THE UNIVERSITY OF HULL

Ecological implications of introducing *Leucaspius delineatus* (Heckel, 1843) and *Pseudorasbora parva* (Temminck and Schlegel, 1842) into inland waters in England

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In Gedenken an
meinen wundervollen Opa, der nie aufgehoert hat, sich Wissen
anzueignen und von dem ich sehr viel gelernt habe.

Kurt Kramer

Du kannst Tränen vergießen,
weil er gegangen ist.
Oder Du kannst lächeln,
weil er gelebt hat.
Du kannst die Augen schließen und Beten,
dass er wiederkehrt.
Oder Du kannst die Augen öffnen
und all das sehen, was er hinterlassen hat.
(VerfasserIn unbekannt)

Widmung

Diese Doktorarbeit widme ich meinen Eltern,

Hannelore und Reinhard Beyer,

für ihre stete Unterstuetzung in allen Lebenslagen.

Dedication

I dedicate this doctoral dissertation to my parents,

Hannelore and Reinhard Beyer,

for their constant support in all my endeavours.

"All animals are equal, but some animals are more equal than others."

George Orwell, Animal Farm, 1951

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Abstract

Non-native species invasions threaten the structure, function and biodiversity of ecosystems worldwide, and those of non-native fishes pose amongst the greatest threats to inland waters of the U.K. This PhD investigated the establishment, dispersal and ecological implications of introducing the two non-native fish species, sunbleak *Leucaspius delineatus* (Heckel, 1843) and topmouth gudgeon *Pseudorasbora parva* (Temminck and Schlegel, 1842) to inland waters of England. The introduction and initial dispersal of both species can be attributed to the commercial fish trade. Species-specific variability of life history, growth and morphological traits was examined in sunbleak (12 sites) and topmouth gudgeon (3 sites) to assess their role in establishment success. The drift dynamics, i.e. timing and intensity (propagule pressure), of sunbleak and topmouth gudgeon were assessed for source populations to determine dispersal potential. Potential risks for native species posed by these two alien cyprinids were assessed with respect to the parasite fauna and overlaps in resource use. For sunbleak, these were also examined in terms of social integration of this species into a native fish assemblage. Biological resistance to topmouth gudgeon invasion was evaluated by stomach flushing and gut content analysis of native piscivorous fishes.

Inter-population variability in life histories and morphological characters were observed in both sunbleak and topmouth gudgeon. Populations of both species matured at small body sizes and between the ages 1 and 2. The fish were of good body condition and exhibited high reproductive investment.

In both species, dispersal from source waters followed a diel pattern, with higher rates at night than during the day (e.g. maximum drift densities during May of 2004 and 2005: 9-10 sunbleak per 1000 m^{-3} at about 23:00 hrs; 40-52 topmouth gudgeon per 1000 m^{-3} at about 05:00 hrs). Downstream of one source population, microhabitat use of topmouth gudgeon was found to overlap with native species (brown trout *Salmo trutta* L., European chub *Leuciscus cephalus* (L.), bullhead *Cottus gobio* L., stoneloach *Barbatula barbatula* (L.); both brown trout and chub were observed to prey on topmouth gudgeon. However, predation intensity may be density-dependent and of insufficient level to impede topmouth gudgeon establishment, which was facilitated in the receiving stream by the consistent propagule pressure from on-line source populations. Sunbleak diet and microhabitat use also overlapped with native species (roach *Rutilus rutilus* (L.) and common bream *Abramis brama* (L.)) as young larvae, but this decreased with age. Social network analysis of sunbleak-native species interactions revealed that sunbleak creates significantly stronger social bonds with the native species than do natives amongst themselves.

No macro-parasites were found in topmouth gudgeon, but two 'Category II' non-native parasites *Neoergasilus japonicus* (Harada, 1930) and *Ergasilus briani* (Markewitsch, 1932) were found in some populations of sunbleak. The potential for sunbleak to spread beyond their current distribution in England and the species' social integration behaviour may facilitate the dispersal of these parasites, which may spread faster among communities invaded by sunbleak than in those where this non-native species is absent. The results of this PhD study are discussed within their wider context and their relevance to non-native species risk analysis and management.

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1. General Introduction

1.2 General Introduction

The problem of accidental or deliberate introductions and translocations of species is growing in recognition and threatens the biodiversity of ecosystems on a global scale (Diamond, 1985; Glowka *et al.*, 1994; Williamson, 1996; Williamson and Fitter, 1996; Mooney and Hobbs, 2000; Bøhn *et al.*, 2004). Non-native species invasions are now considered one of the foremost threats to natural ecosystems and biodiversity. At the same time, they can create enormous costs to agriculture, forestry, fisheries, and other human enterprises, as well as to human health. In the U.S.A. (the only country where a comprehensive review has been completed), invasion negatively effects some 52 % of all imperilled species (Wilcove *et al.*, 1998).

The process of species invasion (Figure 1.1) has been described to consist of four consequent stages: introduction, establishment, dispersal and impact (Rosecchi *et al.*, 2001; Kolar and Lodge, 2002). These stages are not exclusive of each other but are interlinked. The success of each stage will depend on the survival of the new species after introduction and will be defined by the prevailing environmental and biotic conditions (Baltz and Moyle, 1993) as well as species-specific traits, such as life history and ecomorphology (Kolar and Lodge, 2002). The establishment of non-native species in a novel environment can be influenced by abiotic conditions and disturbance levels, characteristics of native species and community structure, and properties of invading species as well as the numbers of individuals introduced (Von Holle and Simberloff, 2005). Important throughout the invasion process is the frequency (propagule pressure) with which a species is introduced to the targeted location, and the potential of the physical environment and the native community to mediate or resist invasion (Byers, 2002a). A species that has been introduced only once may be less likely to establish than a species that has been introduced on several separate occasions (Simberloff and Von Holle, 1999). Repeated invasions of a community by new species may not only disturb the resident populations, but may also alter the habitat, which in turn would favour other invaders (Simberloff and Von Holle, 1999). Recent studies have concluded that the presence of one non-native species may predispose habitat to invasions. This phenomenon, called ‘invasional meltdown’, is the accumulation of synergistic impacts produced by multiple introductions over time. This ‘invasional meltdown’ poses a great threat to both aquatic and terrestrial ecosystems and has implications for prevention, monitoring and research efforts to mitigate species invasions (Simberloff and Von Holle, 1999; Ricciardi, 2001).

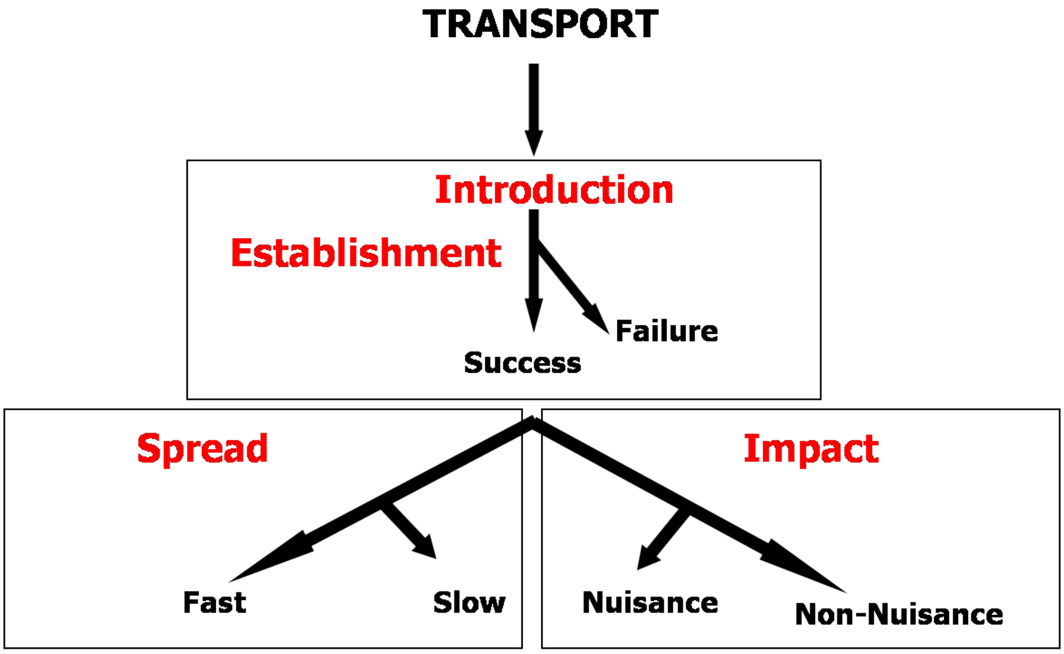

Figure 1.1: Schematic view of the invasion process as described by Kolar and Lodge (2002).

Worldwide, freshwater fishes are a valuable resource for human consumption, recreational activities, education and scientific purposes. Fish are also major components of aquatic biodiversity, which is now under threat from non-native species invasions. Lassuy (1995) summarized factors of extinctions for 40 North American fishes and found that introduced species were the cause in 27 (68 %) cases. An analysis of factors cited in the U.S. Endangered Species Act (ESA) 1991 revealed introduced species as a cause of endangerment of 70 % of fish species, decline of 58 % of fish species and as a continuing threat to 12 % of fish species. The majority of studies (77 %) that examined the potential effects of non-native fish species have documented a decline of native fishes following the introduction of exotic or transplanted species (Ross, 1991b). A variety of ecological effects on native species and communities have been attributed to non-native fishes. These include:

1) habitat alterations, e.g. introduced grass carp *Ctenopharyngodon idella*, Valenciennes 1844, feed extensively on macrophytes, and can subsequently cause habitat degradation (e.g. Small *et al.*, 1985; Petridis, 1990);
2) introduction of pathogens, e.g. the eel parasite, *Anguillicola crassus* (Kuwahara, Niimi and Hagaki, 1974), harmless to its native host the Japanese glass eel *Anguilla japonicus* (Temminck & Schlegel, 1846), is highly pathogenic to the European eel *Anguilla anguilla* (L.) (e.g. Kennedy and Fitch, 1990a; Kirk, 2003);
3) trophic alterations, e.g. vigorous benthic foraging behaviour of invasive carp *Cyprinus carpio* (L.) can result in adverse impacts, with substantial decrease in macrophyte and macroinvertebrate abundance, as well as increased re-suspension of sediments and zooplankton biomass (e.g. Lougheed *et al.*, 1998; Parkos III *et al.*, 2003; Miller and Crowl, 2006);
4) hybridization, e.g. native crucian carp *Carassius carassius* (L.) is threatened by introductions of goldfish *Carassius auratus* (L.) through hybridization in the U.K. (Wheeler, 2000; Hänfling *et al.*, 2005);
5) shifts in habitat use, e.g. introduced brown trout *Salmo trutta* L. caused shifts in habitat use in native *Galaxias auratus*, Johnston 1883, in Tasmania, Australia (Stuart-Smith *et al.*, 2008);
6) decline, endangerment or even extinction of native species, e.g. rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) invasions have caused declines in native fishes and other aquatic biota in many countries including Australia and New Zealand (e.g. Crowl, 1992; Simon and Townsend, 2003); while the decline of some haplochromine cichlids in Lake Victoria, East Africa, has been attributed to the introduction of the Nile perch *Lates niloticus* (L.) (e.g. Ogutu-Ohwayo, 1990; Witte *et al.*, 1992).

Only in a few cases were fish introductions thought not to have an effect, for example despite intensive research addressing aspects of diet, growth, species-habitat and interspecies relationships of both native and introduced species in the

Eel River, California, the introduced Sacramento squawfish *Ptychocheilus grandis* (Ayres, 1854) was not found to have an adverse impact on native coexisting fish species (Brown and Moyle, 1997).

In 2004, Hickley and Chare (2004) reported that approximately 4500 separate fish introductions, representing about 1.5 million fish in total, occur annually in England and Wales. The introduction to, and the movement of fish within the waters of England and Wales are regulated by legislation (Hickley and Chare, 2004) such as the Diseases of Fish Acts of 1937 (amended in 1983), the Salmon & Freshwater Fisheries Act (SAFFA) 1975, the Wildlife and Countryside Act (WCA) 1981 and the Import of Live Fish Act (ILFA) 1980. The latter includes the Prohibition of Keeping or Release of Live Fish (Specified Species) Order 1998 (and subsequent revisions), which displays a list of species that are subject to control. Under Section 30 of the Salmon and Freshwater Fisheries Act (SAFFA) 1975, a person shall be guilty of an offence if he/she introduces any fish or spawn into an inland water, or has in his/her possession any fish or spawn of fish intending to introduce it into an inland water, unless he/she first obtains the written consent of the regulating authority (presently Environment Agency) within whose area the water is situated. Under Section 14 of the Wildlife and Countryside Act (WCA) 1981, it is deemed an offence if any person releases or allows to escape any animal into the wild without a licence, which (a) is not ordinarily resident in and is not a regular visitor to Great Britain in a wild state, or (b) is included in the schedule of non-native animals established in the wild (Schedule 9). Under the Prohibition of Keeping or Release of Live Fish (Specified Species) Order 1998 made under the Import of Live Fish Act (ILFA) 1980, no person shall keep or release any live fish of the specified species in the schedule of non-native species in any part of England and Wales except under the authority of a licence having been granted. Currently 34 individual species and 19 additional genera are specified. Following an extensive consultation, the Prohibition of Keeping or Release of Live Fish (Specified Species) Order was made under the ILFA and came into force on 1 November 1998 to provide better protection for native fish species. Previous controls have not been entirely successful in preventing the unauthorised spread of non-native fish. The above

Order rules that it is an offence to keep or deal in non-native species without an ILFA licence, which is expected to make it easier for the authorities to prevent illegal movements of exotic fish (Hickley and Chare, 2004). However, to date there has only been 1 successful prosecution under this Order since it came into force in 1998 (R. Britton, pers. comm.).

In England and Wales, the Environment Agency is the primary Government authority for environmental protection and plays a major role in the regulation of recreational fishing, while the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) is the Government agency responsible for controlling the import of live fish and aquaculture. Because legislation governing the movement of fish into and within England and Wales is shared between the Environment Agency and other Government organisations, management can be difficult and enables exploitation of any weaknesses in the enforcement system (Hickley and Chare, 2004). This is further fuelled by the high demand for non-native fish (e.g. ornamental, recreational) and the potentially great financial temptation to overcome the legal constraints by introducing these fish without consent (Hickley and Chare, 2004). To make best use of resources and information, CEFAS and the Environment Agency have developed a shared ‘Live Fish Movements Database’ that facilitates effective, joint working with the respective enforcement teams.

Recent compilation of a list of the native fish species in England records 22 species being potamodromous species, including crucian carp *Carassius carassius* (Linnaeus 1758), with an additional 20 species being diadromous species native to England (DAFF, 2002; Maitland, 2004; Hill *et al.,* 2005). Species introductions, along with the effects of fisheries, pollution and land use have been identified as being the greatest threats to fish communities in England (Maitland, 1974; Winfield, 1992; Winfield *et al.*, 1996; Winfield *et al.*, 1998; Winfield *et al.*, 2002) and worldwide (Lowe-McConnell, 1990). Of the fish species introduced into England, 37 % belonged to the cyprinidae family (DAFF, 2002). Cyprinid fish introduced to England have been identified as threats to conservation of rare communities, e.g. coregonids (Winfield, 1992). Also, several diseases and parasite introductions into England have been associated with imported freshwater fish

(Fryer, 1982b; Michel *et al.*, 1986; Boxshall and Frear, 1990; Kennedy and Fitch, 1990b; Austin and Robertson, 1993a; b; Gibson, 1993; Gozlan *et al.*, 2005) and hybridization has been observed between native and introduced species (Wheeler, 2000). However, with the exception of the pikeperch *Sander lucioperca* (L.) (Smith *et al.*, 1998) information on introduced freshwater fish in inland waters of England was very limited in the late 1990s, in particular with regards to their adaptable traits, such as life-histories (Copp *et al.*, 2002a), and the ecological implications of such introductions. Only in more recent years, have small-bodied freshwater fishes, such as sunbleak *Leucaspius delineatus* (Heckel, 1843) and topmouth gudgeon *Pseudorasbora parva* (Temminck and Schlegel, 1842), begun to receive scientific attention in England (e.g. Gozlan *et al.*, 2002; Gozlan *et al.*, 2003b; Pinder and Gozlan, 2003; Pinder and Gozlan, 2004; Pinder *et al.*, 2005b).

The sunbleak (Plate 1.1) and the topmouth gudgeon (Plate 1.2), originating from the Ponto-Caspian region and southeast Asia respectively, were introduced into England in the mid 1980’s, both to the same commercial fish farm in Hampshire (Farr-Cox *et al.*, 1996; Gozlan *et al.*, 2002; Gozlan *et al.*, 2003b). Both species have potential as carriers of non-native pathogens and are now found in inland water bodies of England and Wales (Figure 1.2 and Figure 1.3) (Beyer *et al.*, 2005; Gozlan *et al.*, 2005; Pinder *et al.*, 2005b). This is of considerable concern as these aspects are used in assessing the risks associated with non-native species (Kolar and Lodge, 2002; Gozlan *et al.*, 2006). Both sunbleak and topmouth gudgeon are included in the ILFA list (Defra, 1998), making it an offence to move either species without a licence.

Sunbleak and topmouth gudgeon belong to the Family Cyprinidae, the largest family of freshwater fishes (Nelson, 1994). Both species are small-bodied, with adult sizes rarely exceeding 100 mm in fork length (Šebela and Wohlgemuth, 1984; Arnold, 1990; Arnold and Längert, 1995; Gozlan *et al.*, 2003b), and they share several life history and behavioural characteristics. They feed mainly on plankton and invertebrates (Weber, 1984; Dussling and Berg, 2001), mature early in life and reproduce rapidly with high effort, and are batch spawners, producing successive batches of eggs during spring and summer (Farr-Cox *et al.*, 1996;

Dussling and Berg, 2001; Rosecchi *et al.*, 2001). During spawning season, the males of both species prepare a nest by cleaning an area (substrate or vegetation) of any algae and detritus for egg deposition (Arnold, 1990; Arnold and Längert, 1995). In the cleaned area, the eggs are deposited in strings. After deposition, the respective male guards the eggs by protecting the immediate area from intruders and potential predators, e.g. gastropods and other fish. In sunbleak it has been observed that the male will also remove any eggs infested with fungi to prevent spreading to the healthy eggs (Ecke, 1985). These traits and behaviours may facilitate the establishment of these species in novel environments. In the U.K., more than 50 % of introduced fish species exhibit parental care (Maitland, 2000), a reproductive strategy uncommon for native species but potentially an advantage for successful establishment (Jeschke and Strayer, 2008). In England, 44 % of all introduced species are nest guarders (DAFF, 2002).

Plate 1.1: Sunbleak *Leucaspius delineatus* (Heckel, 1843) (Picture by A.C. Pinder). The white scale bar is 10 mm long.

Plate 1.2: Topmouth gudgeon *Pseudorasbora parva* (Temminck & Schlegel, 1842) (Picture by A.C. Pinder). The white scale bar is 10 mm long.

Sunbleak are native to much of continental Europe and in some countries, such as Germany, they are now considered threatened despite their apparent adaptability to a variety of environmental conditions (Brezeanu, 1968). Sunbleak are assumed to have been accidentally introduced into England with fish stock purchased from the mainland of Europe (Farr-Cox *et al.*, 1996). Sunbleak are reported mainly from the South and South West of England (Figure 1.2) (Farr-Cox *et al.*, 1996).

In their native areas of Central Europe, sunbleak occur in a variety of habitats and often inhabit small and shallow waters (Arnold and Längert, 1995) but can be found in lakes, reservoirs and canals. Especially during the spawning season, sunbleak can migrate into streams and can tolerate water velocities of 1 to 2 m s^{-1}. In streams, they can be found associated with small rheophilic fish species like the Eurasian minnow *Phoxinus phoxinus* (L.), gudgeon *Gobio gobio* L. and barbel *Barbus barbus* (L.) (Arnold and Längert, 1995). Species most often associated with sunbleak are common carp *Cyprinus carpio* L., three-spined sticklebacks *Gasterosteus aculeatus* L., gudgeon, European eel *Anguilla anguilla* (L.), roach *Rutilus rutilus* (L.), northern pike *Esox lucius* (L.), nine-spined stickleback *Pungitius pungitius* (L.), Eurasian perch *Perca fluviatilis* L. and tench *Tinca tinca* (L.) (Arnold and Längert, 1995).

Sunbleak are shoaling fish that live close to aquatic macrophytes (Arnold and Längert, 1995). Spawning takes place in calm, littoral zones (Brezeanu, 1968), where the water temperature increases more quickly and may speed up the development of the larvae. Vertical plant stems, such as those of reeds and water lilies, are a preferred choice for egg deposition. For reproduction in waters without aquatic vegetation, floating materials like leafs, branches and plastic material may be used (Arnold and Längert, 1995). Sunbleak spawning season has been observed to commence in April/May and finish at the end of June, with preferred water temperatures of 18-19 °C (Brezeanu, 1968). They mature at approximately 1 year old, and deposit their eggs on plants in a depth of 10 to 20 cm (Brezeanu, 1968). In the laboratory, sunbleak eggs take about 24 hours to develop to the eyed stage, and they hatch after 75 hours at 24.7 ^{o}C (Pinder and Gozlan, 2004).

Figure 1.2: Distribution of sunbleak in England and Wales (Farr-Cox *et al.*, 1996; CEH, unpubl. data). The river catchment and size of river at risk from invasion is given: 1) Somerset Levels: drains, rivers and enclosed water bodies (~ 61,000 hectares); 2) Revels Fishery (online): River Stour (96 km); 3) River Frome: main river (65 km); 4) Broadlands Lakes Fishery (online): River Test (31 km); 5) Two Lakes Fishery (enclosed); 6) Stoneham Lakes (online): River Itchen (27 km); 7) Skegness, Lincolnshire (enclosed).

Topmouth gudgeon are native to Southeast Asia, in particular Japan, China, Korea and the River Amur catchment (Barus *et al.*, 1984; Bănărescu, 1990; Gozlan *et al.*, 2002). Topmouth gudgeon were first imported to Romania, Europe from the lower Iangtsekiang River (China) as a contaminant together with planktivorous cyprinids (so-called ‘Chinese carps’) (Barus *et al.*, 1984). Topmouth gudgeon were first reported in 1961 in the River Ialomita (Romania). The species spread widely and relatively quickly as a contaminant of live cyprinid fish consignments, and was first introduced to England *via* a fishery near Romsey in Hampshire

(Gozlan *et al.*, 2002) and has been recorded at 25 locations (Figure 1.3). Extensive populations have developed wherever topmouth gudgeon has been introduced (Wohlgemuth and Šebela, 1987), though there are reports of the species disappearing for no apparent reason after an initial period of population establishment (Copp *et al.*, 2005a). Because of their demonstrated success in establishing populations in novel environments, the topmouth gudgeon is now considered to be amongst the most invasive pest species in Europe (Welcomme, 1992; Gozlan *et al.*, 2005). The species is also considered a nuisance by anglers in catch-and-release fisheries aiming for large-bodied fish, as it rapidly forms large populations and becomes an unwanted major part of the catch. For example, this was the case in Ratherheath Tarn, Cumbria, England, before the species was eradicated from here (Britton and Brazier, 2006).

Topmouth gudgeon demonstrate plasticity in habitat utilisation and inhabit rivers, reservoirs, lakes and other available water bodies (Uchida, 1939; Nakamura, 1969; Arnold, 1990). However, they are not considered lotic fish species, but are able to pass through flowing waters to reach favourable water velocities (Muchaceva, 1950). Topmouth gudgeon have also been found to be abundant in eutrophic waters (Ujiie and Mizuguchi, 1994). In their introduced range, topmouth gudgeon associate with a wide variety of fish species (Arnold, 1990; Ujiie and Mizuguchi, 1994), including: pumpkinseed *Lepomis gibbosus* (L.), gudgeon, Eurasian perch, Amur bitterling *Rhodeus amarus* (Bloch, 1782), crucian carp *Carassius carassius* (L.), goldfish *Carassius auratus* (L.), tubenose goby *Proterhorinus marmoratus* (Pallas, 1814), Eurasian ruffe *Gymnocephalus cernuus* (L.), and Japanese eel (Arnold, 1990; Ujiie and Mizuguchi, 1994). This diversity of communities in which topmouth gudgeon can be found underlines the species' adaptable nature.

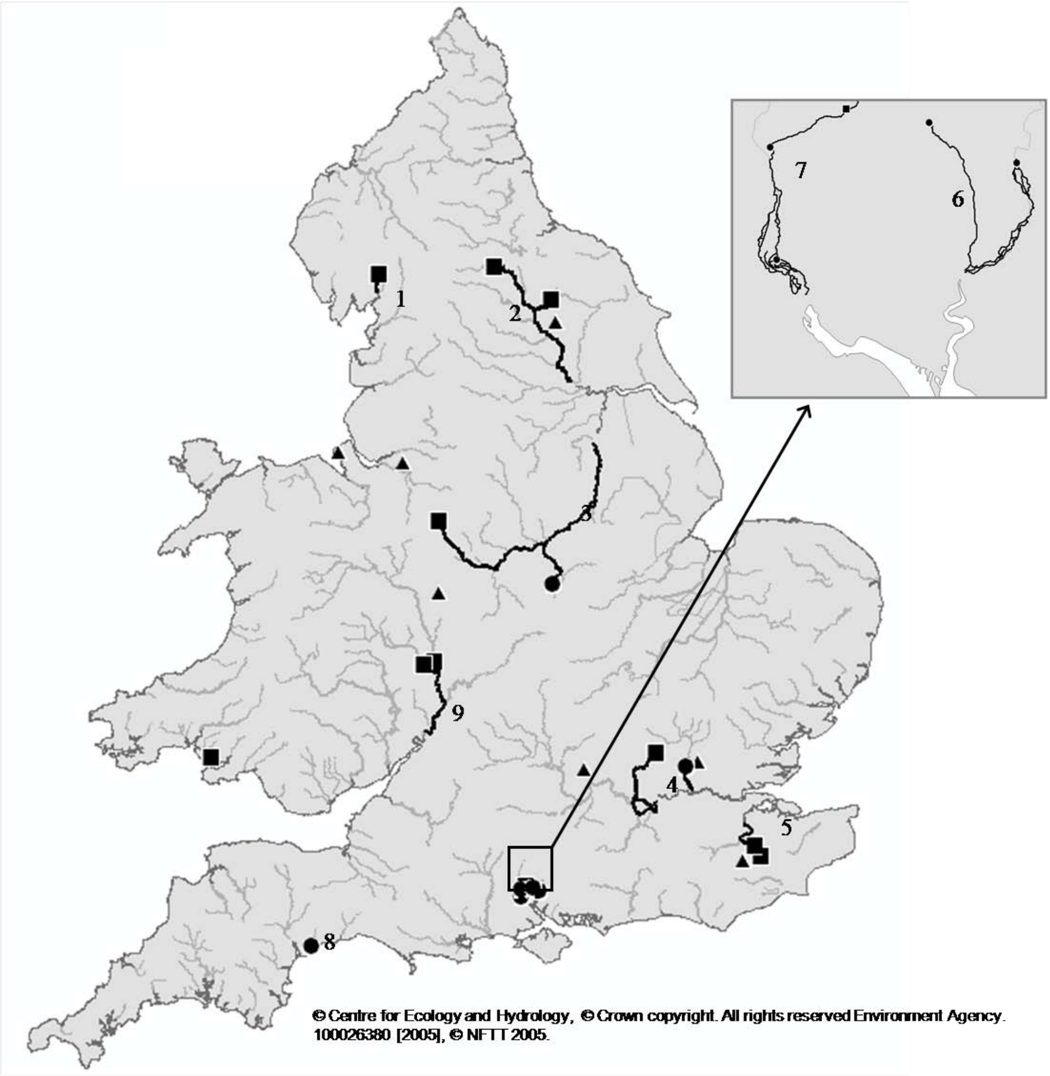

Figure 1.3: Distribution of topmouth gudgeon in England and Wales, November 2005 (●, river; ▲, fully enclosed lake; ■, sites connected to river network; ▬, river length at risk from topmouth gudgeon dispersal; -, river network). Numbers 1–9 indicate river catchment and length of river at risk from invasion (Km): 1, Kent (23); 2, Yorkshire Ouse (160); 3, Trent (330); 4, Thames (157); 5, Medway (72); 6, Itchen (27); 7, Test (31); 8, Otter (4); 9, Severn (96) (Pinder *et al.*, 2005b).

Topmouth gudgeon feed on detritus, zooplankton and phytoplankton, although young-of-the-year can be brought up entirely on dry fish foods in the laboratory (Weber, 1984). With sexual dimorphism occurring, male topmouth gudgeon are on average larger than the females (Šebela and Wohlgemuth, 1984; Arnold, 1990; Adámek and Siddiqui, 1997). During the spawning season, males develop tubercles around the mouth. Following a hierarchical social system, females prefer larger males for mating (Maekawa *et al.*, 1996). Topmouth gudgeon eggs take 6 days to develop until the eyed stage (Maekawa *et al.*, 1996) and hatch after 10 days at 20° C. Generally, this species shows tolerance to the wide temperature range encountered in temperate climates (Rosecchi *et al.*, 1993).

Topmouth gudgeon have been found to feed on eggs and larvae of several fish species (Stein and Herl, 1986; Xie *et al.*, 2000). In some cases, they were observed to be a facultative parasite causing injuries to skin and musculature of other fishes (Trombitskiy and Kakhovskiy, 1987; Libosvárský *et al.*, 1990). An introduced population in a Greek lake demonstrated dietary overlap with three endemic fish species (Rosecchi *et al.*, 1993). In Neusiedler See (Austria), topmouth gudgeon were found to feed extensively on epiphytic chironomid larvae (Wolfram-Wais *et al.*, 1999). The resident species were exploiting other resources, providing abundant resources for the invading topmouth gudgeon to exploit.

Historically, only assumptions have been made as to whether, how and to which extent both species, sunbleak and topmouth gudgeon, have an effect on native fauna of inland waters in England. Information on the species' adaptable traits and the potential implications of their introduction into the country are limited. Therefore, for this PhD thesis project, these two species were chosen for investigation.

1.3 Aims and objectives

The aim of this research was to assess the ecological implications of the introduction, establishment and subsequent invasion of inland waters in England by sunbleak and topmouth gudgeon.

The specific objectives of the study were to:

1) assess the variability of adaptable traits such as life-histories and morphological characters of sunbleak and topmouth gudgeon at different sites, so as to describe the role of adaptable traits in the introduction, establishment and dispersal of these species (Chapter 3);

2) determine the density and timing of movement of sunbleak and topmouth gudgeon *via* drift from source populations into online water bodies, so as to quantify the role of this dispersal pathway in the invasion process (Chapter 4);

3) identify the parasite fauna of sunbleak and topmouth gudgeon in England, as a means of establishing the level of risk of sunbleak and topmouth gudgeon for parasite transmission to native fishes (Chapter 5);

4) assess the level of resource use overlap (diet and habitat) and social integration between the non-native and native fishes, so as to determine whether the invader creates a niche derived at the detriment of native species (Chapter 6); and

5) evaluate the incidence and intensity of native fish predation on (i.e. biological resistance to) topmouth gudgeon in an invaded system, so as to quantify the level of biotic resistance (Chapter 7).

1.4 Structure of the thesis

The thesis is organised in ten sections (eight Chapters plus References and Appendices), which follows the aspects of the invasion process (Figure 1.1). The second chapter describes in detail the study sites that were used. Chapter three presents and discusses the variability of life history traits and morphology of sunbleak and topmouth gudgeon from different geographic locations. In the fourth chapter, drift densities and dispersal from source populations of sunbleak and topmouth gudgeon is investigated. The fifth chapter explores the parasite fauna of several populations of both fish species in their introduced range. Chapter six (part a) presents insights on resource use overlaps between the introduced species (sunbleak, topmouth gudgeon) and the native species during early life and adult stages. The second part of chapter six (part b) utilises social network analysis to determine the social integration of sunbleak into a native fish assemblage during early life. Chapter seven investigates the role of native piscivorous fishes in the potential resistance against topmouth gudgeon invasion. Chapter eight presents a synthesis of the findings and discusses the ecological implications of these findings for sunbleak and topmouth gudgeon invasion, and for the conservation of native fish species. The chapter will further elaborate on recommendations for the management of the two species and further research. The thesis concludes with a list of References and the Appendices which include supplementary information. Parts of this thesis have already been published in refereed journals and presented at international conferences. This is indicated on the front page of each chapter.

2. Study Sites

2.1 Introduction

This chapter identifies and describes the key features of the study area at which field sampling was carried out and/or from which sunbleak or topmouth gudgeon were obtained for further examination. The availability of suitable study sites was a key factor in site selection. An initial assessment of potential sites was carried out to determine their suitability, with guidance sought from Centre for Ecology & Hydrology (CEH) and the local Environment Agency (EA) offices. As a result of the available information and the limited timeframe, the sites described in this Chapter were chosen. Known high densities of sunbleak in the South and South West of England and of topmouth gudgeon in the South and North East of England were expected to ensure an abundant supply of specimens for the investigations.

The investigation was centred in the South and South West of England (see Table 2.1, Figure 2.1, Figure 2.2, Figure 2.3), plus one site, Ratherheath Tarn, near Kendal, Cumbria, in North West England (Figure 2.4). The sites in South East England were Stoneham Lakes and the online Monks Brook, near Eastleigh, Hampshire; Two Lakes Fishery, near Romsey, Hampshire; and Crampmoor Fishery and the online Tadburn Lake stream, near Romsey, Hampshire (Figure 2.1). Sites in South West England included Revels Fishery and the connected Caundle Brook, Dorset and the Somerset Levels and Moors (Figure 2.2, Figure 2.3). Furthermore, material from a population of topmouth gudgeon from the Canal du Fumemorte, Rhone Delta, Camargue (France) was obtained from a collaborator (A. Crivelli, pers. comm.) to complement data collected from the English populations (see Chapter 3; Table 2.1, Figure 2.8).

The timing and duration of the field programmes were driven by factors such as: weather conditions, manpower availability as well as technical and equipment limitations. Assistance with field work was gained from volunteers, undergraduate students, the Centre for Ecology and Hydrology (CEH), the Centre for Environment, Fisheries and Aquaculture Science (Cefas) and the Environment Agency (EA).

Table 2.1: Names, site codes, latitude/longitude and national grid references for each study site selected for this project.

Site	Site Code	Lat/Long	National Grid Reference
	Sunbleak		
Bridgewater-Taunton Canal at Buckland Farm, Somerset	BTC1	51°02'56" N; 2°59'39" W	ST 304 282
Bridgewater-Taunton Canal at Creech St. Michael, Somerset	BTC2	51°01'29" N; 3°02'15" W	ST 274 256
Bridgewater-Taunton Canal, YMCA, Somerset	BTC3	51°07'28" N; 3°00'37" W	ST 294 366
Kings-Sedgemoor Drain at Bradney Bridge, Bawdrip, Somerset	KSD4	51°09'03" N; 2°56'47" W	ST 339 395
Kings-Sedgemoor Drain at Parchey Bridge, Somerset	KSD5	51°08'06" N; 2°55'39" W	ST 352 377
River Huntspill at Woolavington Bridge, Somerset	Hunt6	51°11'19" N; 2°56'19" W	ST 345 437
Sowy River at Grey Lake Bridge, Somerset	Sowy7	51°06'04" N; 2°52'11" W	ST 392 339
River Tone at Hankridge, Somerset	Tone8	51°01'33" N; 3°04'09" W	ST 251 257
Dunwear Pond, Bridgewater, Somerset	Dun9	51°07'06" N; 2°58'48" W	ST 315 359
Durleigh Reservoir, Bridgewater, Somerset	Durl10	51°07'10" N; 3°02'45" W	ST 269 361
Stoneham Lakes, Eastleigh, Hampshire	Stone 11	50°57'14" N; 1°22'48" W	SU 434 173
Two Lakes Fishery, Romsey, Hampshire	TwoL12	51°00'19" N; 1°27'17" W	SU 384 231
Beeches Ponds, Bridgewater, Somerset	N/A	51º07'17" N, 2º58'05" W	ST 323 362
Revels Fishery, Cosmore, Dorset	N/A	50°50'56" N; 2°27'32" W	ST 678 056
	Topmouth gudgeon		
Crampmoor Fishery/Tadburn Lake, Romsey, Hampshire	Tad	51°00'02" N; 1°26'54" W	SU 388 225
Ratherheath Tarn, Kendall, Cumbria	Rath	54°21'21" N; 2°47'42" W	SD 484 959
Canal du Fumemorte, Camargue, France	Fum	43°31' 27" N; 4°42'23" E	N/A

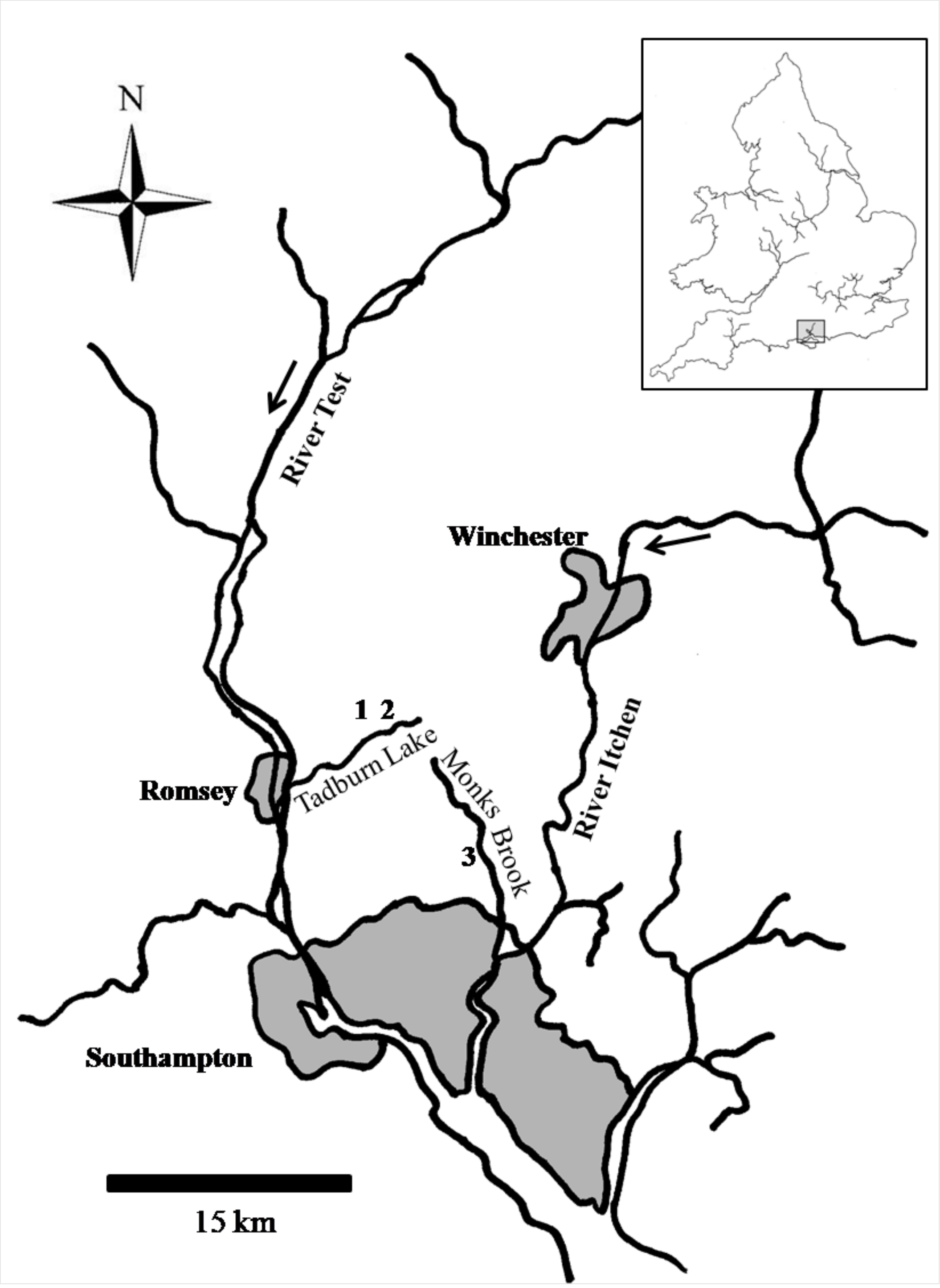

Figure 2.1: Map of the River Itchen and Test catchment in and around Southampton, Hampshire, U.K., indicating the locations of 1) Two Lakes Fishery, 2) Crampmoor Fishery and 3) Stoneham Lakes with a location map in England and Wales inset. Grey areas show urban centres and the arrows the direction of water flow.

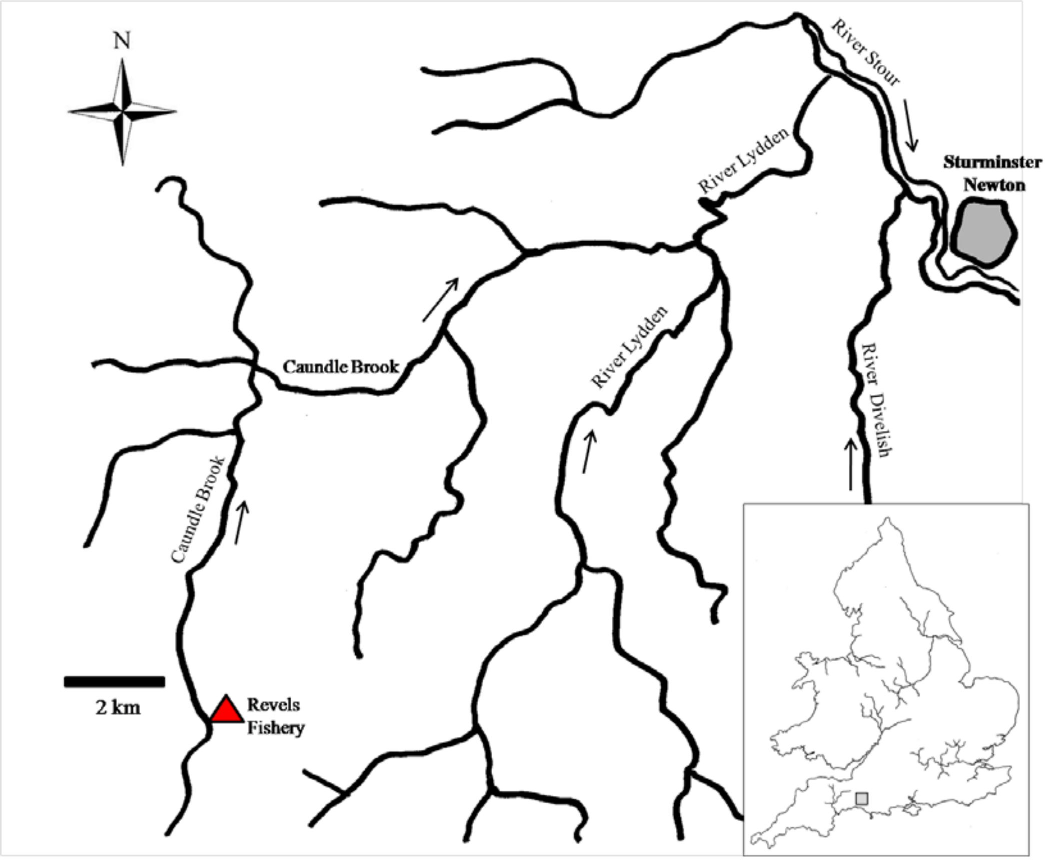

Figure 2.2: Map of the Caundle Brook Catchment with location of Revels Fishery (▲) with a location map in England and Wales inset. Grey areas show urban centres and the arrows the direction of water flow.

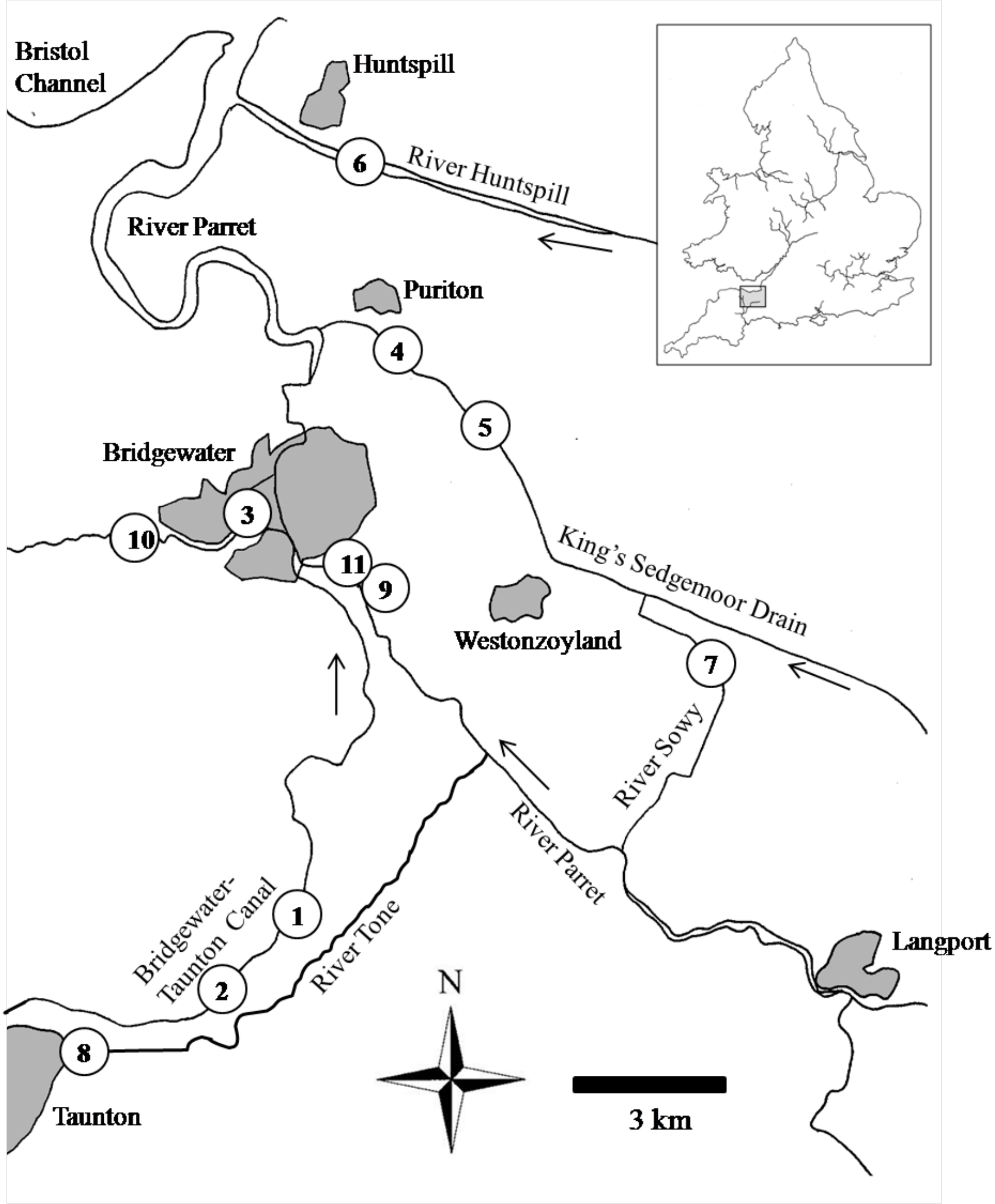

Figure 2.3: Map of the Somerset Levels with sampling locations: 1. Buckland Farm, Bridgewater-Taunton Canal (BTC), 2. Creech St. Michael, BTC, 3. YMCA, BTC, 4. Bradney Bridge, Kings Sedgemoor Drain (KSD), 5. Parchey Bridge, KSD, 6. Woolavington Bridge, River Huntspill, 7. Greylake Bridge, River Sowy, 8. Hankridge, River Tone, 9. Dunwear Pond, 10. Durleigh Reservoir, 11. Beeches Ponds with a location map in England and Wales inset. Grey areas show urban centres and the arrows the direction of water flow.

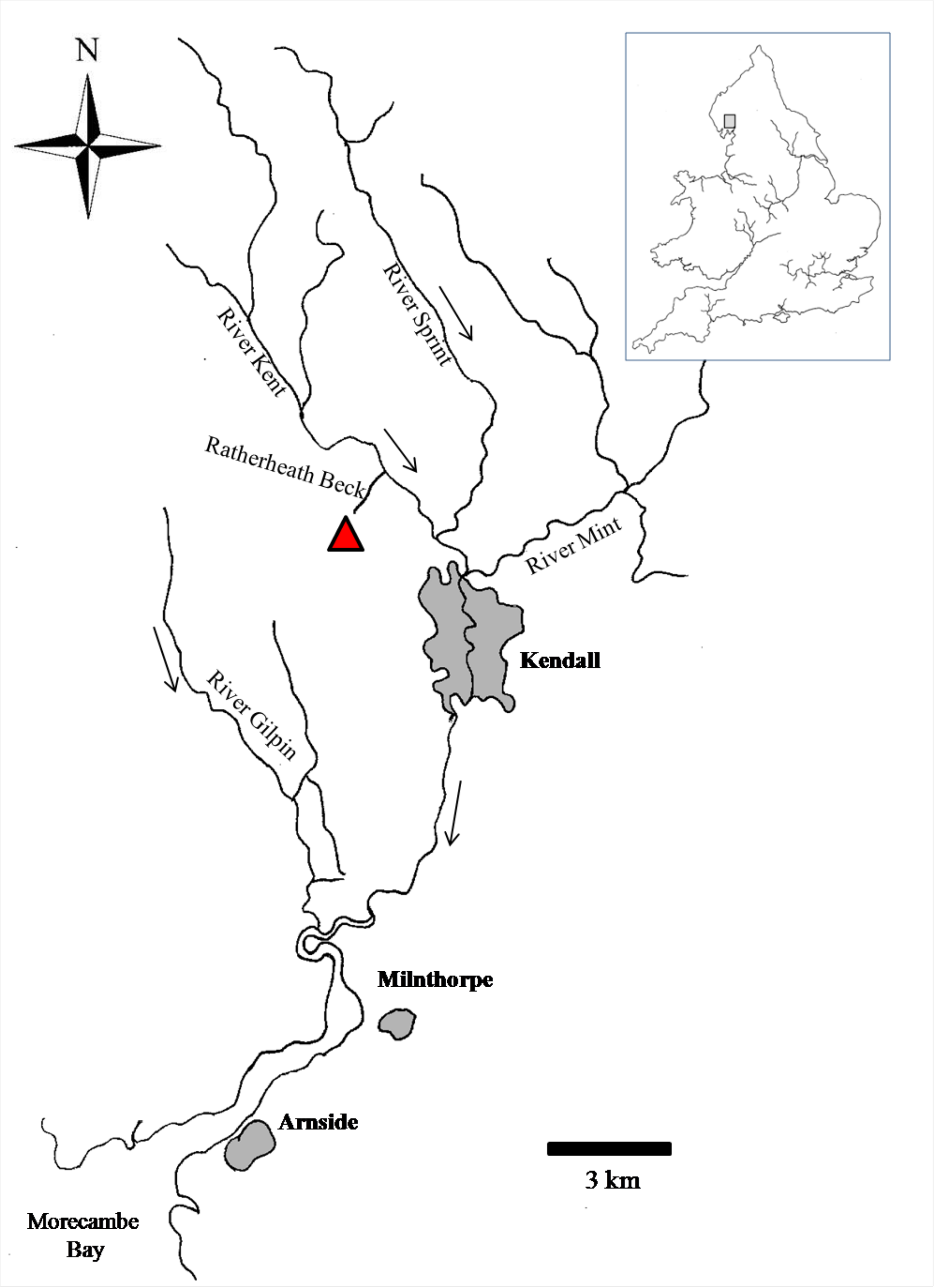

Figure 2.4: Map showing of the River Kent catchment showing the location of Ratherheath Tarn (▲), Cumbria, with a location map in England and Wales inset. Grey areas show urban centres and the arrows the direction of water flow.

2.2 Study sites containing sunbleak

2.2.1 The Stoneham Lakes, Monks Brook and the River Itchen catchment

The Stoneham Lakes coarse fishery (Table 2.1; Figure 2.1) was founded in 1952 by Caustons Angling club and is now run by the Eastleigh and District Angling Club (EADAC). The system consists of three lakes that cover a total area of about 120 hectares (Plate 2.1, Figure 2.5). Park Lake (Plate 2.2), the top-most, and largest of the lakes, is between 1.5 and 3.0 m deep and flows into Shrubbery Lake (Plate 2.3), which is between 1.5 and 4.0 m deep. From here the water flows into Church Lake (Plate 2.4), the smallest of the three lakes, which reaches a depth of 1.2 m. Church Lake has an unscreened outflow that flows underground for approximately 430 m and connects the lakes with Monks Brook (Plate 2.5, Plate 2.6). Monks Brook enters the River Itchen after flowing under motorways and through built up areas of Southampton for 2.0 km downstream of the Stoneham lake’s outflow, at an elevation of about 0.7 m above Ordnance Datum (OD) (National River Flow Archive, 2007a). The River Itchen is 45 km long, rising from springs above Alresford; its sources comprise three main tributaries, the Candover Stream, the Cheriton Stream and the River Alre, but the River Itchen itself does not start until their confluence above Alresford in the Hampshire Downs. The river flows through Winchester and Eastleigh before it flows into Southampton Water (Southern Water, 2007). The River Itchen catchment covers an area of 41,500 hectares and has a mean annual discharge of 5.4 m^3s^{-1} (National River Flow Archive, 2007a). The top of the river banks are typically 20-30 cm above water level, and water levels in summer are often higher than in winter due to weed growth (Environment Agency, 2007b).

The Stoneham Lakes contain some overhanging vegetation both from marginal macrophytes and riparian trees. Parts of the lakes are covered by large patches of yellow water lilies *Nuphar lutea* (L.), white water lilies *Nymphaea alba* (L.) and the common reed *Phragmites* spp., but generally aquatic macrophytes are sparse, occurring only near the lake margins (0 - 0.5 m from bank). For recreational purposes, the riparian vegetation surrounding the lakes is managed and cut by the angling club to prevent it from becoming too dense and creating excessive shading around the margins. The lakes are used as a catch-and-release fishery. The angling society stocks the lakes every few years with native coarse fish, mainly roach and common bream *Abramis brama* (L.). Other native fish species in the lakes are, in decreasing order of numeric importance, perch, rudd *Scardinius erythrophthalmus* (L.), bleak *Alburnus alburnus* (L.), eel, gudgeon, pike, tench and carp. Sunbleak was accidentally introduced into the Stoneham Lakes in the mid 1980s and has since become the most abundant fish species. Their great abundance was confirmed by seine netting carried out at least annually since 2000, during which sunbleak made up between 80 and 90 % of the total catch (R.E. Gozlan, pers. comm.). The large number of sunbleak in the lakes appeared to coincide with reduced natural spawning activity of other species and fishermen had been reporting increasing capture of sunbleak instead of the target species (P. Martin, pers. comm.). No management regarding sunbleak was taking place previous to, and during, the study.

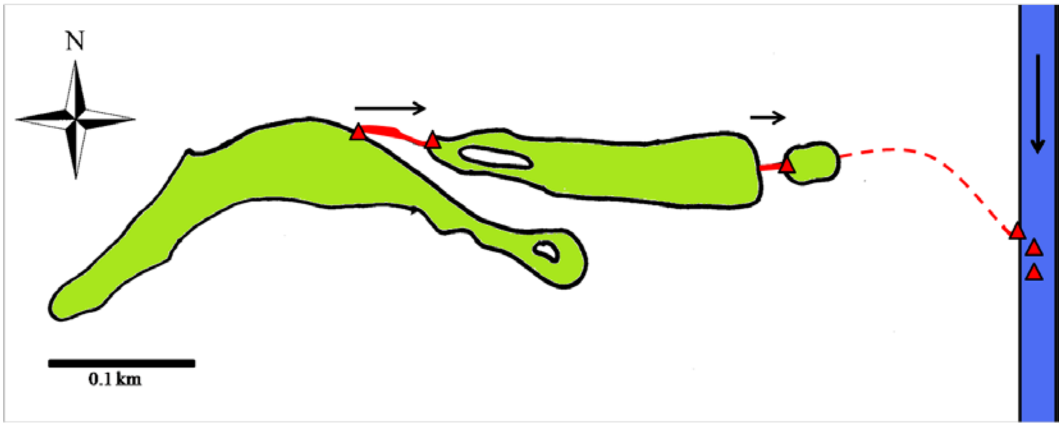

Figure 2.5: Stoneham lakes schematic (arrow: flow direction; green: fishery lakes; blue: Monks Brook; red: connection between water bodies; with continuous lines (▬) being above- and discontinuous lines (---) being under-ground; red triangles (▲) indicate the location of 6 drifts nets used in Chapter 4).

Plate 2.1: Aerial photograph of the three lakes at Stoneham (Flashearth Navteq, 2008d).

Plate 2.2: Park lake, the largest and most westerly of the three lakes at Stoneham (Picture by author).

Plate 2.3: Shrubbery lake, the second-largest of the three lakes at Stoneham (Picture by author).

Plate 2.4: Church lake, the smallest and most easterly of the three lakes at Stoneham (Picture by author). Church lake has an outflow and is online with Monks Brook.

Church Lake is at an elevation of 8.0 m above Ordnance Datum (OD) and outflows into the Monks Brook, which has a catchment of an area of about 43 km^2. Monks Brook has a mean annual discharge of 0.23 m^{3}s^{-1} (National River Flow Archive, 2007b). Monks Brook is a chalk stream with a mostly low-lying catchment developed on impervious Tertiary formations. Along the catchment, mixed land use is represented around the rural headwaters with considerable woodland and substantial urban development. In Monks Brook, submerged vegetation is dominated by patches of water crowfoot *Ranunculus penicillatus* (Dumort.) and yellow cress *Rorippa* spp. Overhanging bankside vegetation along the stream within the study area consisted mainly of bushes and trees, chiefly alder *Alnus glutinosa* (L.) and willow *Salix* spp. Along the banks, hedgerows of bramble *Rubus* spp, hawthorn *Crataegus* spp, laurel *Laurus nobilis* (L.), sycamore *Acer pseudoplatanus* (L.) and ash *Fraxinus excelsior* (L.) provide additional shade. In the study area, Monks Brook is on average approximately 5 m in width and generally shallow (<0.5 m), with sporadic pools of up to 1 m. In areas around public access, e.g. bridges, household debris, such as bicycles and shopping carts, were observed submerged in the water.

Plate 2.5: Monks Brook at the outflow from Stoneham Lakes (Picture by author).

Plate 2.6: Monks Brook ≈200 m downstream of the outflow from Stoneham Lakes (Picture by author). The picture represents the site after a night of heavy rain.

In Monks Brook and the Itchen, 80 % of the total annual discharge is derived from groundwater from Cretaceous chalk aquifers (Mann *et al.*, 1989). Such chalk streams generally have a stable hydrological regime and are rarely subject to floods or droughts because of the low contribution of runoff (Berrie *et al.*, 1998). They are also characterised by high thermal stability, particularly in the head waters, because the groundwater temperature varies less than 10 °C over the annual cycle. The stream bed is composed of flint gravels and cobbles, with areas of silt in the margins and where macrophyte growth occurs for this promotes sedimentation. Chalk streams have high primary productivity, such as abundant flora, so support high secondary productivity of benthic macroinvertebrates (Westlake *et al.*, 1972). Correspondingly, density, biomass and production of fish are also high (Mann *et al.*, 1989). Chalk streams support a diverse fish fauna, which includes brown trout *Salmo trutta* L. and Atlantic salmon *Salmo salar* (L.), which are of great sporting value to anglers. In Monks Brook, bullhead *Cottus gobio* L. and stoneloach *Barbatula barbatula* (L.) are numerically dominant, which is common for chalk streams, while minnows also occur (Mann, 1971). Brown trout, grayling *Thymallus thymallus* (L.), eel, European brook lamprey *Lampetra planeri* (Bloch), three-spined stickleback, roach, pike and ruffe are present at low densities (Riley *et al.*, 2003).

Several areas of the River Itchen catchment have been designated Sites of Special Scientific Interest (SSSI). The river is also a Special Area of Conservation (SAC) that indicates its national and European importance and provides particularly important habitat for plants, invertebrates, fish, birds and mammals (Southern Water, 2007). It is also noted for its populations of the southern damselfly *Coenagrion mercuriale* (Charpentier, 1840), an internationally threatened freshwater macroinvertebrate. The water resources of the catchment are used for public water supply, discharge of treated sewage effluent, fish farming, watercress beds, agriculture, fisheries and recreation (Halcrow Group Ltd, 2007). With a strong fishing influence on river management, the Itchen catchment is one of the country's premier rivers for recreational fishing (Environment Agency, 2007b).

2.2.2 Revels Fishery, Caundle Brook, the River Lydden and Stour catchment

The Revels Fishery, near Cosmore, Sherborne, Dorset, South West England, is positioned within the Blackmore Vale (Figure 2.2). The catch-and-release fishery complex consists of a total of twelve lakes, spread out over 18 acres of land, while the fishing ponds cover an area of about 6 hectares (Figure 2.6, Plate 2.7, Plate 2.8, Plate 2.9). The twelve lakes are separated into three two-lake complexes, one four-lake complex and an extra two-lake complex on a separate property. Sunbleak were found in the main four-lake complex and the adjoining two-lake system for the first time in 1999 (A. Pinder, pers. comm.). A population estimate was not made as sunbleak were too numerous to make this feasible (A. Pinder, pers. comm.). Both complexes eventually flow into Caundle Brook, which in turn flows into the River Lydden and subsequently into the River Stour. The fishery ponds vary in shape and sizes but are all surrounded by trees, such as willows, hedgerows and bushes. The bank side vegetation is managed by vegetation cutbacks. Reeds and water lilies *(Nymphaceae)* are present at the margins of the ponds. None of the ponds exceed a depth of 1.8 m. The fishery is stocked sporadically with 18 species of native and non-native fish, which include pike, common carp, wels catfish *Silurus glanis* (L.), grass carp, tench, common bream, perch, European chub *Leuciscus cephalus* (L.), crucian carp, rudd, roach, common dace *Leuciscus leuciscus* (L.) and golden orfe *Leuciscus idus* (L.). The exact numbers of individual stocked fish were not available.

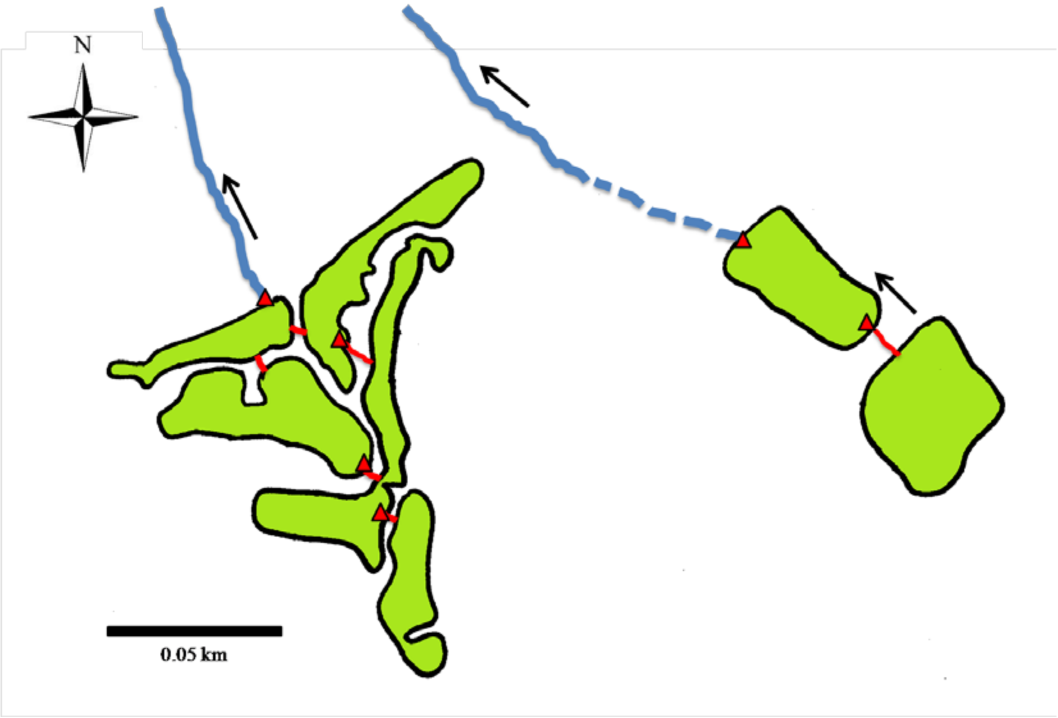

Figure 2.6: Schematic overview of the lakes of Revels Fishery (arrow: flow direction; green: fishery lakes; blue: Caundle Brook (the two arms join together as Caundle Brook ≈200 m downstream of the fishery); red: connection between water bodies; with continuous lines (▬) being above and discontinuous lines (---) being under-ground; red triangles (▲) indicate the location of 6 drifts nets used in Chapter 4).

Plate 2.7: Aerial photograph of Revels Fishery (Flashearth Navteq, 2008c).

Both pond systems containing sunbleak outflow into Caundle Brook, which flows for approximately 15 km until it enters the River Lydden, through which it is subsequently connected to the River Stour. The Brook flows through pasture and agricultural land that is used for cattle and sheep grazing. The banks are mostly natural and rows of trees, such as apple and cherry trees, as well as alders *Alnus* spp., provide overhanging cover for the brook. Hedgerows of bramble contribute the main part of the lower bankside vegetation. The approximate width of Caundle Brook ranges between 0.5 m and 3.50 m until it enters the River Lydden.

The entire Stour catchment covers an area of about 130,000 hectares. The Stour rises on the Greensand, Somerset, has a length of 96 km and falls ≈230 m before it enters the sea at Christchurch in Dorset, South West England. Caundle Brook is underlain predominantly by clay soils (Environment Agency, 1998). Nutrient inputs from farming and low flow during summer put pressure on the system and cause algal blooms in the main catchment, thus reduced dissolved oxygen availability. Flooding and groundwater abstractions are major influences on the catchment. Water crowfoot is the major component of submerged vegetation throughout the catchment and occurs in small patches along the deeper areas (≈1 m) within the study area. Abundant fish species in the catchment are brown trout and Atlantic salmon, as well as minnows, bullheads and stoneloach. Less abundant species are roach, common carp, eel, three-spined stickleback, *Lampetra* spp, chub and pike.

Plate 2.8: View across one of the ponds of the lower four-pond-system at Revels Fishery (Picture by author).

Plate 2.9: View across the northern-most pond of the upper two-pond system at Revels Fishery (Picture by author).

2.2.3 Somerset Levels

The Somerset Levels and Moors (Figure 2.3) a system of connected drain ditches (’rhynes’) and rivers, are recognised as an internationally important wetland of exceptional wildlife (Environment Agency, 2005) and are one of the major British areas of alluvium (Lewin, 1981). The Levels consist of 60,728 ha of low-lying land, which drains into the Severn Estuary. The Levels and Moors are enclosed by low hills and ridges and are underlain by Triassic rocks. The lowland rivers in this area have organic fens alongside peat deposits. Here peat loss may follow drainage and cultivation. Sedimentation is derived partly from offshore sources and also involves marine sedimentation, peat and salt marsh development and fluvial processes (Godwin and Clifford, 1939). The Somerset Levels and Moors are characterised by open landscapes of wet pasture, arable fields, grasslands and wetlands delineated by ditches. Only in a few places, such as the Kings Sedgemoor Drain (see Figure 2.3), does the force of gravity result in surface water discharge. Most drainage channels are closed automatically by a sluice at the seaward side when the sea levels rise above the freshwater level.

Urban development is concentrated on the coastal strip, with small villages throughout the remaining catchment (Environment Agency, 2005). Land use in the catchment is predominantly grazing, dairy farming, with scattered peat workings and willow farming in the lower, and crops in the upper catchment. Flood risk in the lower flood plain is related to the storage capacity of the system. Flooding usually follows a period of prolonged rainfall and/or occurs during summer when artificially penned water levels have decreased the storage capacity of the system. The Somerset Levels and Moors are drained primarily by the Rivers Brue and Axe as well as the River Huntspill (see Figure 2.3). In addition to these major water courses, numerous river channels and ditches drain each catchment. Seasonal factors and flooding issues complicate the maintenance of water levels to suit agricultural and environmental purposes. In the summer, water levels are maintained relatively high to provide wet fences, stock watering and assist nature conservation. During the winter, most of the pens are removed and water levels throughout the area are lowered to accommodate increased rainfall and runoff to decrease flood risk. As a result, dry winter periods often cause extremely low flows in the drainage channels. Summer penning of water courses can lead to a concentration of pollutants (e.g. heavy metals, nutrients) and consequently marked diurnal fluctuations in dissolved oxygen levels. Diffuse pollutants from urban areas and roads entering the water courses and agricultural inputs (e.g. fertilisers, herbicides and pesticides) have a major impact on the nutrient levels in the surrounding watercourses.

The Somerset Levels can be divided into three zones according to a generalised hydrological response to rainfall. The first is the upland area with predominantly impermeable soils, in particular the headwaters of the River Brue catchment (see Figure 2.3). A combination of steeper slopes and impermeable soils mean that the area is characterised by low base flow and a very quick response to rainfall events (i.e. < 10 hr). The second zone is the upland areas with predominantly permeable, highly-fissured limestone ‘karstic’ geology. The third is the lowland area of the flood plain and coastal strip.

On the Levels, the main tree and shrub cover is from willows with a few shelterbelts of poplar. They support a wide variety of plant species, as well as common plants such as marsh marigold *Caltha palustris* (L.), meadowsweet *Filipendula ulmaria* (L.) and ragged robin *Lychnis flos-cuculi* (L.). Throughout the catchment there are bands of willow-dominated scrub around peat workings and nature reserves. Willows are cultivated, along with reed beds. Generally, the Somerset Levels have a high biodiversity, both in terms of species and habitats, and contain a number of important environmentally designated sites. The Somerset Levels and Moors are a designated Ramsar site and are also designated a Special Protection Area, classified for rare and vulnerable birds (Environment Agency, 2005). In addition, the area supports a population of Eurasian otter *Lutra lutra* (L.).

The Somerset Levels are highly valued by anglers, with angling occuring on the River Brue and many of the man-made watercourses in the lowlands; the artificial lakes are used for regional and national angling championships. The Somerset waters contain mostly healthy populations of coarse fish, such as bream, chub, roach, pike, common carp, common bream, perch, three-spined stickleback, eels, dace, roach, rudd, ruffe, gudgeon, as well as brown trout, sunbleak and hybrids of roach and bream (Langler and Smith, 2001). The River Parrett in particular holds eels and elvers during January through to May (see Figure 2.3). Sunbleak was first recorded in the Somerset Levels (Kings-Sedgemoor Drain) in 1990 and the species has since spread throughout the catchment (Farr-Cox *et al.*, 1996).

The River Tone (see Figure 2.3), a tributary of the river, rises in the Brendon Hills near Raleigh’s Cross (Environment Agency, 1997). From the source to the confluence, the Parrett is about 33 km long and drops about 370 m in altitude. The River Tone catchment, as part of the Somerset Levels, covers an area of ≈ 41,400 hectares which is underlain predominantly by Old Red Sandstone (Environment Agency, 2000a). In 1998, 84 % of the River Tone water course was of good or very good chemical quality and 16 % of fairly good quality (Environment Agency, 2000b). A total 63.1 km of the course of the River Tone are used as a salmonid (Game) fishery and 29.1 km as cyprinid (Coarse) fishery. The sampling site at Hankridge, in Taunton on the River Tone (Plate 2.10, Figure 2.3) is muddy and turbid. Few overhanging trees and hedgerows comprise the bank side vegetation.

The Bridgewater-Taunton Canal leaves the River Tone at Firepool Lock in Taunton (Figure 2.3). Where the Canal enters Bridgewater at Hamp, a weir enables excess water to run into the River Parrett. The Bridgewater-Taunton Canal ends at Bridgewater Docks where it enters *via* a lock. The canal has an overall length of approximately 24.5 km. Three sites were sampled on the Canal: at the YMCA in Bridgewater, at Buckland Farm between Bridgewater and Taunton (Plate 2.11, Figure 2.3) and at Creech St. Michael, near Taunton (Plate 2.12, Figure 2.3). One sampling site was at the Durleigh Reservoir (Plate 2.13, Figure 2.3), which is fed underground by the Bridgewater-Taunton Canal. This lowland reservoir of 33 hectares used to be a trout fishery and is now dedicated to public coarse fishing. Species include carp, roach, perch, tench and pike. Submerged macrophytes are sparse but consist mainly of common reed. Bank side vegetation comprises hedgerows, bushes and overhanging trees such as willows. There is also a wildlife conservation area for birds where fishing is prohibited.

Plate 2.10: River Tone at Hankridge, Taunton (Picture by author).

Plate 2.11: Bridgewater-Taunton Canal at Buckland Farm (Picture by author).

Plate 2.12: Bridgewater-Taunton Canal at Creech St. Michael (Picture by author).

The River Huntspill is an 8 km long artificial channel constructed in the 1940s to serve as a water reservoir (Langler and Smith, 2001). On average it is 60 m wide and has an outfall sluice at its seaward end, and a very large pumping station at the landward end. The river, which is a National Nature Reserve, consists of mostly steep or vertical bank with little bank side vegetation. The unstable clay banks prevent macrophytes from establishing. Bare banks and wave action causes strong bank erosion. Water levels vary between about 3.5 m in summer and 2.9 m in winter. However, previous management actions have included localised attempts to increase bank side vegetation by planting common reed and willow. At the sampling site at Woolavington Bridge (Plate 2.14, Figure 2.3), which is characteristic for the River Huntspill, the river is about 25 m wide and without any vegetation, neither submerged nor overhanging.

Plate 2.13: View across Durleigh Reservoir, Bridgewater (Picture by author).

Plate 2.14: River Huntspill at Woolavington Bridge (Natural England, 2007).

At both sites sampled on the Kings-Sedgemoor Drain - Parchey Bridge (Plate 2.15, Figure 2.3) and Bradney Bridge (Plate 2.16, Figure 2.3) – mean annual discharge $< 5\ m^{-3}s^{-1}$, and submerged macrophytes and overhanging trees and/or bushes are sparse. The River Sowy is the 20 km long Parrett relief channel and connects the River Parrett near Langport with the Kings-Sedgemoor Drain. At the sampling site at Greylake Bridge, the River Sowy (Plate 2.17, Figure 2.3) is approximately 1.5 m deep and lined by pasture used for grazing cows on both sides. Dense patches of submerged macrophytes along the bank include common reed and water lilies.

Plate 2.15: Kings-Sedgemoor Drain at Parchey Bridge (Picture by author).

Plate 2.16: Kings-Sedgemoor Drain at Bradney Bridge, Bawdrip (Picture by author).

Plate 2.17: River Sowy at Greylake Bridge (Picture by author).

Dunwear (Plate 2.18, Figure 2.3) and Beeches Ponds (Plate 2.19, Figure 2.3) near Bridgewater are separate and independent from the Somerset Levels drain network, covering an area of 2.2 and 1.7 hectares respectively. They are used for catch-and-release fishery by Bridgewater and Taunton Angling Club. They contain various species of coarse fish, such as roach and common bream, and now contain dense populations of sunbleak. The date of sunbleak introduction into these ponds is unknown.

Plate 2.18: Dunwear Pond near Bridgewater (Picture by G.H. Copp).

Plate 2.19: Beeches Pond near Bridgewater (Picture by G.H. Copp).

2.2.4 Two Lakes Fishery, Hampshire

Two Lakes fishery is a catch-and-release fishery consisting of five large fishing lakes and a large number of small, interconnected ponds (Figure 2.1, Plate 2.20, Plate 2.21). Submerged macrophytes are mainly water lilies *(Nymphaceae)*, which are particularly numerous in the stock ponds, and common reed *Phragmites* spp. The banks are lined with overhanging trees and bushes. All ponds cover a collective area of about 16 hectares and contain coarse fish, including common bream, roach and common carp. The lakes are not online with any water course but may overflow into surrounding woodland in the winter and during heavy rains. Sunbleak was introduced here in 1986 and has since developed into the most abundant fish species (Farr-Cox *et al.*, 1996). Every few years, the lakes are sporadically drained and treated with lime to remove sunbleak from the waters. To date this practise of control has not been successful in extirpating them from the site.

Plate 2.20: Aerial photograph of Two Lakes Fishery (Flashearth Navteq, 2008e).

Plate 2.21: Two Lakes Fishery overlooking the largest pond (Picture by author).

2.3 Study sites containing topmouth gudgeon

2.3.1 Crampmoor Fishery, Tadburn Lake and the River Test catchment

Crampmoor Fishery (Figure 2.1, Figure 2.7, Plate 2.22, Plate 2.23) near Romsey, Hampshire, is an ornamental aquaculture facility consisting of numerous artificial ponds with focus on golden orfe. Topmouth gudgeon was accidentally brought here in the mid 1980s, and since then the population has thrived (Gozlan *et al.*, 2002). The fishery has an outflow into Tadburn Lake stream (Plate 2.24, Plate 2.25, Plate 2.26), which flows into the River Test approximately 6 km downstream of the fishery. In the various ponds that are used to breed mainly golden orfe, submerged vegetation, such as white water lilies *(Nymphaceae)* and reeds *Phragmites* spp. are used by topmouth gudgeon as spawning substratum. The plastic drain pipes used for irrigation of the ponds have been found to have also been used as spawning substrate (M. Stollery, pers. comm.). The fishery ponds are managed by pond draining and weed cutting. During this time, the water will flow through a drainage pond and pass through a large-meshed seine net before discharging into Tadburn Lake stream.

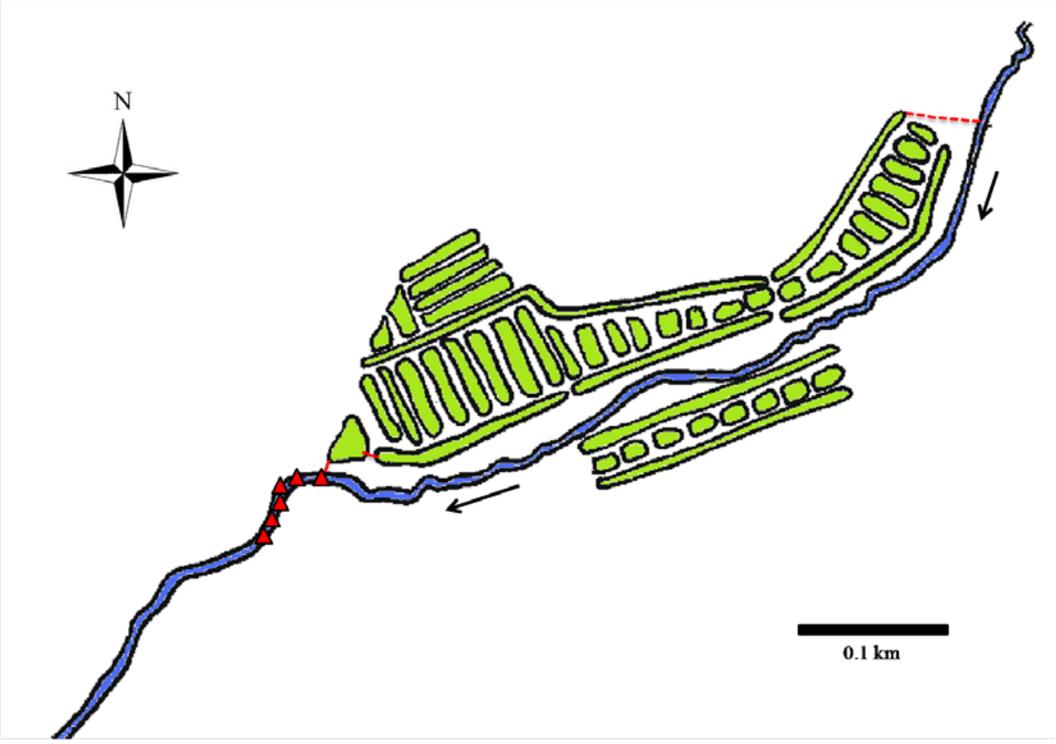

Figure 2.7: Schematic overview of Crampmoor Fishery ponds (arrow: flow direction; green: fishery lakes; blue: Tadburn Lake stream; red: connection between water bodies; with continuous lines (▬) being above - and discontinuous lines (---) being under-ground; red triangles (▲) indicate the location of 6 drifts nets used in Chapter 4). The fishery ponds and drains are connected with each other either permanently and/or temporarily by pipes depending on their use.

Plate 2.22: Aerial photograph of Crampmoor Fishery (Flashearth Navteq, 2008a).

Plate 2.23: Crampmoor Fishery overlooking ponds (Picture by author).

Plate 2.24: Crampmoor Fishery overlooking the drainage pond supplied with net during draining of adjoining fishery ponds (Picture by author).

Plate 2.25: Tadburn Lake stream at approximately 0.1 km downstream of the outflow of Crampmoor Fish Farm looking downstream (Picture by author).

Plate 2.26: Tadburn Lake stream at approximately 0.6 km downstream from the outflow of Crampmoor Fish Farm looking upstream (Picture by author).

Submerged vegetation in Tadburn Lake stream was dominated by patches of water crowfoot and yellow cress. Overhanging bank side vegetation along the stream within the study area was represented by bushes and trees, such as alder, willow, and hedgerows of bramble and hawthorn. Mean width in Tadburn Lake stream, was approximately 1.2 m and depth was generally shallow (<0.3 m), with few deeper areas up to 1.2 m. As a chalk stream, Tadburn Lake stream has an even hydrological regime and thermal stability (Westlake *et al.*, 1972; Berrie *et al.*, 1998). The stream bed consists of flint gravel and cobbles, as well as patches of sand and silt along the study area. The fish community is dominated by bullheads and stoneloach. Topmouth gudgeon are also present and likely to have been introduced to the stream *via* the connection with Crampmoor Fishery. Other fish species include brown trout, chub, *Lampetra* spp., three-spined stickleback, roach, European eel and two other non-native species: golden orfe and mirror carp *Cyprinus carpio* (L.), that most likely also originate from Crampmoor.

The River Test catchment is a lowland chalk river system, rising from the chalk aquifer of the Hampshire Downs. In its lower reaches the Test flows over the Tertiary clay and sand deposits of the Hampshire Basin. The River with its even annual hydrograph response (University of Southampton, 2006) and characteristic chalk river hydrology, supports aquatic habitats of very high nature conservation value that are included within the River Test SSSI (Hampshire Biodiversity Partnership, 2003). There are several areas of species rich flood plain grassland. The lower reaches of the Test show well developed transitions from fen meadow through to brackish flood plain grassland to salt marsh and reed bed.

2.3.2 Ratherheath Tarn, Cumbria, Lake District, North West England

Ratherheath Tarn (Figure 2.4, Plate 2.27, Plate 2.28), in Cumbria, a still water consisting of two connected ponds, is the most northerly site for topmouth gudgeon in England. It is a shallow (mean 1.5 m deep), tree-lined tarn of approximately 2.2 hectares and is managed by Windermere, Ambleside & District Angling Association (WADAA). The Environment Agency classifies Ratherheath Tarn as being 'online' in that it has a surface water outflow to Ratherheath Beck and subsequently the River Kent (Britton and Brazier, 2006). This outflow only functions in high flows during the winter for approximately 3 to 4 months. However, there is also a submerged land drain that functions for much, if not all, of the year, such that water is percolating down through the bed of the most northerly pond.

Sparse submerged vegetation is represented by white water lilies and common reed. The banks are frequented by trees and shrubs that are managed by the Angling club for recreational purposes. Ratherheath Tarn contains tench, bream, common carp, roach and gudgeon. The first topmouth gudgeon specimen was found here in October 2002 and the introduction is thought to have taken place in 2000 (Britton and Brazier, 2006). This could be related to the last stocking of the Tarn with 3,000 juvenile carp in April 2000 (Windermere Ambleside and District Angling Association, 2006), with topmouth gudgeon as an accidental contaminant of this batch. In March 2005, topmouth gudgeon were eradicated from this site using a rotenone-based approach (Britton and Brazier, 2006).

Plate 2.27: Aerial photograph of Ratherheath Tarn (Flashearth Navteq, 2008b).

Plate 2.28: Ratherheath Tarn, overlooking the north basin of the largest pond (Picture by G.H. Copp).

2.3.3 Canal du Fumemorte, Camargue, Rhone Delta, France

Canal du Fumemorte, Camargue region, South France (Figure 2.8, Plate 2.29) lies within the Mediterranean climatic region that is characterised by high evaporation and low rainfall between May and August (Rosecchi *et al.*, 1997). Water levels in the canal vary greatly from year to year. The Canal du Fumemorte is a rain-fed drainage canal for the Rhone part of a seasonally flooded marsh in the Mediterranean region. Fumemorte drains rice field irrigation water and is connected to the Relongues marsh by ditches equipped with sluices (Heurteaux, 1992). The catchment of the Canal du Fumemorte covers an area of about 7,000 hectares and is 14.6 km long (Poizat and Crivelli, 1997). The canal's depth varies between 0.5 and 1.5 m and its width varies between 10 and 15 m. The salinity of Canal du Fumemorte varied from 0.2 to 3.0 mgl^{-1} between 1987 and 1990, but has a mean salinity generally less than 1 gL^{-1} NaCl (Chauvelon, 1998). However, Canal du Fumemorte has generally been classified as a closed freshwater system (Rosecchi and Crivelli, 1995). The bottom of the canal is muddy and submerged vegetation is sparse at the centre. Vegetation such as pondweed *Potamogeton* spp. and common hornwort *Ceratophyllum demersum* (L.) occurs along the margins. Small streams coming off the main canal are mostly terminal and populated by dense beds of submerged macrophytes.

Topmouth gudgeon were first found in the Canal du Fumemorte in 1993 (Rosecchi *et al.*, 1993). The first specimens are assumed to have escaped from a local fish farm (Rosecchi *et al.*, 1997). Canal du Fumemorte harbours fish species such as sand smelt *Atherina boyeri* (Risso 1810), which represents about 80 % of the fish community (Poizat and Crivelli, 1997). Also present are the mullets *Liza ramada* (Risso, 1826) and *Mugil cephalus* (L.), pumpkinseed, black bullhead *Ameirus melas* (Rafinesque, 1820), rudd, European eel, silver bream *Abramis bjoerkna* (L.), common bream, three-spined stickleback, roach, common carp, mosquito fish *Gambusia affinis* (Baird and Girard, 1853), tench, gobies *Gobio* spp, pike, goldfish, pipe fish *Syngnathus abaster* (Risso 1827), bleak, gudgeon and pikeperch.

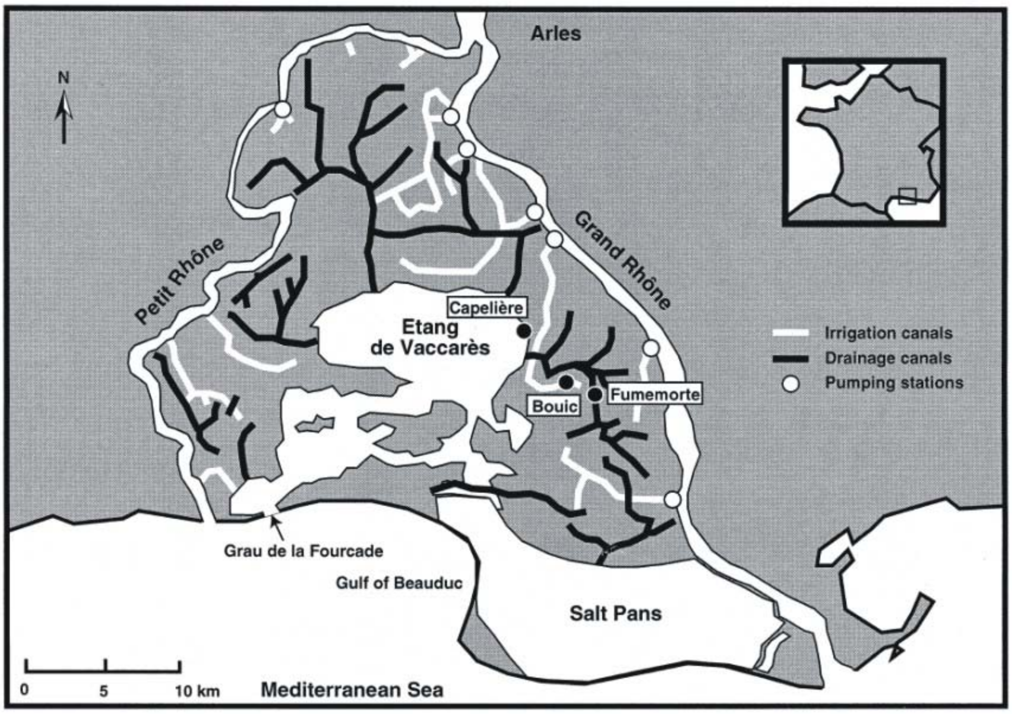

Figure 2.8: Map of Canal du Fumemorte, Rhone Delta, Camargue, France (Rosecchi *et al.*, 2001).

Plate 2.29: Canal du Fumemorte (Parc naturel régional de Camargue, 2007).

3. Life history and morphology

3.1 Introduction

The success of a species after introduction depends largely on its life-history traits (Kolar and Lodge, 2002), which are good predictors of fish invasions (Fausch *et al.*, 2001; Kolar and Lodge, 2002; Vila-Gispert *et al.*, 2005). Invasion theory suggests that adaptation of life histories, including age and length at maturity and reproductive effort, by introduced species to their new habitat is important for successful establishment (Fausch *et al.*, 2001). Knowledge of the life history characteristics of a species will assist in the understanding of the potential with, and the mechanism by which, this species may successfully invade a new environment. This is an aspect that is considered in many risk assessments and ecological niche theory can play an important role during this process. Niche theory asserts that invasion success is facilitated by the intrinsic biological traits of a species, which determine the degree of their 'pre-adaptation' to a new environment (Shea and Chesson, 2002). The biological traits possessed by a species, including life histories, morphological characteristics and habitat requirements (see also Chapter 6), may determine its ability to utilise 'niche opportunities' in a new environment (Shea and Chesson, 2002). Niche theory has been questioned in the past (e.g. Hubbell, 2001); one of the reasons for this criticism was that it did not consider where and under what circumstances a species may subsist, and how it may interact with its surroundings. However, niche theory can be useful as a tool to understand large-scale patterns and alterations in species diversity, distribution and abundance as well as the invasion process (Lohrer, 2001).

Life history theory considers the constraints and/or tradeoffs among individual traits (and fitness) and demographic variables (responses) that are associated with reproduction in different types of environments. The theory makes predictions about relationships between different strategies and the environment, which can be valuable in the study of invasions. Traditional life history theory was displayed as the *r*/*K* selection theory (MacArthur and Wilson, 1967; Pianka, 1970), where:

1) *r* strategists displayed high fecundity, small adult body size, short lifespan, and were able to disperse offspring widely. Organisms within this category were expected to occur mainly in unstable or unpredictable environments.

2) *K* strategists showed large body size, long lifespan, and the production of fewer offspring that generally require extensive parental care until they mature. In stable or predictable environments *K* selection was expected to predominate.

Thus, it would be expected that *r* strategists would generally be better invaders than *K* strategists. This would be governed by *r* strategists having high fecundity, short lifespan and early maturity enabling them to form dense populations within a short timeframe in a new environment. However, the *r/K* concept has been widely criticized (Stearns, 1977; Barbault, 1987; Kuno, 1991; Getz, 1993); it appeared that this traditional view failed to capture some important variation in reproduction of fish. Numerous comparative studies of life history in fish have been carried out and have determined a variety of life history patterns (Wootton, 1984; Winemiller, 1989; Paine, 1990; Winemiller and Rose, 1992; Vila-Gispert and Moreno-Amich, 2002). As a result, three primary life history strategies have been identified, which correspond to the endpoints of a triangular surface arising from trade-offs among three fundamental demographic parameters of survival, fecundity, and reproduction. Through the study of 216 species of North American freshwater and marine fishes, Winemiller and Rose (1992) developed a life history model (Table 3.1), referred to as the ‘W-R model’, which basically separates the *r* strategy of the classic *r/K* model into the periodic and opportunistic strategies and defines the *K* strategy as the equilibrium strategy. However, the model also recognizes intermediate strategies, with the different strategies being considered as adaptive with respect to the relative intensity and predictability of temporal and spatial variation in abiotic environmental conditions, food availability and predation pressure (Winemiller and Rose, 1992).

Life history characteristics of an introduced species that may have been suitable and advantageous in their native habitat may not necessarily be advantageous in the new habitat. For example, early maturity and high reproductive effort may be of advantage in both seasonally fluctuating rivers (e.g. flow, temperature) and man-made reservoirs as it will provide large numbers of offspring while increasing the likelihood of survival of greater numbers. Generally, if a species matures early in life, it can potentially reproduce early in life. Species that mature late in life are exposed for longer time periods to challenges such as predation pressure, food, and habitat availability and quality, before they are able to reproduce for the first time. Consequently, for the duration of their pre-maturation life there would be greater chances of mortality.

The reproductive behaviour of an introduced fish species is also an important factor in their establishment in a new environment. Batch spawning, where mature individuals spawn several times during one spawning season, enables the production of a large number of offspring, which is related to an increased overall fecundity. Such behaviour is often seen in small bodied fish species to increase the maximum fecundity and subsequently ensure recruitment (Cowx, 2001). Fecundity is largely limited by body size. Parental care, where one or both parents care for the eggs and/or young (Clutton-Brock, 1991), enhances survivorship during early life and provides protection from predators. Sunbleak and topmouth gudgeon are batch spawners and the male guards the nest until hatching (Farr-Cox *et al.*, 1996; Dussling and Berg, 2001; Rosecchi *et al.*, 2001), which is expected to facilitate their success as invaders (Jeschke and Strayer, 2008).

Life history characteristics will in part determine the ability of a species to be successful at invading a new water body. It is assumed that this is governed by the combination of the species’ overall life history traits (e.g. fecundity, spawning requirements, reproductive strategy) and its phenotypic plasticity (Bruton, 1986). As the relative growth of morphological traits in fish is related to their overall growth in response to ecological changes (Norton *et al.*, 1995), variations in life-history traits may occur in response to, or in conjunction with morphological adaptations to the prevalent physical and biological conditions (Ľavrinčíková *et al.*, 2005). Classic ‘descriptive’ morphology of fish is based on perceived relationships between morphological characteristics and habitat use (Keast and Webb, 1966). As per Hubbs (1941), fish morphology is related to hydrodynamics of the habitat. As an example, the minnows *Notropis scepticus* (Jordan and Gilbert, 1883) and *Notropis altipinnis* (Cope, 1870) displayed slimmer bodies in fast-flowing habitats while the size of the eyes was related to swift, turbid habitats. Generally, body form and shape, as well as fin morphology are related to the physical habitat type and swimming capabilities, while the morphology of head and mouth is associated with diet. Body shape is the most important factor in the hydrodynamics of fish, which is related to the principles of fluid dynamics regarding movement of water over the body of fish (Webb, 1975; Vogel, 1981). Generally, different factors are important when looking at fish from water bodies displaying differences in velocity, e.g. lentic *vs* lotic. When a species is introduced to a new environment, it is generally expected that morphological plasticity is advantageous to non-native species as it may subsequently be able to subsist in a greater variety of habitats including those of varying flow velocities. It has previously been reported that an inability to adapt to local hydrological regimes results in the failure of non-native fish species to establish despite high propagule pressure (Minckley and Meffe, 1987; Baltz and Moyle, 1993). Tolerance of a wide range of water velocities is also an aspect that is being included in risk assessment protocols for fish, for example Copp *et al*. (2005b; 2005c).

Table 3.1: Overview of the three life history strategies for fish developed by Winemiller and Rose (1992).

Strategy	Typical Characteristics	Typical Environment
Opportunistic	Early maturation High reproductive effort Small adult body size Continuous spawning Low fecundity	Highly disturbed and unpredictable environments
Periodic	Delayed maturation High fecundity Synchronous spawning Large adult body size Low juvenile survivorship (i.e. no parental care)	Seasonal, periodically suitable environments
Equilibrium	Large egg size High juvenile survivorship (i.e. greater parental care) Low fecundity Small and medium adult body size Moderate maturation age	Constant environments

Sunbleak and topmouth gudgeon display early maturation, high reproductive effort, small adult size, batch spawning behaviour and parental care (Pinder and Gozlan, 2003) while their spawning season extends from April/May through to June/July (Brezeanu, 1968; Fishbase, 2008; K. Beyer, pers. obs.). These characteristics suggest an ability to maintain dense populations, thus facilitating the colonization of new habitats (Jeschke and Strayer, 2008). In England, topmouth gudgeon can be found at > 20 locations while sunbleak is mainly found in water bodies in the South of the country (Farr-Cox *et al.*, 1996; Gozlan *et al.*, 2002; Pinder *et al.*, 2005b) (Figure 1.2, Figure 1.3). Both species have formed dense populations where they were introduced, particularly in lentic water bodies. In light of their dispersal, it is relevant to examine intraspecific variability of life history traits as well as their morphology to assess their potential for adaptation to new habitats. The aim of this chapter was to assess the variability of life-history traits and morphological characters of sunbleak and topmouth gudgeon. The specific objectives were to: 1) evaluate size distributions of sunbleak and topmouth gudgeon populations from various sites; 2) examine the morphology of sunbleak and topmouth gudgeon from different locations; and 3) determine reproductive indices of sunbleak and topmouth gudgeon from various locations.

3.2 Materials and methods

3.2.1 Sampling

Fish from each sampling site were utilised for investigations into life history traits and morphological characters. The design and timing of sampling depended on the manpower and equipment availability. This was further driven by location of sites and the spread of sunbleak and topmouth gudgeon in England during the time the PhD research was taking place. The sampling sites were selected because they were known to contain the target species (Farr-Cox *et al.*, 1996; Gozlan *et al.*, 2002). Although, sunbleak and topmouth gudgeon have been sighted in other water bodies in England (Farr-Cox *et al.*, 1996; Pinder *et al.*, 2005b), at the time of the study only the chosen sites were expected to hold dense populations to enable capture of fish of each species required to derive life history traits and morphological characters. A large number of sites containing sunbleak and one site containing topmouth gudgeon were located in the South and South West of England, within easy reach of the base of the PhD researcher who was stationed at CEH Dorset in South West England (see Chapter 2). The topmouth gudgeon sample obtained from the most northerly site in England was collected through collaboration with the Environment Agency. The sample from France was obtained from another collaborator (A. Crivelli, pers. comm.) and was subsequently included in this chapter to complement data from the English populations. When comparing the traits between samples taken at different times of the year, these were considered during interpretation.

Sunbleak were collected at ten sites (see Chapter 2 for description and locations of all sampling sites) in Somerset, southern England between 24 and 26 April 2004. The water bodies included three sites on the Bridgewater-Taunton Canal, two sites on the Kings-Sedgemoor Drain, as well as one site each at Dunwear Pond and Durleigh Reservoir and the Rivers Huntspill, Sowy and Tone (Figure 2.3). In addition, Stoneham’s Shrubbery Lake and Two Lakes Fishery, both in Hampshire, were sampled on 3 June 2003 and 23 May 2003 respectively (Figure 2.1). At each site containing sunbleak, except for Two Lakes Fishery where a pond had been drained and a sample of fish was provided, a seine net (10 m long; 2 m deep; mesh size: 1.5 mm) was swept through the water three times. The seine net was deployed in an arc from the bank using an inflatable dinghy encircling an area of water (Coles *et al.*, 1985; Hughes and Willis, 2000). Based on this sampling method and estimation of the netted area (m^{-2}) using a graduated pole, the density was calculated as the number of individuals per m^{-2}.

Topmouth gudgeon were collected from three sites: Tadburn Lake stream, Hampshire, Southern England (Figure 2.1) on 17 April 2003 and from Canal du Fumemorte, Camargue, Rhone Delta, France (Figure 2.8) on 15 May 2003 (specimens provided by A. Crivelli) using a battery powered DC electrofishing backpack unit with a circular anode (20 cm diameter), and from Ratherheath Tarn, Cumbria, northwestern England (Figure 2.4) on 11 August 2004 using a seine net (50 m long; 2.5 m deep; mesh size: 2.5 mm). The seine net was deployed in an arc from the bank by wading and swimming, and while holding one end of the net encircling an area of water (Coles *et al.*, 1985; Hughes and Willis, 2000).

At each sampling site all sunbleak and topmouth gudgeon were retained and, depending on the number of fish captured at each location, between 2 and 70 fish underwent further analysis per site. Sites where ≤ 5 sunbleak were captured, these were excluded from multivariate analysis of morphology. Such low numbers of fish may disguise patterns in morphological variability that would be revealed by the analysis. Fish were killed by Schedule 1 methods as per the ‘Animals (Scientific Procedures) Act 1986’ with an overdose of 2-Phenoxyethanol followed by severance of the spinal cord at the base of the skull (Home Office, 1986a; b). They were then preserved in 4% formalin for further examination in the laboratory.

Potential shrinkage effects of preservation

Some authors have observed decreased body size after a period of preservation in different types of preservatives (Lux, 1960; Parker, 1963; Stobo, 1972; Engel, 1974; Jawad, 2003). Other authors have reported very limited or no changes in body lengths of different fish species including *Sarotherodon mosambicus* (Peters), *Barbus luteus* (Heckel, 1843) and *Rastrelliger kanagurta* (Cuvier, 1816) (Billy, 1982; Al-Hassan and Abdullah, 1992; Al-Hassan and Shawafi, 1997; Al-Hassan *et al.*, 1999; Al-Hassan *et al.*, 2000; Jawad, 2003). However, it has been observed that preservation in 3.8, 4, 5 and 10 % formalin follows a pattern in a way that the greatest effect on body length and weight, if at all, takes place within the first 24 to 48 hours of preservation (between 2.5 and 4 % shrinkage) (Parker, 1963; Fisher *et al.*, 1998; Cunningham *et al.*, 2000). The effects of preservation on weight (often > 8 %) exceeds the effects on length (mostly < 8%) and the length and weight of shrinkage is inversely related to the initial body size of the fish (Hjorleifsson and Klein-MacPhee, 1992; Johnston and Mathias, 1993). However, the effects of preservation are minimised at lower concentrations of formalin. Therefore, a 4 % formalin solution was used in the preservation of sunbleak and topmouth gudgeon. Shrinkage of these species was not tested during this study, but samples were examined as soon as possible after capture to prevent any longterm effects of preservation.

Schedule 1 methods (Home Office, 1986a; b)

The Animals (Scientific Procedures) Act 1986 makes provision for the protection of animals used for experimental or other scientific purposes in the United Kingdom (Home Office, 1986a). The Code of Practice ‘The Humane Killing of Animals under Schedule 1 to the Animals (Scientific Procedures) Act 1986’, provides detailed information on the methods that should be used to appropriately kill animals covered by the act (Home Office, 1986b). It further describes how death should be confirmed, and safeguards to be adopted to ensure that these methods are performed in a competent manner. For fishes up to 1 kg in body weight, Schedule 1 regulates for killing to take place by 1) applying an ‘overdose of an anaesthetic using a route and an anaesthetic agent appropriate for the size and species of the animal’, and 2) subsequent ‘concussion of the brain by striking the cranium with destruction of the brain before the return of consciousness’. For embryonic and larval fishes, Schedule 1 describes killing to take place by applying an ‘overdose of an anaesthetic using a route and anaesthetic agent appropriate for the size, stage of development and species of the animal’.

3.2.2 Morphological characters

Measurements of morphological characters were taken individually on all sunbleak and topmouth gudgeon, with mensural characters related to swimming capabilities, feeding ability and microhabitat use measured as per Holčik *et al*. (1989). In sunbleak and topmouth gudgeon, 30 and 17 morphological characteristics were recorded respectively (see Table 3.2 for morphological characters and codes). Initial investigations using 30 characters to describe morphological variability in sunbleak (Figure 3.1, Figure 3.2, Figure 3.3) suggested that the use of a reduced number of 17 characters in topmouth gudgeon was sufficient for this purpose and would reveal patterns in morphological variability. All measurements were made to the nearest 0.01 mm and using an electronic caliper. Each fish was weighed wet to the nearest 0.01 g using an electronic balance.

Table 3.2: Morphological characteristics measured in topmouth gudgeon and sunbleak from different populations presented in alphabetical order (see Figure 3.1 to Figure 3.4 for schematic overviews of morphological measurements).

Code	Morphological characters	Sunbleak	Topmouth gudgeon
A – C	anal fin-caudal fin distance	X	
Ab	base of anal fin	X	
Ah	height of anal fin	X	X
Db	base of dorsal fin	X	
Dh	height of dorsal fin	X	X
FL	fork length	X	X
G	gape	X	X
H	maximum body height	X	X
h	minimum body height	X	X
Hd	head depth	X	
Hl	head length	X	
Hw	head width	X	
Ina	inter-nasal distance	X	
Io	inter-orbital distance	X	
Od	orbital diameter		X
Oh	orbital horizontal diameter	X	
Ov	vertical orbital diameter	X	
Pb	base of pectoral fin	X	
Ph	height of pectoral fin	X	X
PreA	pre-anal fin distance	X	X
PreD	pre-dorsal fin distance	X	X
PrO	pre-orbital distance	X	X
PrOp	pre-operculum distance	X	X
PreP	pre-pectoral fin distance	X	X
PreV	pre-ventral fin distance	X	X
SL	standard length	X	X
TL	total length	X	X
Vb	base of ventral fin	X	
Vh	height of ventral fin	X	X
W	maximum body width	X	
w	minimum body width	X	

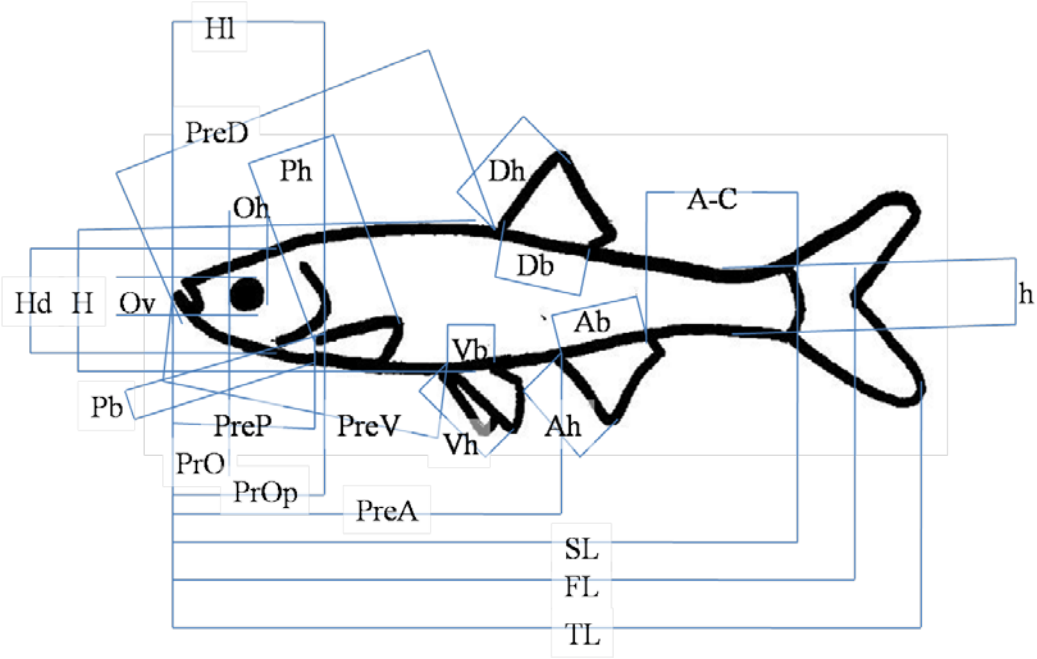

Figure 3.1: Schematic overview of 24 morphological characters recorded in sunbleak (see Table 3.2 for morphological codes).

Figure 3.2: Schematic overview of 5 morphological characters recorded in sunbleak (see Table 3.2 for morphological codes).

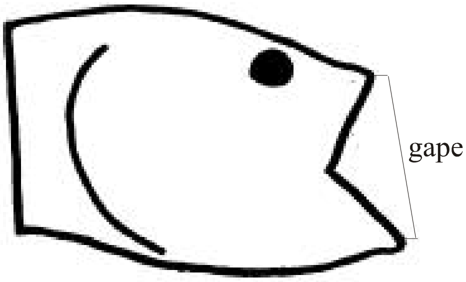

Figure 3.3: Schematic overview of gape (G) measurement recorded in sunbleak and topmouth gudgeon (see Table 3.2 for morphological codes).

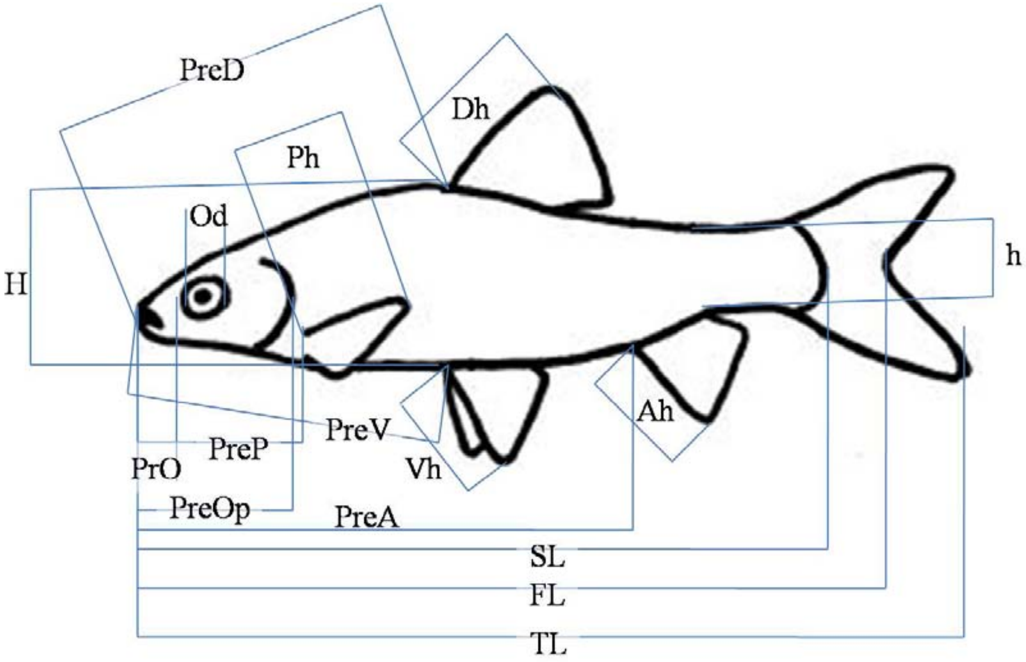

Figure 3.4: Schematic overview of 16 morphological characters recorded in topmouth gudgeon (see Table 3.2 for morphological codes).

3.2.3 Length frequency analysis

Length frequency distributions were derived for the sunbleak and topmouth gudgeon populations used in this chapter. Initial investigations applying >2 mm increments to explain these suggested that 2 mm increments would best describe the modal distributions in the small-bodied cyprinids. Therefore, length frequency distributions were prepared through grouping length classes into 2 mm increments and presented graphically. This was completed to assist description of the populations and allow further explanation of patterns observed during life history and morphological investigations. Length modes may indicate age groups and are generally most pronounced in fish with a short spawning season and fast and uniform growth (Bagenal and Tesch, 1968). Generally, it is possible to determine the mean and/or modal lengths for at least the first few age groups from the length frequency distribution. However, it is expected that this may be more difficult in sunbleak and topmouth gudgeon as they display batch spawning behaviour (Farr-Cox *et al.*, 1996; Rosecchi *et al.*, 2001) and so may produce offspring of several groups of differing lengths during the same year which may be reflected in less distinct lengths groups in subsequent years.

3.2.4 Age determination

Age of each individual topmouth gudgeon was determined using scales. Approximately five scales were taken from above the lateral line around the base of the dorsal fin, where they are first laid down and provide the full growth history of the fish (Bagenal and Tesch, 1978). The age was validated by 1) examining the operculi of 15 % of the sample chosen randomly and 2) using independent estimates of age by a second reader on all scales and the operculi of 15 % of the sample chosen randomly. In sunbleak, age was determined by examining operculi with the age validated by 1) re-examining 15 % of operculi chosen randomly and 2) using independent estimates of age by a second reader on all operculi of the sample.

Based on a study by Gozlan *et al*. (2003b), it was decided that age determination in sunbleak would be carried out by only using operculi. Their study concluded that sunbleak scales were too difficult to age due to their very small size of 0.7 to 1 mm. For topmouth gudgeon, several studies have previously used scales for age determination (Barus *et al.*, 1984; Witkowski, 1991; Rosecchi *et al.*, 1993; Britton *et al.*, 2007) and therefore these were used during this study as well as operculi. Scales and/or operculi were placed in a Petri dish containing a solution of sodium hydroxide solution (NaOH) until the mucus softened and then rinsed in distilled water. The structures were dried, wiped with suitable absorbent paper, and mounted between two microscope slides (Rounesfell and Everhardt, 1953). Age was then determined using images projected with a Projectina scale reading microscope (30x).

Scales

The alternation between rapid summer and slow winter growth of topmouth gudgeon is reflected on the scales by lighter zones and darker zones respectively. The lighter and darker zones represent widely-spaced ridges (summer growth) and tightly-spaced ridges (winter growth) respectively. The scales are aged by counting the annuli, which are formed by closely spaced ridges. The measuring axis for the annual growth zones was chosen as the radius selected from the anterior field (Figure 3.5).

Operculi

The alternation between rapid summer and slow winter growth of topmouth gudgeon and sunbleak is reflected in their opercular bones. The operculi show an alteration of broad opaque (summer) and narrow transparent (winter) rings respectively. The arrangement of these successive light (summer) and dark (winter) zones is related to the pattern of fish growth over the year. The annual rings can be seen as sharp stripes and when counted give the age of the fish. The measuring axis of annual growth zones in the opercular bone is in the centre of the thin shovel-like part, from the highest ridge in the base to the edge (Figure 3.6).

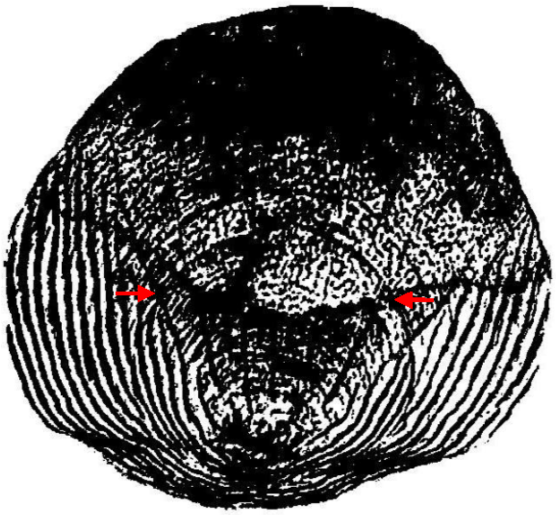

Figure 3.5: Topmouth gudgeon scale with arrows indicating location of annual mark.

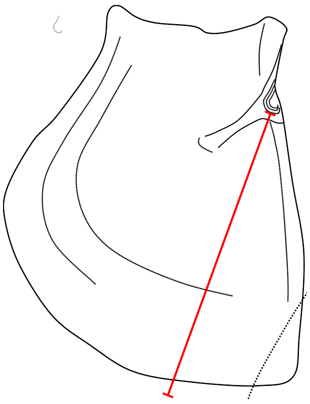

Figure 3.6: Schematic overview of ageing measurement location on sunbleak operculum. Measurements were taken along the line indicated (red line) from the focus to the edge of the operculum.

3.2.5 Back-calculation

Growth is a valuable indicator of fish health because it incorporates the biotic and abiotic parameters an organism is exposed to and can also reflect secondary impacts of chronic stress (Le Cren, 1972; Waters, 1977). Back-calculation allows the determination of the past growth of an individual fish from annual growth patterns inferred from the hard parts of the fish (Francis, 1990). Such calculation is based on the growth relationship between the hard structures used for ageing and fish length (Dahl, 1910; Lea, 1910). Back-calculation of fork length (FL) at age was undertaken using the linear relationship between scale annuli/operculum rings and FL (Creaser, 1926). This gave the following relationships:

$$FL_n = (R_n/R)* FL \qquad \text{after (Lea, 1910)}$$

$$R_n = a + bFL_n \qquad \text{after (Fraser, 1916)}$$

where: a =intercept, b=slope, R_n= radius to growth mark on the scale/operculum, R=the total scale/operculum size at capture, FL_n=fork length at age, FL=fork length at capture.

3.2.6 Fulton's condition factor

Energy intake will allow growth of body tissue and energy storage in muscles and the liver. When increased energy intake takes place, a greater weight may be obtained by a fish than it normally would have obtained at a specific age (Busacker *et al.*, 1990). The Fulton's condition factor K_F, commonly used in fisheries studies, can reveal such excess weight (Le Cren, 1951; Carlander, 1969; Bagenal and Tesch, 1978; Anderson and Gutreuter, 1983; Copp *et al.*, 2002c). To give an indication of the 'physiological state', 'well being' and 'fatness' of sunbleak and topmouth gudgeon at each sampling site, the Fulton's condition index K_F was calculated with the following formula (Murphy and Willis, 1996; Östlund-Nilsson *et al.*, 2005):

$$K_F = (W/FL)*10^5$$

where W is the weight and FL the fork length of the fish. Increased weight of a fish at a given length will be reflected by an elevated condition factor. Reduced condition in fish can be generally associated with a depletion of energy reserves, which can be stored as liver glycogen or body fat (Adams *et al.*, 1985; Evans and Claiborne, 1994). Condition factor decline may be a sign of a change in feeding patterns taking place in form of a behavioural response to stress (Brown *et al.*, 1987).

3.2.7 Gonad examination

Gonads were removed, weighed to the nearest 0.01 g and examined to determine the sex of the fish. Females with ovaries containing non-yolked or indistinguishable eggs were classified as immature, and those with ovaries containing yolked eggs were classified as mature. The gonado-somatic index (GSI) estimates gonad weight relative to somatic body weight, as an indicator of reproductive investment in individual fish (Mills and Eloranta, 1985) and is often used to compare reproductive allocation among populations (Fox and Crivelli, 1998). The GSI was calculated according to:

$$GSI = 100\ (Wg/(Wt-Wg))$$

where Wg is the gonad weight and Wt is the total weight of the fish. Some studies present the gonado-somatic index for mature females only, because the GSI has been deemed an unsuitable indicator for reproductive allocation in males, for example in pumpkinseed (Danylchuk and Fox, 1994). However, for comparative purposes the gonadosomatic-index was calculated for female and male sunbleak and topmouth gudgeon to show the potential differences brought about by the physiological differences in the reproduction between the sexes.

Individual fecundity was calculated by weighing the entire gonad and weighing 50 eggs, both to the nearest 0.01 g, separately and then extrapolating the total number of eggs contained in the gonad (Bøhn *et al.*, 2004). To remove the effect of body length, the relative fecundity as the number of eggs per unit fork length ($\mathrm{Fec}_{\mathrm{FL}}$) of fish was calculated according to:

$$\mathrm{Fec}_{\mathrm{FL}} = \text{number of eggs/fork length.}$$

To remove the effect of body weight, the relative fecundity as the number of eggs per gram body weight ($\mathrm{Fec}_{\mathrm{W}}$) was calculated as follows:

$$\mathrm{Fec}_{\mathrm{W}} = \text{number of eggs/weight.}$$

The described method used to estimate fecundity in sunbleak and topmouth gudgeon is called the ‘gravimetric method’. However, though this method is suitable for most temperate fish, it is not normally used for batch spawning fish species such as sunbleak and topmouth gudgeon. Therefore the results must be carefully interpreted.

The reproductive effort in mature sunbleak and topmouth gudgeon per age was calculated as the relative annual investment in somatic and gonad growth increment according to (Mills and Eloranta, 1985), as:

$$ER = \mathrm{Wg}/(\mathrm{Wg}+\mathrm{Wi})$$

where Wg is the mean gonad weight (g) for each given age class and Wi is the somatic growth increment (g) between consecutive year classes.

3.2.8 Age and length at maturity

Age at maturity was calculated from the proportion of mature individuals in each age-class in each population using the formula of DeMaster (1978):

$$\alpha = \sum_{x=0}^{w} (x)[f(x) - f(x-1)]$$

where α = mean age of maturity; x = age in years; $f(x)$ = proportion of fish mature at age x and w = maximum age in the sample. To calculate the mean length (FL) at maturity as the proportion of mature individuals in each length-class, a length adapted version of this formula (5 mm FL intervals instead of age-classes) (Trippel and Harvey, 1987; Fox, 1994) was used. The length adapted version of this formula using 10 mm length classes, has been found suitable particularly to calculate length at maturity in small-bodied fish species, that mature early in life, and has been applied in many studies on fish of small adult body size, for example on pumpkinseed (Fox and Crivelli, 1998; Copp *et al.*, 2002c; Villeneuve *et al.*, 2005; Fox *et al.*, 2006) and round goby *Neogobius melanostomus* (Pallas 1814) (G.H. Copp, pers. comm.). However, for the present study 5 mm length classes were used to yield sufficiently precise results in these species that display limited size range.

3.2.9 Data analysis

Data from 12 sites for sunbleak and three sites for topmouth gudgeon were used to examine the variability of life histories and morphological characters between the study sites. Three of the 12 sunbleak sampling sites, Durleigh Reservoir, River Tone and River Huntspill, were excluded from the data set for multivariate analyses because only 2, 3 and 5 fish were captured at these sites respectively.

Before assessing the differences between sites, Levene’s test (Dytham, 1999) was used to determine the equality of variances for all variables. Normality was examined using the Kolmogorov-Smirnov test. When data conformed to the requirements of parametric analysis, One-way ANOVA was performed to compare variables between sites and using a Bonferroni post-hoc test to determine differences between groups. When data were not suitable for parametric analysis then non-parametric Kruskal-Wallis test was used to determine those differences. In this case the Mann Whitney U-test served as a post-hoc test to examine differences between groups. All univariate analysis was performed with Minitab 14 (Minitab, Inc., PA, USA).

Before further analysis, each morphological character was corrected for body size by dividing by the standard length (SL). Variability was then calculated as the coefficient of variation (CV) of the size-corrected measure within a population as follows (Fowler *et al.*, 1998):

$$CV = (S.D./\bar{x})*100$$

where S.D. is the standard deviation and x is the mean. The coefficient of variation is presented as a percentage.

Multivariate analysis is carried out when many variables (e.g. morphological characters) and subjects (e.g. individual fish) are present. In fact, linear ordination methods will allow the treatment of related or unrelated ecological variables in a manner that is simultaneous. Each variable would be considered equally important at the start of the analysis, thus revealing any structure in the ecological data (Dolédec and Chessel, 1991). To reveal patterns in morphological variability based on size-corrected mensural characters, principal components analysis (PCA) (Gauch, 1982) by double centring was undertaken. PCA, a factorial method of analysis for quantitative variables, is adequate for determining principal axes that describe relationships between the elements present in a single matrix table (Dolédec and Chessel, 1991). Double centring combines the deviation from the mean for all rows and columns within each matrix (Dolédec and Chessel, 1991). Ordinations of morphological characters of individual specimens were grouped per site (both species) and sex (for topmouth gudgeon only) with scatter stars based upon uniform weightings with 90 % inertia. Using this method, 90 % of samples, displayed by points in the graph, would be found within each ellipse per group (Green, 1971), and would therefore display 90 % of the variation in the species' morphological characters at each site. To remove the proportional importance of each morphological character within the group, uniform weightings were used during the analysis. Parameters per individual were linked to a common centre equal to the mean of the principal component scores (first and second axes) resulting from the PCA. All multivariate analyses were performed using the ADE (Analysis of Environmental Data) Software package (Thioulouse *et al.*, 1997).

3.3 Results

Sunbleak

A total of 475 sunbleak underwent examination of life history parameters and morphology. Between 2 and 53 female and 1 and 23 male sunbleak were investigated at 12 sites (Table 3.3). Overall, except for sunbleak captured from the River Sowy, the number of female sunbleak exceeded the number of males in the samples. A total of only 2, 3 and 5 sunbleak were captured at Durleigh Reservoir (Durl10), River Tone (Tone8) and River Huntspill (Hunt6) respectively. Though the life history parameters from these sites are presented, they were excluded from multivariate analysis of morphology. Differences in the numbers of fish captured between sites may have been influenced by species densities within the different water bodies and/or simultaneously may have been influenced by differences of sampling methodology.

Table 3.3: Numbers of female and male sunbleak investigated for life histories and morphology from 12 sites in England at 1) Bridgewater-Taunton Canal, Buckland Farm (BTC1), 2) Bridgewater-Taunton Canal, Creech St. Michael, Somerset (BTC2), 3) Bridgewater-Taunton Canal, YMCA, Somerset (BTC3), 4) Kings-Sedgemoor Drain, Bradney Bridge, Bawdrip, Somerset (KSD4), 5) Kings-Sedgemoor Drain, Parchey Bridge, Somerset (KSD5), 6) Woolavington Bridge, River Huntspill, Somerset (Hunt6), 7) River Sowy , Grey Lake Bridge, Somerset (Sowy7), 8) Hankridge, River Tone, Somerset (Tone8), 9) Dunwear pond, Somerset (Dun9), 10) Durleigh Reservoir, Somerset (Durl10), 11) Stoneham Lakes, Hampshire (Stone11), 12) Two Lakes Fishery, Hampshire (TwoL12).

Site	Female	Male	Total
BTC 1	38	12	50
BTC 2	39	11	50
BTC 3	33	22	55
KSD 4	21	9	30
KSD 5	49	11	60
Hunt 6	4	1	5
Sowy 7	9	21	30
Tone 8	2	1	3
Dun 9	37	23	60
Durl 10	2	0	2
Stone 11	53	17	70
TwoL 12	52	18	70

Topmouth gudgeon

A total of 160 topmouth gudgeon were examined for their life histories and morphology. Between 16 and 45 female and 15 to 34 male topmouth gudgeon were captured at the Ratherheath Tarn, Cumbria, England, Tadburn Lake stream, Hampshire, England, and Canal du Fumemorte, France (Table 3.4).

Table 3.4: Numbers of female and male topmouth gudgeon investigated for life histories and morphology from two sites in England and one site in France: Ratherheath tarn, Cumbria, England (Rath), Canal du Fumemorte, France (Fum), and Tadburn Lake stream, Hampshire, England (Tad).

Site	Female	Male	Total
Rath	45	15	60
Tad	17	33	50
Fum	16	34	50

3.3.1 Size structure

Sunbleak

Inter-site differences in the size structure of female and male sunbleak were revealed by the length frequency distributions (Figure 3.7 to Figure 3.18). Seine netting revealed that all sunbleak were FL > 29 mm at capture. Limitations in length range of samples may be related to sampling bias from the seine netting methodology or to time of sampling. Sunbleak from Two Lakes Fishery, where a sample had been provided by the fishery manager for examination, provided a minimum fork length of 32 mm. Observed maximum fork lengths in sunbleak did not exceed 68 mm, recorded in a female captured at Durleigh Reservoir (Durl10), at any of the sites. Generally, sunbleak were dominated by fish ranging between 40 and 60 mm. Length distributions of sunbleak revealed body sizes were indicative of a mostly multi-modal distribution possibly related to their batch spawning behaviour. Exceptions were fish from Durleigh Reservoir and the Rivers Tone and Huntspill, as the low number of captured fish allowed only limited interpretation of their size structure. The low numbers of fish in these sites was likely to be related to the nature of the respective habitat (see Chapter 2).

Generally, large size ranges can give an indication as regards recruitment, though maximum size was limited in sunbleak (FL < 70 mm). They are a small bodied fish species rarely exceeding maximum fork lengths of 100 mm (Arnold and Längert, 1995; Gozlan *et al.*, 2003b). For length conversions between FL, TL and SL and length-to-weight regression relationships see Appendix A.

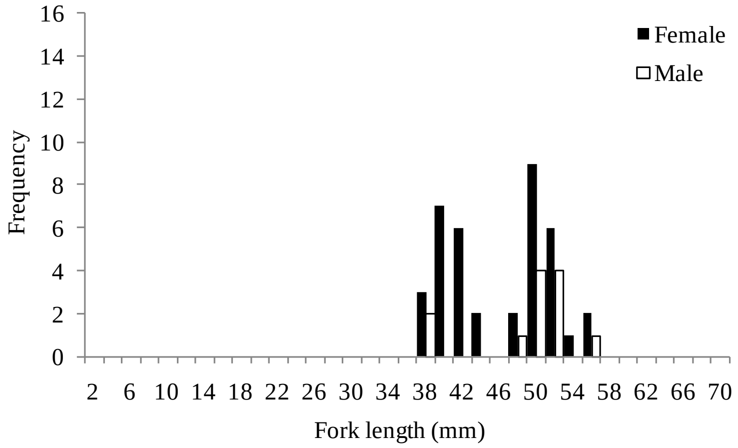

Figure 3.7: Size distribution of female (n=38) and male (n=12) sunbleak from Bridgewater-Taunton Canal at Buckland Farm, Somerset (BTC1).

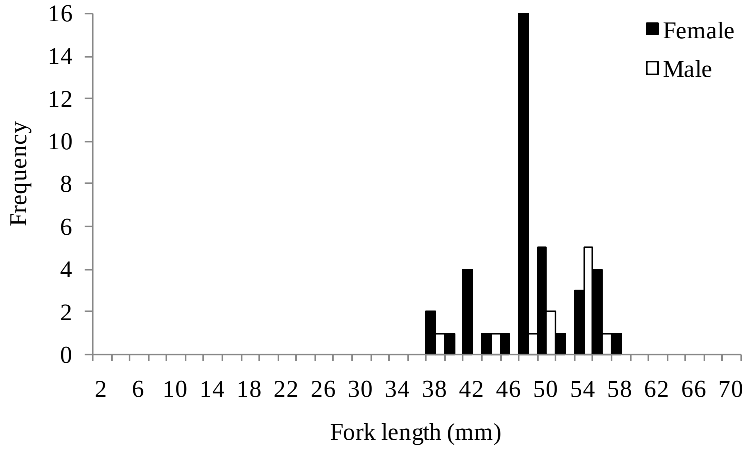

Figure 3.8: Size distribution of female (n=39) and male (n=11) sunbleak from Bridgewater-Taunton Canal at Creech St. Michael, Somerset (BTC2).

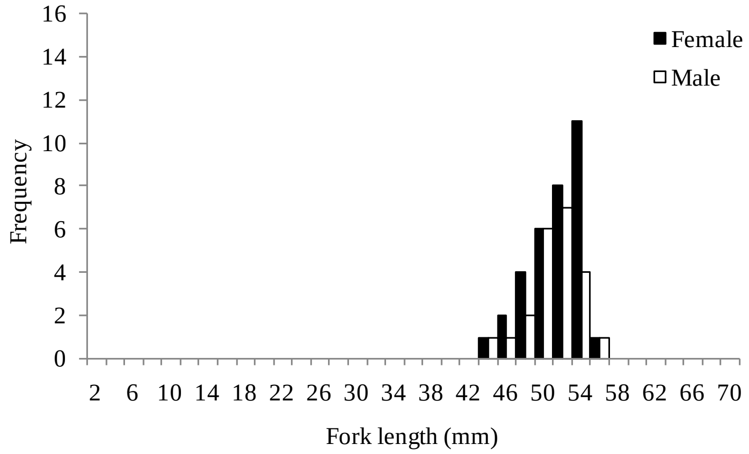

Figure 3.9: Size distribution of female (n=33) and male (n=22) sunbleak from Bridgewater-Taunton Canal at YMCA, Somerset (BTC3).

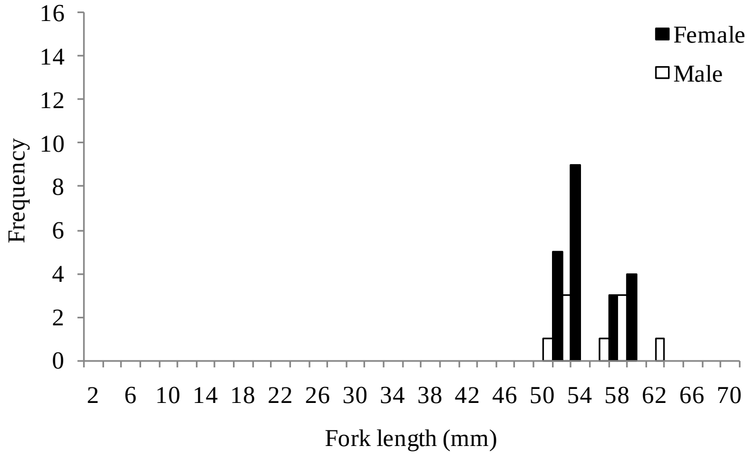

Figure 3.10: Size distribution of female (n=21) and male (n=9) sunbleak from Kings-Sedgemoor Drain at Bradney Bridge, Bawdrip, Somerset (KSD4).

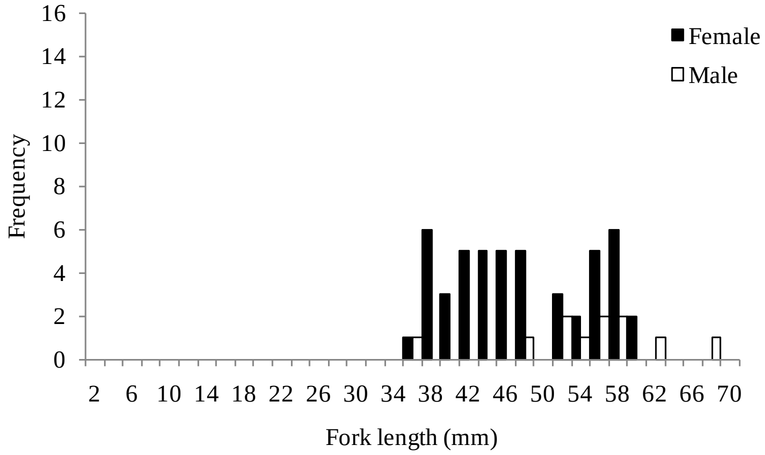

Figure 3.11: Size distribution of female (n=49) and male (n=11) sunbleak from Kings-Sedgemoor Drain at Parchey Bridge, Somerset (KSD5).

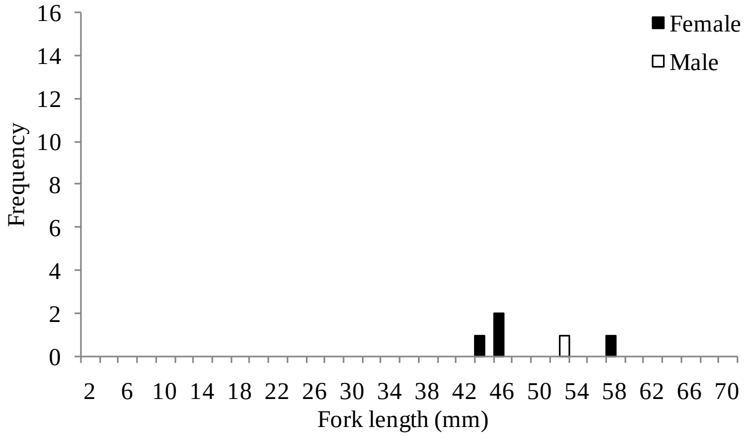

Figure 3.12: Size distribution of female (n=4) and male (n=1) sunbleak from River Huntspill at Woolavington Bridge, Somerset (Hunt6).

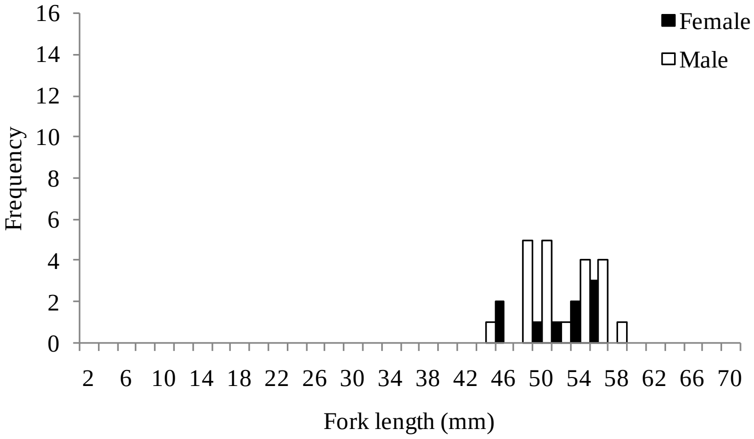

Figure 3.13: Size distribution of female (n=9) and male (n=21) sunbleak from River Sowy at Greylake Bridge, Somerset (Sowy7).

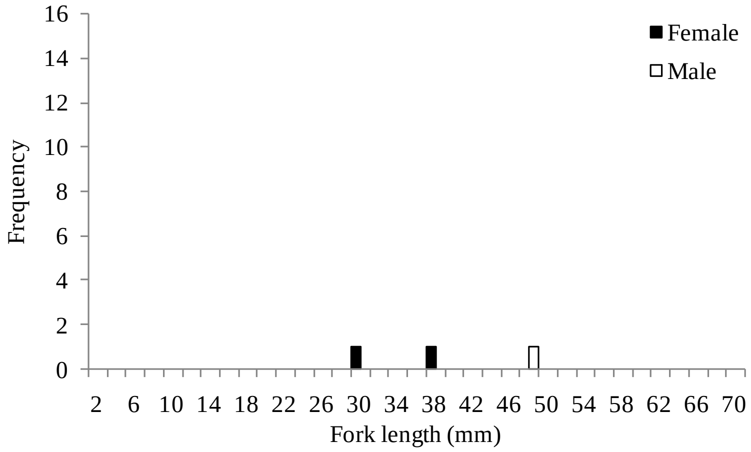

Figure 3.14: Size distribution of female (n=2) and male (n=1) sunbleak from River Tone at Hankridge, Somerset (Tone8).

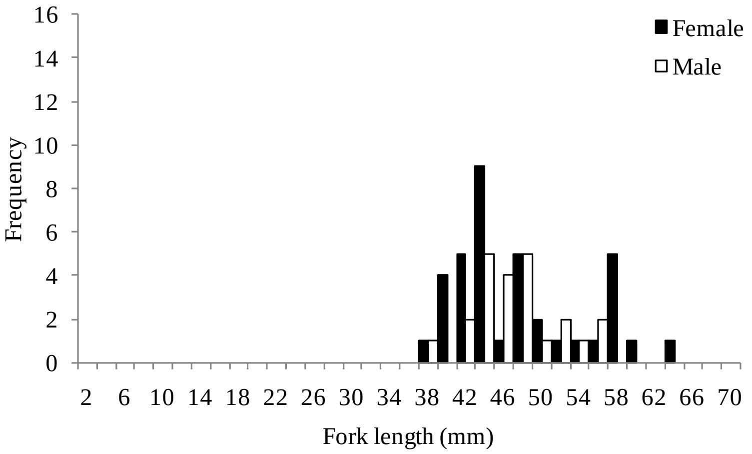

Figure 3.15: Size distribution of female (n=37) and male (n=23) sunbleak from Dunwear Pond, Somerset (Dun9).

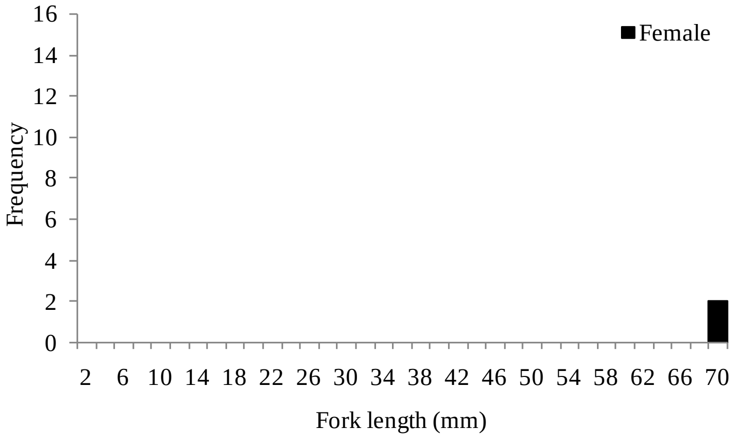

Figure 3.16: Size distribution of female (n=2) sunbleak from Durleigh Reservoir, Somerset (Durl10).

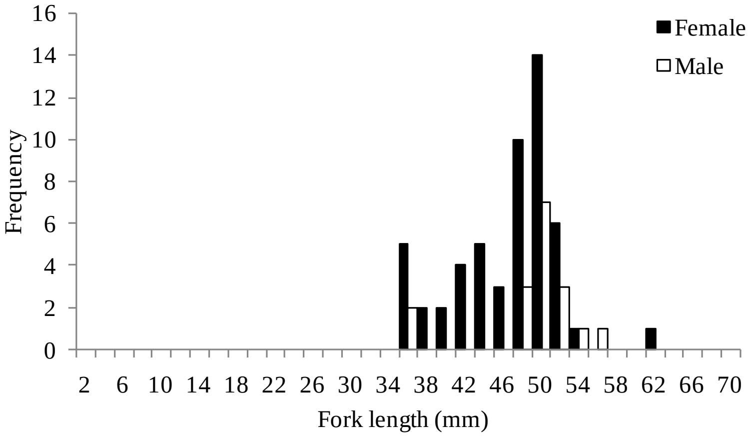

Figure 3.17: Size distribution of female (n=53) and male (n=17) sunbleak from Stoneham Lakes, Hampshire (Stone11).

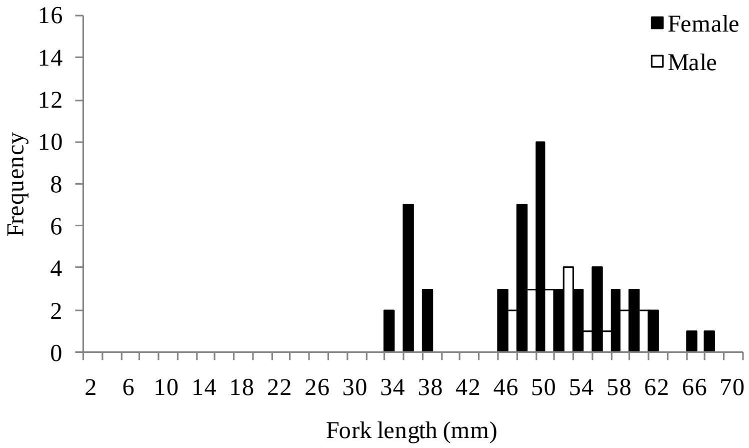

Figure 3.18: Size distribution of female (n=52) and male (n=18) sunbleak from Two Lakes Fishery, Hampshire (TwoL12).

Topmouth gudgeon

The length frequency distributions for each site show limitations in minimum and maximum fork lengths in females and males of topmouth gudgeon (Figure 3.19 to Figure 3.21) with inter-site differences being observed in the size structure. Female topmouth gudgeon ranged in fork length (FL) between 45, 36 and 34 mm to 65, 67 and 55 mm at Ratherheath Tarn (Figure 3.19), Tadburn Lake stream (Figure 3.20) and Canal du Fumemorte (Figure 3.21) respectively. Males ranged between 46, 36 and 38 mm to 58, 69 and 69 mm in fork lengths at Ratherheath Tarn, Tadburn Lake stream and Canal du Fumemorte respectively. While females outnumbered males in the sample from Ratherheath Tarn in Cumbria (F:M=3:1), males were more numerous than females at Tadburn Lake stream (F:M=1:1.9) and Canal du Fumemorte (F:M=1:2.1). Differences in size ranges of captured females and males at all sites may be related to sexual dimorphism which has previously been observed in topmouth gudgeon with males being generally larger than females (Nakamura, 1969; Katano and Maekawa, 1997). Additionally and comparable to sunbleak, topmouth gudgeon showed relatively small maximum body size (FL < 70 mm) as they are a smallbodied fish species not normally exceeding 100 mm fork length (Šebela and Wohlgemuth, 1984; Arnold, 1990). For topmouth gudgeon, length conversions between FL, TL and SL and length-to-weight regression relationships see Appendix A.

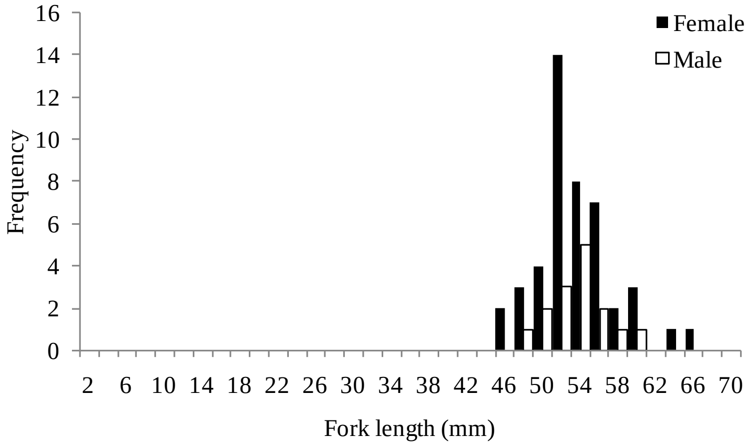

Figure 3.19: Size distribution of female (n=45) and male (n=15) topmouth gudgeon from Ratherheath Tarn, Cumbria.

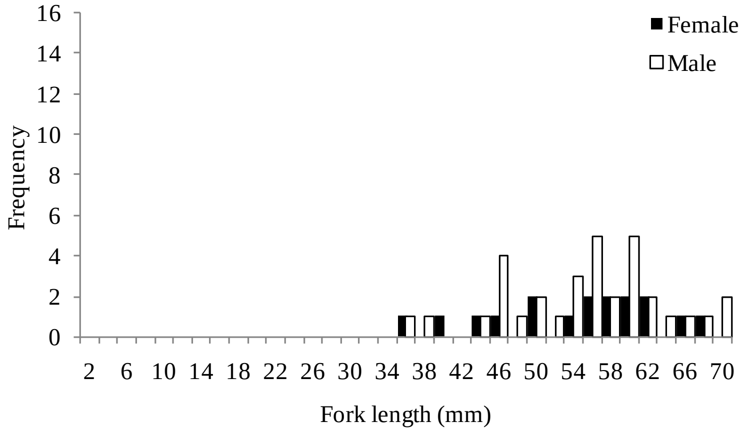

Figure 3.20: Size distribution of female (n=17) and male (n=33) topmouth gudgeon from Tadburn Lake stream, Hampshire.

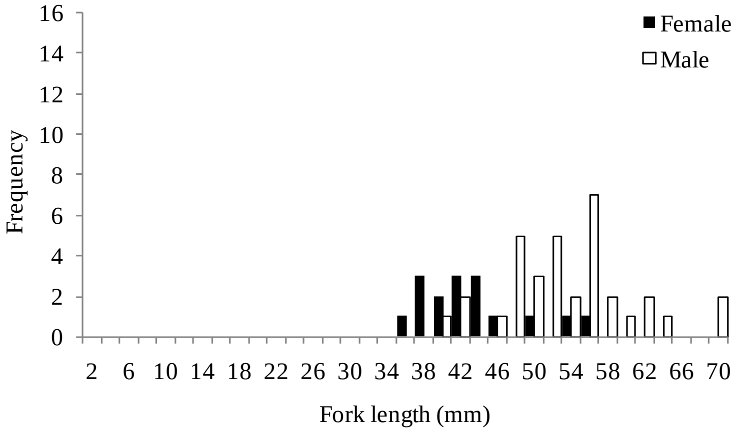

Figure 3.21: Size distribution of female (n=16) and male (n=34) topmouth gudgeon from Canal du Fumemorte, France.

3.3.2 Morphological variability

Sunbleak

Intra-population variability in morphological characters was observed to be up to 25 % for all parameters in sunbleak and topmouth gudgeon with a tendency for the variation to be greater in females than males, and an increase in variation with age in both species (see Appendix A for further details). In sunbleak, statistically significant sexual dimorphism did not occur ($P \geq 0.5$) and therefore the sexes were combined for multivariate analysis of morphological differences between sites (Figure 3.22). Variations in morphology occurred between most sites, with the head parameters ($P < 0.05$), and dorsal, anal and ventral fin lengths ($P < 0.05$) significantly different and increasing this variation. In the PCA with site grouping, the first two components account for 65 % of the variation (Figure 3.22) with the 90 % ellipses revealing overlaps in morphology between most of the nine sampling sites. The morphological characters that best described the overall variability between the sites, i.e. the ones that were being ordinated furthest from the origin, were: base of the anal fin (Ab), pre-anal, pre-dorsal and pre-ventral fin distances (PreA, PreD and PreV), gape (G), height of the pectoral fin (Ph), inter-orbital distance (Io) and minimum body height (h). The sunbleak population from Dunwear Pond, although the respective ellipse is overlapping with all other sites, appear to be morphologically more variable than the other sites (Figure 3.22) and the following characters best describe this variability: base of the anal fin (Ab), pre-anal, pre-dorsal and pre-ventral fin distances (PreA, PreD and PreV), and gape (G). Except for sunbleak from Dunwear Pond, the ellipses appear to orientate mainly along gradients of head and eye parameters (inter-orbital distance Io, inter-nasal distance Ina, head width Hw, head depth Hd, pre-orbital distance PrO, vertical orbital diameter Ov, horizontal orbital diameter Oh, head length Hl) and size of the base of the ventral and dorsal fins (Vb, Db). This orientation is most pronounced in the sunbleak from Two Lakes Fishery, Hampshire and Bridgewater-Taunton Canal at the YMCA, Somerset.

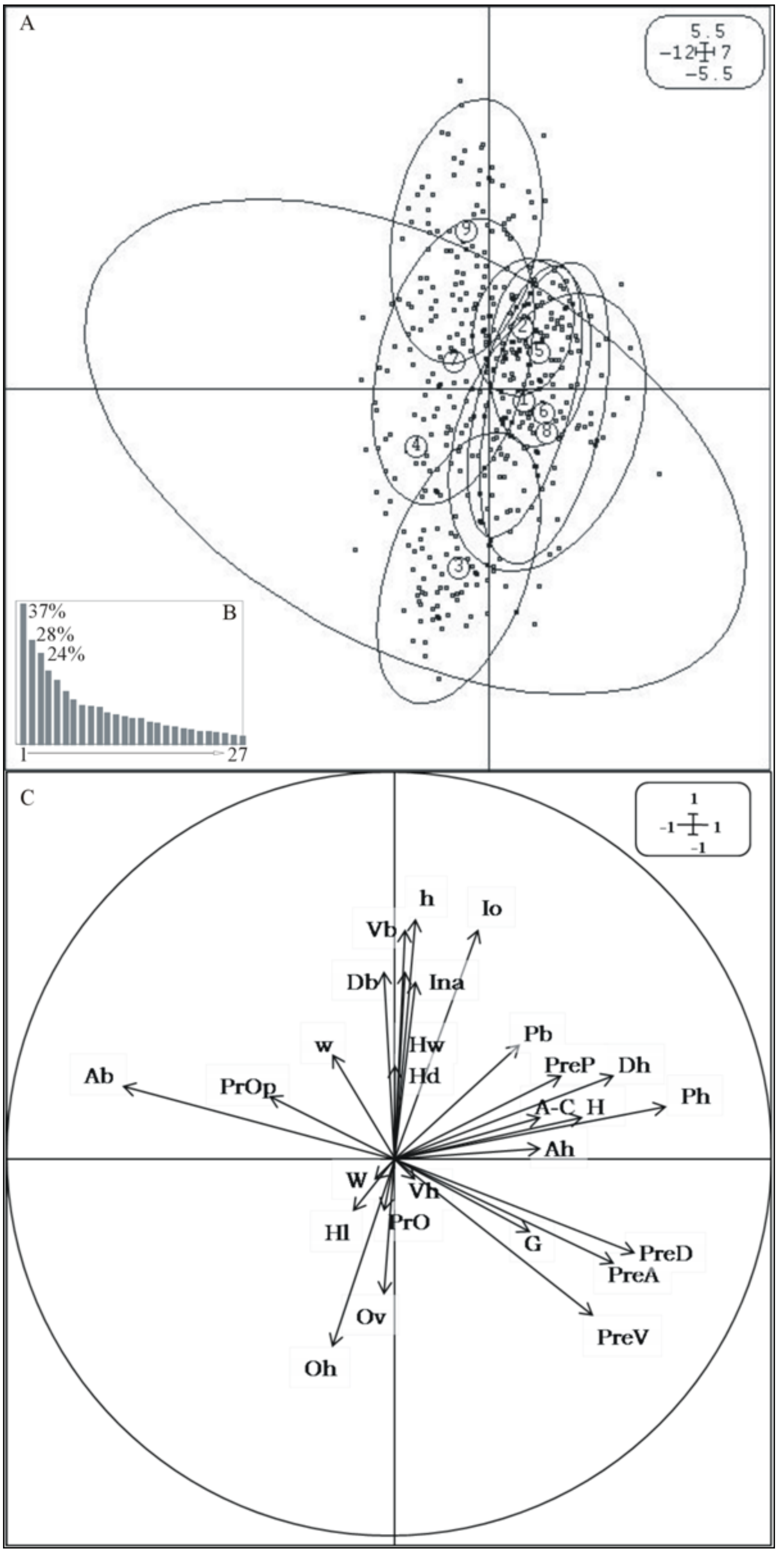

Figure 3.22: Geographical variability of morphological traits of sunbleak from nine sites in England using ordination of principal components with (A) 90 % ellipses for nine site groups (1-Site 1 Bridgewater-Taunton Canal (BTC), Somerset; 1- Site 2 BTC; 3 – Site 3 BTC; 4 – Dunwear Pond, Somerset, 5 – Site 5 Kings-Sedgemoor Drain (KSD), Somerset; 6 – Site 6 KSD, 7 – Site 7 Stoneham Lakes, Hampshire, 8 – Site 8 Sowy River, 9 – Site 9 Two Lakes) with (B) the eigenvalues and (C) the 27 morphological characters. See Table 3.2 for codes.

Topmouth gudgeon

In topmouth gudgeon, morphological variability between sites was analysed separately for each sex because of significant sexual dimorphism in morphological characters in their populations ($P < 0.05$). In the PCA with site grouping, the components one and two account for 52 % of the variation (Figure 3.23), represented by the maximum (H) and minimum (h) body height respectively, which may be related to sexual dimorphism. Morphological variability was best described by the following characters, which were being ordinated furthest from the origin: pectoral and ventral fin heights (Ph, Vh), pre-ventral fin distance (PreV), gape (g) and pre-orbital distance (PrO). Generally, morphological plasticity, augmented by head and fin size parameters as well as body height characters, appeared greater in topmouth gudgeon from Tadburn Lake and France than in fish from Ratherheath Tarn (Figure 3.23), an observation that may be habitat (i.e. velocity) related. Ratherheath Tarn is a lentic rather than a lotic water body, where food resourcing (i.e. gape) and swimming capability (i.e. fin size) may not be as problematic as in high water velocities. Fish from Ratherheath Tarn were best described by the body height (H, h) characteristics.

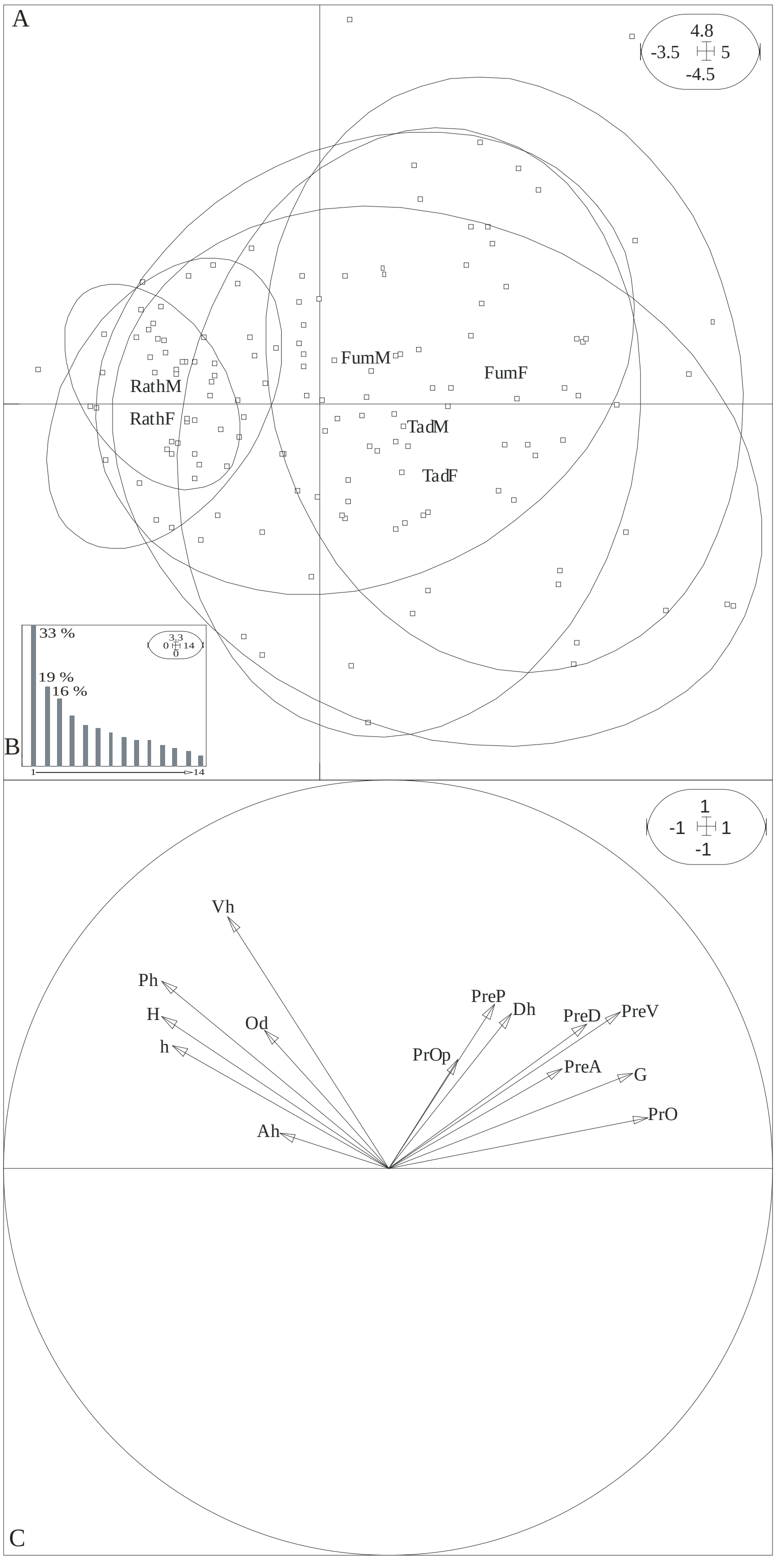

Figure 3.23: Geographical variability of morphological traits of three topmouth gudgeon populations from Ratherheath Tarn, Cumbria (Rath) Tadburn Lake stream, Hampshire (Tad), both England and Canal du Fumemorte, France (Fum) using ordination of principal components with (A) 90 % ellipses site/sex groups and using uniform weightings (male groups are denoted M and females with F) with (B) the eigenvalues and (C) the 14 morphological characters. See Table 3.2 for codes.

3.3.3 Life history variability

Sunbleak

Body size in sunbleak in England (for length conversions and length-weight relationships see Appendix A) was not significantly different in the observed age groups and between males and females (ANOVA F=0.212, $P<0.07$) (Table 3.5). The relatively small standard errors observed in the length at age data may be related to limitations given by the size structure of sunbleak at the different sampling sites (see Figure 3.7 to Figure 3.18). Overall, back-calculated lengths reflect the majority of growth attained at age 1 at all sites, with approximately 10 to 20 mm in fork length gained at maximum age obtained in the samples. No fish of age 5, the maximum age at which sunbleak were observed during the study, were captured at sites with less than 5 fish, at the Bridgewater-Taunton Canal, Creech St. Michael and the YMCA in Somerset and Stoneham Lakes, Hampshire. To prevent masking information on the minimum and maximum lengths at age, the description of back-calculated lengths omits data from sites where less than a total of 5 fish were captured, Durleigh Reservoir, River Tone and River Huntspill, and the lowest densities of 0.1, 0.15 and 0.25 sunbleak per m^{-2} were observed (Table 3.5). The greatest density of 118 sunbleak per m^{-2} was observed at Stoneham Lakes where the lowest overall growth was observed in both females and males (Table 3.5).

In female sunbleak at age 1, mean back-calculated lengths ranged from 31 mm (n = 53) at Stoneham Lakes, Hampshire (Stone11), to 43 mm (n = 21) at Kings-Sedgemoor Drain at Bradney Bridge, Somerset (KSD4) (Table 3.5). At age 2, mean back-calculated lengths ranged from 37 mm (n = 46) at the Stoneham Lakes, Hampshire (Stone11), to 45 mm (n = 21) at Kings-Sedgemoor Drain at Bradney Bridge, Somerset (KSD4). At age 3, mean back-calculated lengths of female sunbleak ranged from 43 mm (n = 4) at the Stoneham Lakes, Hampshire (Stone11), to 49 mm (n = 28) at the Bridgewater-Taunton Canal at the YMCA, Somerset (BTC3). At age 4, mean back-calculated lengths ranged from 46 mm (n = 20) at the Stoneham Lakes, Hampshire (Stone11), to 53 mm (n = 11) at Kings-Sedgemoor Drain at Parchey Bridge, Somerset (KSD5). At age 5, mean back-calculated lengths ranged from 52 mm (n = 1) at the River Sowy, Somerset (Sowy7), to 56 mm (n = 1) at Dunwear Pond, Somerset (Durl10) (Table 3.5).

In male sunbleak, mean back-calculated lengths at age 1 ranged from 29 mm (n = 18) at Two Lakes Fishery, Hampshire, to 43 mm (n = 9) at Kings-Sedgemoor Drain at Bradney Bridge, Somerset (KSD4) (Table 3.5). At age 2, mean back-calculated lengths ranged from 38 mm (n = 20) at River Sowy, Somerset (Sowy7), to 46 mm (n = 9) at Kings-Sedgemoor Drain at Bradney Bridge, Somerset (KSD4). At age 3, mean back-calculated lengths of males ranged from 44 mm (n = 15) at the Stoneham Lakes, Hampshire (Stone11), to 49 mm (n = 9) at Bridgewater-Taunton Canal at Creech St. Michael, Somerset (BTC2). At age 4, mean back-calculated lengths ranged from 47 mm (n = 7) at the Stoneham Lakes, Hampshire (Stone11), to 51 mm (n = 6) at Bridgewater-Taunton Canal at Creech St. Michael, Somerset (BTC2). Male sunbleak at age 5, ranged in their mean back-calculated lengths from 52 mm (n = 3) at River Sowy, Somerset (Sowy7), to 59 mm (male; n = 1) at Kings-Sedgemoor Drain at Bradney Bridge, Somerset (KSD4) (Table 3.5).

Generally, sunbleak in England mature between the ages of 1 and 2 and at small body sizes, with few individual fish representing an exception at some sites and subsequently causing increased inter-site variability (Table 3.6). At sites where females and/or males were found to mature at age 2, which includes Bridgewater-Taunton Canal at the YMCA (BTC3), Kings-Sedgemoor Drain at Bradney Bridge (KSD4), the River Huntspill (Hunt6) and the River Tone (Tone8), all in Somerset, no females and/or male sunbleak in samples were observed at age 1 (Table 3.6). This may also be reflected in the results of the length-at-maturity calculation. The coefficient of variation for age- and length-at-maturity reflects the size and age structure of the samples (Table 3.6). Overall, sunbleak from lentic waters, for example Stoneham lakes and Two Lakes Fishery, appeared to mature at smaller body size than sunbleak from lotic populations such as the Bridgewater-Taunton Canal and Kings-Sedgemoor Drain (Table 3.6).

Mean reproductive effort and gonado-somatic index exhibited the highest inter-site variability of all life history parameters in sunbleak, with the highest values observed in females from Kings Sedgemoor Drain, River Huntspill and Durleigh Reservoir. Consequently there were significant differences in E_R and GSI ($P > 0.01$) between sites. However, this variability between sites may partly be related to bias from time of sampling, and the timing of spawning and the developmental stage of the gonad at this point in time. Overall, reproductive effort and GSI were greater in females than in males.

Fecundity (mean number of eggs per mm fork length and per gram body weight) was high in all sunbleak with 16.0 % and 24.4 % variation between sites. The mean values ranged from approximately 5.9 (Dunwear Pond, Somerset) to 9.5 (Kings Sedgemoor Drain, Bradney Bridge) eggs per mm FL eggs respectively, and 103.9 (Durleigh Reservoir) to 322.5 egg per gram body weight.

Sunbleak from all sites were of good body condition, and with 12.4 % condition varied least of all life history traits between sites (Table 3.6). Condition factor in sunbleak ranged between 0.92 and 1.56.

Table 3.5: Sunbleak density (fish/m^2), approximate year of introduction, latitude (Lat), number of fish in sample (n), mean ± standard error (S.E.) back-calculated fork lengths (FL) at observed ages 1 to 5 at 12 sites in England at 1) Bridgewater-Taunton Canal, Buckland Farm (BTC1), 2) Bridgewater-Taunton Canal, Creech St. Michael, Somerset (BTC2), 3) Bridgewater-Taunton Canal, YMCA, Somerset (BTC3), 4) Kings-Sedgemoor Drain, Bradney Bridge, Bawdrip, Somerset (KSD4), 5) Kings-Sedgemoor Drain, Parchey Bridge, Somerset (KSD5), 6) Woolavington Bridge, River Huntspill, Somerset (Hunt6), 7) River Sowy , Grey Lake Bridge, Somerset (Sowy7), 8) Hankridge, River Tone, Somerset (Tone8), 9) Dunwear pond, Somerset (Dun9), 10) Durleigh Reservoir, Somerset (Durl10), 11) Stoneham Lakes, Hampshire (Stone11), 12) Two Lakes Fishery, Hampshire (TwoL12). —, fish within this age group were not observed.

						Mean back-calculated FL at age in mm ± S.E. (n)				
Site	≈Year of intro-duction	Density (n/m^2)	Lat °N	Sex	n	1	2	3	4	5
BTC 1	1990	5.95	51	Female	38	39 ± 0.4 (38)	43 ± 0.5 (29)	47 ± 0.4 (20)	51 ± 0.6 (11)	53 ± 1.5 (2)
				Male	12	39 ± 0.9 (12)	44 ± 0.9 (11)	47 ± 0.5 (10)	50 ± 0.7 (6)	54 ± 0 (1)
				Combined	50	39 ± 0.4 (50)	43 ± 0.4 (40)	47 ± 0.3 (30)	50 ± 0.7 (17)	53 ± 1.0 (3)
BTC 2	1990	6.15	51	Female	39	36 ± 0.2 (39)	41 ± 0.3 (31)	48 ± 0.4 (19)	51 ± 0.4 (10)	—
				Male	11	36 ± 0.5 (11)	42 ± 0.5 (10)	49 ± 0.5 (9)	51 ± 0.3 (6)	—
				Combined	50	36 ± 0.2 (50)	41 ± 0.2 (41)	48 ± 0.3 (28)	51 ± 0.3 (16)	—
BTC 3	1990	4.95	51	Female	33	38 ± 0.4 (33)	45 ± 0.4 (33)	49 ± 0.4 (28)	50 ± 0.6 (16)	—
				Male	22	38 ± 0.2 (22)	45 ± 0.3 (22)	48 ± 0.3 (17)	51 ± 0.5 (8)	—
				Combined	55	38 ± 0.3 (55)	45 ± 0.2 (55)	49 ± 0.3 (45)	50 ± 0.4 (24)	—
KSD 4	1990	1.5	51	Female	21	43 ± 0.2 (21)	45 ± 0.3 (21)	48 ± 0.3 (21)	51 ± 0.2 (17)	55 ± 1.3 (2)
				Male	9	43 ± 0.2 (9)	46 ± 0.6 (9)	48 ± 0.7 (9)	51 ± 0.9 (6)	59 ± 0 (1)
				Combined	30	43 ± 0.2 (30)	45 ± 0.2 (30)	48 ± 0.3 (30)	51 ± 0.3 (23)	56 ± 1.6 (3)
KSD 5	1990	18.85	51	Female	49	36 ± 0.5 (49)	43 ± 0.8 (33)	49 ± 1.1 (20)	53 ± 1.9 (11)	55 ± 1.7 (3)
				Male	11	34 ± 0.8 (11)	40 ± 1.0 (10)	46 ± 1.3 (10)	51 ± 1.7 (8)	56 ± 0.4 (2)
				Combined	60	35 ± 0.4 (60)	42 ± 0.7 (43)	48 ± 0.8 (30)	52 ± 1.3 (19)	55 ± 1.0 (5)
Hunt 6	1990	0.25	51	Female	4	30 ± 2.1 (4)	38 ± 3.0 (4)	43 ± 5.0 (4)	44 ± 0.6 (2)	—
				Male	1	34 ± 0 (1)	39 ± 0 (1)	48 ± 0 (1)	—	—
				Combined	5	31 ± 1.8 (5)	38 ± 2.4 (5)	44 ± 3.5 (5)	44 ± 0.6 (2)	—
Sowy 7	1990	12.25	51	Female	9	36 ± 1.9 (9)	40 ± 1.5 (8)	45 ± 1.3 (8)	50 ± 0.9 (6)	52 ± 0 (1)
				Male	21	31 ± 1.1 (21)	38 ± 0.9 (20)	44 ± 1.0 (18)	48 ± 0.8 (10)	52 ± 0.4 (3)
				Combined	30	33 ± 1.0 (30)	38 ± 0.8 (28)	44 ± 0.8 (26)	49 ± 0.6 (16)	52 ± 0.3 (4)
Tone 8	1990	0.15	51	Female	2	30 ± 1.0 (2)	35 ± 0 (1)	—	—	—
				Male	1	35 ± 0 (1)	42 ± 0 (1)	44 ± 0 (1)	45 ± 0 (1)	—
				Combined	3	31 ± 1.7 (3)	38 ± 3.6 (2)	44 ± 0 (1)	45 ± 0 (1)	—
Dun 9	1990	3.45	51	Female	37	34 ± 0.7 (37)	41 ± 0.9 (31)	46 ± 1.1 (26)	52 ± 1.8 (9)	56 ± 0 (1)
				Male	23	34 ± 0.8 (23)	40 ± 0.8 (22)	44 ± 0.8 (22)	50 ± 2.7 (3)	—
				Combined	60	34 ± 0.5 (60)	41 ± 0.6 (53)	45 ± 0.7 (48)	51 ± 1.5 (12)	56 ± 0 (1)
Durl 10	1990	0.1	51	Female	2	46 ± 1.0 (2)	52 ± 0.7 (2)	59 ± 0.7 (2)	66 ± 0.3 (2)	—
				Male	0	—	—	—	—	—
				Combined	2	46 ± 1.0 (2)	52 ± 0.7 (2)	59 ± 0.7 (2)	66 ± 0.3 (2)	—

Table 3.5 continued:

						Mean back-calculated FL at age in mm ± S.E. (n)				
Site	≈Year of intro-duction	Density (n/m^2)	Lat °N	Sex	n	1	2	3	4	5
Stone 11	1986	117.55	50	Female	53	31 ± 0.5 (53)	37 ± 0.5 (46)	43 ± 0.6 (35)	46 ± 0.8 (20)	—
				Male	17	31 ± 1.0 (17)	39 ± 0.9 (15)	44 ± 0.8 (15)	47 ± 1.0 (7)	—
				Combined	70	31 ± 0.5 (70)	38 ± 0.5 (61)	43 ± 0.5 (50)	47 ± 0.7 (27)	—
TwoL 12	1986	—	51	Female	52	30 ± 0.5 (52)	40 ± 0.7 (40)	47 ± 0.9 (32)	51 ± 1.4 (20)	54 ± 2.3 (4)
				Male	18	29 ± 0.8 (18)	40 ± 0.9 (18)	46 ± 1.0 (16)	51 ± 1.8 (10)	—
				Combined	70	29.7 ± 0.4 (70)	40 ± 0.6 (58)	46 ± 0.7 (48)	51 ± 1.1 (30)	54 ± 2.3 (4)

Table 3.6: Mean fork length at maturity (FL_{M}) in mm, mean age at maturity (Age_{M}) in years, mean ± standard error (S.E.) gonadosomatic index (GSI) in %, mean ± standard error (S.E.) reproductive effort (*ER*), mean ± standard error (S.E.) number of eggs per mm fork length (Fec_{FL}), mean ± standard error (S.E.) number of eggs per gram (g) body weight (Fec_{W}) and mean ± standard error (S.E.) Fulton's condition factor (K_F) for mature individuals of sunbleak at 12 sites in England at 1) Bridgewater-Taunton Canal, Buckland Farm (BTC1), 2) Bridgewater-Taunton Canal, Creech St. Michael, Somerset (BTC2), 3) Bridgewater-Taunton Canal, YMCA, Somerset (BTC3), 4) Kings-Sedgemoor Drain, Bradney Bridge, Bawdrip, Somerset (KSD4), 5) Kings-Sedgemoor Drain, Parchey Bridge, Somerset (KSD5), 6) Woolavington Bridge, River Huntspill, Somerset (Hunt6), 7) River Sowy , Grey Lake Bridge, Somerset (Sowy7), 8) Hankridge, River Tone, Somerset (Tone8), 9) Dunwear pond, Somerset (Dun9), 10) Durleigh Reservoir, Somerset (Durl10), 11) Stoneham Lakes, Hampshire (Stone11), 12) Two Lakes Fishery, Hampshire (TwoL12). Mean, minimum (Min.), maximum (Max.) values, coefficient of variation (CV), sample number (n) as well as water body typology are presented. —, data not available.

			Life history and condition						
	Typology	Sex	FL_{M}	Age_{M}	Mean GSI ± S.E.	Mean *ER* ± S.E.	Fec_{FL} ± S.E.	Fec_{W} ± S.E.	Mean *KF* ± S.E.
BTC1	lotic	Female	37	1.3	7.3 ± 0.8	0.76 ± 0.21	6.6 ± 0.5	227.7 ± 20.5	1.56 ± 0.94
		Male	37	1.0	4.9 ± 1.9	0.23 ± 0.01	—	—	1.38 ± 0.19
BTC2	lotic	Female	39	1.1	8.4 ± 0.6	0.49 ± 0.10	8.1 ± 0.6	258.9 ± 19.4	1.44 ± 0.06
		Male	37	1.0	3.9 ± 0.9	0.16 ± 0.02	—	—	1.41 ± 0.13
BTC 3[1]	lotic	Female	42	2.0	9.4 ± 0.7	0.10 ± 0.03	9.3 ± 0.5	290.1 ± 17.8	1.29 ± 0.04
		Male	37	2.0	2.2 ± 0.1	0.28 ± 0.02	—	—	1.29 ± 0.03
KSD 4[2]	lotic	Female	42	2.0	8.2 ± 0.8	0.52 ± 0.11	9.5 ± 0.8	278.4 ± 22.2	1.17 ± 0.04
		Male	47	2.0	3.1 ± 1.1	1.24 ± 1.01	—	—	1.18 ± 0.09
KSD 5	lotic	Female	39	1.2	12.5 ± 1.5	0.45 ± 0.07	6.4 ± 0.6	211.0 ± 19.0	1.40 ± 0.06
		Male	37	1.0	2.4 ± 0.5	0.82 ± 0.63	—	—	1.03 ± 0.16
Hunt 6[3]	lotic	Female	42	2.0	12.0 ± 4.4	0.35 ± 0	7.9 ± 1.0	319.0 ± 51.4	1.12 ± 0.04
		Male	52	2.0	2.2 ± 0	—	—	—	0.92 ± 0.00
Sowy 7	lotic	Female	42	1.0	9.1 ± 1.4	0.71 ± 0.42	9.2 ± 1.1	247.9 ± 39.2	1.46 ± 0.07
		Male	42	1.0	3.1 ± 0.2	0.18 ± 0.02	—	—	1.26 ± 0.06
Tone 8[4]	lotic	Female	37	2.0	3.0 ± 0	0.35 ± 0	—	—	1.08 ± 0.17
		Male	47	2.0	1.7 ± 0	—	—	—	1.23 ± 0.00
Dun 9	lentic	Female	37	1.0	6.7 ± 0.6	0.51 ± 0.27	5.9 ± 0.6	221.8 ± 24.4	1.34 ± 0.07
		Male	37	1.0	1.8 ± 0.2	0.11 ± 0.08	—	—	1.20 ± 0.10
Durl 10[5]	lentic	Female	67	4.0	12.8 ± 5.9	—	6.9 ± 13.1	103.9 ± 214.0	1.37 ± 0.05
		Male	—	—	—	—	—	—	—
Stone 11	lentic	Female	32	1.0	8.3 ± 0.4	0.51 ± 0.14	8.9 ± 0.6	322.5 ± 22.5	1.43 ± 0.06
		Male	32	1.0	1.6 ± 0.2	0.21 ± 0	—	—	1.33 ± 0.12
TwoL 12	lentic	Female	35	1.3	8.1 ± 0.6	0.39 ± 0.15	7.9 ± 0.5	281.4 ± 21.3	1.45 ± 0.09
		Male	47	1.3	1.3 ± 0.5	0.05 ± 0.02	—	—	1.08 ± 0.02
Mean			41	1.5	5.8	0.42	7.9	251.1	1.28
S.E.			1.6	0.2	0	0.07	0.4	18.5	0.03
Min			32	1.0	1.3	0.05	5.9	103.9	0.92
Max			67	4.0	12.8	1.24	9.5	322.5	1.56
CV			18.4	46.0	65.4	69.7	16.0	24.4	12.6
n			23	23	23	20	11	11	23

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[1] No fish at age 1 observed in sample.

[2] No fish at age 1 observed in sample.

[3] No fish at age 1 observed in sample.

[4] No males at age 1, 2 or 3 observed in sample

[5] No males in sample

Topmouth gudgeon

Some variability was observed in body sizes at age of topmouth gudgeon between sites (Table 3.7) (for length conversions and length-weight relationships see Appendix A). Mean length at age was greater in males than in female topmouth gudgeon except at age 3 fish from Tadburn Lake stream. The majority of length was gained during the first year of life with subsequent increments of approximately 6 to 30 mm in fork length until maximum observed age in the samples per site (Table 3.7). The greatest length at age was observed at age 1 in fish from Canal du Fumemorte, France, while the greatest mean length at age 3 was observed at this site. Overall, topmouth gudgeon sampled from France grew faster than the ones from the English samples. With a mean 25 mm (n = 45) and 27 mm (n = 15) fork length in females and males at age 1 respectively, the lowest length at this age was recorded at Ratherheath Tarn. Maximum mean back-calculated fork length was observed at age 4 at Tadburn lake stream, though this was based on only one male specimen. When small standard errors are observed in the samples, these may be related to limitations given by the size structure of the topmouth gudgeon sample at the respective site (see Figure 3.19 to Figure 3.21).

Overall, topmouth gudgeon mature between ages 1 and 2, with females maturing earlier than males, and at small body sizes (Table 3.8). Length at maturity in females ranged from 46 mm at Canal du Fumemorte to 49 mm at both, Ratherheath Tarn and Tadburn Lake stream. In males, the values range between 45 mm at Tadburn Lake stream and 53 mm at Ratherheath Tarn. The latter value appears to be rather exaggerated and may have been augmented by the size structure of the topmouth gudgeon in this water body (see Figure 3.19 to Figure 3.21) as well as the timing of sampling. However, overall variation in length-at-maturity between sites was considerably lower than age-at-maturity (Table 3.8).

Gonado-somatic index and reproductive effort exhibited the highest inter-site variability of all life history parameters, with the mean values generally greater in females than in males (Table 3.8). Mean female GSI at Canal du Fumemorte was greater than in the two English sites, while mean male GSI was greatest at Ratherheath Tarn. However, variability between sites is probably to some extent driven by differences in timing of sampling as well as the size of fish used.

Fecundity (mean number of eggs per mm fork length and per gram body weight) in topmouth gudgeon with 30.4 % and 27.5 % varied considerably between sites. The mean values ranged from approximately 5.9 (Ratherheath Tarn) to 10 (Canal du Fumemorte) eggs per mm FL eggs respectively, and 126.5 (Tadburn Lake stream) to 208.5 egg per gram body weight. However, differences in mean numbers of eggs may be related to the timing of sampling or may be an artefact of the gravimetric method used.

Topmouth gudgeon from all sites were of good body condition, and with 6 % condition factor varied least of all life history traits between sites (Table 3.8), though the highest value was observed in females from Ratherheath Tarn.

Table 3.7: Topmouth gudgeon density (fish/m^2), approximate year of introduction, latitude (Lat), number of fish in sample (n), and mean back-calculated fork lengths (FL) ± standard error (S.E.) at observed ages 1 to 4 from two sites in England and one site in France: Ratherheath tarn, Cumbria, England (Rath), Canal du Fumemorte, France (Fum), and Tadburn Lake stream, Hampshire, England (Tad). —, fish within this age group were not observed.

Site	≈Year of intro-duction	Density (n/ m^2)	Lat °N	Sex	n	Mean back-calculated FL at age in mm ± S.E. (n)			
						1	2	3	4
Rath	2000	6.1*	54	Female	45	25 ± 0.4 (45)	39 ± 0.4 (38)	52 ± 0.6 (17)	57 ± 0.8 (3)
				Male	15	27 ± 0.8 (15)	47 ± 1.5 (10)	52 ± 0.6 (5)	57 ± 0 (1)
				Combined	60	25 ± 0.4 (60)	41 ± 0.6 (48)	52 ± 0.5 (22)	57 ± 0.6 (4)
Tad	1985	2.6	50	Female	17	38 ± 0.8 (17)	50 ± 1.5 (10)	59 ± 1.4 (2)	—
				Male	33	41 ± 0.8 (33)	52 ± 0.8 (14)	58 ± 1.8 (4)	63 ± 0 (1)
				Combined	50	40 ± 0.7 (50)	51 ± 0.8 (24)	58 ± 1.2 (6)	63 ± 0 (1)
Fum	1993	N/A	43	Female	16	42 ± 0.5 (16)	49 ± 1.4 (2)	—	—
				Male	34	44 ± 0.5 (34)	53 ± 1.3 (14)	61 ± 1.1 (2)	—
				Combined	50	43 ± 0.4 (50)	53 ± 1.2 (16)	61 ± 1.1 (2)	—

*the density value for Ratherheath Tarn, Cumbria, was taken from Britton *et al.* (2006)

Table 3.8: Mean fork length at maturity (FL$_M$) in mm, mean age at maturity (Age$_M$) in years, mean ± standard error (S.E.) gonadosomatic index (GSI) in %, mean ± standard error (S.E.) reproductive effort (*ER*), mean ± standard error (S.E.) number of eggs per mm fork length (Fec$_{FL}$), mean ± standard error (S.E.) number of eggs per gram (g) body weight (Fec$_W$) and mean ± standard error (S.E.) Fulton's condition factor (K_F) for mature individuals of topmouth gudgeon from two sites in England and one site in France: Ratherheath tarn, Cumbria, England (Rath), Tadburn Lake stream, Hamsphire, England (Tad) and Canal du Fumemorte, France. Mean, standard error (S.E.), minimum (Min.), maximum (Max.) values, coefficient of variation (CV) and sample number (n) are presented. —, data not available.

			Life history and condition						
	Typology	Sex	FL$_M$	Age$_M$	Mean GSI ± S.E.	Mean *ER* ± S.E.	Fec$_{FL}$ ± S.E.	Fec$_W$ ± S.E.	Mean K_F ± S.E.
Rath	lentic	Female	49	1.8	13.6 ± 1.5	0.45 ± 0.21	6.4 ± 0.4	141.69 ± 9.53	1.65 ± 0.03
		Male	53	2.0	7.0 ± 1.6	0.26 ± 0.13	—	—	1.47 ± 0.07
Tad	lotic	Female	49	1.0	10.8 ± 0.8	0.23 ± 0.04	5.9 ± 0.2	126.54 ± 7.50	1.43 ± 0.06
		Male	45	1.7	1.1 ± 0.9	0.03 ± 0.01	—	—	1.44 ± 0.52
Fum	lotic	Female	46	1.0	16.8 ± 3.0	0.24 ± 0	10.0 ± 1.1	208.52 ± 35.60	1.41 ± 0.10
		Male	47	1.1	1.3 ± 0.2	0.04 ± 0.01	—	—	1.41 ± 0.04
Mean			48	1.4	8.43	0.21	7.4	158.9	1.47
S.E.			1.1	0.2	2.64	0.06	1.3	25.2	0.04
Min			45	1.0	1.07	0.03	5.9	126.5	1.41
Max			53	2.0	16.84	0.45	10.0	208.5	1.65
CV			5.6	31.6	76.7	75.2	30.4	27.5	6.3
n			6	6	6	6	3	3	6

3.4 Discussion

3.4.1 Body size

Sunbleak and topmouth gudgeon are small-bodied fish species which rarely exceed fork lengths of 100 mm (Šebela and Wohlgemuth, 1984; Arnold, 1990; Arnold and Längert, 1995; Gozlan *et al.*, 2003b; Britton and Davies, 2007). This study was no exception to these findings as the maximum fork lengths were 68 mm (female; Durleigh Reservoir) and 66 mm (male; Kings-Sedgemoor Drain, Parchey Bridge) in sunbleak and 67 mm (female; Tadburn Lake stream) and 69 mm (male; Tadburn Lake stream) in topmouth gudgeon. Small body size in both species is expected to aid successful invasion. As the majority of growth is obtained during the first year of life and before maturation, the remaining energy can be expended on reproduction while growth remains low during the remaining years of life (Table 3.5; Table 3.7). This trade-off would certainly assist in successful establishment, as high reproductive effort coupled with batch spawning and parental care behaviour requires a large amount of energy.

Inter-site variability in body size at age may to some extent be related to water velocity variations and its influence on growth (Fausch, 1984). Although flow velocity may increase the encounter with drifting food, to maintain the position in the flow requires a large amount of energy and limits feeding time (Takashi Asaeda and Manatunge, 2005). Such mechanisms may be reflected in reduced growth at lotic sites (i.e. greater water velocities). Such processes have previously resulted in reduced growth of topmouth gudgeon in native water bodies (Takashi Asaeda and Manatunge, 2005). However, such mechanisms may not explain inter-population variations in body size at age observed in topmouth gudgeon from the different sites. Length at age was lowest at Ratherheath Tarn, Cumbria, England, while it was greatest in topmouth gudgeon from Canal du Fumemorte, France (Table 3.7). In fact, density parameters may play an important role in shaping these characteristics. For example, Katano and Maekawa (1997) have previously observed decreased growth of female topmouth gudgeon with increased density. Density-based conclusions for slower growth of topmouth gudgeon in the Cumbrian lake have been made by Britton *et al*. (2007). Essentially, since the introduction of topmouth gudgeon, density-dependent pressures may have facilitated a high degree of intraspecific competition for resources in the lake resulting in resource limitations, which may have subsequently caused slower growth and increased age-at-maturity (Britton *et al.*, 2007).

In Somerset, most sites were lotic water bodies while only Durleigh Reservoir and Dunwear Pond were lentic. Length at age in sunbleak from Dunwear Pond was similar to fish from lotic water bodies in Somerset. Both sunbleak populations from Hampshire are from lentic water bodies with fish from Stoneham Lakes growing slower than from all other sites though this was not statistically significant ($P > 0.05$). However, it is possible that the high density of sunbleak at this site (118 fish/m^{-2}), may have outweighed the benefits of inhabiting a low velocity habitat (i.e. increased growth through decreased energy expenditure) and subsequently reduced length at age through density-related effects (i.e. decreased growth) (Burrough and Kennedy, 1979; Bromley, 1989; Bohlin *et al.*, 2002; Bøhn *et al.*, 2004). Further aspects to consider in this evaluation are different sources of stress that the sunbleak may be exposed to at Stoneham Lakes, for example parasites, which may cause stress in individuals but not mortality (see Chapter 5 for details on the parasite fauna of sunbleak at this site). Density values were not available from Two Lakes Fishery as the sunbleak sample was provided by the fishery manager for investigation.

3.4.2 Morphology

Significant sexual differences in morphology did not occur in sunbleak but were observed in topmouth gudgeon, in which it has previously been recorded in its introduced range (Barus *et al.*, 1984; Jankovic, 1985; Maekawa *et al.*, 1996; Kotusz and Witkowski, 1998). This sexual dimorphism is related to the species' reproductive behaviour where large size is important for males and their reproductive success as the female prefers to mate with larger males (Maekawa *et al.*, 1996). Information on the morphology of topmouth gudgeon in its native range is not available. Sunbleak has not been reported to display sexual dimorphism, neither in its introduced range (Pipoyan, 1996) nor in its native range (Arnold and Längert, 1995). In both species, females and males were found to differ in reproductive allocation likely to be related to differences in physiological and physical gonad characteristics.

Morphological variation between sunbleak populations was best described by fin size parameters (i.e. anal and pectoral fin), pre-fin distances (pre-anal, pre-dorsal, pre-ventral), gape, interorbital distance and minimum body height. Head morphology is generally related to the diet while the fin lengths would be related to swimming abilities, which would subsequently be driven by the prevalent environmental conditions (i.e. food availability and flow velocities) at the different sites. A fish swims by developing thrust using its whole body while using the caudal fin as the main propulsion and steering device to propel forward in the water (Videler, 1993). This takes place with the help of contracting muscles in the body (using up stored energy). The dorsal, anal, pectoral and ventral fins are utilised mainly for stabilisation and positioning of the fish within the water and act in support of propulsion. Variation in head and eye parameters may concur with previous studies on the sensory abilities of sunbleak, which concluded that sunbleak rely more heavily on optical rather than chemical senses (Devicina and El-Attar-El-Saied, 1988; Arnold and Längert, 1995).

Increasing variability in morphological parameters of topmouth gudgeon may be increased by dominant males in a given sample, since females prefer males of larger body size for mating (Katano and Maekawa, 1997). Further, predation pressure and flow velocity may influence morphological variability and thus plasticity in topmouth gudgeon (Takashi Asaeda and Manatunge, 2005). Greater morphological plasticity of topmouth gudgeon in France and Tadburn Lake stream (both lotic waters) than in fish from Ratherheath Tarn (lentic) may be related to differences in water velocities between sites. Variation in head and fin size parameters in topmouth gudgeon may be explained by differences in flow velocities between sites, which are most likely greater at Canal du Fumemorte and Tadburn Lake stream than at Ratherheath Tarn. In greater velocities, the encounter with drifting food may be increased (Fausch, 1984; Hill and Grossman, 1993), while swimming ability is required to be better and fin size larger than in a low velocity environment.

3.4.3 Reproduction

Both species matured at small sizes (Sunbleak: Females, $FL_M \leq 39$ mm, Males, $FL_M \leq 47$ mm; Topmouth gudgeon: Females, $FL_M \leq 49$ mm, Males, $FL_M \leq 53$ mm), with variability of sizes at maturity exhibited between females and males within and between populations (Table 3.6, Table 3.8). In sunbleak, size-at-maturity ranged from 32 mm in females and males (Stoneham Lakes, Hampshire) to 42 mm (females; Bridgewater Taunton Canal, YMCA, Kings-Sedgemoor Drain, Bradney Bridge, River Sowy) and 42 mm (males; River Sowy). The high values for females at Durleigh Reservoir ($FL_M = 67$ mm) and males at the River Huntspill ($FL_M = 52$ mm) and the River Tone ($FL_M = 47$ mm) were excluded from the discussion because of the low numbers of specimens and subsequent unclear size structure of fish at these sites (Figure 3.12; Figure 3.14; Figure 3.16). Sunbleak from lotic water bodies, Stoneham Lakes and Two Lakes Fishery, matured at smaller body sizes and displayed slower growth than specimens from lentic waters. This may be related to the prevalent water velocities, temperature and/or productivity of the water body. Differences in length-at-maturity with river populations maturing at greater body sizes than lake populations, has been recorded in other fish species, for example the river blenny *Salaria fluviatilis* (Asso, 1801) (Neat *et al.*, 2003). Generally, variability of size at maturity occurs in fish and has also been found in introduced European populations of small-bodied pumpkinseed (summarised in Villeneuve *et al.*, 2005). However, variability in size at maturity in sunbleak and topmouth gudgeon may be influenced by the species' reproductive behaviour and the composition of members, in size and number, among social groups.

Sunbleak matured between the ages of 1 and 2 (Females and Males: $Age_M \leq 2$) with variations between females and males at Bridgewater-Taunton Canal at Buckland Farm (BTC1), Creech St. Michael (BTC2) and Kings-Sedgemoor Drain (KSD5). Some of the inter-site variation was augmented by sunbleak from the Bridgewater-Taunton Canal, Creech St Michael, Somerset (BTC3), the Kings-Sedgemoor Drain, Bradney Bridge (KSD4), Somerset, the River Huntspill (Hunt6), the River Tone (Tone8) and Durleigh Reservoir (Durl10) because no fish of age 1 were observed at these sites, which was possibly related to the sampling method used. The sample from the latter site also did not contain fish of ages 2 or 3 and therefore the age-at-maturity ($Age_M = 4$) can be regarded as an artefact of the sample composition. Topmouth gudgeon matured between the ages 1 and 2 with specimens from Ratherheath Tarn maturing later (Females: $Age_M = 1.75$; Males: $Age_M = 2.00$) than at the remaining sites. Generally, maturation after 1 or 2 years will provide sunbleak and topmouth gudgeon with a characteristic that will aid recruitment and subsequent establishment. The reduced amount of time spent exposed to pressures such as predation, feeding and potentially variation in habitat quality will at the same time increase the chance for survival.

As expected, reproductive effort and gonadosomatic indices were higher in females than in males in both species owing to the physiological and physical differences in gonad characteristics reflected in gonadal weight (W_g) which subsequently is integrated into the equations used to calculate these parameters (see Method section 3.2.7 for details). Inter-site variability in reproductive effort and gonadosomatic index, which was observed in sunbleak and topmouth gudgeon, is likely to be related to differences in gonadal developmental stage at the time of sampling and potentially spawning times within the different water bodies. Batch spawning incorporates the production of several batches of eggs in one season, with the gonads containing oocytes of different developmental stages. So, when the fish were captured, the gonad at the gonadal stage at capture was investigated, which may have been different from the gonadal developmental stage in specimens from a different site. When looking at the inter-site comparison of reproductive investment from this angle, it becomes clear that such comparison is particularly difficult in batch-spawning fish species. However, reproductive investment is high in both species enabling them to form dense populations (i.e. early maturity, short generation time) and ensure successful establishment soon after introduction. Parental care may further assist in this process and warrant survival of the large numbers of eggs (Clutton-Brock, 1991).

Generally, variability in reproductive effort of fish can take place in response to variations in population density. The effect of density on reproductive effort in sunbleak and topmouth gudgeon can only be speculated upon. Warren (1973) and Dahlgren (1979) observed reduced reproductive effort with increased density in the guppy *Poecilia reticulata* (Peters). Laboratory experiments using topmouth gudgeon in their native range found that when population density is high, females displayed an increase of reproductive effort and decreased body size while males increased in body length (Katano and Maekawa, 1997). Such regulatory processes may assist females in increasing their reproductive success (Katano and Maekawa, 1997).

In sunbleak, relative fecundity was relatively high, as predicted by records of high reproductive effort, and ranged between 5.9 and 9.5 eggs per mm fork length and 103.9 and 322.5 eggs per g body weight. The greatest fecundity per gram body weight was observed at Stoneham Lakes, in fish with the slowest growth (Table 3.5, Table 3.6). It may be that there was a trade-off between body size and fecundity. Relative fecundity was also high in topmouth gudgeon, with 5.9 to 10.0 eggs per mm fork length and between 126.5 and 208.5 eggs per gram body weight. High fecundities were observed in topmouth gudgeon from Canal du Fumemorte, France, where relatively large males also occurred. This may be related to the species' reproductive behaviour where the female regulates towards a greater fecundity when larger males are available as mates (Maekawa *et al.*, 1996). However, a different study also investigating, amongst other parameters, the fecundity in topmouth gudgeon from Ratherheath Tarn, Cumbria (Britton *et al.*, 2007), reports greater fecundities than observed in the present study (351 eggs per gram body weight). This is likely related to differences in timing of sampling; August 2004 (this study) *vs* March 2005 (Britton *et al.*, 2007), but it could also indicate an amount of underestimation of relative fecundity using the gravimetric method.

For species that spawn their eggs at multiple times during the spawning season, measuring the diameter of the eggs would allow for a more robust fecundity dataset to be produced (Bagenal and Braum, 1978). The results suggest that in batch spawning fish species, such as sunbleak and topmouth gudgeon, the gonads would normally contain developing eggs of different sizes governed by the maturation of different batches that are shed at differing successive periods throughout the spawning season. It is for this reason that it is useful to record the diameter of the different size groups within the gonad to enable a more accurate estimation of the fecundity in individual fish.

Prevalence of sunbleak and topmouth gudgeon being in good body condition, with relatively low variations between sites, may be related to sufficient energy intake and energy storage (Busacker *et al.*, 1990). This may favour withstanding the requirements of new habitats and support successful establishment and dispersal. The condition factor of fish is also related to individual reproductive investment (e.g. GSI) (Lambert and Dutil, 1997). Good body condition coupled with high reproductive effort in topmouth gudgeon and sunbleak is, therefore, important to ensure the species' successful establishment.

3.4.4 Conclusions

Intra-population variability in life histories of sunbleak and topmouth gudgeon may be attributed to their batch-spawning behaviour. Individuals that stem from different batches of the same year may exhibit variations in growth rates and age and size at first maturation. Inter-population variability observed in life histories and/or morphology in sunbleak or topmouth gudgeon populations may be influenced by variations in water quality, but could also be related to variations in population density (see also Table 3.5 and Table 3.7) and/or fish community structure at the different sites. Temperature variations may also play a role in this process as it is known to influence recruitment success (Mills and Mann, 1985; Nunn *et al.*, 2003; Britton *et al.*, 2004). However, inter-population variability in life histories is common in fish, be they introduced or native (Vila-Gispert *et al.*, 2002; Villeneuve *et al.*, 2005).

Variability in age and length of maturation can be influenced by latitude (Copp *et al.*, 2002a; Vila-Gispert *et al.*, 2002). With decreasing latitude, fish follow a rather opportunistic (early maturation, batch spawning, small body size, short life-span) strategy (Vila-Gispert *et al.*, 2002). Due to habitat seasonality, many North American and European fish populations follow a periodic strategy (large clutches, delayed maturation). However, in their non-native range sunbleak and topmouth gudgeon appear to have adapted intermediate life history strategies, displaying aspects of opportunistic (early maturity, high reproductive effort, small adult body size), periodic (fast growth during early life, high fecundity) and equilibrium (parental care) strategists. In light of the *r/K* model, these are characteristics (except for the parental care), typical for *r* strategists and particularly beneficial in unstable or unpredictable environments (MacArthur and Wilson, 1967; Pianka, 1970). By virtue of their introduction into a new environment, the fish are exposed to unpredictable environmental circumstances. However, when applying the W-R life history model (see Introduction Section 3.1 and Table 3.1 for further details), which also describes the typical environments that species within each life history group may persist in, it appears that the combination of different life history characteristics from all 3 of the strategies, topmouth gudgeon and sunbleak would be expected to be able to persist in most types of environments. Both species display at least one typical characteristic suited to highly disturbed and unpredictable environments (opportunistic strategy), seasonal, periodically suitable environments (periodic strategy) and constant environments (equilibrium). However, in studies of invasions, traditional life history theory may be considered but increased attention has to be given to potentially intermediate strategies. This is also interesting when considering characteristics of native fish species in England, where for example parental care does not occur but is displayed by numerous established non-native fish species (Maitland, 2000).

Based on the results it is expected that when sunbleak and topmouth gudgeon are introduced into a new water body, they would be equipped with characteristics that may enable them to form dense populations within 1 to 2 years after introduction (e.g. short lag time, high propagule pressure). High reproductive effort and fecundity, early maturity, small body size and short generation time in a combined manner, facilitate establishment success. Variability in parameters that enable biological adaptation and/or integration will increase the likelihood of the species to fit into the new environment after introduction and persist. In light of this, it is paramount that the human-mediated translocation and/or introduction of these species are prevented.

3.5 Chapter summary

Morphological variability between invasive populations can involve different characters in different populations (Gillespie and Fox, 2003) and is not necessarily accompanied by life history differentiation but may rather be related to the species' reproductive behaviour. Sunbleak and topmouth gudgeon possess several life history attributes that enable these species to successfully invade new water bodies (Perdices and Doadrio, 1992a; b). Early maturation, short generation time and high reproductive effort aids quick establishment and the creation of dense populations in new environments. Nest-guarding by males, which may increase egg survival, and batch spawning (Cassou and LeLouarn, 1991) further increase overall survival rate during early life. Parental care is a trait that is not found in native fish species while > 50 % of the non-native species with parental care have successfully established in U.K. waters (Maitland, 2000) and is considered a characteristic that facilitates invasion success (Jeschke and Strayer, 2008). The introduction of topmouth gudgeon and sunbleak into online lakes and/or enclosed lakes that are located in flood plains serves as an ideal springboard for successful invasion. Such areas act as sources for new recruits and transition zones before further dispersal and recruitment in the wild. The processes of sunbleak and topmouth gudgeon dispersal from such sources are presented in Chapter 4.

4. Drift and dispersal of sunbleak and topmouth gudgeon[6]

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[6] Data from parts of this study were presented at the FSBI Conference in July 2004: Beyer, K., Gozlan, R.E. & Copp, G.H. ‘Escapees of potentially invasive fishes from an ornamental aquaculture facility: the case of topmouth gudgeon *Pseudorasbora parva*’; and at the 15th ICAIS Conference in September 2007: Beyer, K., Gozlan, R.E. & Copp, G.H. ‘Aspects of successful invasion by topmouth gudgeon’.

4.1 Introduction

Dispersal and colonisation of new habitats are part of the invasion process and crucial for the success of invaders (Davis and Thompson, 2000). Information on these mechanisms may help to determine the lag phase[7] and colonisation rate of an invader (Crooks and Soule, 1999). Ecological knowledge of introduced species is important because it provides the basis for predictions about the potential impact on native taxa (Harvey *et al.*, 2002). Sound management of non-native species must be based on the characterisation of introduction pathways and on the ability to predict potential future dispersal and subsequent distribution. Quantification of drift from a source population may assist in the making of such predictions and can be useful when carrying out risk assessments (Copp *et al.*, 2005b; 2005c). This is supported by several studies, which report the frequency with which individuals of a species are introduced into a new environment as an important factor for a species' establishment success (Beirne, 1975; Veltman, 1996; Green, 1997; Von Holle and Simberloff, 2005).

It is not only the abiotic (e.g. temperature) and biotic (e.g. community structure) variances in a novel environment, or the properties of the new species (e.g. life history) that determine whether an introduced species establishes or not, but also the number of individuals that are introduced (Von Holle and Simberloff, 2005). Propagule pressure is a measure of the number of individuals introduced and the frequency of their introduction into a new ecosystem (Williamson and Fitter, 1996) and has only recently started to receive attention in the application to introduced fish species, with previous application limited to terrestrial invasions (Duggan *et al.*, 2006; Copp *et al.*, 2007). Propagule pressure is positively correlated with the establishment success of non-native species (Williamson, 1996; Colautti and MacIsaac, 2004) and so appears to be an important mechanism that should be considered in the invasion ecology of introduced fishes. The level of propagule pressure on a targeted location will, amongst other factors, determine whether the physical environment and the native community may mediate or

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[7] 'Lag phase' is the amount of time following a species' introduction which is needed to increase its population to a size that will allow successful establishment and dispersal. This phase may be influenced by the size- and age-at-maturity size of the introduced species.

resist a potential invasion (Byers, 2002a). It is generally expected that a species that is introduced on a single occasion is less likely to establish than a species introduced on several separate occasions.

The spread of an introduced non-native fish is a crucial part of the invasion process (Rosecchi *et al.*, 2001; Kolar and Lodge, 2002) and is limited by the opportunity to disperse from the new environment. For example, dispersal is possible from lentic environments when these are connected with fluvial systems or a floodplain lake. Downstream movement of freshwater fishes may be: 1) passive when fishes drift without orientation in association with the water flow; 2) active-passive, when fishes move downstream with only weak resistance to the current; or 3) active (Pavlov, 1994). Mass downstream movement of young fishes occur in many freshwater fishes and can reach up to 12,000 specimens 1000 m^{-3} (Cyprinidae, Percidae, Osmeridae) in large rivers (Pavlov *et al.*, 1981), with drift timing, frequency and intensity being species specific and associated with developmental stages of fish (Pavlov, 1994; Jurajda, 1998; Reichard, 2002; Reichard *et al.*, 2002b; Reichard *et al.*, 2002c; Reichard *et al.*, 2004; Reichard and Jurajda, 2007).

Depending on community structure and spawning season, drift densities as well as timing and species vary widely between water bodies, which may further be explained by differences in hydrological regimes. A study on fish drift in the River Lohajang, Tangail, Bangladesh reports larval drift densities between 1000 and 9300 fish 1000 m^{-3} (de Graaf *et al.*, 1999). A study examining interannual patterns of drift in the Rivers Morava and Kyjovka, two lowland rivers within the Danube Basin (Czech Republic), reports peak densities ranging between 80 and 1354 fish 1000 m^{-3} between years and rivers, 98 % of which were represented by cyprinids (Reichard *et al.*, 2002b). Larval fish drift in a study on the River Lee with overall means not exceeding 10 fish larvae 1000 m^{-3} in 1993, and 1995 reports much lower densities (Copp *et al.*, 2002b). However, the low drift densities were generally attributed to the hydrological regime of the River Lee (Copp *et al.*, 2002b).

Drift of fishes is reported to follow a diurnal pattern with the greatest proportion of drift taking place during the hours of darkness (Brown and Armstrong, 1985; Corbett and Powles, 1986; de Graaf *et al.*, 1999; Carter and Reader, 2000; Araujo-Lima *et al.*, 2001; Copp *et al.*, 2002b; Reichard *et al.*, 2002b; Reichard *et al.*, 2004; Zitek *et al.*, 2004a) as well as a seasonal pattern (de Graaf *et al.*, 1999; Carter and Reader, 2000; Reichard *et al.*, 2002b; Zitek *et al.*, 2004a). The diurnal drift pattern has previously been related to larval photosensitivity (Reichard *et al.*, 2002a), predation avoidance (Araujo-Lima and Oliveira, 1998) or water temperature (Zitek *et al.*, 2004a). Generally, fish drift is related with flow velocity (Copp *et al.*, 2002b).

In England, populations of sunbleak and topmouth gudgeon occur in water bodies, many of which are connected to river catchments that are of conservation importance due to the presence of wild Atlantic salmon and brown trout populations (see Chapter 1 for distribution maps). The likelihood of non-native species dispersing into the online water courses is high, particularly in cases where measures to prevent outfall from source populations have not been applied. However, the dynamics of this dispersal mechanism have not previously been examined for sunbleak and topmouth gudgeon. Indeed, studies of fish drift in England are scarce (Copp *et al.*, 2002b). It is important to determine the intensity with which topmouth gudgeon and sunbleak are dispersing, because of their potential to spread beyond their current distribution in their non-native range (Gozlan *et al.*, 2003b; Pinder *et al.*, 2005b). The potential for drift and dispersal is a key determinant of invasion success. Therefore, the present study aimed to examine the density and timing of movement of sunbleak and topmouth gudgeon *via* drift from source populations into connected river catchments, so as to quantify the role of this dispersal pathway in the species' invasion process. The specific objectives where to: 1) quantify the density of drift of topmouth gudgeon and sunbleak larvae from source populations into connected streams/brooks, 2) determine if diel drift patterns occur, and 3) enumerate the extent to which sunbleak or topmouth gudgeon have invaded online water bodies as a result of this drift.

4.2 Materials and methods

4.2.1 Data collection

Drift rates and patterns of sunbleak and topmouth gudgeon movement out of source fisheries into recipient streams were measured using drift nets (EFE & GB Nets, Bodmin, Cornwall, U.K.). The drift nets (Plate 4.1; Figure 4.1) had a rectangular to conical shape with a net (1 mm mesh size) leading to an end opening to which a removable 500 ml plastic bottle was attached. The bottle created a zero-velocity zone at the end of the net that reduced the amount of potential damage to the captured fish due to the force of water passing through the net (Peňáz *et al.*, 1992). This approach also reduced the amount of time needed to collect the sample from the net, as each bottle could be quickly replaced by an empty one. Each drift net had a rectangular opening of 0.24 m x 0.40 m, with a 0.65 m long net leading to a 3 cm diameter end opening. During sampling, each net was fixed at the bottom using metal stakes, normally just below the water's surface and filtered the water depth to 0.24 m (= height of the net). In instances where the upper part of a net was above the water line, the depth of water filtered was measured at the beginning and the end of net exposure to determine the estimated volume of filtered water. The water velocity was recorded at the net entrances during the study using a flow meter (Log IT).

Plate 4.1: Drift net placed below the outflow from Crampmoor Fishery inside Tadburn Lake stream.

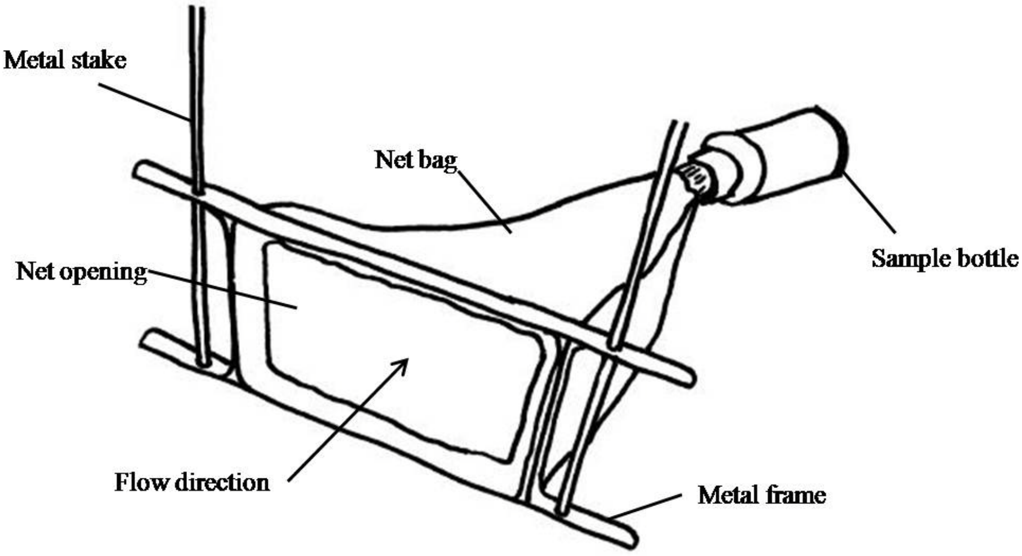

Figure 4.1: Schematic drawing of a drift net as used to estimate drift densities for topmouth gudgeon and sunbleak. The rectangular opening of the net measures 0.24 m x 0.40 m, with the 0.65 m long net leading to a 3 cm diameter end opening.

4.2.1.1 Movement from source populations

Drift of sunbleak was quantified at Revels Fishery, Dorset in 2004 and at Stoneham Lakes Fishery, Hampshire in 2004 and 2005. Topmouth gudgeon drift was quantified at Crampmoor Fishery, Hampshire in 2004 and 2005. For locations and description of study sites see Chapter 2.

When placing the nets in the stream, it was assumed that fish movement *via* drift would be passive (i.e. similar to suspended matter) and as such drift density should be positively related to stream power, which is a function of velocity and the stream bed gradient (Faulkner and Copp, 2001). The influence of net location in relation to the cross section of the stream was dismissed, because Tadburn Lake stream was narrow in the area of sampling(~ 2 m). Monks Brook was relatively faster flowing, slightly wider and the bottom was made of concrete, so nets were placed at differing distances from the outflow. To prevent bias due to water velocity variations between net locations, water velocity was recorded in front of each net every time the bottle was emptied.

Revels Fishery, Dorset

Fish drift was determined at Revels Fishery between April and June 2004 (see Chapter 2 for site description; see Appendix B for details on sampling dates and timing). These months were considered representative of the spawning periods of sunbleak and were chosen because intra-annual variations in fish drift may result from increased reproduction. In each sampling period, six drift nets were set over two replicate 24-hr periods per month. To reveal diel drift patterns, drift nets were set at 11:00 hr with samples being taken every 6 hours, and removed at 11:00 hr of the following day. At Revels Fishery, two and four nets were allocated for sampling in the two- and five-lake-systems, respectively (see Figure 2.6 in Chapter 2 for drift net locations). The nets were placed at inflows between lakes and at the outflow into Caundle Brook.

Owing to limitations in manpower availability in 2005, Revels Fishery was sampled in 2004 only.

Stoneham Lakes Fishery, Hampshire

At Stoneham Lakes, fish drift was determined at Stoneham Lakes between April and June 2004 and 2005 (see Appendix B for details on sampling dates and timing). These months were considered representative of the spawning period of sunbleak and were chosen because intra-annual variations in fish drift may result from variations in reproductive success between years. In both years, six drift nets were set at 11:00 hr over two replicate 24-hr periods per month with samples being taken every 6 hours, and removed at 11:00 hr on the following day. Although diel patterns in drift densities were observed in 2004, numbers of drifting fish were relatively low, so emptying the nets every six hours was deemed to be sufficient for drift quantification in 2005. Three drift nets were set between the three separate lakes and at the outflow into Monks Brook, to calculate the rate of drift between established source populations of sunbleak (see Figure 2.5 in Chapter 2 for drift net locations). Three further drift nets were set below the Stoneham Lakes’ outflow into the adjacent Monks Brook to identify drift into the wild.

Crampmoor Fishery, Hampshire

Fish drift was determined at Crampmoor Fishery between April and June 2004 and 2005 (see Appendix B for details on sampling dates and timing). These months were considered representative of the spawning periods of topmouth gudgeon and were chosen because intra-annual variations in fish drift may result from reproduction. In 2004, six drift nets were set at 11:00 hours over two replicate 24-hr periods per month with drift samples being taken every 6 hours, and removed at 11:00 hr of the following day. Because drift sampling was not possible inside Crampmoor Fishery, nets were set in subsequent order below the fish farm’s outflow into the adjacent stream (see Figure 2.7 in Chapter 2 for drift net locations). Owing to high densities of topmouth gudgeon drift observed during 2004, this site was chosen to investigate diel pattern in more detail in 2005. Therefore, six drift nets were set at 11:00 hours over two replicate 24-h periods in

April, May and June 2005, with drift samples being taken every 3 hours, and removed at 11:00 hr on the following day.

Owing to extensive sampling effort and manpower limitations, only this site containing topmouth gudgeon was chosen for this more detailed insight into the diel drift pattern (3 hr periods). This decision was further justified with the belief that this knowledge would be even more important for topmouth gudgeon as they are already more widespread in England than sunbleak (Figure 1.2, Figure 1.3).

To examine seasonal dynamics of topmouth gudgeon drift from the source water body, drift sampling was carried out on a monthly basis from July 2004 to March 2005. The nets were set at 8:00 hr for a 24 hour period once per month and emptied every 12 hours, and removed at 8:00 hr the following day. Owing to manpower limitations and commitments to field and laboratory work over the remainder of the study, the timing during this monthly sampling was adapted accordingly.

Sample processing

Fish larvae collected in the drift were killed by overdose of 2-Phenoxyethanol, whereas adult fish captured were killed by severance of the spinal cord at the base of the skull according to Schedule 1 methods as per the ‘Animals (Scientific Procedures) Act 1986’ (Home Office, 1986a; b). All samples were preserved in 4 % formalin for further examination in the laboratory. Shrinkage effect of preservation on body size of captured fish was not tested. For further details on potential shrinkage effects of fish preservation and on Schedule 1 methods, refer to Section 3.2 of Chapter 3.

Fish eggs, larvae and adults were identified to species (Arnold and Längert, 1995; Pinder, 2001; Maitland, 2004; Pinder, 2005) and their fork length (mm) to the nearest 0.1 mm recorded. Ontogenetic stages of larvae were defined according to the developmental framework presented by Pinder and Gozlan (2004) for sunbleak and in Appendix C for topmouth gudgeon, based on the functional capabilities according to their physiological and morphological development.

4.2.1.2 Dispersal within the recipient water body

The following part of the study was carried out in 2003, because of the known occurrence of sunbleak in Stoneham Lakes and Revels Fishery, and topmouth gudgeon in Crampmoor Fishery. At this point it was also known that all three fisheries had outflows into the wild. The results of this work lead to the development of the question whether the species are exiting these fisheries and to what extent this would take place. This question was the initial starting point for the drift investigation carried out in 2004 and 2005. Drift investigations in 2003 would not have been possible due to equipment in-availability and the time of the spawning season.

Field surveys were carried out to assess the extent to which Tadburn Lake Stream (River Test basin, Hampshire), Monks Brook (River Itchen basin, Hampshire), and Caundle Brook (River Stour basin, Dorset) had been invaded by either sunbleak or topmouth gudgeon. To measure the dispersal of these non-native fish species, randomly-chosen 50 m electro-fishing surveys were carried out in summer 2003 in the streams adjacent to the three fisheries and below the fishery outflows (Tadburn Lake stream ≈4.0 km; Monks Brook ≈5.0 km; Caundle Brook ≈13 km). All sites were electro-fished, wading from downstream to upstream using pulsed DC single pass backpack electric fishing gear (Output: 50 – 100 Hz PDC with an operating current of 1 to 2 Amps). Immobilized fish were collected, identified to species, and their fork lengths were measured to the nearest 0.01 mm. For each transect the following habitat variables (averaging five random measurements along each transect) were recorded: distance from fishery (km), width in cm, Dep, depth in cm, bottom substrate types as a percentage of %Sa, sand (> 0.06 - 0.2 cm), %Gr, gravel (> 0.2 – 4.0 cm), %Pe, pebbles (> 4.0 – 6.4), and %Co, cobbles (> 6.4 cm), Vel, water velocity, SVe, percentage of submerged vegetation, Lig, percentage of ligneous debris and the OhV, percentage of overhanging cover. Habitat methodology used follows the methods used in many studies on the habitat use in fish (Grossman and Freeman, 1987; Watkins *et al.*, 1997; Cerny *et al.*, 2003; Carter *et al.*, 2004; Klaar *et al.*, 2004; Davey *et al.*, 2005; Gozlan and Copp, 2005). Water velocity was determined semi-quantitatively as described in Carter *et al.* (2004), using a dip-net pole; upon immersion of the pole, (1) no ripple effect around the pole was noted as zero water velocity; (2) a gentle ripple effect (broken water) around the pole indicated a weak velocity (> 0 but < 5 cm s^{-1}); (3) a moderate ripple effect around the pole represented a moderate velocity (5 – 10 cm s^{-1}).

To enable quantification of drift at a location far below the topmouth gudgeon source population and in close proximity of the River Test, six drift nets were placed immediately next to each other across Tadburn Lake stream 5.5 km below the fishery on 9 and 12 April 2005. This location was 0.5 km upstream from where Tadburn Lake stream enters the River Test. Landowners did not give permission to fish in Tadburn Lake stream further downstream of this point. This additional sampling effort in 2005 was expected to provide a snapshot picture of topmouth gudgeon the furthest downstream as was possible in light of these restrictions. This sampling took place further downstream than the random electro-fishing surveys carried out during 2003 and was deemed important in light of the native Salmonid population in the River Test and the association of topmouth gudgeon with the rosette-like agent (RLA) (Gozlan *et al.*, 2005).

4.2.1.3 Data analysis

Drift density

To enable calculation of drift density, the water velocity (m s^{-1}) at net entrances was measured using a Log IT water velocity meter, which was fixed to one of the six drift nets during each sampling period. In addition, each time the contents of the bottles were emptied, the flow velocity was measured as a precaution in case of recording failure. In such cases, the mean entrance water velocity was used to determine the volume of water filtered. The recorded flow velocity at the net entrance allowed calculation of the volume of filtered water (= volume of water passing through the net). The volume of water for each sample was calculated as follows (Allan and Russek, 1985; Faulkner and Copp, 2001):

$$V_{FW} = Vel_{NE} * Area_{NE} * SI$$

where V_{FW} is the volume of filtered water (m^{-3}), Vel_{NE} is the net entrance velocity, in m s^{-1}, $Area_{NE}$ is the cross-sectional area of net entrance, in m^2, and SI is the sample interval, in s.

To remove the effects of variability in water velocity, the drift density DD per sample was calculated as follows:

$$DD = n_{dev} / V_{FW}$$

where n_{dev} is the number of individuals at different developmental stages and V_{FW} volume of filtered water (m^{-3}).

Filter efficiency

When using drift nets to determine drift density, it is possible that the filter efficiency (net filtration performance) can be affected by an accumulation of organic detritus in the net (‘clogging’) (Waters, 1969). However, only few and more recent studies on riverine drift have actually accounted for a potential ‘clogging effect’ in their studies (e.g. Faulkner and Copp, 2001; Peterka *et al.*, 2004; Reichard *et al.*, 2004). To assess whether ‘clogging’ of the nets with organic debris would bias the calculations of water volumes filtered, the organic debris (air dried) weight (= O_t in g) was determined to the nearest 0.1 g for every drift sample taken. It was expected that if the weight of organic debris was statistically indifferent between samples, a ‘clogging effect’ would be discounted. This was deemed suitable as all samples covered a time period of ≤ 12 hours (Faulkner and Copp, 2001). Because of high numbers of adult individuals captured in the drift nets, these were included in the data analysis but treated separately where appropriate.

Statistical analysis

Differences in drift densities (i.e. numbers of larvae/eggs per volume of filtered water) between developmental intervals of drifting species, between sampling nets, between periods of day, and between sampling dates, months, seasons and years were tested using the non-parametric Kruskal-Wallis test (Sokal and Rohlf, 1998). This was due to a large numbers of zeros (‘no fish’) in the fish drift data set. When there were no differences, data were combined into groups as appropriate. To permit statistical comparisons of drift densities at Crampmoor Fishery between 2004 and 2005, data for the latter year were combined according to daytime (08:00 – 17:00 hr), dusk (20:00 hr), night (23:00 – 02:00 hr) and dawn (5:00 hr). For comparison, seasons were combined according to spring (March - May), summer (June - August), autumn (September – November) and winter (December – February). Before non-parametric analyses were chosen, normality and equality of variances were disproved of using the Kolmogorov-Smirnov and Levene’s test statistics, respectively.

Finally, in order to determine differences in community composition between random electro-fishing surveys downstream of the fisheries, the catch per unit effort (CPUE) was determined as the number of fish per unit of time (hour) fished. To determine whether data for macro-habitat and the adult fish CPUE conformed to the requirements of parametric statistical testing, normality and equal variances using the Kolmogorov-Smirnov and Levene’s statistics were applied. When data did not conform to these requirements, differences in macro-habitat and adult fish CPUE between random surveys were examined using the non-parametric Kruskal-Wallis test. The relationship between CPUE (per hour) and the distance from the upstream fishery was tested using Pearson’s correlation.

4.3 Results

4.3.1 Movement from source populations

Revels Fishery, Dorset

At Revels Fishery, a total of 16 specimens of sunbleak were observed in the drift samples of 2004 (Table 4.1). No other fish species were recorded in the drift. Sunbleak were found drifting only between 17:00 hr and 05:00 hr between ponds within the fishery (Table 4.1). Additionally, a total of 116 sunbleak eggs attached to vegetation were found drifting on 18th May 2004 recorded from a net placed directly at the outflow of the fishery into the online Caundle Brook.

Stoneham Lakes, Hampshire

At Stoneham Lakes, 5 species of fish were observed from drift nets, including sunbleak, roach and minnow with 1 perch occurring in 2004 and 1 bream in 2005 (Table 4.1). In 2004 and 2005, 26 and 35 specimens of sunbleak were observed respectively. Drift from Stoneham consisted mainly of larval sunbleak. Roach was the only other species of which larval stages (L2) were observed drifting. For each species, all larvae and length groups of adults were combined as ‘larvae’ and ‘adults’, respectively, because no differences were observed in drift densities between the different larval stages ($P > 0.1$) or between the different length groups ($P > 0.9$). At Stoneham Lakes, sunbleak drifted with a mean density of 0.4 ± 0.2 and 0.6 ± 0.4 larvae 1000 m^{-3} in 2004 and 2005 respectively. Maximum density of larval sunbleak drifting reached 9 fish 1000 m^{-3} and 10 fish 1000 m^{-3} on 27 May 2004 and 22 May 2005, respectively. No larval stage L1 sunbleak drifted in 2004 or 2005 (Table 4.1; Figure 4.2; Figure 4.3; Figure 4.4; Figure 4.5). Variability in the proportion of the remaining 4 larval stages in the total drift was probably related to inter-annual variations in the timing of sunbleak spawning and timing of sampling in Stoneham Lakes. However, drift densities between years were not significantly different (Kruskal-Wallis $H = 0.01$, $P = 0.981$).

Drift densities at Stoneham differed significantly between nets (Kruskal-Wallis $H = 13.45$, $P > 0.1$), as a consequence of significantly lower ($H = 260.57$, $P < 0.001$) discharge between the lakes (nets 1 - 3) than from the outflow fishery into Monks Brook (nets 4 - 6). Drift quantities in the latter three nets were significantly higher than in the between-lake nets ($P < 0.05$).

Stoneham drift densities were significantly higher at night than during the day (Kruskal-Wallis $H = 10.68$, $P < 0.05$) (Figure 4.2; Figure 4.3). Mean larval drift was greatest between 23:00 and 5:00 hr in both years. During 2005, mean larval drift between 17:00 and 23:00 hr was slightly higher than observed for the same time period during 2004.

Densities of drifting larval sunbleak varied over time with a peak on 26th May 2004 and 21st May 2005 (Figure 4.4; Figure 4.5). In both years, 2004 and 2005, densities of drift were lower in April than during other months (Kruskal-Wallis $H = 275.19$, $P < 0.001$).

Adult fish density varied between April, May and June in both years but did not differ significantly ($P > 0.05$) (Figure 4.6; Figure 4.7). Adults found in drift nets were deemed to follow active-passive movement.

Crampmoor Fishery, Hampshire

A total of seven fish species were observed in drift nets at Crampmoor Fishery with a total of 558 topmouth gudgeon collected over the two sampling years (Table 4.1). Of those, 247 specimens were captured in 2004 and 239 specimens in 2005. Topmouth gudgeon larvae were the only species of which early life stages were observed in the drift during both 2004 and 2005 (Table 4.1). Mean drift was 3 ± 1 and 7 ± 2 larval topmouth gudgeon 1000 m^{-3} in 2004 and 2005 respectively. Maximum drift densities reached 40 and 52 topmouth gudgeon larvae 1000 m^{-3} on 24 May 2004 and 12 May 2005 respectively. There were no significant differences in drift densities between nets or between larval stages (Kruskal-Wallis, $P > 0.10$).

Larval drift densities differed significantly between periods of day ($H = 39.64$, $P < 0.001$) with densities at dawn (05:00 hr) being significantly higher than other periods of day (Figure 4.8, Figure 4.9). In 2004, 6-hourly sampling already revealed this diel pattern of topmouth gudgeon drift, with densities being greatest between 23:00 and 5:00 hr (Figure 4.8). However, a more detailed pattern emerged from the 3-hourly sampling where the greatest densities were recorded between 2:00 and 5:00 hr (Figure 4.9).

Drift densities differed significantly between sampling dates ($H = 21.10$, $P = 0.032$) and between months of intensive 24 hour surveys ($H = 19.14$, $P < 0.001$). Drift densities were not significantly different between years (Kruskal-Wallis $H = 0.04$, $P = 0.846$), while numbers of fish 1000 m^{-3} were significantly higher during May than during other months in both years (Kruskal-Wallis $H = 47.90$, $P < 0.001$) and varied with time (Figure 4.10, Figure 4.11 and Figure 4.12).

Topmouth gudgeon were captured in drift nets throughout the year indicating substantial propagule pressure was exerted on Tadburn Lake stream by this species during the spawning season (April, May and June) as well as in the remaining months of the year (Figure 4.12).

Table 4.1: Number of specimens, mean and standard error (S.E.) of fork length (FL) in mm, the number of eggs (No of eggs) and the proportion (in %) of each step [Larval stages (L1 – L5), Juvenile (J) and Adult (A)] of fishes collected from Crampmoor Fishery, Stoneham Lakes and Revels Fishery during drift sampling in 2004 and 2005.

Location	Year	Common name	Scientific name	n	Mean FL	SE	No of eggs	L1	L2	L3	L4	L5	J	A
Crampmoor Fishery	2004	Topmouth gudgeon	*Pseudorasbora parva*	247	29.3	0.9	0	2.1	22.7	18.3	0.3	N/A	15.8	33.3
		Golden Orfe	*Leuciscus idus*	8	78.0	0.5	0	0	0	0	0	0	0	100.0
		Mirror Carp	*Cyprinus carpio*	1	64.0	0	0	0	0	0	0	0	100.0	0
		Three-Spined Stickleback	*Gasterosteus aculeatus*	1	35.1	1.3	0	0	0	0	0	0	0	100.0
		Stoneloach	*Barbatula barbatula*	3	77.7	12.4	0	0	0	0	0	0	0	100.0
		Bullhead	*Cottus gobio*	2	57.1	1.7	0	0	0	0	0	0	0	100.0
		Lampetra spp	*Lampetra* spp	1	123.0	0	0	0	0	0	0	0	100.0	0
	2005	Topmouth gudgeon	*Pseudorasbora parva*	239	23.3	1.2	0	25.1	23.4	1.3	0.0	N/A	38.9	11.3
		Golden Orfe	*Leuciscus idus*	4	78.8	0.5	0	0	0	0	0	0	0	100.0
		Mirror Carp	*Cyprinus carpio*	0	0	0	0	0	0	0	0	0	0	0
		Three-Spined Stickleback	*Gasterosteus aculeatus*	6	33.7	0.9	0	0	0	0	0	0	0	100.0
		Stoneloach	*Barbatula barbatula*	1	56.0	0	0	0	0	0	0	0	0	100.0
		Bullhead	*Cottus gobio*	8	57.9	2.6	0	0	0	0	0	0	0	100.0
		Lampetra spp	*Lampetra spp*	0	0	0	0	0	0	0	0	0	0	0
Stoneham Lakes Fishery	2004	Sunbleak	*Leucaspius delineatus*	26	23.2	3.6	0	0	15.4	26.9	3.8	23.1	0	30.8
		Roach	*Rutilus rutilus*	4	14.3	4.2	0	0	50.0	0	0	0	50.0	0
		Minnow	*Phoxinus phoxinus*	7	44.0	0	0	0	0	0	0	0	0	100.0
		Bream	*Abramis brama*	0	0	0	0	0	0	0	0	0	0	0
		Perch	*Perca fluviatilis*	1	98.0	0	0	0	0	0	0	0	0	100.0
	2005	Sunbleak	*Leucaspius delineatus*	35	18.5	2.6	0	0	22.9	20.0	8.6	25.7	0	22.9
		Roach	*Rutilus rutilus*	1	24.5	0	0	0	0	0	0	0	100.0	0
		Minnow	*Phoxinus phoxinus*	1	45.0	0	0	0	0	0	0	0	0	100.0
		Bream	*Abramis brama*	1	87.0	0	0	0	0	0	0	0	100.0	0
		Perch	*Perca fluviatilis*	0	0.0	0	0	0	0	0	0	0	0	0
Revels	2004	Sunbleak	*Leucaspius delineatus*	16	49.0	3.2	116	0	0	0	12.5	0	0	87.5

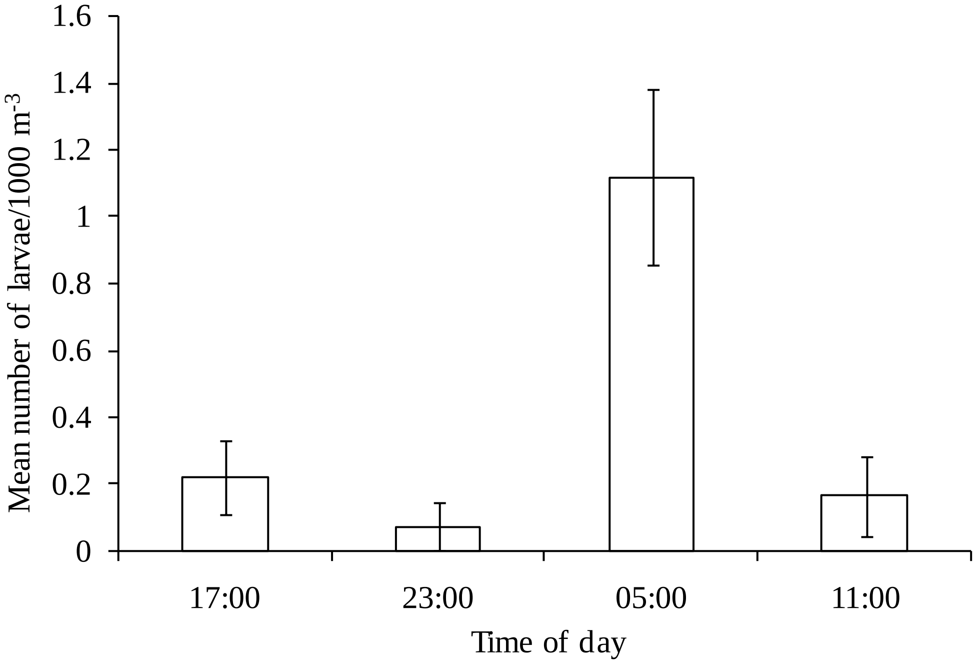

Figure 4.2: Mean drift densities 1000 m^{-3} and standard error bars for larval sunbleak captured during intensive 24 hour drift sampling at Stoneham Lakes Fishery during 2004.

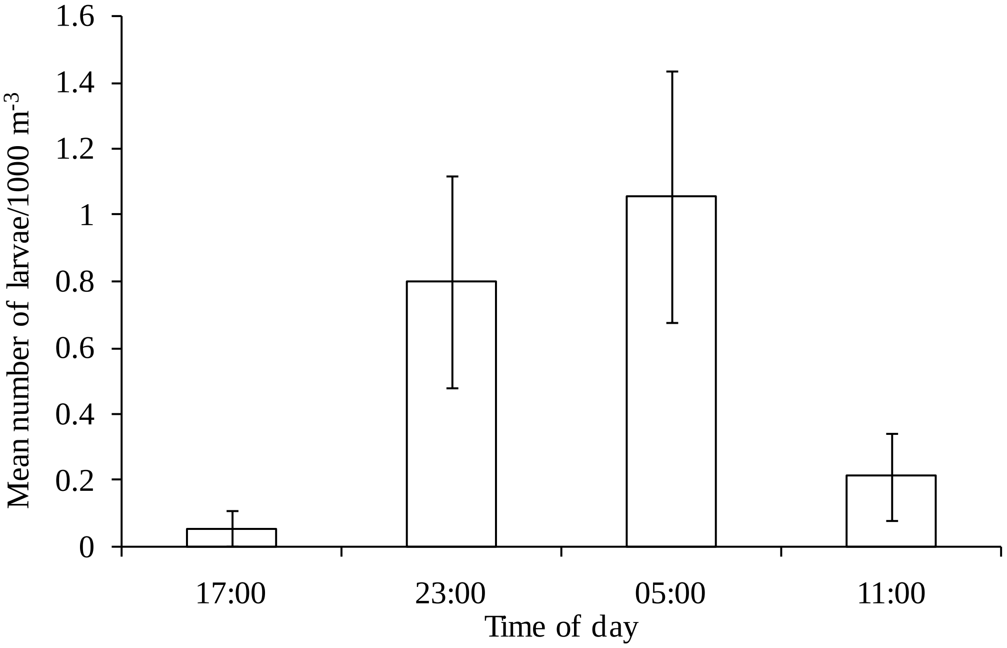

Figure 4.3: Mean drift densities 1000 m^{-3} and standard error bars for larval sunbleak captured during intensive 24 hour drift sampling at Stoneham Lakes Fishery during 2005.

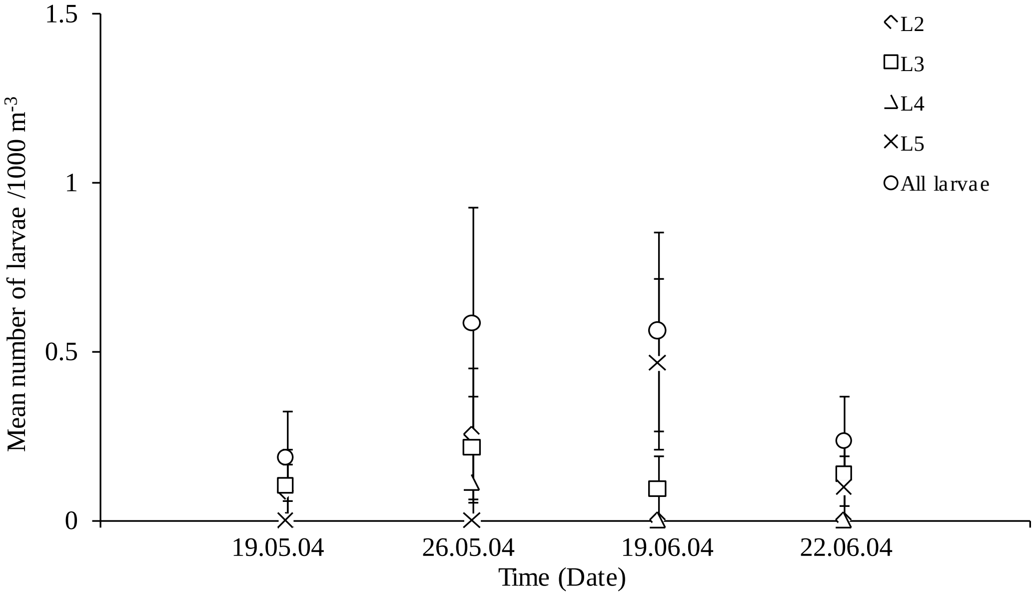

Figure 4.4: Mean number of sunbleak larvae 1000 m^{-3} and standard error bars captured in six drift nets over six 24 hour intervals during May and June of 2004 (every 6 h with nets set at 11:00 hours) at Stoneham Lake Fishery. No sunbleak larvae were observed in drift samples during April 2004.

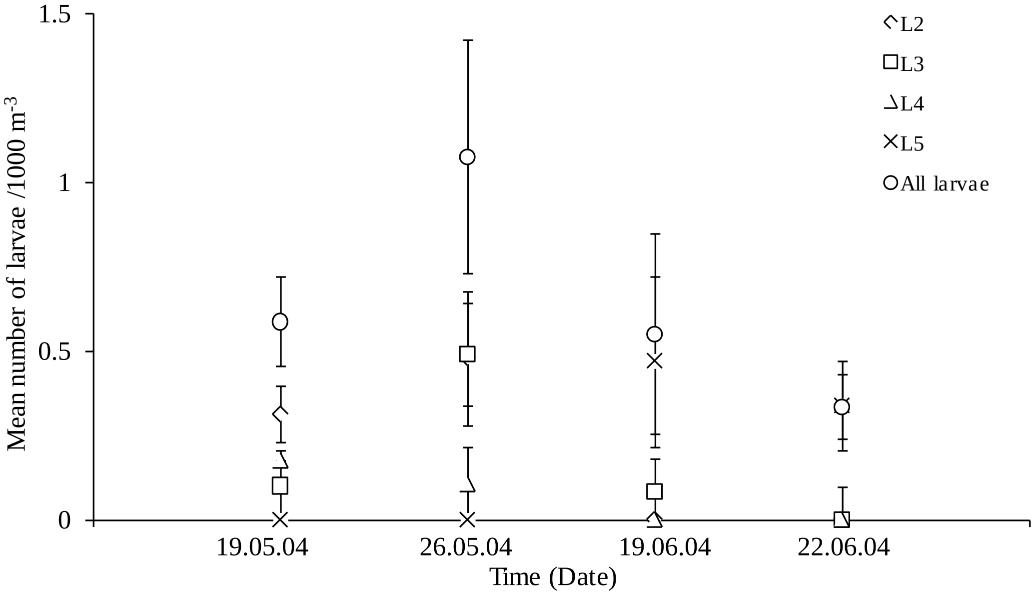

Figure 4.5: Mean number of sunbleak larvae 1000 m^{-3} and standard error bars captured in six drift nets over six 24 hour intervals during May and June of 2005 (every 6 h with nets set at 11:00 hours) at Stoneham Lake Fishery. No sunbleak larvae were observed in drift samples during April 2005.

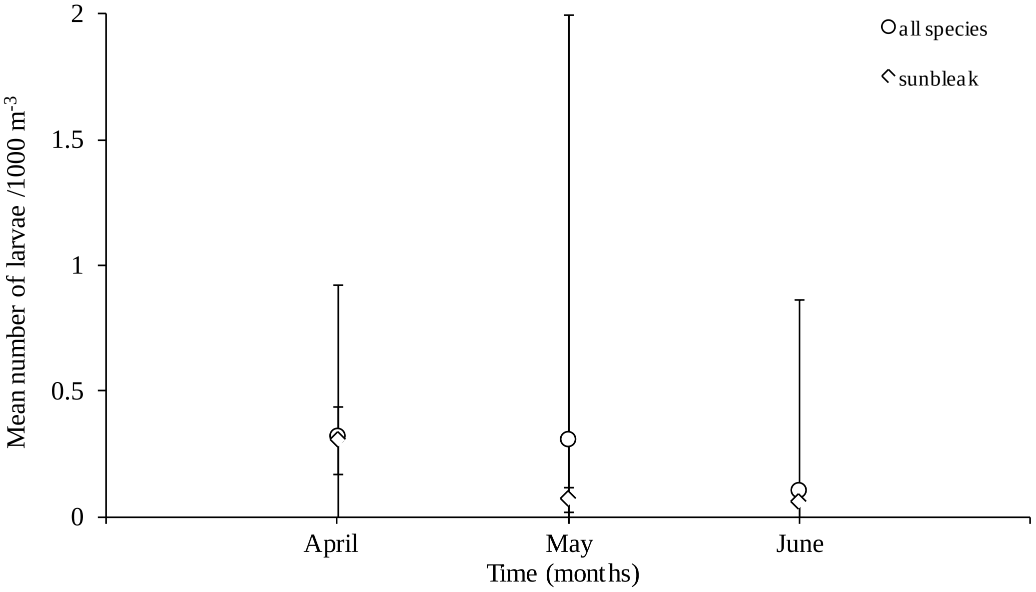

Figure 4.6: Mean densities 1000 m^{-3} and standard error bars of sunbleak and all adult fish captured in drift nets at Stoneham Lake Fishery during 2004.

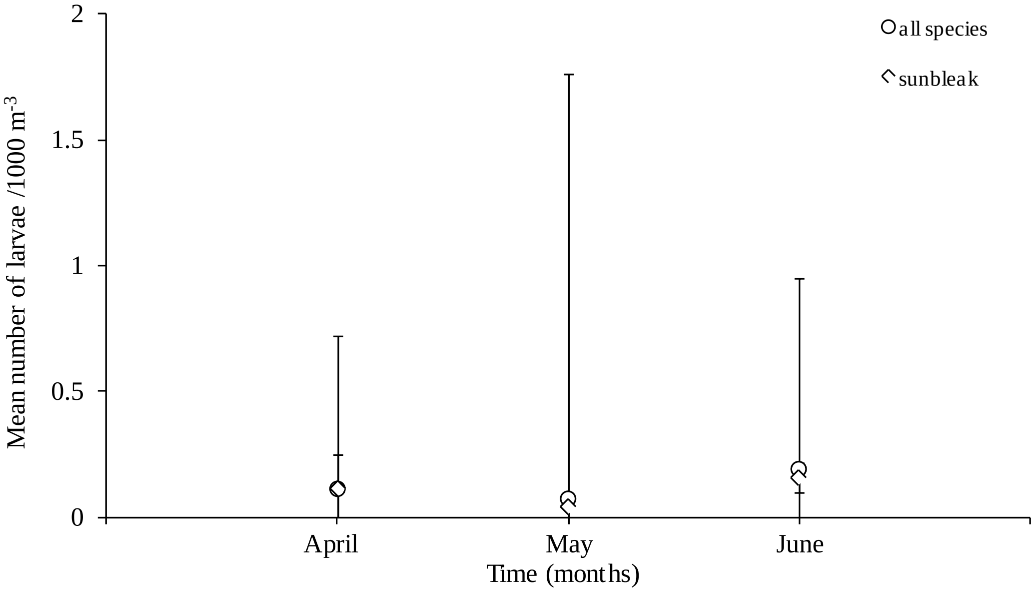

Figure 4.7: Mean densities 1000 m^{-3} and standard error bars of sunbleak and all adult fish captured in drift nets at Stoneham Lake Fishery during 2005.

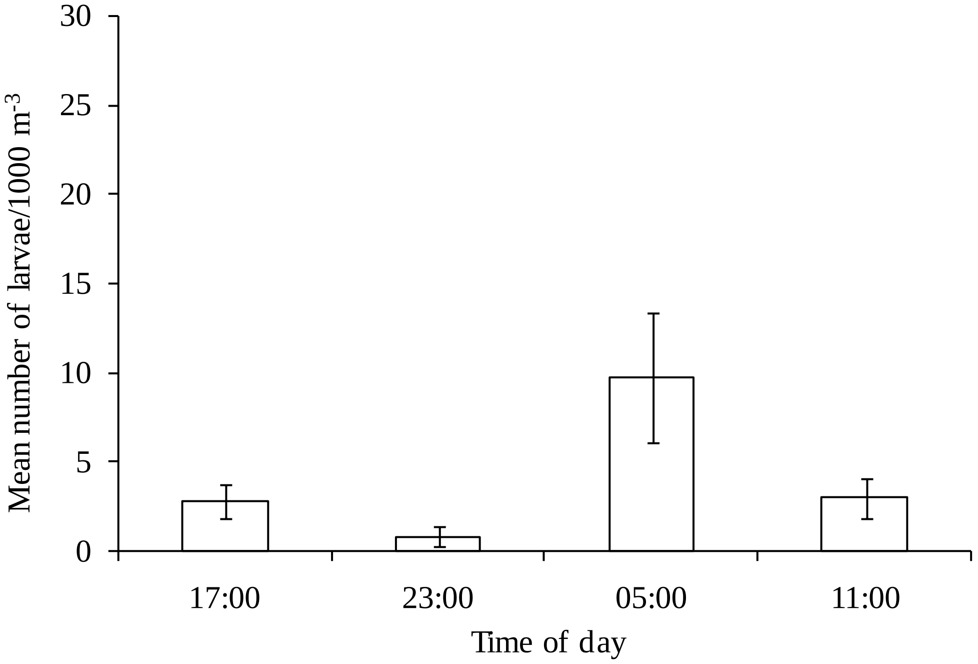

Figure 4.8: Mean drift densities 1000 m^{-3} and standard error bars for larval topmouth gudgeon captured during intensive 24 hour drift sampling at Crampmoor Fishery during May 2004.

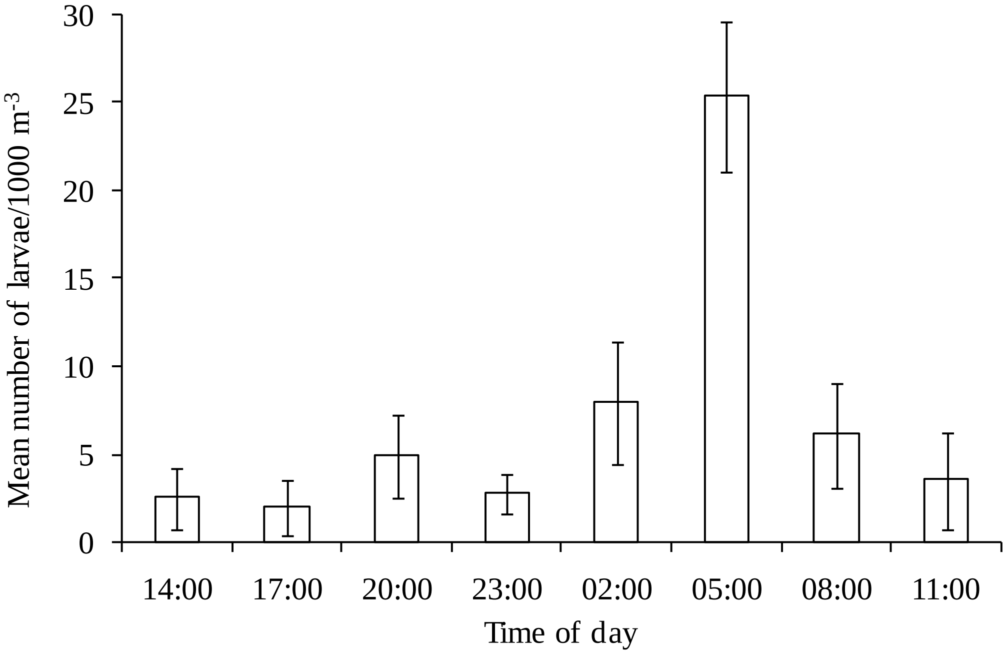

Figure 4.9: Mean drift densities 1000 m^{-3} and standard error bars for larval topmouth gudgeon captured during intensive 24 hour drift sampling at Crampmoor Fishery during May 2005.

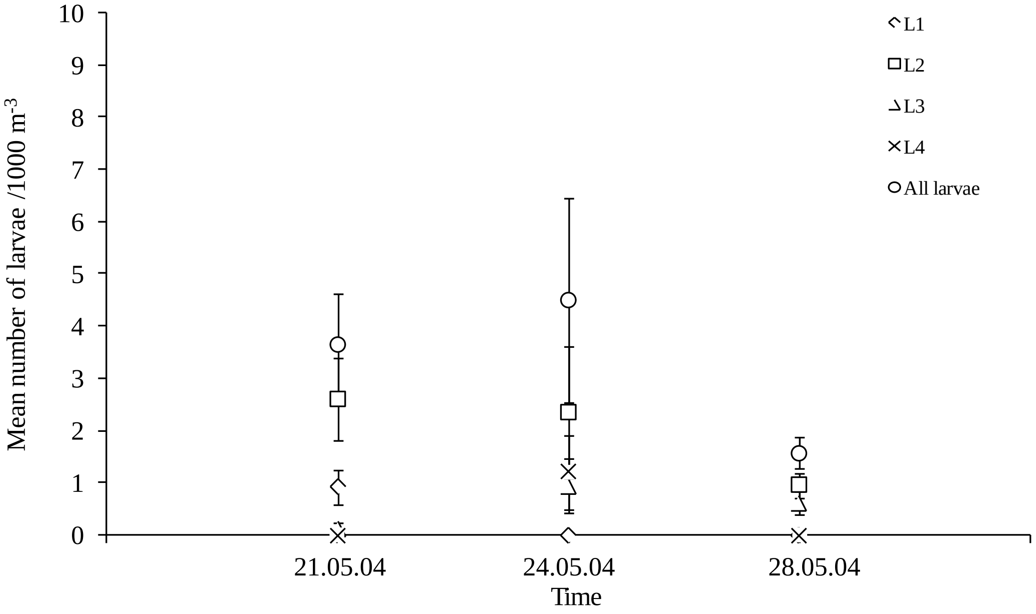

Figure 4.10: Mean larval topmouth gudgeon drift densities 1000 m^{-3} and standard error bars during 2004 at Crampmoor Fishery. Samples were captured in six drift nets over six 24 hr intervals (samples taken every 6 hrs with nets set at 11:00 hr).

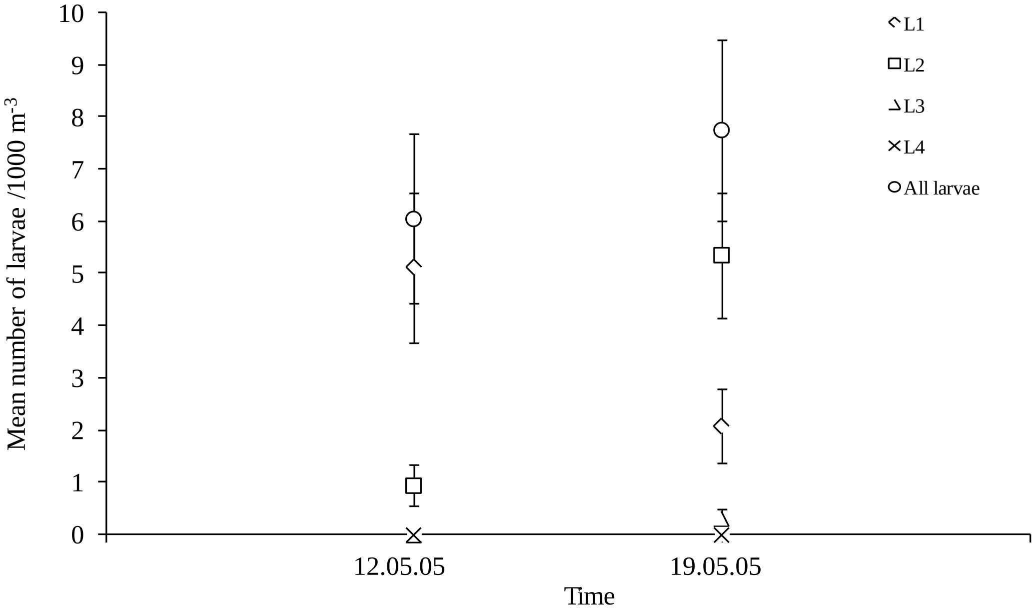

Figure 4.11: Mean larval topmouth gudgeon drift densities 1000 m^{-3} and standard error bars during 2005 at Crampmoor Fishery. Samples were captured in six drift nets over six 24 hr intervals (samples taken every 6 hrs with nets set at 11:00 hr).

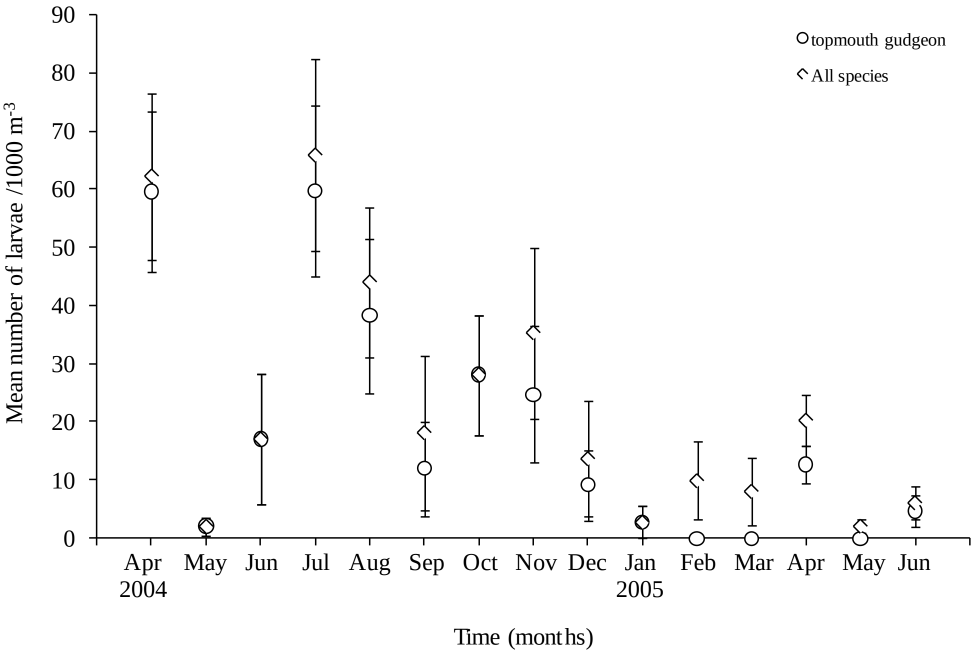

Figure 4.12: Mean densities 1000 m^{-3} and standard error bars of all adult fish captured at Crampmoor Fishery. Samples were captured during 24 hr sampling between April 2004 and June 2005.

4.3.2 Dispersal within the recipient water body

No sunbleak were observed in Caundle Brook, into which Revels Fishery discharges (Table 4.2). In Monks Brook, only 2 sunbleak were captured within a 2.1 km stretch downstream of the Stoneham Lakes. Meso-scale habitat character in Monks Brook did not differ significantly between random surveys (Kruskal-Wallis $H = 73.61$; $P = 0.760$).

Surveys in Tadburn Lake stream revealed 11 species of fish downstream of the fishery. These include non-native topmouth gudgeon, golden orfe and carp. In the 4 km stretch of Tadburn Lake stream sampled downstream of Crampmoor Fishery, topmouth gudgeon was confirmed in the upper 2.1 km section. The distribution of topmouth gudgeon in the catchment was limited and decreased downstream (Figure 4.13). Topmouth gudgeon occurrence was significantly correlated with distance from the fishery ($n = 20$; $r = 0.836$; $P \leq 0.01$). Other species significantly correlated with distance from the fishery were chub ($n = 20$; $r = 0.611$; $P \leq 0.01$) and three-spined stickleback ($n=20$; $r = 0.75$; $P \leq 0.01$). A significant inverse correlation to the distance from the fishery was observed in brown trout (n=20; r = -0.436; $P \leq 0.05$). There were no significant differences in habitat variables measured between random transects in either of the streams surveyed ($P > 0.5$) (Table 4.3, Table 4.4, Table 4.5).

During random electro-fishing surveys of 2003, no topmouth gudgeon were confirmed more than 4 km downstream of the Crampmoor Fishery. However, drift netting in April 2005 at 5.5 km below the fishery revealed individual adults moving further downstream towards the entrance into the online River Test. As there were no differences, either between periods of day (Kruskal-Wallis $H = 0.48$, $P = 0.488$) or between nets (Kruskal-Wallis $H = 2.47$, $P = 0.781$), all data were combined for each species (Figure 4.14). Based on information collected by the Environment Agency, three topmouth gudgeon were captured in a smolt trap in April 2005, in the River Test, 9.5 km downstream of the fishery (Environment Agency, unpubl. data), confirming that topmouth gudgeon had dispersed in the river. Owing to the absence of another known population of topmouth gudgeon online with the River Test, it is believed that these specimens originated from Crampmoor Fishery.

For details on the CPUE (per hr) of fish captured during random electro-fishing surveys downstream of the respective fisheries in Caundle Brook, Monks Brook and Tadburn Lake stream refer to Appendix D.

Table 4.2: Proportion of the specimens, mean and standard error (S.E.) of CPUE in %, mean and standard error of CPUE (per hour) and the mean and standard error (S.E.) of fork length (FL) in mm from random surveys downstream of three fishery facilities in England. See Appendix D for details on fish capture during random electro-fishing surveys. —, fish not captured.

	Caundle Brook						Monks Brook						Tadburn Lake stream					
Species	Mean CPUE (%)	S.E.	Mean CPUE (hour)	S.E.	Mean FL	S.E.	Mean CPUE (%)	S.E.	Mean CPUE (hour)	S.E.	Mean FL	S.E.	Mean CPUE (%)	S.E.	Mean CPUE (hour)	S.E.	Mean FL	S.E.
C. gobio	72.817	10.539	4.348	0.960	44.9	0.7	35.539	9.455	1.742	0.496	47.0	0.8	70.249	3.478	2.776	0.542	43.7	0.3
L. cephalus	0.037	0.037	0.003	0.003	104.0	0	1.061	0.286	0.060	0.016	33.9	0.4	1.775	0.551	0.045	0.017	117.7	2.0
Lampetra spp.	—	—	—	—	—	—	0.229	0.095	0.014	0.005	134.0	5.1	3.823	0.949	0.113	0.028	124.5	2.5
P. phoxinus	17.857	9.073	1.487	0.810	43.6	1.2	52.952	8.594	3.252	0.744	39.3	0.7	0.114	0.114	0.002	0.002	71.0	0
G. aculeatus	5.507	1.658	0.458	0.153	32.5	1.7	0.673	0.430	0.038	0.019	24.9	2.1	7.078	2.339	0.255	0.111	28.7	0.5
B. barbatula	0.882	0.357	0.070	0.029	78.6	6.0	5.692	1.330	0.333	0.081	65.8	1.8	8.601	1.152	0.262	0.048	75.1	1.6
S. trutta	0.687	0.248	0.045	0.017	155.2	33.9	2.397	0.659	0.107	0.024	98.3	8.7	7.125	2.188	0.132	0.027	189.3	5.7
R. rutilus	0.294	0.204	0.025	0.017	48.6	4.3	0.231	0.121	0.009	0.004	76.0	45.0	0.057	0.057	0.001	0.001	78.0	0
A. anguilla	1.696	1.575	0.013	0.008	500.0	150.0	0.737	0.221	0.032	0.010	229.7	26.4	0.389	0.168	0.009	0.003	391.8	37.2
G. gobio	0.223	0.186	0.018	0.014	98.6	5.8	—	—	—	—	—	—	—	—	—	—	—	—
P. flesus	—	—	—	—	—	—	0.434	0.240	0.019	0.010	133.2	22.6	—	—	—	—	—	—
C. carpio	—	—	—	—	—	—	—	—	—	—	—	—	0.056	0.039	0.001	0.001	305.0	145.0
L. delineatus	—	—	—	—	—	—	0.054	0.037	0.004	0.003	47.3	0.3	—	—	—	—	—	—
P. parva	—	—	—	—	—	—	—	—	—	—	—	—	0.734	0.341	0.025	0.010	47.5	1.3

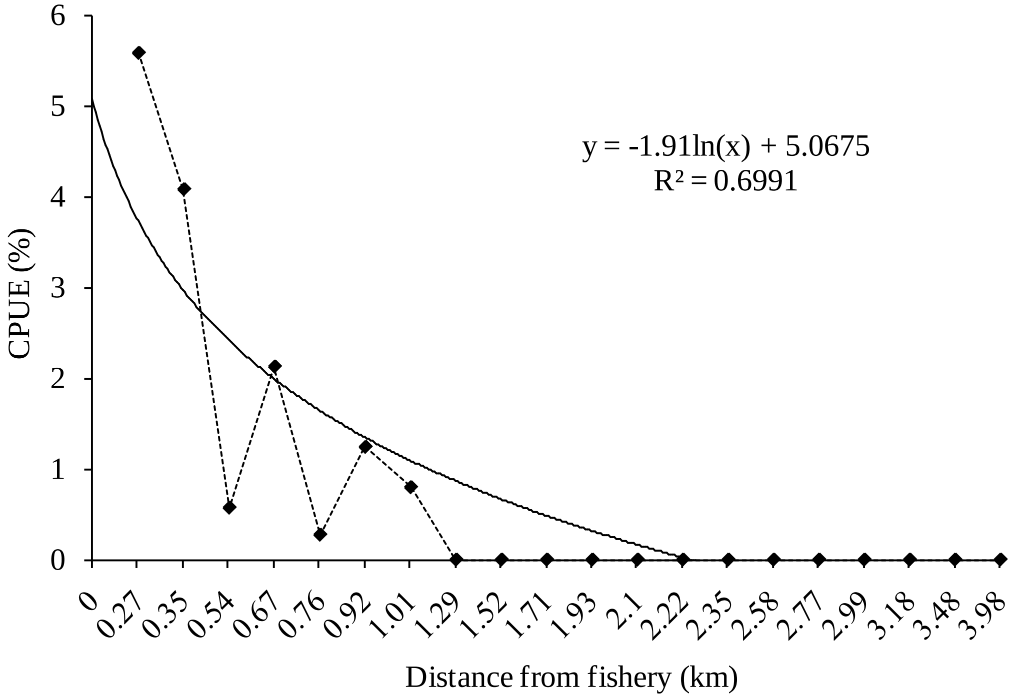

Figure 4.13: CPUE of topmouth gudgeon in Tadburn Lake stream with distance from Crampmoor Fishery (n = 20; $P \leq 0.01$).

Table 4.3: Meso-scale habitat observed during 15 random electro-fishing surveys in Monks Brook, Hampshire: Distance, distance from Stoneham Lake outflow (km); Width (cm); Dep, water depth (cm); SVe, per cent submerged vegetation (%); OhV, per cent overhanging cover (%); Lig, per cent ligneous debris (%);%Sa, per cent sand; %Gr, per cent gravel; %Pe, per cent pebbles; %Co, per cent cobbles; Vel, water velocity [1: zero water velocity; 2: weak velocity (> 0 but < 5 cm s^{-1}); 3) moderate velocity (5 – 10 cm s^{-1})].

Distance (km)	Width (cm)	Dep (cm)	%Sa	%Gr	%Pe	%Co	Vel	SVe (%)	Lig (%)	OhV (%)
0.08	250	25	0	0	100	0	2	5	5	10
0.17	270	25	0	0	100	0	2	5	5	15
0.21	310	30	0	0	100	0	2	10	5	20
0.39	250	25	0	50	50	0	2	10	5	50
0.48	450	18	5	10	5	80	2	0	10	90
0.6	250	35	10	45	45	0	2	0	5	90
0.72	200	30	5	10	85	0	2	10	5	90
0.87	250	35	10	40	50	0	2	5	5	50
0.95	320	45	5	45	50	0	2	5	5	50
1.17	300	40	0	40	60	0	2	5	5	80
1.24	350	45	0	40	50	10	2	15	5	50
1.49	300	40	0	50	50	0	2	5	5	50
1.71	400	50	0	20	60	20	2	10	5	80
1.93	300	45	0	20	70	10	3	5	5	50
2.18	310	45	0	10	70	20	3	5	5	20

Table 4.4: Meso-scale habitat observed during 20 random electro-fishing surveys in Tadburn Lake stream, Hampshire: Distance, distance from Crampmoor Fishery (km); width (cm); Dep, water depth (cm); SVe, per cent submerged vegetation (%); OhV, per cent overhanging cover (%); Lig, per cent ligneous debris (%); %Si, per cent silt; %Sa, per cent sand; %Gr, per cent gravel; %Pe, per cent pebbles; %Co, per cent cobbles; Vel, water velocity [1: zero water velocity; 2: weak velocity (> 0 but < 5 cm s^{-1}); 3) moderate velocity (5 – 10 cm s^{-1})].

Distance (km)	Width (cm)	Dep (cm)	%Si	%Sa	%Gr	%Pe	%Co	Vel	SVe (%)	Lig (%)	OhV (%)
0.27	95	20	10	50	30	10	0	2	10	30	75
0.35	105	15	5	15	70	10	0	2	0	20	70
0.54	90	20	5	10	80	5	0	3	5	30	95
0.67	125	15	0	15	80	5	0	2	10	5	80
0.76	120	15	0	20	70	10	0	2	5	5	80
0.92	100	25	0	20	70	10	0	2	5	5	50
1.01	150	35	0	10	80	10	0	2	10	10	50
1.29	135	30	0	20	70	10	0	2	10	5	70
1.52	140	25	0	0	50	50	0	2	5	5	50
1.71	130	35	0	0	0	100	0	3	0	5	95
1.93	125	30	0	40	50	10	0	2	5	5	80
2.1	160	45	0	30	60	10	0	2	5	5	80
2.22	190	35	0	10	50	40	0	2	5	5	80
2.35	250	25	0	0	30	70	0	2	15	5	30
2.58	140	20	0	0	40	60	0	2	10	5	50
2.77	250	40	0	10	40	50	0	2	5	5	85
2.99	290	55	0	10	30	60	0	2	5	5	85
3.18	310	50	0	0	20	80	0	3	15	5	30
3.48	280	55	0	0	10	90	0	3	15	5	40
3.98	320	45	0	0	0	100	0	3	15	5	50

Table 4.5: Meso-scale habitat observed during 9 random electro-fishing surveys in Caundle Brook, Dorset: Distance, distance from Revels Fishery (km); width (cm); Dep, water depth (cm); SVe, per cent submerged vegetation (%); OhV, per cent overhanging cover (%); Lig, per cent ligneous debris (%); %Si, per cent silt; %Sa, per cent sand; %Gr, per cent gravel; %Pe, per cent pebbles; %Co, per cent cobbles; Vel, water velocity [1: zero water velocity; 2: weak velocity (> 0 but < 5 cm s^{-1}); 3) moderate velocity (5 – 10 cm s^{-1})].

Distance (km)	Width (cm)	Dep (cm)	%Si	%Sa	%Gr	%Pe	%Co	Vel	SVe (%)	Lig (%)	OhV (%)
0.39	35	30	0	5	50	40	5	2	5	5	10
3.38	35	35	0	5	10	80	5	2	5	5	10
3.44	40	10	0	20	30	50	0	2	5	5	10
3.59	350	100	0	5	40	40	10	2	5	10	10
4.46	350	90	0	20	60	10	10	2	10	40	10
8.17	300	90	0	5	40	50	5	3	10	5	20
9.96	400	95	0	5	30	60	5	3	10	5	10
11.46	550	110	0	5	20	70	5	3	5	5	5
13.29	600	120	0	5	20	70	5	3	10	5	5

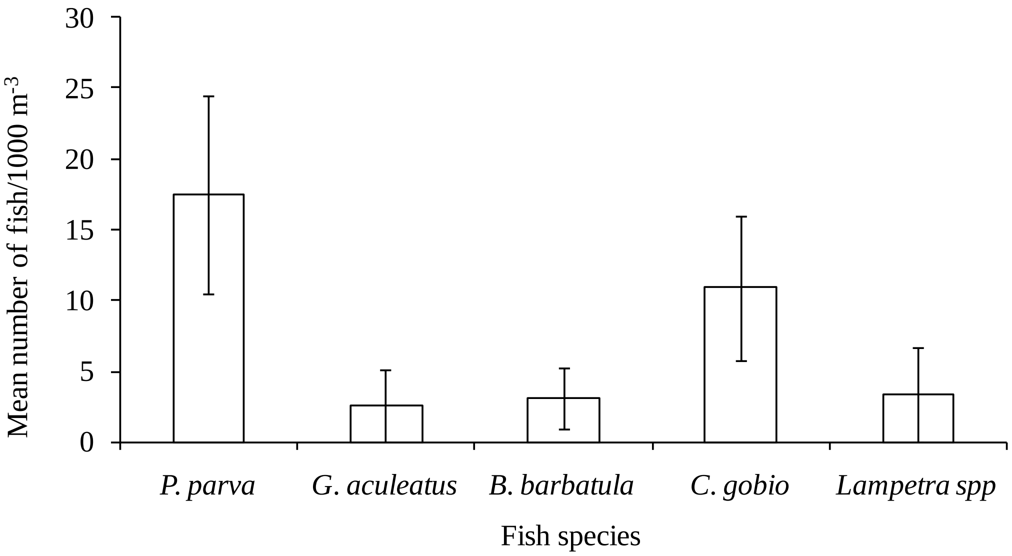

Figure 4.14: Mean numbers and standard error of adult fish 1000 m^{-3} captured in six drift nets during two 24-hour sampling intervals at 5.5 km downstream of Crampmoor Fishery in Tadburn Lake stream during April 2005.

4.4 Discussion

The drift densities observed at the three fisheries were much lower than natural drift densities observed in studies on fish drift in large European rivers (Reichard *et al.*, 2002b). One of lowest drift densities published were found at the River Lee, England, where overall means did not exceed 10 fish larvae 1000 m^{-3} (Copp *et al.*, 2002b). However, comparison with other data is difficult as the fisheries that were examined in this chapter represent comparably small water bodies, which are online with small streams or brooks. In light of this, it is believed that the drift densities can be considered as relatively high particularly from Crampmoor Fishery where overall mean drift was 3 ± 1 and 7 ± 2 larval topmouth gudgeon 1000 m^{-3} in 2004 and 2005 respectively. Maximum drift densities reached 40 and 52 larval topmouth gudgeon 1000 m^{-3} at this fishery in 2004 and 2005 respectively. At Stoneham Lakes Fishery, sunbleak drifted with a mean density of 0.4 ± 0.2 and 0.6 ± 0.4 larvae 1000 m^{-3} in 2004 and 2005 respectively, while maximum values reached 9 and 10 larvae 1000 m^{-3}.

Larval downstream movement *via* drift is of particular ecological importance for initial distribution of non-native species and may be driven by the density of the source population (Reichard *et al.*, 2004), particularly for topmouth gudgeon (Chapter 3). High drift density represents strong propagule pressure on the receiving Tadburn Lake stream, which may promote topmouth gudgeon invasion success. However, a system under pressure from a new species may provide resistance against such invasion, for example in form of adverse environmental conditions or strong predation pressure by piscivorous predators (Elton, 1958; Robinson and Wellborn, 1988). Such assumption was initially made when only limited dispersal of topmouth gudgeon below the fishery outflow in Tadburn Lake stream was observed in 2003 (Figure 4.13). An insight into whether Tadburn Lake stream may be able to overcome the strong propagule pressure by mediating invasion resistance *via* native predators is presented in Chapter 7.

Despite dense populations in the Stoneham Lakes (see Chapter 3), sunbleak drift densities were low. Here, drift may have been related to the habitat unsuitability at locations where water would exit either of the lakes. These areas are anthropogenically graduated, relatively deep (>1.5 m) and provide little shelter in form of submerged or overhanging vegetation, characteristics that sunbleak appear to be associated with during early life (Pinder *et al.*, 2005a) (see also Chapter 6). However, dispersal of sunbleak *via* drift from fisheries was higher than in the native species, which was likely related to high densities of sunbleak in the lakes while young-of-the-year of native species were low in numbers.

In both species, drift densities were greatest during the dark, between 23:00 hr and 5:00 hr. Such diurnal drift patterns are common in freshwater fish (Copp *et al.*, 2002b; Reichard *et al.*, 2004; Zitek *et al.*, 2004a), with highest drift densities reported for some cyprinid species between 22:00 and 04:00 h in European rivers. Drift patterns of this type may be associated with larval photosensitivity (Reichard *et al.*, 2002a) or predator avoidance (Araujo-Lima and Oliveira, 1998), while drift is generally related with flow velocity and thus the water volume passing through the net (Copp *et al.*, 2002b).

In topmouth gudgeon, the highest proportions drifting were larval stage 1 (L1) during May 2004, and stages 1 (L1) and 2 (L2) during May 2005. In sunbleak, larval stages 2 (L2) and 3 (L3) dominated drift during May 2004 and 2005. During June of both years, sunbleak at larval stage 5 contributed the greatest proportion to the total drift. In both species, L2 represents the onset of the anterior swimbladder and air is first evident at L3 (Pinder and Gozlan, 2004; Appendix C). Drift is driven by species-specific ontogeny and the differences in reproductive cycles that exist between species and potentially between years (Zitek *et al.*, 2004a; Zitek *et al.*, 2004b). Fishes undergo a series of ontogenetic changes during their early life, which are linked to their performance-related capabilities (Balon, 1975; Balon, 1990). A change in body size during ontogeny is therefore associated with a change in the maximum sustainable water velocity (Flore and Keckeis, 1998). The differential sustainable water velocity will subsequently determine the propensity of fish at different developmental stages to drift.

Generally, some movement of fish at the different life stages was observed at all three fisheries. Larval drift may have been passive initially but in part active-passive in older larvae displaying increased swimming capability (Pinder, 2001). Adult fish captured in drift samples were probably moving actively and possibly active-passively during increased velocities. However, to confirm this, studies on the swimming behaviour under differential current velocities in sunbleak and topmouth gudgeon would be required.

Generally, adult fish movement from fisheries may be driven by foraging behaviour and food resource availability (Fredrich *et al.*, 2003; Winter and Fredrich, 2003; Takashi Asaeda and Manatunge, 2005). Other reasons for adult fish movements may be related to spawning, natural dispersal and competition and/or predation avoidance (Fredrich *et al.*, 2003). High densities of topmouth gudgeon moving from the fishery will increase propagule pressure from the fishery outfall on Tadburn Lake stream. Here passive dispersal *via* larval drift from the fishery is coupled with potentially active movement of older individuals. Downstream movements of non-native fishes from source populations, either as active migrations or as passive drift during early life, would appear to be an important dispersal mechanism to facilitate invasion success.

In 2003 and 2004, numerous topmouth gudgeon were observed in Tadburn Lake stream as far as 5.5 km downstream of the source population. No sunbleak were found downstream of Revels Fishery, and two individuals were observed in Monks Brook. The habitat available within the streams may be suitable for utilisation by both, sunbleak and topmouth gudgeon, (Arnold, 1990; Arnold and Längert, 1995) and their establishment is not expected to have been impeded by the prevalent environmental conditions. For example, water velocity in Tadburn Lake stream was observed to be mostly within the preferred range of topmouth gudgeon (< 7 cm s^{-1}) as observed under experimental conditions (Asaeda *et al.*, 2005; Sunardi *et al.*, 2005).

After introduction into a new environment, the mechanisms with which non-native freshwater fish may potentially disperse from source populations are generally expected to be comparable to natural movements of fish. The number of individuals taking part in the downstream movement of non-native freshwater fish from a source population may be closely related to fish density within the source population (Reichard *et al.*, 2004). It would subsequently be expected, that if reproduction takes place within a source population, the number of individuals moving downstream may be increased. This number is further altered if reproductive effort of the respective species is high, which applies to sunbleak and topmouth gudgeon (see Chapter 3).

The extent and character of fish movements during all life stages and the success of a non-native species is dependent on initial downstream movements during early life into fluvial systems such as river catchments (Pavlov, 1994). Drift is crucial for colonization of new habitats and is important as a regular source of introduction into the downstream catchment and may promote the success of establishment. Such success may alter the potential impacts on native fish species. Tadburn Lake Stream and Monks Brook flow into the Rivers Test and Itchen, respectively. These rivers are of conservation value due to their high densities of Atlantic salmon and brown trout. Both rivers are designated as ‘Sites of Special Scientific Interest’ (SSSI) and ‘Special Areas of Conservation’ (SAC) (Hampshire Biodiversity Partnership, 2003; Halcrow Group Ltd, 2007; Southern Water, 2007). Salmonids in the River Test may initially benefit from topmouth gudgeon as an additional food source (see also Chapter 7), or they may be adversely affected by the recently discovered micro-parasite RLA associated with topmouth gudgeon (Gozlan *et al.*, 2005). Further, topmouth gudgeon has potential to prey on eggs and larvae of other fish species (Stein and Herl, 1986; Xie *et al.*, 2000), and as a facultative parasite on other fishes (Trombitskiy and Kakhovskiy, 1987; Libosvárský *et al.*, 1990). The drift and dispersal from source populations provides access for non-native species into the wild and increases the risk of exposure to native fish species and vice versa. In this way, the risk that a species like topmouth gudgeon, which has previously been found to have negative impacts on other fish species, may display similar behaviour (predation, facultative parasitism) in the new environment, and may be affecting native species could be increased (Copp *et al.*, 2005b; Copp *et al.*, 2007). The risk of native species exposed to the RLA is also increased (Gozlan *et al.*, 2005). Furthermore, the risk of RLA potentially entering the River Test *via* topmouth gudgeon and Tadburn Lake stream from the source population was increased in various interlinking steps: 1) introduction of topmouth gudgeon into an online fishery, 2) fishery outlet was not equipped with a permanent ‘outfall prevention measure’, 3) fishery water draining through outlet into the stream, 4) high reproductive effort of topmouth gudgeon in the fishery (see also Chapter 3), 5) larval drift, and 6) active and/or active-passive movement of adult topmouth gudgeon downstream.

Many studies have investigated larval drift of fish in their natural environments (Pavlov, 1994; Jurajda, 1998; Copp *et al.*, 2002b; Reichard, 2002; Reichard *et al.*, 2002b; Reichard *et al.*, 2002c; Reichard *et al.*, 2004; Reichard and Jurajda, 2007), but specific studies quantifying non-native fish drift are few. Though in some studies, non-native fish sporadically occur in the drift, the importance of this is not actually discussed (Reichard *et al.*, 2002b). This is surprising as such knowledge would enable conclusions on whether propagule pressure is an important component of the invasion process. It is clear that the potential for dispersal and propagule pressure are important elements of risk assessments of non-native freshwater fishes (Copp *et al.*, 2005b; 2005c).

When applying propagule pressure as a measure to freshwater fish invasions that are related to live fish movements, it is important to consider the following possible scenarios:

1) Propagule pressure from outside the region: A non-native fish species can be introduced as a contaminant of live fish movements into new environments. One or more individuals of a non-native species may be introduced on a single occasion or on several separate occasions and would thus be creating propagule pressure.
2) Propagule pressure within the region: At a location (e.g. online aquaculture facility), that has received one or more individuals of a particular non-native fish species, and this species has successfully reproduced and formed a dense population. A potential for escapism from this source population (i.e. providing new recruits through reproduction and outlet into the wild) will create propagule pressure within the region.

The results show that great propagule pressure is created by topmouth gudgeon dispersing from a source population, while limited pressure is being created by sunbleak escaping from Stoneham Lakes and Revels Fishery. This highlights the importance of preventing outfall from source populations containing non-native fish.

During the study, few native species occurred in the larval drift. This may be related to differences in the timing of the spawning season between species and possibly to the conditions provided by the fisheries. While it is unlikely that fish in the investigated fisheries actively avoid drifting, in some studies it has been reported that some species occur less often in drift than would be expected based on their abundance in the fish assemblage (Kennedy and Vinyard, 1997; Reichard *et al.*, 2002b) and are assumed to avoid drift. As an example, chub spent time in low flow patches to avoid drifting in the River Morava (Reichard *et al.*, 2002b). Other species avoiding drift in the River Morava include barbel, nase *Chondrostoma nasus* L., dace and perch.

At Crampmoor Fishery, management entails the draining of water from holding ponds after retaining the fish species of commercial interest (e.g. golden orfe). Eventually, the water of the fishery ponds (see Figure 2.7 in Chapter 2) enters into Tadburn Lake stream through the fishery’s outlet. During pond draining, a large meshed net (> 1 cm) is placed between the entrance from the long draining pond into the smaller holding pond to capture any fish escaping. However, due to the large mesh size of the net it is likely for small topmouth gudgeon and larvae to pass through. They would subsequently have access to the online stream *via* the unscreened outlet. This is reflected in the data collected at this site. In contrast, management at Revels Fishery and Stoneham Lake Fishery (see Figure 2.5 and Figure 2.6 for a schematic overview of the fisheries) does not normally entail pond draining (K. Beyer, pers. obs.). Here, fishery management includes the cutting of bankside vegetation causing an amount of floating materials, which may be suitable spawning material for sunbleak (K. Beyer, pers. obs.). This vegetation may float towards the fishery’s outlet and subsequently access the online brooks. At Revels Fishery, 116 sunbleak eggs attached to floating vegetation were observed and captured in a drift net that was placed at the outlet into Caundle Brook. Though, eggs were not observed in drift nets at Stoneham Lakes, vegetation management takes place here annually in April/May (K. Beyer, pers. obs.). This coincides with the spawning season of sunbleak so it is paramount that not only larval and adult fish movement through the outlet is prevented but also floating vegetation should not be able to pass through. It is recommended that a permanent sustainable filtering system to prevent any outfall should be applied at all three fisheries investigated. Such a system could for example comprise a gravel filter, through which the water must pass. However, a filtering system should serve not only the purpose to prevent fish and vegetation passing through. Ideally, it should also be combined with a mechanism that kills any possible parasites (e.g. non-native parasites with free-living life stages) and disease (e.g. transferred *via* water) (see also Chapter 5).

Drift should be an integrated aspect of management, regulation and monitoring of aquaculture facilities. With regard to spatial dynamics and the health of native populations in the wild, the movement of adults and larval drift of non-native species are factors shaping the structure and functioning of self-sustaining fish populations and have to be monitored using active surveillance techniques, particularly at places where new introductions are likely to occur, e.g. water bodies likely to receive live fish stock. Any potential recipient water body requires measures to be put into place: 1) to prevent the introduction of an unwanted species, 2) for fish introduction audit (e.g. species identification and sorting) of live fish before stocking, 3) if the water body is online, measures to prevent outfall of any developmental stage of fish (eggs, larvae, adults) and potential spawning substrate (eggs can attach to those) into those online water bodies (e.g. permanent gravel filter) and 4) if the water body is used by the angling community, ensure accidental transfer (e.g. *via* the angler's holding nets) to a different water body is prevented (e.g. education).

It is important to remember that any outfall of topmouth gudgeon and sunbleak from such source populations represents the movement of two non-native fish species, which are regulated by the Import of Live Fish Act (ILFA). The problem that arises from this issue is that we are now dealing with the (semi-)natural spread of sunbleak and topmouth gudgeon, which is nonetheless facilitated by anthropogenic measures (e.g. outlets from fisheries into the wild). This highlights the importance for studies on the drift and dispersal of non-native fish species to combine both, anthropogenic and natural mechanisms of dispersal. These two aspects are inevitably interlinked, particularly in non-native fish species which are associated with live fish movements. The measures controlling the movement of fish need to be strictly applied to all vectors for dispersal, be they large scale (e.g. aquaculture trade) or small scale (e.g. outlets of fisheries containing non-native species).

4.5 Chapter summary

Larval drift of sunbleak and topmouth gudgeon was observed from three fisheries taking place mainly during the hours of darkness. Topmouth gudgeon drifted at greater densities than sunbleak. Movement of adult specimens was also observed during the spawning season in both species as well as throughout the year in topmouth gudgeon (this was not tested in sunbleak). The study demonstrates that still waters connected to river catchments play an important role in determining the risk of non-native fish dispersal into water courses, and the rate of escape into online water bodies such as streams and brooks is regulated by the type of outflow connection. Such online water bodies act as ‘drip feeds’, with the type of outlet influencing the propagule pressure of non-native fishes on receiving streams.

5. The parasite fauna of sunbleak and topmouth gudgeon[8]

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[8] Data from part of this study have been published as: Beyer, K., Kochanowska, D., Longshaw, M., Feist, S. W. & Gozlan, R. E. (2005). A potential role for invasive sunbleak in the further dissemination of a non-native parasite. *Journal of Fish Biology* 67, 1730-1733; and were presented at the 14th ICAIS Conference in May, 2006 as: Beyer, K. & Gozlan, R. E. 'Fish Alien Parasites'.

5.1 Introduction

The dispersal of non-native pathogens and parasites *via* both native and non-native fish hosts represents a threat to indigenous fishes (Kennedy, 1976; Fryer, 1982a; Hoffman and Schubert, 1984; Boxshall and Frear, 1990; Kennedy, 1994). Such organisms may harm, and cause decline in, native fishes that have not co-evolved with them. During host-parasite co-evolution, concomitant immunity may exist in the host that is continuously infected (Brown and Grenfell, 2001). When introduced to new areas, parasites can often adapt quickly to new hosts with negative consequences for the host. For example, the eel parasite *A. crassus*, originally from Japan and harmless to its native host the Japanese eel is highly pathogenic to the European eel (Kennedy and Fitch, 1990a; Kirk, 2003). Numerous examples of the impact of pathogen and parasite introductions have been documented worldwide (Johnsen and Jensen, 1991; Blanc, 2001a; Gozlan *et al.*, 2006). In England, a variety of pathogens, such as the yeast *Debaryomyces hansenii* and furunculosis *Aeromonas salmonicida,* have been imported *via* the aquaculture trade, some of which have subsequently caused disease and increased mortality in salmonids and other fish species (Austin and Robertson, 1993a; b; Gibson, 1993; Mitchell, 2001; Irianto and Austin, 2002). In England and Wales, the Environment Agency has listed 8 non-native parasite species as ‘Category II’ — i.e. ‘those parasites novel to England and Wales and/or those that may harbour a significant disease potential when introduced to waters where they do not already exist’ (Environment Agency, 1999; 2007a; Institute of Fisheries Management, 2007). Two parasite species, *Paraergasilus longidigitus* (copepod) and *Atractolytocestus huronensis* (Lytocestid tapeworm), were removed from this list in 2007. This decision was made by the Environment Agency’s internal ‘Category II Review Group’, because neither *P. longidigitus* nor *A. huronensis* was deemed to pose a threat to wild fish populations.

Through high selection pressure, parasites have evolved into manipulating their hosts to ensure the completion of their life cycle (Lafferty and Morris, 1996; Poulin, 2000). Parasite infections may modify host behaviour, its microhabitat, and subsequently increase its vulnerability to predation through disorientation and reduced stamina, that alter host response capabilities (Crowden and Broom, 1980; Poulin and Fitzgerald, 1989; Belk and Lydeard, 1994). An infected individual may be forced to divert a large part of their energy into their immune system to counteract the infection (Wedekind, 1992). The type of parasite and the level of infection, driven by prevalent environmental conditions, will determine the amount of energy expended by the host in battling the infection.

Active phenotype matching behaviour in fish shoals is thought to be an adaptation to prevent predation by visual predators, which are most likely to attack the ‘odd one out’ (Landeau and Terborgh, 1986; Theodorakis, 1989; Ward and Krause, 2001). Parasitised fish are more likely to occupy peripheral shoal positions (sometimes nearer the water surface), have greater distance to neighbouring fish than un-parasitised fish and be excluded from the shoal by uninfected fish which may demonstrate a preference for uninfected shoals (Dugatkin *et al.*, 1994; Barber and Huntingford, 1996; Krause and Godin, 1996; Barber *et al.*, 1998; Ward *et al.*, 2002). Parasites with a phenotypic effect on their hosts may also cause their hosts to be avoided by conspecifics during mating (Rosenqvist and Johansson, 1995; Barber, 2002).

Previous studies have focussed on the effects of parasites on natural fish populations in native habitats (Loot *et al.*, 2004). But invasions provide great opportunities to investigate how parasites may affect and regulate host populations (Torchin *et al.*, 2003). An interesting study on the impact of an acanthocephalan parasite on amphipod hosts, which are normally photophobic, showed no alteration in infected invaders but caused a change in native resident hosts towards photophily (Bauer *et al.*, 2000). Despite numerous known impacts of introduced pathogens on native fishes, there is a lack of information on the role of introduced species as hosts for novel parasites and their implications for fish biodiversity (Gozlan *et al.*, 2006).

Elsewhere, introduced hosts have been found to be less parasitized than the same species in its native range (Torchin *et al.*, 2003), and less parasitized than native species in the novel environment (Shea and Chesson, 2002; Ondračková *et al.*, 2005). In their study, Torchin *et al.* (2003) concluded that there was no difference in the susceptibility of introduced versus native populations, but that instead parasites may simply be lost during the invasion process and host-specificity may limit their potential to adapt to new hosts. The hypothesis where the success of an introduced species could be associated with the partial loss of native parasite fauna has been supported by a study on the European shore crab *Carcinus maenas* (Torchin *et al.*, 2001), where uninfected, introduced crab populations were significantly larger and had a greater biomass than native ones.

In their native European range, sunbleak have been found associated with a variety of metazoan parasites, such as monogeneans, digeneans, acanthocephalans, cestodes and the branchiuran *Argulus* sp. (Arnold, 1990; Arnold and Längert, 1995; Moravec, 2001). In its native Asian range (Japan and Korea), topmouth gudgeon hosts various species of copepods and digeneans (Harada, 1930; Kim *et al.*, 1979; Chai *et al.*, 1985; Kang *et al.*, 1985; Sohn, 1991; Aohagi *et al.*, 1992). Amongst these parasites, the digenean *Clinostomum complanatum* can also cause infections in humans (Yamashita, 1938; Hirai *et al.*, 1987; Yoshimura *et al.*, 1991). Amongst introduced continental European populations of topmouth gudgeon, nematodes, acanthocephalans, and monogeneans have been found (Bianco, 1988; Rosecchi *et al.*, 1993; Šimková *et al.*, 2004). Although topmouth gudgeon and sunbleak have been associated with various parasite species in their native and non-native range, no information on their parasite fauna in England was available at the outset of this study. The aim of this chapter was to determine the parasite fauna of sunbleak and topmouth gudgeon in England.

5.2 Material and methods

Sampling

The standard protocol used by CEFAS parasitologists, to carry out parasitological investigations such as for this study, requires the use of a sample of 30 fish and renders this sample size as being sufficient to detect whether a population carries a certain parasite or not (Fernando *et al.*, 1972). Therefore, a total of 30 live sunbleak each were collected on 1 July 2004 from Beeches Pond, Somerset (Site 1), using backpack electro fishing gear (Output: 50 – 100 Hz PDC with an operating current of 1 to 2 Amps) with a circular anode (20 cm diameter) deployed from a small inflatable dinghy, and on 30 June 2004 from Parchey Bridge, Kings-Sedgemoor Drain, Somerset (Site 2) and on 12 October 2003 from Shrubbery Lake, Hampshire (Site 3) by seine netting (see Chapter 2). When seine netting was carried out to obtain fish samples (Coles *et al.*, 1985; Hughes and Willis, 2000), the micro-mesh seine net used was 10 m long and 2 m deep with a mesh size of 1.5 mm. The net was deployed in an arc from the bank using an inflatable dinghy encircling an area of water. This was done as many times as was necessary to obtain 30 fish. In the case of electrofishing, the current was deployed until the required number of fish had been obtained. A total of 30 topmouth gudgeon each were collected from Tadburn Lake, Hampshire on 19 May 2003, using backpack electrofishing gear (Output as above) with a circular anode (20 cm diameter) and from Ratherheath Tarn, Cumbria on 11 August 2004 by seine netting (as described above). All fish captured were immediately transferred to a bucket of water before being transported to the CEFAS laboratory in Weymouth. Sampling effort (one sample per site) and timing (sampling dates) was driven by limitations in manpower and equipment availability. The sunbleak and topmouth undergoing parasitological investigation were of adult morphology. The individual fork lengths were not measured and the sex of fish was not recorded as this was not a requirement set out by the standard protocol used (Fernando *et al.*, 1972). This did, however, prevent measures of size and sex selectivity by parasites.

The fish were transported alive to the laboratory and immediately examined for external parasites. The fish were then killed with an overdose of benzocaine followed by severance of the spinal cord at the base of the skull. All external surfaces including the gills, skin and fins, as well as all internal organs and the body cavity, were examined for parasites under a stereo-microscope (Nikon SMZ-10a). Separately, liver, kidney and gall bladder were gently squashed between a glass slide and cover slip with the addition of a drop of distilled water, and examined by phase-contrast microscopy and differential contrast microscopy on a Nikon Eclipse E800 microscope, Nikon U.K. Ltd, Surrey, U.K. All parasites observed were removed from the host, enumerated and where possible, identified to species using identification keys (Bykhovskaya-Pavlovskaya *et al.*, 1964; Shulman, 1966; Blair, 1974; 1977; Fryer, 1982a; Khotenovsky, 1985; Brown *et al.*, 1986; Bauer, 1987; Chubb *et al.*, 1987; Lom and Dyková, 1992; Abdelhalim *et al.*, 1993; Alston *et al.*, 1993; Moravec, 1994; Environment Agency, 1999). Samples of parasites were fixed in 10 % formalin. Digital images of parasites were taken using the Lucia^{TM} image archiving system (Nikon U.K. Ltd, Kingston-upon-Thames, England).

Data analysis

Parasite prevalence was expressed as percentage (%) and was calculated as the total number of fish infected by one parasite species ($n_{\text{infected fish}}$) divided by the total number of fish sampled (n_{fish}) multiplied by 100 (Bush *et al.*, 1997):

$$\text{Prevalence (\%)} = (n_{\text{infected fish}} / n_{\text{fish}})*100$$

Mean intensity was calculated as the total number of parasites of any particular species found in infected hosts ($n_{\text{parasites in infected fish}}$), divided by the number of infected hosts ($n_{\text{infected fish}}$) (Bush *et al.*, 1997):

$$\text{Mean intensity} = n_{\text{parasites in infected fish}} / n_{\text{infected fish}}$$

Mean abundance was calculated as the total number of individuals of one parasite species ($n_{\text{parasites in all infected fish}}$) found divided by total number of fish sampled (n_{fish}) (Bush *et al.*, 1997):

$$\text{Mean abundance} = n_{\text{parasites in all infected fish}} / n_{\text{fish}}$$

The data were compiled into three data matrices comprising of 90 individual sunbleak-by-9 parasite taxa.

Correlation matrix principal components analysis (PCA) (Gauch, 1982) was applied to reveal patterns in the distribution and occurrence of parasites in sunbleak hosts between different sites. Ordination of parasite occurrence with 90 % inertia was based on uniform weighting. Prior to analysis, all data were converted to presence/absence matrices in order to facilitate comparison between quantitative parasite taxa and the semi-quantitative ones. All multivariate analysis was performed using the ADE (Analysis of Environmental Data) Software package (Thioulouse *et al.*, 1997).

To assess differences in quantitatively collected data between sites, Levene's test (Dytham, 1999) was used to determine the equality of variances for all variables and normality was examined using the Kolmogorov-Smirnov test (Zar, 1999). When data did not conform to the requirements of parametric analysis (homogeneity of variances, normal distribution), non-parametric Kruskal-Wallis test was performed to compare parasite abundance between sampling sites. Although this test is less powerful than a one-way ANOVA, it will decrease the probability of a Type I error (Fowler *et al.*, 1998). As the Kruskal-Wallis test does not provide a *post hoc* test to determine which group differs from which, Fisher's least significant difference (LSD) test was carried out (Fowler *et al.*, 1998). All uni-variate analyses were performed with Minitab 14 (Minitab, Inc., PA, USA).

The index of dispersion (ID) was calculated to assess the parasite distribution patterns amongst the host population (Elliott, 1977; Duerr *et al.*, 2003; Luque *et al.*, 2005):

$$ID = s^2 / \overline{x}$$

where s^2 is the variance and $\overline{x}$ is the mean. A dispersion index where ID < 1 indicates a regular distribution of the parasite amongst their host population, ID ≈ 1 denotes a random distribution and ID > 1 denotes an overdispersed (contagious) distribution (Fowler *et al.*, 1998). The significance of ID was tested using the *d* statistical test:

$$d = \sqrt{2\chi^2} - \sqrt{2\nu - 1}$$

where d is a normal variable with zero mean and unit standard deviation, χ^2 is the distribution and ν is the number of degrees of freedom. Values of d higher than 1.96 indicate an overdispersed (contagious or aggregated) distribution (Elliott, 1977).

The Berger-Parker index (D_{BP}) of dominance was calculated for each parasite infracommunity (all parasites found on each fish host form a parasite infracommunity), per individual fish where appropriate (Magurran, 1988), presents the proportional importance of the most dominant parasite species and is calculated as follows:

$$D_{BP} = N_{max}/N$$

where N_{max} is the number of individuals in the most abundant species and N is the number of all individuals. The index is expressed in the reciprocal form ($1/ D_{BP}$) so that increases in the index value describe a decrease in dominance or an increase in diversity.

5.3 Results

Investigations of the topmouth gudgeon populations did not reveal the presence of any macro-parasites. In contrast, eight different parasite taxa, including two non-native parasitic copepods, *Neoergasilus japonicus* (Harada, 1930) and *Ergasilus briani* (Markewitsch, 1932), and unidentified digenean metacercariae, were recorded in sunbleak (Table 5.1; Plate 5.1). The metacercariae were not identified to species as correct identification of most digenean metacercariae generally requires molecular tools (M. Longshaw, pers. comm.), and could not be completed in this study. Abundance of the different parasite taxa differed between sites, with *Diplostomum spathaceum* (Rudolphi, 1819) being most the abundant in Beeches Pond (site 1) and Kings-Sedgemoor Drain (site 2), while *N. japonicus* was most abundant in Shrubbery Lake (site 3).

The PCA ordination plot for the different parasites (components 1 and 2, representing *N. japonicus* and *E. briani* respectively), accounted for 42 % of the variation in the data (Figure 5.1), and revealed an overlap in the parasite occurrence of sunbleak from Somerset (sites 1 and 2). In contrast, the parasite fauna of sunbleak from Shrubbery Lake (site 3) appeared to be distinct. The principal parasites discriminating the sites from each other (longest vectors in the correlation circle) were *Diplostomum spathaceum* (Rudolphi, 1819), *Posthodiplostomum cuticola* (von Nordmann, 1832), *E. briani*, *Rhabdochona* sp. (Raillet, 1916) and *N. japonicus* (Figure 5.1). The strong vector for *D. spathaceum* most likely distinguishes site 3 from the other sites. Sites 1 and 2 may be discriminated from each other due to absence/presence of *P. cuticola*.

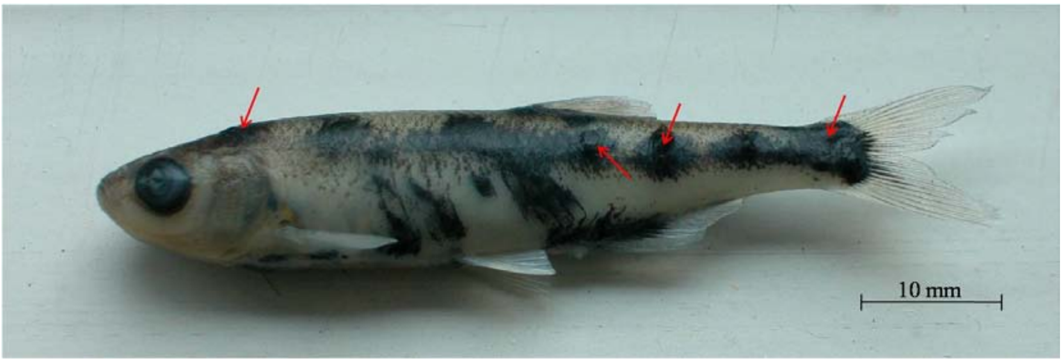
The parasites *Rhabdochona* sp and *Myxidium rhodei* (Léger, 1905) were not included in the calculation because they were too numerous to be counted individually. The remaining parasites displayed an aggregated pattern of distribution amongst their host population (Table 5.2) that is common in many parasite systems (Luque *et al.*, 2005). The Berger-Parker index ($1/D_{BP}$ ± S.E.) revealed values of 1.23 ± 0.7, 0.87 ± 0.04 and 1.77 ± 0.12 for sites 1, 2 and 3 respectively, describing the highest diversity and lowest dominance of a particular parasite species in sunbleak from site 3.

Table 5.1: Parasite fauna of sunbleak *L. delineatus* from three different sites (Site 1-Beeches Pond; Site 2 - Kings-Sedgemoor Drain; Site 3 – Shrubbery Lake). Ecological terminology follows (Bush *et al.*, 1997); n/a = items too numerous to be counted individually; — parasite taxa not observed. Significant differences between sites are indicated by *, $P \leq 0.01$).

	Parasite species	*Myxidium rhodei* (Myxozoa)	*Diplozoon cf. paradoxum* (Monogenea)	*Rhipidocotyle illense* (Digenea)	*Diplostomum spathaceum* (Digenea)	*Posthodiplostomum cuticola* (Digenea)	Unidentified digenean metacercariae	*Ergasilus briani* (Copepoda)	*Neoergasilus japonicus* (Copepoda)	*Rhabdochona sp.* (Nematoda)
	Site of Infection	Kidney	Gills	Muscle tissue	Eye lens	Skin	Gall bladder, skin	Gills	Skin, fins	Visceral cavity
Site 1	Prevalence (%)	—	3.33	6.67	90.00	—	—	33.33	—	—
	Mean abundance ± S.E.	—	0.03 ± 0.03	0.20 ± 0.17	2.3 ± 0.37*	—	—	0.8 ± 0.24*	—	—
	Mean intensity ± S.E.	—	1.00 ± 0.00	3.00 ± 2.00	2.56 ± 0.37	—	—	2.40 ± 0.37	—	—
Site 2	Prevalence (%)	—	10.00	33.33	96.67	86.67	—	10.00	—	—
	Mean abundance ± S.E.	—	0.17 ± 0.10	1.43 ± 0.54*	15.5 ± 2.14*	6.60 ± 2.56	—	0.10 ± 0.06	—	—
	Mean intensity ± S.E.	—	1.67 ± 0.33	4.30 ± 1.19	16.03 ± 2.15	7.62 ± 2.91	—	1.00 ± 0.00	—	—
Site 3	Prevalence (%)	46.70	6.70	—	10.00	—	3.30	13.30	43.30	100.00
	Mean abundance ± S.E.	n/a	0.07 ± 0.25	—	0.13 ± 0.43*	—	0.03 ± 0.18	0.13 ± 0.35	1.43 ± 2.18	n/a
	Mean intensity ± S.E.	n/a	1.00 ±0.00	—	1.33 ± 0.58	—	1.00 ± 0.00	1.00 ± 0.00	3.31 ±2.18	n/a

(a) *N. japonicus* (BF)

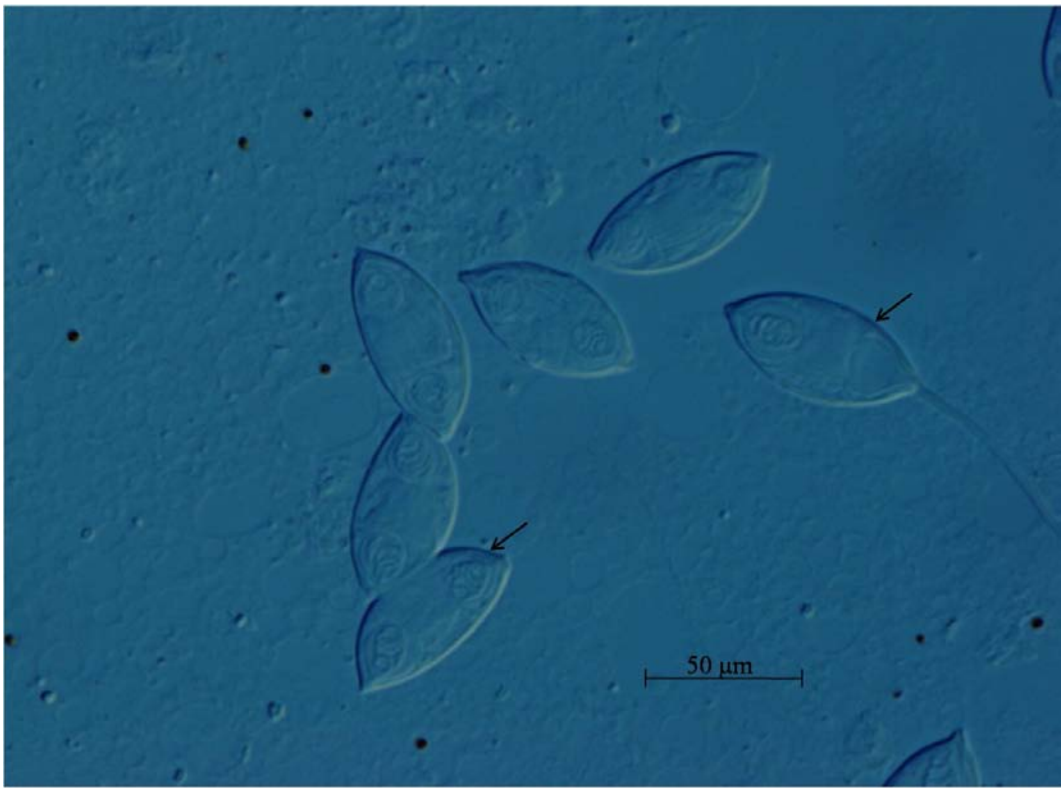
(b) *E. briani* (BF)



(c) Sunbleak infected with *P. cuticola*

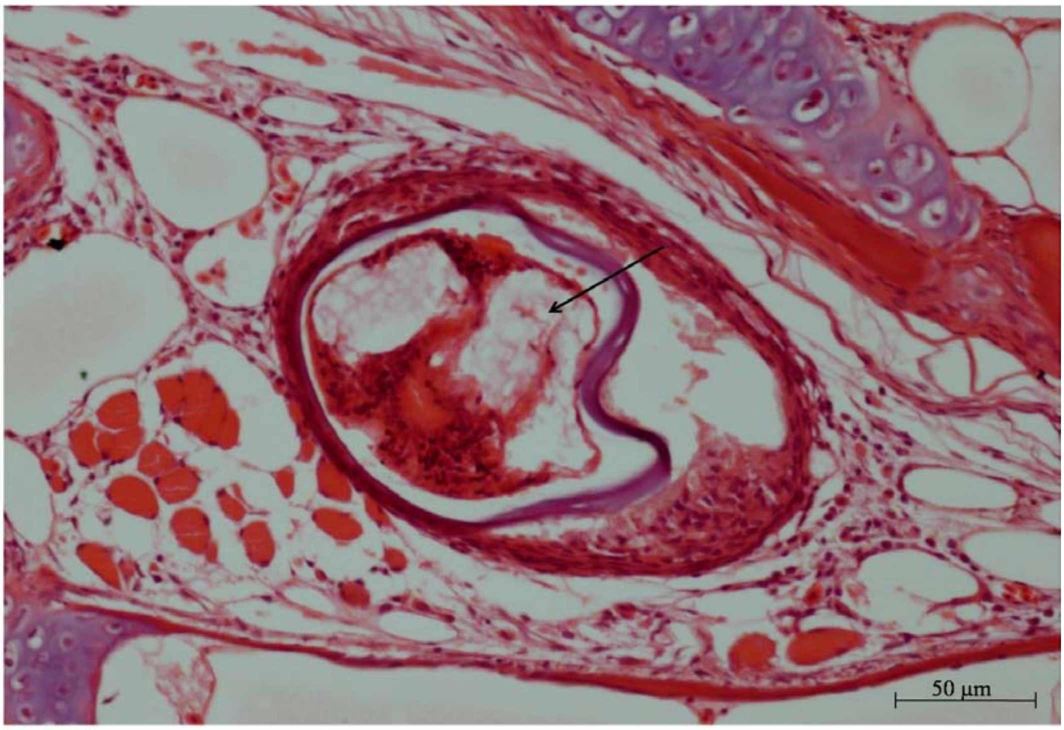
Plate 5.1: Microscopic images (Brightfield microscopy = BF; Differential interference microscopy = DIF) of parasites found in sunbleak *L. delineatus*: (a) *Neoergasilus. japonicus*, (b) *Ergasilus briani* (c) *Posthodiplostomum cuticola* on sunbleak, (d) *Diplozoon cf. paradoxum*, (e) *Myxidium rhodei*, (f) unidentified digenean metacercariae.

(d) *D. cf. paradoxum* (BF)



(f) *M. rhodei* (DIF)

Plate 5.1 continued: Microscopic images (Brightfield microscopy = BF; Differential interference microscopy = DIF) of parasites found in sunbleak *L. delineatus*: (a) *Neoergasilus. japonicus*, (b) *Ergasilus briani* (c) *Posthodiplostomum cuticola* on sunbleak, (d) *Diplozoon cf. paradoxum*, (e) *Myxidium rhodei*, (f) unidentified digenean metacercariae.



(g) Unidentified digenean metacercariae (BF)

Plate 5.1 continued: Microscopic images (Brightfield microscopy = BF; Differential interference microscopy = DIF) of parasites found in sunbleak *L. delineatus*: (a) *Neoergasilus. japonicus*, (b) *Ergasilus briani* (c) *Posthodiplostomum cuticola* on sunbleak, (d) *Diplozoon cf. paradoxum*, (e) *Myxidium rhodei*, (f) unidentified digenean metacercariae.

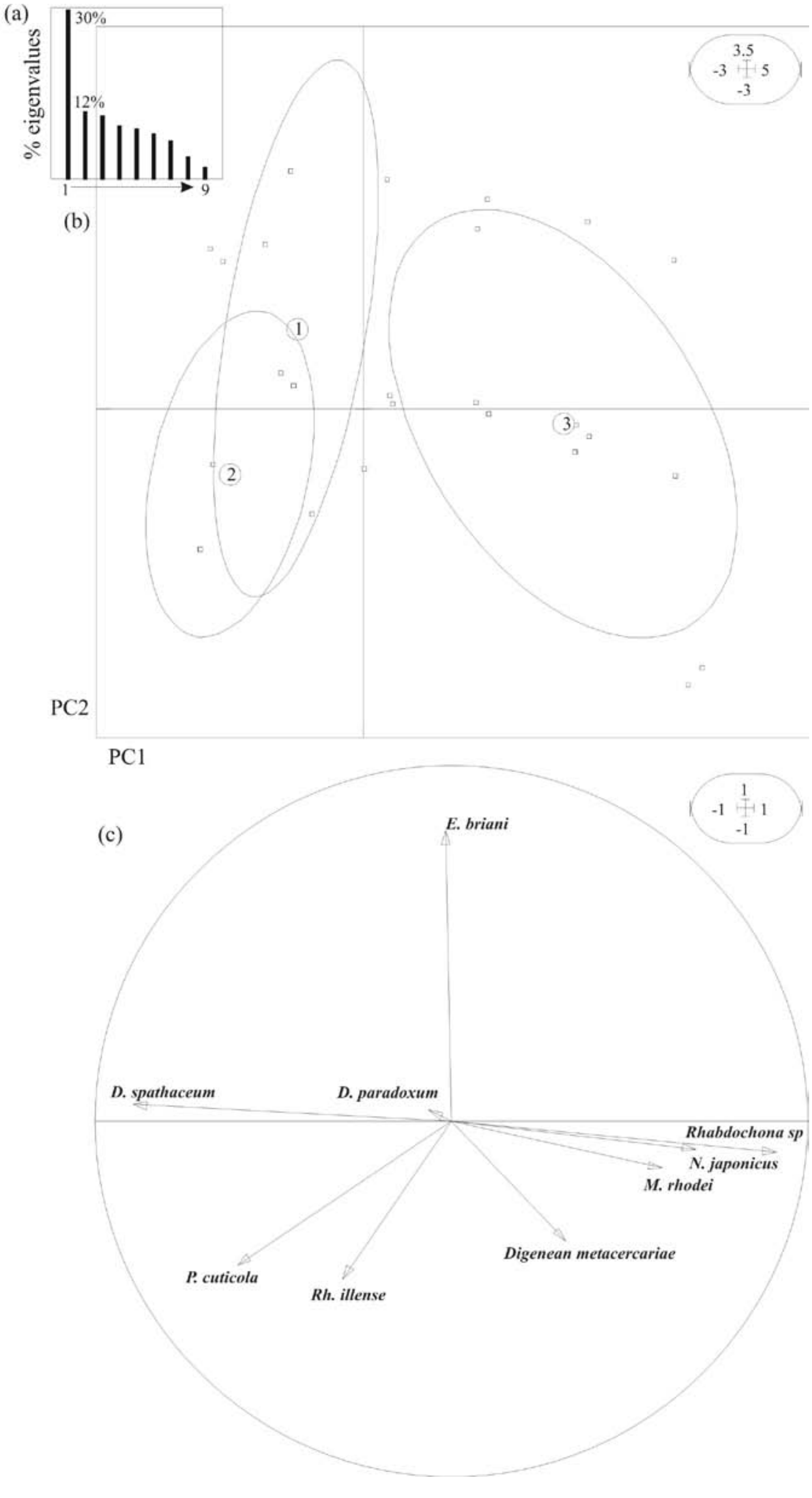


Figure 5.1: (a) Eigenvalues, (b) ordination plot of principal components one and two (representing *N. japonicus* and *E. briani* respectively) for sunbleak parasite fauna (absence/presence) from Beeches Pond (1), Kings-Sedgemoor Drain (2), and Shrubbery Lake (3), with 90 % ellipses based on uniform weightings, and (c) the correlation circle for nine parasite taxa.

Table 5.2: Values of the index of dispersion (ID) and *d* test for parasites sunbleak in England combined for all sites at which they occurred. The total number (n) of fish that were included in the calculation and the mean number and standard error (S.E.) of parasites per individual sunbleak are presented.*

Parasites	ID	d	n	mean ± S.E.
Diplozoon cf. paradoxum (Monogenea)	1.43	2.63	90	0.09 ± 0.04
Rhipidocotyle illense (Digenea)	6.21	16.24	60	0.82 ± 0.29
Diplostomum spathaceum (Digenea)	15.55	39.30	90	5.98 ± 1.02
Posthodiplostomum cuticola (Digenea)	29.78	34.01	30	6.60 ± 2.56
Unidentified digenean metacercariae	0.97	-0.07	30	0.07 ± 0.05
Ergasilus briani (Copepoda)	2.22	6.60	90	0.33 ± 0.09
Neoergasilus japonicus (Copepoda)	3.30	6.29	30	1.43 ± 0.40

* *M. rhodei* and *Rhabdochona sp.* were not included because they were too numerous to be counted individually.

5.4 Discussion

5.4.1 Overview

This chapter represents the first investigation into the parasite fauna of sunbleak and topmouth gudgeon in England and reveals contrasting roles of two non-native fish species, one being a host to native and non-native parasites (sunbleak), while no parasites were found in the other (topmouth gudgeon).

5.4.2 Sunbleak

The non-native (Category II) ergasilids, *N. japonicus* and *E. briani* observed in sunbleak, are of Asian and Eurasian origin, respectively (Markewitsch, 1934; Yin, 1956; Yin, 1962) and so far have displayed localised distribution in England (Fryer and Andrews, 1983; Alston and Lewis, 1994). *E. briani* and *N. japonicus* were first introduced into Yorkshire and West Sussex respectively in the early 1980s (Mugridge *et al.*, 1982; Alston and Lewis, 1994). This introduction into England was associated with fish translocations (Alston and Lewis, 1994). There have been no previous reports of these ergasilids in south west England. These ergasilid copepods go through a direct and fast life cycle comprising free-living stages of nauplii and copepodids, followed by the adult stage during which only fertilized females attach themselves to the skin, gills or fins of fish to produce egg sacs (Urawa *et al.*, 1980; Alston *et al.*, 1996). Both copepods are capable of swimming, thus spread easily between hosts by releasing larvae into the water, and are non-host-specific (Pónyi and Molnár, 1969). They may cause damage to their fish host by their attachment, because their antennae are modified as powerful organs of attachment, and feeding mechanism (El-Rashidy and Boxshall, 1999). Within its native range, sunbleak has previously been reported to host *E. briani* (Grabda, 1971). In both North America (Hayden and Rogers, 1998; Hudson and Bowen, 2002) and England (Beyer *et al.*, 2005), *N. japonicus* has been found in non-native fish associated with aquaculture (Kennedy, 1975), but it has not previously been found in sunbleak. *N. japonicus* exhibits a fast life cycle of 21 days at 20 °C and high fecundity as a female can produce an average 1425 eggs (at 20 °C) during their life (Urawa *et al.*, 1991). The distribution of *N. japonicus* in England is limited to a few locations (Alston and Lewis, 1994) but with the potential for sunbleak to disperse beyond its current distribution in England, there is particular concern that the spread of *N. japonicus* to new areas of England may be exacerbated (Beyer *et al.*, 2005).

The absence/presence of certain parasite taxa in sunbleak and thus the discrepancies between the different sites may be determined by the life cycle and the absence/presence of the suitable intermediate hosts such as in the digeneans (Marcogliese and Compagna, 1999; Ondračková *et al.*, 2004). Digeneans display life cycles that normally involve a mollusc and a fish as first and second intermediate hosts, with a piscivorous fish or bird as the definite host (Taskinen *et al.*, 1991; Donald *et al.*, 2004). Differences in sunbleak parasite fauna between sites may stem from the differences in the invertebrate host communities at the different sites. The invertebrate hosts required differ in that *D. spathaceum* uses *Lymnaea* spp (Morley *et al.*, 2005), *P. cuticola* requires *Planorbis* spp (Ondračková *et al.*, 2004), and *Rhipidocotyle illense* (Ziegler, 1883) uses *Anodonta* spp and *Unio* spp (Molloy *et al.*, 1996; Kortet *et al.*, 2004). Overall, discrepancies between sites related to absence/presence of suitable intermediate hosts may have been driven by temporal sampling bias. However, sampling of intermediate invertebrate hosts was not completed here.

The digeneans *P. cuticola* and *D. spathaceum*, when in large numbers, have been found to cause high rates of mortalities in sunbleak populations in their native habitats (Arnold, 1990). Metacercariae of *D. spathaceum* are particularly harmful, capable of suppressing immunological response and causing blindness and even death of the host fish (Crossland *et al.*, 1971; Wootten, 1974; McKeown and Irwin, 1997). *D. spathaceum*, a common parasite of freshwater fishes, is widely distributed, alters feeding behaviour in infected fish and increases predation by birds (Crowden and Broom, 1980; Moravec, 1985; Chappell *et al.*, 1994). Sunbleak are ideal intermediate hosts for *D. spathaceum* as they can be easily taken by the piscivorous bird host because of their small body size (Petrushevski and Shulman, 1961; Wootten, 1974). *P. cuticola*, an agent of black spot disease in Europe, is found on the surface of the fish, making the host more susceptible to predators due to its increased visibility (Giles, 1987; Ondračková *et al.*, 2002). In some of the investigated sunbleak, the infection covered the lateral line organ which could potentially affect the fish's ability to sense movements in its immediate surrounding, thus increasing their vulnerability. However, to confirm that this would have taken place in the sunbleak populations, detailed behavioural investigations of sunbleak parasitized with *P. cuticola* vs non-parasitized (control) would be required.

The monogenean *Diplozoon paradoxum* (Von Nordmann, 1832) follows a direct life cycle (Llewellyn, 1957; Wiles, 1968) and is known to cause mortalities in fish hosts (Schaeperclaus *et al.*, 1990). *Rhabdochona* spp. and *M. rhodei*, insect- and oligocheate-transmitted respectively, are common intestinal parasites of freshwater fishes with low host specificity (Moravec and Coy Otero, 1987; Kepr, 1991; Moravec, 1995; Marcogliese, 2001; Svobodova and Kolarova, 2004).

The most common distribution pattern in natural parasite-host interactions is the 'overdispersed' or 'aggregated distribution' (Anderson and May, 1978; Shaw *et al.*, 1998). Overdispersion indicates an increased potential of parasite transmission to new hosts as well as both unpredictability and great variation in the level and composition of infections and disease transmission in native co-habiting fish. This is relevant for all parasites found during this study that exhibited low host specificity, in particular the two non-native ergasilids. Essentially, this suggests that the likelihood of these parasites being transferred to fish of a different (i.e. native) species may be increased.

It is difficult to know whether sunbleak were hosting the Category II parasites prior to their invasion of the investigated sites, and so may have introduced the parasites to this site or not. These parasites are non-host-specific and sunbleak form dense populations so as such may provide a large number of hosts increasing the likelihood for parasite transmission. As regards fishery management, it is equally important to: 1) prevent the further dispersal of sunbleak *via* trade or *via* potential outflows from source populations, 2) prevent movement of sunbleak known to be infected with non-native (Category II) parasites, and 3) control any movements of native fish from sources known to contain non-native (Category II) parasites. However, research needs to continue to gain more specific insights into the potential effects of the current Category II parasites in order to keep the list up to date and provide fishery managers with the appropriate knowledge on which to base decisions as regards fish movements. Generally, it is necessary that firmer regulation of sunbleak populations carrying non-native parasites is applied, e.g. eradication. As for the management of parasites potentially associated with non-native fish species, special attention should be given to research into the type of life cycle that parasites may display, as it has been suggested that Direct Life Cycle (DLC) parasites are more likely to establish in a new environment (either on a non-native or native host) than Indirect Life Cycle (ILC) parasites, which require an intermediate host (Petrushevski, 1961; Dobson and May, 1986; Bauer, 1991).

5.4.3 Topmouth gudgeon

Although topmouth gudgeon are known elsewhere to be associated with a variety of pathogens, e.g. copepods (Harada, 1930), metacercariae of *Clonorchis sinensis* (Kim *et al.*, 1979; Kang *et al.*, 1985), metacercariae of *Echinochasmus japonicus* (Chai *et al.*, 1985), metacercariae of *Metorchis orientalis* (Sohn, 1991), metacercariae of *Clinostomum complanatum* (Aohagi *et al.*, 1992), monogeneans *Dactylogyrus* spp (Šimková *et al.*, 2004), acantocephalans *Pomphorhynchus* *bosniacus* (Rosecchi *et al.*, 1993) and pike fry rhabdovirus (PFR) (Ahne and Thomsen, 1986), no parasites were found in the investigated populations in England. The absence of parasites in two topmouth gudgeon populations may be an indication of a general low level of parasitism in topmouth gudgeon populations in England. The observed English populations may have derived from a small subset of possibly uninfected source populations. However, this conclusion is based on the results of two topmouth gudgeon populations investigated (one sample of 30 fish per site) within a discrete sampling period, while seasonal effects may be masked. There are currently 25 recorded topmouth gudgeon populations in England (Pinder *et al.*, 2005b), and so to confirm this conclusion for other introduced populations in England, further parasitological investigations are necessary.

However, an association has recently been suggested between topmouth gudgeon in England and an intracellular eukaryotic disease, similar to the rosette agent that is pathogenic to salmonids in North America (Gozlan *et al.*, 2005). The topmouth gudgeon in which the disease was found did not show any external signs of infection nor did their internal organs (Gozlan *et al.*, 2005). The disease was determined using molecular tools and cohabitation studies (Gozlan *et al.*, 2005), and could not have been identified using standard parasitological protocols as used during the present study. Consideration of the type of tools used for fish health monitoring is paramount in the management of live fish movement and the associated prevention of further novel pathogen introductions into and/or translocations within England. Topmouth gudgeon being a non-native host for a disease, which could not be detected using standard parasitological investigatory tools, is of major concern specifically as regards the species' close association with the aquaculture trade (introduction into and translocation within England) (Pinder *et al.*, 2005b). In the previous chapter (Chapter 4), it is shown that topmouth gudgeon have escaped from an aquaculture facility into the wild; the online river system (River Test, Hampshire). This river harbours valuable salmonid stock and the possibility that this novel disease may be transferred to these salmonids is apparent. The risk of such an infection for salmonids in England could have been much reduced if: 1) the disease had been detected in the healthy host population during health checks before introduction into England; 2) ‘spill-over’ of non-native topmouth gudgeon from source populations into the wild (see also Chapter 4) had been prevented and/or 3) topmouth gudgeon had not been introduced into England. The described situation raises great concern as regards the mechanisms of the emergence of novel pathogens and the role of their facilitation *via* anthropogenic means. Also, though it has been suggested that health monitoring on introduced fish needs to be carried out before they are transported across borders, imported species are still not subject to specific sanitary surveillance (Austin and Robertson, 1993b; Blanc, 2001a; Copp *et al.*, 2005b; Gozlan *et al.*, 2006).

5.4.4 Conclusions

The geographical distribution of most parasite species is limited by the distribution of the potential host population and/or environmental constraints for different stages of the parasite life cycle (Dobson and Carper, 1992). Temperature changes affect parasite life cycles and transmission, and the host biology (Marcogliese, 2001). Global changes in temperature may facilitate the future establishment of novel species and their parasites, as well as to increase the rate of parasite transmission (Dobson and Carper, 1992; Gozlan *et al.*, 2006). Increasing water temperature may facilitate establishment and spread of new fish species, introduced into England *via* aquaculture trade. Consequently, the probability of parasites spreading to native fish populations will increase. In addition, it is predicted that some introduced pathogens will show increased survival, impact and prevalence (Gozlan *et al.*, 2006). Furthermore, temperature increases may cause behavioural changes in the native species and result in exposure to pathogens they may not have been exposed to otherwise. Policy development in England and Wales needs to incorporate the assessment of the potential effects of climate change on the causes, development and transmission of parasites and disease. A start could be made by determining potential areas of colonization by new host species and areas where novel parasites are likely to persist. This could be done by identifying the potential species likely to be introduced using risk assessment methodology such as that developed by Copp *et al.* (2005b), and using mathematical modelling for prediction and mapping techniques to overlay environmental data of areas where the respective species may be able to persevere. Such information may assist in the prevention and management of future introductions.

5.5 Chapter summary

Sunbleak were associated with numerous different parasite species at the three different sites. Generally, overdispersion was found in most parasite species and indicates an increased potential of parasite transmission to new hosts, e.g. native co-habiting fish. This is particularly paramount in the parasites with low host-specificity, including the two non-native ergasilids. In England, the distribution of non-native *N. japonicus* is limited to a few locations (Alston and Lewis, 1994) but with the potential for sunbleak to spread beyond its current distribution, there is particular concern that *N. japonicus* may be disseminated to new areas of the country (Beyer *et al.*, 2005).

No parasites were found in topmouth gudgeon, which may be an indication of a general low level of parasitism in topmouth gudgeon populations in England. However, this could not be confirmed on the basis of the results from the limited number of investigated populations. The lack of macro-parasites may be substantiated in the discovery of topmouth gudgeon being a healthy host of an intracellular pathogen (RLA) by Gozlan *et al*. (2005), which may pose a risk to native salmonid species in England (Gozlan *et al.*, 2005).

6. Interactions and overlaps in resource use between sunbleak and topmouth gudgeon with native fish species[9]

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[9] Part of this chapter has been published in: Beyer, K., Copp, G.H. & Gozlan, R.E. (2007) Microhabitat use of non-native topmouth gudgeon *Pseudorasbora parva* within a stream fish assemblage. *Journal of Fish Biology* 71 (Suppl. D): 224–238. Another part of this chapter has been published in: Pinder A.C, Gozlan, R.E, Beyer, K. & Bass, J.A.B. (2005) Ontogenetic induced shifts in the ecology of sunbleak, *Leucaspius delineatus* during early development. *Journal of Fish Biology* 67 (Suppl. B): 205–217. The latter paper utilised dietary and habitat information as regards ontogenetic shifts for sunbleak only. Further publication of aspects regarding the interactions and overlaps between sunbleak and native fish species are in preparation.

The structure of this chapter

Introduced species may affect other species by displacing or even eliminating native species, and, as such, cause changes that may affect other species and potentially disrupt the structure and functioning of an ecosystem. There are various ways that sunbleak and topmouth gudgeon may interact with native fish species of a new environment. This chapter presents work carried out on the biological and social interactions of these two introduced cyprinids with native species to determine whether a basis of resource co-exploitation exists. Firstly, potential overlap in diet and habitat use between native fishes and sunbleak during early life was investigated in a lake system. Secondly, the microhabitat use of native fishes and adult topmouth gudgeon was investigated in a small stream. In the second part of this chapter, the interactions between sunbleak and native fishes are examined in the first known application of social network analysis to determine the level of social integration of an invasive species into a native species assemblage. This social network analysis concentrated on the early life stages, when the presence of a new species on the growth of a native species may be particularly important because ontogenetic development determines survival and influences the contribution to recruitment (Fuiman and Higgs, 1997; Pinder and Gozlan, 2004).

A. Potential overlaps in diet and microhabitat use

6.1 Introduction

Invasion success is greatly influenced by the ability of the introduced species to adapt to and utilise the available resources in the new environment (Fausch *et al.*, 2001). Resource partitioning in general is a common phenomenon in nature (Toft, 1985; Ross, 1986; Schoener, 1986), and species may segregate by habitat and trophic order (Schoener, 1974; Schoener, 1986). Spatial segregation of species due to differences in use of resources, such as food and microhabitat, is important for community structure (Ross, 1986; Schoener, 1986; Arlettaz, 1999; Young, 2001), which is sensitive to shifts in resource use that may result from non-native species introductions (Werner, 1984). Information on the processes that create intra-specific and inter-specific differences in resource use in fish communities subjected to fish introductions is vital to explain the influence of the introduced species on community dynamics and structure.

Important microhabitat variables associated with diet and spatial segregation in fish are water depth, water velocity, vegetation and substratum size (Gorman and Karr, 1978; Harvey and Stewart, 1991; Facey and Grossman, 1992; van Snik Gray and Stauffer, 1999). Other factors that influence microhabitat use, thus emphasizing the plasticity of resource use and behaviour (Dill, 1983) include: predation pressure (or risk), food availability and quality, and the constraints of a physical nature and competition at the inter- and intra-specific levels (Baltz *et al.*, 1982; Harvey and Stewart, 1991; Facey and Grossman, 1992; Hill and Grossman, 1993). Fish respond to these factors at an individual level due to differences in morphology, behaviour or physiological and physical abilities that are size- or species-specific. Native species’ response to the presence of a new species may cause changes in resource use (microhabitat, food) and consequentially encourage interactive segregation.

In communities subject to non-native species introductions, it is important to determine whether any apparent differences or overlaps in resource use are likely to reflect competitive interactions between the native and introduced species. However, it is not easy to distinguish between the selective and interactive mechanisms of differential resource use, and as a consequence there are relatively few demonstrated cases of actual competition. As such, the role of competition in determining microhabitat and dietary resource use of native and non-native species remains poorly studied. Furthermore, investigations on the impacts of introduced species have mainly focussed on the adult stages of the organism in question (Courtenay, 1995). This inevitably ignores the fact that the environmental requirements of fishes can change quite dramatically over the course of their ontogeny. The early life stages determine the potential of the young to grow and become valuable reproductive adults, and this is an important factor in determining invasion success and survival. The ontogenetic changes associated with development are not only morphological, but also physiological, behavioural and ecological (Copp and Kováč, 1996). The potential impact of introduced species on native species may vary during ontogeny, so it is important to investigate how ontogenetic shifts in resource use of the invasive species may affect native species during their early life (Polis, 1984; Werner and Hall, 1988), with due consideration for the quantity and quality of available habitat, which will influence the form and extent of potential shifts in resource use (Schramm, 1987; Werner and Hall, 1988; Belk and Lydeard, 1994; Schaefer *et al.*, 1994).

Relatively little information is available on the diet and habitat use of sunbleak and topmouth gudgeon in their introduced ranges (Arnold, 1990; Rosecchi *et al.*, 1993; Wolfram-Wais *et al.*, 1999; Hliwa *et al.*, 2002; Pinder *et al.*, 2005a), and this is particularly acute as regards the overlap in resource use with native species. The first aim of this chapter was to determine the incidence of overlap in resource use, in terms of food and habitat, between sunbleak and coexisting native fish species during early life and adult stages. The second aim was to determine the incidence of overlap in habitat use between topmouth gudgeon and coexisting native fish species. This information will enable a better understanding of the mechanisms that govern community structure of invaded fish assemblages (Schoener, 1974). It will also provide insights into the effects of non-native species on resource use of native species that will be of value to environmental managers and policy-makers. The specific objectives were to: 1) evaluate the diet of sunbleak during early life, and test for overlaps in resource use with native fish species, 2) examine the microhabitat use of sunbleak, particularly during early life, and test for overlaps in resource use with native fish species, and 3) assess the microhabitat use of topmouth gudgeon and test for potential overlaps in microhabitat use with native species.

6.2 Material and methods

6.2.1 Data collection

The investigations were carried out in the Stoneham Lakes system and in Tadburn Lake stream, both in Hampshire (see Sections 2.2.1 and 2.3.1 in Chapter 2 for site descriptions). At Stoneham Lakes, weekly sampling was undertaken during May, June and July in 2002 and 2003, and fortnightly in August and September 2003. At Stoneham Lakes, the aim was to assess overlaps in resource use during early life. Sunbleak spawning is known to take place between April/May until the end of June (Brezeanu, 1968), and the period from activation to the end of the larval period, when larvae become juveniles, lasts 96 days (Pinder and Gozlan, 2004). For this reason the sampling time chosen was representative of the spawning season. Sampling dates and numbers of fish at different developmental stages captured at Stoneham Lakes is presented in Table 6.2.

In Tadburn Lake Stream, sampling was undertaken on seven occasions between 15 June and 6 September 2004, in eight to twenty-one day intervals. The sampling times in the stream were chosen to represent the habitat use of topmouth gudgeon and coexisting native species during summer months. The sampling intervals of 8 to 21 days were to ensure that any sampling disturbance that could have occurred had passed. Sampling dates and numbers of fish at different size classes captured at Tadburn Lake stream is presented in Table 6.8.

At both sites, fish were sampled using the Point Abundance Sampling strategy by electrofishing (PASE) for small fishes as proposed by Copp & Peňáz (1988). A total of 1269 point samples were collected in the Stoneham Lakes over the two sampling years. In a 500 m stretch of Tadburn Lake stream, 60 point samples were taken per date, a total of 420 point samples over all sampling dates combined.

PASE was applied using a Deka II 3000 backpack (Output: 50 – 100 Hz PDC with an operating current of 1 to 2 Amps) with a circular anode (15 cm diameter), whereby all sample points were selected randomly (Copp and Garner, 1995). In Stoneham Lakes, the point samples were collected using an inflatable dinghy and moving across the area of the lakes in a random manner (see Figure 2.1 in Chapter 2). In Tadburn Lake stream, sampling was undertaken by wading in an upstream direction from within a 500 m stretch of the water course, beginning at approximately 700 m and ending at 200 m downstream of Crampmoor Fishery (see Figure 2.1 in Chapter 2). In all cases, each sampling point was at least 5 m from the previous point and was approached quietly; the sample was taken rapidly by dipping the active anode into the water, followed by a hand net dipped below the anode and lifted directly up through the area affected by the electrical current to capture any immobilized fish. The hand net (1 mm mesh size) had a 50 cm diameter and was fitted to a 2.0 m long pole. All stunned fish were collected using the hand net and then transferred into a bucket of water. Except for sunbleak, all adult fish caught were immediately identified to species, measured and returned to the water. All fish larvae and all sunbleak caught were sacrificed by overdose of 2-Phenoxyethanol (free embryo, larva) or by Schedule 1 methods as prescribed in the ‘Animals (Scientific Procedures) Act 1986’ (juvenile/adult) (Home Office, 1986a; b) and preserved in 4 % formalin for identification in the laboratory. Shrinkage effect of preservation on body size of captured fish was not tested. For further details on potential shrinkage effects of fish preservation and on Schedule 1 methods, refer to Section 3.2 of Chapter 3.

At each discrete sampling point, the following 13 quantitative and semi-quantitative environmental variables were recorded: distance from bank (DiB) in cm (measured using a graduated pole; or estimated visually for distances > 2m), water depth (Dep) in cm (using a graduated pole), distance to nearest cover (DNC) in cm (using a graduated pole), bottom substratum type as a percentage of clay (%Cl: < 0.05 µm), silt (%Si: > 0.05 µm—0.06 cm), sand (%Sa: 0.06—0.2

cm), gravel (%Gr: 0.2—4.0 cm), pebbles (%Pe: > 4.0—6.4 cm), cobbles (%Co: > 6.4), percentage of submerged vegetation (SVe), percentage of roots or other ligneous matter (Lig), percentage of overhanging cover (OhV), whether the discrete sampling point was in the sun or shaded (Shd). Water velocity (Vel) was determined semi-quantitatively as in Carter *et al.* (2004), using a dip-net pole; upon immersion of the pole, (1) no ripple effect around the pole was noted as zero water velocity; (2) a gentle ripple effect (broken water) around the pole indicated a weak velocity (> 0 but < 5 cm s^{-1}); (3) a moderate ripple effect around the pole represented a moderate velocity (5 – 10 cm s^{-1}).

In the laboratory, all specimens were examined using a binocular microscope, identified to species and categorised according to their developmental interval (Pinder, 2001; Pinder and Gozlan, 2004). Ontogenetic stages of development were defined according to the framework developed by Pinder & Gozlan (2004) and based on shifts in capabilities and ecology during early development.

Gut content examination

To determine diet, entire specimens of L1 to L3 of bream, rudd, roach and sunbleak were squashed between two glass microscope slides and then mounted using a glass cover slip and Hydramount solution. For more developed specimens (L4 and later developmental steps), the anterior one third of the gut was extracted and then mounted on a slide in the same way. The mounted samples were examined using a stereo-microscope, and prey items were identified to species where possible (Henry, 1922; Petkovski, 1973; Pontin, 1978; Amoros, 1984; Fitter and Manuel, 1986). Gut fullness was expressed as a percentage of total gut capacity, as this is one of the preferred methods to minimise errors effectively in dietary studies (Hyslop, 1980). For sampling dates with a large number of fish samples, a random sub-sample of 5 gut contents were examined for each developmental stage of each species. A total of 520 larval fish underwent dietary analysis (see Table 6.2 for numbers of fish and species that underwent dietary analysis). Food availability in the Stoneham Lakes was not examined.

6.2.2 Data analysis

Diet at Stoneham Lakes

Prior to analysis, all dietary items were transformed to percentages to assist comparisons between the abundance of quantitative (= prey items that could be counted one by one, e.g. rotifers) with semi-quantitative (= prey items that could not be counted one by one, e.g. aufwuchs) prey items. Guts that were empty or less than 10 % full were excluded from the analyses because they were not deemed to be representative as gut evacuation times of food items in larval fish guts can be very short, i.e. often only 1 - 2 hours (Mills *et al.*, 1984; Pedersen, 1984). Prey species abundance, richness *S* and diversity *H* were analysed for all fish species at all developmental intervals. The Shannon diversity Index *H* was calculated as follows:

$$H = -\sum_{i=1}^{s} p_{\mathrm{i}} \ln(p_{\mathrm{i}})$$

where p_{i} is the proportional abundance of each species (abundance of the species per total abundances, known here as $\mathrm{p_i = n_i / N}$). To examine differences in prey diversity and abundance between and within samples, between species, and between developmental intervals within species, paired t-tests were carried out.

Principal component analysis (PCA) (Gauch, 1982; Shea, 1985) by double centring was applied to identify patterns in the diet, and specifically whether any overlaps may be observed between sunbleak and coexisting species during early development. PCA is adequate for determining principal axes that describe relationships between the elements present in a single matrix table (Dolédec and Chessel, 1991). Double centring combines the deviation from the mean for all rows (species/developmental stage) and columns (percentage contributions of dietary items) within each matrix (Dolédec and Chessel, 1991). Ordinations of the diet of individual specimens were grouped per developmental stage (Pinder and Gozlan, 2004) with scatter stars based upon uniform weightings with 90 % inertia. Using this method, 90 % of samples, displayed by points in the graph, would be placed within each ellipse per group (Green, 1971), and would therefore display 90 % of the variation in the species' diet at each developmental stage. An overlap between the ellipses indicates resource use overlap between groups. To remove the proportional importance of prey groups, uniform weightings were used during the analysis. Parameters per individual were linked to a common centre equal to the mean of the principal component scores (first and second axes) resulting from the PCA.

To further examine dietary overlaps between different species at different developmental intervals, the Schoener Dietary Overlap Index α (Schoener, 1970; Wallace and Ramsey, 1983; Vinni *et al.*, 2000) was calculated using:

$$\alpha = 1 - 0.5 \left(\sum_{i=1}^{n} \left| \mathrm{Pxi} - \mathrm{P\,yi} \right| \right)$$

where Pxi = proportion of food category i in the diet of species x; Pyi = proportion of food category i in the diet of species y; n = number of food categories; where α = 1 indicates complete dietary overlap, whereas α = 0 means that no overlap exists.

Habitat use at Stoneham Lakes and Tadburn Lake stream

With the exception of water velocity and sun/shade, which were recorded directly as categories, the environmental variables measured in the Stoneham Lakes were converted to semi-quantitative categories based on frequency distributions of the variables observed during sampling: DiB (≤ 25 cm, 26 –100, 101–150, 151–400, 401–870 cm); Dep (≤ 20 cm, 21 –40, 41–60, 61–80, 81–100, 101–120, 121–190 cm); DNC (0 cm, < 50, 51–100, ≥ 100 cm); %Cl and SVe as (0 %, 1–50 %, 51–100%); %Si, %Sa, %Gr and OhV (0 %, 1–25 %, 26–50, 51–100%); %Lig (absent, present); and %LaS (combining %Pe and %Co; 0 %, 1–25 %, 26–50, 51–100%).

With the exception of water velocity and sun/shade, environmental variables collected in Tadburn Lake Stream were attributed to semi-quantitative categories based on frequency distributions of the variables observed during sampling: DiB

(≤14 cm, 15–30, 31–42, 43–54, >55 cm); Dep (≤ 7 cm, 8–14.9, 15–18.9, 19–28.9, ≥ 29 cm); DNC (≤23 cm, 24–39, 40–51, 52–68, 69–85, 86–107, 108–123, 124–153 cm); %Si (0 %, 1–15 %, 16–50 %); %Sa, %Gr, %Pe (0 %, 1–25 %, 26–50, >50–100 %); %Co (0 %, 1–30 %); SVe, Lig and OhV (0 %, 1–10 %, 11–30, 31–50, >50–100 %).

The mean number of fish per sample and the frequency of occurrence were calculated for each developmental interval (Stoneham Lakes) or size class (Tadburn Lake stream). Fish species that occurred in < 3 % of point samples were excluded from microhabitat analysis (Copp, 1992b). Low frequency occurrence species are more likely to be extreme outliers, and may disguise patterns in the electivity profiles of the more abundant species that would be revealed by subsequent multivariate analysis (Chessel *et al.*, 1987; Copp, 1992b; Pilcher and Copp, 1997). Electivity indices were calculated to determine preference/avoidance of different ontogenetic intervals and size classes of sunbleak during early life and size classes of topmouth gudgeon for environmental variables in the Stoneham Lakes and Tadburn Lake stream, respectively. The habitat electivities (E) were calculated as the difference between the frequency of a species at a particular developmental interval or size class having a given category of environmental variable (Fc) and the frequency of that species in all samples (Fa): E = Fc – Fa (Copp, 1992b). Negative values approaching –0.5 indicate avoidance, and positive values approaching +0.5 indicate preference (Copp, 1992b). Deviations from expected occurrence of fish and environmental categories, as well as co-occurrences between fish species/size classes and temporal variations in fish occurrences, were compared using the non-parametric Kruskal-Wallis test after checking for normality (Kolmogorov Smirnov) and equality of variances (Levene’s test). Associations between species/developmental intervals or size classes with environmental variables were examined using Pearson correlations, as were associations between species/developmental intervals or size classes.

To provide composites of microhabitat use at each site and to identify shifts in microhabitat use and overlaps between non-native and native coexisting species, the corresponding samples-by-species and the samples-by-variables matrices, which included samples void of fish, were subjected to canonical correspondence analysis (CCA) (ter Braak, 1986; ter Braak and Verdonschot, 1995). The samples-by-species matrices were constructed using the species of a certain developmental stage or size class observed in each point sample. The samples-by-variables matrices were constructed using the category of each environmental variable recorded for each point sample. This analysis was used to evaluate the wideness of microhabitat for each developmental/size class of fish, combining variables into the best artificial gradients that make the most of niche separation. For the CCA calculation, weighted averages were used as estimates of the species optimum, expecting that the response curve for that species was normal. Maximum microhabitat use separation is presented by the eigenvalue of the ordination axis (Mercier *et al.*, 1992; ter Braak and Verdonschot, 1995). From the CCA, plots were produced, combining the ordinations for samples, species and environmental vectors (ter Braak, 1986). The distance between individual fish displayed as symbols in the CCA diagrams approximates the dissimilarity of their species composition, as was determined by their chi-square distance. Individual fish species/size class points in the diagram are displayed in order of predicted increase (in direction of the arrow) of the particular environmental variable value indicated. Univariate analyses were carried out using Minitab 14 (Minitab, In., PA, USA). Multivariate analyses were performed using the ADE (Analysis of Environmental Data) software package (Thioulouse *et al.*, 1997) and the computer program CANOCO for Windows, version 4.5 (ter Braak and Smilauer, 2002).

6.3 Results

6.3.1 Sunbleak at Stoneham Lakes

A total of 5996 fish representing ten species were collected during sampling at Stoneham Lakes in 2002 and 2003, respectively; consisting of bleak, common bream, common carp, gudgeon, perch, pike, roach, rudd, tench and sunbleak (see Table 6.1 for information on species and developmental codes; see Table 6.2 for numbers and species of fish captured per sampling date). Of these, a total of 520 specimens were subjected to dietary analysis (see Table 6.2 for numbers of fish that were subjected to dietary analysis).

Table 6.1: List of fish species in alphabetical order of Latin name, with name and developmental code (species indicated using the initials of the respective scientific name; developmental codes are: FE = free embryo, 1 to 5 = larval intervals 1 to 5; see Pinder, 2001) captured at the Stoneham Lakes, Southern England, between May and July 2002 and between May and September 2003. Species without a code occurred in too few samples to be included in the analyses.

Latin name	Common name	Code
Alburnus alburnus	Bleak	–
Abramis brama	Common bream	Ab1
		Ab2
		Ab3
		Ab4
		Ab5
Cyprinus carpio	Common carp	–
Esox lucius	Pike	–
Gobio gobio	Gudgeon	–
Leucaspius delineatus	Sunbleak	LdFe
		Ld1
		Ld2
		Ld3
		Ld4
		Ld5
		LdJ
		LdAd
Perca fluviatilis	Perch	Pf
Rutilus rutilus	Roach	Rr1
		Rr2
		Rr3
		Rr4
		Rr5
Scardinius erythrophtalmus	Rudd	SeFe
		Se1
		Se2
		Se3
		Se4
		Se5
Tinca tinca	Tench	–

Table 6.2: Numbers of bleak, bream, common carp, and gudgeon at different developmental stage captured over time at the Stoneham Lakes, Southern England, between May and July 2002 and between May and September 2003. The number of point samples (PAS) taken at each date, the number of fish used for dietary analysis and total numbers are also presented (Fe, free embryo; L1, larval stage 1; L2, larval stage 2; L3, larval stage 3; L4, larval stage 4; L5, larval stage 5; J, juvenile stage; Ad, adult stage).

			Bleak	Bream							Carp	Gudgeon	Pike
Date	No of PAS	Total no of fish	L2	L1	L2	L3	L4	L5	J	Ad	L1	L2	L2
07/05/2002	50	1	0	0	0	0	0	0	0	0	0	0	0
14/05/2002	50	57	0	9	1	0	0	0	0	0	0	0	0
21/05/2002	50	116	0	0	1	0	0	0	0	0	0	0	0
29/05/2002	50	412	0	0	6	0	0	0	0	0	0	0	0
05/06/2002	50	383	0	0	33	0	0	0	0	0	0	0	0
11/06/2002	44	373	0	0	0	0	0	0	0	0	0	0	0
18/06/2002	40	340	0	0	3	0	0	0	0	0	0	0	0
25/06/2002	40	398	0	0	0	0	13	27	0	0	0	0	0
02/07/2002	40	666	0	0	0	0	37	43	1	0	0	0	0
10/07/2002	40	269	0	0	0	0	0	52	0	1	0	0	0
Total	*454*	*3015*	*0*	*9*	*44*	*0*	*50*	*122*	*1*	*1*	*0*	*0*	*0*
06/05/2003	21	0	0	0	0	0	0	0	0	0	0	0	0
13/05/2003	60	115	0	4	1	0	0	0	0	0	0	0	1
20/05/2003	60	326	3	0	4	0	0	0	0	0	0	1	0
27/05/2003	60	252	1	0	6	0	0	0	0	0	0	1	0
03/06/2003	60	384	3	2	16	1	0	0	0	0	2	0	0
09/06/2003	60	327	0	0	0	0	0	0	0	0	0	0	0
17/06/2003	60	670	1	0	1	0	1	3	0	0	0	0	0
23/06/2003	60	428	0	0	0	0	7	6	0	0	0	0	0
08/07/2003	53	107	0	0	0	0	35	14	0	0	0	0	0
22/07/2003	60	146	0	0	0	0	0	57	0	0	0	0	0
04/08/2003	31	49	0	0	0	0	0	0	0	0	0	0	0
18/08/2003	59	86	0	0	0	0	0	0	0	0	0	0	0
03/09/2003	60	28	0	0	0	0	0	0	0	0	0	0	0
19/09/2003	60	12	0	0	0	0	0	0	0	0	0	0	0
29/09/2003	40	4	0	0	0	0	0	0	0	0	0	0	0
14/10/2003	60	30	0	0	0	0	0	0	0	0	0	0	0
28/10/2003	8	17	0	0	0	0	0	0	0	0	0	0	0
Total	*872*	*2981*	*8*	*6*	*28*	*1*	*43*	*80*	*0*	*0*	*2*	*2*	*1*
Total 02/03	1326	5996	8	15	72	1	93	202	1	1	2	2	1
No. of individuals used for dietary analysis		520	0	9	15	0	0	42	0	0	0	0	0

Table 6.2 continued: Numbers of sunbleak, tench and perch at different developmental stage captured over time at the Stoneham Lakes, Southern England, between May and July 2002 and between May and September 2003. The number of point samples (PAS) taken at each date, the number of fish used for dietary analysis and total numbers are also presented (Fe, free embryo; L1, larval stage 1; L2, larval stage 2; L3, larval stage 3; L4, larval stage 4; L5, larval stage 5; J, juvenile stage; Ad, adult stage).

	Sunbleak								Tench	Perch		
Date	FE	L1	L2	L3	L4	L5	J	Ad	L1	L5	J	Ad
07/05/2002	0	1	0	0	0	0	0	0	0	0	0	0
14/05/2002	1	26	2	0	0	0	0	0	0	0	0	0
21/05/2002	1	58	23	0	0	0	0	0	0	1	0	0
29/05/2002	1	45	178	115	2	0	0	1	0	0	0	0
05/06/2002	0	19	65	192	15	0	0	1	0	0	0	0
11/06/2002	1	31	51	167	29	0	0	0	0	0	1	0
18/06/2002	0	5	3	53	37	18	1	1	0	1	44	0
25/06/2002	0	1	0	3	7	104	0	1	0	0	20	1
02/07/2002	0	0	0	0	34	207	0	6	0	3	39	4
10/07/2002	0	0	0	7	7	61	3	0	0	0	25	0
Total	*4*	*186*	*322*	*537*	*131*	*390*	*4*	*10*	*0*	*5*	*129*	*5*
06/05/2003	0	0	0	0	0	0	0	0	0	0	0	0
13/05/2003	6	27	67	0	0	0	0	0	0	0	0	0
20/05/2003	0	1	132	46	0	0	0	0	0	0	0	0
27/05/2003	0	1	111	0	0	0	0	0	0	0	0	0
03/06/2003	0	70	198	26	13	0	0	0	1	0	0	0
09/06/2003	0	23	258	8	0	0	0	0	0	0	0	0
17/06/2003	0	0	3	8	327	228	0	0	0	0	5	0
23/06/2003	0	0	0	38	188	152	0	0	0	0	5	0
08/07/2003	0	0	0	0	5	4	43	0	0	0	2	0
22/07/2003	0	0	0	0	0	27	29	7	0	0	18	0
04/08/2003	0	0	0	0	0	19	22	7	0	0	0	0
18/08/2003	0	0	0	0	0	4	25	31	0	0	4	0
03/09/2003	0	0	0	0	0	0	0	13	0	0	1	0
19/09/2003	0	0	0	0	0	2	6	4	0	0	0	0
29/09/2003	0	0	0	0	0	0	0	4	0	0	0	0
14/10/2003	0	0	0	0	0	0	0	16	0	0	0	0
28/10/2003	0	0	0	0	0	0	0	17	0	0	0	0
Total	*6*	*122*	*769*	*126*	*533*	*436*	*125*	*99*	*1*	*0*	*35*	*0*
Total 02/03	10	308	1091	663	664	826	129	109	1	5	164	5
No. of individuals used for dietary analysis	0	126	72	41	25	20	0	0	0	0	0	0

Table 6.2 continued: Numbers of roach and rudd at different developmental stage captured over time at the Stoneham Lakes, Southern England, between May and July 2002 and between May and September 2003. The number of point samples (PAS) taken at each date, the number of fish used for dietary analysis and total numbers are also presented (Fe, free embryo; L1, larval stage 1; L2, larval stage 2; L3, larval stage 3; L4, larval stage 4; L5, larval stage 5; J, juvenile stage; Ad, adult stage).

	Roach							Rudd					
Date	L1	L2	L3	L4	L5	J	Ad	FE	L1	L2	L3	L4	L5
07/05/2002	0	0	0	0	0	0	0	0	0	0	0	0	0
14/05/2002	7	0	0	0	0	0	0	3	8	0	0	0	0
21/05/2002	13	8	0	0	0	0	0	0	9	2	0	0	0
29/05/2002	1	7	31	2	0	0	0	0	15	8	0	0	0
05/06/2002	0	31	5	2	0	0	0	0	2	8	10	0	0
11/06/2002	0	0	87	0	0	0	0	0	2	3	0	1	0
18/06/2002	0	0	9	17	139	3	2	0	0	0	2	2	0
25/06/2002	0	0	0	6	161	22	31	0	0	0	0	1	0
02/07/2002	0	0	0	25	204	40	23	0	0	0	0	0	0
10/07/2002	0	0	0	2	61	16	28	0	0	0	0	1	5
Total	*21*	*46*	*132*	*54*	*565*	*81*	*84*	*3*	*36*	*21*	*12*	*5*	*5*
06/05/2003	0	0	0	0	0	0	0	0	0	0	0	0	0
13/05/2003	0	0	0	0	0	0	0	3	6	0	0	0	0
20/05/2003	0	95	33	0	0	0	0	0	11	0	0	0	0
27/05/2003	0	17	43	21	37	0	0	0	2	12	0	0	0
03/06/2003	9	7	25	0	0	0	0	0	0	0	11	0	0
09/06/2003	9	20	0	0	0	0	0	0	0	8	0	1	0
17/06/2003	0	0	0	8	85	0	0	0	0	0	0	0	0
23/06/2003	0	1	0	2	2	26	0	0	0	1	0	0	0
08/07/2003	0	0	0	0	0	2	0	0	0	0	0	0	2
22/07/2003	0	0	0	0	0	8	0	0	0	0	0	0	0
04/08/2003	0	0	0	0	0	1	0	0	0	0	0	0	0
18/08/2003	0	0	0	0	0	13	9	0	0	0	0	0	0
03/09/2003	0	0	0	0	0	14	0	0	0	0	0	0	0
19/09/2003	0	0	0	0	0	0	0	0	0	0	0	0	0
29/09/2003	0	0	0	0	0	0	0	0	0	0	0	0	0
14/10/2003	0	0	0	0	0	0	14	0	0	0	0	0	0
28/10/2003	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	*18*	*140*	*101*	*31*	*124*	*64*	*23*	*3*	*19*	*21*	*11*	*1*	*2*
Total 02/03	39	186	233	85	689	145	107	6	55	42	23	6	7
No. of individuals used for dietary analysis	21	20	20	20	38	0	0	0	24	5	0	0	0

Because there were no significant differences in prey diversity (*P* = 0.39) and abundance (*P* = 0.71) of prey items within and between samples over time of sunbleak, roach, rudd and bream, all prey data were grouped together for each species at each developmental stage (Table 6.3; Table 6.4). Rotifers and *Euglena* sp were the most common prey in all fish species examined, whereas cladocerans represented only minor dietary components. The predominant food for all species at developmental interval L1 was detritus, and accounted for over 50 % of the gut content in all species at this stage. Detritus appeared to be the major component of all species intervals until L4 when preference shifted to other dietary items. Highest prey diversity was observed in bream at L5, and the lowest in sunbleak at L4 (Table 6.4). A general increase in prey diversity, i.e. increase in the amount of different types of prey, with development was observed, with guts being generally fuller in native species than in sunbleak (Table 6.4).

Table 6.3: Mean percentage contributions ± S.E. of prey items to the diet of larval bream, roach, rudd and sunbleak at different developmental stage (L1, larval stage 1; L2, larval stage 2; L3, larval stage 3; L4, larval stage 4; L5, larval stage 5). Rudd were not examined for diet at stages 3, 4 and 5. Bream were not examined for diet at stages 3 and 4.

			Bream						Rudd			
			L1		L2		L5		L1		L2	
			Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Cladocera	Chydoridae	*Acroperus* spp	0	0	0	0	0	0	0	0	0	0
	Bosminidae		0	0	1.78	1.43	13.23	2.70	3.77	1.98	0	0
	Chydoridae		0	0	0	0	0.11	0.07	1.57	1.57	6.00	6.00
	Daphniidae		0	0	0	0	0	0	0.65	0.65	0	0
	Sididae		0	0	0	0	1.80	0.57	0	0	0	0
Crustacea	Copepoda		0	0	0	0	10.61	2.31	0	0	0	0
	Indeterminate microcrustacea		0	0	0	0	0	0	3.24	2.22	0.04	0.04
Diatoms			0	0	0	0	0	0	0.03	0.03	0	0
Egg capsules			2.35	1.82	5.02	1.44	3.86	1.00	1.00	1.25	0	0
Diptera	Chironomid larvae		0	0	0	0	0.15	0.08	0.08	0	6.00	6.00
Pollen grains			0	0	2.16	1.34	0.09	0.05	0.05	0	0	0
Protista	Amoeba		0	0	7.02	3.11	6.75	1.89	1.13	0.74	1.37	1.17
		Euglena spp	11.47	3.49	13.84	3.75	5.38	1.10	12.09	3.21	15.39	8.94
	Ciliates		0.17	0.17	0.14	0.14	0	0	0.05	0.03	0	0
		Vorticella	0	0	0.12	0.12	0	0	0	0	0	0
	Indeterminate protozoan stalk		1.34	1.24	0.75	0.75	0	0	5.66	2.60	0	0
	Other indeterminate protozoans		1.36	0.80	0.05	0.05	0	0	0.04	0.03	0	0
Rotifera			5.09	3.76	20.92	5.63	39.16	3.74	5.53	3.06	12.20	10.76
Filamentous algae			0.72	0.61	0	0	0	0	0.01	0.01	0	0
Detritus			64.38	3.59	37.14	4.22	18.59	2.52	51.74	4.91	50.00	7.75
Other indeterminate prey items			13.13	2.30	5.36	2.43	0.26	0.18	0.18	1.66	9.00	5.57

Table 6.3 continued: Mean percentage contributions ± S.E. of prey items to the diet of larval bream, roach, rudd and sunbleak at different developmental stage (L1, larval stage 1; L2, larval stage 2; L3, larval stage 3; L4, larval stage 4; L5, larval stage 5). Rudd were not examined for diet at stages 3, 4 and 5. Bream were not examined for diet at stages 3 and 4.

			Roach									
			L1		L2		L3		L4		L5	
			Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Cladocera	Chydoridae	*Acroperus* spp	0	0	0	0	0	0	0	0	0	0
	Bosminidae		0.94	0.83	0.67	0.46	4.16	3.23	6.17	2.94	0.33	0.21
	Chydoridae		0.49	0.29	0.18	0.18	0.02	0.02	0	0	0.02	0.01
	Daphniidae		0	0	0	0	0.12	0.12	0	0	0	0
	Sididae		0	0	0	0	0.60	0.60	0	0	0	0
Crustacea	Copepoda		0	0	0	0	0	0	0	0	0.02	0.01
	Indeterminate microcrustacea		0.86	0.75	0	0	3.65	2.65	0.02	0.02	0.01	0.01
Diatoms			0.11	0.11	0	0	0	0	0.03	0.03	0	0
Egg capsules			0.35	0.26	6.12	1.44	3.18	1.04	2.49	0.83	4.04	0.70
Diptera	Chironomid larvae		0	0	0.07	0.07	0.11	0.07	0.18	0.15	0.02	0.02
Pollen grains			0	0	0	0	0.15	0.13	0	0	0.26	0.12
Protista	Amoeba		0.04	0.04	2.98	1.06	2.73	0.96	3.65	1.25	0.81	0.21
		Euglena spp	21.30	2.72	13.07	1.94	22.34	3.92	15.71	3.01	6.56	1.23
	Ciliates		0.67	0.30	0.18	0.18	0.06	0.05	0.10	0.07	0.02	0.01
		Vorticella	0.32	0.32	0	0	0.24	0.24	0	0	0	0
	Indeterminate protozoan stalk		0.32	0.26	0.64	0.44	0.13	0.13	1.06	0.59	0.47	0.27
	Other indeterminate protozoans		0.83	0.83	0.11	0.11	0	0	0.03	0.03	0.01	0.01
Rotifera			5.52	2.47	27.48	5.71	10.77	3.17	28.27	6.61	59.15	3.55
Filamentous algae			0	0	0	0	0	0	0.04	0.04	0	0
Detritus			55.00	2.86	43.25	5.95	50.50	4.49	42.00	5.68	25.43	2.75
Other indeterminate prey items			13.25	1.71	5.25	1.56	1.25	0.71	0.25	0.25	2.86	0.72

Table 6.3 continued: Mean percentage contributions ± S.E. of prey items to the diet of larval bream, roach, rudd and sunbleak at different developmental stage (L1, larval stage 1; L2, larval stage 2; L3, larval stage 3; L4, larval stage 4; L5, larval stage 5). Rudd were not examined for diet at stages 3, 4 and 5. Bream were not examined for diet at stages 3 and 4.

			Sunbleak									
			L1		L2		L3		L4		L5	
			Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Cladocera	Chydoridae	*Acroperus* spp	0	0	0	0	0	0	0	0	0	0
	Bosminidae		1.43	0.51	5.37	1.65	1.77	0.84	0.38	0.38	1.54	0.74
	Chydoridae		0.15	0.15	0.94	0.76	0.22	0.13	0	0	0.08	0.08
	Daphniidae		0	0	0	0	0	0	0	0	0	0
	Sididae		0	0	0	0	0	0	0	0	0.11	0.06
Crustacea	Copepoda		0	0	0	0	0	0	0	0	3.26	1.63
	Indeterminate microcrustacea		1.28	0.82	0.92	0.61	0.04	0.04	0.08	0.04	0.03	0.03
Diatoms			0.52	0.40	0.13	0.13	0	0	0	0	0	0
Egg capsules			1.85	0.40	3.45	0.93	3.44	0.85	1.58	1.32	3.67	0.93
Diptera	Chironomid larvae		0	0	0	0	0.10	0.08	0.04	0.04	0.07	0.06
Pollen grains			0	0	0.14	0.09	0	0	0	0	0.44	0.06
Protista	Amoeba		1.05	0.33	1.75	0.54	1.73	0.55	0.18	0.07	1.89	0.63
		Euglena spp	17.27	1.24	14.86	1.79	26.02	1.84	10.93	1.22	4.86	2.23
	Ciliates		0.39	0.17	0.14	0.13	0.33	0.32	0	0	0.06	0.06
		Vorticella	0.02	0.02	0.30	0.22	0	0	0	0	0	0
	Indeterminate protozoan stalk		5.64	1.57	5.03	1.45	4.72	1.15	0.09	0.09	0.65	0.40
	Other indeterminate protozoans		0.15	0.09	0.20	0.15	0.08	0.08	0	0	0.01	0.01
Rotifera			3.00	0.66	6.64	1.53	9.14	1.88	0.32	0.16	60.03	7.80
Filamentous algae			0.47	0.18	0	0	0	0	0	0	0	0
Detritus			54.34	1.83	52.68	2.67	48.88	3.51	86.40	1.56	22.12	5.54
Other indeterminate prey items			12.06	0.94	7.18	1.05	3.53	1.33	0	0	1.18	0.81

Table 6.4: Mean values and standard error (S.E.) for gut fullness (%), Shannon diversity indices *H* and sample sizes (n) for common bream, roach, rudd and sunbleak at each developmental interval (L1, larval stage 1; L2, larval stage 2; L3, larval stage 3; L4, larval stage 4; L5, larval stage 5). Rudd were not examined for diet at stages 3, 4 and 5. Bream were not examined for diet at stages 3 and 4.

Developmental interval	Species	Shannon diversity index *H*	Gut fullness (%) ± S.E.	n
L1	Bream	0.75	48.89 ± 8.20	9
	Roach	0.76	65.95 ± 5.46	21
	Rudd	0.66	50.83 ± 5.47	24
	Sunbleak	0.70	48.02 ± 2.36	126
L2	Bream	1.23	51.67 ± 6.45	15
	Roach	1.09	64.25 ± 4.66	20
	Rudd	0.50	69.00 ± 8.12	5
	Sunbleak	0.93	56.94 ± 2.87	72
L3	Roach	1.05	81.25 ± 4.10	20
	Sunbleak	1.17	65.02 ± 3.67	41
L4	Roach	1.19	82.25 ± 4.64	20
	Sunbleak	0.38	83.50 ± 5.78	25
L5	Bream	1.42	40.26 ± 3.11	42
	Roach	0.81	43.68 ± 3.76	38
	Sunbleak	0.99	36.32 ± 5.75	20

With all Schoener dietary overlap indices (α) above 0.56, there was clear dietary overlap between bream, roach, rudd and sunbleak during early life at all examined developmental intervals (Figure 6.1). This indicated that there was more than 56 % dietary overlap between sunbleak and the respective native species at each developmental interval. The most pronounced overlaps occurred between sunbleak and rudd at L1 and between sunbleak and roach at L3 (Figure 6.1). The lowest overlaps occurred between sunbleak and roach at L4 (Figure 6.1). A general tendency of decrease in dietary overlap was observed during development. Because dietary overlap was strong between sunbleak and native species up to developmental interval L4 (Figure 6.1), principal component analysis is presented for L5 only. A clear dietary overlap was observed between bream, roach and sunbleak at larval stage 5, as indicated by the overlapping ellipses, each of which includes 90 % of all sample points for the respective species (Figure 6.2). This overlap was pronounced between roach and sunbleak, whereas bream had a slightly different and more diverse diet (Table 6.3; Table 6.4; Figure 6.2). At this stage, predominant prey for roach and sunbleak were rotifers and *Euglena sp.*, whereas they were Bosminidae and Copepoda for bream.

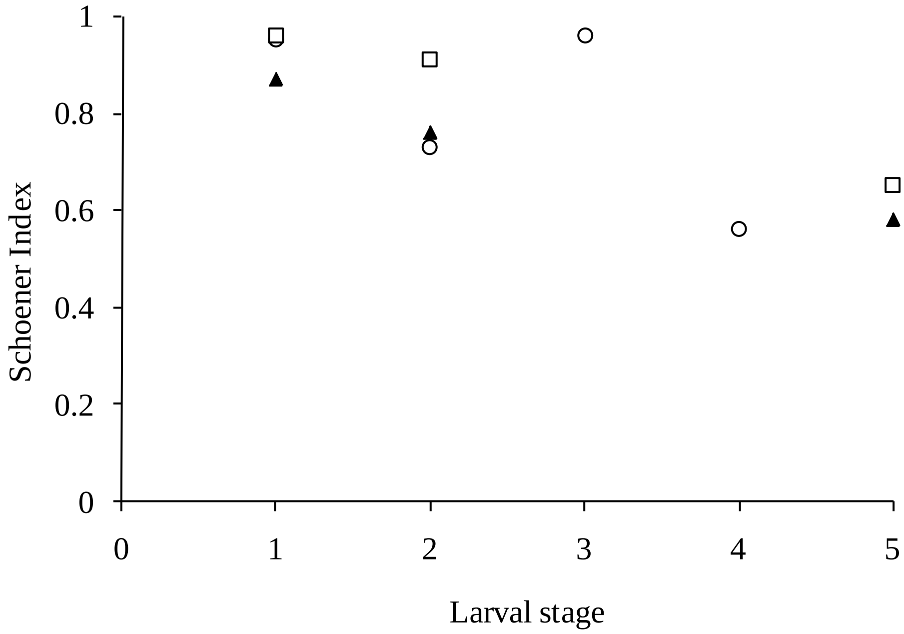

Figure 6.1: Schoener dietary overlap index (α) between larval sunbleak and rudd (☐), sunbleak and roach (o), sunbleak and bream (▲), during early development (1, larval stage 1; 2, larval stage 2; 3, larval stage 3; 4, larval stage 4; 5, larval stage 5). Rudd were not examined for diet at stages 3, 4 and 5. Bream were not examined for diet at stages 3 and 4.

Canonical correspondence analysis (CCA) for fish from the Stoneham lakes during early life revealed the most influential variables characterising microhabitat selection were (in decreasing order by vector length (ter Braak and Verdonschot, 1995)): distance from bank, water depth, distance to nearest cover (DNC), overhanging cover and shade, with variations between species and developmental intervals (Figure 6.3). The analysis suggests minor microhabitat shifts within species and between developmental intervals as well as apparent overlaps of sunbleak with native fishes. Thresholds for sunbleak and roach between larval intervals and juvenile/adult life stages were also suggested, as older fish preferred deeper water further away from the bank. Overlaps in habitat use between sunbleak and native species during early life correspond largely with overhanging vegetation and distance to nearest cover. Pearson correlation of sunbleak with environmental variables revealed no significant association with the latter variables but with several others (Table 6.5), as do native species. Sunbleak developmental intervals L1 to L3 were significantly negatively associated with distance from bank, water depth and percentage of sand. Weak habitat electivities were observed for the free embryo interval while with progressing development these electivities became stronger (Figure 6.4). Throughout development a preference of deeper water and distances further away from the bank were observed. An initial avoidance of sandy substrate during larval stages 1 to 3 shifted to preference during later life stages. A similar shift was observed for ligneous debris. The opposite observation was observed for other environmental variables, for example, an initial preference for overhanging vegetation during earlier stages decreased with progressing development. Sunbleak occurrence was significantly associated with the native species at various early life intervals (Table 6.6).

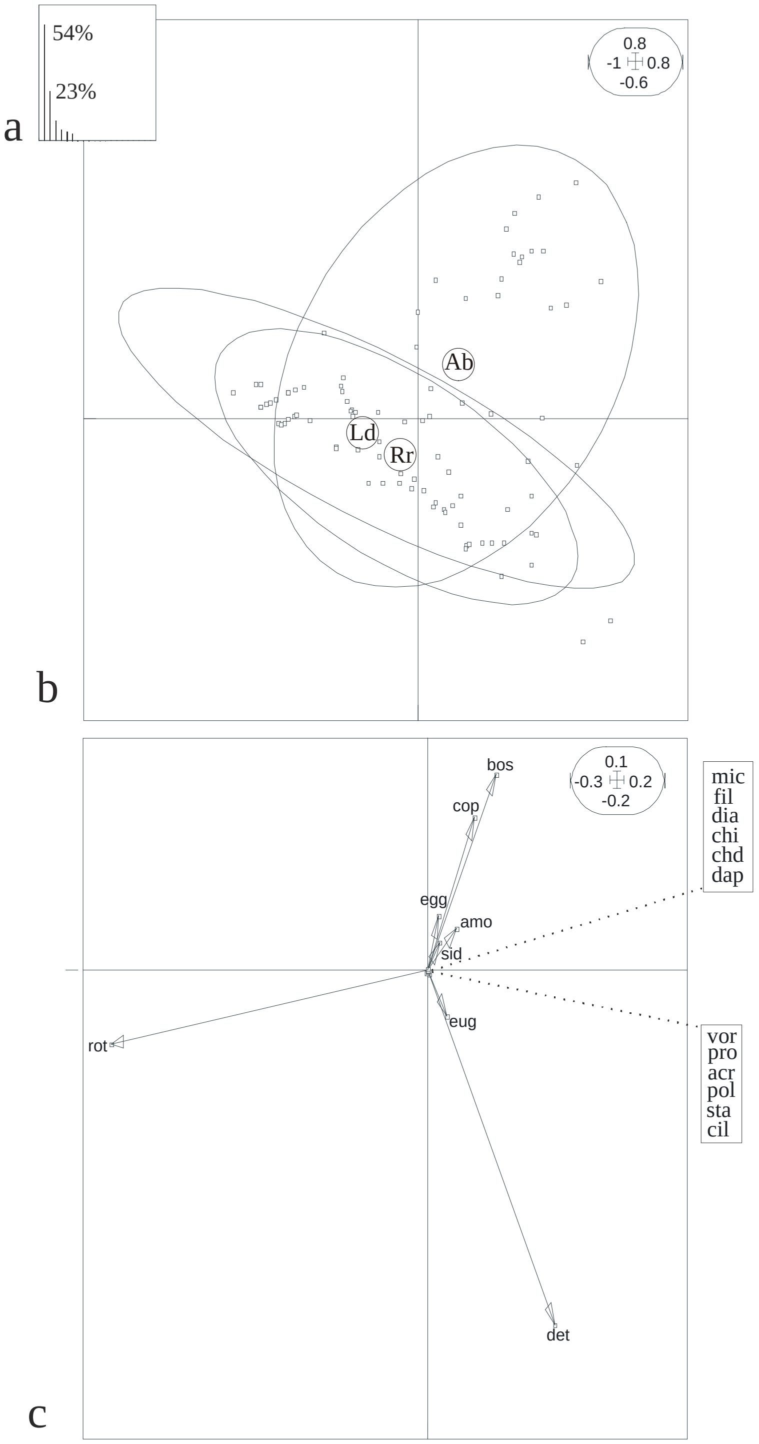

Figure 6.2: Principal component analysis of the fish by diet items matrix based on the 19 dietary items consumed: (a) eigen values, (b) Ordination of individual sunbleak (Ld), roach (Rr) and bream (Ab) at larval step 5 (dots and ellipses) with ellipses based on uniform weightings and (c) correlation circle for the dietary items. Codes for dietary items are: rot: Rotifera, det: detritus (aufwuchs), eug: *Euglena* sp, egg: egg capsules, amo: Rhizopoid Amoeba, bos: *Bosmina* sp. cop: Copepod, acr: *Acroperus* sp, sid: Sididae, dap: *Daphnia* sp, pol: Pollen grains, fil: Filamentous Algae, chd: Chydoridae, dia: Diatom, vor: vorticellid, cil: ciliate, prot: protozoa (unidentified), mic: microcrustacea (unidentified).

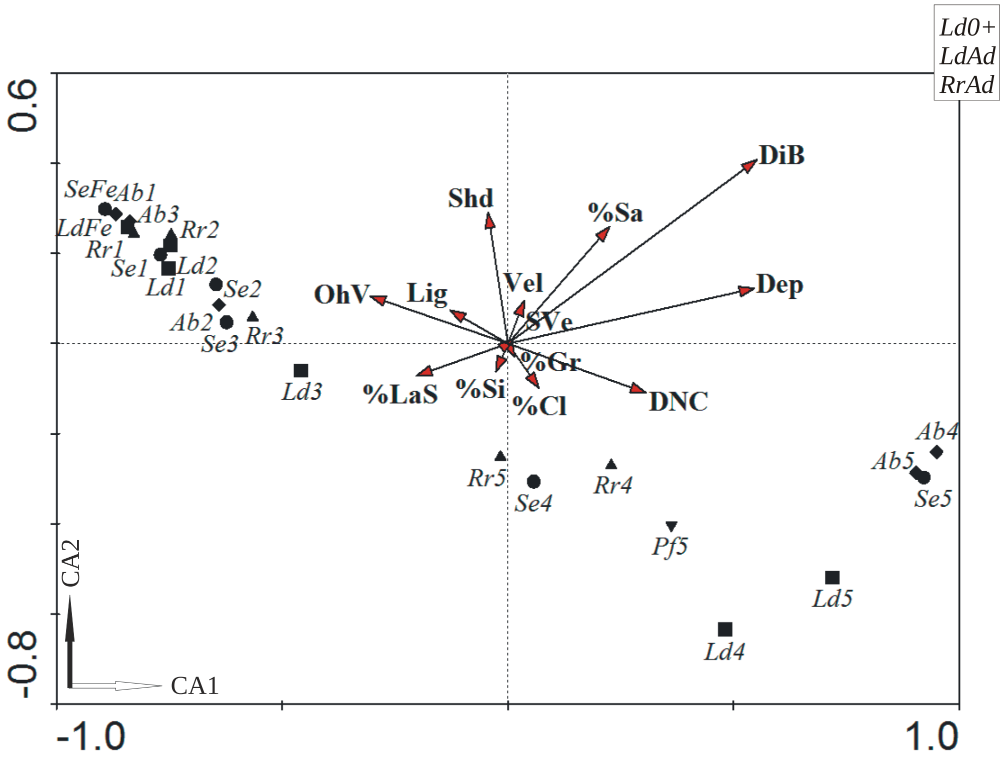

Figure 6.3: Canonical correspondence analysis biplot for fish and environmental variables associations (horizontal: CA1; vertical: CA2) at the Stoneham Lakes, Southern England in 2002 and 2003. Correlation for the 13 habitat variables indicated by vectors with the length of the vectors indicating their relative influence on the ordinations (DiB, distance to bank; DNC, distance to cover; Dep, water depth; SVe, per cent submerged vegetation; OhV, per cent overhanging vegetation; Shade, presence or absence of sun; Lig, per cent ligneous debris; %Cl, per cent clay; %Si, per cent silt; %Sa, per cent sand; %Gr, per cent gravel; %LaS, per cent large substrata, Vel, water velocity). See Table 6.1 for species and developmental codes (Ld, sunbleak, Se, rudd, Rr, roach, Ab, bream, Pf, perch; Fe, free embryo; 1, larval stage 1; 2, larval stage 2; 3, larval stage 3; 4, larval stage 4; 5, larval stage 5; J, juvenile stage; Ad, adult stage).

Table 6.5: Pearson correlations between species/developmental intervals and 13 environmental variables in the Stoneham Lakes in 2002 and 2003. Positive (+) and negative (-) and statistically significant relationships are indicated as: * $P < 0.05$ and ** $P < 0.01$ (n = 483). See method section for details on environmental variables and Table 6.1 for species codes (DiB, distance to bank; DNC, distance to cover; Dep, water depth; SVe, per cent submerged vegetation; OhV, per cent overhanging vegetation; Shade, presence or absence of sun; Lig, per cent ligneous debris; %Cl, per cent clay; %Si, per cent silt; %Sa, per cent sand; %Gr, per cent gravel; %LaS, per cent large substrata, Vel, water velocity; Ld, sunbleak, Se,rudd, Rr, roach, Ab, bream, Pf, perch; 1, larval stage 1; 2, larval stage 2; 3, larval stage 3; 4, larval stage 4; 5, larval stage 5).

	DiB	Dep	%Cl	%Si	%Sa	%Gr	%LaS	SVe	Lig	OhV	Shd	DNC	Vel
Ab1													
Ab2													
Ab3													
Ab4													
Ab5		*+											
Pf5													
Rr1	*-	*-							**+				
Rr2													
Rr3													
Rr4												**+	
Rr5												**+	
SeFe													
Se1	*-			*+									
Se2	*-	**+			*-								
Se3									**+				
Se4													
Se5													
LdFe													
Ld1	**-	**-			**-		**+						
Ld2	**-	**-			*-	*+		*-	*+				
Ld3	*-	*-											*-
Ld4													
Ld5											*-	*+	

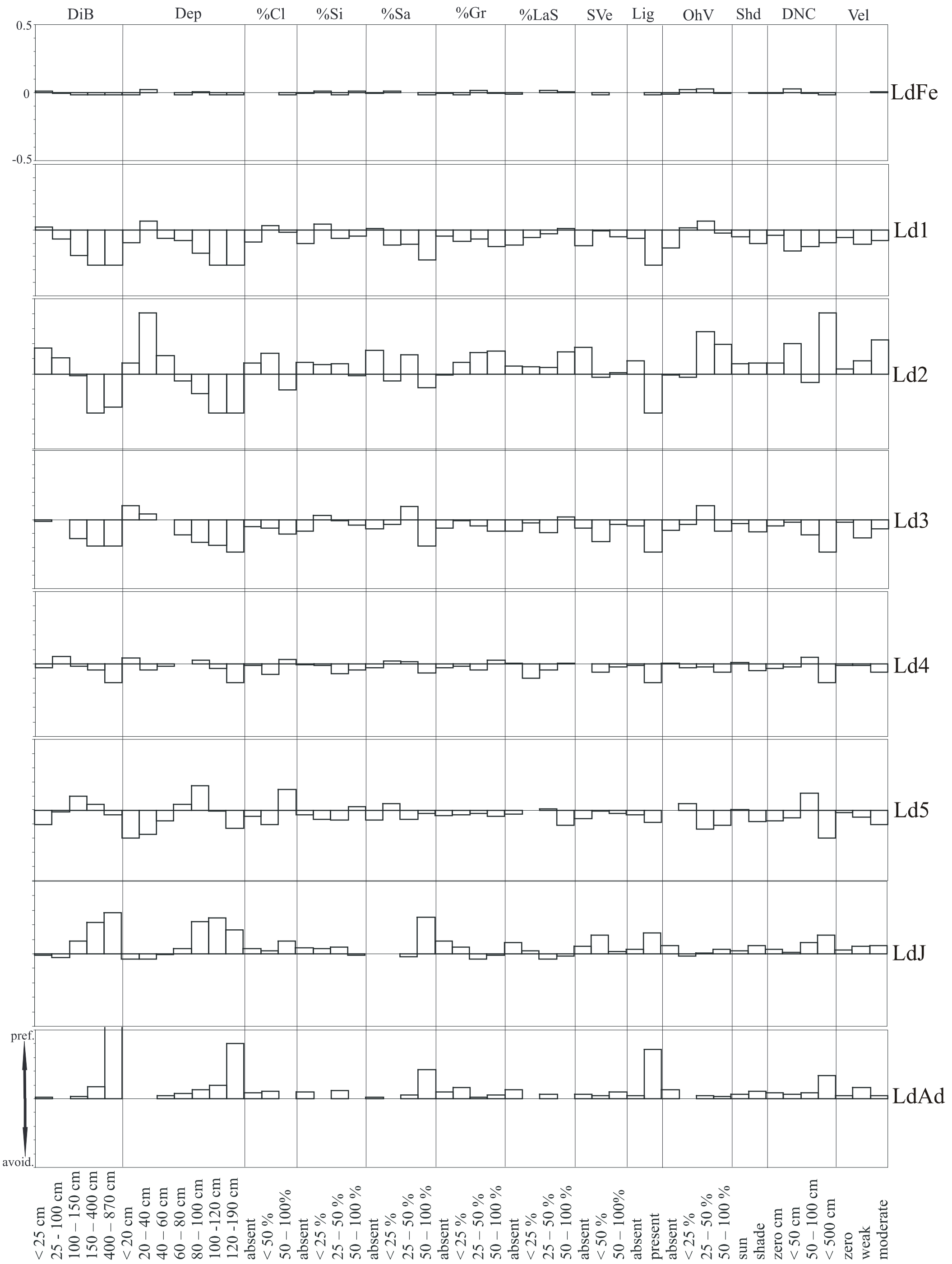

Figure 6.4: Microhabitat electivity profiles (preference = values approaching +0.5; avoidance = values approaching -0.5) for sunbleak (Ld) during different life stages at Stoneham Lakes, Southern England between May and July 2002 and between May and September 2003. See method section for details environmental variables and Table 6.1 for developmental codes (DiB, distance to bank; DNC, distance to cover; Dep, water depth; SVe, per cent submerged vegetation; OhV, per cent overhanging vegetation; Shade, presence or absence of sun; Lig, per cent ligneous debris; %Cl, per cent clay; %Si, per cent silt; %Sa, per cent sand; %Gr, per cent gravel; %LaS, per cent large substrata, Vel, water velocity; Fe, free embryo; 1, larval stage 1; 2, larval stage 2; 3, larval stage 3; 4, larval stage 4; 5, larval stage 5; J, juvenile stage; Ad, adult stage).

Table 6.6: Pearson correlation of frequencies of occurrence between different life stages of sunbleak and native species (see Table 6.1 for developmental codes; Ld, sunbleak, Se,rudd, Rr, roach, Ab, bream, Pf, perch; 1, larval stage 1; 2, larval stage 2; 3, larval stage 3; 4, larval stage 4; 5, larval stage 5; J, juvenile stage; Ad, adult stage) at Stoneham Lakes, Southern England in 2002 and 2003. Significance is indicated as * $P < 0.05$ and ** $P < 0.01$.

	LdFe	Ld1	Ld2	Ld3	Ld4	Ld5	LdJ	LdAd
Ab1			*	*				
Ab2			*					
Ab3					*			
Ab4						*	*	*
Ab5			*					
AbJ								
Pf5		**	**	**				
Pf0+		*	*		*		*	**
Rr1		**						
Rr2	*							
Rr3					**	**		
Rr4			**		*			
Rr5		**	**	**			**	
RrJ					**	**		
RrAd					*	**	**	
SeFe			**				**	
Se1	**							
Se2	*		**					
Se3			*					
Se4			**	**				
Se5								
LdFe	—	**						
Ld1		—	**	**				
Ld2			—	*				
Ld3				—				
Ld4					—	**	**	
Ld5						—		**
LdJ							—	
LdAd								—

6.3.2 Topmouth gudgeon at Tadburn Lake stream

In Tadburn Lake stream, a total of 1195 fish representing 11 species of fish were recorded during 2004 and underwent examination of microhabitat overlaps (see Table 6.7 for species, codes and size classes; see Table 6.8 for numbers of fish and species at different size classes). Topmouth gudgeon, bullhead and stoneloach were the most abundant species, followed by brown trout, chub, *Lampetra* spp and three-spined stickleback, roach, eel, golden orfe and carp. The latter four species occurred too infrequently to be considered further. The CCA (Figure 6.5) was based on all samples combined from the different sampling dates because temporal variation in fish microhabitat use during the study period was observed in a few species size classes only: microhabitat use of brown trout at size class 3 (St3, see Table 6.7 for size classes) during September differed significantly from previous months (Kruskal–Wallis, $P < 0.01$) and topmouth gudgeon microhabitat use by size classes 2 (Pv2) and 4 (Pv4) (see Table 6.7 for size classes) during June and September 2004 differed significantly from other months, respectively (Kruskal–Wallis, $P < 0.01$).

Table 6.7: List of fish species, codes and corresponding size classes (mm fork length) captured in Tadburn Lake stream, Southern England, between June and September 2004. Species without a code occurred in too few point samples to be included in the analyses. For length distributions on which size classes are based refer to Appendix E.

Latin name	Common name	Code	Size class (mm FL)
Barbatula barbatula	stoneloach	Nb1	< 55
		Nb2	56 – 84
		Nb3	> 85
Cottus gobio	bullhead	Cg1	< 51
		Cg2	52 – 60
		Cg3	61 – 74
		Cg4	75 – 93
		Cg5	> 94
Cyprinus carpio	carp	–	–
Gasterosteus aculeatus	three-spined stickleback	Ga	16 – 46
Lampetra spp	*Lampetra* spp	Lp1	< 85
		Lp2	86 – 140
		Lp3	> 141
Leuciscus cephalus	European chub	Lc1	< 106
		Lc2	107 – 119
		Lc3	120 – 130
		Lc4	> 130
Leuciscus idus	golden orfe	–	–
Pseudorasbora parva	topmouth gudgeon	Pv1	18 - 29
		Pv2	30 - 49
		Pv3	50 – 59
		Pv4	> 60
Salmo trutta	brown trout	St1	< 100
		St2	101 - 149
		St3	150 - 159
		St4	>160

Table 6.8: Numbers of fish species at different size classes captured at Tadburn Lake stream in 2004. The number of point samples (PAS) taken at each date and the total numbers of fish are also presented. For species codes and size classes see Table 6.7. For length distributions on which size classes are based refer to Appendix E.

Species/ Size Class	15/06/2004	05/07/2004	13/07/2004	30/07/2004	09/08/2004	24/08/2004	06/09/2004	*Totals*
Cg1	1	8	20	4	2	4	7	*46*
Cg2	9	8	14	10	17	6	2	*66*
Cg3	5	3	29	14	9	7	6	*73*
Cg4	10	18	30	6	15	13	16	*108*
Cg5	18	5	3	0	2	1	0	*29*
Ga	2	16	1	2	0	9	4	*34*
Lc1	17	7	14	5	9	4	9	*65*
Lc2	10	17	7	3	0	0	5	*42*
Lc3	16	5	6	2	2	0	7	*38*
Lc4	12	2	0	0	0	0	2	*16*
Lp1	1	1	1	1	0	0	0	*4*
Lp2	1	0	1	0	1	1	1	*5*
Lp3	0	1	1	1	0	0	0	*3*
Nb1	0	0	0	10	1	0	0	*11*
Nb2	5	2	9	7	0	1	3	*27*
Nb3	11	7	19	10	4	1	3	*55*
Pp1	13	21	8	21	1	0	0	*64*
Pp2	90	46	42	23	36	44	57	*338*
Pp3	8	13	10	10	7	15	13	*76*
Pp4	3	6	1	2	3	2	1	*18*
St1	0	2	0	1	0	3	3	*9*
St2	5	0	7	1	0	2	0	*15*
St3	4	4	2	2	1	2	1	*16*
St4	9	4	8	3	1	2	2	*29*
Total no of fish	250	196	233	138	111	117	142	*1195*
No of PAS	60	60	60	60	60	60	60	420

The main environmental variables that characterised (in order of decreasing importance and ordinate furthest from the origin) the habitat use of young fishes in Tadburn Lake Stream were the proportions of sand and gravel, water depth, the distance to nearest cover, the distance from the bank and the amount of overhanging vegetation (Figure 6.5). Topmouth gudgeon occurrence was significantly associated with only a few of these environmental variables (positive correlation: % pebbles, ligneous debris; negative correlation: distance to nearest cover) and these were limited to specimens of the two smaller size classes 1 and 2

(Figure 6.6; Table 6.9; see Table 6.7 for size classes). This is corroborated by the few habitat electivities of topmouth gudgeon (Figure 6.6). Chub demonstrated the greatest level of habitat associations with significant correlations observed of chub of different size classes with distance from the bank, water depth, % cobbles, overhanging vegetation and % sandy substrate (Table 6.9). Topmouth gudgeon were significantly associated with at least two size classes of every native fish species, with the exception of the single size-class three-spined stickleback (Table 6.10). Indeed, particularly small topmouth gudgeon (Pv2, see Table 6.7 for size classes) were associated with numerous species and size classes of native species (Table 6.10).

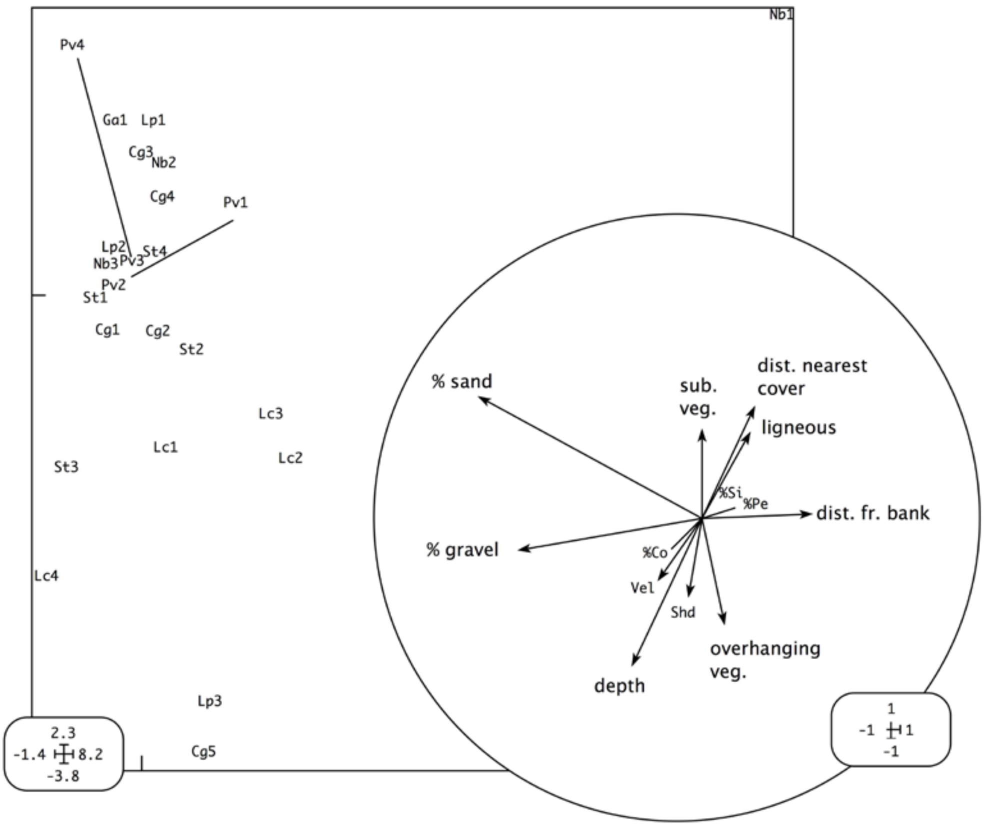

Figure 6.5: Canonical correspondence analysis ordination for fish (CA1 and CA2) in Tadburn lake stream, Southern England in 2004, with inset correlation circle for the environmental vectors. The lengths of the vectors indicate their relative influence on the ordinations. See method section for environmental variables and Table 6.7 for species codes and size classes (DiB, distance to bank; DNC, distance to cover; Dep, water depth; SVe, per cent submerged vegetation; OhV, per cent overhanging vegetation; Shade, presence or absence of sun; Lig, per cent ligneous debris; %Cl, per cent clay; %Si, per cent silt; %Sa, per cent sand; %Gr, per cent gravel; %Pe, per cent pebbles, %Co, per cent cobbles; Vel, water velocity; Cg, bullhead; Ga, three-spined stickleback; Lc, chub; Lp, *Lampetra* spp; Nb, stoneloach; Pv, topmouth gudgeon; St, brown trout).

Table 6.9: Pearson correlations between species/size classes and 12 environmental variables in Tadburn Lake stream in 2004. Positive (+) and negative (-) and statistically significant relationships are indicated as: * $P < 0.05$ and ** $P < 0.01$ (n = 420). See method section for details on environmental variables and Table 6.7 for species codes and size classes (DiB, distance to bank; DNC, distance to cover; Dep, water depth; SVe, per cent submerged vegetation; OhV, per cent overhanging vegetation; Shade, presence or absence of sun; Lig, per cent ligneous debris; %Cl, per cent clay; %Si, per cent silt; %Sa, per cent sand; %Gr, per cent gravel; %Pe, per cent pebbles, %Co, per cent cobbles; Vel, water velocity; Cg, bullhead; Ga, three-spined stickleback; Lc, chub; Lp, *Lampetra* spp; Nb, stoneloach; Pv, topmouth gudgeon; St, brown trout).

	DiB	Dep	%Si	%Sa	%Gr	%Pe	%Co	SVe	Lig	OhV	Shd	DNC	Vel
Cg1													
Cg2													
Cg3								**+					
Cg4									*+				
Cg5		**+		*-									
Ga		*-			*+								
Lc1	*+	*+					**+						
Lc2				*-						*+			
Lc3	*+												
Lc4		**+											
Lp1													
Lp2													
Lp3										**+			
Nb1	*+			*-	*-	**+							
Nb2													
Nb3													
Pv1						*+							
Pv2									*+			*-	
Pv3													
Pv4													
St1													
St2							*						
St3													
St4			*										

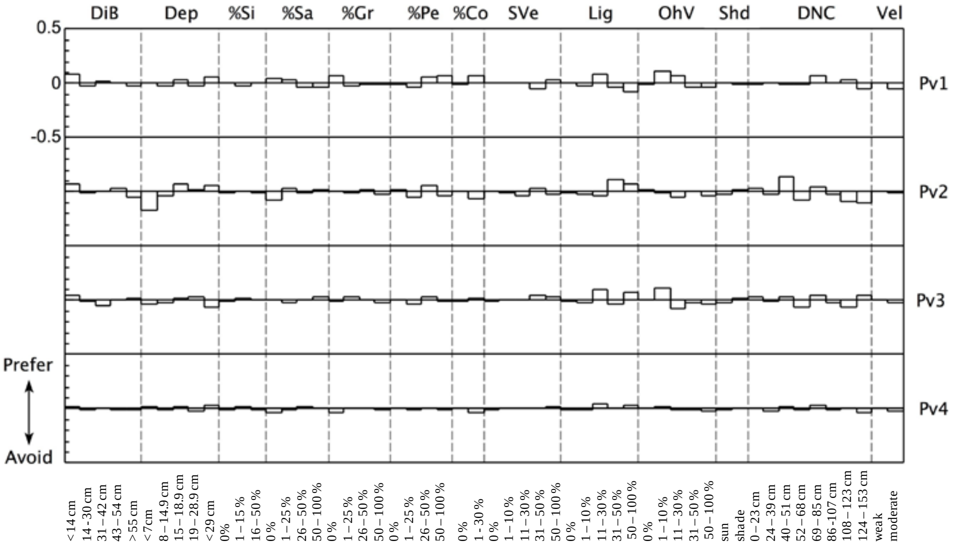

Figure 6.6: Microhabitat electivity profiles (preference = values approaching +0.5; avoidance = values approaching -0.5) for topmouth gudgeon at different size classes between June and September 2004 in Tadburn Lake Stream, Southern England. See method section for details on the environmental variables and Table 6.7 for species codes and size classes (DiB, distance to bank; DNC, distance to cover; Dep, water depth; SVe, per cent submerged vegetation; OhV, per cent overhanging vegetation; Shade, presence or absence of sun; Lig, per cent ligneous debris; %Cl, per cent clay; %Si, per cent silt; %Sa, per cent sand; %Gr, per cent gravel; %Pe, per cent pebbles, %Co, per cent cobbles; Vel, water velocity; Cg, bullhead; Ga, three-spined stickleback; Lc, chub; Lp, *Lampetra* spp; Nb, stoneloach; Pv, topmouth gudgeon; St, brown trout).

Table 6.10: Pearson correlations (*, *P* <0.05; **, *P*<0.01) of frequencies of occurrence between fish species/size classes at Tadburn Lake stream, Southern England in 2004. See Table 6.7 for species codes and size classes (Cg, bullhead; Ga, three-spined stickleback; Lc, chub; Lp, *Lampetra* spp; Nb, stoneloach; Pv, topmouth gudgeon; St, brown trout).

	Pv1	Pv2	Pv3	Pv4
Cg1				*
Cg2	*	**		**
Cg3		**		**
Cg4	**	**	**	
Cg5		**		
Ga		*		
Lc1		**		
Lc2		**	*	
Lc3		**		
Lc4		**		
Lp1	*			
Lp2				
Lp3				*
Nb1	**			
Nb2		**	**	**
Nb3		**	**	**
Pv1	—	**		
Pv2		—	**	**
Pv3			—	**
Pv4				—
St1	*	*	*	
St2	**	*		
St3	*	**	**	**
St4	**	**	**	**

6.4 Discussion

6.4.1 Overview

The data highlight overlaps in the diet between sunbleak and native fishes (roach, bream, rudd) during early development. This overlap was strongest up to larval stage 4, which was related to larvae feeding mainly on detritus, a largely unlimited resource. However, at larval stage 5 while overlaps between sunbleak and roach were still strong, larval bream appeared to increasingly differentiate their diet; predominant prey for roach and sunbleak were rotifers and *Euglena* sp., compared to Bosminidae and Copepoda for bream at larval stage 5.

The study highlighted overlaps in the microhabitat use of native species and those of introduced sunbleak during early development. Generally, overlaps between sunbleak and native species during early life were related to overhanging vegetation and the distance to the nearest cover. Alongside these overlaps, slight shifts in habitat use were observed in sunbleak and native fish species with progressing development. For example, older larvae were more frequently occupying areas of deeper water at increased distance from the bank.

The results revealed overlaps in microhabitat use between topmouth gudgeon and native fish species at different size classes in Tadburn Lake stream. This overlap can be described mainly by the proportions of sand and gravel, water depth and the distance from bank and cover. The study further highlights an aspect in the habitat use of topmouth gudgeon. They displayed only few associations with environmental variables, highlighting the species' plasticity in habitat use.

6.4.2 Overlaps in diet and habitat use at Stoneham Lakes

Overlaps in resource use during early life could influence the fitness and survival of native and non-native species, and initiate changes in their habitat use during the early development and lead to differential intra-specific resource use during later life (Polis, 1984). Strong dietary overlaps between sunbleak and native fish species during early development indicates a sharing of food resources within the invaded fish assemblage (Figure 6.1, Figure 6.2). However, overlaps were mainly based on detritus, which is of low nutritional value (Bowen *et al.*, 1995). The importance of detritus in the diet of all species investigated may reflect the unlimited nature of this food resource. The diet overlaps between sunbleak and native species during early life, at least for the larval stages 1 to 4, may simply reflect the prey availability in the Stoneham Lakes. The observed overlaps may be regulated by similar energy requirements at the same developmental intervals, irrespective of the species.

A higher frequency of full guts in native fishes compared to non-native ones have been observed elsewhere (Feyrer *et al.*, 2003) and, along with generally greater prey diversity in the native species, may indicate that early life stages of native fishes are more efficient at exploiting resources which are familiar to them. With progressive development, intra- and inter-specific segregation and dietary shifts could occur in an increasingly selective manner, and this would be influenced by increasing physical and physiological functional capabilities (Mark *et al.*, 1989; Pinder and Gozlan, 2004; Gozlan and Copp, 2005; Pinder *et al.*, 2005a). With increasing development, larvae were also more suited to feed on more mobile prey items (e.g. rotifers). For example, the development of fins (= increased swimming capability) and increasing body pigmentation (= camouflage to protect from predators) play an important role in this (Thetmeyer and Kils, 1995; Pinder, 2001; Urho, 2002; Pinder and Gozlan, 2004).

Conclusions on how prey availability in the lakes may have affected the diet of larvae at Stoneham Lakes could not be made as food availability was not examined during the study. Accurate measurements of prey availability would have required intense replicate sampling alongside (i.e. at the same location as) point abundance samples. However, even if samples were taken from the same location as the larval fish, they may have taken prey from elsewhere. Conversely, prey availability in Stoneham Lakes may be influenced by keystone predators that affect the trophic structure in lakes (Kurmayer and Wanzenböck, 1996). For example, young-of-the-year perch have previously been found to predate heavily on cladocerans causing their decreased availability as prey for larval fish. At Stoneham Lakes, cladocerans contributed only a limited amount to the diet of the larval fish.

Shifts in habitat use during early life are an integrated response to the progressive increase in functional capabilities and interspecific mechanisms (Kováč, 2002). At Stoneham Lakes, larvae of sunbleak and native species tended to be associated with littoral habitats and moved out into the pelagic zone as they matured (Figure 6.3). Such behaviour has been previously reported for fish larvae (Copp and Garner, 1995). Ontogenetic shifts and differential inter-specific resource use observed during this study are both common phenomena in fish (Werner and Gilliam, 1984; Ross, 1986) and ontogenetic changes in habitat preferences have been observed in several studies of fish-habitat relationships of cyprinids (Copp, 1990; 1992a). Such changes are generally linked to the development of overall body morphology and the sensory organs (Kotrschal and Palzenberger, 1992; Copp and Kováč, 1996; Sagnes *et al.*, 1997).

Spawning period of sunbleak extends from April/May through to June/July, which represents a spawning period that is longer than that of most native cyprinid species (Table 6.11). In combination with their batchspawning behaviour (Farr-Cox *et al.*, 1996; Dussling and Berg, 2001), this increases the possibility for some of the sunbleak larvae to be present in environmental conditions that may promote survival (Humphries *et al.*, 2002). This aspect may play an important role in their establishment success. The prolonged presence of sunbleak larvae may affect species composition and food resources for other larvae and small fish at Stoneham Lakes. In support of this suggestion, it has been reported by anglers that numbers of native cyprinids have reduced since the introduction of sunbleak, while sunbleak numbers have increased.

Table 6.11: Overview of the spawning period of fish species observed at Stoneham Lakes, according to Fishbase (2008).

Common name	February	March	April	May	June	July
Bleak				xxxx	xxxx	xxxx
Bream				xxxx	xxxx	xxxx
Carp				xxxx	xxxx	xxxx
Gudgeon				xxxx	xxxx	
Perch		xxxx	xxxx	xxxx	xxxx	
Pike	xxxx	xxxx	xxxx	xxxx		
Roach				xxxx	xxxx	
Rudd				xxxx	xxxx	
Sunbleak			xxxx	xxxx	xxxx	xxxx
Tench				xxxx	xxxx	xxxx

It is possible that the timing of sampling of fish larvae may have influenced the results of this study. Generally, the timing of spawning would have directly affected the numbers of larvae available for capture. Additionally, the spawning behaviour of sunbleak vs the native species (batchspawning vs non-batchspawning) would have increased the likelihood of sunbleak larvae at different developmental stages to be captured in point samples.

6.4.3 Overlaps in habitat use at Tadburn Lake stream

Habitat use of fish in Tadburn Lake Stream appears to be size-structured; small topmouth gudgeon were associated with the proportion of sand, whereas larger size classes of specimens of larger-bodied species (e.g. *Lampetra* spp, brown trout, chub) were found in relatively deeper waters of > 19.0 cm (Figure 6.5). Topmouth gudgeon is a species particularly plastic in their habitat use, and in their associations with other species (Arnold, 1990), and this is corroborated by the limited number of microhabitat preferences/avoidances (= habitat electivities) observed in Tadburn Lake stream (Table 6.10).

The potential for adverse impacts (e.g. through competition) with native species is also apparent in the numerous positive associations of topmouth gudgeon with native fishes (Table 6.10), and these may suggest either shared resource use (Elliott, 1973; Forseth and Jonsson, 1994) or predation by natives (i.e. potential biological resistance). The facultative piscivorous brown trout and chub (Elliott, 1967; Hellawell, 1971; Mann, 1976a; Forseth and Jonsson, 1994) are species likely to exert predation pressure on topmouth gudgeon in Tadburn Lake stream, and segregation in terms of their resource use has previously been reported in chub (Gyurko and Nagy, 1965). Brown trout are flexible in terms of habitat use and have been observed to undertake shifts in habitat use elsewhere (Elliott, 1994; Näslund *et al.*, 1998; Heggenes *et al.*, 2002; Klemetsen *et al.*, 2003). Renowned for their strong intraspecific interactions (Fausch, 1984), brown trout in the present study were associated with topmouth gudgeon (Table 6.10). See also Chapter 7 for further information on predator-prey interactions between brown trout and chub with topmouth gudgeon and the potential for biological resistance in Tadburn Lake stream.

Native small-bodied, benthic species such as bullhead and stoneloach, which had clear overlaps in microhabitat use with topmouth gudgeon, have previously been found to be more likely to repartition resources, rather than compete for them (Welton *et al.*, 1991; Copp *et al.*, 1994a; Davey *et al.*, 2005). In other English water courses, both of these native species have been found to demonstrate preferences for shallow waters with moderate-to-high velocities and medium-to-large sized substrata (Copp, 1992b; Copp *et al.*, 1994a; Davey *et al.*, 2005). Stoneloach were associated with submerged vegetation, which is commonly observed elsewhere (Copp *et al.*, 1994b; Carter *et al.*, 2004; Figure 6.4). Habitat overlap with native fishes appears to be less pronounced for the largest size-class of topmouth gudgeon (Figure 6.4).

Topmouth gudgeon appear to co-exploit microhabitat resources together with native species. Favourable life history traits and drift from a source upstream of the study site (see Chapters 3 and 4) indicate the importance of such resource overlaps within such a small stream that is directly connected to a river whose fish stock is of major economic importance. Few and weak habitat associations in topmouth gudgeon indicate a wide and plastic breadth of microhabitat use.

It is unlikely that the introduction of topmouth gudgeon has caused habitat shifts in the native fish species in Tadburn Lake stream, as the native species do not display atypical habitat use. Topmouth gudgeon occur in still and running waters (Arnold, 1990; Jankovic and Karapetkova, 1992; Rosecchi *et al.*, 1993; Adámek and Siddiqui, 1997; Sunardi *et al.*, 2005; Sunardi *et al.*, 2007a; Sunardi *et al.*, 2007b), and the species can withstand a variety of environmental conditions (Ujiie and Mizuguchi, 1994), including brief periods of piscicide concentrations that are lethal to other fish species (Allen *et al.*, 2006). Despite being able to form populations under lotic conditions (Sunardi *et al.*, 2005; Sunardi *et al.*, 2007a; Sunardi *et al.*, 2007b), topmouth gudgeon occur in higher densities in lentic conditions, with at least one study suggesting that canals are the species' preferred habitat (Adámek and Siddiqui, 1997). The high densities may be the result of food rather than habitat availability, as the species displays great habitat plasticity, as well as the species' reproductive behaviour (Rosecchi *et al.*, 2001), which involves batch spawning and nest guarding. This reproductive strategy requires a large amount of energy, which is expected to increase under conditions of elevated velocity (Asaeda *et al.*, 2005; Sunardi *et al.*, 2007b). Topmouth gudgeon establishment in Tadburn Lake stream has not been impeded by the ambient water velocities, which at <5 cm s^{-1} are the water velocity preferences (<7 cm s^{-1}) observed in the laboratory under experimental conditions (Asaeda *et al.*, 2005;

Sunardi *et al.*, 2005). The present study provides evidence of great plasticity in topmouth gudgeon habitat use, which is assumed to be one of the factors that have facilitated the species' successful invasion of European inland waters.

6.4.4 Conclusions

Spatial and trophic dimensions are important when describing overlaps in resource use between native and non-native species. However, the success of an introduced non-native species, such as sunbleak and topmouth gudgeon, may not merely depend on out-competing the native species but to take advantage of the environment and integrate into the existing community (see also Chapter 6B). Successful invaders may thus be those species that are able to exploit available resources without inciting major changes in the invaded environment.

6.5 Part A: Chapter summary

The chapter provides valuable ecological insights into the functioning of the aspects of resource use of sunbleak and topmouth gudgeon and overlaps with native fish species in two water bodies of Southern England. Overlaps in diet and habitat use between sunbleak and native fish species during early life indicate a co-exploitation of similar resources, while this becomes increasingly differentiated between species with progressing development. Overlaps in habitat between topmouth gudgeon and co-existing species were observed at different size classes. Habitat associations were limited in topmouth gudgeon indicating the species' plasticity in habitat use. Based on the results, it may be more important for sunbleak and topmouth gudgeon to successfully establish in the respective communities and exploit available resources to ensure survival. A disruption of the new habitat and its community may not aid the invasion success of a non-native species.

B. Social integration of sunbleak into a native fish assemblage

6.6 Introduction

Network theory is commonly applied to identify local and global traits of interconnected nodes (also called ‘actors’), such as brain cells or websites on the internet (Newman, 2003c). Despite its potential to quantify disease spread (Newman, 2002) and social interactions between individuals within and between groups, network theory has rarely been used to examine the social structure of animal groups (Lusseau, 2003; Croft *et al.*, 2004; Croft *et al.*, 2006). Indeed, social network analysis may assist in the better understanding of the integration of invasive species and may be particularly useful in uncovering new and important social traits used in colonisation. In this chapter, the network approach was used to characterise the social organisation of a native larval fish assemblage that has received an invasive fish species.

Many organisms form groups with benefits that have been traditionally explained by performance in predator-prey interactions and locomotion efficiency (Magurran, 1990; Pitcher and Parrish, 1993). More recent studies have suggested that abilities that enable social group-living may rather reveal honest information about individual performance, which may have evolved as amplifiers of individual quality (Barber and Folstad, 2000). The drivers of social organisation include responses to predator pressure and interspecific competition that can determine the success or failure of entire populations. For group living organisms, such as shoaling fishes, social structure may be particularly important following the introduction of a new species, which may compete within the shoal for positions normally occupied by native fishes (Witte *et al.*, 1992). In this study, it is not the impact of an invasive species on the social organisation of natives that was examined, but rather its social integration into the fish assemblage.

In most organisms, early life is a crucial phase for growth and subsequent survival to recruitment. During their early life, fishes undergo a series of ontogenetic changes in morphology, behaviour, physiology, ecological interactions and thus in their performance-related capabilities (Balon, 1975; Balon, 1990). The present study aimed to: 1) determine whether invasive species integrate into the native species social network during their early life; 2) assess whether any of the social ties between invasive and native species of particular developmental intervals are more common than others; and 3) detect whether the invasive species is more strongly socialising with con-specifics than native species with each other. This is the first study that has utilised social network analysis to examine the integration of an introduced species into the social network of native species. This integration may be a key attribute of successful invaders.

6.7 Material and methods

6.7.1 What are ‘Social Networks’?

A social network is a set of organisms with some pattern of contacts or interactions between them (Wasserman and Faust, 1994). There are a variety of networks that can range from regular to random networks (Figure 6.7) (Watts and Strogatz, 1998). In Figure 6.7, the dots in the diagrams are the actors[10], for example fish or persons, and the lines are the social ties[11] between them. The networks all consist of 16 actors (Figure 6.7). When looking at the ‘Regular Network’ diagram, imagine this is a group of 16 persons. Each of those persons only knows or socially interacts with 4 other persons in the group. This results in the network consisting of many small groups, which is also called ‘clustering’ (see Appendix F for glossary of social network terms) (Watts and Strogatz, 1998). Each person in the network is the same because they know or socially interact with the same amount of people. However, for information to reach every person in the network it takes quite a long time, because the distance between two persons is quite long because not everyone knows or socially interacts with each other. If these 16 persons would be connected randomly as in the ‘Random Network’ diagram, then they would form a random network (Figure 6.7) (Watts and Strogatz, 1998). In the random network, because everyone knows or socially interacts with everyone, there is almost no clustering because there are no small groups. In this type of network, information can spread fast (Figure 6.7). Small-world networks are characterized by containing complementary elements from

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[10] Actors can also be called ‘nodes’.

[11] Social ties can also be called ‘edges’.

regular networks and random networks (Figure 6.7) (Watts and Strogatz, 1998). By inserting few shortcuts into a regular network it is possible to obtain a small-world network with, for example, small groups and short distances. Having both short local and global distances in a network affect possibilities for efficient diffusion and spreading of data, information and epidemics in such networks (see Appendix F for glossary of social network terms).

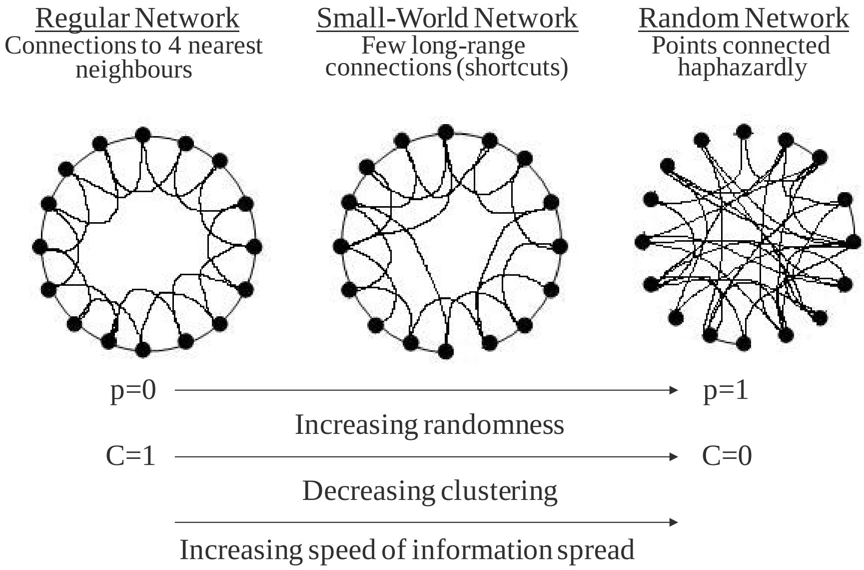

Figure 6.7: Overview of the characteristics of regular, small-world and random networks (adapted from Watts & Strogatz, 1998). ●, actors; ▬, social ties; C, clustering coefficient; p, index of randomness; see Appendix F for glossary of social network terms.

6.7.2 Applying social network theory to fish populations

A social network is a set of organisms, such as fish or groups of fish with some pattern of contacts or interactions between them (Wasserman and Faust, 1994). About 50 % of juvenile teleost fish species live in shoals and about 25 % maintain this behavioural trait throughout their lives (Shaw, 1978). Shoaling behaviour has several benefits for individual fish such as increased detection speed of food during foraging and protection from predation (Pitcher *et al.*, 1982; Magurran, 1990). In light of the dynamic nature of fish shoals, it is important to examine the interactions between individual fish within and between shoals, as well as across whole populations. This will give insights into the social organisation of fish shoals. Using information on the interactions between individual fish, social networks can be created (Newman, 2003c) (Figure 6.8). From these networks, in which the individual fish are inter-connected *via* social ties, standard network measures (L, path length[12], C, clustering coefficient[13] and k, mean degree[14]; see Appendix F for glossary of social network terms) can be calculated to describe the networks.

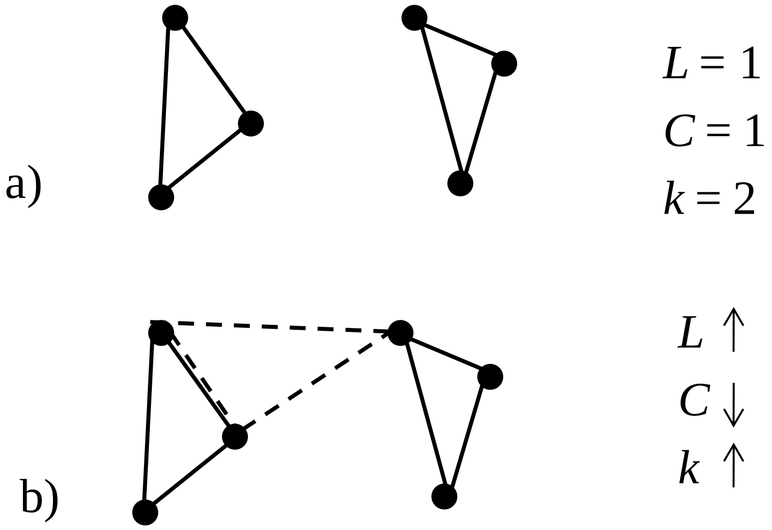

Figure 6.8: Indicative overview of social network parameters using a) two groups of 3 individuals each and b) showing one group of 6 individuals that are inter-connected. ●, actors; ▬, social ties; L, path length, C, clustering coefficient and k, mean degree; see Appendix F for glossary of social network terms (adapted from Croft, 2003).

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[12] Path length L is the distance between pairs of actors in the network. Mean path-length is the mean of these distances between all pairs of actors. L describes a global property of the network. It can be used to predict how quickly information and disease may spread in an animal population (e.g. in a population of size N, disease can be expected to spread more quickly for lower values of L). See also 'geodesic distance'.

[13] Clustering coefficient C is a measure of the cliquishness of the network, calculated as the mean value of all potential social connections that occur in the local ('direct') neighbourhood. C describes an average local property of the network, and measures the likelihood that two associates of a node are associates themselves. A higher clustering coefficient indicates a greater 'cliquishness'.

[14] Degree k is equivalent to the number of social ties that an actor has with other actors in the network. k is calculated as the mean number of social ties per actor in the network. The degree k_i of an actor is the number of actors, $|N_i|$, in its neighbourhood N_i.

The application of social network analysis to interactions in animal populations has great potential. For example, it may assist in the progress of research and analysis of co-operative behaviour, the transmission of information *via* social interactions and the mechanisms of disease and/or parasite transmission (Watts and Strogatz, 1998; Abramson and Kuperman, 2001; Latora and Marchiori, 2001). It is also possible to predict a network's resistance to predation and the subsequent loss of individuals (Lusseau, 2003), as well as to examine social segregation (Newman, 2003a). Up to date information regarding the structure and properties of social networks for wild animal populations is scarce.

6.7.3 Applying social network analysis to the data set from Stoneham Lakes

The data used for Chapter 6B are those used for the analysis of microhabitat use at Stoneham Lakes and presented in Table 6.2 of Chapter 6A. The method of data collection is also described in Chapter 6A (Section 6.2.1). Here, the data are utilised to examine social integration, as they were deemed to be suitable for sunbleak as they are known to aggregate in shoals during early life and as adults (Rüppell and Gößwein, 1972; Siegmund and Wolff, 1973a; b; Andoerfer, 1980; Arnold and Längert, 1995; Pinder and Gozlan, 2004) and this was also observed at Stoneham Lakes (K. Beyer, pers. obs.; see also Chapter 6A). Each sample was considered as a random sub-sample of whole groups of individual fish. Fish that were found in the same sample were considered to be socially associated. Based on the behavioural ecology of sunbleak and other native species, the assumption of social associations within groups of fish was warranted (Rüppell and Gößwein, 1972; Siegmund and Wolff, 1973a; b; Andoerfer, 1980; Arnold and Längert, 1995; Pinder and Gozlan, 2004).

To further understanding on the social aspects of an invaded fish assemblage during early life, this study examined the inter-species developmental interval interactions within fish shoals at Stoneham Lakes. From information on these interactions, social networks could be constructed. In these social networks, the fish species at the different developmental intervals (actors, nodes) were inter-connected by their social ties (so-called 'edges') (see Appendix F for a glossary of terms used). To describe the networks, local and global properties (*k*, mean degree, *C*, clustering coefficient, and *L*, mean path length, respectively; see Appendix F for glossary of social network terms) (Watts and Strogatz, 1998; Newman, 2003b; c) were calculated. To explain the mean number of social ties of an individual actor in a network, the degree k_υ of connectivity was calculated. The connectivity of an actor υ, is the number of its social ties. The mean path *L* length is the geodesic distance[15] averaged over all actors in the network. If *d* is the length of the shortest path between the actors *i* and *j*, then the mean path length *L* is *d (i,j)* averaged over all pairs of actors. The local neighbourhood[16] Γ_ϑ of an actor υ is then:

$$\Gamma_\vartheta = \{i : d(i,\vartheta) = 1\}, \text{ so } \vartheta \notin \Gamma_\vartheta .$$

The local clustering coefficient measures the likelihood that two associates of an actor are associates themselves and is calculated with the following equation:

$$C_\vartheta = |E(\Gamma_\vartheta)| / \binom{k_\vartheta}{2},$$

where k_υ is the degree of connectivity and $|E(.)|$ gives the number of social ties for the respective network. The mean clustering coefficient *C* is the $C\upsilon$ averaged over all actors in the network. With the mean clustering coefficient *C*, the cliquishness[17] within the networks was calculated.

In the present study, the network actors do not represent individual animals as is the case in previous studies on the social organisation of animal groups (Lusseau, 2003; Croft *et al.*, 2004)[18], but they each represent individuals at the same developmental intervals, i.e. with the same functional capabilities. During early

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[15] Geodesic distance is the number of social ties in a shortest path length connecting two fish. See Appendix F for glossary of terms.

[16] For a set A of actors (fishes), the 'local neighbourhood' of A is the union of the social ties of the actors (fishes), and so it is the set of all actors (fishes) socially tied to at least one actor (fish) of A.

[17] Cliquishness is a term used when in a network the number of 'cliques' are examined. 'Cliques' are groups within which every fish is directly socially tied to every other fish in the network. See Appendix F for glossary of terms.

[18] These studies used 'mark-and-recapture' (Croft *et al.*, 2004) or recognized individual animals (Lusseau, 2003); the application of neither technique was feasible during the present study of fish during early life.

ontogeny the yolk sac disappears and physiological features such as the mouth, the anterior and posterior swim bladder chambers and the fin rays develop (Pinder, 2001). Simultaneously, the independence and moving capabilities of the fish improve during each developmental stage. During development, the young fish are increasingly able to avoid predators, control their position in the water column and investigate their habitat. At larval stage 5, with the formation of scales and the lateral line, they can detect the movements of nearby organisms. Most importantly, larvae at each of those developmental intervals are correlated with similar physical, physiological and social functional capabilities. These capabilities at each larval interval are comparable to the ones of the native species occurring at the study site (Pinder, 2001). Thus, for this study, it was decided to treat each specimen of fish per species and per developmental interval as the same individual.

For calculation of network parameters, fish-by-fish matrices were constructed using the species of a certain developmental stage observed in each point sample. These matrices were used to calculate the degrees k, clustering coefficients C, and path lengths L for each sample. Samples with one or no fish were excluded from the analysis, because the network parameters are based on social interactions. Complete networks[19] were analysed per sampling date representing all species categories for their clustering and mean geodesic distances. From the complete networks, ego-networks[20] for each developmental category of sunbleak and native species were analysed by choosing ego-actors[21] and then running them for each developmental interval of each species categories observed in each network.

The Student's *t*-test was used to compare properties between ego-networks and developmental intervals within and between species. Levene's test was used to determine equality of variances for all variables, and normality was tested using

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[19] A complete network is a simple network in which every pair of fish is socially connected.

[20] Based on the selection of one fish (in this case the 'ego') within the network and includes all other fish to whom the 'ego'-fish has (or could have) social ties. The ego-network approach examines the whole fish population by means of census, rather than by sample.

[21] Ego-actor is the fish on which the calculation of the respective ego-network is based.

Kolmogorov-Smirnov test. To examine the coefficient of determination (r^2) regressions were generated for ego-network size against time based on the developmental categories. All statistical tests were performed with Minitab 14 (Minitab, Inc, PA, USA). Social network analysis was carried out using the UCINET software package (Borgatti *et al.*, 2002).

6.8 Results

Ten fish species were captured at Stoneham Lakes: bleak, bream, common carp, gudgeon, perch, pike, roach, rudd, sunbleak and tench. The most common species in the samples were bream, roach, rudd and sunbleak (see Chapter 6A for more details on the fish captured at Stoneham Lakes).

For all complete networks per date, each species-developmental interval presented social ties with a mean 52.34 % ± 3.82 (degree k ± S.E.) of all other fish (species-developmental interval) in each network with a minimum of 22.22 % and a maximum of 100 % (Figure 6.9). Mean path length L over all fish in the complete networks was low at 1.19 (± 0.04), ranging from 1 to 1.65 (Figure 6.10). This indicated that information within these networks may be rapidly transmitted (Watts and Strogatz, 1998; Newman, 2002; Croft, 2003). Mean clustering coefficient C for all fish in the complete networks per date (± S.E.) was 0.29 (± 0.04; Min. = 0; Max. = 0.5); these are low values indicating only a limited amount of cliquishness (Figure 6.10).

For all species, there was a general tendency of decrease in ego-network size during early life (Figure 6.11a). The mean number of fish with which each individual sunbleak were socially associated (3.57 ± 0.45) decreased significantly ($r^2 = 0.98$; $P \leq 0.05$) with age and with improved corresponding capabilities of the larvae (Figure 6.11a). Except for developmental steps 2 and 3, the ego-network size in sunbleak and in the native species was generally similar. Path length L was found to be 1 for all sunbleak and native species ego-networks, indicating a short path length between fishes. Mean degree k of the ego-networks per sunbleak developmental interval was 59.25 % (S.E. ± 4.94) (Figure 6.11b) indicating that sunbleak at each developmental interval were socially connected with a mean 59.25 % of all fish within the network. The mean degree *k* was, except for developmental stage 4, significantly greater than for the native species developmental intervals. The degree of connectedness of sunbleak and native species ego-networks decreased, but not significantly. Mean clustering for all actors (Figure 6.11c) in all sunbleak ego-networks was 0.29 (S.E.±0.02). Except for intervals 4 and 5, all other sunbleak intervals displayed significantly different clustering from the native species intervals. Sunbleak generally favoured social ties with native species of similar developmental intervals until after larval interval 5, the metamorphic transition to juvenile development, after which sunbleak established stronger social ties with younger developmental intervals of native species.

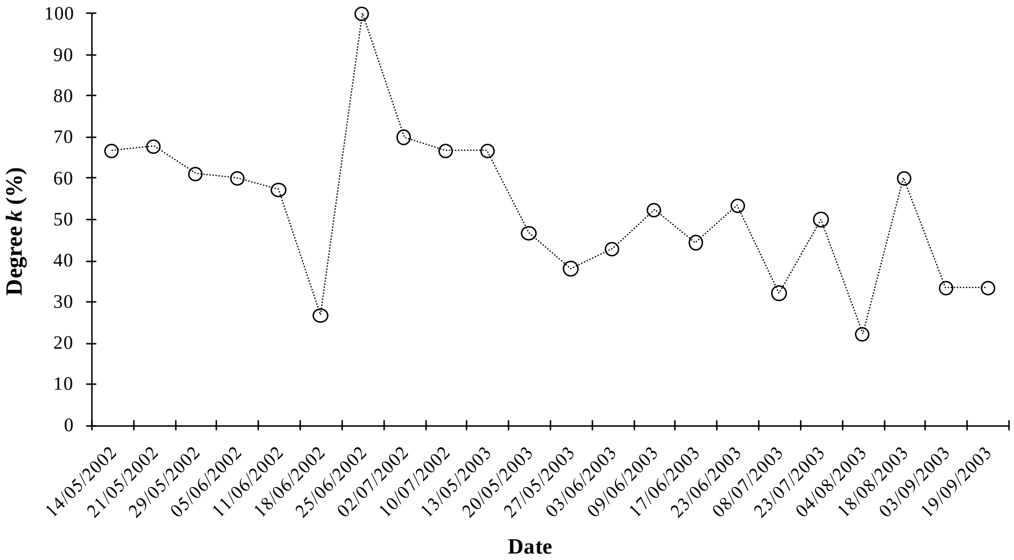

Figure 6.9: Mean degree *k* of connectivity (%) for complete social networks for larval fish in the Stoneham lakes, Hampshire in 2002 and 2003 per sampling date.

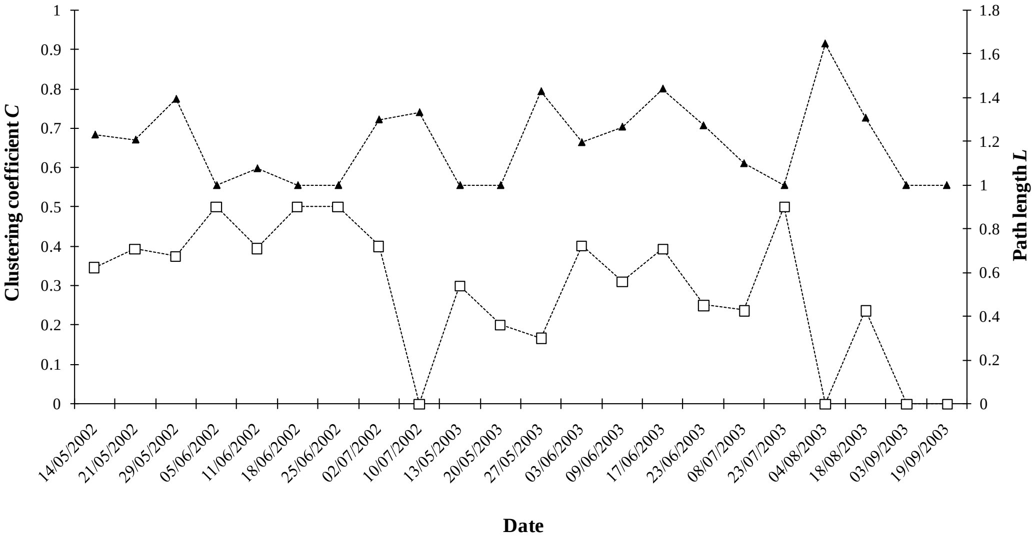

Figure 6.10: Mean clustering coefficients *C* (□) and mean path length *L* (▲) for complete social networks for larval fish in the Stoneham lakes, Hampshire in 2002 and 2003 per sampling date.

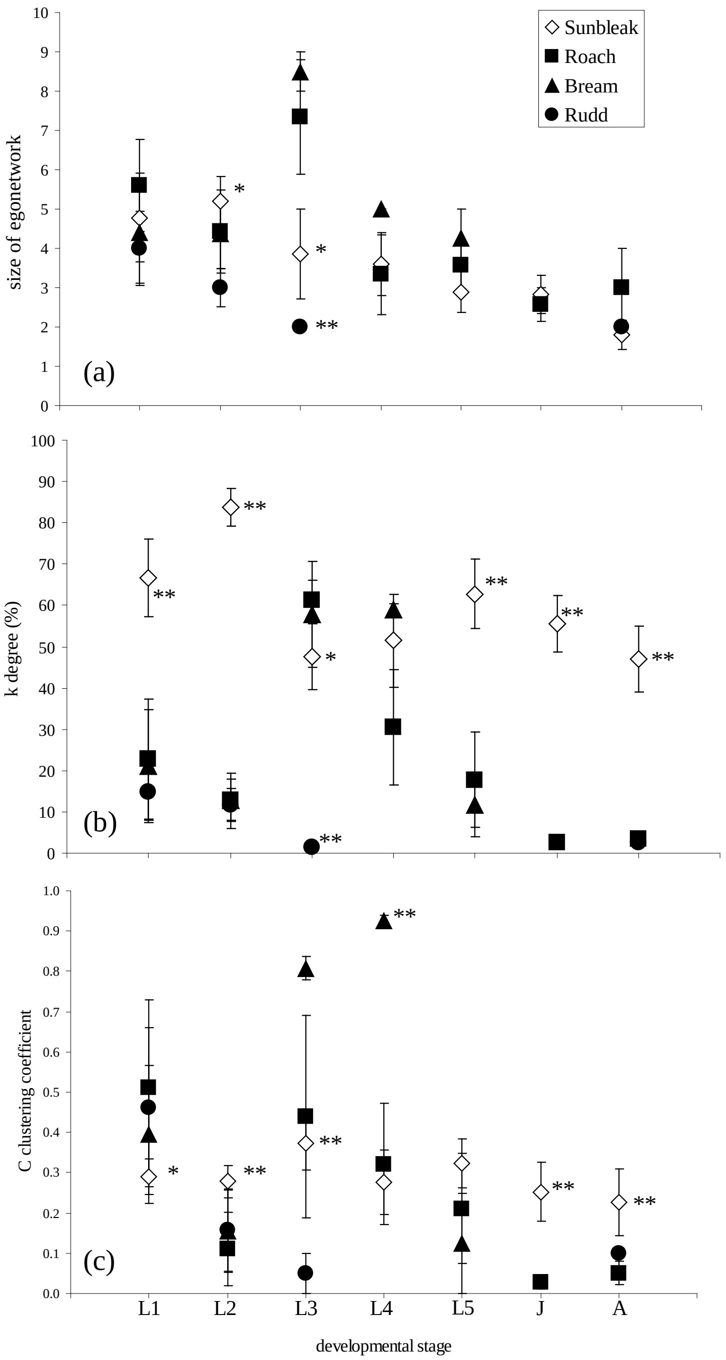

Figure 6.11: (a) Size of ego-networks per developmental interval for sunbleak, roach, bream and rudd. Statistically significant differences are presented as ** at $P < 0.01$ and as * at $P < 0.05$. The decrease in ego-networks size with time was significant ($y = -0.5223x + 5.656$; $r^2 = 0.98$; $P < 0.05$) in sunbleak. (b) Degree *k* of the connectivity of the ego-networks developmental intervals of sunbleak, roach, bream and rudd. (c) Clustering coefficients *C* per ego-network at each developmental interval of sunbleak, roach, bream and rudd (L1, larval stage 1; L2, larval stage 2; L3, larval stage 3; L4, larval stage 4; L5, larval stage 5; J, juvenile stage; A, adult stage).

6.9 Discussion

The social networks constructed for this fish assemblage exhibited characteristics of ‘Small World Models’ (Watts and Strogatz, 1998). The observed social networks with low clustering coefficients and short path lengths (Figure 6.10), displayed attributes of both, random and regular networks, which is typical of these models (Watts and Strogatz, 1998). Low clustering indicates that populations are more susceptible to epidemics, as infections may spread rapidly between fish and through the entire network (Newman, 2003b; see also Chapter 5). The occurrence of similarities with a small world network is of particular interest because short path length in such structured networks is associated with the rapid transmission of information between fish (Watts and Strogatz, 1998; Newman, 2002; Croft, 2003).

Sunbleak displayed numerous social ties with native fishes. Well-connected networks are evidence of this, with each species developmental interval directly tied to an average of 52 % in the complete networks (Figure 6.9) and to 59 % in the ego-networks (Figure 6.11b). In general, during early life the ties between sunbleak and native fish species are much stronger than those that link native species to each other. The success of establishment and subsequent invasion may be highlighted not only by the capacity of the alien species to adapt to the new environment, but also in its capacity to integrate into the native fish community. The low level of clustering amongst the studied fish groups suggests that individuals prefer to maintain social associations among species of similar larval developmental status. Before reaching the juvenile period, the similar physiological developmental level at same developmental intervals may force them to form groups and exploit similar resources (Pinder *et al.*, 2005a). This relates to the hypothesis of Gozlan *et al.* (2003b) that the small adult size of sunbleak could be an advantage over the young-of-the-year of other species as sunbleak juveniles and adults preferred to form groups with native species of lesser developmental status.

Repeated occurrence of pair-wise associations between sunbleak and native species of similar developmental stages suggests a potential for the development of cooperative behaviour (Dugatkin, 1997), which may further increase the advantages for an invasive species. The influences of habitat use, site fidelity and active choice of social partners and their reflection in the networks call for confirmation in further studies. However, active preference/avoidance of individuals as social partners has previously been found in female guppies by Croft *et al.* (2004).

Sunbleak at the early developmental stages, and also in later life, may choose to shoal with fish of similar phenotype to prevent attacks from predators that may be attracted by odd individuals in a group (Theodorakis, 1989; Peuhkuri, 1998; Mathis and Chivers, 2003). In laboratory and field studies, several fish species were found to form shoals according to body size (Ranta and Lindström, 1990; Krause, 1994; Krause and Godin, 1994; Krause *et al.*, 1996b; Krause *et al.*, 1996a; Peukhuri *et al.*, 1997). The structure and position of sunbleak within in a shoal may have also been influenced by illumination levels, as individual animals in shoals were previously found to be closer together increased light (Dobler, 1977). However, the above studies focus in their work on adult fish and little is known on early life shoaling.

In conclusion, this new insight into the social relationship among alien and native fish species during early life reveals the potential for alien species not only to transfer new infectious disease but also to spread them faster among the native community. This is crucial due to the non-native parasites hosted by sunbleak (see also Beyer *et al.*, 2005). The study of the parasite fauna of sunbleak revealed that it is a host for two non-native copepodid parasites, *Neoergasilus japonicus* and *Ergasilus briani*, which are of Asian and Eurasian origin, respectively (Chapter 5). The results of the social network analysis raise concerns over the speed of transmission of these non-native parasites within the social networks. The social aspects of parasite and/or disease transmission could be a useful tool in invasion ecology and potentially in risk assessments.

6.10 Part B: Chapter summary

This was the first attempt to describe the social integration of an alien fish into the social network of a native fish assemblage. It was shown that invasive sunbleak were more strongly interconnected with native species than the native species with each other. The social networks revealed characteristics of a ‘small world’ (Watts and Strogatz, 1998). The findings may indicate potential traits of successful invaders and the implication for the spread of disease. Finally, the success of establishment and subsequent invasion may be highlighted not only by the capacity of the new species to adapt to the new environment, but also in its capacity to penetrate the social circle of the native community.

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7. Potential for biotic resistance against topmouth gudgeon invasion[22]

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[22] Data from parts of this chapter were presented at the ICAIS Conference in May 2006: Beyer, K., Gozlan, R.E. & Copp, G.H. ‘Home vs Guests – The Game is on Against Aliens’. Another part of this chapter has been published in: Beyer, K., Miranda, R., Copp, G.H. & Gozlan, R.E. (2006) Biometric data and bone identification of topmouth gudgeon *Pseudorasbora parva* and sunbleak *Leucaspius delineatus*. *Folia Zoologica* 55(3), 287–292.

7.1 Introduction

Biological resistance was recognized as the earliest and strongest factor affecting the probability of establishment of introduced species (Moyle and Light, 1996). Successful invasion may be inhibited by species-rich communities due to great resource availability and predator abundance (Fox and Fox, 1986; Pimm, 1991; McCann *et al.*, 1998; Stachowicz *et al.*, 1999; Byers and Noonburg, 2003). Native predators may prey on introduced species (Trowbridge, 1995). An investigation into the non-native green alga *Codium fragile* on the rocky shores of New Zealand reported that 6 of 11 native grazers, which included four gastropods and two echinoids, preyed to some extent on the introduced alga (Trowbridge, 1995). Some of the native predators had a preference to feed on the new species while others favoured native subspecies or exhibited no preference. However, in some cases predation by native species on introduced ones has greatly inhibited the new species' establishment (Robinson and Wellborn, 1988; Baltz and Moyle, 1993). For example, predation by native fish on a newly introduced clam *Corbicula tluminea*, which is native to South East Asia, prevented the clam's establishment in a reservoir in Texas, USA (Robinson and Wellborn, 1988). In a study on stream fish assemblages in California, USA, native fish feeding on non-native fish species was a particularly important factor in the resistance against their invasion (Baltz and Moyle, 1993). However, Baltz and Moyle (1993) also noted that this resistance applied to streams that were largely undisturbed by anthropogenic pressures. In some streams, the persistence of native fish assemblages has been reported despite frequent invasions by introduced fish species in low numbers (Moyle *et al.*, 1982; Moyle and Vondracek, 1985). Such observations corroborate hypotheses of biotic resistance. Interestingly, Ross (1991a) noted that established stream fish assemblages are rarely successfully invaded by introduced fishes. Their study concluded that these assemblages were structured mainly by competition and predation (Ross, 1991a).

Trophic guilds and feeding habits vary widely between fish, while specialisation on one particular prey category throughout their entire life cycle rarely takes place

(Noble *et al.*, 2007). Few European freshwater fish species have specialist feeding habitats. Noble *et al.* (2007) present a summary of trophic guilds in fish and propose a standardized guild classification for use in freshwater fish across Europe, which is generally based on the dominance of food items in the diet. The classes for trophic guilds are: 1) planktivores (feeding on high proportions of zooplankton and/or phytoplankton), 2) herbivores (feeding on high proportions of plant material), 3) detritivores (feeding on high proportions of detritus), 4) omnivores (diet 'generalist' including a wide range of flora and fauna), 5) insectivores/invertivores (feeding on high proportions of invertebrates/insects), 6) benthivores (feeding on high proportions of benthic organisms), 7) piscivores (diet consists of > 75 % fish) and 8) parasite (parasitic feeding mode) (Noble *et al.*, 2007). However, Noble *et al.* (2007) also accept that some fish species do not fit into distinct classes, and for those, consider joint groups such as 'insectivores/piscivores'. The acknowledgement of intermediate or joint trophic strategies is important for example when studying piscivorous fish species, where some fish species are 'obligate piscivores' (those that rely entirely on fish as prey; e.g. pike) and others are considered as 'facultative piscivores' (those that only partially depend on a piscivorous diet; e.g. salmonids, eel, perch).

In inland waters of England a potential fish predator of introduced fish species is the pike, which becomes an obligate piscivore in its first year of life (Mann, 1976b; 1982). Facultative piscivorous fishes are perch, brown trout, Atlantic salmon, chub and eel (Elliott, 1967; Hellawell, 1971; Elliott, 1972; 1975b; a; Mann, 1976a; Mann, 1978; Lammens *et al.*, 1985; Mann and Blackburn, 1991; Forseth and Jonsson, 1994). Many piscivorous fish species are opportunistic foragers, taking the most abundant available prey (Britton and Shepherd, 2005). It is, therefore, expected that any native co-occurring piscivorous species could mediate an amount of predatory resistance against an introduced fish species. This would be particularly important in locations where large numbers of the non-native species disperse into receiving waters (see Chapter 4).

Indeed, biological resistance in the form of predation may be a factor limiting the dispersal of topmouth gudgeon observed in Tadburn Lake stream (see Chapter 4). This water course is of particular interest because it receives high propagule pressure (drift densities) of topmouth gudgeon (Chapter 4). In Tadburn Lake stream, there are no obligate piscivores (see also Chapters 4 and 6A) and so facultative predators were used for this investigation. The facultative piscivores present were eel, brown trout and chub. As eel numbers were low, chub and brown trout only were used for investigations into their diet and they overlapped in their microhabitat use with topmouth gudgeon (Chapter 6). These species have previously been found to feed on fish in inland waters of England (Elliott, 1967; Hellawell, 1971), and so had the potential to mediate biological resistance against topmouth gudgeon. Consequently, both were used as model native predators and their role in potential biotic resistance against invasion was examined. Quantification of potential resistance against non-native fish mediated by native predators could provide knowledge that may be incorporated into non-native species risk assessments (Copp *et al.*, 2005b; 2005c).

The purpose of the work presented in this chapter was to provide a ‘snapshot’ insight into the incidence and intensity of predation on topmouth gudgeon by native piscivorous fish species in Tadburn Lake stream. The study was localised in space and time. Studies attempting to assess the potential for biological resistance in ecosystems with high propagule pressure are scarce. The aim of the present study was to assess the extent of native fish predation exerted on non-native fishes, and more specifically to estimate the level of biotic resistance against topmouth gudgeon in Tadburn Lake stream. The specific objectives were to 1) determine the incidence of predation on topmouth gudgeon by brown trout and chub and 2) quantify the intensity of predation by these two native predators on topmouth gudgeon.

7.2 Materials and methods

Field work

To investigate the incidence of predation on topmouth gudgeon by brown trout and chub, the gut contents of the latter two species were examined during three sampling surveys carried out within 18 days of each other (28 April, 10 May, and 16 May 2005). Fish were captured in a 1 km stretch of Tadburn Lake Stream between 0.2 and 1.2 km downstream of Crampmoor Fishery. On each date, the stream was sampled using a back-pack electrofishing unit (fitted with a 15 cm diameter anode) in an upstream direction (Output: 50 – 100 Hz PDC with an operating current of 1 to 2 Amps). Immobilized fish were placed in a bucket and identified to species level, counted, and measured for fork length (to the nearest 1.0 mm). Brown trout and chub were also weighed to the nearest 0.1 g. All fish, except brown trout (79 specimens) and chub (63 specimens), were immediately returned to the stream alive.

The gut contents of live brown trout were obtained by stomach flushing using mechanised pressure (Strange and Kennedy, 1981; Georges and Gaudin, 1984; Kamler and Pope, 2001), which reduces the impact (i.e. mortality) of the study on this species of conservation interest. Strange and Kennedy (1981) report that stomach flushing allows the removal of 98.9 % of stomach contents and that it has a very limited effect on survival (99.3 % survival). Also, the technique can be used on relatively small fish (> 4 cm length) (Strange and Kennedy, 1981). The stomach flushing apparatus consisted of a polyethylene tube (≈5 mm diameter, ≈50 cm length that was fitted at one end with a 100 ml syringe (the pump end) and at the other end with a 5 ml pipette (the probe end). Prior to flushing, each brown trout was anesthetized using 2-Phenoxyethanol according to their length and placed horizontally in a fine-mesh net. The syringe was filled with water, then the fish was held with the mouth open over the receiving tray, and the probe end of the flushing apparatus was inserted gently through the mouth into the stomach — this was facilitated by the initial flow of water from the probe end as the syringe was gently squeezed down. The water pressure flushed out the stomach contents through the oesophagus and into the tray. This process was repeated either five times or until no more items were expelled from the fish, whichever occurred first. The contents of the tray were then filtered through a fine-meshed net and preserved in 10 % formalin. Brown trout were then placed into a recovery bucket containing only oxygenated water and, upon recovery, were returned to Tadburn Lake stream alive.

Stomach flushing was deemed unsuitable for chub, because of the anatomy of the digestive tract in this species (Harder, 1975). In the field and soon as possible after capture, all 63 chub were sacrificed by Schedule 1 methods as per the ‘Animals (Scientific Procedures) Act 1986’ (Home Office, 1986a; b), using an overdose of 2-Phenoxyethanol followed by severance of the spinal cord at the base of the skull (refer to Section 3.2 of Chapter 3 for further details on Schedule 1 methods). Each individual was subsequently dissected to remove the intestinal tract, which was preserved in 10 % formalin for subsequent processing in the laboratory. Expelling of stomach contents either during electrofishing or during the exposure to 2-Phenoxyethanol was not observed. However, small quantities may have been expelled, which may not have been visible to the naked eye.

Dietary examinations and/or surveys to confirm the presence of other piscivorous fauna, such as mammals (e.g. otters) and/or birds (e.g. cormorants *Phalacrocorax carbo carbo* (L.)), were not undertaken. However, both species are reported to prey on freshwater fish species in inland waters of England (Roche *et al.*, 1995; Britton *et al.*, 2002; Copp and Roche, 2003; Britton and Shepherd, 2005; Britton *et al.*, 2005; Miranda *et al.*, 2008).

To determine benthic food availability, six kick samples were taken along the same stretch of stream that was electrofished on 12 May 2005 covering all available habitat. Kick sampling was carried out to provide a snapshot of the available food resource within the stream and was carried out within the 18-day period of fish sampling. Samples were collected using Hynes’ method as described by Macan

(1958): a micro-mesh net fixed onto a 50 x 50 cm square wooden frame was held against the stream bed and the area immediately upstream of the net was disturbed. The content of the net was then preserved in 10 % formalin for processing in the laboratory.

Laboratory processing

The anterior third of the alimentary tract was examined in each of the chub (Hellawell, 1971), whereby the gut was cut at point of entry into the abdomen and a second cut was made at the first bend where the intestine runs anteriorly. The gut contents were removed and then stored in 10 % formalin.

The individual gut items from each fish and the kick samples were sorted and identified to at least family level and, where possible, to species (Henry, 1922; Scourfield and Harding, 1966; Macan, 1971; Petkovski, 1973; Harding and Smith, 1974; Elliott and Humpesch, 1983; Amoros, 1984; Fitter and Manuel, 1986; Elliott *et al.*, 1988; Edington and Hildrew, 1995; Bass, 1998; Savage, 1999; Wallace *et al.*, 2003). In each sample the presence of one or more food organisms or plant material which could not be enumerated was regarded as *one* occurrence of that dietary item. When a gut contained several different food items they were counted. Fish in the guts were counted, measured to the nearest 0.1 mm and identified to species either from whole specimens or from bones found. When the body length of topmouth gudgeon as a prey item could not be determined directly (due to deterioration from digestion), the approximate body lengths were regressed from bone lengths (Table 7.1, Figure 7.1).

Regression relationships between head bone lengths and body size (standard length and body weight) were established[23] (Beyer *et al.*, 2006). Forty topmouth gudgeon

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[23] This work was part of a collaborative study between the author and Dr. R. Miranda, at University of Navarra who is a fish bone specialist and has been published as Beyer *et al.* (2006).

across a range of sizes (mean SL = 56 mm, S.E. = 1.37, n = 40, min. = 36, max. = 71 mm) were killed with an overdose of 2-Phenoxyethanol. In the laboratory, each specimen was measured for their standard length (SL, to the nearest 0.1 mm) and weight (Wt, to nearest 0.01 g). The standard length was used in this baseline study, as this measure had been used in previous studies on fish bones (Copp and Kováč, 2003; Hajkova *et al.*, 2003). Length conversions between fork (FL), total (TL) and standard (SL) lengths are presented in Appendix A. As per Copp & Kováč (2003), each individual was then boiled until the flesh was easily removable after which the bones were left to air dry. Some bones were lost due to breakage during this process. Shrinkage of bones during air drying was not tested. The number of bones (n) used for analysis and the regression parameters are given in Table 7.1, with bone images utilised for identification and measurements presented in Figure 7.1.

Information on bone vs body size regression relationships are used for investigations of interactions between fish and their predators. In most cases, such knowledge is only available for native prey species but not introduced ones. The biometry of bones in topmouth gudgeon has not been examined previously. Therefore, these data provide essential information for assessing the relative contribution of topmouth gudgeon to the diet of piscivorous predators in invaded water bodies, but potentially wherever this species may occur.

Table 7.1: Number of specimens of topmouth gudgeon, regression slope, intercept values, and coefficients of determination for linear and logarithmic relationships of bone sizes (BL, in mm) regressed against standard length (BL = *b*SL ± *a*) and body weight ($BL = a\mathrm{Wt}^b$) for the left (L) and right (R) sides of fish (mean SL = 55.5 mm, S.E. = 1.4, n = 40) from an aquaculture facility in Hampshire. All models were significant at $P \leq 0.001$.

		Standard length (mm)			Body weight (g)		
	n	r^2	*a*	*b*	r^2	*a*	*b*
R-dentary	31	0.912	-5.672	22.617	0.939	0.054	3.763
L-dentary	34	0.898	-5.733	22.925	0.909	0.066	3.625
R-maxilla	34	0.913	-1.435	22.838	0.885	0.110	3.322
L-maxilla	30	0.911	-4.770	24.074	0.906	0.089	3.557
R-premaxilla	23	0.917	-7.272	28.814	0.911	0.154	3.260
L-premaxilla	24	0.917	-0.508	24.434	0.918	0.123	3.755
R-pharyngeal	31	0.931	-6.423	22.984	0.900	0.061	3.685
L-pharyngeal	32	0.902	-4.025	21.913	0.855	0.070	3.524
R-cleithrum	30	0.904	-0.577	7.557	0.885	0.002	3.469
L-cleithrum	33	0.929	-4.233	8.047	0.928	0.002	3.652
R-operculum	33	0.900	+4.396	12.395	0.904	0.034	3.005
L-operculum	33	0.904	+2.903	12.750	0.882	0.030	3.085

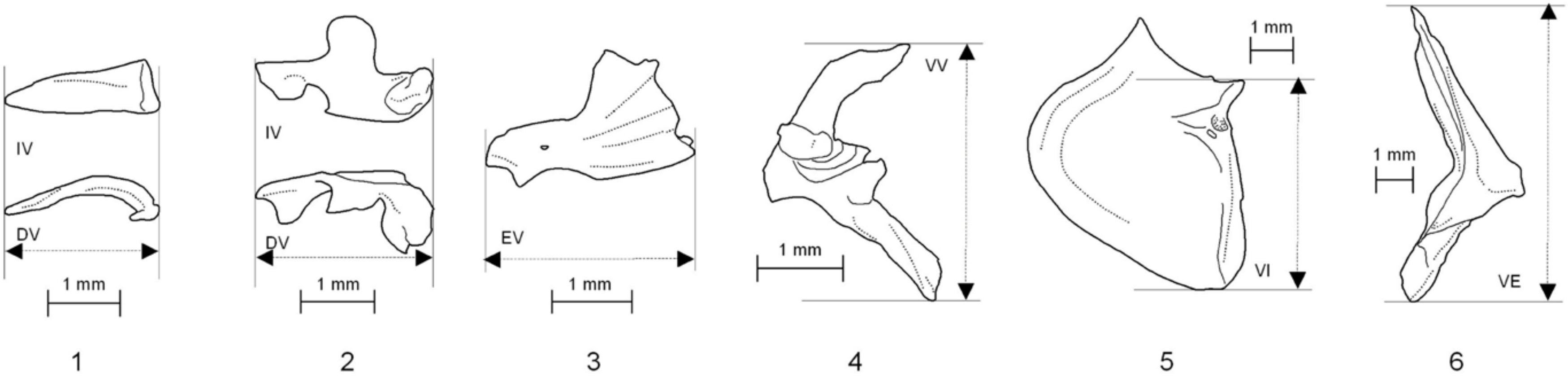

Figure 7.1: Measurements of pre-maxillae (1), maxillae (2), dentaries (3), pharyngeals (4), operculi (5) and cleithra (6) taken from topmouth gudgeon. The abbreviations are EV (external view), IV (internal view), DV (dorsal view) and VV (ventral view). All bones shown are from the left body side (Beyer *et al*., 2006).

Data analysis

The presence of each type of food item was regarded as *one* occurrence of that item to calculate the relative frequency of the occurrence of food items in the diet. The total number of occurrences of all food categories and the relative contributions made by each were computed for each predatory species as the proportional occurrence (%) of each food item ($n_{\text{diet item}}$) in the total diet per fish species with all individuals ($n_{\text{total number of diet items per fish species}}$) combined:

$$\text{Proportional occurrence (\%)} = (n_{\text{diet item}} / n_{\text{total number of diet items per fish species}})*100.$$

This method expresses the frequency of occurrence of the item in the diet and was favoured against the more commonly utilised method of evaluating the frequency of occurrence of predators in which a particular prey type would be observed (Hellawell, 1971). Predation on topmouth gudgeon was estimated as the mean number of prey per examined individual predator:

$$\text{Predation}_{\text{TMG}} = \text{number of prey/examined predator.}$$

Pearson’s correlation was applied to investigate how accurately predator size describes topmouth gudgeon size as prey.

Catch-per-unit-effort (CPUE) was calculated as the number of fish captured per hour of fishing and as follows: CPUE = n/f_{hr}, where n is the number of fish and f_{hr} is the fishing effort or the time (in hrs) fished.

Ivlev's index of electivity (E) was calculated for topmouth gudgeon as diet item contributors in both of the native predatory species investigated, as:

$$E = (Ri – Pi)/ (Ri + Pi),$$

where Ri is the relative abundance of topmouth gudgeon in the diet and Pi is the relative abundance of topmouth gudgeon in the local environment (= n_{TMG} km^{-1} of fished stream) as determined by electrofishing surveys (Ivlev, 1961). Index values can range from −1 to +1, with values nearing these extremes representing avoidance of the prey item or selection for the prey item, respectively. Values near zero indicate a prey species was consumed in proportion to its encounter rate in the environment.

To determine whether parametric or non-parametric statistical methods should be used, the equality of variances and normality of the data was tested using Levene’s and Kolmogorov-Smirnov statistics respectively. To determine differences in the diet composition between sampling days, between species, and between length groups within species, the non-parametric Kruskal-Wallis test was used (Sokal and Rohlf, 1998).

7.3 Results

During the three surveys, 610 fish represented by 11 different fish species were captured. The most common species captured were brown trout, chub, topmouth gudgeon and bullheads (Figure 7.2). The smallest fish encountered were sticklebacks, topmouth gudgeon and bullheads (Table 7.2). Species with the greatest body size were eels, brown trout, *Lampetra* spp, carp and chub. Mean sizes and weights of the examined predators are presented in Table 7.3. The removal of chub did not result in reduced capture over time. On 28 April, 10 May and 16 May 2005 a total of 14, 32 and 17 chub were captured respectively. It is possible that new individuals moved into the study area between the sampling dates from elsewhere in Tadburn Lake stream to the ‘habitat-patches’ that have become vacant.

The benthic fauna of Tadburn Lake stream consisted mainly of insects (53.1%), followed by Gastropoda (17.7%), and Crustacea (11.5%), with minor proportions of Hirudinea and Lamellibranchia and unidentifiable aquatic insects (Table 7.4). Of the insects, the most abundant taxon was Ephemeropterans (22.1%), which are indicators of good water quality (Hawkes, 1997; Walley and Hawkes, 1997) as well as being a valuable aquatic food source for resident insectivores.

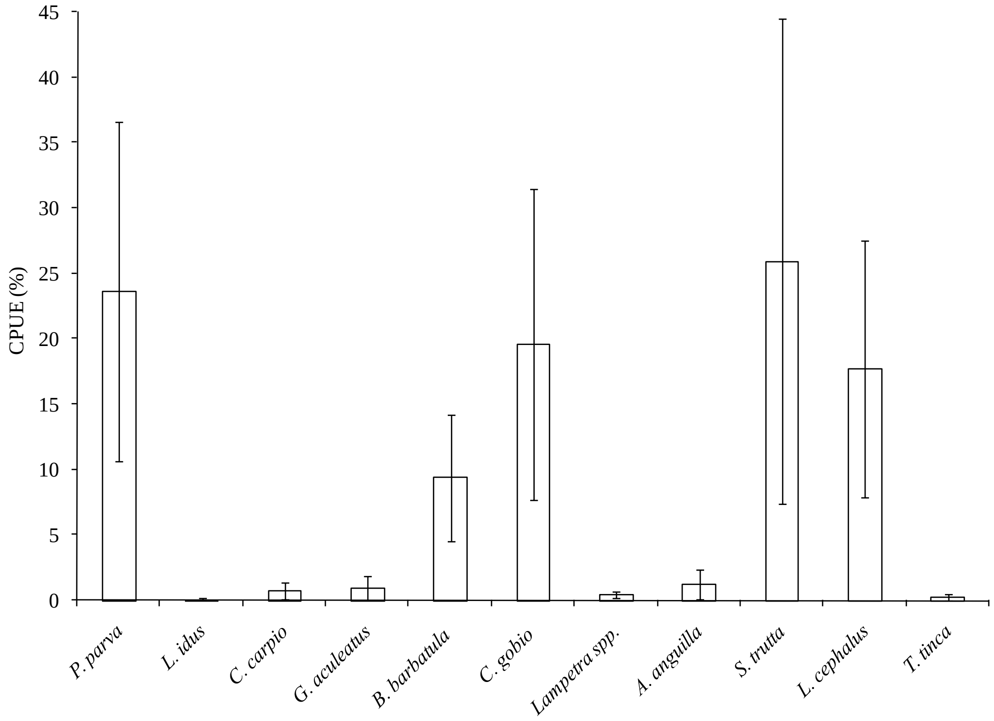

Figure 7.2: Mean and standard error bars of % proportion of total CPUE per species observed during surveys in Tadburn Lake stream within 1.2 km downstream of Crampmoor Fishery.

Table 7.2: Mean, standard errors (S.E.), minimum (Min) and maximum (Max) fork lengths (mm) of fish captured during electrofishing surveys in Tadburn Lake stream on 28 April, 10 and 16 May 2005 (also see Figure 7.2). n, number of fish.

Common name	Scientific name	Mean (mm)	S.E.	Min	Max	n
Topmouth gudgeon	*P. parva*	50	3	32	82	213
Golden Orfe	*L. idus*	100	0	100	100	1
Mirror Carp	*C. carpio*	152	55.3	71	258	4
Three-Spined Stickleback	*G. aculeatus*	35	0.4	32	38	7
Stoneloach	*B. barbatula*	94	4	71	111	81
Bullhead	*C. gobio*	54	2	42	73	151
Lampe	*Lampetra* spp	165	15	150	180	4
Eel	*A. anguilla*	318	12	295	350	6
Brown Trout	*S. trutta*	199	7	108	312	79
Chub	*L. cephalus*	152	2	122	194	63
Tench	*T. tinca*	89	0	89	89	1

Table 7.3: Mean, standard error (S.E.), minimum (min) and maximum (max) fork lengths (mm) and weights (g) of chub and brown trout in length groups captured in Tadburn Lake stream on 28 April, 10 and 16 May 2005 that underwent dietary analysis. n, number of fish. See Figure 7.3 and Figure 7.4 for length frequencies on which length groups are based).

		Fork Length (mm)				Weight (g)				
Species	Length groups	Mean	S.E.	Min	Max	Mean	S.E.	Min	Max	n
Chub	1	137	1	122	149	36.2	1.4	21.5	59.3	35
	2	170	2	155	194	70.7	3.5	49.3	112.2	28
Brown Trout	1	128	2	108	139	27.9	2.0	11.5	56.6	24
	2	169	4	152	190	59.2	4.7	30.7	86.6	13
	3	233	3	201	257	159.0	6.3	95.7	200.0	31
	4	292	4	272	312	200.0*	0.0	200.0	200.0	11

* Due to malfunctioning of the balance above 200 g, no means were calculated for fish weighing > 200 g.

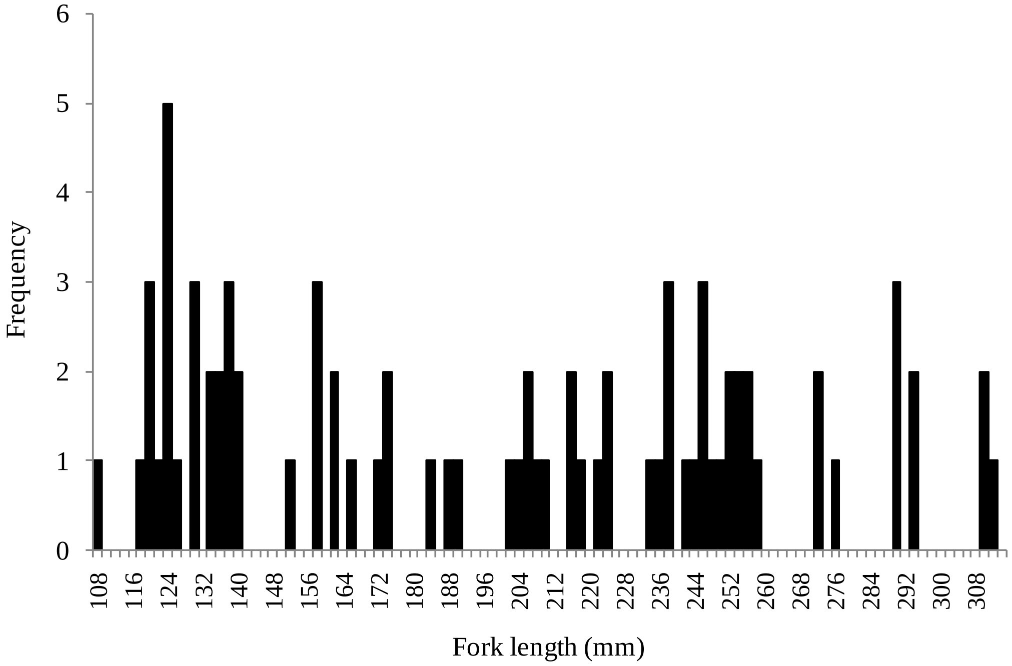

Figure 7.3: Length frequencies of brown trout captured in Tadburn Lake stream on 28 April, 10 and 16 May 2005 and examined for diet.

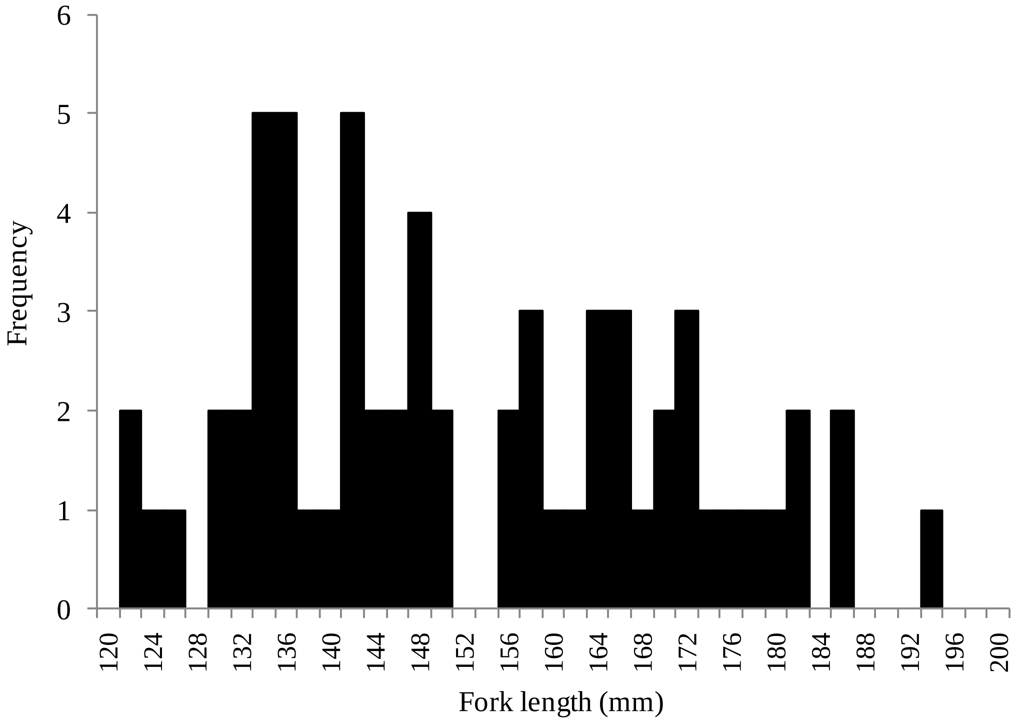

Figure 7.4: Length frequencies of chub captured in Tadburn Lake stream on 28 April, 10 and 16 May 2005 and examined for diet.

Gut analyses revealed the occurrence of topmouth gudgeon in the diet of 30 % of chub and 34 % of brown trout investigated. Diet composition was not significantly different between these two species, and was not different between sampling days or lengths groups within species (see Appendix G for diet data set and Appendix H for details on statistical results). The diet of both species did not contain hirudineans, gastropods or lamellibranchs, which were all present in the benthic fauna (Table 7.4). Plant material occurred in the diet of a considerable proportion of brown trout and chub (Table 7.5), as did aquatic and aerial insects. Organisms of terrestrial origin occurred infrequently in the diet.

Fish in brown trout and chub diet were only represented by topmouth gudgeon (except for indeterminate fish eggs) and accounted for approximately 7 % (S.E. ± 1.25) and 8 % (S.E. ± 1.65) respectively. The mean number of topmouth gudgeon consumed per trout was 0.42 (S.E. ± 0.08). Chub consumption of topmouth gudgeon was slightly lower, averaging 0.35 (S.E. ± 0.72) per fish. Correlation of body size between predator and topmouth gudgeon prey was insignificant for chub ($n = 22$, $r_{[0.413]} = 0.214$, $P > 0.05$) but was significant for brown trout ($n = 33$,

$r_{[0.436]} = 0.458$, $P \leq 0.01$) (Figure 7.5; Figure 7.6). Ivlev's dietary electivity index for topmouth gudgeon was -0.82 for trout and -0.66 for chub, suggesting that topmouth gudgeon was taken as a prey item less often than expected.

Table 7.4: Mean and standard errors (S.E.) for proportional occurrence of invertebrates in six kick samples taken of the benthic fauna in Tadburn Lake stream on 12 May 2005.

			Occurrence (%)	
			Mean	S.E.
Hirudinea	Erpobdellidae	*Erpobdell* spp	7.35	1.55
Gastropoda	Hydrobiidae	*Potamopyrgus* spp	8.86	0.51
	Ancylidae	*Ancylus* spp	8.86	0.51
Lamellibranchia		*Anodonta* spp	1.52	1.52
Crustacea	Decapoda	*Astacus* spp	1.52	1.52
	Amphipoda	*Gammarus pulex*	8.86	0.51
	Isopoda	*Asellus* spp	1.11	1.11
Insects	Plecoptera	*Leuctra* spp	2.90	1.84
	Trichoptera		4.29	1.97
	Ephemeroptera	*Baetis* spp	7.35	1.55
	Ephemeroptera	*Leptophlebia* spp	7.35	1.55
	Ephemeroptera	*Ephemera* spp	7.35	1.55
	Hemiptera		1.11	1.11
	Coleoptera	*Limnius* spp	2.63	1.69
	Diptera	*Simulium* spp	7.20	1.51
	Diptera	*Tipula* spp	4.02	1.82
	Diptera	Chironomidae	8.86	0.51
Indeterminate aquatic insects			8.86	0.51

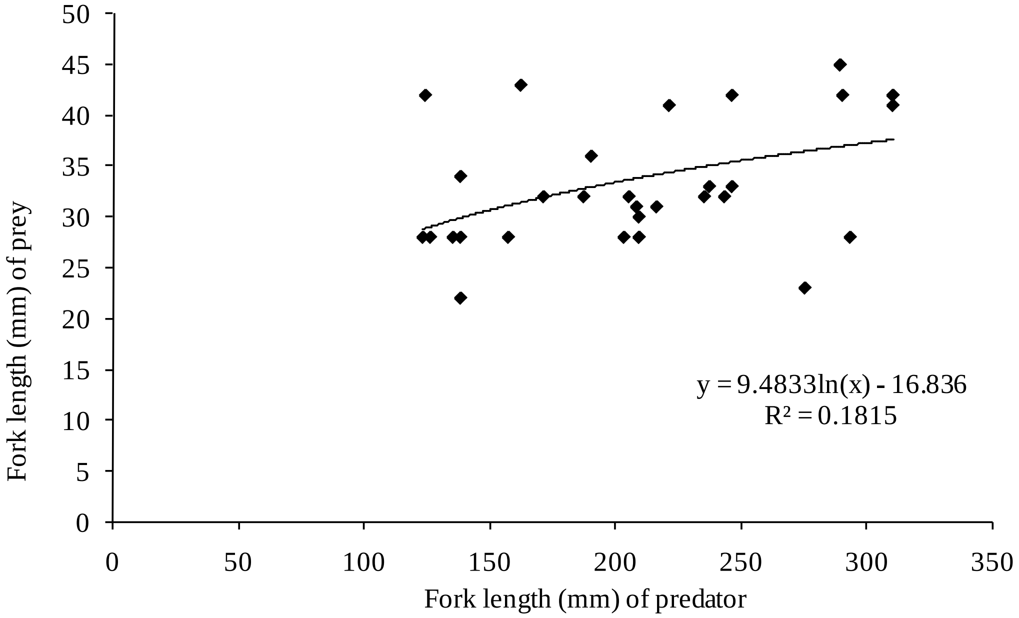

Figure 7.5: Correlation between body sizes of predator brown trout and topmouth gudgeon taken as prey in Tadburn Lake stream on 28 April, 10 and 16 May 2005 (n = 33, $r_{[0.436]} = 0.458$, $P \leq 0.01$).

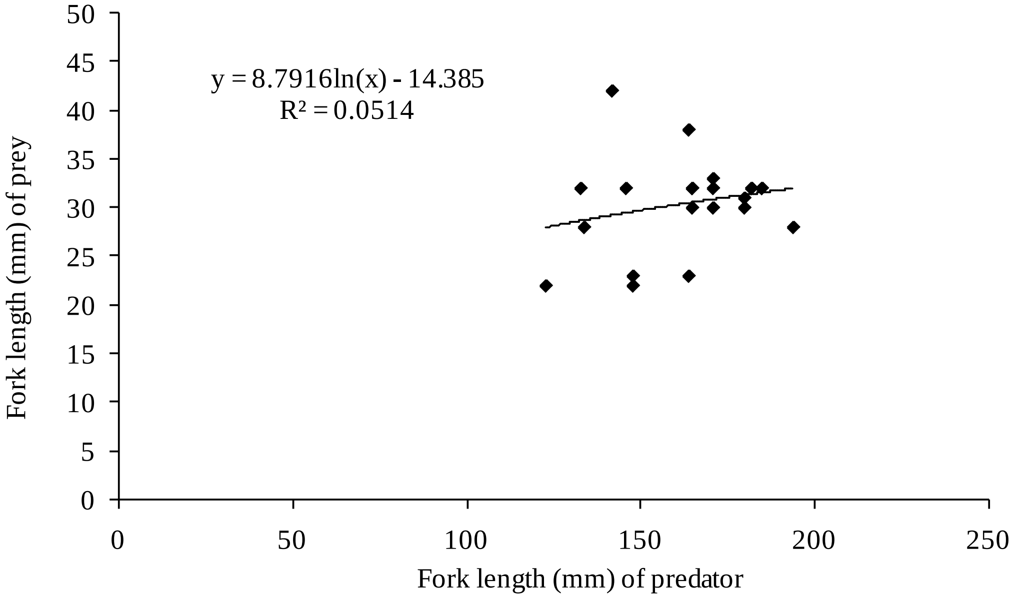

Figure 7.6: Correlation between body sizes of predator chub and topmouth gudgeon taken as prey in Tadburn Lake stream on 28 April, 10 and 16 May 2005 (n = 22, $r_{[0.413]} = 0.214$, $P > 0.05$).

Table 7.5: Mean and standard errors (S.E.) of dietary composition as percentage contributions of each food item to the total diet of chub (n = 63) and brown trout (n = 79) from Tadburn Lake stream in April/May 2005.

			Trout		Chub	
			Occurrence (%)		Occurrence (%)	
			Mean	S.E.	Mean	S.E.
Plant material	Total Plant Material		24.68	2.18	31.42	2.85
Fish		*P. parva*	7.14	1.22	7.83	1.65
		Indeterminate fish eggs	0.21	0.21	0.00	0.00
		Total fish	7.35	1.25	7.83	1.65
Aquatic Insects						
Diptera	Chironomidae	Tanypodinae	0.57	0.29	0.00	0.00
		Orthocladinae	0.44	0.26	0.00	0.00
		Simulidae	0.54	0.32	0.13	0.13
	Indeterminate Chironomidae		5.42	1.02	14.54	1.73
	Tipulidae	Dicranota	0.38	0.38	0.14	0.14
Coleoptera	Gyrinidae	Gyrinidae	0.37	0.26	0.00	0.00
Trichoptera	Limnephilidae	Limnephiloida	1.84	0.92	0.31	0.31
	Leptoceridae	*Athripsodes* spp	7.50	1.53	8.01	2.06
	Indeterminate Trichoptera		0.16	0.16	3.24	1.04
Hemiptera	Gerroidea	Mesovelidae	0.44	0.26	0.00	0.00
Ephemeroptera	Leptophlebidae	Paraleptophlebia	0.39	0.23	0.00	0.00
	Baetidae	*Baetis* spp	2.15	0.84	0.44	0.32
	Ephemeridae	*Ephemera* spp	0.43	0.31	3.71	1.36
	Indeterminate Ephemeridae		0.60	0.35	0.37	0.26
Apterygota		Collembola	0.18	0.18	0.00	0.00
Neuroptera	Sisyridae		0.46	0.38	0.33	0.33
Exopterygota	Hemiptera	Corixidae	0.32	0.23	0.00	0.00
Indeterminate Aquatic Insects			0.00	0.00	1.29	0.65
		Total Aquatic Insects	23.71	2.17	17.48	1.70
Aquatic Crustaceans						
Copepoda	Cyclopoidae		1.15	0.52	0.13	0.13
Decapoda	Astacidae		1.41	0.81	0.41	0.30
Amphipoda	Gammaridae	*Gammarus pulex*	6.86	1.15	8.64	1.36
	Total Aquatic Crustaceans		9.41	1.38	8.64	1.36
Aerial Insects						
Diptera	Nematocera		8.60	1.32	10.13	1.63
	Tipulidae		1.67	0.65	0.53	0.37
	Indeterminate Aerial Diptera		5.99	1.25	11.03	1.62
Coleoptera		Beetle	2.56	0.65	0.26	0.26
	Curculionoidea	Weevil	0.63	0.39	0.32	0.32
Hemiptera	Heteroptera		0.87	0.44	0.13	0.13
	Indeterminate Aerial Insects		3.79	0.95	3.07	0.94
		Total Aerial Insects	24.74	2.08	12.08	1.62
Terrestrial Insects						
Crustacea	Isopoda	*Asellus* spp	1.64	0.51	1.19	0.70
Dermaptera		Earwig	0.74	0.40	0.00	0.00
Arthropoda	Diplopoda	Millipede	0.71	0.37	0.00	0.00
Terrestrial items	Araneida		1.20	0.45	0.00	0.00
	Nematoda		1.02	0.47	0.00	0.00
	Trematoda		1.18	0.70	0.00	0.00
Detritus			1.10	0.50	0.98	0.56

7.4 Discussion

7.4.1 Overview

Fish were only represented by topmouth gudgeon and accounted for around 7 % (S.E. ± 1.25) and 8 % (S.E. ± 1.65) of the total brown trout and chub diet respectively. Ivlev's dietary electivity index for topmouth gudgeon was -0.82 for trout -0.66 for chub, suggesting that topmouth gudgeon was taken as a prey item less frequently than expected. Neither brown trout nor chub were selective towards topmouth gudgeon in their prey, while both species fed on the remaining food resources of Tadburn Lake stream.

7.4.2 Potential for biological resistance in Tadburn Lake stream

Species-poor communities are thought by some to be more susceptible to invasion by non-native species than species-rich communities (Stachowicz *et al.*, 1999; Byers and Noonburg, 2003), but the evidence is equivocal (Ricciardi, 2001). Various covariates have to be accounted for when examining invasion processes that may affect the relationship between species diversity and invasibility[24] (Naeem *et al.*, 2000; Shea and Chesson, 2002). Tadburn Lake stream contained a fish assemblage of 11 different species, including three non-native fishes (golden orfe, mirror carp, and topmouth gudgeon). All three of the non-native species originated from Crampmoor Fishery, which lies upstream, but only topmouth gudgeon seems to pose a threat of invasion (see also Chapter 4). Of the native species, chub occurs in high numbers uncharacteristic of trout streams such as this, and may have the potential to impose a competitive threat to co-existing fish species. Chub have long been known to express homing behaviour (Libosvárský, 1966; Allouche *et al.*, 1999), which may include patch defence behaviours, as suggested for some other cyprinids (Peňáz *et al.*, 2002; Robalo *et al.*, 2003). Such behaviour may include increased feeding on prey fish that may pose a 'threat to their patch'. Patch defence behaviour in chub from Tadburn Lake stream, however, was not tested.

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[24] Invasibility is the likelihood that an environment will be successfully invaded by a non-native species.

Predation by brown trout and chub on topmouth gudgeon was low, representing 7 % and 8 % of total diet respectively. Based on these results, it would appear that this predation was too low to have any perceivable impact on the number of topmouth gudgeon in Tadburn Lake stream. In fact, topmouth gudgeon do not appear to be a preferred prey of the native predators (Ivlev, 1961), though they were the only fish species consumed. A generally lower selectivity by brown trout and chub for fish as prey was observed when compared with other studies (Elliott, 1967; Hellawell, 1971). It is possible that this could have been influenced by 'predator avoidance' of topmouth gudgeon, a behaviour which has been observed elsewhere in this species (Takashi Asaeda and Manatunge, 2005). Potential predator avoidance (Takashi Asaeda and Manatunge, 2005) coupled with favourable life history traits (Chapter 3) in topmouth gudgeon may enhance their establishment success (Reusch, 1998). The topmouth gudgeon population receives a steady supply of new recruits with drift from the fishery (Chapter 4) and reproductive effort in the stream is high (Chapter 3). Biological resistance by native predators captured during this study may be discounted. The present results, in combination with the exclusion of food resource limitations, support the previous assumption that Tadburn Lake stream provides a transit area for establishment and further dispersal of topmouth gudgeon in the wild (see also Chapter 4).

The results showed that chub and brown trout were non-selective for topmouth gudgeon as prey. However, it is important to consider that these results are based on a 'snapshot' study that was limited in space and time. Also, owing to the absence of an obligate predator in Tadburn Lake stream, two facultative predators were investigated, which may by nature only have limited potential to facilitate biological resistance *via* predation against introduced fish species, as they only partially depend on a piscivorous diet. As a result, it appeared that even a comparably large number of facultative predators (79 brown trout, 63 chub) may have only very limited potential to mediate biological resistance against topmouth gudgeon. The actual removal of all chub on each sampling date was not expected to have biased the results. The number of chub captured on each date ranged from 14, 32 and 17 chub on 28 April, 10 May and 16 May 2005 respectively. It is possible that new individuals of chub moved into the study area from elsewhere in the stream to inhabit habitat patches previously occupied by the chub that had been removed (Peňáz *et al.*, 2002; Robalo *et al.*, 2003).

Eel are also facultative predators, but only 6 individuals were captured during the study. The number of topmouth gudgeon consumed by those fish is unknown, but in light of the low number of eels, was not considered. The composition of the fish assemblage as regards piscivorous predators and their ecology in Tadburn Lake stream may lead to the conclusion to consider the introduction of an obligate piscivore (e.g. pike) into the system. This may be with the intention of creating the biological resistance. However, introducing a species with an ecological trait that does not naturally exist in an ecosystem may have disastrous consequences. Additionally, the obligate piscivore may not be selective for topmouth gudgeon, but may actually feed on native fish species, which are a familiar prey to them. As for the management of Tadburn Lake stream and its unwanted topmouth gudgeon population, which originates from the fishery upstream (Chapter 4) as well as from reproduction within the stream (K. Beyer, pers. obs.), it is recommended that: 1) outfall of non-native species is prevented from the fishery itself (see also Chapter 4 for more details) [Prevention] and 2) regular fish surveys are carried out during which all topmouth gudgeon are removed and destroyed [Control].

During electrofishing surveys carried out by the Environment Agency on 20 September 2001, 3 September 2003 and 20 August 2004 in Tadburn Lake stream, topmouth gudgeon were only observed in 2001 (Environment Agency, unpubl. data). This was surprising based on the results presented in this Chapter as well as Chapters 3 and 4. However, the 2001 survey reported that the species was ‘abundant’. The classification for an ‘abundant’ species ranges between 100 and 999 individuals of that species (Environment Agency, unpubl. data).

Comparison of the results is difficult as published studies investigating the ecology of native predators in relation to introduced species and their potential to create ecological resistance against fish invasions is scarce (Baltz and Moyle, 1993). In England, with the exception of Miranda *et al.* (2008), no other study has investigated this aspect previously. However, it appears that the feeding ecology of native predators may be an important factor, alongside with propagule pressure (see Chapter 4), promoting topmouth gudgeon's success at least at the study site. Interestingly, the study by Miranda *et al*. (2008) investigating whether native piscivorous otters may prey preferentially on non-native fish species in the Somerset Levels, South West England, revealed that the opportunistic otters fed only rarely (sunbleak) or not at all (pumpkinseed) on non-native fishes but rather on native fishes (eel, three-spined stickleback).

Other studies have investigated aspects for stream fish assemblages and the potential for invasion by new species (Moyle *et al.*, 1982; Moyle and Vondracek, 1985; Ross, 1991a; Baltz and Moyle, 1993). However, these studies have the general conclusion that streams and/or stream fish assemblages may be relatively resilient against non-native fish invasions, which contradicts the results of the present study. Baltz and Moyle (1993) reported that predation by native fish was a major factor in creating biological resistance against non-native fish invasions in streams that were largely undisturbed. This may highlight two important conclusions made from the present investigation: 1) The ecology of the native predators and subsequent low predation pressure may not contribute sufficiently to create a resistance against topmouth gudgeon; and 2) A large section of Tadburn Lake stream flows through an urban area on its way to the River Test, while providing public access on either bank (i.e. potential for anthropogenic disturbance).

Dietary studies in fish can be prone to bias as the results can be influenced by a variety of factors including the timing of sampling, feeding behaviour and body size of the fish (Windell and Bowen, 1978). It is possible that chub may not have been feeding heavily due to spawning (Fishbase, 2008), though this was not confirmed during this study. Elsewhere, larger specimens of brown trout were observed to feed more frequently on fish than smaller brown trout (Klemetsen *et al.*, 2003), while such size-related differences were not observed during the present study (see Results Section 7.3 and Appendix H for details). In both brown trout and chub, predation may be increased during darkness, because feeding behaviour is associated with drift (Elliott, 1973; Roussel *et al.*, 1999). However, the general diet of the native predators from Tadburn Lake stream was consistent with other studies (Hellawell, 1971; Elliott, 1973; Mann, 1976a). Food supply of the stream was of good quality (Hawkes, 1997; Walley and Hawkes, 1997), so the native predators may have no need to be selective towards topmouth gudgeon. The macro-invertebrate communities that were found in the samples are relatively diverse, including several members of the pollution sensitive orders of mayflies (Ephemeroptera), stoneflies (Plecoptera) and caddisflies (Trichoptera) (Hawkes, 1997; Walley and Hawkes, 1997).

7.4.3 Conclusions

Elton (1958) was the first to describe biotic resistance in relation to species diversity as a small-scale phenomenon, but it is also consistent with large-scale patterns of invasions (Byers and Noonburg, 2003). The examination of invasion processes requires knowledge of the life histories and propagule pressure of invaders and quantification of predation by native species. Several studies have confirmed that increased propagule intensity will increase successful establishment of introduced species (Beirne, 1975; Veltman, 1996; Green, 1997). In this study, propagule pressure was most likely greater than biological resistance created by facultative predators, which favoured establishment of topmouth gudgeon within the catchment downstream of the original introduction. A similar process, where propagule pressure by non-native species overwhelmed ecological resistance has been observed in forest under story plants (Von Holle and Simberloff, 2005). This study by Von Holle and Simberloff (2005) was the first study that demonstrated the dominance of propagule pressure over other covariate factors (e.g. the physical environment, number of resident species), which may influence the invasion success of a non-native species. No studies have been published as regards to such mechanisms in fish. The present study was localised in space and time and impacts of ecological resistance on topmouth gudgeon might be different elsewhere. However, the high propagule pressure (see Chapter 4) in combination with topmouth gudgeon taken as prey less frequently than expected by brown trout and chub, may have had profound implications on ecosystem invasibility.

7.5 Chapter summary

Topmouth gudgeon were taken less frequently than expected by brown trout and chub. The facultative predators, chub and brown trout, examined as part of the investigations into the potential for biological resistance and invasion by topmouth gudgeon, appeared not to provide sufficient predation pressure to mediate such resistance. Additionally, it is expected that propagule pressure of topmouth gudgeon was too great to be overcome by predation from facultative native predators (see Chapter 4).

8. General Discussion

8.1 Synthesis of the findings

8.1.1 Aims and objectives

The aim of this PhD thesis was to assess the ecological implications of the introduction, establishment and subsequent invasion of inland waters in England by sunbleak and topmouth gudgeon. The specific objectives were to:
1) assess the variability of adaptable traits such as life-histories and morphological characters of sunbleak and topmouth gudgeon at different sites, so as to describe the role of adaptable traits in the introduction, establishment and dispersal of these species (Chapter 3);
2) determine the density and timing of movement of sunbleak and topmouth gudgeon *via* drift from source populations into online water bodies, so as to quantify the role of this dispersal pathway in the invasion process (Chapter 4);
3) identify the parasite fauna of sunbleak and topmouth gudgeon in England, as a means of establishing the level of risk of sunbleak and topmouth gudgeon for parasite transmission to native fishes (Chapter 5);
4) assess the level of resource use overlap (sunbleak: diet and habitat; topmouth gudgeon: habitat) and social integration between the non-native (sunbleak only) and native fishes, so as to determine whether the invader occupies a niche derived at the detriment of native species. (Chapter 6); and
5) evaluate the incidence and intensity of native fish predation on (i.e. biological resistance to) topmouth gudgeon in an invaded system, so as to quantify the level of biotic resistance (Chapter 7).

The different objectives were further specified and addressed in Chapters 3 to 7, with the findings presented in a synthesized manner in the following Sections 8.1.2 and 8.1.3.

8.1.2 Synthesis of the findings: Sunbleak

Inter-population variation was observed in the life history traits and morphological characters of sunbleak in inland waters of England (Chapter 3). Sunbleak populations all matured between the ages of 1 and 2 (Females and males: $\text{Age}_M \leq 2$ yr), and at small body sizes (Females: $\text{FL}_M \leq 39$ mm; Males: $\text{FL}_M \leq 47$ mm); maturation observed later in life and at larger body sizes in some sites was a consequence of sample structure (see Chapter 3 for details). In general, sunbleak were of good body condition, and reproductive investment (e.g. GSI, fecundity, *ER*) by the species was high in all populations. The parasite fauna in three of the sunbleak populations varied between sites (Chapter 5), and this may have been an influencing factor in the observed inter-population variability of biological traits.

Of particular concern amongst the parasite fauna was the presence of two non-native copepodid parasites, *Neoergasilus japonicus* and *Ergasilus briani*. In light of the potential for sunbleak to spread beyond their current distribution in their non-native range (Gozlan *et al.*, 2003b), be it *via* natural dispersal or accidental movement *via* live fish consignments, this may contribute to the further dissemination of these 'Category II' parasites in England (i.e. sunbleak as a potential vector for non-native parasites). Indeed, sunbleak were found to disperse from source populations *via* downstream drift (Chapter 4), which followed a diel pattern of passage from the on-line water bodies (Stoneham Lakes, Hampshire; Revels Fishery, Dorset). The drift densities (i.e. 'propagule pressure') exerted by these water bodies on the adjacent streams (Monks Brook, Hampshire; Caundle Brook, Dorset) generally increased with declining light levels, with sunbleak drifting at highest densities during hours of darkness. At Stoneham Lakes Fishery, sunbleak drifted with a mean density of 0.4 ± 0.2 larvae 1000 m^{-3} and 0.6 ± 0.4 larvae 1000 m^{-3} in 2004 and 2005 respectively. Maximum drift densities reached 9 and 10 larvae 1000 m^{-3} in 2004 and 2005 respectively.

A closer examination of the sunbleak population at Stoneham Lakes revealed clear overlaps in resource use (diet and microhabitat) between the native species and sunbleak during early life. These overlaps decreased during the progress of larval development, and were a good example of how the young stages of large-bodied native fishes may have to recruit through a phase of resource co-exploitation with adults of small-bodied alien species (Chapter 6A). Use of social network analysis in the study of sunbleak interactions with native fishes revealed that sunbleak had integrated into the Stoneham Lakes' fish assemblage and created significantly stronger social bonds with the native species than the natives established between themselves (Chapter 6B), which may indicate the potential for rapid parasite transmission within these networks, particularly from non-native to native species (Newman, 2003b).

8.1.3 Synthesis of the findings: Topmouth gudgeon

Variations were observed in the biological traits between the studied topmouth gudgeon populations. For example, at the most northern site at Ratherheath Tarn female topmouth gudgeon matured at age 2, whereas females from southern England and France were found to mature at age 1. The northernmost population of topmouth gudgeon also possessed lower morphological plasticity than the other two introduced populations. Length at maturity was found to be $FL_M \leq 49$ mm in females and $FL_M \leq 53$ mm in males at Ratherheath Tarn, while at Tadburn Lake stream females also matured at $FL_M \leq 49$ mm but males at $FL_M \leq 45$ mm. Female topmouth gudgeon from France matured at $FL_M \leq 46$ mm, while males matured at $FL_M \leq 47$ mm.

Densities of larval topmouth gudgeon in the drift (propagule pressure) entering the adjacent Tadburn Lake stream from Crampmoor Fishery were relatively high (Chapter 4), with a peak at about 05:00 hrs. Overall mean drift density was 3 ± 1 and 7 ± 2 larval topmouth gudgeon 1000 m^{-3}, with maximum densities reaching 40 and 52 larval topmouth gudgeon 1000 m^{-3} in 2004 and 2005 respectively. Despite these fish being macroparasite-free (Chapter 5), a study by Gozlan *et al.* (2005) identified topmouth gudgeon from Tadburn Lake stream as the healthy host of an intracellular pathogen (rosette like agent – RLA) that is potentially lethal to some fish species. Microhabitat use of topmouth gudgeon was found to overlap with native species including brown trout, chub, bullhead, stoneloach (Chapter 6A). The potential of two native predators (brown trout and chub) to mediate biotic resistance against topmouth gudgeon invasion of Tadburn Lake stream (Chapter 7) revealed that predation pressure from these two facultative piscivores failed to overcome the strong propagule pressure. The strong propagule pressure resulted from high reproductive investment of topmouth gudgeon

(Chapter 3), that produced increased densities of larvae to drift from the source populations (Chapter 4).

8.2 Ecological implications of topmouth gudgeon and sunbleak introductions

8.2.1 Life history and morphology of sunbleak and topmouth gudgeon

Sunbleak and topmouth gudgeon are small-bodied fish species which generally do not exceed a fork length of 100 mm (Šebela and Wohlgemuth, 1984; Arnold, 1990; Arnold and Längert, 1995; Gozlan *et al.*, 2003b), though lengths exceeding 70 mm are rarely observed. The present study revealed maximum fork lengths were 68 mm (female; Durleigh Reservoir) and 66 mm (male; Kings-Sedgemoor Drain, Parchey Bridge) in sunbleak and 67 mm (female; Tadburn Lake stream) and 69 mm (male; Tadburn Lake stream) in topmouth gudgeon. In both species, the majority of growth was obtained during the first year of life and before maturation; the remaining energy can be invested into reproduction while growth remains low during the remaining years of life (Table 3.5, Table 3.7). Such trade-off is expected to assist in the species' successful establishment because high reproductive effort coupled with batch spawning and parental care behaviour is energetically expensive.

Some examples of small bodied freshwater fish species that are invasive elsewhere include the mosquitofish *Gambusia affinis* (Baird & Girard, 1853) (FL ≤ 60 mm) (Crivelli, 1995; Scoppettone *et al.*, 2005), round goby (FL≤ 150 mm) (L'avrinčíková *et al.*, 2005), bighead goby *Neogobius kessleri* (Günther, 1861) (FL ≤ 170 mm) (Copp *et al.*, 2005a; Kováč and Siryová, 2005) and the guppy (Males: FL ≤ 30 mm; Females: FL ≤ 60 mm) (Arthington, 1989). However, important aspects to consider when looking at these invasive species are the respective pathways and the contribution of each pathway to the species' introduction into the new environment. For example, mosquitofish were intentionally introduced into a variety of systems as a biocontrol for mosquitoes (Crivelli, 1995; Rehage and Sih, 2004; Scoppettone *et al.*, 2005). At least for these initial introductions it would be known where and when such introductions would have taken place. When evaluating the pathways for sunbleak and topmouth gudgeon, a different picture emerges. Both species have been evidentially linked to live fish movements as accidental contaminants (Copp *et al.*, 2007). This highlights the necessity to consider pathways and their potentially varying characteristics when managing introduced freshwater fish species.

Significant sexual differences in morphology were observed in topmouth gudgeon, and this has been previously recorded elsewhere in its introduced range (Barus *et al.*, 1984; Jankovic, 1985; Maekawa *et al.*, 1996; Kotusz and Witkowski, 1998). Sexual dimorphism is related to their reproductive behaviour, where large size is important for male topmouth gudgeon and their reproductive success (Maekawa *et al.*, 1996), as females generally prefer to mate with males of larger body size. Sunbleak has not been found to display sexual dimorphism (Arnold and Längert, 1995; Pipoyan, 1996). In both species, females and males were found to differ in reproductive allocation related to differences in physiological and physical gonad characteristics. Overall, morphological variability between fish from different sampling location was largely attributed to the characteristics of the respective environment (i.e. flow velocities) and the subsequent swimming abilities required.

Both species mature at a small body size, with intra- and inter-population variation in sizes at maturity between females and males (Table 3.6, Table 3.8). Size-at-maturity in sunbleak ranged from 32 mm in females and males (Stoneham Lakes, Hampshire) to 42 mm (females; Bridgewater Taunton Canal, YMCA, Kings-Sedgemoor Drain, Bradney Bridge, River Sowy) and 42 mm (males; River Sowy). Sunbleak from lentic waters, Stoneham Lakes and Two Lakes Fishery, matured at smaller body sizes than fish from lotic waters. Such differences may be attributed to prevalent water velocities, food availability, habitat, competition and/or temperature, although this would require confirmation during further research. Variations in length-at-maturity with river populations maturing at greater body sizes than lake populations, has been recorded in fish species elsewhere (Neat *et al.*, 2003).

Maturation after only 1 or 2 years may provide sunbleak and topmouth gudgeon with a characteristic that will aid recruitment and subsequent establishment. The amount of time immature fish are exposed to pressures including predation, feeding and potential variation in habitat quality is reduced. Additionally, reproductive investment is high in both species (e.g. GSI, *ER*), which enables them to form dense populations and ensure successful establishment soon after introduction (e.g. early maturity, short generation time).

Morphological variability between invasive populations can involve different characters in different populations (Gillespie and Fox, 2003) and is not necessarily accompanied by life history differentiation but instead may be related to the species' reproductive behaviour. Sunbleak and topmouth gudgeon have several life history attributes that enable them to successfully invade new water bodies (Perdices and Doadrio, 1992a; b). Nest-guarding by males, which increases egg survival, and batch spawning (Cassou and LeLouarn, 1991) may further increase overall survival rate during early life. In the U.K., parental care is a characteristic not displayed in native fish species while > 50 % of established non-native fishes utilise parental care in their reproduction (Maitland, 2000). Invasion success is deemed to be aided by parental care as this ensures increased survival of eggs and larvae (Jeschke and Strayer, 2008). The introduction of topmouth gudgeon and sunbleak into online and/or enclosed lakes that are located in flood plains serve as a valuable facilitator for successful establishment and subsequent dispersal. Such systems act as sources for new recruits and transition zones before further dispersal and recruitment in the wild. Ultimately, the reproductive traits assist establishment, but dispersal is dependent on the connection of the non-native habitat with fluvial systems such as rivers.

Variability in age and length at maturation can be influenced by latitude (Copp *et al.*, 2002a; Vila-Gispert *et al.*, 2002). In general, with decreasing latitude, many fishes follow an opportunistic (early maturation, batch spawning, small body size, short life-span) strategy (Vila-Gispert *et al.*, 2002). Generally, and due to habitat seasonality, many North American and European fish populations follow a periodic strategy (large clutches, delayed maturation). However, sunbleak and topmouth gudgeon appear to have adopted intermediate life history strategies and display aspects of opportunistic (early maturity, high reproductive effort, small adult body size), periodic (fast growth during early life, high fecundity) and equilibrium (parental care) strategists in their non-native range. In light of the *r/K* model (for further explanation see Section 3.1 in Chapter 3), these are traits, which are characteristic for *r* strategists and advantageous in unstable or unpredictable environments (MacArthur and Wilson, 1967; Pianka, 1970). Upon their introduction into a new environment, the fish are likely to be exposed to unpredictable environmental conditions. Though, when applying the ‘Winemiller and Rose’ life history model (Winemiller and Rose, 1992), which also describes the typical environments that species within each life history group may persevere in, it appears that the combination of various life history characteristics from all 3 of the strategies, topmouth gudgeon and sunbleak would be expected to be able to persist in a variety of different environments. Both species display at least one characteristic suited to highly disturbed and unpredictable environments (opportunistic strategy), seasonal, periodically suitable environments (periodic strategy) and constant environments (equilibrium).

Based on the results it may be expected that when sunbleak and topmouth gudgeon arrive at a new location, they would be equipped with characteristics that may enable them to form dense populations within 1 to 2 years after first introduction. In combination, high reproductive effort and fecundity, early maturity, small body size and short generation time, facilitate establishment success. Parental care will further assist in this process and potentially permit survival of eggs (Clutton-Brock, 1991). Variability in parameters that enable biological adaptation and/or integration will increase the likelihood of the species to fit into the new environment after introduction and potentially to persist. However, whether establishment occurs is dependent on other factors as well, e.g. potential for dispersal, propagule pressure, and biological resistance and ecosystem resilience.

8.2.2 Drift and dispersal of sunbleak and topmouth gudgeon

The drift observed at the three fisheries (sunbleak: Revels Fishery, Dorset; Stoneham Lakes, Hampshire; topmouth gudgeon: Crampmoor Fishery, Hampshire) was much lower than natural drift densities reported elsewhere (de Graaf *et al.*, 1999; Copp *et al.*, 2002b; Reichard *et al.*, 2002b). Owing to the respective community structure and spawning season, drift densities as well as timing and species vary widely between waters bodies, which may further be explained by differences in hydrological regimes. One of lowest drift densities was recorded from the River Lee, England, where overall means did not exceed 10 fish larvae 1000 m^{-3} (Copp *et al.*, 2002b). Reichard *et al.* (2002b) examined inter-annual patterns of drift in the rivers Morava and Kyjovka, two lowland rivers within the Danube Basin (Czech Republic), and observed peak densities ranging between 80 and 1354 fish 1000 m^{-3} between years and rivers, 98 % of which were represented by cyprinids. Finally, larval drift densities between 1000 and 9300 fish 1000 m^{-3} were reported from the River Lohajang, Tangail, Bangladesh (de Graaf *et al.*, 1999).

Generally, comparison with fish drift observed in this study with results from elsewhere is problematic. Here, the study sites were relatively small water bodies, online with small streams or brooks. Considering this, the drift densities were regarded as relatively high, particularly from Crampmoor Fishery where overall mean drift was 3 ± 1 and 7 ± 2 larval topmouth gudgeon 1000 m^{-3} in 2004 and 2005 respectively. Here, maximum drift densities reached 40 and 52 larval topmouth gudgeon 1000 m^{-3} in 2004 and 2005 respectively. At Stoneham Lakes Fishery, sunbleak drifted with a mean density of 0.4 ± 0.2 and 0.6 ± 0.4 larvae 1000 m^{-3} in 2004 and 2005 respectively, with maximum values reaching 9 and 10 larvae 1000 m^{-3}.

Despite a high fish density as observed during surveys in the Stoneham Lakes (see Chapter 3), sunbleak drift densities were surprisingly low. In this case, drift may have been related to inadequate habitat typology at the outfalls of the lakes. These areas are anthropogenically modified, relatively deep (>1.5 m) and offer limited amounts of shelter by way of submerged or overhanging vegetation -

environmental features that sunbleak appear to be associated with during early life (Pinder *et al.*, 2005a) (see Chapter 6A). Nevertheless, overall drift was greater in sunbleak than in the native species, which is probably related to the high density of sunbleak in the lakes as opposed to low numbers of young-of-the-year of native species.

Dense topmouth gudgeon drift represents great propagule pressure on the receiving Tadburn Lake stream, which may well promote topmouth gudgeon invasion of the River Test. However, a system exposed to such an amount of pressure from an introduced species may provide resistance against their invasion, for instance by way of unfavourable environmental conditions or strong predation pressure by native piscivorous predators (Elton, 1958; Robinson and Wellborn, 1988). This supposition was originally made when limited dispersal of topmouth gudgeon below the fishery outflow in Tadburn Lake stream was observed in 2003 (Figure 4.13). Though, at least for aspects of predation pressure (i.e. biological resistance), it was concluded that this was not strong enough as provided by the two facultative piscivores brown trout and chub.

Larval drift of sunbleak and topmouth gudgeon was observed occurring during darkness (topmouth gudgeon: Crampmoor Fishery, Hampshire; sunbleak: Stoneham Lakes, Hampshire; Revels Fishery, Dorset). In both species, movement of adult specimens was also observed during the spawning season. In topmouth gudgeon (this was not tested in sunbleak), adult fish escapement from fisheries was recorded throughout the remaining months between (and inclusive of) July 2004 and March 2005. Based on the results, it can be concluded that connected lakes are important determinants of risk of non-native fish dispersal into water courses. The rate of outfall into online water bodies (e.g. streams, brooks) is related to the type of outflow connection. An online water body may act as ‘drip feed’, with the outlet type regulating the propagule pressure of non-native fishes on the receiving streams.

The further dispersal of fish from the site of introduction will be determined by: 1) the opportunity to drift/disperse (e.g. connection to adjacent water bodies), 2) drift density, and 3) the suitability of the new environment. Water bodies in the vicinity of high-risk entry points for non-native fishes (e.g. aquaculture facilities, stocked systems) are under a particularly elevated threat of invasion as they are regular recipients of live fish.

8.2.3 Parasites in sunbleak

The non-native (Environment Agency Classification: Category II) ergasilids, *N. japonicus* and *E. briani* observed in sunbleak (Markewitsch, 1934; Yin, 1956; Yin, 1962) have limited distribution in England (Fryer and Andrews, 1983; Alston and Lewis, 1994). *E. briani* and *N. japonicus* were first introduced into Yorkshire and West Sussex respectively in the early 1980s (Mugridge *et al.*, 1982; Alston and Lewis, 1994). Their introduction into England was associated with fish translocations (Alston and Lewis, 1994).

E. briani has previously been recorded in sunbleak within its native range (Grabda, 1971). In both North America (Hayden and Rogers, 1998; Hudson and Bowen, 2002) and England (Beyer *et al.*, 2005; this study), *N. japonicus* has been found in non-native fish associated with aquaculture (Kennedy, 1975), but has not previously been reported in sunbleak. The distribution of *N. japonicus* in England is limited to a few locations (Alston and Lewis, 1994) but with the potential for sunbleak to disperse beyond their current distribution in England, it is likely that the spread of *N. japonicus* to new areas of England may be exacerbated (Beyer *et al.*, 2005).

8.2.4 Parasites in topmouth gudgeon

Even though topmouth gudgeon are reportedly associated with a variety of parasite species elsewhere (Harada, 1930; Kim *et al.*, 1979; Chai *et al.*, 1985; Kang *et al.*, 1985; Bianco, 1988; Sohn, 1991; Aohagi *et al.*, 1992; Rosecchi *et al.*, 1993; Šimková *et al.*, 2004), no parasites were found in the English topmouth gudgeon populations studied. These populations may have originated from a small subset of perhaps uninfected source populations, which may have acted as an ecological advantage during the colonisation process (Dobson and Carper, 1992;

Torchin *et al.*, 2001). This notion is derived from the hypothesis that the success of an introduced species may be associated with the partial loss of its native parasite fauna (Torchin *et al.*, 2001; Clay, 2003; Torchin *et al.*, 2003). Though, this assumption is based on results from two topmouth gudgeon populations, which were examined within a distinct sampling period. In fact, topmouth gudgeon have been reported from 25 different locations in England (Pinder *et al.*, 2005b). To verify this conclusion is true for other introduced populations in England, parasitological investigations at the remaining locations would be necessary.

8.2.5 Overlaps in resource use (diet, habitat) between sunbleak and native species

Overlaps in resource use during early life might affect the fitness and survival of native species, initiate changes in their habitat use during the early development and lead to differential intra-specific resource use during later life (Polis, 1984). Strong dietary overlaps between sunbleak and native fish species during early development indicates a sharing of food resources within the invaded fish assemblage (Figure 6.1, Figure 6.2). However, overlaps were mainly based on detritus, an abundant food resource of low nutritional value (Bowen *et al.*, 1995). Diet overlaps between sunbleak and native species during early life, at least for the larval stages 1 to 4, may reflect the prey availability in the Stoneham Lakes. The observed overlaps may be regulated by comparable energy requirements at the same developmental intervals, irrespective of the species being native or non-native.

A higher frequency of full guts in native species as compared to non-native ones have been reported elsewhere (Feyrer *et al.*, 2003) and, along with generally greater prey diversity in the native species, may indicate that early life stages of native species are more efficient at exploiting resources. With advancing development, selective intra- and inter-specific separation and dietary shifts may occur, governed by increasing physical and physiological functional abilities (Mark *et al.*, 1989; Pinder and Gozlan, 2004; Gozlan and Copp, 2005; Pinder *et al.*, 2005a). With progressing development, larvae were also increasingly capable to prey on more mobile dietary items (e.g. rotifers). For example, the development of fins (= improved swimming capability) and increasing body pigmentation (= camouflage as protection from predators) are important role in this mechanism (Thetmeyer and Kils, 1995; Pinder, 2001; Urho, 2002; Pinder and Gozlan, 2004).

Shifts in habitat use during early life are an integrated response to the progressive increase in functional capabilities and interspecific mechanisms (Kováč 2002). Larvae of sunbleak and native species were associated with littoral habitats and moved out into the pelagic zone with progressing development (Figure 6.3). Similar behaviour has previously been observed for larvae of other fishes (Copp and Garner, 1995). Ontogenetic shifts and differential inter-specific resource use are common in fish (Werner and Gilliam, 1984; Ross, 1986) and ontogenetic changes in habitat preferences have been reported in several studies of fish-habitat relationships of cyprinids (Copp, 1990; 1992a). Such alterations are commonly related to the development of overall body morphology and the sensory organs (Kotrschal and Palzenberger, 1992; Copp and Kováč, 1996; Sagnes *et al.*, 1997).

8.2.6 Overlaps in resource use (habitat) between topmouth gudgeon and native species

The potential for adverse impacts (e.g. through competition with native species) is evident in the various positive associations of topmouth gudgeon with native fishes (Table 6.10), for example through shared resource utilization (Elliott, 1973; Forseth and Jonsson, 1994). However, topmouth gudgeon co-exploited microhabitat resources together with the native species. It is unlikely that the introduction of topmouth gudgeon has incited habitat shifts in the native fish species in Tadburn Lake stream, because the native species were not demonstrating uncharacteristic habitat use. Elsewhere in their introduced range, topmouth gudgeon sustain populations in still and running waters (Arnold, 1990; Jankovic and Karapetkova, 1992; Rosecchi *et al.*, 1993; Adámek and Siddiqui, 1997; Sunardi *et al.*, 2005; Sunardi *et al.*, 2007a; Sunardi *et al.*, 2007b), and the species can endure a variety of environmental conditions (Ujiie and Mizuguchi, 1994). Notwithstanding the ability to form populations in lotic waters (Sunardi *et al.*, 2005; Sunardi *et al.*, 2007a; Sunardi *et al.*, 2007b), topmouth gudgeon occur in greater densities in lentic conditions (Adámek and Siddiqui, 1997). The high densities may be the consequence of food rather than habitat availability, as the species exhibits great habitat plasticity, as well as the species' reproductive behaviour (Rosecchi *et al.*, 2001), which involves batch spawning and nest guarding. This reproductive tactic necessitates a large amount of energy, which is expected to increase in waters of elevated velocity (Asaeda *et al.*, 2005; Sunardi *et al.*, 2007b). Topmouth gudgeon establishment in Tadburn Lake stream has not been hindered by the ambient water velocities, which at <5 cm s^{-1} are the water velocity preferences (<7 cm s^{-1}) observed in the laboratory under experimental conditions (Asaeda *et al.*, 2005; Sunardi *et al.*, 2005). Topmouth gudgeon is a species known to be especially plastic in their habitat use, and in their associations with other species (Arnold, 1990), and this belief is also confirmed by the limited amount of microhabitat preferences/avoidances (= habitat electivities) observed during the investigations in Tadburn Lake stream (Table 6.10).

It is essential to consider the spatial and trophic dimensions when describing overlaps in resource use between native and non-native species. However, the success of an introduced species, such as sunbleak and topmouth gudgeon, may not simply depend on out-competing the native species but to make use of the environment and integrate into the new community (see also Section 8.2.7). This suggests that successful invaders may be those species that are able to exploit accessible resources without inciting major changes in the invaded environment.

8.2.7 Social integration of sunbleak into a native fish assemblage

The social networks of the fish assemblage at Stoneham Lakes Fishery exhibited characteristics of 'Small World Models' (Watts and Strogatz, 1998). Low clustering coefficients and short path lengths (Figure 6.10), exhibited features of random as well as regular networks, which is characteristic of these models (Watts and Strogatz, 1998). Overall, the results from the network analysis suggest that populations are more at risk to epidemics, as infections may spread more rapidly between native and non-native fishes within the fish assemblage (Watts and Strogatz, 1998; Newman, 2002; Croft, 2003; Newman, 2003b). Overall, the results provide a new insight into the social relationship among sunbleak and native fish species during early life and reveal the potential for alien species not only to transfer new infectious diseases but also to spread them faster among the native community. Generally, these findings may indicate potential traits of successful invaders and the implication for the spread of disease. The success of establishment and subsequent invasion may be highlighted not only by the capacity of the alien species to adapt to the new environment, but also in its capacity to integrate into the native fish community.

8.2.8 Potential for biotic resistance against topmouth gudgeon

Predation by the facultative predators, brown trout and chub, on topmouth gudgeon was low, and it was concluded that this predation was too low to have any influence on the abundance of topmouth gudgeon in Tadburn Lake stream. In fact, topmouth gudgeon did not appear to be a preferred prey (Ivlev, 1961). The proportions of fish consumed by chub and brown trout elsewhere were greater than in Tadburn Lake stream (e.g. Elliott, 1967; Hellawell, 1971).

Owing to the absence of an obligate predator (e.g. pike) in Tadburn Lake stream, two facultative predators were examined. These may by nature only have limited potential to facilitate biological resistance *via* predation against introduced fish species (Noble *et al.*, 2007). Facultative predators only partially depend on a piscivorous diet; as a result, it appeared that even a comparably large number of facultative predators (79 brown trout, 63 chub) may have only very limited potential to mediate biological resistance against topmouth gudgeon. The present study was localised in space and time and impacts of ecological resistance on topmouth gudgeon might be different elsewhere. However, the high propagule pressure (see Chapter 4) in combination with topmouth gudgeon taken as prey less frequently than expected by brown trout and chub (see Chapter 7), may have affected ecosystem invasibility.

8.2.9 Ecological perspectives

The association of sunbleak with two non-native parasites (Chapter 5), resource use overlaps (Chapter 6A), the strong social bonds between sunbleak and the natives (Chapter 6B), and their low drift densities (Chapter 4) are important aspects shaping the species' invasion success. It has to be noted that even if some ecological aspects of a species are not of particular concern, others may be (i.e. the hosting of non-native parasites). In such a case, even low densities of drift are of concern because they represent a vector for parasite dissemination. With sunbleak's potential for integration, interaction and adaptability, the low numbers of drift may simply be enough to integrate into native fish communities.

Topmouth gudgeon's plasticity (Chapter 3), in particular their resource use (Chapter 6A), are important factors counteracting potential limitations imposed by the species' general preference for lentic habitats. This enables topmouth gudgeon to co-exploit available microhabitat resources together with the native species. This flexibility aids the ability of topmouth gudgeon to sustain populations in a variety of environments, with this also dependent on the quantity and quality of food resources and spawning substrate, as well as water quality and competition.

Elton (1958) described biotic resistance in relation to species diversity as a small-scale phenomenon, but it is also consistent with large-scale patterns of invasions (Byers and Noonburg, 2003). The examination of invasion processes requires knowledge of the life histories and propagule pressure of invaders and quantification of predation by native species. Several studies have confirmed that increased propagule intensity will increase successful establishment of introduced species (Beirne, 1975; Veltman, 1996; Green, 1997). In this study, propagule pressure was greater than biological resistance created by the facultative predators, which is expected to have aided the successful establishment of topmouth gudgeon within the catchment downstream of the original introduction. This conclusion is based upon a study, which was 1) limited in space and time, and 2) based on the investigation of two facultative piscivores within a system devoid of obligate piscivores. Biological resistance may be much greater in systems which are exposed to similar propagule pressure from topmouth gudgeon, but contain obligate piscivores (e.g. pike) (Noble *et al.*, 2007). An obligate piscivore, which would rely entirely on fish as prey, would generally be expected to feed on greater amounts of fish than a facultative piscivore. Essentially, if the topmouth gudgeon were to be of similar densities as in Tadburn Lake stream, biological resistance mediated by obligate piscivores may be greater than observed during the present study.

In the inland waters of England, sunbleak and topmouth gudgeon interact and integrate (Chapter 6) with native species, utilising their species-specific plasticity in biological traits, e.g. reproduction and morphology (Chapter 3), to increase the likelihood of successfully establishing a population in the novel environment. Therefore, biological and social plasticity, such as the establishment of strong social bonds of sunbleak with native species (Chapter 6B), appear to be key elements in the success of topmouth gudgeon and sunbleak in English inland waters. The small size, early maturity and high reproductive effort, supported by good body condition, of sunbleak and topmouth gudgeon ensure fast turnovers of introduced populations, and compensate for the naturally high mortality rates associated with these traits. Reproductive success and subsequent successful establishment is further supported by the species' batch-spawning behaviour and parental care (Farr-Cox *et al.*, 1996; Rosecchi *et al.*, 2001; Gozlan *et al.*, 2003a).

Topmouth gudgeon and sunbleak may create a problem for the receiving waters, e.g. those connected to non-native species introduction 'hotspots' such as aquaculture facilities and/or those that are likely to receive fish through live fish movements. This is particularly evident for Crampmoor Fishery. After the initial introduction of topmouth gudgeon, a lag phase potentially afforded an opportunity for the species to reproduce and establish a dense population. Intensive downstream drift of the resulting larvae exerted elevated propagule pressure on the receiving water course (Tadburn Lake stream). So, despite being introduced to a single fishery, the conditions of the fishery served to amplify the propagule pressure on the receiving stream. For topmouth gudgeon, this provided a highly suitable reproductive site and a mechanism for natural dispersal (Chapter 4). Larval downstream movement *via* drift is of particular ecological importance for initial distribution of non-native species and may be driven by the density of the source population (Reichard *et al.*, 2004). This drift is vital for colonization of new environments and important for subsequent invasion success. Additionally, the elevated drift densities (propagule pressure) into a stream of relatively high fish density and low species diversity, characterised by facultative rather than obligate native piscivores, provided low potential for native biological resistance against topmouth gudgeon, thus facilitating the species' invasion success.

8.3 Management implications and recommendations

8.3.1 Current legislation

Since the early 1970s, numerous national and international policies and legislation have been introduced in Europe to protect freshwater fishes and their habitats (Ramsar Convention 1971; Bern Convention 1979; Convention on Biological Diversity 1992; Habitats Directive 1992), to regulate trade of certain species (CITES 1975), and to protect migratory species (Bonn Convention 1979 and 1994). The Habitats Directive 1992 requires Special Areas of Conservation (SACs) to be designated for other species, and for habitats. These two directives are the basis of the creation of the Natura 2000 network, which forms an ecological network in the territory of the European Union. This legislation is designed to protect the most seriously threatened habitats and species across Europe. Natura 2000 is the centrepiece of nature and biodiversity policy within the European Union (EU).

The EU Water Framework Directive (WFD) came into force on 22 December 2000 and established a new, integrated approach to the protection, improvement and sustainable use of Europe's rivers, lakes, estuaries, coastal waters and groundwater. The key purpose of the WFD is the protection and enhancement of aquatic ecosystems in Europe. To conform to the WFD, countries must adhere to the criteria set out with the aim to restore the ecological quality of their aquatic habitats. One of the main criteria in the determination of water quality status is the presence of appropriate fish communities in freshwaters. Unfortunately, most legislation and directives do not consider impacts related to fisheries and introduced species. Small-scale approaches, such as applied in this PhD, are vital in providing the knowledge and the tools to implement such international policy successfully on a large-scale. Overall, the WFD now drives much of the legislation and management activities related to non-native species in the U.K.

The Wildlife and Countryside Act (WCA) 1981 and 1985 is currently the major part of legislation concerning conservation. This Act aims to protect species and habitats of importance in the U.K. The major piece that concerns the control of alien fish species in England and Wales is the Import of Live Fish Act (ILFA) 1980 (including the Prohibition of Keeping or Release of Live Fish (Specified Order) Order 1998), which aims to regulate the importation and keeping of listed fish species within England and Wales. Acts like the Salmon and Freshwater Fisheries Act 1975 (SAFFA 1975) aim to further protect selected species including salmon, trout (including sea trout), freshwater fish and eels. SAFFA 1975 describes ‘freshwater fish’ as “any fish living in freshwater exclusive of salmon and trout and of any kinds of fish which migrate to and from tidal waters and of eels” (Minister of Agriculture Fisheries and Food, 2000). However, this definition excluded anadromous fish other than salmon and sea trout and, as a consequence, species for example shads, smelt and lampreys were not covered by freshwater fisheries legislation (Minister of Agriculture Fisheries and Food, 2000).

In England and Wales, the Environment Agency is the primary Government authority for environmental protection and plays a major role in the regulation of recreational fishing, while the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) is the Government agency responsible for controlling the import of live fish. CEFAS carries out aquatic scientific research and consultancy and is generally acting under the Department of Environment, Food and Rural Affairs (Defra). Defra carries policy responsibility as regards the introcudction of species, which are not ordinarily resident or regular visitors in the wild state. Defra's responsibilities cover species protection, plant and animal health, licensing of intentional introductions, marine issues such as ballast water exchange, and fisheries. However, enforcement of legislation lies with the Home Office. Natural England, England’s statutory conservation agency, provides scientific advice to government, licensing authorities for releases, and instigates practical management activity. Border control responsibility as regards non-native species lies with HM Revenue and Customs.

Because legislation governing the movement of fish into and within England and Wales is shared between the Environment Agency and other Government organisations, management can be difficult and enables exploitation of weaknesses in the enforcement system (Hickley and Chare, 2004). This is further promoted by the high demand (e.g. ornamental, recreational demand) for non-native fish and the potentially great temptation (e.g. financial reward) to overcome the legal constraints by introducing these fish without consent (Hickley and Chare, 2004). To make best use of resources and information, CEFAS and the Environment Agency have developed a shared 'Live Fish Movements Database' that facilitates effective, joint working with the respective enforcement teams. However, the development of new legislation that amalgamates both aspects of fish introductions and live fish movements may simplify non-native species management in England and Wales. To begin with, it is essential to effectively utilise the existing powers through enhanced liaison and co-ordination between those bodies holding the relevant powers.

8.3.2 Management of freshwater fish introductions in England and Wales

Generally, non-native species risk assessments concentrate upon pre-introduction scenarios (Copp *et al.*, 2005b; 2005c). However, post-introduction risk management of a non-native species is equally important, especially to ensure appropriate spending of available resources, e.g. priority should be given to management of 'high risk' sites. It is for this reason that this Section largely separates pre-introduction and post-introduction management recommendations, and finally provides some ideas on where and how funding solutions for these activities may potentially be sought.

8.3.2.1 Pre-introduction recommendations

The advancement of globalisation[25] and the European trade policies favour future introductions into England and Wales, especially ornamental fish species through

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[25] Globalisation is often defined as the process of increasing international integration in economic, political, social and cultural spheres, whereby actions beyond national boundaries constrain and influence national outcomes.

the aquarium trade (Copp *et al.*, 2007). Stringent measures need to be employed to prevent accidental introductions of unwanted species. At borders, thorough species identification and enforcement of more strict quarantine measures are needed. Species imports for the purpose of fish trade need to be thoroughly monitored to prevent unnecessary introductions of non-native species and associated parasites into England. Appropriately trained personnel (in species identification), forming ‘rapid response teams’ (RRTs), need to be in place to prevent future introductions of novel alien fish and parasite species. Enforcement of these RRTs may suitably lie with the Environment Agency in collaboration with the Department for Environment, Food and Rural Affairs (Defra).

Potential future invaders have to be identified using risk assessments, which are based on available information of species’ biological traits (Copp *et al.*, 2005b; 2005c). Knowledge relating to the species’ habitat use, diet, variability of species-specific traits, reproductive behaviour and invasion history is vital for these protocols. The social aspects of an introduction should be given more weight and the potential for integration of a species on this level may be included into considerations of risk assessments for non-native species. Further, in combination with the potential of parasite spread with increased socialisation these aspects should be combined when looking at the potential of new species for successful establishment in England and Wales. Also, despite their uncertainty, habitat suitability indices and dispersion models may assist in the advancement of prediction, prevention and early detection of invaders (Inglis *et al.*, 2006).

It is of particular concern that although it has been suggested that health monitoring on introduced fish needs to be carried out before they are transported across borders, imported species are still not being thoroughly monitored for pathogens (Austin and Robertson, 1993b; Blanc, 2001b). However, border inspections are recommended although they are likely to be very expensive. Additionally, little appears to be known of the parasites that are considered to be ‘high-risk’, so thorough evaluation of the actual effects of the parasites included into lists (e.g. Environment Agency) would be useful to evaluate the real risk associated with them so as to be able to prioritise subsequent action when new parasite species are found. Steps forward in this direction may include: 1) further research into the risks of different parasites, e.g. the ones that are included in the Category II-list, 2) identifying the risks of other potential parasites that are likely to be introduced, 3) improve health check protocols as regards the tools used to identify parasites and disease in fish, and 4) improve skills of personnel undertaking health checks and increase the number of personnel undertaking these health checks.

The following questions may be worth considering when reviewing the methodology with which live fish movements are undertaken (see also Akhter, 2003):

1) Has a health check been carried out at origin, e.g. ‘Disease-Free’ Certification?
2) What methods are used for such health checks in different countries? Are these compatible with the requirements in England and Wales?
3) Has a species check been carried out at origin, e.g. species certification by qualified personnel?
4) Is the training provided to personnel carrying out species checks compatible between different countries?
5) Quarantine at origin: before movement to new location?
6) Quarantine at arrival: before introduction into the local facilities?
7) Has all water and equipment used during transport been disinfected and sterilised at arrival location?
8) Has a species check taken place at arrival location by qualified personnel?
9) Is cataloguing of live fish movements by the Environment Agency and Defra taking place? If possible, disease certification and the outcomes should be made public so as to enable potential customers to carry out their personal quality assessment.

Essentially, an increasingly global approach should be used when drawing up legislation that aims at preventing fish introductions from elsewhere (e.g. EU level legislation). For example, many rivers pass through a number of different countries and subsequently a non-native fish invading such rivers may become an international issue; i.e. biogeography is more important than geographical barriers.

Fish introduction ‘hotspots’, such as aquaculture facilities and water bodies used for recreational fishing activities, need to be identified and categorised into online or closed water bodies, so as to further identify the risk of potentially connected water bodies. It would be important to determine potential areas of colonization by new host species and areas where novel parasites are likely to persist (‘high risk areas’), e.g. using remote sensing. Such information may assist in the prevention and management of future introductions.

8.3.3.1 Post-introduction recommendations

Post-introduction management of non-native species may be largely described by two broad scenarios:

1) Rapid detection, rapid response and potential eradication to address introduced species management with the aim of a species’ extirpation soon after initial introduction (i.e. prevention of a problem).
2) If a species is already established and widespread when it is first discovered, then the management approach should address the ecosystem recovery, the removal of the potential suppression of the native species, and related socio-economic aspects (i.e. deal with potential impacts).

An Early Warning Network (EWN) system should be set up that includes an interconnected communication network between stakeholders, e.g. anglers, regulating agencies and rapid response teams (RRT) who will be able to take rapid action in form of immediate decision-making when a new non-native species is reported. Within the EWN, results of research on non-native species (see Section 8.4 for examples) will be supplied for use in practical application in management as soon as it is available. The power of decision-making would need to rest within each of the task groups of the network. Rapid response and preparedness is vital for successful management of biological invasions. Similar early warning systems have recently been recommended for integration into the non-native species strategy in the U.K. under the ‘Early Detection, Surveillance, Monitoring and Rapid Response’ objective (Defra, 2007).

Small-scale control of introduced species may be achieved on a case by case basis by introducing stricter measures for each facility involved in the fish trade, and ensuring education of fishery-managers on the urgency of the prevention of non-native species overspill into the natural environment. It is recommended that fisheries and aquaculture facilities that are subject to species introductions, particularly ones that are located online with inland water bodies such as streams and rivers, may employ a permanent sustainable filtering system, e.g. gravel filter, through which the outflow must pass. This would provide a physical barrier to fish leaving the facility and potentially entering the connected water body. With regard to spatial dynamics and the health of native populations in the wild, the movement of adults and larval drift of non-native species are factors that may affect the structure and functioning of self-sustaining native fish populations and must be controlled. However, such filtering systems should ideally serve not only the purpose to prevent fish passing through. In fact, it should also be combined with a mechanism that kills any possible parasites (e.g. non-native parasites with free-living life stages) and disease (e.g. transferred *via* water) (see also Chapters 4 and 5).

After the initial discovery of a non-native species it should be assessed if eradication[26] may provide a suitable approach (Wheeler, 1998; Genovesi, 2005; Hill and Cichrab, 2005; Allen *et al.*, 2006; Britton and Brazier, 2006), for example when the benefits outweigh the costs. Such a condition would be met when the removal of the non-native species would essentially benefit the health of the native fish population, which had previously been impeded by the presence of the said non-native. Eradication protocols may be adapted from the one previously used for the eradication of topmouth gudgeon (Britton and Brazier, 2006). In Europe, introduced species eradications are scarce, probably due to limited awareness of the public and decision makers (Genovesi, 2005). In many cases

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[26] Eradication is the complete removal of a population in a set area within a defined timeframe.

(e.g. large water bodies, presence of protected species), eradication may not provide an option, so mitigation measures including stringent quarantine and population reduction could be applied (i.e. control and containment).

Before eradication can be undertaken a feasibility assessment needs to be carried out, and a variety of requirements need to be met (Wittenberg and Cock, 2001; GISP, 2005):

1) Each individual of the population must be targeted, i.e. each individual must be vulnerable to the eradication method employed,
2) The target species must be removed faster than they reproduce, and
3) The risk of re-introduction of the systems must be zero (i.e. pathway closure).

Before eradication could be attempted numerous factors need to be accounted for; for example the characteristics of the target species and native communities (fauna and flora). It is also important that the potential cost of the eradication is assessed, and whether sufficient resources (e.g. finance, manpower) are available to carry out a complete removal of the species. Additionally, the type of system from which a species is to be eradicated is important when evaluating the feasibility of this undertaking. An enclosed lake versus an online river system offer obvious reasons for the feasibility of eradication. Enclosed systems are more likely to meet the above requirements for eradication. Once a species has invaded a river system, eradication is very problematic and expensive, although this has previously been done in Norwegian rivers (Johnsen and Jensen, 1991). In this case, control (e.g. regular surveys during which specimens are removed and destroyed) and mitigation (e.g. assist ecosystem recovery) should be applied.

It is necessary to gain a large amount of knowledge of the natural environment to be able to potentially improve the ecological status of a system after, for example eradicating an unwanted introduced species. Here, management strategies will be supported by the Habitats Directive 1992 and on the larger scale by the Water Framework Directive, which delegates the restoration of ecological quality of aquatic habitats. Further, a consistent approach to habitat conservation may aid the environment to potentially mediate ecological resistance against future invasions by introduced species. This is important because some introduced species may be more likely to be successful in ecosystems that are already disturbed (Byers, 2002b). One of the reasons for this is the anthropogenic alteration of environments (e.g. eutrophication; the selective removal of top predators), which was found to predispose those habitats to invasions (Byers, 2002b).

Freshwater fish are of great economical importance to England and Wales in that catch-and-release fishing are among the most popular recreational activities for all ages of the population. The economic value of angling is estimated at > £ 3.6 billion per annum (Environment Agency, 2004). Of great importance in the plight against biological invasions is general public awareness, but particularly stakeholders such as recreational anglers and fishery managers. All stakeholders need to be educated about ILFA listed species and potential species that may be introduced in future, so they will be able to identify and subsequently notify the responsible regulating bodies to take rapid action. In recreational fisheries, invaders such as topmouth gudgeon and sunbleak may be able to go unnoticed due to their small size and form dense populations assisted by their favourable life history characteristics. As a result, the species can become a nuisance by sheer numbers, i.e. the likelihood to catch target species is much decreased. Additionally, the risk of introduction and transfer of disease to valuable recreational fish stock would rise.

8.3.3.1 Potential sources for finance of recommended activities

Generally, financial resources are crucial for non-native species management and they need to be spent where they are most needed, e.g. ‘high risk’ sites. It is generally considered that obtaining sufficient funding to address the management recommendations may be difficult to gain. Solutions for administration and financing bodies may have to be sought through combined consultation with the variety of government bodies currently involved with non-native species legislation and management, e.g. Defra, Environment Agency. However, it may be necessary to create new legal authority and provide emergency funding to support rapid responses to emerging invasions. In the following some ideas on sources of financial support are outlined:

1) **Government tax of 'high risk' activities:** Fish traders dealing in live fish species should be taxed according to risk. This applies to national and international trade of live specimens. Such tax may then be used to carry out non-native species pre- and post-introduction management methods. Essentially, prevention of a problem will be more cost-effective than the potential costs to the economy as a result of introduction when nothing is done.
2) **Charge for fish movement consents:** Currently, consents are granted to stakeholders free of charge. Seeing the potential risks related to the movement of live fish (e.g. overspill from source populations into the wild), it may seem only fair that a charge may be recuperated from such 'high risk' activity. This appears particularly reasonable, for example, because currently eradications of introduced species are undertaken by the Environment Agency and paid for by public funds.
3) **Emergency funding to combat non-native species:** Emergency funding should be given when a 'biosecurity emergency' in the event of the incursion of a new organism that has potential to cause significant economic or environmental loss. This should be provided by the government upon rapid consideration and consultation. Generally, such funding will ensure rapid response in urgent cases, with the aim of protecting the native fauna.

8.3.3 Recommendations for the management of sunbleak and topmouth gudgeon

Prevention of further introductions

Further dispersal of topmouth gudgeon and sunbleak should be prevented. The introduction into and the dispersal of both species within inland waters in England is largely attributed to live fish movements (Copp *et al.*, 2007). Implications and recommendations relating to the potential prevention of further introductions of both species are presented and discussed in Section 8.3.2. Generally, it is recommended:

1) To stop 'high risk' activities (i.e. closure of pathways) that are most likely to be the cause of further introductions (e.g. live fish movements into water

bodies, which are connected to river catchments but are not equipped with permanent outfall prevention measures), and

2) For open pathways, to carry out stringent audits of live fish being moved to prevent introductions of unwanted species.

Prevention of further dispersal

It is recommended, that the outlets of all fisheries (recreational and ornamental) are equipped with sustainable permanent filtering systems, e.g. gravel filter, through which the outflow must pass. This would provide a physical barrier to fish leaving the facility and potentially entering the connected water body. As previously recommended, such filtering system should also prevent passage of parasites and disease (see also Section 8.3.2; Chapters 4 and 5), though setup of such system may prove difficult as well as being costly.

Eradication and/or Control

Eradication of known topmouth gudgeon populations should ideally be undertaken where benefits outweigh the costs. The eradication of topmouth gudgeon from Ratherheath Tarn, Cumbria, is a good example (Britton and Brazier, 2006) and a similar eradication protocol may be adapted for use elsewhere. In England and Wales, where suitable, eradication is currently being undertaken by the Environment Agency. In Ratherheath Tarn a dense population of topmouth gudgeon was extirpated using rotenone after great effort was put into the removal of the native stock. Eradication was costly but has so far been a success (e.g. spawning of native species has been observed) and is expected to have been beneficial on the long term for the fishery. Places where eradication is not feasible, for example because costs outweigh the benefits, should be quarantined to prevent further dispersal. A ‘decision support system’ which collates and utilises available information may be necessary to aid in the decision-making process.

It may not always be possible to eradicate completely (see Section 8.3.2 for an explanation). Essentially, as soon as new sightings of topmouth gudgeon and/or sunbleak are reported, it should be evaluated how management should be applied (i.e. risk-based approach). At this stage, risk management plays a crucial role because it is essential that available resources are used where they are most needed (‘high risk’ locations). Cost-benefit analysis for populations observed to evaluate whether or not removal is an option or quarantine to prevent further dispersal (even with enclosed water bodies).

When risk analysis suggests that eradication is not feasible, it is recommended that regular fishing surveys be carried out during which non-native species are removed [control]. Additionally, during such surveys, by controlling spawning substrata (e.g. removal of topmouth gudgeon or sunbleak eggs attached to substrata) it may be possible to reduce numbers of offspring during the spawning season. Such regular surveys are recommended for Tadburn Lake stream and the River Test catchment (topmouth gudgeon escaped from Crampmoor Fishery), Monks Brook and the River Itchen catchment (sunbleak escaped from Stoneham Lakes Fishery), as well as Caundle Brook and the River Lydden (outfall of sunbleak eggs from Revels Fishery) (see Chapter 2 for locations of the catchments).

Public awareness and education

Topmouth gudgeon and sunbleak distribution is largely related to live fish movements and many of the locations where the species have been found to form dense populations are fisheries (recreational and ornamental) (Copp *et al.*, 2007) and so their managers and anglers ought to be supplied with information of species identification. All stakeholders need to be supplied with training as well as ID cards containing a picture of the species and depicting their pertinent morphological features that will assist in identification. Such ID cards should be supplied to all potential ‘hotspots’ for introductions. It is further paramount that education as regards fish introductions is available to all stakeholders. In addition, it may be useful to prepare ‘What-to-Do’ leaflets, which should describe which steps should be taken when a specimen is captured that corresponds to an ID card. An example of an ID card prepared for invasive round goby invading the Great Lakes, North America (Minnesota Sea Grant, 2008) can be seen in Appendix I. Such ID cards and leaflets are relatively cheap to produce and work well as educational tools for stakeholders. On the whole, and this applies to regions within which water bodies have already been invaded by topmouth gudgeon and sunbleak or may potentially be introduced to in future, education about fish introductions and the implications of invasions should be incorporated in school curricula.

On a larger and more wide-ranging scale, an educational video about fish introductions and/or non-native species in general, could be used as a tool to reach a wide audience including schools, colleges, universities, and fishery managers. Part of this video, may be titled: 'The story of the topmouth gudgeon'. However, the production of this may be expensive.

The 'Do-Nothing' Approach

Generally, the 'do-nothing' approach is an option that should not be taken lightly. It is important that a full risk assessment be carried out when new sightings of topmouth gudgeon and/or sunbleak are reported. In light of the potential for dispersal of both species to disperse beyond their current distribution as well as their association with non-native parasites (sunbleak; see Chapter 5 and Beyer *et al.*, 2005) and an intracellular pathogen that is potentially lethal to native fish species (topmouth gudgeon; Gozlan *et al.*, 2005), the 'do-nothing' approach is unlikely to be suitable.

In actual fact, some steps including the evaluation of associated disease and/or parasites and the prevention of further dispersal are likely to be essential in all cases, which also involve subsequent management. Essentially, the 'do-nothing' approach is only justifiable when the cost of eradication and/or control outweighs the cost of the potential species' impact.

Parasites and Disease

An issue that should be continued to be addressed are the non-native parasites that are associated with sunbleak in the England and Wales. It is important to know whether Category II–Parasites cause problems for the host fish. The Environment

Agency’s internal ‘Category II Review Group’ is responsible to review and update the list of classified parasite species.

The risk of an infection with the novel intracellular pathogen RLA, through the exposure to topmouth gudgeon as a healthy carrier, for salmonids in England may be reduced by preventing further ‘spill-over’ of topmouth gudgeon from source populations into the wild (see also Chapter 4) and preventing further introductions into and translocations within the country. The described situation raises great concern as regards the mechanisms of the emergence of novel pathogens and the role of their facilitation *via* anthropogenic means. Also, though it has been suggested that health monitoring on introduced fish needs to be carried out before they are transported across borders, imported species are still not subject to specific sanitary surveillance (Austin and Robertson, 1993b; Blanc, 2001a; Copp *et al.*, 2005b; Gozlan *et al.*, 2006). This is in thorough need of rectification.

Gozlan *et al.* (2005) reported that topmouth gudgeon in which RLA was found, did not reveal any external signs of infection nor did their internal organs (Gozlan *et al.*, 2005). The disease was determined using molecular tools and cohabitation studies (Gozlan *et al.*, 2005), and could not have been identified using standard parasitological protocols as used during the present study (Fernando *et al.*, 1972). A similar protocol is used by personnel carrying out health checks under Section 30 of the Salmon and Freshwater Fisheries Act (SAFFA) 1975. Based on these health checks, the Environment Agency grants licences for live fish movements between water bodies within England and Wales. Consideration of the type of tools used for fish health monitoring is paramount in the management of live fish movement and the associated prevention of further novel pathogen introductions into and/or translocations within England. Topmouth gudgeon being a non-native host for a disease, is of major concern particularly in light of the species’ close association with the aquaculture trade (introduction into and translocation within England) (Pinder *et al.*, 2005b). Furthermore, this management should be applied to all fish movements because topmouth gudgeon is associated with live fish movements as an accidental contaminant (Copp *et al.*, 2007).

Biotic resistance

As for the management of Tadburn Lake stream and its unwanted topmouth gudgeon population, which originates from Crampmoor Fishery upstream (Chapter 4) as well as from reproduction within the stream (K. Beyer, pers. obs.), it is recommended that: 1) outfall is prevented from the fishery (see also Chapter 4 for more details) [prevention] and 2) regular fish surveys are carried out downstream of the fishery during which all topmouth gudgeon are removed and destroyed [control]. The composition of the fish assemblage as regards piscivorous predators and their ecology in Tadburn Lake stream may lead to the conclusion to consider the introduction of an obligate piscivore (e.g. pike) into the system to facilitate biological resistance against topmouth gudgeon. However, introducing a species with an ecological trait that does not naturally exist in an ecosystem may have disastrous consequences. However, despite the introduction of an obligate piscivore being considered an unlikely option for Tadburn Lake stream, this may be an option that could be useful elsewhere.

To improve the potential for a native ecosystem to mediate resistance against an invasion, it is recommended to ensure overall habitat protection and conservation. Habitat enhancements and reducing anthropogenic disturbances where possible may not only conform to the aims of the Water Framework Directive, but also increase the likelihood for the systems to facilitate biological resistance against an invasion.

Updating of Existing Risk Assessments

1) Pre-Introduction Risk Assessment

Social aspects are not currently part of non-native fish species risk assessments (Copp *et al.*, 2005b). In light of the conclusions made based on the social network analysis regarding the social integration of sunbleak into a native fish assemblage and the potentially rapid transmission of parasites, risk assessments may require review and consideration of the social aspects of non-native species.

2) **Post-Introduction Risk Assessment**

At present, risk assessments only deal with pre-introduction scenarios, while post-introduction risk assessment is crucial in determining priorities in management and the application of resources where they are most needed.

Modelling

To determine potential habitats that may be invaded by topmouth gudgeon, sunbleak and other non-native species in future, the use of models such as habitat match modelling and for example CLIMEX and BIOLIM/ANUCLIM (Duncan *et al.*, 2001; Kriticos and Randall, 2001). Such models incorporate information for example rainfall and temperature, and have been previously used to predict the distribution of terrestrial fauna and flora (Duncan *et al.*, 2001; Kriticos and Randall, 2001). The outputs of such analyses may assist risk assessment and enable determination of priority locations (e.g. matching habitats) that require attention (e.g. increased risk). This information will allow categorisation of ‘high risk’ versus ‘low risk’ locations and enable to identify where resources need to be invested first (i.e. application of non-native species management measures).

It is also possible to investigate how a non-native species may impact ecosystems using the ecosystem trophic mass balance analysis (Ecopath) (Christensen and Walters, 2004). Ecopath has traditionally been used to determine how fisheries and the environment may affect ecosystems but may be useful in revealing further aspects in invasion ecology. Trophic aspects of a non-native species play an important role in the identification of the level of risk that the species may pose to the native fish community and the environment (Copp *et al.*, 2005b). Non-native piscivores may pose an increased threat to native fish species by feeding on them (e.g. Nile perch), while herbivores may cause habitat alterations through excessive feeding on aquatic macrophytes (e.g. grass carp). Utilisation of Ecopath may enable prediction of potential impacts based on trophic information of the potential non-native species, complementing risk assessment and prioritisation of ‘high risk’ versus ‘low risk’ locations for management. Stable isotope analysis may aid in the collection of the necessary trophic data required for Ecopath modeling.

Recreational and ornamental fisheries

Recreational fisheries may suffer from potential fish losses due to potential disease introduction through accidental introduction of healthy carrier topmouth gudgeon. Indirect financial losses may be caused by angler avoidance because, for example nuisance from capture of dense small-bodied sunbleak and/or topmouth gudgeon. These problems may be decreased if fishery management incorporates regular removal exercises using for example a seine net suitable for the size of the fishery. Removal (and subsequent destruction) may afford considerable population reduction, while at the same time reducing potential dispersal (i.e. propagule pressure). Further measures to be applied include the application of permanent filtering system at the outlet (if the fishery is online) and education of anglers. These have been discussed above.

8.4 Further research

This PhD research provides a large amount of information on the ecological aspects of the invasion of inland waters in England by sunbleak and topmouth gudgeon. However, some gaps are yet to be filled and recommendations on how to do this are presented here.

8.5.1 Topmouth gudgeon

Social aspects of invasion

The results of the social network analysis raise concerns over the speed of transmission of non-native parasites within social networks containing sunbleak (Chapter 6B). The social aspects of parasite and/or disease transmission within invaded fish assemblages could be a useful tool in invasion ecology and potentially in risk assessments. This is substantiated in light of topmouth gudgeon’s association with RLA (Gozlan *et al.*, 2005) and social network analysis may reveal aspects of the transfer mechanism of this pathogen between topmouth gudgeon and native conspecifics.

Potentially, parts of these aspects could be investigated using cohabitation studies and/or mesocosm experiments:

1) **Cohabitation studies**

   Cohabitation challenges (St-Hilaire *et al.*, 2001; Gozlan *et al.*, 2005; Drennan *et al.*, 2007) may be carried out using suitably sized systems (e.g. tanks) that will allow social interactions between fishes to take place (controls: mock cohabitations; treatments: pathogen cohabitation). Each system should be equipped with independent re-circulating water systems while all tanks in a system should receive identical types and amounts of water. Initially, cohabitation investigations may use native fish species (e.g. species that are likely to come into contact with topmouth gudgeon as indicated by fish communities in water bodies that have already been invaded) and topmouth gudgeon known to be healthy carriers of RLA. Each fish would require marking for individual recognition to allow for subsequent social network analysis. Behavioural observations will allow confirmation and comparison of social interactions while molecular tools would need to be used for detection of RLA in the native species exposed to topmouth gudgeon. It is essential that experimental investigations, such as recommended above, carry out all activities following stringent protocols including hygiene and disinfection of equipment used etc.

2) **Mesocosm experiments**

   A similar approach as described for cohabitation studies may be used, while for mesocosm experiments the experimental system used should simulate real-life conditions as closely as possible. Basically, cohabitation studies may be carried out on a much larger scale.

Parasite Fauna

The absence of macroparasite fauna in two topmouth gudgeon populations in England as well as one population in France, calls for confirmation of a ‘Parasite Lost’ hypothesis and/or the theory of a common origin for England (see Chapter 5 for details). This would require the examination of topmouth gudgeon from the remaining locations in England where the species currently occurs (see Figure 1.3; Pinder *et al.*, 2005b).

Disease

Attention should be given to the identification of topmouth gudgeon populations that are actual carriers of the emerging intracellular disease RLA (Gozlan *et al.*, 2005), which is a potential threat to freshwater fish diversity. This needs to be done not just for conservation purposes but also to enable prioritisation of subsequent action. To date, only topmouth gudgeon from one English location (Gozlan *et al.*, 2005) were found to be associated with RLA. It is yet unknown whether the remaining populations in England and Wales (see Figure 1.3; Pinder *et al.*, 2005b) are healthy carriers of the disease. It is recommended this be identified. Sites where RLA occurs in topmouth gudgeon may be classed as 'high risk' sites and eradication feasibility assessment may be applied immediately. Topmouth gudgeon populations in which RLA is not identified may be assessed for eradication feasibility following RLA-associated sites.

Invasibility and Biotic Resistance

The ecology of the two native facultative predators (brown trout, chub) and subsequent low predation pressure may not contribute sufficiently to create a resistance against topmouth gudgeon in Tadburn Lake stream. The role of piscivorous predators in creating biotic resistance and ecosystem resilience against topmouth gudgeon invasion elsewhere is unclear. This requires investigation in future research on the diet of native piscivorous predators in combination with quantification of propagule pressure of topmouth gudgeon elsewhere.

A large section of Tadburn Lake stream flows through an urban area on its way down to the River Test, while providing direct access on either bank (see Figure 2.1 in Chapter 2). Anthropogenic disturbance has been found to increase the likelihood for successful invasion of streams by non-native species elsewhere (Byers, 2002b). The role of anthropogenic disturbance in the invasibility by topmouth gudgeon was outside the scope of this PhD. However, whether this may be an important aspect in the invasion success of topmouth gudgeon should be tested. Such research requires much effort in that indices for anthropogenic disturbance need to be developed while streams need to be investigated that have already been invaded by topmouth gudgeon (‘treatment stream’) and streams void of the fish species (‘control stream’).

Other locations in England

Topmouth gudgeon have been reported from 25 locations in England and Wales. During the present study, examinations were limited to two of those sites. To confirm and evaluate the results of this study, aspects (e.g. life histories, morphology, habitat use) of the topmouth gudgeon from the remaining sites need to be investigated. A variety of steps may be followed during further investigations into topmouth gudgeon elsewhere:

1) If possible, utilise information on live fish movements (i.e. EA/Cefas database),
2) Identification of water bodies that may receive fish through live fish movements,
3) Determine size of water body, composition of the native community, biotic and abiotic conditions,
4) Identify whether the water is connected to the wild (e.g. stream, river etc.),
5) Ascertain the size (length) of fish moved, and
6) Establish whether topmouth gudgeon occur in the water body.

The results may enable not only improvement of management of topmouth gudgeon in the country, but also, identification of potential spread that may have taken place since 2005 in which Pinder *et al*. (2005b) identified the 25 sites containing topmouth gudgeon.

8.5.2 Sunbleak

Social aspects of sunbleak invasion

As a comparison with the results of the present study and to confirm whether social networks display similar characteristics as in the fish assemblage at Stoneham Lakes in Hampshire, social networks could be examined in the Somerset Levels. Further, a more intense investigation could take place using adult specimen and applying mark-and-recapture techniques (Croft *et al.*, 2004). One approach may include the capture of all adult specimens of fish within a defined area and marking (e.g. visible implant fluorescent elastomer) them to enable individual recognition upon eventual recapture. The marking technique used by Croft *et al.* (2003) may be one that could be followed in such investigation. Mortality and potential tag loss as well as the potential effect of the identification mark on shoaling behaviour should be tested in control experiments. The mark–recapture experiment in the wild may entail simultaneously release of all captured fish into the same area where they had originated, and following a re-sampling protocol (Croft *et al.*, 2004). Increasing the knowledge using this novel approach may provide further specific insights into the social aspects of freshwater fish invasions.

Repeated occurrence of pair-wise associations between sunbleak and native species of similar developmental stages suggests a potential for the development of cooperative behaviour (Dugatkin, 1997), which may further increase the advantages for an invasive species. The influences of habitat use, site fidelity and active choice of social partners and their reflection in social networks call for confirmation in further studies.

8.5.3 Freshwater fish invasions

Parasite life cycles

It has been suggested that Direct Life Cycle (DLC) parasites are more likely to establish in a new environment (either on a non-native or native fish host) than Indirect Life Cycle (ILC) parasites, which require an intermediate host (Petrushevski, 1961; Dobson and May, 1986; Bauer, 1991). Therefore research into the type of life cycle that parasites potentially associated with introduced fish species may display is warranted. Non-native species risk assessments identifying ‘high risk’ fish species for future introduction, may assist in identification of ‘high risk’ parasites. Once identified, the life cycle of these parasites (if not yet known) requires identification. Essentially, DLC parasites can be determined by carrying out ‘single host species’ (e.g. 1 fish species) cohabitation experiments. This basically excludes the availability of intermediate hosts and would deny a DLC parasite to fulfil its life cycle. Parasite risk assessment may incorporate DLC vs ILC risk classification (e.g. DLC: high risk; ILC: decreased risk).

Propagule pressure vs biotic resistance

Studies investigating the relationships between propagule pressure of non-native fish species and covariate factors (e.g. the physical environment, number of resident species, predation by native species) are virtually non-existent. Though, this appears to be an important element of invasion success (see Chapters 4 and 7).

Biological control methods

Pheromones are now used in pest control for example against sea Lampes *Petromyzon marinus*, Linnaeus, 1758, in the Great Lakes (Sorensen and Stacey, 2004). Pheromones have great potential to supplement and increase the efficiencies of other control strategies including the trapping for removal or sterilisation, and barriers to prevent spread. It is recommended that research into the use and the development of specific pheromones to control non-native fish species in England is intensified (Sorensen and Stacey, 2004). Initially, two research directions could be considered:

1) **Disruption of spawning**: Sex-pheromones are important in the successful reproduction of many fish species (Dulka *et al.*, 1987; Irvine and Sorensen, 1993; Sorensen and Stacey, 2004). Essentially, if a pheromone that disrupts the reproductive behaviour of a non-native species (e.g. topmouth gudgeon, sunbleak) could be identified and synthesized, this may assist in population reduction, while reducing the species' potential dispersal (i.e. propagule pressure).
2) **Phermone-baited traps**: Control strategies may include the use of traps that are equipped with pheromones as bait. The pheromones used here would need to be identified and synthesized, but are likely related to reproductive and/or migration behaviour and act as attractant for the target fish non-native fish species. Specimens captured in traps should subsequently be destroyed.

Are invasive species better 'dispersers'?

Dispersal is an important element of a species' invasion success (Rehage and Sih, 2004), but it is unclear whether invaders are simply better dispersers than unsuccessful introduced species or native species themselves. In fact, it has been suggested that an underlying behavioural trait (boldness) may be a key factor in this mechanism (Rehage and Sih, 2004). Rehage and Sih (2004) investigated the link between dispersal, boldness, and invasiveness in two invasive Gambusia species and two congeners in experimental streams. Invasive Gambusia was more likely to: 1) disperse, 2) disperse sooner, 3) travel a greater distance, and 4) exhibit greater dispersal tendencies than their close relatives. Owing to the findings of the study by Rehage and Sih (2004), and the results on the potential for dispersal by topmouth gudgeon and sunbleak (Chapter 4), further analyses of behavioural mechanisms in the study of invasive species may be warranted. Such research may largely depend on experimental systems appropriate to the size and behaviour of the species under investigation. For example, experimental streams could be used which enable the investigation of dispersal mechanisms from a source population. Such a setup may enable testing of a large number of species (native and non-native), while field investigations need to be carried out to ascertain experimental results.

Social aspects of invasions

Knowledge on social aspects of introduced species could be a useful tool in invasion ecology and potentially in risk assessments. It may therefore be useful to continue to explore the role of social characteristics in species invasions as well as the mechanism of social integration into native communities. This could be done by utilising social network approach used in Chapter 6B and applying it to social fish species elsewhere. To address social aspects of invasions, experiments with differing levels of realism and control (e.g. littoral cages, outdoor pools, laboratory aquaria) may be conducted. The use of native and non-native species in these experiments may give important insights that may be incorporated into risk assessments.

Climate Change and parasites associated to non-native fish species

Global changes in temperature may facilitate the future introduction and establishment of novel species and their parasites, as well as to increase the rate of parasite transmission (Dobson and Carper, 1992; Gozlan *et al.*, 2006). Policy development in England and Wales needs to incorporate the assessment of the potential effects of climate change on the causes, development and transmission of parasites and disease. A start could be made by determining potential areas of colonization by new host species and areas where novel parasites are likely to persist. This could be done by identifying the potential species likely to be introduced using risk assessment methodology such as that developed by Copp *et al.* (2005b), and using mathematical modelling for prediction and mapping techniques to overlay environmental data of areas where the respective species may be able to persevere. Such information may assist in the prevention and management of future introductions.

Modelling using CLIMEX, BIOLIM/ANUCLIM and Ecopath may assist in more precise and multidimensional descriptions of invasion processes (see also Section 8.3.3). Naturally, the basis for such modelling is ecological information on the respective species.

Ecology vs anthropogenic aspects of fish invasions

It is evident, that examining ecological aspects of invasions by itself will not result in reliable conclusions to be made. When attempting to determine invasion mechanisms, a range of biological parameter such as life history traits of the invader, its association with anthropogenic sources and propagule pressure should be quantified together with ecosystem resistance (predation pressure, habitat availability etc.).

Parasitology and ecology of fish invasions

Investigating the parasitology and the ecology of invasive fish species alongside each other is seldom done. Yet, such combined research is essential when aiming to understand the mechanisms underlying the dispersal of parasite associated with introduced and/or invasive species.

8.5 Concluding remarks

It is unlikely that all future introductions of new species into England will be prevented, however it would be possible to reduce the risk of these introductions through more effective importation, control and eradication procedures, including a better defined policy on the implementation of stocking and translocations practices regulated under Section 30 of the Salmon and Freshwater Fisheries Act (SAFFA) 1975. Furthermore, the development of new legislation that incorporates aspects of fish introductions and live fish movements into one may simplify non-native species management. Prevention in the form of trade agreements, border inspections, and early detection and eradication of species that circumvent border inspections may offer the greatest benefits for the least cost. Integrated management is vital to assure the conservation of native fish stocks and habitat in England. The government should provide funding and encouragement for cost effective programs to slow the spread of existing invasive species in order to protect still un-invaded ecosystems. In general, a greater understanding of the attributes that drive the success of an introduced species will be vital for the continued development of protocols with which to evaluate the risks and potential implications of non-native species. The present study has investigated a variety of aspects that are of critical importance in the environmental biology of two introduced species and their success in a new environment. It describes several biological traits in topmouth gudgeon and sunbleak that may initiate potential impacts on native co-existing species. This work is an important contribution in gaining knowledge on the ecology of small-bodied freshwater fishes that have been introduced to inland water bodies in England and their ecological implications. This information, in light of the potential for topmouth gudgeon and sunbleak to spread beyond their current distribution along with the ever-increasing number of introduced species causing harm to native populations world-wide, is essential for management and conservation of native species and their habitats.

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10. Appendices

Appendix A

Table A10.1: Coefficients of linear regression for the three types of length measures in sunbleak (TL=total length, FL=fork length, SL=standard length) at nine locations in England at Bridgewater-Taunton Canal, Buckland Farm (BTC1), Bridgewater-Taunton Canal, Creech St. Michael, Somerset (BTC2), 3) Bridgewater-Taunton Canal, YMCA, Somerset (BTC3), Kings-Sedgemoor Drain, Bradney Bridge, Bawdrip, Somerset (KSD4) 5) Kings-Sedgemoor Drain, Parchey Bridge, Somerset, River Sowy , Grey Lake Bridge, Somerset (Sowy7), Dunwear pond, Somerset (Dun9), Stoneham Lakes, Hampshire (Stone11), Two Lakes Fishery, Hampshire (TwoL12). Coefficients are not presented for 3 sites at River Huntspill (Hunt6), River Tone (Tone8) and Durleigh Reservoir (Durl10).

Site	y	x	a	b	r^2	n	Significance
BTC1	FL	SL	0.95	-2.4508	0.986	50	$P < 0.001$
	FL	TL	1.0273	-6.8149	0.9577		$P < 0.001$
	SL	TL	0.9771	-8.9811	0.9464		$P < 0.001$
BTC2	FL	SL	0.9985	-4.6641	0.9918	50	$P < 0.001$
	FL	TL	1.0038	-6.6082	0.9886		$P < 0.001$
	SL	TL	1.0047	-10.862	0.9851		$P < 0.001$
BTC3	FL	SL	0.9894	-4.3751	0.9321	55	$P < 0.001$
	FL	TL	0.8952	0.8614	0.8902		$P < 0.001$
	SL	TL	0.9368	-6.3434	0.9282		$P < 0.001$
KSD4	FL	SL	0.8248	5.076	0.6109	30	$P < 0.001$
	FL	TL	0.8974	0.5932	0.89		$P < 0.001$
	SL	TL	0.6431	11.364	0.4106		$P < 0.001$
KSD5	FL	SL	0.7985	0.7298	0.8684	60	$P < 0.001$
	FL	TL	0.8735	2.1576	0.888		$P < 0.001$
	SL	TL	0.9194	-1.4944	0.9892		$P < 0.001$
Sowy7	FL	SL	0.9108	-0.6025	0.9688	70	$P < 0.001$
	FL	TL	0.948	-2.1341	0.9698		$P < 0.001$
	SL	TL	0.8765	-3.2817	0.9682		$P < 0.001$
Dun9	FL	SL	0.9099	-0.4061	0.9827	30	$P < 0.001$
	FL	TL	0.9456	-1.1754	0.959		$P < 0.001$
	SL	TL	0.8687	-1.8955	0.9608		$P < 0.001$
Stone11	FL	SL	0.9992	-4.8775	0.9863	60	$P < 0.001$
	FL	TL	1.0538	-7.0099	0.9842		$P < 0.001$
	SL	TL	1.0493	-11.695	0.9639		$P < 0.001$
TwoL12	FL	SL	0.9273	-1.8492	0.9961	70	$P < 0.001$
	FL	TL	0.9869	-3.9289	0.9921		$P < 0.001$
	SL	TL	0.9143	-5.4457	0.9863		$P < 0.001$
All English Populations	FL	SL	0.9453	-2.3087	0.9778	475	$P < 0.001$
	FL	TL	0.9439	-1.8287	0.9482		$P < 0.001$
	SL	TL	0.8927	-4.0599	0.9281		$P < 0.001$

Table A10.2: Coefficients of linear regression of length against weight (LnW=bLnFL+a) for males, females and both sexes combined for sunbleak from at nine locations in England at Bridgewater-Taunton Canal, Buckland Farm (BTC1), Bridgewater-Taunton Canal, Creech St. Michael, Somerset (BTC2), 3) Bridgewater-Taunton Canal, YMCA, Somerset (BTC3), Kings-Sedgemoor Drain, Bradney Bridge, Bawdrip, Somerset (KSD4) 5) Kings-Sedgemoor Drain, Parchey Bridge, Somerset, River Sowy , Grey Lake Bridge, Somerset (Sowy7), Dunwear pond, Somerset (Dun9), Stoneham Lakes, Hampshire (Stone11), Two Lakes Fishery, Hampshire (TwoL12). Coefficients are not presented for 3 sites at River Huntspill (Hunt6), River Tone (Tone8) and Durleigh Reservoir (Durl10).

Site	Sex	a	b	r^2	n	Significance
BTC1	Male	-0.288	0.829	0.182	12	NS
	Female	-0.288	0.822	0.206	38	P<0.010
	Both	-0.291	0.827	0.114	50	P<0.050
BTC2	Male	-0.811	1.949	0.522	11	P<0.010
	Female	-0.927	2.127	0.557	39	P<0.001
	Both	-0.929	2.139	0.561	50	P<0.001
BTC3	Male	-1.610	3.423	0.600	22	P<0.001
	Female	-0.744	1.797	0.259	33	P<0.010
	Both	-1.099	2.482	0.400	55	P<0.001
KSD4	Male	-0.421	0.292	0.050	9	NS
	Female	-0.266	0.003	0.050	21	NS
	Both	-0.330	0.123	0.072	30	NS
KSD5	Male	-0.282	0.768	0.148	11	P<0.001
	Female	-0.977	2.172	0.723	49	P<0.001
	Both	-0.799	1.803	0.575	60	P<0.001
Sowy7	Male	-1.143	2.531	0.229	21	P<0.050
	Female	-1.908	4.103	0.702	9	P<0.010
	Both	-1.457	3.162	0.322	30	P<0.010
Dun9	Male	-1.498	3.037	0.377	23	P<0.010
	Female	-1.476	3.105	0.619	37	P<0.001
	Both	-1.502	3.115	0.527	60	P<0.001
Stone11	Male	-0.621	1.466	0.553	17	P<0.001
	Female	-0.785	1.763	0.497	53	P<0.001
	Both	-0.757	1.714	0.516	70	P<0.001
TwoL12	Male	-3.089	6.066	0.986	18	P<0.001
	Female	-0.828	1.892	0.458	52	P<0.001
	Both	-0.931	2.077	0.471	70	P<0.001

Table A10.3: Coefficients of linear regression for the three types of length measures in topmouth gudgeon (TL=total length, FL=fork length, SL=standard length) populations from Ratherheath Tarn (n=60), Tadburn Lake stream (n=50) and Canal du Fumemorte (n=50).

	y	x	a	b	r^2	n	Significance
Ratherheath	FL	SL	1.159	-1.859	0.945	60	*P*<0.001
	FL	TL	0.778	7.345	0.780	60	*P*<0.001
	SL	TL	0.628	10.459	0.722	60	*P*<0.001
Tadburn	FL	SL	1.070	2.243	0.992	50	*P*<0.001
	FL	TL	0.920	0.055	0.989	50	*P*<0.001
	SL	TL	0.856	-1.800	0.988	50	*P*<0.001
Fumemorte	FL	SL	1.123	0.161	0.990	50	*P*<0.001
	FL	TL	0.945	-1.507	0.990	50	*P*<0.001
	SL	TL	0.836	-1.184	0.986	50	*P*<0.001
Combined	FL	SL	1.095	1.198	0.985	160	*P*<0.001
	FL	TL	0.908	0.302	0.960	160	*P*<0.001
	SL	TL	0.820	-0.258	0.951	160	*P*<0.001

Table A10.4: Coefficients of linear regression of length against weight (LnW=bLnFL+a) for males, females and both sexes combined in topmouth gudgeon populations from Ratherheath Tarn, Cumbria, Tadburn Lake Stream and Canal du Fumemorte, France.

	Sex	a	b	r^2	n	Significance
Ratherheath	Male	-1.408	3.192	0.296	15	*P*<0.050
	Female	-2.009	4.396	0.761	45	*P*<0.001
	Both	-1.896	4.164	0.621	60	*P*<0.001
Tadburn	Male	-2.839	5.790	0.930	33	*P*<0.001
	Female	-2.541	5.275	0.894	17	*P*<0.001
	Both	-2.721	5.586	0.915	50	*P*<0.001
Fumemorte	Male	-2.643	5.425	0.913	34	*P*<0.001
	Female	-2.100	4.426	0.898	16	*P*<0.001
	Both	-2.306	4.816	0.924	50	*P*<0.001

Table A10.5: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in sunbleak from Bridgewater-Taunton Canal at Buckland Farm, Somerset (BTC1). See Table 3.2 in Chapter 3 for morphological codes.

	All						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
TL	51.32	0.79	30.93	41.32	60.82	50	53.08	1.61	31.03	41.32	60.17	12	50.77	0.89	30.42	43.13	60.82	38
FL	45.91	0.83	34.08	36.45	55.92	50	47.79	1.59	30.39	36.75	55.41	12	45.32	0.95	34.60	36.45	55.92	38
SL	41.17	0.79	31.20	32.15	50.67	50	43.06	1.50	26.83	32.19	49.34	12	40.57	0.92	31.82	32.15	50.67	38
% of standard length																		
h	8.37	0.07	0.24	6.99	9.25	50	8.50	0.11	0.14	7.65	8.90	12	8.32	0.08	0.27	6.99	9.25	38
H	21.50	0.14	1.04	20.03	24.53	50	21.53	0.28	0.93	20.03	23.25	12	21.49	0.17	1.10	20.13	24.53	38
A - C	20.85	0.20	1.99	17.85	23.23	50	20.61	0.50	2.99	18.02	22.80	12	20.92	0.21	1.72	17.85	23.23	38
PreD	55.68	0.21	2.26	53.49	58.91	50	56.19	0.55	3.68	53.97	58.91	12	55.52	0.22	1.78	53.49	58.47	38
Dh	17.10	0.08	0.29	16.34	19.94	50	16.99	0.09	0.11	16.38	17.52	12	17.13	0.10	0.35	16.34	19.94	38
Db	11.78	0.09	0.37	9.94	12.94	50	11.83	0.13	0.21	11.35	12.86	12	11.76	0.11	0.42	9.94	12.94	38
PreA	65.26	0.19	1.76	61.95	68.31	50	64.85	0.41	2.06	61.96	66.71	12	65.39	0.21	1.65	61.95	68.31	38
Ah	15.82	0.06	0.20	15.03	17.20	50	15.70	0.10	0.11	15.03	16.34	12	15.86	0.08	0.22	15.06	17.20	38
Ab	16.43	0.05	0.14	14.77	16.99	50	16.35	0.16	0.32	14.77	16.92	12	16.46	0.05	0.09	16.00	16.99	38
PreV	47.16	0.14	0.96	45.20	50.79	50	47.37	0.29	1.00	45.92	48.78	12	47.10	0.16	0.95	45.20	50.79	38
Vh	12.83	0.09	0.37	11.29	14.25	50	13.08	0.14	0.23	12.06	13.94	12	12.76	0.10	0.40	11.29	14.25	38
Vb	3.69	0.04	0.09	3.03	4.41	50	3.67	0.09	0.10	3.27	4.41	12	3.70	0.05	0.09	3.03	4.28	38
PreP	25.41	0.11	0.56	21.34	26.38	50	25.48	0.18	0.40	24.12	26.28	12	25.38	0.13	0.62	21.34	26.38	38
Ph	16.31	0.11	0.59	14.63	17.64	50	16.07	0.23	0.64	15.14	17.64	12	16.39	0.12	0.57	14.63	17.64	38
Pb	4.39	0.03	0.04	4.01	5.33	50	4.41	0.04	0.02	4.21	4.60	12	4.38	0.04	0.05	4.01	5.33	38
PreO	12.24	0.08	0.35	9.81	12.99	50	12.05	0.27	0.88	9.81	12.78	12	12.29	0.07	0.19	11.42	12.99	38
PreOp	4.95	0.05	0.13	4.40	6.38	50	4.92	0.09	0.10	4.40	5.67	12	4.96	0.06	0.14	4.40	6.38	38
Gape	3.06	0.01	0.01	2.82	3.24	50	3.07	0.03	0.01	2.82	3.22	12	3.05	0.01	0.01	2.88	3.24	38
Hd	17.44	0.08	0.30	16.15	19.35	50	17.56	0.22	0.60	16.22	19.35	12	17.40	0.08	0.21	16.15	18.33	38
Io	7.38	0.06	0.15	5.92	7.93	50	7.28	0.11	0.14	6.63	7.89	12	7.41	0.06	0.16	5.92	7.93	38
Oh	8.65	0.03	0.05	8.23	9.52	50	8.69	0.07	0.06	8.23	9.17	12	8.64	0.04	0.05	8.33	9.52	38
Ov	8.45	0.02	0.03	8.12	8.88	50	8.47	0.04	0.02	8.20	8.68	12	8.45	0.03	0.03	8.12	8.88	38
Hw	11.95	0.07	0.24	11.09	13.58	50	12.00	0.19	0.44	11.30	13.58	12	11.94	0.07	0.18	11.09	12.76	38
Hl	17.67	0.07	0.21	17.05	19.41	50	17.89	0.17	0.33	17.23	19.41	12	17.60	0.07	0.17	17.05	19.17	38
Ina	2.86	0.03	0.04	2.47	3.47	50	2.83	0.08	0.07	2.51	3.47	12	2.87	0.03	0.03	2.47	3.22	38
W	12.16	0.08	0.30	11.20	13.92	50	12.21	0.16	0.29	11.39	12.85	12	12.14	0.09	0.31	11.20	13.92	38
w	3.07	0.03	0.05	2.62	4.24	50	3.10	0.07	0.05	2.62	3.55	12	3.06	0.04	0.05	2.87	4.24	38

Table A10.6: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in sunbleak from Bridgewater-Taunton Canal at Creech St. Michael, Somerset (BTC2). See Table 3.2 in Chapter 3 for morphological codes.

	All						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
TL	53.75	0.70	24.48	42.23	62.48	50	55.30	1.61	28.38	42.23	59.49	11	53.31	0.77	23.20	43.26	62.48	39
FL	47.87	0.71	24.95	36.63	56.70	50	49.58	1.62	28.94	36.63	54.48	11	47.39	0.78	23.48	37.56	56.70	39
SL	43.14	0.71	25.08	32.19	51.27	50	44.81	1.58	27.52	32.38	49.39	11	42.67	0.79	24.06	32.19	51.27	39
% of standard length																		
h	8.79	0.07	0.24	7.54	9.91	50	9.13	0.07	0.06	8.83	9.65	11	8.70	0.08	0.25	7.54	9.91	39
H	21.78	0.20	2.04	20.06	25.33	50	20.58	0.15	0.24	20.06	21.62	11	22.12	0.23	2.04	20.17	25.33	39
A - C	20.41	0.19	1.86	16.48	22.82	50	20.08	0.39	1.69	18.00	21.88	11	20.50	0.22	1.91	16.48	22.82	39
PreD	56.01	0.24	2.91	53.46	60.45	50	55.57	0.39	1.71	53.49	57.70	11	56.13	0.29	3.23	53.46	60.45	39
Dh	17.41	0.04	0.08	17.00	17.89	50	17.46	0.10	0.10	17.04	17.88	11	17.40	0.04	0.07	17.00	17.89	39
Db	11.64	0.06	0.19	10.20	12.53	50	11.62	0.10	0.11	11.04	12.01	11	11.65	0.08	0.22	10.20	12.53	39
PreA	65.68	0.11	0.64	63.62	66.98	50	66.02	0.13	0.18	65.30	66.58	11	65.59	0.14	0.74	63.62	66.98	39
Ah	16.10	0.08	0.31	14.87	17.52	50	15.66	0.17	0.30	15.05	16.90	11	16.23	0.08	0.24	14.87	17.52	39
Ab	17.30	0.11	0.65	15.49	19.57	50	17.67	0.30	0.97	15.49	19.57	11	17.19	0.12	0.53	15.66	19.27	39
PreV	47.28	0.16	1.31	45.02	49.85	50	47.47	0.35	1.36	45.74	49.85	11	47.23	0.18	1.32	45.02	49.07	39
Vh	12.94	0.04	0.10	12.30	13.83	50	12.97	0.06	0.04	12.73	13.47	11	12.93	0.06	0.12	12.30	13.83	39
Vb	3.76	0.02	0.02	3.32	4.07	50	3.73	0.04	0.02	3.55	3.95	11	3.77	0.03	0.03	3.32	4.07	39
PreP	27.31	0.08	0.34	24.54	27.99	50	27.05	0.27	0.78	24.54	27.75	11	27.38	0.07	0.20	25.24	27.99	39
Ph	15.46	0.04	0.09	15.08	16.46	50	15.41	0.07	0.05	15.08	15.75	11	15.47	0.05	0.10	15.08	16.46	39
Pb	4.33	0.03	0.04	4.01	4.95	50	4.30	0.06	0.04	4.01	4.54	11	4.34	0.03	0.04	4.03	4.95	39
PreO	11.70	0.08	0.31	10.85	13.25	50	11.42	0.10	0.12	10.85	12.04	11	11.78	0.09	0.34	11.01	13.25	39
PreOp	5.01	0.04	0.07	4.57	5.75	50	5.07	0.11	0.14	4.57	5.75	11	5.00	0.04	0.05	4.57	5.47	39
Gape	2.96	0.02	0.01	2.65	3.18	50	2.98	0.04	0.02	2.74	3.18	11	2.95	0.02	0.01	2.65	3.15	39
Hd	18.50	0.04	0.08	18.12	19.53	50	18.55	0.08	0.07	18.14	18.89	11	18.49	0.05	0.08	18.12	19.53	39
Io	7.21	0.03	0.03	6.87	7.64	50	7.06	0.03	0.01	6.87	7.17	11	7.25	0.03	0.03	6.94	7.64	39
Oh	8.55	0.04	0.07	8.05	8.99	50	8.58	0.08	0.07	8.09	8.99	11	8.54	0.04	0.07	8.05	8.97	39
Ov	8.64	0.04	0.07	7.91	9.01	50	8.70	0.10	0.10	7.91	8.98	11	8.62	0.04	0.06	8.07	9.01	39
Hw	12.61	0.03	0.04	12.25	13.01	50	12.61	0.05	0.02	12.41	12.86	11	12.61	0.03	0.04	12.25	13.01	39
Hl	17.55	0.03	0.06	16.98	18.01	50	17.67	0.06	0.04	17.30	17.92	11	17.52	0.04	0.06	16.98	18.01	39
Ina	3.01	0.03	0.05	2.68	3.55	50	2.96	0.06	0.04	2.68	3.30	11	3.02	0.04	0.05	2.72	3.55	39
W	12.61	0.04	0.07	12.19	13.31	50	12.54	0.09	0.08	12.20	13.00	11	12.63	0.04	0.06	12.19	13.31	39
w	4.17	0.05	0.15	2.69	5.25	50	4.21	0.14	0.21	3.68	5.25	11	4.15	0.06	0.14	2.69	4.70	39

Table A10.7: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in sunbleak from Bridgewater-Taunton Canal at YMCA, Somerset (BTC3). See Table 3.2 in Chapter 3 for morphological codes.

	All						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
TL	55.20	0.39	8.28	45.13	59.20	55	54.79	0.66	9.46	45.13	58.54	22	55.47	0.48	7.56	48.51	59.20	33
FL	50.28	0.37	7.45	43.01	54.93	55	49.99	0.59	7.73	43.01	54.93	22	50.47	0.47	7.41	43.72	54.30	33
SL	45.37	0.38	7.82	37.29	49.48	55	45.00	0.63	8.71	37.29	49.48	22	45.61	0.47	7.33	39.99	49.31	33
% of standard length																		
h	8.33	0.06	0.18	7.20	9.10	55	8.34	0.09	0.19	7.55	8.93	22	8.32	0.08	0.19	7.20	9.10	33
H	21.30	0.11	0.61	20.12	22.95	55	20.96	0.12	0.33	20.19	22.40	22	21.52	0.14	0.69	20.12	22.95	33
A - C	18.57	0.11	0.67	15.77	19.91	55	18.62	0.12	0.30	17.49	19.40	22	18.54	0.17	0.93	15.77	19.91	33
PreD	56.32	0.22	2.76	51.06	59.93	55	56.20	0.33	2.37	53.07	58.34	22	56.40	0.31	3.08	51.06	59.93	33
Dh	16.67	0.10	0.51	14.86	19.49	55	16.75	0.15	0.47	16.01	19.01	22	16.62	0.13	0.53	14.86	19.49	33
Db	11.38	0.05	0.17	10.38	12.91	55	11.35	0.06	0.08	10.59	11.96	22	11.40	0.08	0.23	10.38	12.91	33
PreA	65.08	0.15	1.25	61.70	68.37	55	64.97	0.22	1.07	62.45	66.97	22	65.15	0.21	1.39	61.70	68.37	33
Ah	15.54	0.06	0.21	14.50	16.96	55	15.53	0.10	0.24	14.65	16.96	22	15.54	0.08	0.19	14.50	16.80	33
Ab	17.27	0.11	0.62	14.21	18.79	55	17.35	0.07	0.12	16.66	17.96	22	17.21	0.17	0.95	14.21	18.79	33
PreV	49.17	0.14	1.07	47.22	51.41	55	49.17	0.23	1.17	47.22	51.11	22	49.17	0.18	1.03	47.33	51.41	33
Vh	12.57	0.06	0.18	11.33	13.95	55	12.53	0.10	0.23	11.33	13.84	22	12.59	0.07	0.15	12.04	13.95	33
Vb	3.21	0.04	0.07	2.71	4.01	55	3.21	0.05	0.06	2.71	3.65	22	3.20	0.05	0.08	2.84	4.01	33
PreP	23.31	0.18	1.79	21.50	28.51	55	23.20	0.29	1.88	21.50	27.97	22	23.39	0.23	1.76	21.63	28.51	33
Ph	14.86	0.10	0.50	13.70	17.17	55	14.87	0.15	0.47	13.74	17.17	22	14.85	0.13	0.54	13.70	16.80	33
Pb	4.10	0.05	0.13	3.60	5.65	55	4.05	0.07	0.10	3.65	5.04	22	4.12	0.07	0.16	3.60	5.65	33
PreO	11.61	0.10	0.57	9.02	12.60	55	11.66	0.17	0.62	9.34	12.60	22	11.58	0.13	0.55	9.02	12.52	33
PreOp	4.69	0.05	0.12	3.32	5.15	55	4.73	0.06	0.07	4.25	5.14	22	4.67	0.07	0.15	3.32	5.15	33
Gape	2.94	0.02	0.03	2.45	3.22	55	2.97	0.03	0.02	2.63	3.22	22	2.91	0.03	0.03	2.45	3.17	33
Hd	17.38	0.05	0.12	16.27	18.22	55	17.36	0.08	0.14	16.27	18.09	22	17.40	0.06	0.11	16.61	18.22	33
Io	6.44	0.06	0.19	5.83	8.45	55	6.38	0.06	0.09	6.05	7.06	22	6.47	0.09	0.26	5.83	8.45	33
Oh	9.27	0.04	0.11	8.42	10.49	55	9.34	0.07	0.12	8.70	10.49	22	9.22	0.06	0.10	8.42	9.93	33
Ov	9.10	0.04	0.08	8.38	9.93	55	9.14	0.05	0.05	8.75	9.81	22	9.08	0.05	0.09	8.38	9.93	33
Hw	12.16	0.04	0.10	11.38	13.19	55	12.06	0.07	0.09	11.38	12.59	22	12.23	0.05	0.09	11.79	13.19	33
Hl	19.18	0.09	0.47	18.20	22.53	55	19.26	0.17	0.63	18.55	22.53	22	19.13	0.11	0.38	18.20	21.26	33
Ina	3.05	0.03	0.07	2.32	3.91	55	3.06	0.06	0.07	2.32	3.51	22	3.05	0.04	0.06	2.35	3.91	33
W	12.39	0.08	0.34	11.28	14.04	55	12.29	0.10	0.24	11.52	13.78	22	12.46	0.11	0.41	11.28	14.04	33
w	3.19	0.04	0.07	2.36	4.08	55	3.15	0.05	0.05	2.36	3.53	22	3.22	0.05	0.08	2.74	4.08	33

Table A10.8 Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in sunbleak from Kings-Sedgemoor Drain at Bradney Bridge, Bawdrip, Somerset (KSD4). See Table 3.2 in Chapter 3 for morphological codes.

	All						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
TL	59.79	0.61	11.34	53.15	67.25	30	60.09	1.31	15.52	55.77	67.25	9	59.66	0.70	10.18	53.15	64.74	21
FL	54.24	0.58	10.26	49.84	61.31	30	54.26	1.31	15.44	49.84	61.31	9	54.24	0.64	8.70	50.72	59.43	21
SL	49.82	0.62	11.43	44.78	55.88	30	49.24	1.15	11.95	44.78	54.23	9	50.06	0.74	11.58	45.36	55.88	21
% of standard length																		
h	8.98	0.11	0.35	8.07	9.92	30	9.08	0.22	0.42	8.12	9.92	9	8.94	0.13	0.34	8.07	9.79	21
H	21.66	0.16	0.77	19.43	22.86	30	21.84	0.31	0.89	20.38	22.86	9	21.58	0.19	0.74	19.43	22.66	21
A - C	18.62	0.20	1.17	16.73	20.99	30	19.00	0.36	1.15	18.04	20.99	9	18.47	0.23	1.15	16.73	20.12	21
PreD	58.41	0.15	0.68	55.34	59.73	30	58.54	0.22	0.45	57.52	59.68	9	58.36	0.19	0.79	55.34	59.73	21
Dh	17.69	0.08	0.17	16.78	18.83	30	17.68	0.14	0.19	16.78	18.13	9	17.70	0.09	0.17	17.09	18.83	21
Db	12.26	0.08	0.20	11.09	13.29	30	12.25	0.16	0.22	11.43	12.88	9	12.26	0.10	0.20	11.09	13.29	21
PreA	61.36	0.53	8.48	56.10	66.56	30	62.96	0.90	7.25	58.82	65.74	9	60.67	0.61	7.76	56.10	66.56	21
Ah	15.73	0.07	0.13	15.12	16.46	30	15.57	0.11	0.11	15.12	15.98	9	15.80	0.08	0.13	15.23	16.46	21
Ab	17.04	0.26	2.08	13.10	18.49	30	17.48	0.46	1.89	13.98	18.49	9	16.86	0.32	2.14	13.10	18.18	21
PreV	49.57	0.14	0.59	47.47	51.18	30	49.84	0.22	0.44	49.04	51.18	9	49.45	0.17	0.64	47.47	50.82	21
Vh	13.20	0.12	0.40	12.04	14.37	30	13.08	0.10	0.09	12.57	13.51	9	13.26	0.16	0.54	12.04	14.37	21
Vb	3.50	0.06	0.11	2.82	4.03	30	3.59	0.10	0.08	3.04	4.03	9	3.46	0.07	0.12	2.82	4.00	21
PreP	25.13	0.11	0.33	23.64	25.88	30	25.36	0.13	0.15	24.66	25.86	9	25.03	0.14	0.39	23.64	25.88	21
Ph	17.53	0.12	0.41	15.75	18.84	30	17.31	0.23	0.47	15.75	18.00	9	17.63	0.13	0.38	16.19	18.84	21
Pb	4.15	0.03	0.03	3.95	4.85	30	4.10	0.02	0.01	4.01	4.24	9	4.17	0.04	0.04	3.95	4.85	21
PreO	11.79	0.06	0.12	11.35	13.20	30	11.89	0.17	0.27	11.37	13.20	9	11.75	0.06	0.07	11.35	12.18	21
PreOp	4.83	0.05	0.08	4.15	5.52	30	4.98	0.10	0.09	4.56	5.52	9	4.77	0.06	0.07	4.15	5.06	21
Gape	3.01	0.03	0.02	2.77	3.26	30	2.95	0.05	0.03	2.77	3.24	9	3.04	0.03	0.02	2.82	3.26	21
Hd	17.92	0.07	0.13	17.35	19.41	30	18.04	0.17	0.27	17.71	19.41	9	17.87	0.06	0.07	17.35	18.37	21
Io	7.36	0.04	0.04	7.02	7.70	30	7.28	0.08	0.05	7.02	7.68	9	7.40	0.04	0.03	7.06	7.70	21
Oh	8.04	0.06	0.11	7.50	8.89	30	8.05	0.13	0.15	7.57	8.89	9	8.03	0.07	0.10	7.50	8.76	21
Ov	8.14	0.05	0.07	7.55	9.09	30	8.20	0.12	0.13	7.87	9.09	9	8.11	0.05	0.05	7.55	8.49	21
Hw	12.51	0.07	0.14	11.93	13.15	30	12.48	0.13	0.15	11.99	13.07	9	12.52	0.08	0.14	11.93	13.15	21
Hl	20.95	0.20	1.14	18.55	24.88	30	21.20	0.50	2.27	19.43	24.88	9	20.84	0.18	0.71	18.55	21.74	21
Ina	2.86	0.05	0.08	2.09	3.54	30	3.03	0.08	0.06	2.63	3.54	9	2.79	0.06	0.08	2.09	3.23	21
W	12.50	0.09	0.23	11.11	13.31	30	12.52	0.17	0.27	11.47	13.31	9	12.49	0.10	0.22	11.11	13.07	21
w	2.78	0.04	0.05	2.40	3.21	30	2.76	0.08	0.06	2.47	3.16	9	2.79	0.04	0.04	2.40	3.21	21

Table A10.9: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in sunbleak from Kings-Sedgemoor Drain at Parchey Bridge, Somerset (KSD5). See Table 3.2 in Chapter 3 for morphological codes.

	All						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
TL	52.97	1.17	81.62	40.04	81.06	60	57.04	2.89	91.67	40.04	73.30	11	52.06	1.25	76.58	40.38	81.06	49
FL	48.43	1.08	70.13	35.46	72.26	60	53.33	2.37	62.00	35.49	66.04	11	47.32	1.17	66.52	35.46	72.26	49
SL	43.03	1.00	59.92	30.23	64.20	60	47.67	2.23	54.86	30.23	58.95	11	41.98	1.07	56.17	30.47	64.20	49
% of standard length																		
h	8.81	0.08	0.41	7.59	10.25	60	8.51	0.13	0.19	7.90	9.04	11	8.88	0.09	0.44	7.59	10.25	49
H	21.40	0.13	1.03	19.23	23.65	60	21.66	0.43	1.99	19.95	23.65	11	21.34	0.13	0.83	19.23	23.32	49
A - C	18.11	0.17	1.75	15.44	20.84	60	18.43	0.34	1.29	16.84	19.85	11	18.04	0.19	1.85	15.44	20.84	49
PreD	57.91	0.22	2.84	53.75	61.56	60	57.80	0.63	4.41	53.75	61.38	11	57.93	0.23	2.57	54.27	61.56	49
Dh	17.84	0.14	1.16	14.45	19.98	60	17.48	0.40	1.75	14.65	19.98	11	17.92	0.14	1.03	14.45	19.78	49
Db	11.53	0.08	0.34	10.43	13.57	60	11.54	0.20	0.44	10.65	12.81	11	11.53	0.08	0.33	10.43	13.57	49
PreA	64.82	0.20	2.45	61.94	69.11	60	64.93	0.43	1.99	61.94	66.73	11	64.79	0.23	2.59	62.07	69.11	49
Ah	16.01	0.09	0.52	14.43	17.77	60	16.11	0.23	0.58	14.69	17.55	11	15.98	0.10	0.51	14.43	17.77	49
Ab	16.19	0.11	0.69	14.72	18.82	60	15.72	0.16	0.27	14.91	16.46	11	16.30	0.12	0.73	14.72	18.82	49
PreV	49.40	0.15	1.28	46.25	53.06	60	49.07	0.26	0.77	47.61	50.25	11	49.47	0.17	1.38	46.25	53.06	49
Vh	12.91	0.09	0.50	12.02	14.60	60	13.13	0.23	0.57	12.04	14.16	11	12.86	0.10	0.48	12.02	14.60	49
Vb	3.84	0.04	0.10	2.74	4.38	60	3.62	0.12	0.17	2.74	4.26	11	3.89	0.04	0.07	3.16	4.38	49
PreP	25.80	0.15	1.41	23.12	28.92	60	25.74	0.47	2.39	23.21	28.10	11	25.81	0.16	1.23	23.12	28.92	49
Ph	16.88	0.10	0.56	14.30	18.89	60	16.46	0.26	0.72	14.30	17.41	11	16.97	0.10	0.49	14.94	18.89	49
Pb	4.16	0.04	0.08	3.53	4.98	60	4.07	0.08	0.06	3.61	4.46	11	4.18	0.04	0.09	3.53	4.98	49
PreO	11.59	0.07	0.33	10.12	12.77	60	11.74	0.21	0.49	10.33	12.77	11	11.56	0.08	0.29	10.12	12.73	49
PreOp	4.59	0.08	0.37	3.39	6.09	60	4.56	0.26	0.73	3.39	6.01	11	4.60	0.08	0.30	3.74	6.09	49
Gape	2.81	0.03	0.06	2.28	3.37	60	2.83	0.11	0.12	2.28	3.37	11	2.80	0.03	0.05	2.33	3.23	49
Hd	17.02	0.09	0.48	15.66	18.78	60	17.39	0.22	0.55	16.37	18.64	11	16.94	0.10	0.44	15.66	18.78	49
Io	6.93	0.06	0.21	5.78	8.13	60	7.07	0.15	0.26	6.52	8.13	11	6.89	0.06	0.20	5.78	7.76	49
Oh	8.58	0.05	0.18	7.86	9.55	60	8.68	0.08	0.07	8.14	9.15	11	8.56	0.06	0.20	7.86	9.55	49
Ov	8.78	0.04	0.08	8.05	9.32	60	8.72	0.10	0.10	8.09	9.06	11	8.79	0.04	0.08	8.05	9.32	49
Hw	11.95	0.05	0.15	11.09	12.75	60	11.87	0.11	0.12	11.56	12.60	11	11.96	0.06	0.16	11.09	12.75	49
Hl	18.84	0.11	0.67	16.91	20.77	60	18.41	0.21	0.47	16.91	19.30	11	18.94	0.12	0.67	17.13	20.77	49
Ina	3.48	0.05	0.16	2.71	4.17	60	3.14	0.09	0.08	2.71	3.51	11	3.56	0.06	0.15	2.76	4.17	49
W	11.62	0.11	0.66	9.49	14.12	60	11.70	0.42	1.95	10.19	14.12	11	11.60	0.09	0.41	9.49	13.83	49
w	3.24	0.07	0.32	2.01	4.06	60	3.11	0.15	0.24	2.41	3.90	11	3.27	0.08	0.34	2.01	4.06	49

Table A10.10: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in sunbleak from River Huntspill at Woolavington Bridge, Somerset (Hunt6). See Table 3.2 in Chapter 3 for morphological codes.

	All						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
TL	52.83	2.61	11.05	48.02	62.13	5	54.60	—	—	—	—	1	52.39	3.32	12.68	48.02	62.13	4
FL	48.33	2.55	11.80	43.74	57.36	5	50.57	—	—	—	—	1	47.77	3.21	13.45	43.74	57.36	4
SL	43.22	2.28	11.80	39.01	51.41	5	44.77	—	—	—	—	1	42.84	2.90	13.55	39.01	51.41	4
% of standard length																		
h	8.19	0.27	7.39	7.20	8.80	5	8.11	—	—	—	—	1	8.21	0.35	8.49	7.20	8.80	4
H	21.02	0.61	6.46	19.10	22.84	5	20.55	—	—	—	—	1	21.14	0.77	7.28	19.10	22.84	4
A - C	18.17	0.46	5.70	17.25	19.33	5	19.23	—	—	—	—	1	17.91	0.49	5.47	17.25	19.33	4
PreD	57.62	0.96	3.72	54.93	60.73	5	58.39	—	—	—	—	1	57.42	1.21	4.22	54.93	60.73	4
Dh	17.02	1.57	20.63	12.06	21.90	5	17.42	—	—	—	—	1	16.92	2.02	23.91	12.06	21.90	4
Db	11.86	0.60	11.30	10.50	14.06	5	11.44	—	—	—	—	1	11.97	0.76	12.73	10.50	14.06	4
PreA	66.03	1.34	4.53	62.68	69.65	5	63.48	—	—	—	—	1	66.67	1.52	4.55	62.68	69.65	4
Ah	15.28	0.67	9.86	12.94	16.82	5	15.10	—	—	—	—	1	15.32	0.87	11.32	12.94	16.82	4
Ab	16.22	1.05	14.47	12.52	18.18	5	18.18	—	—	—	—	1	15.72	1.20	15.22	12.52	17.89	4
PreV	49.79	0.70	3.13	48.14	51.92	5	49.01	—	—	—	—	1	49.99	0.86	3.46	48.14	51.92	4
Vh	13.57	0.68	11.20	11.73	15.88	5	13.36	—	—	—	—	1	13.62	0.87	12.84	11.73	15.88	4
Vb	3.45	0.27	17.65	2.84	4.33	5	3.10	—	—	—	—	1	3.53	0.33	18.87	2.84	4.33	4
PreP	23.81	2.02	18.97	19.19	29.48	5	19.19	—	—	—	—	1	24.97	2.14	17.13	21.24	29.48	4
Ph	16.13	0.31	4.24	15.14	16.80	5	15.14	—	—	—	—	1	16.38	0.23	2.86	15.83	16.80	4
Pb	4.37	0.13	6.51	4.11	4.80	5	4.20	—	—	—	—	1	4.41	0.15	7.02	4.11	4.80	4
PreO	11.31	0.33	6.54	10.39	12.38	5	11.53	—	—	—	—	1	11.25	0.42	7.48	10.39	12.38	4
PreOp	5.03	0.37	16.54	4.14	6.02	5	5.43	—	—	—	—	1	4.93	0.46	18.78	4.14	6.02	4
Gape	2.81	0.25	20.01	1.96	3.33	5	3.08	—	—	—	—	1	2.74	0.31	22.79	1.96	3.33	4
Hd	18.02	0.36	4.45	17.31	19.05	5	17.67	—	—	—	—	1	18.11	0.45	4.96	17.31	19.05	4
Io	7.25	0.35	10.90	6.72	8.62	5	6.72	—	—	—	—	1	7.39	0.42	11.46	6.72	8.62	4
Oh	9.04	0.45	11.21	8.01	10.29	5	8.35	—	—	—	—	1	9.21	0.54	11.75	8.01	10.29	4
Ov	8.91	0.40	9.97	7.95	9.95	5	8.51	—	—	—	—	1	9.01	0.50	11.02	7.95	9.95	4
Hw	12.12	0.37	6.91	11.19	13.40	5	11.19	—	—	—	—	1	12.35	0.38	6.13	11.60	13.40	4
Hl	19.06	0.30	3.49	18.08	19.84	5	18.78	—	—	—	—	1	19.13	0.37	3.91	18.08	19.84	4
Ina	3.34	0.13	8.99	3.02	3.71	5	3.71	—	—	—	—	1	3.24	0.13	7.72	3.02	3.46	4
W	11.94	0.78	14.69	9.41	13.64	5	11.28	—	—	—	—	1	12.10	0.99	16.36	9.41	13.64	4
w	3.77	0.34	19.97	3.05	4.87	5	3.22	—	—	—	—	1	3.91	0.40	20.30	3.05	4.87	4

Table A10.11: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in sunbleak from River Sowy at Greylake Bridge, Somerset (Sowy7). See Table 3.2 in Chapter 3 for morphological codes.

	All						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
TL	56.15	0.73	7.01	47.97	64.10	29	56.01	0.86	7.06	47.97	64.10	21	56.51	1.46	7.33	50.32	61.50	9
FL	51.09	0.70	7.42	43.02	57.66	29	50.91	0.81	7.26	43.02	57.66	21	51.58	1.51	8.25	45.39	55.95	9
SL	45.94	0.65	7.63	39.30	52.84	29	45.79	0.71	7.13	39.30	52.84	21	46.35	1.52	9.27	39.63	50.53	9
% of standard length																		
h	8.59	0.08	4.97	7.48	9.87	29	8.58	0.11	5.75	7.48	9.87	21	8.62	0.06	2.07	8.44	8.93	9
H	21.53	0.16	3.89	20.16	23.67	29	21.31	0.15	3.30	20.16	22.42	21	22.12	0.33	4.16	20.99	23.67	9
A - C	17.86	0.27	8.01	15.04	20.77	29	17.80	0.33	8.61	15.04	20.77	21	18.03	0.42	6.64	15.72	19.63	9
PreD	56.54	0.31	2.91	53.74	60.08	29	56.41	0.32	2.58	54.19	58.48	21	56.89	0.75	3.75	53.74	60.08	9
Dh	17.45	0.22	6.71	14.75	19.08	29	17.30	0.27	7.24	14.75	19.08	21	17.86	0.31	4.84	16.23	18.79	9
Db	11.46	0.17	8.06	9.54	13.05	29	11.42	0.22	8.83	9.54	13.05	21	11.57	0.25	6.06	10.62	12.51	9
PreA	64.64	0.36	3.00	58.23	68.06	29	64.37	0.46	3.28	58.23	68.06	21	65.33	0.44	1.90	63.49	67.16	9
Ah	15.86	0.14	4.78	14.37	17.80	29	15.91	0.17	5.02	14.50	17.80	21	15.74	0.24	4.26	14.37	16.48	9
Ab	15.98	0.21	7.23	12.87	18.22	29	16.02	0.28	7.89	12.87	18.22	21	15.88	0.31	5.48	14.65	17.21	9
PreV	48.58	0.24	2.62	46.37	51.62	29	48.60	0.32	3.04	46.37	51.62	21	48.54	0.17	1.00	47.76	49.22	9
Vh	13.53	0.14	5.46	12.32	14.71	29	13.34	0.16	5.34	12.32	14.70	21	14.04	0.20	4.06	13.22	14.71	9
Vb	3.12	0.07	12.82	2.54	3.99	29	3.19	0.09	13.46	2.54	3.99	21	2.93	0.08	8.06	2.58	3.29	9
PreP	25.32	0.16	3.42	24.01	27.16	29	25.35	0.17	3.15	24.01	26.72	21	25.25	0.38	4.27	24.07	27.16	9
Ph	16.61	0.22	7.08	14.28	18.86	29	16.37	0.25	7.13	14.28	18.86	21	17.23	0.36	5.86	15.77	18.52	9
Pb	4.47	0.08	9.33	3.53	5.33	29	4.46	0.09	9.68	3.53	5.33	21	4.49	0.14	8.96	3.92	5.25	9
PreO	12.03	0.16	7.27	10.37	13.91	29	11.99	0.19	7.24	10.37	13.91	21	12.16	0.33	7.75	11.25	13.73	9
PreOp	4.54	0.13	15.93	3.07	6.51	29	4.60	0.18	17.74	3.07	6.51	21	4.39	0.14	8.90	3.99	4.99	9
Gape	3.13	0.06	10.20	2.49	3.88	29	3.09	0.07	9.88	2.49	3.57	21	3.23	0.13	10.97	2.87	3.88	9
Hd	17.79	0.13	4.03	16.25	19.43	29	17.77	0.17	4.36	16.25	19.43	21	17.86	0.21	3.25	17.26	18.93	9
Io	7.77	0.10	6.93	6.30	8.77	29	7.77	0.13	7.87	6.30	8.77	21	7.75	0.11	3.85	7.43	8.31	9
Oh	8.88	0.09	5.47	8.11	9.78	29	8.94	0.10	5.33	8.11	9.64	21	8.70	0.17	5.67	8.12	9.78	9
Ov	8.81	0.08	4.94	8.09	9.77	29	8.90	0.09	4.80	8.13	9.77	21	8.56	0.13	4.34	8.09	9.18	9
Hw	12.41	0.14	6.20	11.23	14.85	29	12.18	0.11	4.15	11.23	13.31	21	13.01	0.36	7.93	11.81	14.85	9
Hl	18.81	0.17	4.86	16.65	20.43	29	18.97	0.21	4.96	16.65	20.43	21	18.39	0.26	3.96	17.56	19.69	9
Ina	3.30	0.06	9.74	2.67	4.18	29	3.35	0.07	9.84	2.85	4.18	21	3.17	0.10	8.69	2.67	3.65	9
W	12.30	0.13	5.72	11.12	14.03	29	12.13	0.14	5.16	11.12	13.55	21	12.74	0.26	5.84	11.87	14.03	9
w	2.75	0.09	18.59	2.20	4.24	29	2.85	0.12	19.43	2.29	4.24	21	2.50	0.10	10.77	2.20	2.92	9

Table A10.12: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in sunbleak from River Tone at Hankridge, Somerset (Tone8). See Table 3.2 in Chapter 3 for morphological codes.

	All						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
TL	41.76	5.73	23.75	32.10	51.92	3	51.92	—	—	—	—	1	36.69	4.58	17.68	32.10	41.27	2
FL	37.47	4.82	22.29	29.49	46.15	3	46.15	—	—	—	—	1	33.13	3.64	15.54	29.49	36.77	2
SL	33.45	4.62	23.92	26.24	42.06	3	42.06	—	—	—	—	1	29.15	2.91	14.12	26.24	32.06	2
% of standard length																		
h	8.86	0.26	5.08	8.35	9.17	3	8.35						9.12	0.05	0.78	9.07	9.17	2
H	23.17	1.21	9.02	20.78	24.67	3	20.78	—	—	—	—	1	24.36	0.31	1.81	24.05	24.67	2
A - C	14.43	2.22	26.67	10.14	17.57	3	17.57	—	—	—	—	1	12.87	2.73	30.00	10.14	15.60	2
PreD	56.70	1.46	4.47	54.15	59.22	3	59.22	—	—	—	—	1	55.43	1.28	3.26	54.15	56.71	2
Dh	21.13	1.37	11.21	18.43	22.83	3	18.43	—	—	—	—	1	22.49	0.34	2.14	22.15	22.83	2
Db	12.87	0.46	6.25	11.96	13.47	3	11.96	—	—	—	—	1	13.33	0.14	1.53	13.19	13.47	2
PreA	68.62	1.79	4.53	66.00	72.05	3	66.00	—	—	—	—	1	69.92	2.13	4.30	67.80	72.05	2
Ah	15.30	0.43	4.85	14.44	15.76	3	15.76	—	—	—	—	1	15.07	0.62	5.85	14.44	15.69	2
Ab	16.87	0.19	1.92	16.58	17.22	3	16.81	—	—	—	—	1	16.90	0.32	2.68	16.58	17.22	2
PreV	51.53	1.06	3.58	49.89	53.52	3	51.19	—	—	—	—	1	51.71	1.82	4.98	49.89	53.52	2
Vh	15.03	1.25	14.37	12.72	17.00	3	12.72	—	—	—	—	1	16.18	0.82	7.17	15.36	17.00	2
Vb	4.06	0.44	18.61	3.43	4.90	3	3.85	—	—	—	—	1	4.16	0.73	24.92	3.43	4.90	2
PreP	28.98	1.60	9.56	26.32	31.85	3	26.32	—	—	—	—	1	30.31	1.54	7.17	28.77	31.85	2
Ph	16.64	0.90	9.35	15.36	18.37	3	16.19	—	—	—	—	1	16.87	1.51	12.64	15.36	18.37	2
Pb	4.40	0.38	14.83	3.65	4.84	3	4.71	—	—	—	—	1	4.24	0.60	19.83	3.65	4.84	2
PreO	11.95	0.76	11.02	11.01	13.45	3	11.01	—	—	—	—	1	12.42	1.03	11.77	11.38	13.45	2
PreOp	4.97	0.39	13.61	4.33	5.68	3	4.33	—	—	—	—	1	5.30	0.38	10.16	4.92	5.68	2
Gape	3.11	0.29	16.05	2.59	3.59	3	3.14	—	—	—	—	1	3.09	0.50	22.79	2.59	3.59	2
Hd	19.61	1.02	8.98	18.59	21.65	3	18.59	—	—	—	—	1	20.12	1.52	10.72	18.60	21.65	2
Io	7.20	0.24	5.74	6.94	7.67	3	6.94	—	—	—	—	1	7.32	0.35	6.75	6.97	7.67	2
Oh	10.33	0.56	9.31	9.22	10.98	3	9.22	—	—	—	—	1	10.88	0.09	1.19	10.79	10.98	2
Ov	10.17	0.61	10.34	8.96	10.86	3	8.96	—	—	—	—	1	10.78	0.08	1.07	10.70	10.86	2
Hw	12.92	0.31	4.19	12.29	13.26	3	12.29	—	—	—	—	1	13.23	0.03	0.36	13.19	13.26	2
Hl	20.68	2.22	18.63	17.33	24.89	3	17.33	—	—	—	—	1	22.35	2.54	16.05	19.82	24.89	2
Ina	3.43	0.17	8.67	3.24	3.77	3	3.28	—	—	—	—	1	3.51	0.27	10.78	3.24	3.77	2
W	12.31	0.12	1.66	12.16	12.54	3	12.22	—	—	—	—	1	12.35	0.19	2.19	12.16	12.54	2
w	3.53	0.47	23.15	3.03	4.47	3	4.47	—	—	—	—	1	3.06	0.03	1.42	3.03	3.09	2

Table A10.13: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in sunbleak from Dunwear Pond, Somerset (Dun9). See Table 3.2 in Chapter 3 for morphological codes.

	All						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
TL	50.39	0.82	40.81	42.02	67.26	60	49.47	1.06	25.97	42.39	60.92	23	50.96	1.16	50.15	42.02	67.26	37
FL	46.47	0.80	38.05	36.58	62.52	60	46.04	0.96	20.99	36.58	54.16	23	46.74	1.15	49.34	36.58	62.52	37
SL	41.88	0.73	32.06	31.28	57.54	60	41.39	0.88	17.88	32.37	50.02	23	42.18	1.06	41.36	31.28	57.54	37
% of standard length																		
h	8.54	0.05	0.14	7.61	9.21	60	8.63	0.07	0.10	8.02	9.14	23	8.48	0.07	0.16	7.61	9.21	37
H	20.71	0.13	0.95	14.86	21.84	60	20.77	0.11	0.29	19.76	21.84	23	20.68	0.19	1.35	14.86	21.84	37
A - C	15.61	0.25	3.71	12.09	21.63	60	15.79	0.44	4.43	12.09	20.46	23	15.45	0.30	3.30	12.75	21.63	37
PreD	56.87	0.72	30.17	16.38	61.75	60	57.71	0.31	2.28	55.55	61.75	23	56.32	1.12	46.46	16.38	58.99	37
Dh	16.08	0.15	1.27	12.32	18.05	60	15.86	0.21	1.06	13.11	17.86	23	16.20	0.19	1.36	12.32	18.05	37
Db	11.59	0.11	0.69	9.32	13.62	60	11.68	0.19	0.86	9.32	13.21	23	11.53	0.12	0.57	10.23	13.62	37
PreA	64.51	0.88	45.70	14.93	68.46	60	65.40	0.32	2.29	62.21	68.46	23	63.96	1.39	71.41	14.93	68.25	37
Ah	14.72	0.13	1.00	12.47	16.79	60	14.49	0.23	1.22	12.47	16.17	23	14.82	0.16	0.90	12.69	16.79	37
Ab	18.40	0.58	20.00	9.99	48.22	60	17.83	0.42	4.10	14.74	21.38	23	18.73	0.89	29.42	9.99	48.22	37
PreV	49.12	0.68	27.12	12.66	62.36	60	49.80	0.22	1.09	47.88	51.95	23	48.68	1.07	42.54	12.66	62.36	37
Vh	11.86	0.18	1.96	3.93	14.23	60	12.04	0.18	0.74	10.05	14.04	23	11.77	0.27	2.68	3.93	14.23	37
Vb	3.88	0.08	0.39	2.46	5.22	60	3.72	0.14	0.47	2.46	5.22	23	3.98	0.09	0.31	2.86	5.22	37
PreP	25.59	0.22	2.83	14.86	28.19	60	26.03	0.19	0.80	25.04	28.19	23	25.29	0.32	3.87	14.86	27.46	37
Ph	15.08	0.24	3.30	3.77	17.67	60	15.19	0.19	0.86	13.39	17.64	23	14.98	0.36	4.81	3.77	17.67	37
Pb	4.09	0.05	0.15	3.29	5.17	60	4.12	0.08	0.16	3.40	5.17	23	4.06	0.06	0.14	3.29	4.70	37
PreO	12.12	0.08	0.39	10.83	13.52	60	12.12	0.12	0.35	10.95	12.97	23	12.10	0.11	0.43	10.83	13.52	37
PreOp	5.78	0.08	0.36	4.59	7.27	60	5.67	0.14	0.44	4.66	7.27	23	5.82	0.09	0.32	4.59	7.01	37
Gape	2.64	0.04	0.07	2.11	3.35	60	2.60	0.05	0.05	2.24	3.24	23	2.65	0.05	0.09	2.11	3.35	37
Hd	18.06	0.09	0.43	16.83	19.42	60	18.25	0.11	0.27	17.23	19.42	23	17.93	0.12	0.49	16.83	19.42	37
Io	6.72	0.10	0.53	3.36	8.02	60	6.67	0.17	0.66	3.36	7.52	23	6.77	0.11	0.46	4.67	8.02	37
Oh	9.02	0.05	0.15	7.99	9.77	60	9.06	0.07	0.12	8.48	9.68	23	8.97	0.07	0.18	7.99	9.77	37
Ov	8.87	0.05	0.17	7.72	9.97	60	8.91	0.06	0.10	8.38	9.64	23	8.81	0.08	0.22	7.72	9.97	37
Hw	12.60	0.20	2.40	11.09	20.85	60	12.35	0.10	0.21	11.09	13.17	23	12.74	0.32	3.68	11.25	20.85	37
Hl	20.26	0.17	1.79	17.48	27.90	60	20.68	0.35	2.89	19.02	27.90	23	19.94	0.16	0.99	17.48	22.16	37
Ina	3.08	0.06	0.18	1.88	4.04	60	3.00	0.09	0.18	1.88	3.97	23	3.12	0.07	0.18	2.15	4.04	37
W	12.64	0.13	0.95	11.26	18.78	60	12.55	0.10	0.25	11.35	13.27	23	12.70	0.19	1.39	11.26	18.78	37
w	3.71	0.05	0.16	2.90	4.73	60	3.69	0.07	0.12	3.14	4.23	23	3.72	0.07	0.18	2.90	4.73	37

Table A10.14: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in sunbleak from Durleigh Reservoir, Somerset (Durl10). See Table 3.2 in Chapter 3 for morphological codes.

	All						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
TL	76.11	0.86	1.60	75.25	76.97	2	—	—	—	—	—	—	76.11	0.86	1.60	75.25	76.97	2
FL	68.25	0.13	0.26	68.12	68.37	2	—	—	—	—	—	—	68.25	0.13	0.26	68.12	68.37	2
SL	61.24	0.58	1.34	60.66	61.82	2	—	—	—	—	—	—	61.24	0.58	1.34	60.66	61.82	2
% of standard length																		
h	8.73	0.04	0.65	8.69	8.77	2	—	—	—	—	—	—	8.73	0.04	0.65	8.69	8.77	2
H	24.07	0.48	2.83	23.59	24.56	2	—	—	—	—	—	—	24.07	0.48	2.83	23.59	24.56	2
A - C	18.70	0.14	1.09	18.55	18.84	2	—	—	—	—	—	—	18.70	0.14	1.09	18.55	18.84	2
PreD	58.48	0.11	0.27	58.36	58.59	2	—	—	—	—	—	—	58.48	0.11	0.27	58.36	58.59	2
Dh	17.06	0.01	0.12	17.05	17.08	2	—	—	—	—	—	—	17.06	0.01	0.12	17.05	17.08	2
Db	11.69	0.33	3.99	11.36	12.02	2	—	—	—	—	—	—	11.69	0.33	3.99	11.36	12.02	2
PreA	69.16	0.73	1.50	68.43	69.90	2	—	—	—	—	—	—	69.16	0.73	1.50	68.43	69.90	2
Ah	14.29	0.64	6.35	13.65	14.94	2	—	—	—	—	—	—	14.29	0.64	6.35	13.65	14.94	2
Ab	16.26	1.23	10.71	15.03	17.49	2	—	—	—	—	—	—	16.26	1.23	10.71	15.03	17.49	2
PreV	47.68	1.64	4.86	46.04	49.32	2	—	—	—	—	—	—	47.68	1.64	4.86	46.04	49.32	2
Vh	12.08	1.21	14.15	10.87	13.29	2	—	—	—	—	—	—	12.08	1.21	14.15	10.87	13.29	2
Vb	3.62	0.25	9.95	3.36	3.87	2	—	—	—	—	—	—	3.62	0.25	9.95	3.36	3.87	2
PreP	23.61	0.15	0.90	23.46	23.76	2	—	—	—	—	—	—	23.61	0.15	0.90	23.46	23.76	2
Ph	16.13	1.06	9.33	15.07	17.20	2	—	—	—	—	—	—	16.13	1.06	9.33	15.07	17.20	2
Pb	4.42	0.02	0.56	4.40	4.43	2	—	—	—	—	—	—	4.42	0.02	0.56	4.40	4.43	2
PreO	11.91	0.06	0.66	11.86	11.97	2	—	—	—	—	—	—	11.91	0.06	0.66	11.86	11.97	2
PreOp	4.18	0.87	29.32	3.31	5.05	2	—	—	—	—	—	—	4.18	0.87	29.32	3.31	5.05	2
Gape	2.64	0.15	7.86	2.49	2.78	2	—	—	—	—	—	—	2.64	0.15	7.86	2.49	2.78	2
Hd	17.34	0.03	0.26	17.31	17.37	2	—	—	—	—	—	—	17.34	0.03	0.26	17.31	17.37	2
Io	7.28	0.49	9.43	6.79	7.76	2	—	—	—	—	—	—	7.28	0.49	9.43	6.79	7.76	2
Oh	7.82	0.30	5.47	7.52	8.13	2	—	—	—	—	—	—	7.82	0.30	5.47	7.52	8.13	2
Ov	7.79	0.37	6.67	7.42	8.16	2	—	—	—	—	—	—	7.79	0.37	6.67	7.42	8.16	2
Hw	11.72	0.26	3.19	11.46	11.99	2	—	—	—	—	—	—	11.72	0.26	3.19	11.46	11.99	2
Hl	16.30	0.80	6.94	15.50	17.10	2	—	—	—	—	—	—	16.30	0.80	6.94	15.50	17.10	2
Ina	3.00	0.06	2.90	2.93	3.06	2	—	—	—	—	—	—	3.00	0.06	2.90	2.93	3.06	2
W	14.35	0.47	4.62	13.88	14.82	2	—	—	—	—	—	—	14.35	0.47	4.62	13.88	14.82	2
w	2.49	0.47	26.80	2.02	2.97	2	—	—	—	—	—	—	2.49	0.47	26.80	2.02	2.97	2

Table A10.15: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in sunbleak from Stoneham Lakes, Hampshire (Stone11). See Table 3.2 in Chapter 3 for morphological codes.

	All						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
TL	50.47	0.63	27.49	38.96	67.65	70	52.28	1.30	28.62	38.96	60.10	17	49.88	0.70	26.24	39.25	67.65	53
FL	46.17	0.67	31.01	34.16	61.68	70	47.95	1.33	29.98	34.16	55.11	17	45.60	0.76	30.57	34.24	61.68	53
SL	41.26	0.67	31.39	28.63	55.75	70	43.00	1.34	30.64	28.63	49.49	17	40.70	0.76	30.92	29.38	55.75	53
% of standard length																		
h	8.96	0.06	0.22	7.85	10.13	70	9.06	0.10	0.17	8.27	10.06	17	8.93	0.07	0.23	7.85	10.13	53
H	20.78	0.13	1.16	18.37	24.64	70	20.50	0.30	1.57	19.07	24.64	17	20.87	0.14	1.02	18.37	23.00	53
A - C	16.61	0.17	2.06	13.17	21.10	70	16.88	0.41	2.89	14.19	21.10	17	16.53	0.18	1.81	13.17	20.80	53
PreD	56.52	0.28	5.46	53.63	66.20	70	57.09	0.68	7.83	53.63	66.07	17	56.34	0.30	4.69	53.71	66.20	53
Dh	16.42	0.11	0.92	13.43	17.98	70	16.91	0.23	0.89	13.96	17.98	17	16.26	0.13	0.84	13.43	17.85	53
Db	12.52	0.12	0.94	10.15	16.75	70	12.37	0.20	0.71	10.17	13.46	17	12.56	0.14	1.02	10.15	16.75	53
PreA	65.38	0.14	1.36	61.68	67.62	70	65.60	0.24	0.97	64.13	67.62	17	65.31	0.17	1.48	61.68	67.47	53
Ah	14.85	0.09	0.58	12.99	17.06	70	14.54	0.23	0.90	13.07	16.95	17	14.95	0.09	0.45	12.99	17.06	53
Ab	17.71	0.14	1.32	14.58	20.64	70	17.30	0.29	1.42	15.22	19.11	17	17.84	0.15	1.24	14.58	20.64	53
PreV	48.98	0.16	1.73	41.87	51.05	70	48.76	0.47	3.76	41.87	50.81	17	49.05	0.14	1.11	46.75	51.05	53
Vh	11.68	0.11	0.79	10.18	14.79	70	12.00	0.23	0.89	10.61	14.79	17	11.57	0.12	0.73	10.18	14.08	53
Vb	3.55	0.06	0.22	2.59	4.46	70	3.42	0.10	0.18	2.70	4.42	17	3.59	0.07	0.24	2.59	4.46	53
PreP	25.21	0.14	1.33	22.33	27.84	70	24.50	0.37	2.28	22.33	27.27	17	25.44	0.13	0.83	23.07	27.84	53
Ph	15.47	0.10	0.63	13.49	16.98	70	15.63	0.20	0.66	14.04	16.88	17	15.42	0.11	0.63	13.49	16.98	53
Pb	4.13	0.04	0.11	3.29	4.80	70	4.22	0.09	0.14	3.29	4.65	17	4.11	0.04	0.10	3.35	4.80	53
PreO	12.52	0.07	0.38	10.98	14.42	70	12.77	0.19	0.61	11.75	14.42	17	12.44	0.07	0.29	10.98	13.55	53
PreOp	5.14	0.07	0.37	3.90	6.67	70	5.09	0.13	0.30	3.90	6.16	17	5.16	0.09	0.39	3.90	6.67	53
Gape	2.64	0.03	0.05	2.21	3.55	70	2.64	0.06	0.05	2.37	3.20	17	2.65	0.03	0.05	2.21	3.55	53
Hd	17.39	0.07	0.36	16.01	19.46	70	17.34	0.14	0.33	16.33	18.42	17	17.40	0.08	0.37	16.01	19.46	53
Io	7.06	0.05	0.19	5.68	8.02	70	6.75	0.10	0.18	5.68	7.34	17	7.15	0.06	0.16	6.10	8.02	53
Oh	8.36	0.04	0.10	7.77	9.13	70	8.48	0.09	0.12	7.93	9.07	17	8.32	0.04	0.09	7.77	9.13	53
Ov	8.20	0.03	0.07	7.58	9.12	70	8.21	0.07	0.09	7.58	8.71	17	8.20	0.04	0.07	7.62	9.12	53
Hw	12.27	0.05	0.16	11.46	13.41	70	12.29	0.10	0.18	11.71	13.21	17	12.26	0.05	0.16	11.46	13.41	53
Hl	18.13	0.09	0.53	16.84	19.78	70	18.38	0.20	0.67	16.84	19.70	17	18.05	0.09	0.47	17.02	19.78	53
Ina	3.16	0.05	0.14	2.37	4.09	70	3.04	0.08	0.11	2.48	3.73	17	3.19	0.05	0.15	2.37	4.09	53
W	12.85	0.07	0.38	11.46	14.00	70	12.80	0.15	0.38	11.46	13.59	17	12.86	0.09	0.39	11.62	14.00	53
w	3.57	0.07	0.31	2.38	5.27	70	3.72	0.15	0.39	2.79	5.27	17	3.52	0.07	0.28	2.38	4.55	53

Table A10.16: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in sunbleak from Two Lakes Fishery, Hampshire (TwoL12). See Table 3.2 in Chapter 3 for morphological codes.

	All						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
TL	53.62	0.97	65.95	37.37	73.51	70	55.85	1.14	23.52	49.26	64.44	18	52.85	1.23	79.01	37.37	73.51	52
FL	48.99	0.96	64.74	32.01	66.61	70	51.35	1.06	20.13	45.12	59.15	18	48.17	1.23	78.23	32.01	66.61	52
SL	43.58	0.89	55.89	27.01	59.55	70	45.77	0.93	15.65	40.30	52.34	18	42.81	1.14	68.10	27.01	59.55	52
% of standard length																		
h	9.51	0.06	0.30	8.07	11.16	70	9.97	0.10	0.20	9.38	11.16	18	9.35	0.07	0.23	8.07	10.42	52
H	21.09	0.09	0.61	19.23	22.88	70	20.94	0.15	0.40	19.23	21.89	18	21.15	0.11	0.68	19.52	22.88	52
A - C	18.33	0.21	3.12	14.49	22.56	70	19.04	0.39	2.80	14.66	22.56	18	18.08	0.24	3.04	14.49	22.35	52
PreD	55.38	0.15	1.62	52.28	58.27	70	55.43	0.29	1.47	53.54	58.22	18	55.36	0.18	1.70	52.28	58.27	52
Dh	17.15	0.10	0.72	14.96	19.12	70	17.07	0.21	0.83	15.11	18.94	18	17.18	0.12	0.69	14.96	19.12	52
Db	12.34	0.07	0.39	10.65	14.03	70	12.27	0.15	0.39	10.65	13.13	18	12.36	0.09	0.40	11.34	14.03	52
PreA	63.50	0.17	2.05	61.00	66.95	70	63.07	0.30	1.66	61.00	65.61	18	63.64	0.20	2.13	61.04	66.95	52
Ah	15.04	0.13	1.17	12.69	17.83	70	15.27	0.27	1.33	13.19	17.10	18	14.96	0.15	1.11	12.69	17.83	52
Ab	17.21	0.17	1.97	14.00	22.58	70	17.58	0.38	2.60	15.27	22.58	18	17.08	0.18	1.73	14.00	20.56	52
PreV	46.61	0.14	1.33	42.86	48.66	70	46.83	0.22	0.85	44.50	48.66	18	46.54	0.17	1.49	42.86	48.61	52
Vh	12.97	0.14	1.31	11.14	16.32	70	12.68	0.17	0.52	11.14	14.10	18	13.07	0.17	1.57	11.16	16.32	52
Vb	4.31	0.05	0.15	3.32	5.15	70	4.27	0.11	0.20	3.32	5.15	18	4.32	0.05	0.14	3.38	5.14	52
PreP	24.97	0.11	0.90	22.90	26.91	70	25.22	0.23	0.93	23.48	26.77	18	24.88	0.13	0.87	22.90	26.91	52
Ph	15.76	0.13	1.22	11.61	18.28	70	16.29	0.23	0.92	14.45	17.85	18	15.57	0.15	1.20	11.61	18.28	52
Pb	4.33	0.03	0.07	3.66	4.84	70	4.40	0.06	0.06	3.83	4.84	18	4.30	0.04	0.07	3.66	4.84	52
PreO	11.32	0.07	0.32	8.10	12.51	70	11.46	0.08	0.11	11.00	12.00	18	11.26	0.09	0.38	8.10	12.51	52
PreOp	5.36	0.04	0.14	4.51	6.28	70	5.40	0.08	0.12	4.86	6.28	18	5.35	0.05	0.15	4.51	6.19	52
Gape	2.62	0.03	0.08	1.95	3.30	70	2.69	0.08	0.10	1.95	3.25	18	2.59	0.04	0.07	2.14	3.30	52
Hd	17.65	0.07	0.39	16.33	19.25	70	17.76	0.16	0.46	16.33	18.84	18	17.61	0.08	0.37	16.52	19.25	52
Io	7.84	0.04	0.10	7.13	8.58	70	7.84	0.07	0.09	7.13	8.56	18	7.84	0.05	0.11	7.22	8.58	52
Oh	8.66	0.05	0.21	7.30	9.56	70	8.79	0.10	0.18	8.03	9.56	18	8.61	0.06	0.21	7.30	9.53	52
Ov	8.65	0.05	0.17	7.47	9.50	70	8.84	0.09	0.15	8.12	9.49	18	8.59	0.06	0.17	7.47	9.50	52
Hw	12.38	0.07	0.38	11.15	13.71	70	12.70	0.13	0.31	11.75	13.71	18	12.27	0.08	0.37	11.15	13.40	52
Hl	19.21	0.09	0.58	17.25	21.21	70	19.32	0.14	0.35	18.25	20.53	18	19.17	0.11	0.66	17.25	21.21	52
Ina	3.75	0.06	0.26	2.91	5.42	70	3.62	0.11	0.23	2.94	4.62	18	3.79	0.07	0.26	2.91	5.42	52
W	12.61	0.08	0.48	11.22	14.16	70	12.73	0.17	0.53	11.32	14.16	18	12.57	0.09	0.46	11.22	13.98	52
w	3.42	0.06	0.23	2.32	4.60	70	3.43	0.16	0.44	2.32	4.60	18	3.42	0.06	0.16	2.57	4.12	52

Table A10.17: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in topmouth gudgeon from Ratherheath Tarn, Cumbria. See Table 3.2 in Chapter 3 for morphological codes.

	Combined						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
Tl	58.20	0.57	7.62	49.67	71.71	60	57.74	0.79	5.29	50.68	63.40	15	58.36	0.72	8.28	49.67	71.71	45
Fl	52.63	0.50	7.43	45.36	65.35	60	52.82	0.79	5.76	46.36	58.29	15	52.57	0.62	7.96	45.36	65.35	45
Sl	47.02	0.42	6.97	41.28	57.97	60	47.33	0.61	5.00	41.94	51.53	15	46.91	0.53	7.56	41.28	57.97	45
% of standard length																		
H	25.07	0.10	2.97	23.31	26.95	60	24.98	0.22	3.44	23.33	26.95	15	25.10	0.11	2.82	23.31	26.69	45
h	11.93	0.07	4.26	10.86	12.85	60	12.02	0.12	3.82	11.27	12.85	15	11.90	0.08	4.41	10.86	12.82	45
PreD	49.79	0.08	1.29	48.55	50.92	60	50.13	0.14	1.10	49.03	50.83	15	49.68	0.09	1.28	48.55	50.92	45
Dh	20.63	0.07	2.68	19.09	21.87	60	20.70	0.15	2.79	19.75	21.85	15	20.61	0.08	2.67	19.09	21.87	45
PreA	68.59	0.35	3.96	49.30	70.76	60	68.54	0.26	1.49	67.12	69.95	15	68.60	0.46	4.51	49.30	70.76	45
Ah	16.99	0.08	3.65	15.02	17.94	60	16.74	0.18	4.10	15.02	17.87	15	17.08	0.09	3.40	15.46	17.94	45
PreV	49.91	0.14	2.16	48.13	55.24	60	49.65	0.18	1.43	48.34	51.05	15	50.00	0.17	2.34	48.13	55.24	45
Vh	16.47	0.07	3.50	15.15	17.80	60	16.63	0.17	4.06	15.15	17.80	15	16.42	0.08	3.28	15.21	17.47	45
PreP	28.66	0.12	3.28	26.05	30.71	60	28.38	0.21	2.85	27.33	30.21	15	28.75	0.14	3.37	26.05	30.71	45
Ph	16.16	0.10	4.74	14.28	17.68	60	16.49	0.20	4.65	14.59	17.68	15	16.05	0.11	4.61	14.28	17.09	45
PrO	7.58	0.07	7.07	6.59	9.03	60	7.50	0.13	6.45	6.63	8.44	15	7.61	0.08	7.29	6.59	9.03	45
Od	6.72	0.03	3.62	6.08	7.16	60	6.66	0.07	3.91	6.25	7.06	15	6.74	0.04	3.51	6.08	7.16	45
PreOp	24.93	0.39	12.03	2.43	26.06	60	25.50	0.10	1.52	24.58	25.95	15	24.74	0.51	13.92	2.43	26.06	45
G	3.73	0.03	7.25	2.98	4.27	60	3.75	0.06	6.68	3.30	4.09	15	3.72	0.04	7.49	2.98	4.27	45

Table A10.18: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in topmouth gudgeon from Tadburn Lake Stream, Hampshire. See Table 3.2 in Chapter 3 for morphological codes.

	Combined						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
Tl	58.56	1.26	15.20	40.15	75.02	50	58.66	1.52	14.89	40.15	75.02	33	58.36	2.30	16.25	40.17	74.12	17
Fl	53.95	1.16	15.27	35.77	68.52	50	54.16	1.41	14.98	35.77	68.52	33	53.54	2.11	16.27	35.94	67.24	17
Sl	48.31	1.08	15.87	31.68	62.23	50	48.48	1.31	15.55	31.82	62.23	33	47.98	1.97	16.95	31.68	61.52	17
% of standard length																		
H	23.24	0.23	6.88	19.74	27.47	50	23.20	0.23	5.63	20.41	25.97	33	23.31	0.51	9.01	19.74	27.47	17
h	11.41	0.12	7.57	9.36	12.98	50	11.53	0.15	7.55	9.36	12.98	33	11.18	0.20	7.39	9.99	12.93	17
PreD	50.42	0.30	4.14	45.22	54.63	50	50.37	0.41	4.71	45.22	54.63	33	50.52	0.35	2.85	47.68	53.68	17
Dh	22.00	0.21	6.73	19.51	25.55	50	22.05	0.25	6.58	19.51	24.82	33	21.91	0.38	7.20	19.57	25.55	17
PreA	69.64	0.24	2.42	66.36	73.74	50	69.54	0.32	2.68	66.36	73.74	33	69.83	0.31	1.86	67.22	72.07	17
Ah	15.71	0.70	31.43	11.34	48.94	50	16.41	1.03	36.14	13.58	48.94	33	14.36	0.28	8.15	11.34	16.18	17
PreV	50.78	0.23	3.24	47.04	53.26	50	50.70	0.31	3.47	47.04	53.26	33	50.94	0.35	2.82	47.81	53.02	17
Vh	15.58	0.21	9.70	11.66	18.33	50	15.85	0.23	8.26	12.38	18.28	33	15.07	0.43	11.77	11.66	18.33	17
PreP	29.14	0.50	12.14	25.95	51.79	50	29.39	0.74	14.41	26.05	51.79	33	28.65	0.35	5.00	25.95	30.94	17
Ph	14.49	0.18	8.76	11.79	17.25	50	14.68	0.21	8.38	11.88	17.25	33	14.12	0.32	9.20	11.79	16.44	17
PrO	8.77	0.12	9.32	6.75	10.21	50	8.82	0.13	8.18	7.65	10.21	33	8.68	0.24	11.48	6.75	10.19	17
Od	5.80	0.10	11.66	4.40	7.47	50	5.70	0.12	12.44	4.40	7.47	33	6.01	0.14	9.56	5.09	6.88	17
PreOp	25.05	0.22	6.34	21.52	29.26	50	25.13	0.25	5.60	22.77	27.99	33	24.88	0.47	7.75	21.52	29.26	17
G	4.59	0.11	16.19	3.07	6.05	50	4.63	0.11	14.25	3.07	6.05	33	4.51	0.22	19.95	3.21	5.82	17

Table A10.19: Mean, standard error (S.E.), minimum (Min), maximum (Max), and coefficient of variation (CV) for mensural characters of morphology in topmouth gudgeon from Canal du Fumemorte, France. See Table 3.2 in Chapter 3 for morphological codes.

	Combined						Male						Female					
Character	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n	Mean	S.E.	CV	Min	Max	n
Tl	53.70	1.22	16.06	37.04	73.66	50	57.11	1.27	12.98	41.74	73.66	34	46.46	1.58	13.57	37.04	60.14	16
Fl	49.25	1.16	16.64	34.15	68.50	50	52.49	1.20	13.32	38.09	68.50	34	42.35	1.52	14.36	34.15	55.15	16
Sl	43.70	1.03	16.61	29.51	60.57	50	46.51	1.09	13.64	33.79	60.57	34	37.72	1.31	13.94	29.51	48.76	16
% of standard length																		
H	23.57	0.26	7.65	20.09	27.31	50	23.31	0.30	7.51	20.09	26.03	34	24.14	0.46	7.61	20.14	27.31	16
h	11.08	0.13	8.01	9.03	13.05	50	11.35	0.14	7.15	9.71	13.05	34	10.50	0.19	7.37	9.03	11.91	16
PreD	50.80	0.26	3.58	47.32	55.19	50	50.36	0.27	3.11	47.32	53.52	34	51.73	0.50	3.87	47.94	55.19	16
Dh	23.08	0.25	7.64	17.67	27.55	50	23.58	0.20	4.93	21.61	25.61	34	22.01	0.58	10.55	17.67	27.55	16
PreA	69.50	0.27	2.77	62.29	72.76	50	69.13	0.35	2.97	62.29	72.76	34	70.27	0.35	1.96	67.46	72.33	16
Ah	15.67	0.19	8.79	12.16	18.28	50	16.14	0.19	6.70	13.48	18.28	34	14.66	0.36	9.71	12.16	17.48	16
PreV	51.33	0.28	3.83	46.99	54.78	50	50.66	0.32	3.74	46.99	53.79	34	52.75	0.31	2.36	50.56	54.78	16
Vh	16.60	0.20	8.49	12.18	20.18	50	17.04	0.17	5.85	14.79	18.83	34	15.68	0.43	11.00	12.18	20.18	16
PreP	28.32	0.23	5.79	24.62	31.18	50	27.84	0.29	6.06	24.62	31.18	34	29.34	0.23	3.17	27.24	31.04	16
Ph	15.20	0.26	11.98	9.98	18.48	50	15.77	0.30	11.05	9.98	18.48	34	13.99	0.34	9.75	10.49	15.84	16
PrO	8.56	0.12	10.00	6.73	10.68	50	8.47	0.14	9.45	6.73	10.26	34	8.75	0.24	10.99	6.97	10.68	16
Od	6.32	0.11	12.10	4.67	8.02	50	6.12	0.11	10.30	4.67	8.01	34	6.75	0.22	12.83	4.86	8.02	16
PreOp	24.75	0.20	5.69	21.54	28.94	50	24.62	0.21	4.93	21.54	27.84	34	25.03	0.44	7.04	22.84	28.94	16
G	5.01	0.09	12.49	3.38	6.27	50	5.02	0.09	10.48	3.42	5.92	34	4.98	0.20	16.40	3.38	6.27	16

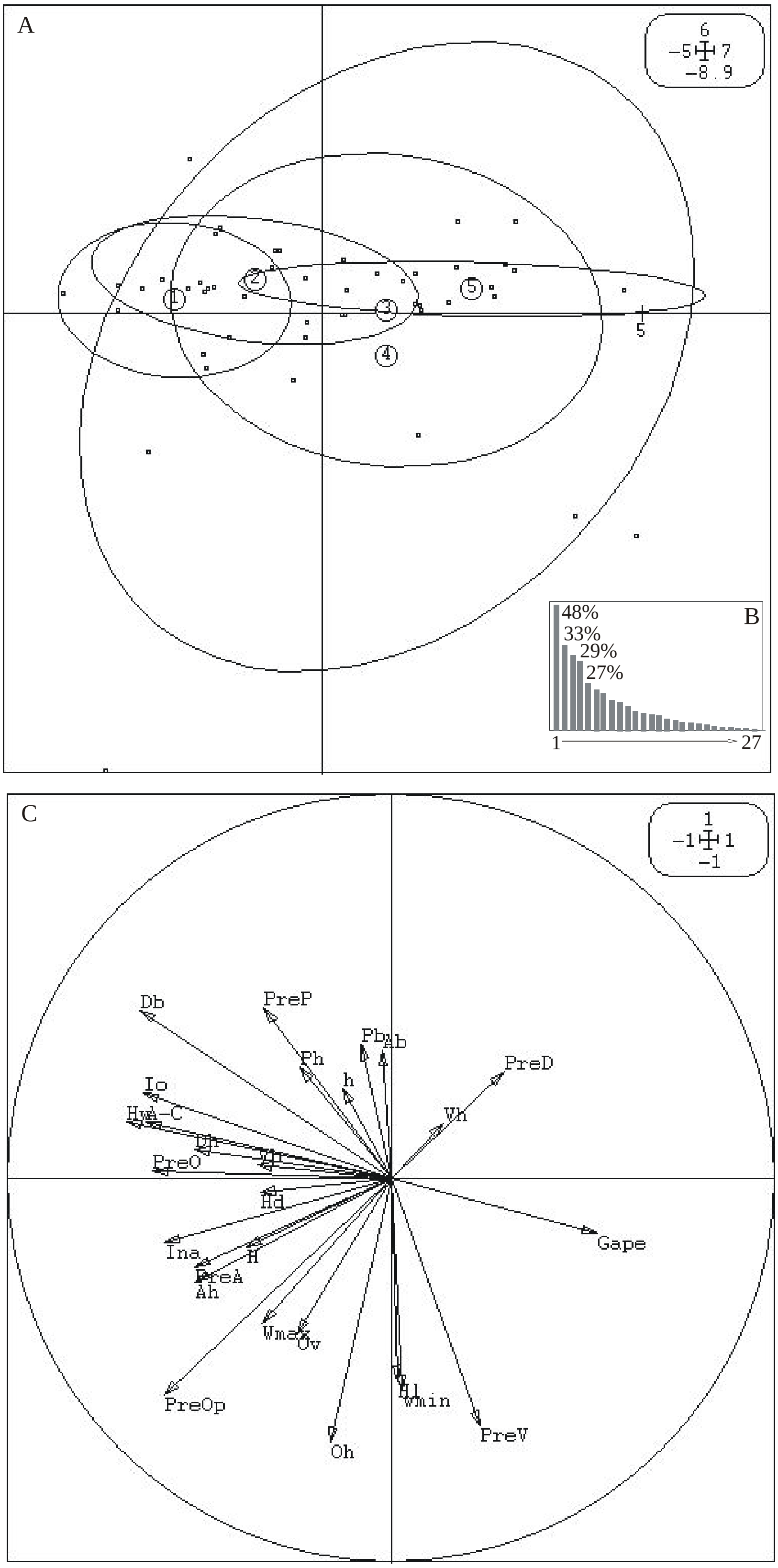

Figure A10.1: Morphological traits of sunbleak from Bridgewater-Taunton Canal at Buckland Farm, Somerset (BTC1) using ordination of principal components with (A) ellipses age groups and using uniform weightings (age groups are denoted as 1 to 5) with (B) the eigenvalues and (C) the 27 morphological characters.

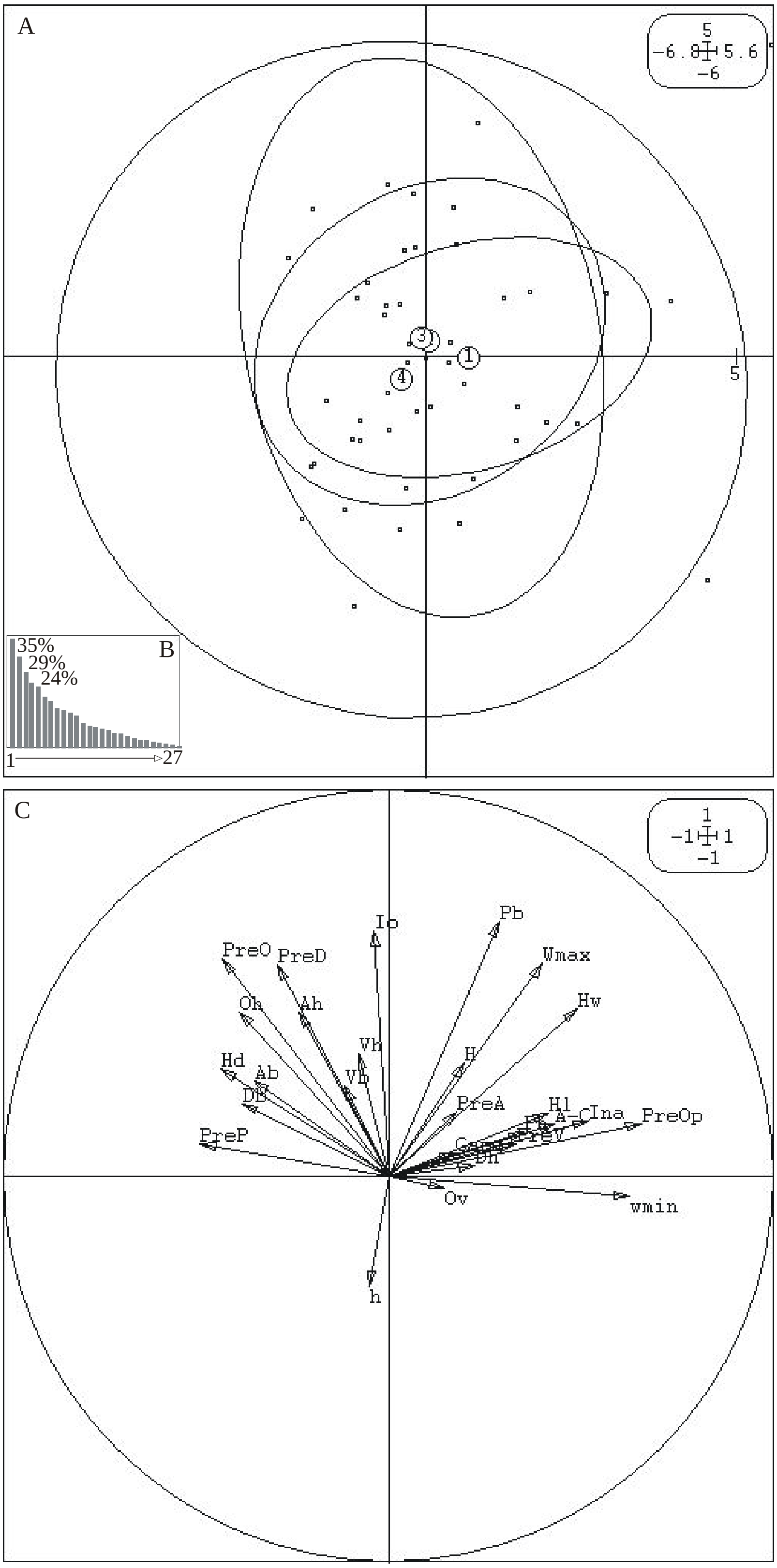

Figure A10.2: Morphological traits of sunbleak from Bridgewater-Taunton Canal at Creech St. Michael, Somerset (BTC2) using ordination of principal components with (A) ellipses age groups and using uniform weightings (age groups are denoted as 1 to 4) with (B) the eigenvalues and (C) the 27 morphological characters.

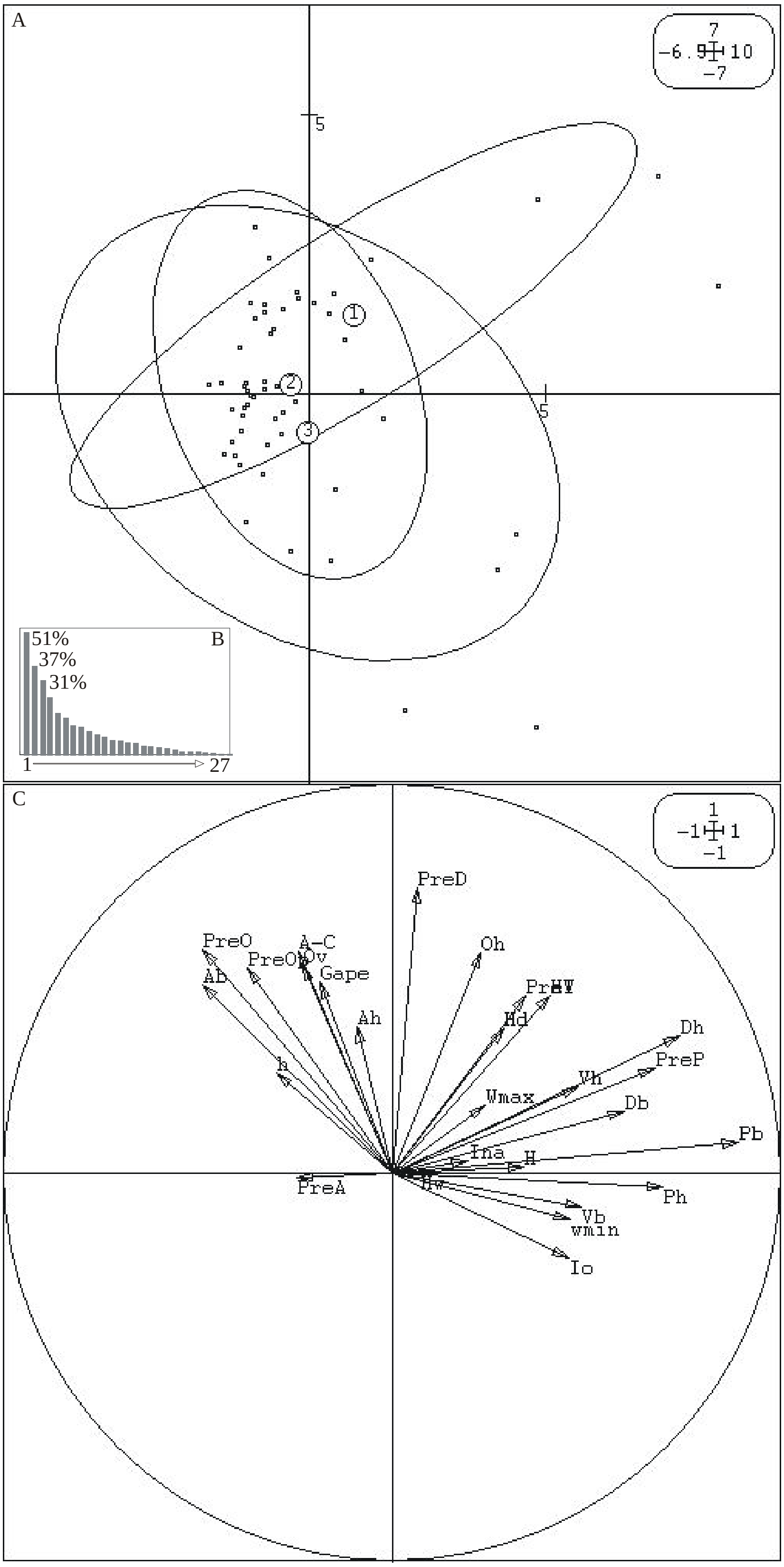

Figure A10.3: Morphological traits of sunbleak from Bridgewater-Taunton Canal at YMCA, Somerset (BTC3) using ordination of principal components with (A) ellipses age groups and using uniform weightings (age groups are denoted as 1 to 3) with (B) the eigenvalues and (C) the 27 morphological characters.

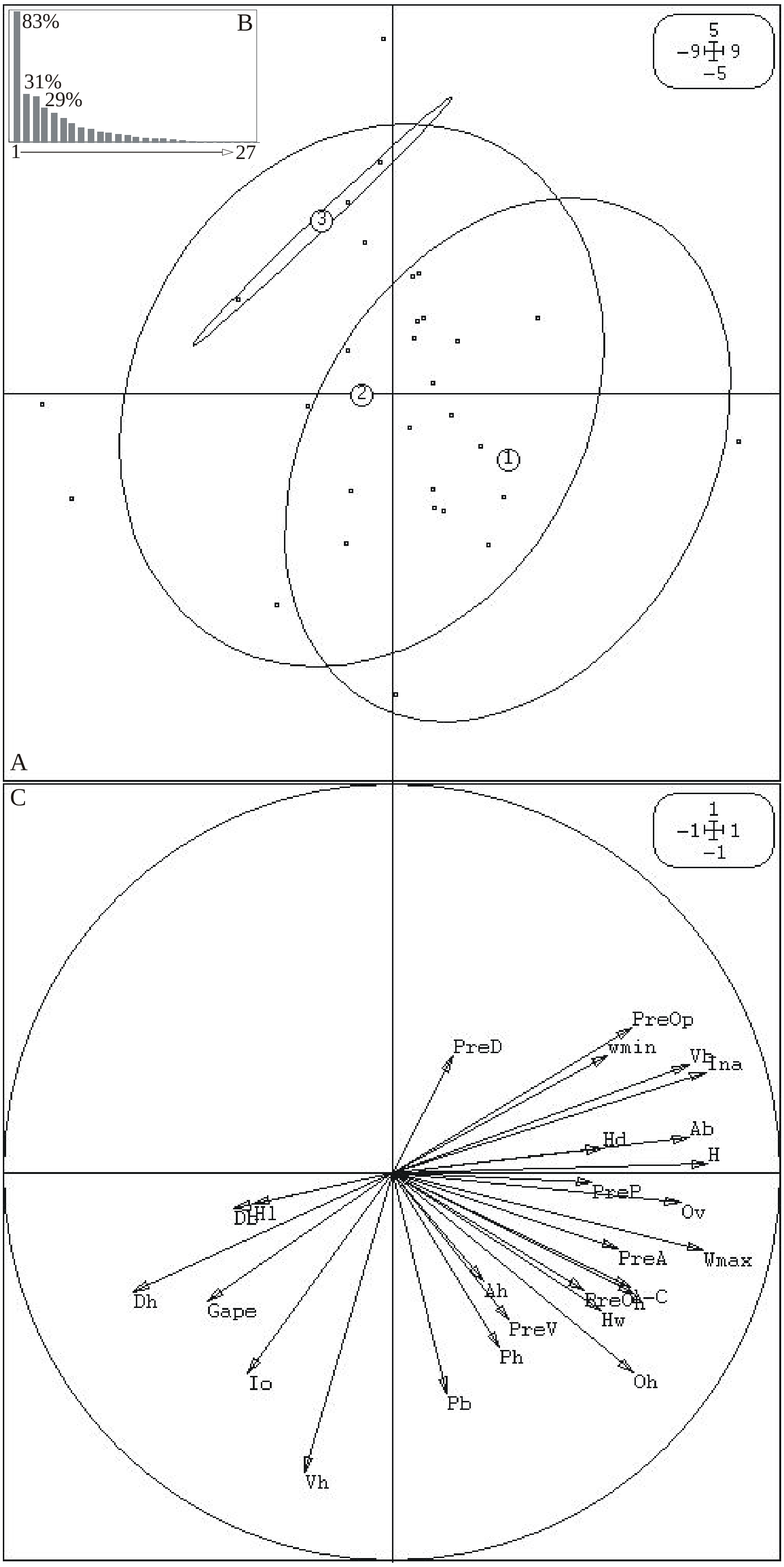

Figure A10.4: Morphological traits of sunbleak from Kings-Sedgemoor Drain at Bradney Bridge, Bawdrip, Somerset (KSD4) using ordination of principal components with (A) ellipses age groups and using uniform weightings (age groups are denoted as 1 to 3) with (B) the eigenvalues and (C) the 27 morphological characters.

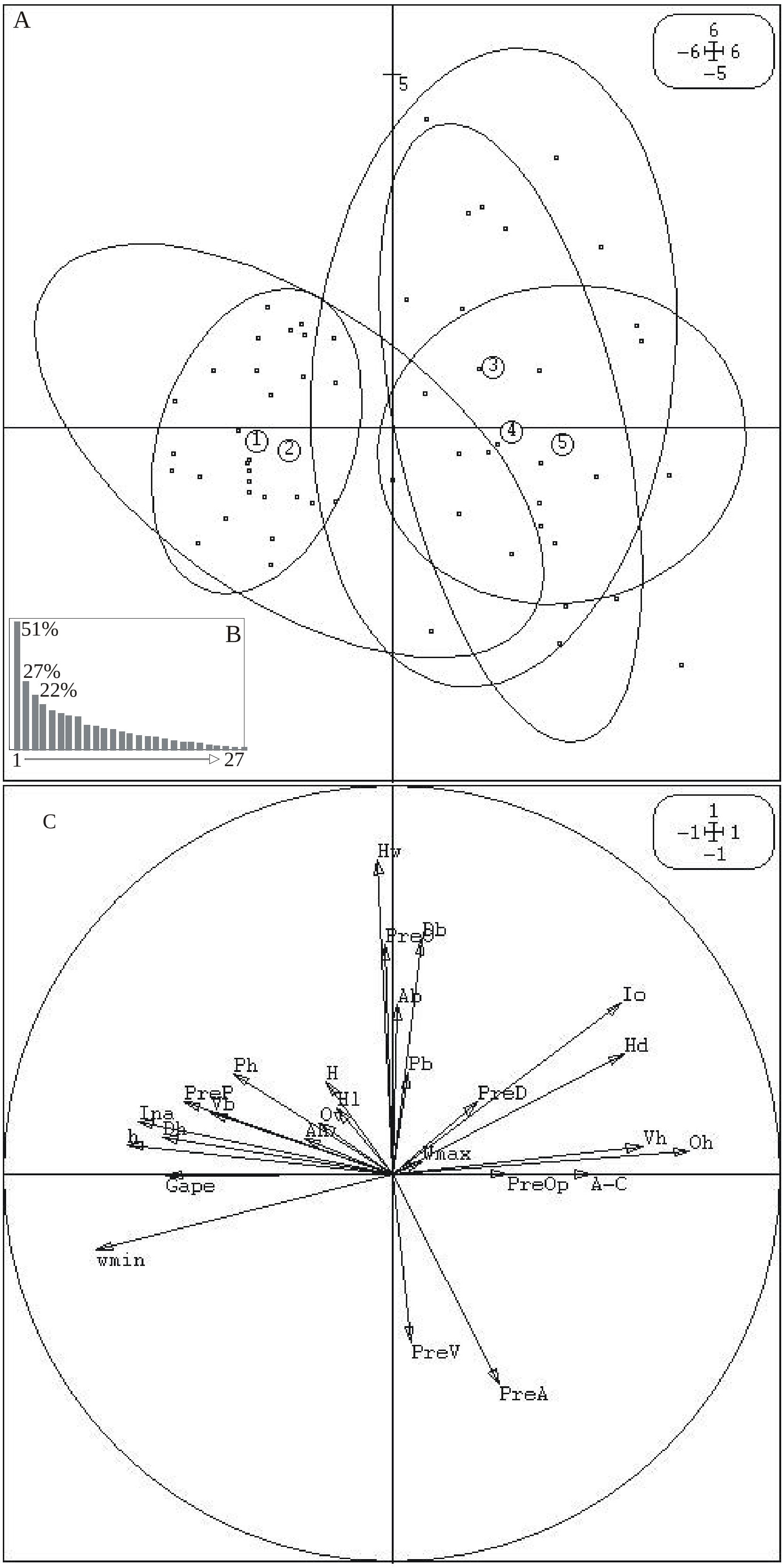

Figure A10.5: Morphological traits of sunbleak from Kings-Sedgemoor Drain at Parchey Bridge, Somerset (KSD5) using ordination of principal components with (A) ellipses age groups and using uniform weightings (age groups are denoted as 1 to 4) with (B) the eigenvalues and (C) the 27 morphological characters.

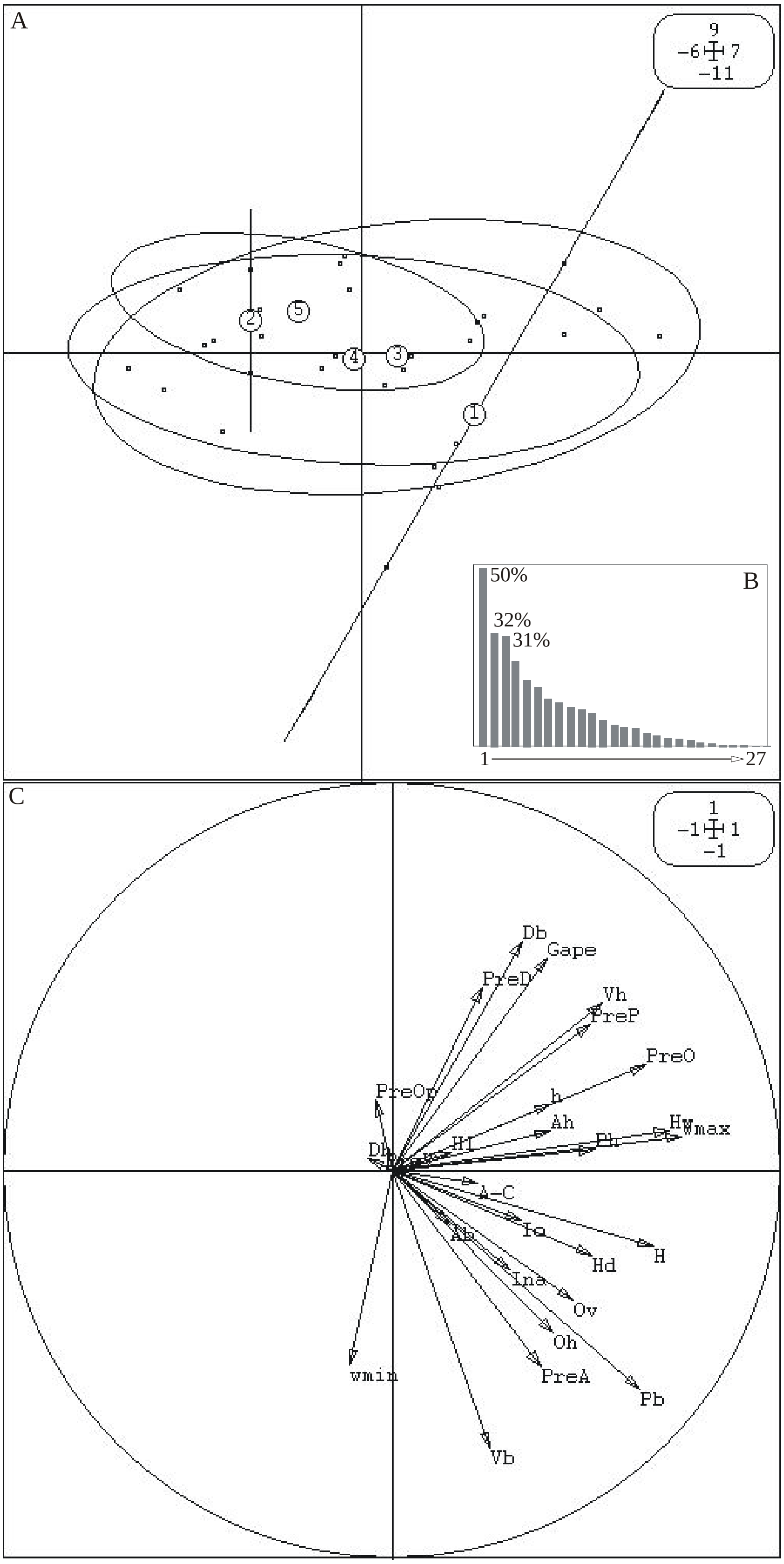

Figure A10.6: Morphological traits of sunbleak from River Sowy at Greylake Bridge, Somerset (Sowy7) using ordination of principal components with (A) ellipses age groups and using uniform weightings (age groups are denoted as 1 to 4) with (B) the eigenvalues and (C) the 27 morphological characters.

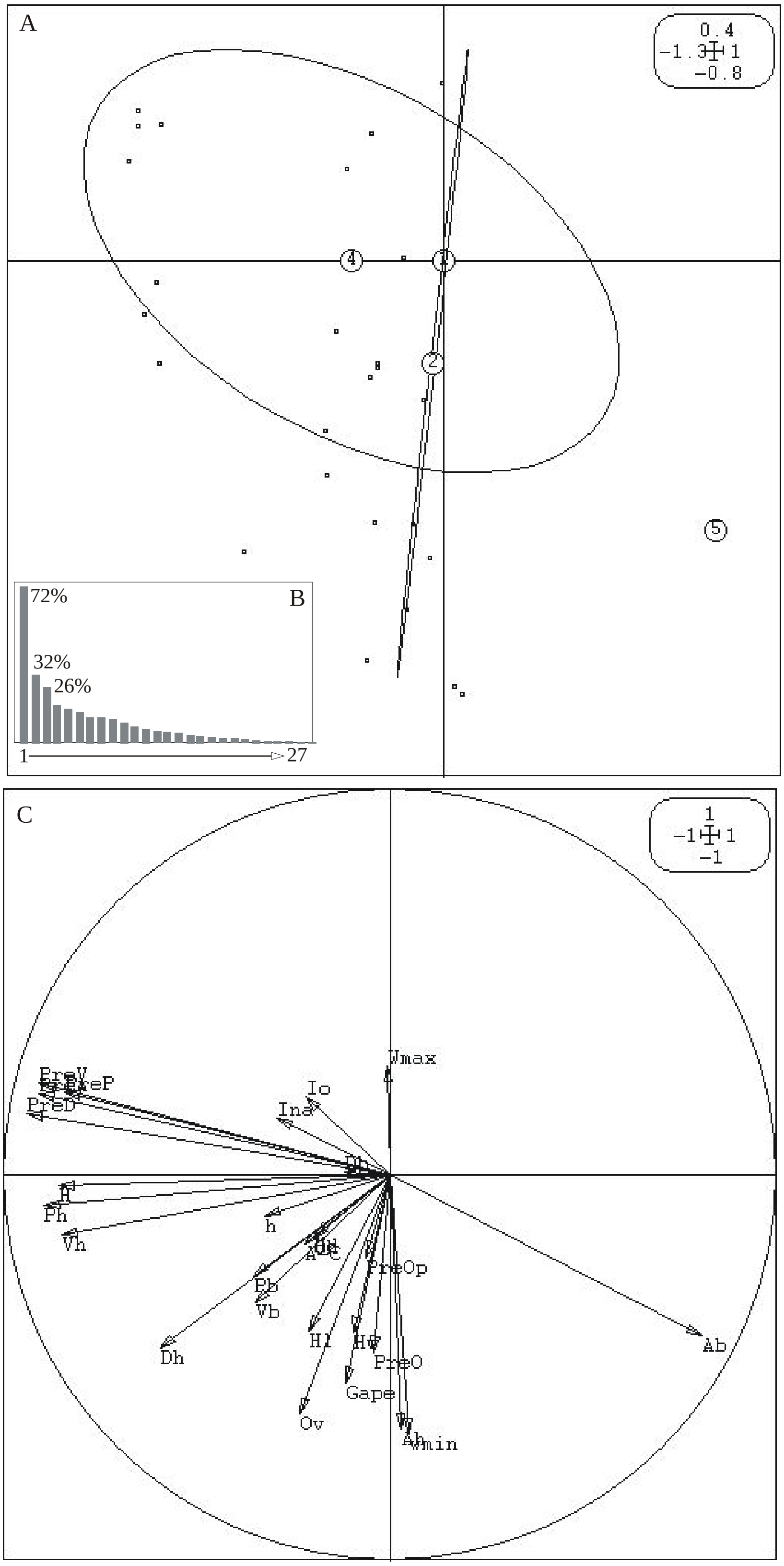

Figure A10.7: Morphological traits of sunbleak from Dunwear Pond, Somerset (Dun9) using ordination of principal components with (A) ellipses age groups and using uniform weightings (age groups are denoted as 1 to 4) with (B) the eigenvalues and (C) the 27 morphological characters.

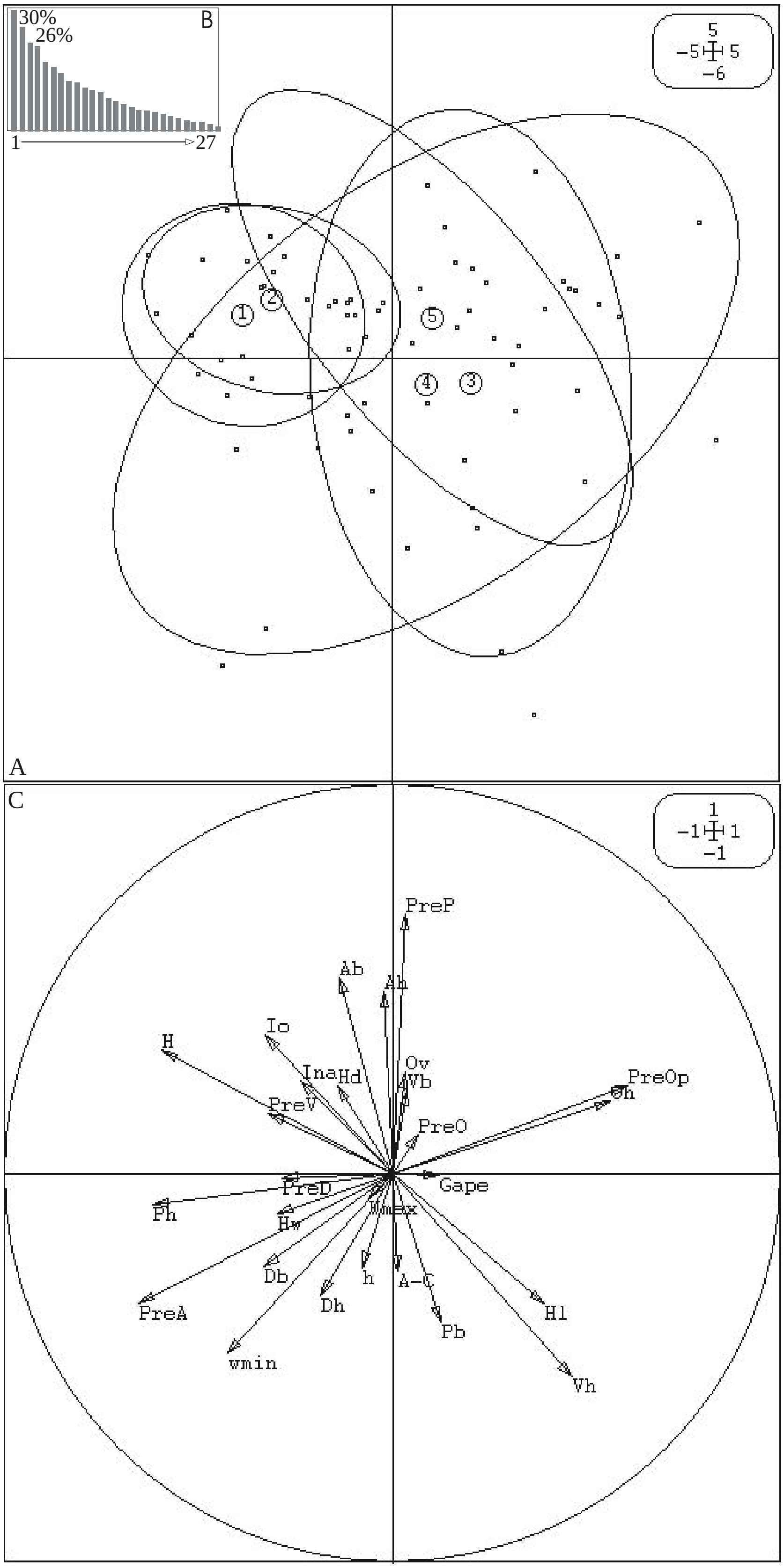

Figure A10.8: Morphological traits of sunbleak from Stoneham Lakes, Hampshire (Stone11) using ordination of principal components with (A) ellipses age groups and using uniform weightings (age groups are denoted as 1 to 5) with (B) the eigenvalues and (C) the 27 morphological characters.

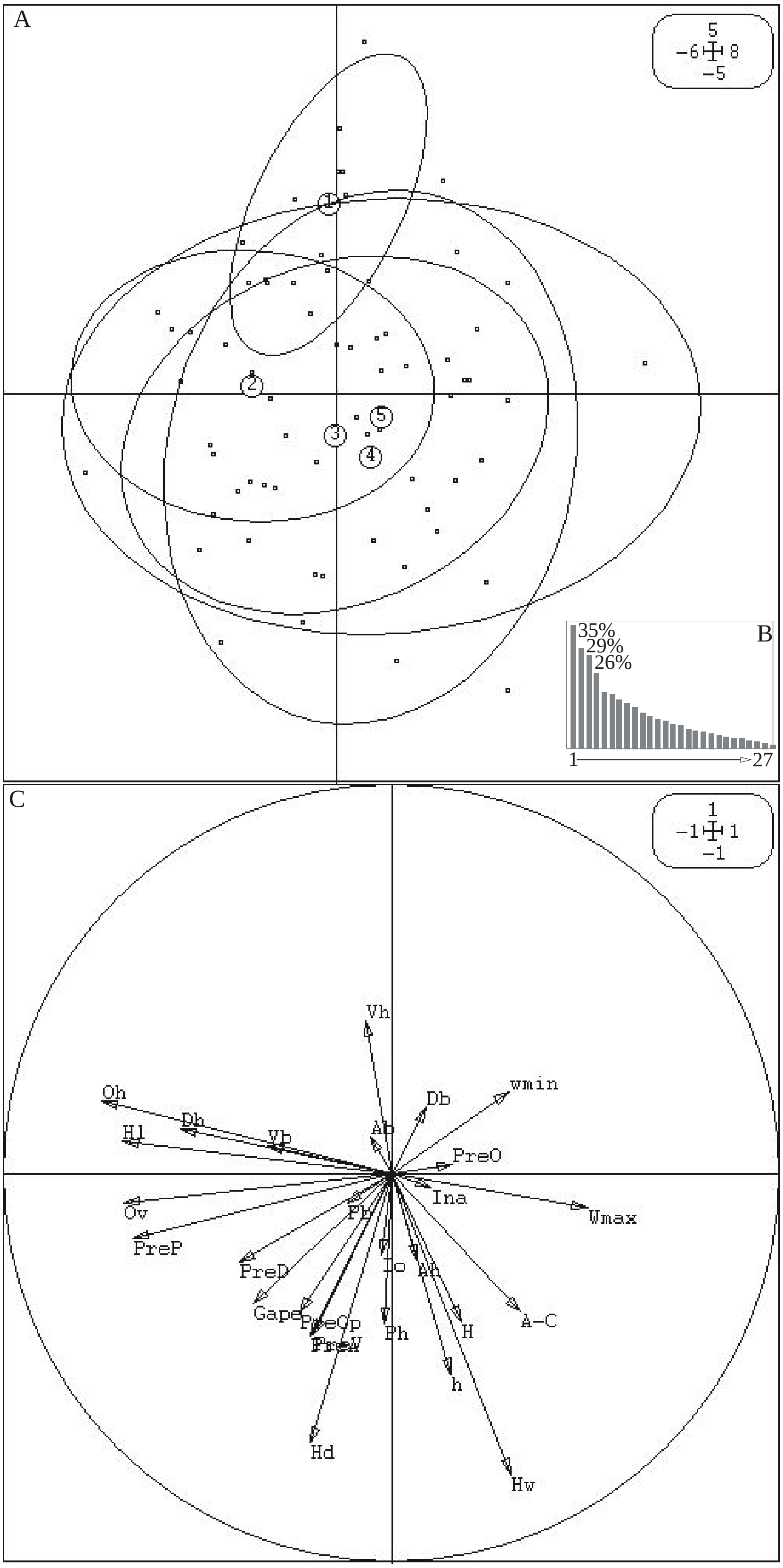

Figure A10.9: Morphological traits of sunbleak from Two Lakes Fishery, Hampshire (TwoL12) using ordination of principal components with (A) ellipses age groups and using uniform weightings (age groups are denoted as 1 to 5) with (B) the eigenvalues and (C) the 27 morphological characters.

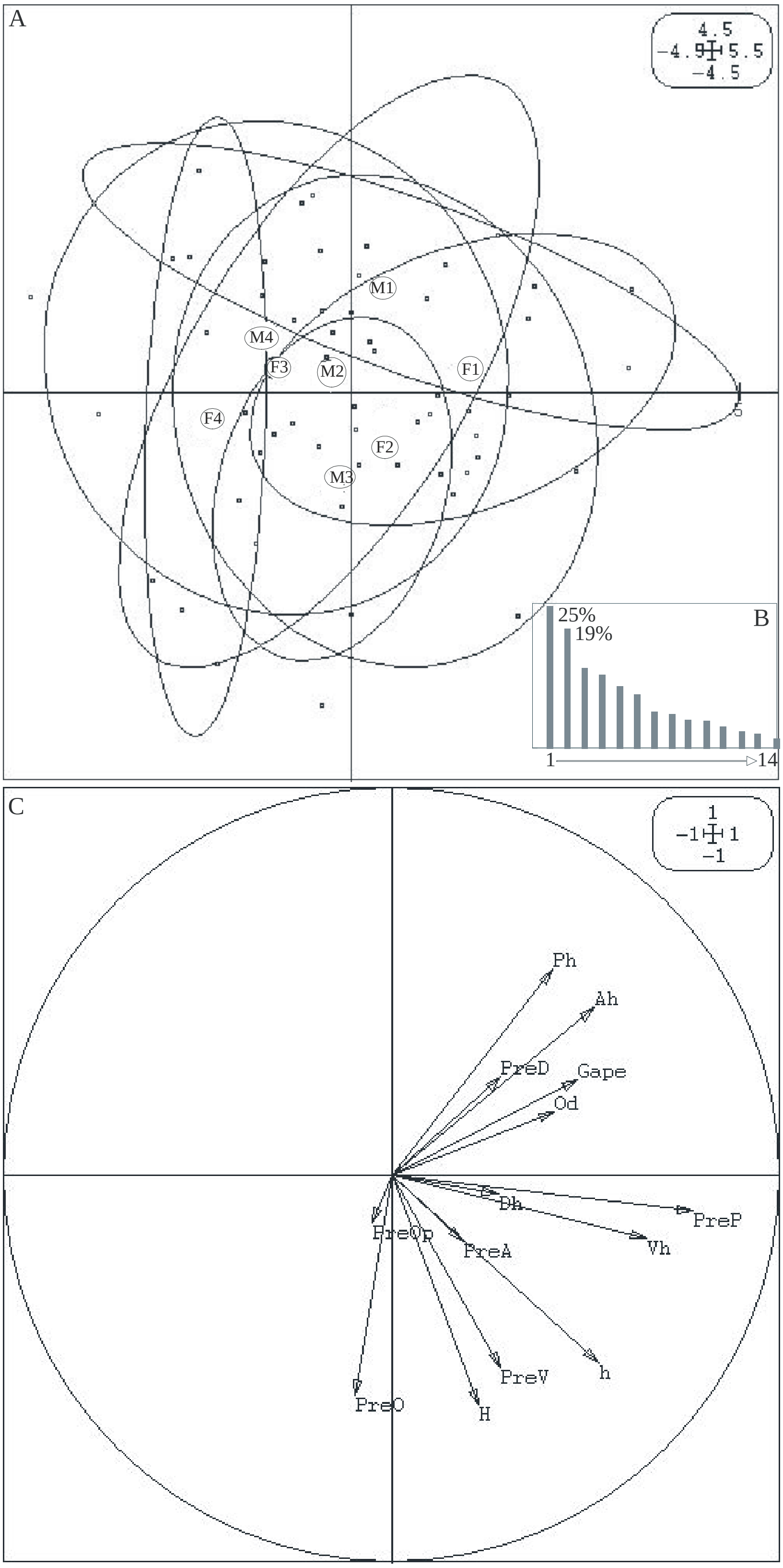

Figure A10.10: Morphological traits of topmouth gudgeon from Ratherheath Tarn, Cumbria (Rath) using ordination of principal components with (A) ellipses age/sex groups and using uniform weightings (male groups are denoted M and females with F; age groups are denoted as 1 to 4) with (B) the eigenvalues and (C) the 14 morphological characters.

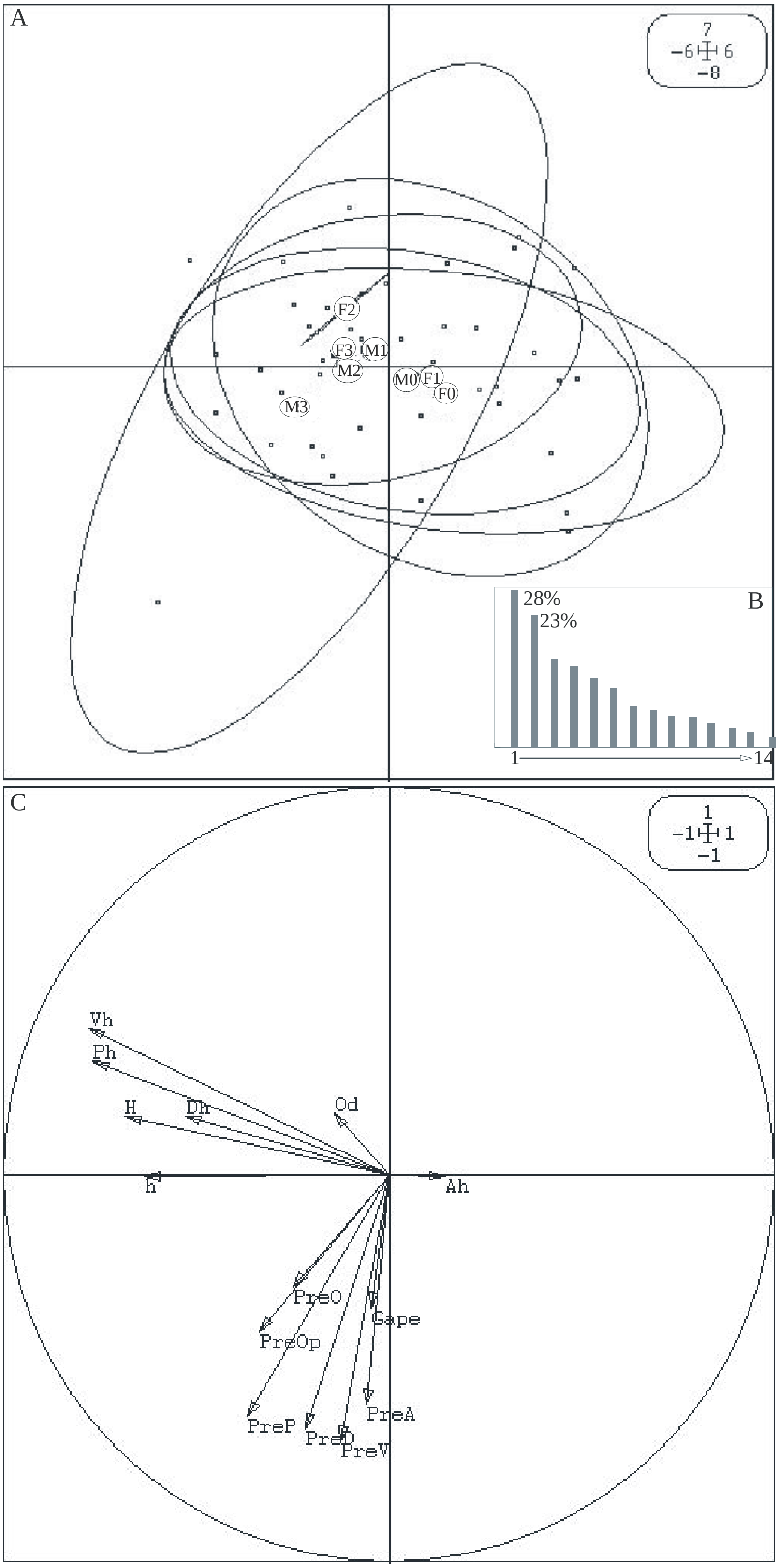

Figure A10.11: Morphological traits of topmouth gudgeon from Tadburn Lake stream, Hampshire (Tad) using ordination of principal components with (A) ellipses age/sex groups and using uniform weightings (male groups are denoted M and females with F; age groups are denoted as 0 to 4) with (B) the eigenvalues and (C) the 14 morphological characters.

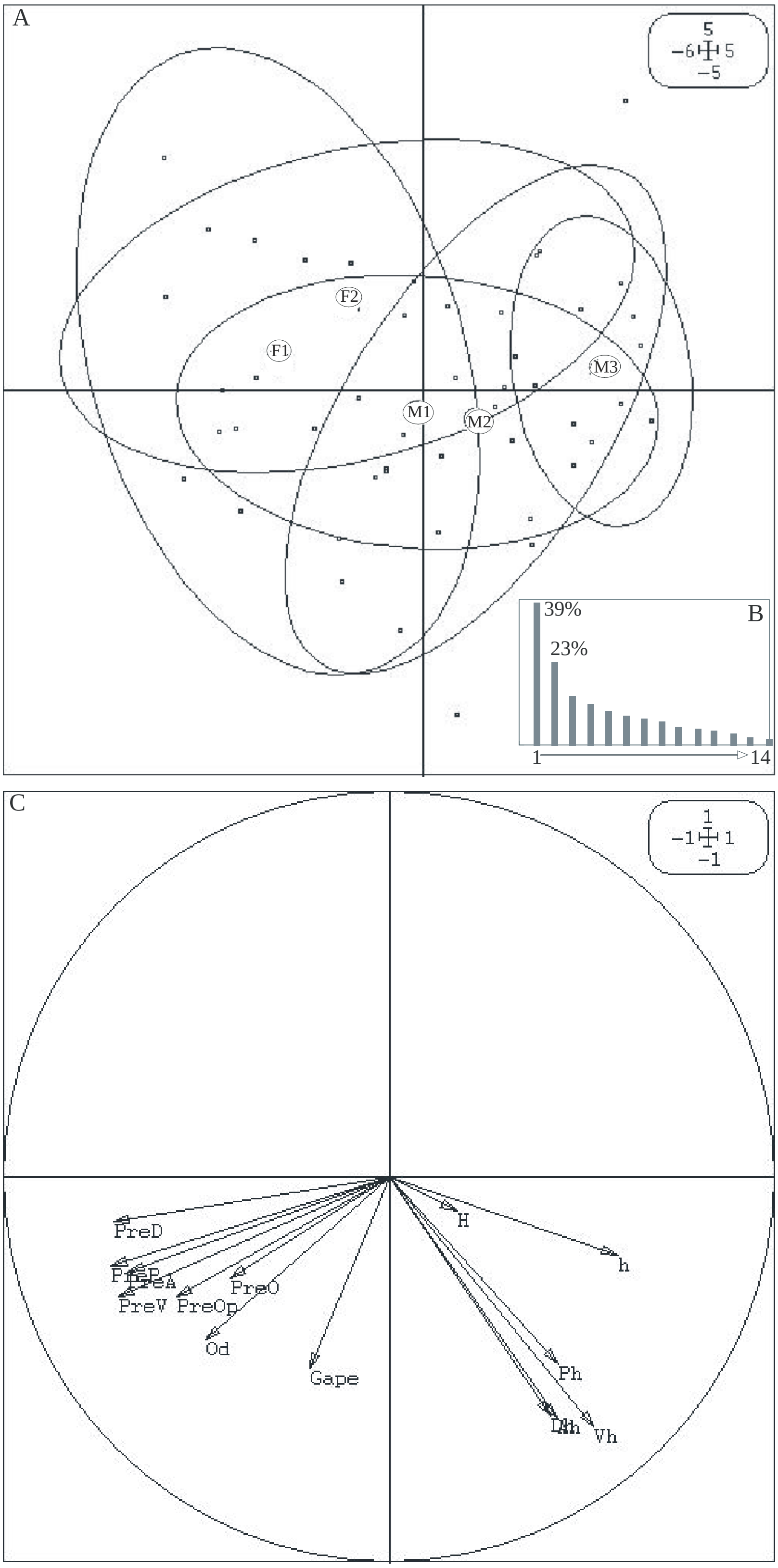

Figure A10.12: Morphological traits of topmouth gudgeon from Canal du Fumemorte, France, Hampshire (Fum) using ordination of principal components with (A) ellipses age/sex groups and using uniform weightings (male groups are denoted M and females with F; age groups are denoted as 1 to 3) with (B) the eigenvalues and (C) the 14 morphological characters.

Appendix B

Table B10.20: Dates and timing of 24-hour drift sampling during 2004 and 2005 and seasonal sampling dates at Revels Fishery, Dorset, Stoneham Lakes, Hampshire, and Crampmoor Fishery, Hampshire. Net set times and bottle changing times are also indicated.

	Revels Fishery		Stoneham Lakes		Crampmoor Fishery	
	2004	2005	2004	2005	2004	2005
Time of bottle change	Set at 11:00 h	—	Set at 11:00 h	Set at 11:00 h	Set at 11:00 h	Set at 11:00 h
14:00	—	—	—	—	—	12—13 Apr 2005 14—15 Apr 2005 12—13 May 2005 19—20 May 2005 27—28 Jun 2005 30 Jun—1 Jul 2005
17:00	07—08 Apr 2004 15—16 Apr 2004 17—18 May 2004 24—25 May 2004 17—18 Jun 2004 24—25 Jun 2004	—	09—10 Apr 2004 17—18 Apr 2004 19—20 May 2004 26—27 May 2004 19—20 Jun 2004 22—23 Jun 2004	10—11 Apr 2005 15—16 Apr 2005 14—15 May 2005 21—22 May 2005 25—26 Jun 2005 28—29 Jun 2005	11—12 Apr 2004 19—20 Apr 2004 21—22 May 2004 24—25 May 2004 28—29 May 2004 21—22 Jun 2004 24—25 Jun 2004	12—13 Apr 2005 14—15 Apr 2005 12—13 May 2005 19—20 May 2005 27—28 Jun 2005 30 Jun—1 Jul 2005
20:00	—	—	—	—	—	12—13 Apr 2005 14—15 Apr 2005 12—13 May 2005 19—20 May 2005 27—28 Jun 2005 30 Jun—1 Jul 2005
23:00	07—08 Apr 2004 15—16 Apr 2004 17—18 May 2004 24—25 May 2004 17—18 Jun 2004 24—25 Jun 2004	—	09—10 Apr 2004 17—18 Apr 2004 19—20 May 2004 26—27 May 2004 19—20 Jun 2004 22—23 Jun 2004	10—11 Apr 2005 15—16 Apr 2005 14—15 May 2005 21—22 May 2005 25—26 Jun 2005 28—29 Jun 2005	11—12 Apr 2004 19—20 Apr 2004 21—22 May 2004 24—25 May 2004 28—29 May 2004 21—22 Jun 2004 24—25 Jun 2004	12—13 Apr 2005 14—15 Apr 2005 12—13 May 2005 19—20 May 2005 27—28 Jun 2005 30 Jun—1 Jul 2005
02:00	—	—	—	—	—	12—13 Apr 2005 14—15 Apr 2005 12—13 May 2005 19—20 May 2005 27—28 Jun 2005 30 Jun—1 Jul 2005
05:00	07—08 Apr 2004 15—16 Apr 2004 17—18 May 2004 24—25 May 2004 17—18 Jun 2004 24—25 Jun 2004	—	09—10 Apr 2004 17—18 Apr 2004 19—20 May 2004 26—27 May 2004 19—20 Jun 2004 22—23 Jun 2004	10—11 Apr 2005 15—16 Apr 2005 14—15 May 2005 21—22 May 2005 25—26 Jun 2005 28—29 Jun 2005	11—12 Apr 2004 19—20 Apr 2004 21—22 May 2004 24—25 May 2004 28—29 May 2004 21—22 Jun 2004 24—25 Jun 2004	12—13 Apr 2005 14—15 Apr 2005 12—13 May 2005 19—20 May 2005 27—28 Jun 2005 30 Jun—1 Jul 2005
08:00	—	—	—	—	—	12—13 Apr 2005 14—15 Apr 2005 12—13 May 2005 19—20 May 2005 27—28 Jun 2005 30 Jun—1 Jul 2005
11:00	07—08 Apr 2004 15—16 Apr 2004 17—18 May 2004 24—25 May 2004 17—18 Jun 2004 24—25 Jun 2004	—	09—10 Apr 2004 17—18 Apr 2004 19—20 May 2004 26—27 May 2004 19—20 Jun 2004 22—23 Jun 2004	10—11 Apr 2005 15—16 Apr 2005 14—15 May 2005 21—22 May 2005 25—26 Jun 2005 28—29 Jun 2005	11—12 Apr 2004 19—20 Apr 2004 21—22 May 2004 24—25 May 2004 28—29 May 2004 21—22 Jun 2004 24—25 Jun 2004	12—13 Apr 2005 14—15 Apr 2005 12—13 May 2005 19—20 May 2005 27—28 Jun 2005 30 Jun—1 Jul 2005
Seasonal Sampling (12hr net change)	—	—	—	—	17 Jul 2004 16 Aug 2004 17 Sep 2004 17 Oct 2004 19 Nov2004 17 Dec 2004	23 Jan 2005 16 Feb 2005 16 Mar 2005

Appendix C

Post-hatching development and morphology of topmouth gudgeon *Pseudorasbora parva*

Introduction

The theory of saltatory ontogeny states that during development, some fish species go through a sequence of stabilised states, separated by periods of rapid change or ‘thresholds’ (Balon, 1990). Developmental steps are separated by morphological and physiological ‘development thresholds.’ The difference between each threshold is the development of an organ or feature that, when functioning, affords the fish new capabilities to survive more easily or more efficiently. During early life, fish go through many morphological changes that along with changes in habitat and other abilities determine the survival of the fish over time. Until the fish is fully grown the environment requirements change with development.

The aim of the present study is to describe the post-hatching development of the topmouth gudgeon in relation to the theory of saltatory ontogeny and to examine morphological characters during post-hatching development. This information is important when examining aspects of the invasion process such as drift and dispersal of topmouth gudgeon in relation to its early life.

Materials and methods

In May 2004, eggs were acquired naturally in tanks from adult broodstock originating from the Crampmoor Fishery (see Chapter 2 for site description). After spawning, the eggs were immediately transferred to an 80 l capacity rearing aquarium. Ontogenetic development after hatching was assessed for topmouth gudgeon using the reference specimens reared in the aquarium, which was fitted with a small air stone to provide aeration and water circulation.

Water temperatures in the tanks were recorded hourly, throughout the study period, using TinyTag® recording equipment. The timescale used against development is presented as accumulated degree days post-hatching (a^{o}d), where a^{o}d = sum of mean daily temperatures (°C). Time is presented in days, hours and minutes after hatching. After hatching on the 31 May 2004, larvae in the aquarium were fed with *Artemia* sp. (brine shrimp) nauplii complemented with a mixture of ground dried flakes. Samples of fish were taken at regular intervals after hatching. Individuals from each sample were anaesthetized with 2-Phenoxyethanol, examined under a binocular microscope and preserved in 4 % formaldehyde solution. Measurements were made to the nearest 0.1 mm using an ocular graticule fitted to the binocular microscope. Lengths are given as notochord length (NCL) for specimens prior to flexion of the urostyle and total length (TL) after urostyle flexion. Both preserved and living specimens were used to determine developmental intervals for topmouth gudgeon. Fourteen morphological characters (Table A3.1) related to swimming capacity and feeding behaviour were measured, following the techniques of (Holčík *et al.*, 1989).

Table C10.21: Morphological characters measured in topmouth gudgeon *P. parva* during early life presented in alphabetical order.

Code	Morphological characters
H	maximum body height
H	minimum body height
Hd	head depth
Iio	inner inter-orbital distance
laco	maximum body width
lapc	minimum body width
NCL	notochord length for pre-flexion of the urostyle
Oh	orbital horizontal diameter
Oo	outer inter-orbital distance
Ov	vertical orbital diameter
Ph	height of pectoral fin
PoO	post-orbital distance
PrO	pre-orbital distance
PrP	pre-pectoral fin distance
SL	standard length
TL	total length

Results

Laboratory investigations on ontogenetic development of topmouth gudgeon during early life lasted 1330 degree days and were accompanied by observations on functional and morphological changes up until the topmouth gudgeon reached the juvenile phase (Figures A3.1, A3.2; Table A3.2). After hatching the free embryos and larvae in the aquarium in the tank room were kept at an average temperature of 20.18^{o} C with a minimum of 19.67^{o} C and a maximum of 20.76^{o} C. The post-hatching periods of development represented one free embryo step and four larval steps. The timescale from hatching to the end of the larva period, when the larvae became juveniles for the first time, lasted 65 days.

Free embryo phase

The free embryo phase began with hatching on the 31 May 2004 at 10:00 and ended with the disappearing of the yolk sac and the mouth became visible 24 h to 47.5 h (01.06.04, 10:00; 02.06.04, 9:30). At this stage, the appearance of the topmouth gudgeon was typical of cyprinids, with the head bent down over the yolk and a finfold surrounding the body.

Larva 1

Larval stage 1 lasted from 97.5 h (4.06.04, 11:50) to 557 h (23.06.04, 15:10). This stage was characterised by the yolk sac disappearing almost entirely and ended with the beginning of urostyle flexion. This flexion increased throughout this larval stage. As the caudal fin started forming rays started to form and at the end of this larval step rays were visible in the entirety of the caudal fin when the caudal fin started to fork. The posterior swim bladder was formed and this should aid the buoyancy of the larva. The gut started to form and a small amount of ingested food was visible suggesting that the mouth was functional at this point. The visible amount of food inside gut increased though this larval stage. The gills also started to form. The mouth at such an early stage was terminal. Faint pigment was visible on the swimbladder area. While the anal finfold reduced the anal fin started to form and was clearly visible at 432 h after hatching. At the beginning of the stage there was an orange pigment around the eye of the larvae but this soon disappeared and changed to a dark pigment above the eye and dark melanophores on the top and side of the head, along the vertebra and on the underside of the larvae.

Larva 2

Larval stage 2 lasted from 557 h (23.06.04, 15:10) to 721 h (30.06.04, 11:10) The beginning of this stage was signified by the anterior swimbladder becoming visible. The anterior swimbladder was however, at this stage, not particularly inflated and very small in relation to the posterior swimbladder. As the dorsal finfold began to disconnect from the dorsal fin; the dorsal fin began to develop and the caudal fin was nearly fully developed and was forked although it did not display the final ray count. Only a little caudal finfold was left at this point of development. The flexion of the urostyle was complete. The anal fin also became more developed in this stage. There were a few melanophores on the side of the larva and on the underside.

Larva 3

This interval was observed from 936 h (09.07.04, 10:15) to 1110.5 h (16.07.04, 16:30) after hatching. The dorsal fin became fully formed and was fully disconnected from the dorsal finfold which indicated the onset of larval interval3 4. Although there was still some residual caudal finfold, the caudal fin was fully formed and forked. This developmental interval was characterised by the straight gut structure becoming looped and folded. This would allow the larvae to gain an increasing amount of energy from ingested foods. The anterior swimbladder became inflated and hence much bigger although it was slightly smaller than the posterior swimbladder. The pelvic fin became visible. All other fins, including the anal fin, were fully formed. The mouth was in its final superior position. There was also a clear acceleration in growth in this stage. The topmouth gudgeon from this stage became much darker with more melanophores now being found on the entire body of the fish, being more pronounced on its back.

Larva 4

Larval stage 4 lasted from 1247 h (21.07.04, 9:00) to 1439 h (29.07.04, 8:50). The onset of larval interval 4 was determined by the complete disappearance of the finfold and all fins, including the pelvic fin, were fully formed. Scales started to develop first on the sides of the larvae.

Juvenile period

The first fully scaled fish, with the lateral line organ fully formed and distinct, were observed at 1583 h (04.08.04, 9:00). This marked the transition from larval to juvenile interval.

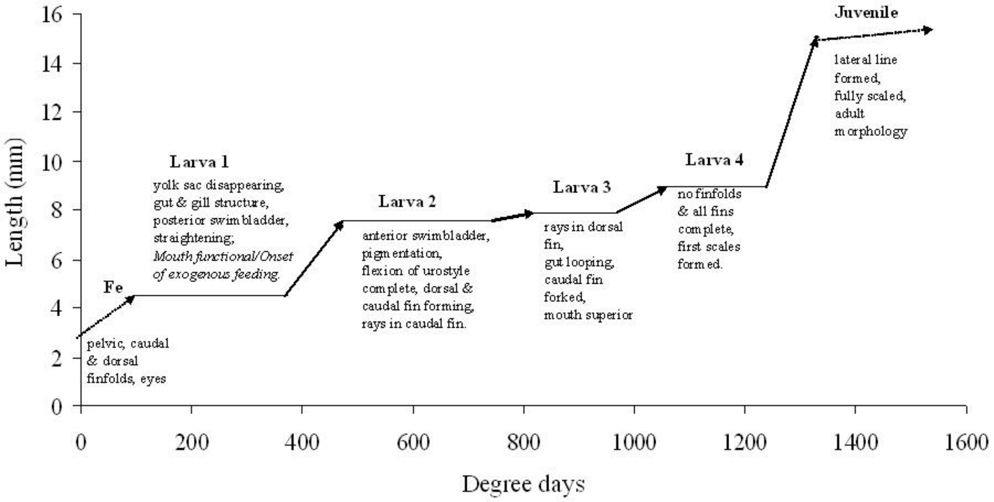

Figure C10.13: Growth in developmental intervals of topmouth gudgeon *P. parva* during early life from hatching through to the juvenile period were investigated in the laboratory from the 1 June 2004.

Table C10.22: Growth in total length of topmouth gudgeon *P. parva* during early life investigated in the laboratory after hatching on the 31 May 2004.

Development Step	Mean TL (mm)	S.E.	Min	Max	Mean increment between steps (mm)
FE	4.27	0.02	4.26	4.29	-
L1	5.24	0.90	3.86	7.29	0.97
L2	7.10	0.71	6.14	7.86	1.86
L3	8.41	0.64	7.00	8.86	1.31
L4	12.89	1.87	10.43	15.00	4.49
Juvenile	16.43	1.54	15.00	18.57	3.54

The first two components of the PCA accounted for 49 % of the variation, with ellipses representing the early life stages suggesting a gradual transformation in morphology throughout the larval period (Figure A3.2). A shift was noticeable between larval interval 4 and the juvenile period. The morphological variables that contributed most to changes between steps were pre-orbital distance, the orbital diameter and the minimum body width.

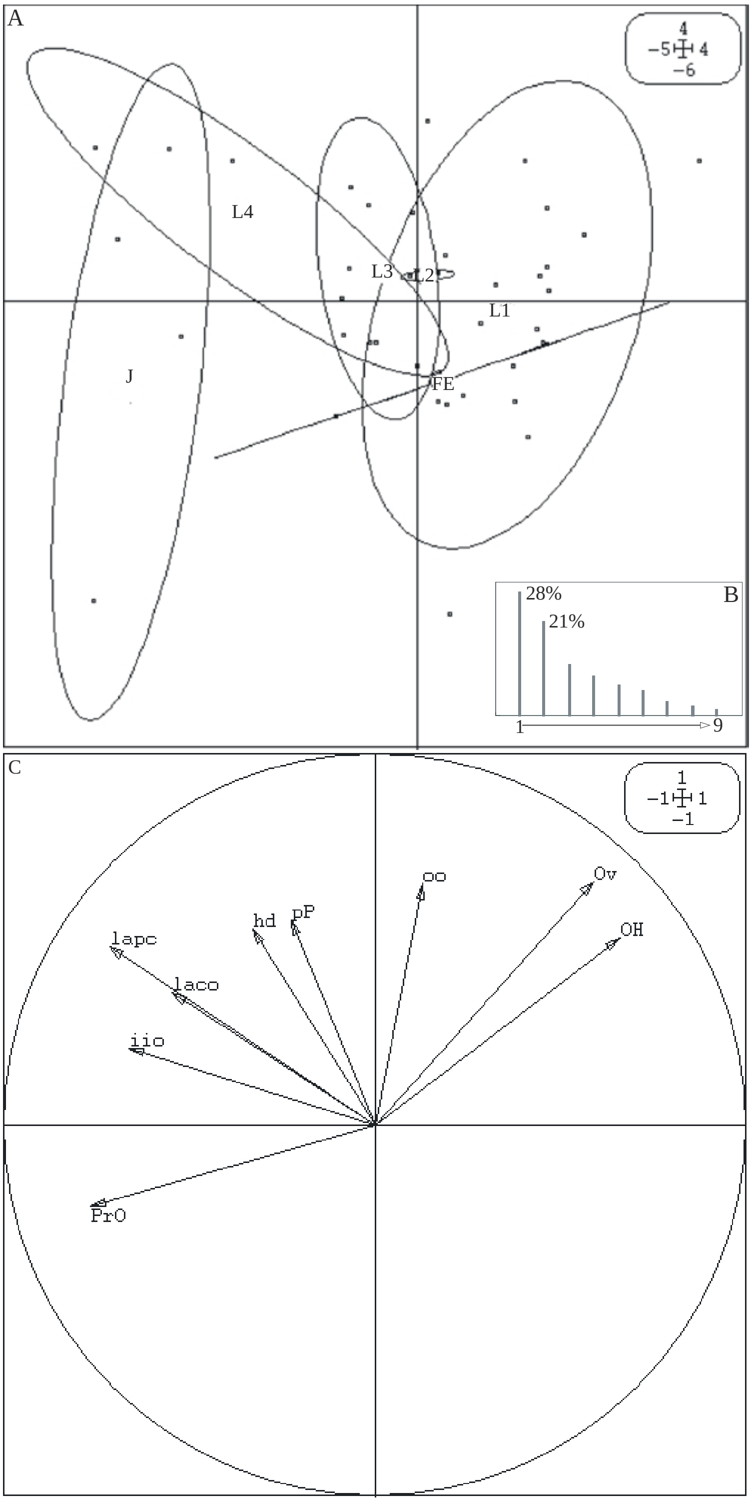

Figure C10.14: Principal components analysis of morphological traits of the developmental steps of topmouth gudgeon *P. parva*, where FE-free embryo, L1 - Larva 1, L2 - Larva 2, L3 - Larva 3, L4 - Larva 4 and J – Juvenile.

Discussion

The transition from free embryo to larva is a time of considerable morphological change in fishes (Kováč, 1995), which is evident in the early ontogeny of the topmouth gudgeon (Figures A3.1, A3.2). The larvae also developed and gained use of many features as they got older which distinguished them, both in size and ability from younger larvae and gave them a distinct advantage. Recent work (Peňáz, 2001) recognised six larval intervals in fish during early life. However, inter-specific variation is recognised, for example the sofie *Chondrostoma toxostoma* (Vallot, 1836) has eight larval intervals (Gozlan *et al.*, 1999) and the sunbleak *Leucaspius delineatus* displays five larval intervals (Pinder and Gozlan, 2004). During the present study on topmouth gudgeon the free embryo interval was followed by four larval intervals.

In larval interval 1 the yolk sac disappeared almost entirely and the larvae developed gills for gaseous exchange. Also mouth and gut were formed, which facilitate exogenous feeding necessary to replace the yolk as a food source. The caudal fin was beginning to form which, when fully functional, increase the larva's mobility and subsequent ability to search for food. At the Larva 2 interval, the buoyancy was enabled by the start of the anterior swimbladder development. The gut became folded in larval interval 3, which would allow the larva to retrieve an increased amount of energy from its food and thus increase its distinct advantage over larvae at earlier life stages. There was clear acceleration in larval development in the topmouth gudgeon during larval interval 3. The final larval interval 4 represents the positioning of the mouth in its final position, the completion of the fins and the start of the formation of scales. This is the preparation interval for development into a juvenile.

The post-hatching development of topmouth gudgeon follows the theory of saltatory ontogeny in relation to the functional physiology and physical characters. However, the external morphology appears to develop rather gradually.

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Appendix D

Table D10.23: Catch per unit of time (number of fish captured per hour) of all fish species observed in Monks Brook, Hampshire during 15 random electrofishing surveys in distance from Stoneham Lake outflow (km).

Distance from fishery (km)	Bull head	Chub	*Lam petra* spp	Minnow	Stickle back	Stone loach	Brown Trout	Roach	Eel	Sun bleak	Floun der	Total CPUE (per hr)
0.08	0.84	0.10	0.02	9.06	0.14	0.53	0.04	0.00	0.03	0.00	0.00	10.78
0.17	0.78	0.00	0.02	7.69	0.07	0.53	0.04	0.04	0.00	0.04	0.00	9.22
0.21	0.15	0.00	0.00	1.15	0.00	0.15	0.00	0.03	0.03	0.00	0.00	1.50
0.39	0.57	0.00	0.00	4.17	0.03	0.63	0.07	0.00	0.13	0.00	0.00	5.60
0.48	0.18	0.00	0.00	2.98	0.27	0.44	0.18	0.00	0.04	0.00	0.00	4.09
0.60	0.24	0.20	0.05	4.33	0.04	0.64	0.07	0.00	0.00	0.02	0.02	5.60
0.72	0.12	0.08	0.02	5.20	0.02	0.68	0.03	0.00	0.00	0.00	0.00	6.15
0.87	0.58	0.18	0.05	5.08	0.00	0.60	0.03	0.00	0.00	0.00	0.00	6.50
0.95	0.64	0.07	0.00	5.69	0.00	0.78	0.04	0.00	0.00	0.00	0.00	7.22
1.17	2.31	0.03	0.00	0.89	0.00	0.00	0.34	0.03	0.09	0.00	0.09	3.77
1.24	6.38	0.07	0.00	0.20	0.00	0.00	0.09	0.00	0.02	0.00	0.07	6.82
1.49	2.77	0.09	0.00	0.66	0.00	0.00	0.20	0.00	0.06	0.00	0.11	3.89
1.71	2.26	0.06	0.00	0.49	0.00	0.00	0.14	0.00	0.00	0.00	0.00	2.94
1.93	3.36	0.00	0.04	0.52	0.00	0.00	0.12	0.00	0.04	0.00	0.00	4.08
2.18	4.97	0.03	0.00	0.70	0.00	0.00	0.20	0.03	0.03	0.00	0.00	5.97

Table D10.24: Catch per unit effort (per hour) of all fish species observed in Tadburn Lake stream, Hampshire during 20 random electrofishing surveys in distance from Crampmoor Fishery (km).

Distance from fishery (km)	Bull head	Chub	*Lam petra* spp	Minnow	Stickle back	Stone loach	Brown Trout	Roach	Eel	Sun bleak	Floun der	Total CPUE (per hr)
0.27	1.39	0.19	0.03	0.00	0.80	0.23	0.03	0.00	0.00	0.16	0.00	2.81
0.35	0.90	0.13	0.00	0.00	0.43	0.16	0.02	0.00	0.00	0.07	0.00	1.71
0.54	3.26	0.07	0.21	0.00	2.18	0.26	0.13	0.00	0.02	0.04	0.00	6.16
0.67	3.32	0.28	0.21	0.00	0.31	0.01	0.16	0.00	0.00	0.09	0.00	4.39
0.76	8.83	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.03	0.00	9.10
0.92	3.77	0.09	0.43	0.00	0.09	0.03	0.09	0.00	0.06	0.06	0.00	4.60
1.01	7.78	0.00	0.18	0.00	0.04	0.22	0.04	0.00	0.02	0.07	0.00	8.36
1.29	5.83	0.00	0.03	0.00	0.35	0.75	0.10	0.00	0.03	0.00	0.00	7.08
1.52	2.55	0.00	0.04	0.00	0.27	0.65	0.29	0.00	0.00	0.00	0.00	3.80
1.71	2.78	0.00	0.17	0.00	0.08	0.65	0.05	0.00	0.00	0.00	0.00	3.72
1.93	5.29	0.00	0.16	0.00	0.04	0.51	0.04	0.00	0.00	0.00	0.00	6.04
2.10	1.37	0.00	0.37	0.00	0.34	0.29	0.09	0.00	0.00	0.00	0.01	2.47
2.22	1.07	0.00	0.16	0.00	0.00	0.19	0.31	0.00	0.00	0.00	0.00	1.72
2.35	0.49	0.05	0.05	0.00	0.00	0.11	0.45	0.00	0.02	0.00	0.00	1.18
2.58	1.08	0.02	0.04	0.00	0.04	0.16	0.04	0.00	0.00	0.00	0.00	1.38
2.77	1.64	0.02	0.02	0.00	0.02	0.11	0.24	0.00	0.00	0.00	0.00	2.07
2.99	0.79	0.01	0.00	0.00	0.03	0.09	0.21	0.00	0.00	0.00	0.00	1.13
3.18	0.49	0.01	0.11	0.00	0.07	0.04	0.19	0.00	0.03	0.00	0.00	0.93
3.48	0.98	0.03	0.02	0.03	0.02	0.22	0.03	0.02	0.02	0.00	0.00	1.35
3.98	1.92	0.00	0.04	0.00	0.00	0.32	0.13	0.00	0.00	0.00	0.01	2.43

Table D10.25: Catch per unit effort (per hour) of all fish species observed in Caundle Brook, Dorset during 9 random electrofishing surveys in distance from Revels Fishery (km). Sunbleak were not observed.

Distance from Fishery (km)	Bull head	Chub	Minnow	Stickle back	Stone loach	Brown trout	Roach	Eel	Gud geon	Total CPUE (per hr)
0.39	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.20
3.38	4.13	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	4.17
3.44	4.21	0.00	0.80	0.00	0.08	0.04	0.00	0.00	0.00	5.13
3.59	5.04	0.00	0.04	0.36	0.00	0.11	0.00	0.00	0.00	5.55
4.46	7.00	0.00	0.03	0.77	0.00	0.14	0.00	0.00	0.00	7.94
8.17	9.18	0.00	0.00	0.48	0.08	0.05	0.00	0.00	0.00	9.78
9.96	6.06	0.00	1.17	0.34	0.06	0.03	0.00	0.00	0.00	7.66
11.46	2.30	0.00	6.30	1.37	0.20	0.00	0.10	0.07	0.03	10.37
13.29	1.05	0.03	5.05	0.80	0.23	0.00	0.13	0.03	0.13	7.43

Appendix E

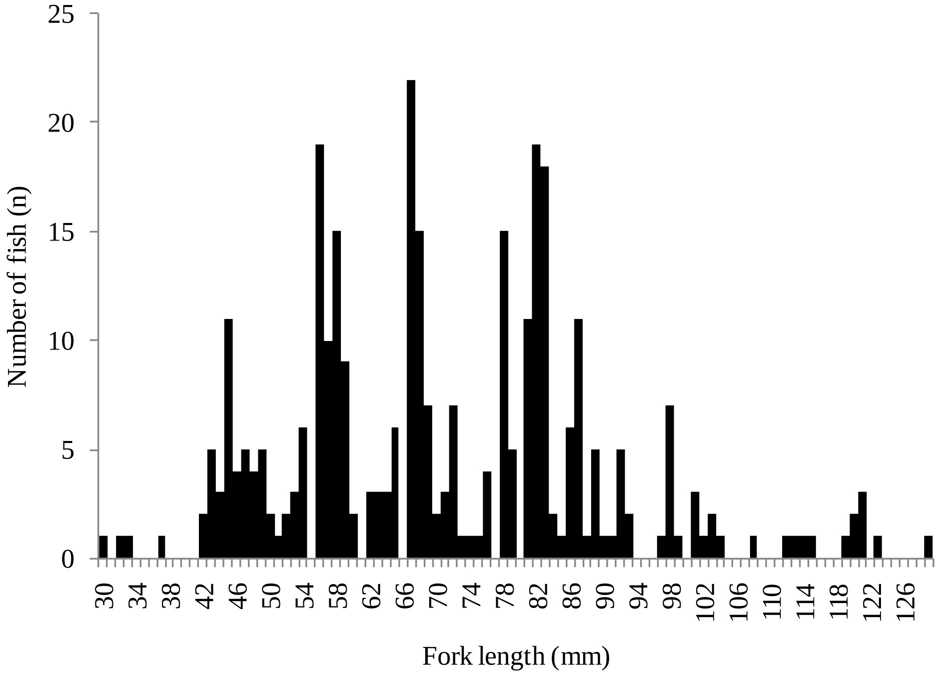


Figure E10.15: Length distribution of bullheads (Cg) captured during point abundance sampling of Tadburn Lake stream between June and September 2004. Based on this, fish were grouped into 5 length classes and subsequently subjected to multivariate analysis of microhabitat use.

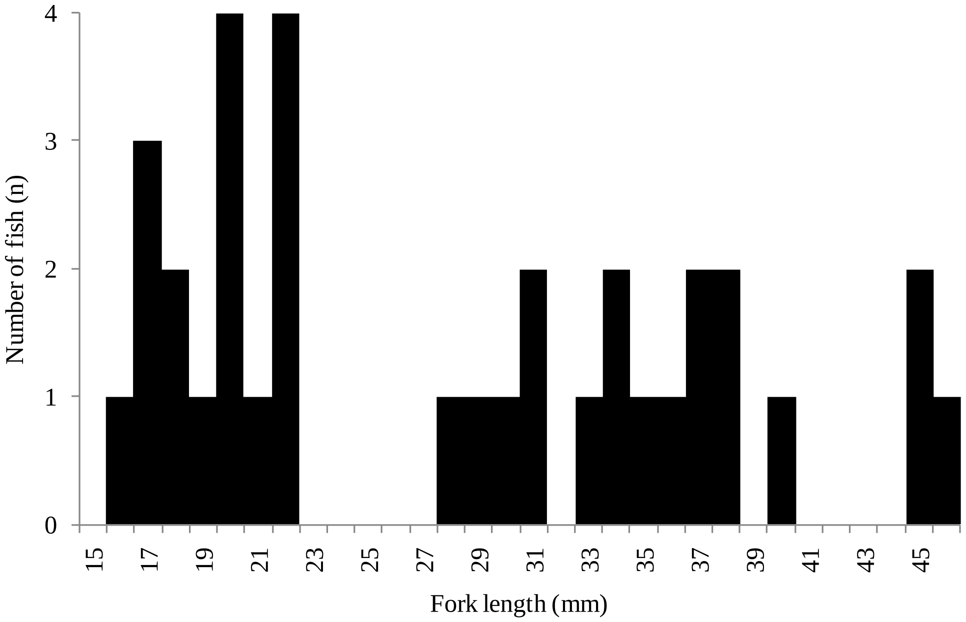


Figure E10.16: Length distribution of three-spined sticklebacks (Ga) captured during point abundance sampling of Tadburn Lake stream between June and September 2004. Based on this, all fish were subjected to multivariate analysis of microhabitat use.

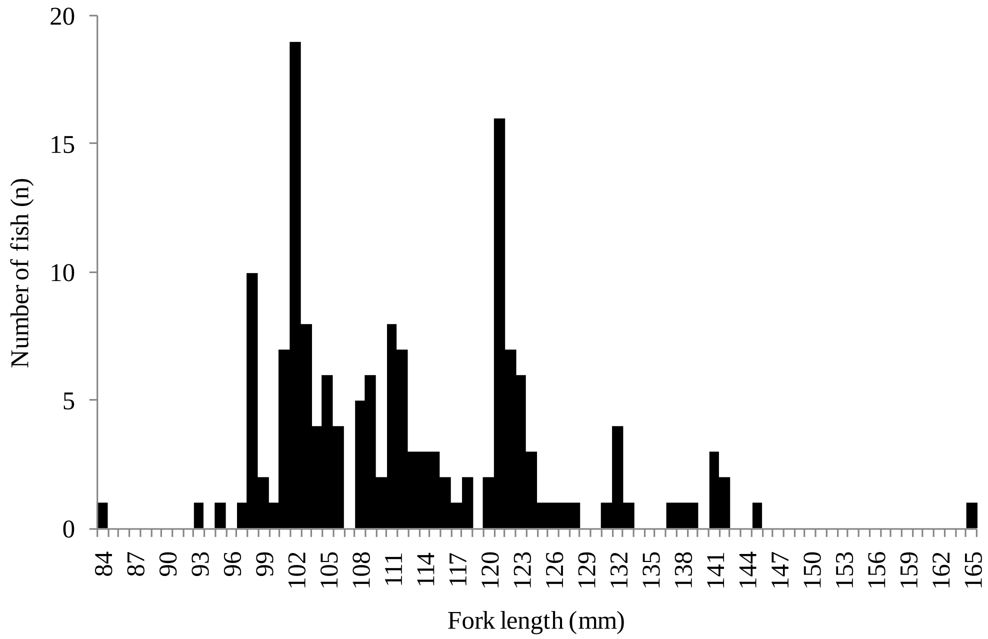


Figure E10.17: Length distribution of chub (Lc) captured during point abundance sampling of Tadburn Lake stream between June and September 2004. Based on this, fish were grouped into 4 length classes and subsequently subjected to multivariate analysis of microhabitat use.

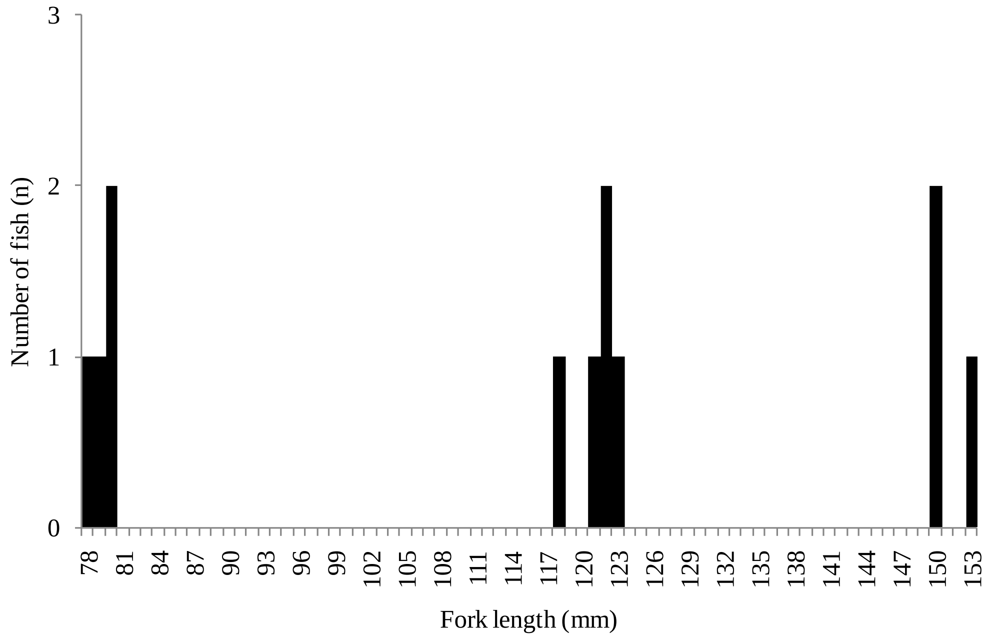


Figure E10.18: Length distribution of *Lampetra* spp (Lp) captured during point abundance sampling of Tadburn Lake stream between June and September 2004. Based on this, fish were grouped into 3 length classes and subsequently subjected to multivariate analysis of microhabitat use.

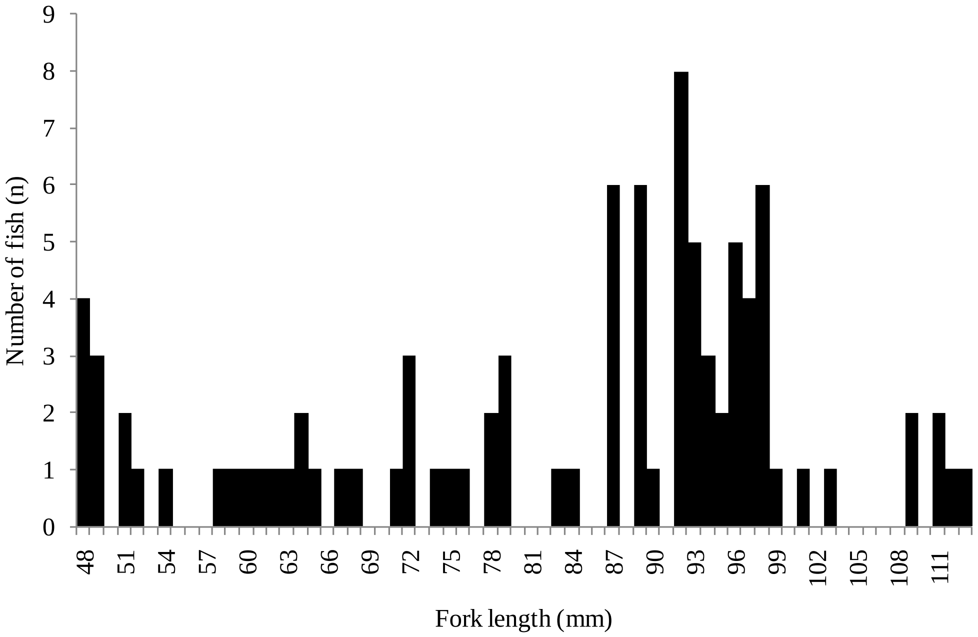


Figure E10.19: Length distribution of stoneloach (Nb) captured during point abundance sampling of Tadburn Lake stream between June and September 2004. Based on this, fish were grouped into 3 length classes and subsequently subjected to multivariate analysis of microhabitat use.

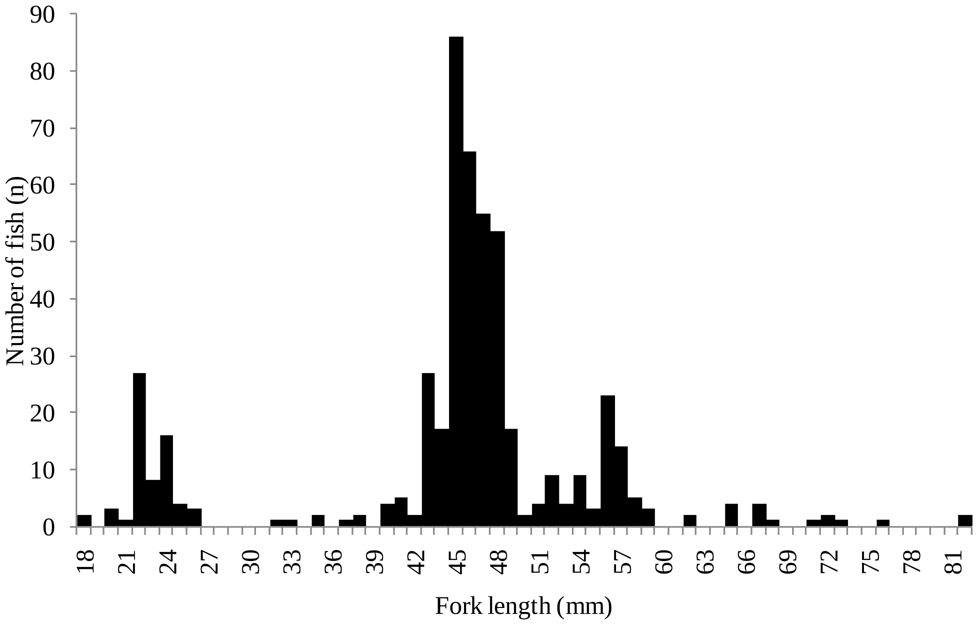


Figure E10.20: Length distribution of topmouth gudgeon (Pv) captured during point abundance sampling of Tadburn Lake stream between June and September 2004. Based on this, fish were grouped into 4 length classes and subsequently subjected to multivariate analysis of microhabitat use.

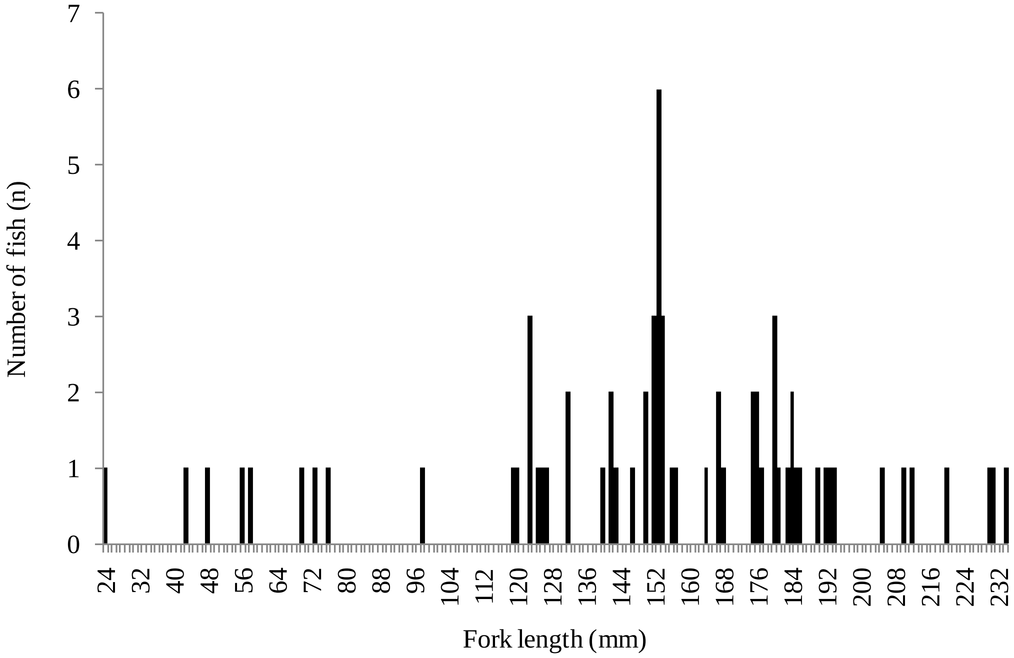


Figure E10.21: Length distribution of brown trout (St) captured during point abundance sampling of Tadburn Lake stream between June and September 2004. Based on this, fish were grouped into 4 length classes and subsequently subjected to multivariate analysis of microhabitat use.

Appendix F

Glossary of terms used in the study of Social Networks

This glossary was partly adapted for social networks of fish; for more details on social network analysis used in Chapter 6B refer to: Watts and Strogatz 1998, Wasserman & Faust, 1994.

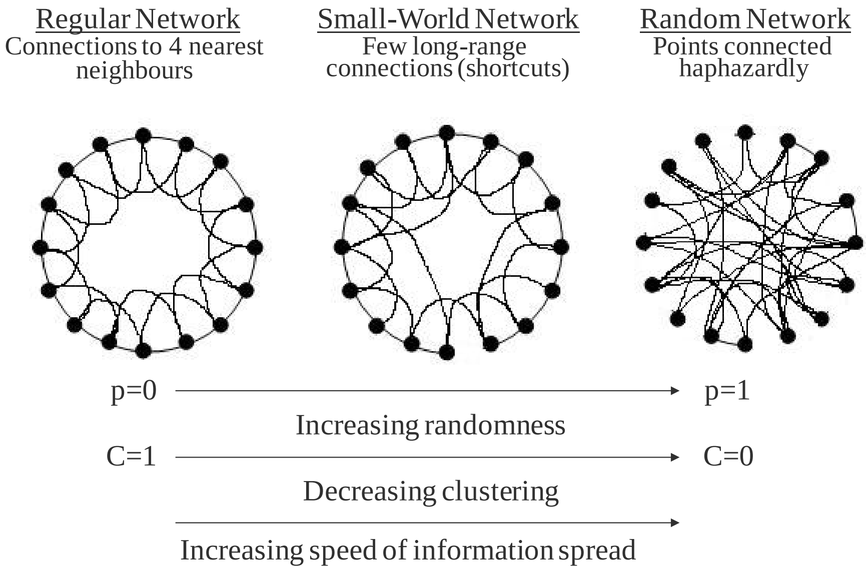
Actor	Individual animal (fish) within a network. In the case of social networks at Stoneham Lakes, each individual per fish species at a particular developmental stage was treated as the same ‘actor’. See also ‘node’.
Clique	Groups are identified as ‘cliques’ if every actor is directly socially tied to every other actor.
Cliquishness	Term used when in a network the numbers of cliques are examined. A higher clustering coefficient indicates a greater 'cliquishness'. See also ‘Clique’ and ‘Clustering coefficient’.
Clustering	Likelihood that two associates of a node are associates themselves. See also ‘Clique’, ‘Cliquishness’ and ‘Clustering coefficient’.
Clustering coefficient C	A measure of the cliquishness of the network, calculated as the mean value of all potential social connections that occur in the local neighbourhood. C describes an average local property of the network, and measures the likelihood that two associates of a node are associates themselves. A higher clustering coefficient indicates a greater 'cliquishness'. See also ‘Clique’, ‘Cliquishness’ and ‘Clustering coefficient’.
Complete network	A complete network is a simple network in which every pair of distinct nodes is connected by an edge.
Connectivity	Connectivity of a node υ is the number of its social ties. See also ‘social tie’.
Degree k_υ	Is equivalent to the number of social ties that an actor has with other actors in the network. k is calculated as the mean number of social ties per actor in the network. The degree k_i of an actor is the number of actors, $\|N_i\|$, in its neighbourhood N_i.
Edge	The social relationships between the ‘actors’. See also ‘social tie’
Ego	Actor on which the calculation of the respective ego-network is based. See also ‘ego-network’.

Ego-network	Based on the selection of one actor (in this case the ‘ego’) within the network and includes all other actors to whom the ‘ego’-actor has (or could have) ties. The ego-network approach examines the whole fish population by means of census, rather than by sample. See also ‘ego’.
Ego-network size	The number of all actors to whom the ‘ego’-actor has social ties
Geodesic distance	The distance between two actors in a network is the number of edges in a shortest path length connecting them. This is also known as the geodesic distance. See also ‘path length’.
Global neighbourhood	Direct and indirect connections between actors in a network.
Global network properties	Characteristics of direct and indirect connections (‘social ties’) between actors in a network. Also see ‘global neighbourhood’.
Grouping	Level of ‘clustering’. See also ‘cliquishness’.
Local neighbourhood	Direct neighbourhood of each actor in the network. For a set A of actors, the local neighbourhood of A is the union of the social ties of the actors, and so it is the set of all actors socially tied to at least one actor of A.
Local network properties	Characteristics of direct connections (‘social ties’) between actors in a network. Also see ‘local neighbourhood’.
Node υ	Individual animals (fish) within a network. See also ‘actor’.
Path length L	Distance between pairs of actors in the network. Mean path-length is the mean of these distances between all pairs of actors. L describes a global property of the network. It can be used to predict how quickly information and disease may spread in an animal population (e.g. in a population of size N, disease can be expected to spread more quickly for lower values of L). See also ‘geodesic distance’.
Random network	See ‘Small world network’.
Regular network	See ‘Small world network’.

Small world model

See ‘Small world network’.

Small world network (adapted from Watts & Strogatz, 1998)



There are a variety of networks that can range from regular to random networks. In the above diagrams, the dots are the actors (nodes), for example fish or people, and the lines are the social ties between them. The networks above all consist of 16 actors. When looking at the ‘Regular Network’ diagram, imagine for example this is a group of 16 people. Each of those persons only knows 4 other persons in the group. This results in the regular network consisting of many small groups. This is also called ‘clustering’. Each person in the network is the same because they know the same amount of people. However, for information to reach every person in the network it takes quite a long time, because the distance between two people is quite long because not everyone knows each other. If these 16 persons would be connected randomly as in the ‘Random Network’ diagram then they would form a random network. In the random network, because everyone knows everyone, there is almost no clustering because there are no small groups. In this type of network, information can spread fast. Small-world networks are characterized by containing complementary elements from regular networks and random networks. By inserting very few shortcuts into a regular network it is possible to obtain a small-world network with for example small groups and short distances. Having both short local and global distances in a network affect possibilities for efficient diffusion and spreading of data, information & epidemics in such networks.

Small world phenomenon	Is the hypothesis that the chain of social acquaintances required to connect one arbitrary i to another arbitrary person anywhere in the world is generally short.
Social tie	The social relationships between the ‘actors’. See also ‘edge’.
Standard network measures	Includes path length (L), clustering coefficient, (C) and mean degree (k). The values of L, C and k can be used to describe the structural properties of the network.

Appendix G

Diet of chub and brown trout at Tadburn Lake stream

Table G10.26: Dietary items of 79 brown trout captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

					Trout				
				Sample No	1	2	3	4	5
				Length group	2	3	1	2	2
				Fork Length (mm)	205	290	119	247	205
				Weight of fish (g)	96.4	>200	14.6	167.5	95.7
Plant material				Macrophytes	1	0	1	1	1
				Thistle seed	0	0	0	0	0
				Debris and detritus	1	1	1	1	1
				Total Plant Material	2	1	2	2	2
Fish				*P. parva*	1	1	0	0	0
				Indet. fish eggs	0	0	0	0	0
Aquatic Insects	Diptera	Chironomidae	Tanypodae	larvae	0	0	0	0	0
				adult	0	0	0	0	0
			Orthocladinae	larvae	0	0	0	0	0
				adult	0	0	0	0	0
			Simuliidae	*Simulium vernum* gp	0	0	0	0	0
				Simulium ornatum larva	0	0	0	0	0
				Simulium spp	0	0	0	0	0
			Indet. Chironomidae	pupae	0	0	1	0	0
				larvae	0	0	0	0	0
				adult	0	0	0	0	0
				other	0	0	1	0	0
		Tipulidae	Dicranota	larvae	0	0	0	0	0
				adult	0	0	0	0	0
	Coleoptera	Gyrinidae		larvae	0	0	0	0	0
				adult	0	0	0	0	0
	Trichoptera	Limnephilidae	Limnephiloida	larvae	0	0	0	0	0
				larvae with case	0	1	0	0	0
				adult	0	0	0	0	0
		Leptoceridae	Athripsodes	larva	0	0	0	0	0
				larvae with case	1	1	0	0	1
			Indet. Trichoptera	larvae	0	0	0	0	0
	Hemiptera	Gerroidea	Mesovelidae		0	0	0	0	0
	Ephemeroptera	Leptophlebidae	Paraleptophlebia	larvae	0	0	0	0	0
				adult	0	0	0	0	0
		Baetidae		larvae	0	0	0	0	0
				adult	0	0	0	0	0
		Ephemeridae	Ephemera spp	larva	0	0	0	0	0
			Ephemera spp	adult	0	0	0	0	0
			other		0	0	0	0	0
	Apterygota		Collembola		0	0	0	0	0
	Neuroptera	Sisyridae		larva	0	0	0	0	0
				adult	0	0	0	0	0
	Exopterygota	Hemiptera	Corixidae		0	0	0	0	0
				Indet. Aquatic Insects	0	0	0	0	0
Aquatic Crustaceans		Copepoda	Cyclopoidae		0	0	0	0	0
		Decapoda	Astacidae	juvenile	0	0	0	0	0
				adult	0	0	0	0	0
		Amphipoda	Gammaridae	*Gammarus pulex*	1	0	0	0	0
Aerial Insects		Diptera	Nematocera		0	0	0	0	0
			Tipulidae		0	0	0	1	0
		Indet. Aerial Diptera		Diptera (fly)	0	0	1	0	0
				Diptera Wing (fly)	0	0	0	0	0
		Coleoptera		Beetle	1	0	0	0	0
			Curculionoidea	Weevil	0	0	0	0	0
		Hemiptera	Heteroptera		0	0	0	0	0
		Indet. Aerial Insects		insect head capsule	0	2	0	0	0
				insect cuticle fragment	0	0	0	0	0
				other	0	2	0	0	0
			Total Aerial insects		1	2	0	1	0
Terrestrial Insects		Crustacea	Isopoda	*Asellus* spp	0	0	0	0	0
		Dermaptera		Earwig	0	0	0	0	2
		Arthropoda	Diplopoda	Millipede	0	0	0	0	0
			Araneida		0	0	0	0	0
			Nematoda		0	0	0	0	0
			Trematoda		0	0	0	0	0
Mud, sand etc.			Mud, sand etc.		0	0	0	0	0

Table G10.26 cont'd: Dietary items of 79 brown trout captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Trout									
	Sample No	6	7	8	9	10	11	12	13	14	15
	Length group	3	2	1	2	1	1	2	4	4	2
	Fork Length (mm)	310	203	135	209	157	117	217	293	275	223
	Weight of fish (g)	>200	96.5	31.2	106.2	30.7	18.4	134.5	>200	>200	147.7
Plant material	Macrophytes	0	0	0	0	0	1	0	0	0	0
	Thistle seed	0	0	0	0	0	0	0	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1	1	1
	Total Plant Material	1	1	1	1	1	2	1	1	1	1
Fish	*P. parva*	3	1	1	3	1	0	0	1	1	0
	Indet. fish eggs	14	0	0	0	0	0	0	0	0	0
Tanypodae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	0	0	0	0
	Simulium ornatum larva	0	0	0	0	0	0	0	0	0	0
	Simulium spp	0	0	0	0	0	0	0	0	0	0
Indet. Chironomidae	pupae	0	0	0	0	0	1	0	0	12	0
	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
	other	0	0	0	0	0	1	0	0	12	0
Dicranota	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	0	0	0	0	0	0	2	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Athripsodes	larva	0	0	0	0	0	0	0	0	0	0
	larvae with case	1	3	1	1	1	0	1	0	1	0
Indet. Trichoptera	larvae	0	0	0	0	0	0	0	0	0	0
Mesovelidae		0	0	0	0	0	0	0	0	0	0
Paraleptophlebia	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Baetidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Ephemera spp	larva	0	0	0	0	0	0	0	0	0	0
Ephemera spp	adult	0	0	0	0	0	0	0	0	0	0
other		1	0	0	0	0	0	0	0	0	1
Collembola		0	0	0	0	0	0	0	0	0	0
Sisyridae	larva	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Hemiptera	Corixidae	0	0	0	1	0	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0	0	0	0	0	0
Cyclopoidae		0	0	0	0	0	0	0	0	0	0
Astacidae	juvenile	0	0	0	0	0	0	1	1	0	0
	adult	0	0	0	1	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	0	0	1	1	2	0	0	0	2	0
Nematocera		0	0	0	6	0	0	0	0	0	15
Tipulidae		0	0	0	0	0	1	0	0	0	1
Indet. Aerial Diptera	Diptera (fly)	0	0	0	0	0	0	0	0	0	0
	Diptera Wing (fly)	0	0	0	0	0	1	0	0	0	0
	Beetle	0	0	0	0	1	0	0	0	1	0
Curculionoidea	Weevil	0	1	0	0	0	0	0	0	0	0
Heteroptera		1	0	0	0	0	0	0	0	0	0
Indet. Aerial Insects	insect head capsule	0	0	0	0	0	0	0	0	0	0
	insect cuticle fragment	0	0	0	0	0	0	0	0	0	0
	other	0	0	0	0	0	0	0	0	0	0
Total Aerial Insects		1	1	0	6	1	1	0	0	1	16
Isopoda	*Asellus* spp	0	0	1	1	0	0	0	0	1	0
Dermaptera	Earwig	0	0	0	0	0	0	0	0	0	0
Diplopoda	Millipede	0	0	0	0	0	0	0	0	0	1
Araneida		0	0	0	0	0	0	0	0	0	0
Nematoda		0	0	0	1	0	0	0	0	0	0
Trematoda		0	0	0	0	0	0	0	0	0	0
Mud, sand etc.		0	0	0	0	0	0	0	0	1	0

Table G10.26 cont'd: Dietary items of 79 brown trout captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Trout									
	Sample No	16	17	18	19	20	21	22	23	24	25
	Length group	4	2	4	2	4	2	3	2	2	1
	Fork Length (mm)	257	237	254	208	251	162	246	187	184	157
	Weight of fish (g)	>200	165.5	>200	130.7	>200	52	189.1	86.6	83.2	48.2
Plant material	Macrophytes	0	0	0	0	0	0	0	0	0	0
	Thistle seed	0	0	0	0	0	0	0	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1	1	1
	Total Plant Material	1	1	1	1	1	1	1	1	1	1
Fish	*P. parva*	0	0	0	1	0	0	1	1	0	0
	Indet. fish eggs	0	0	0	0	0	0	0	0	0	0
Tanypodae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	0	0	0	0
	Simulium ornatum larva	0	0	0	0	0	0	0	0	0	0
	Simulium spp	0	0	0	0	0	0	0	0	0	0
Indet. Chironomidae	pupae	0	0	0	1	0	0	0	0	0	1
	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
	other	0	0	0	1	0	0	0	0	0	1
Dicranota	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	2	0	0	1	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Athripsodes	larva	0	1	0	1	0	0	0	0	0	0
	larvae with case	0	1	1	1	1	0	0	2	3	0
Indet. Trichoptera	larvae	0	0	0	0	0	0	0	0	0	0
Mesovelidae		0	0	0	0	0	0	0	0	0	0
Paraleptophlebia	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Baetidae	larvae	0	0	0	0	0	2	0	1	7	0
	adult	0	0	0	0	0	0	0	0	0	0
Ephemera spp	larva	0	0	0	0	0	0	0	0	0	0
Ephemera spp	adult	0	0	0	0	0	0	0	0	0	0
other		0	0	0	0	0	0	0	0	0	0
Collembola		0	0	0	0	0	0	0	0	0	0
Sisyridae	larva	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Hemiptera	Corixidae	0	0	0	0	0	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0	0	0	0	0	0
Cyclopoidae		0	0	0	0	0	0	0	0	0	0
Astacidae	juvenile	0	0	0	0	0	0	1	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	0	0	0	1	0	5	0	2	3	1
Nematocera		12	40	27	2	21	31	0	15	57	0
Tipulidae		0	1	0	0	0	0	0	0	0	0
Indet. Aerial Diptera	Diptera (fly)	0	0	0	0	0	0	0	0	0	0
	Diptera Wing (fly)	1	0	0	0	0	0	0	0	0	0
	Beetle	0	4	0	0	0	1	0	0	0	0
Curculionoidea	Weevil	0	0	0	0	0	0	0	0	0	0
Heteroptera		0	0	1	0	0	0	0	0	1	0
Indet. Aerial Insects	insect head capsule	1	0	0	0	1	0	0	0	0	0
	insect cuticle fragment	0	0	0	0	0	0	0	0	0	0
	other	1	0	0	0	1	0	0	0	0	0
Total Aerial Insects		13	45	28	2	22	32	0	15	58	0
Isopoda	*Asellus* spp	0	0	0	0	1	0	0	0	1	0
Dermaptera	Earwig	0	0	0	0	0	0	0	0	0	0
Diplopoda	Millipede	0	0	0	0	0	0	0	0	0	0
Araneida		1	1	0	0	1	0	0	0	0	0
Nematoda		0	1	0	0	0	0	0	0	0	0
Trematoda		0	0	0	0	0	0	0	0	0	0
Mud, sand etc.		0	0	0	0	0	0	0	0	0	0

Table G10.26 cont’d: Dietary items of 79 brown trout captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Trout									
	Sample No	26	27	28	29	30	31	32	33	34	35
	Length group	1	1	1	1	1	1	1	1	1	1
	Fork Length (mm)	152	171	133	139	130	123	138	173	123	126
	Weight of fish (g)	36	66.3	56.6	30.5	27.2	27.6	30.7	61.4	23.7	26.7
Plant material	Macrophytes	0	0	0	0	0	0	0	0	0	0
	Thistle seed	0	0	0	0	0	0	0	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1	1	1
	Total Plant Material	1	1	1	1	1	1	1	1	1	1
Fish	*P. parva*	0	1	0	0	0	0	0	0	1	1
	Indet. fish eggs	0	0	0	0	0	0	0	0	0	0
Tanypodae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	0	0	0	0
	Simulium ornatum larva	0	0	0	0	0	0	0	0	0	0
	Simulium spp	0	0	0	0	0	0	0	0	0	0
Indet. Chironomidae	pupae	0	0	0	1	0	0	0	0	0	0
	larvae	0	1	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
	other	0	1	0	1	0	0	0	0	0	0
Dicranota	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0	0	1	0	0	0
	larvae with case	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Athripsodes	larva	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	0	1	1	1	0	0	1	0	0
Indet. Trichoptera	larvae	0	0	0	0	0	0	0	0	0	0
Mesovelidae		0	0	0	0	0	0	0	0	0	0
Paraleptophlebia	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Baetidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Ephemera spp	larva	0	0	0	0	0	0	0	0	0	0
Ephemera spp	adult	0	0	0	0	0	0	0	0	0	0
other		0	0	0	0	0	0	0	0	0	0
Collembola		0	0	0	0	0	0	0	0	0	0
Sisyridae	larva	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Hemiptera	Corixidae	0	0	0	0	0	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0	0	0	0	0	0
Cyclopoidae		0	0	1	0	0	0	0	1	0	0
Astacidae	juvenile	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	2	1	0	0	0	0	0	1	1	2
Nematocera		0	0	8	2	1	0	3	2	2	4
Tipulidae		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Diptera	Diptera (fly)	0	0	0	0	0	0	0	0	0	0
	Diptera Wing (fly)	0	0	0	0	2	0	3	0	2	1
	Beetle	0	0	0	0	0	0	0	0	0	0
Curculionoidea	Weevil	0	0	0	0	0	0	0	0	0	0
Heteroptera		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Insects	insect head capsule	0	0	0	0	0	0	1	0	0	0
	insect cuticle fragment	0	0	0	0	0	0	1	0	0	0
	other	0	0	0	0	0	0	2	0	0	0
Total Aerial Insects		0	0	8	2	1	0	5	2	2	4
Isopoda	*Asellus* spp	0	0	0	0	0	0	0	0	0	0
Dermaptera	Earwig	0	0	0	0	0	0	0	0	0	0
Diplopoda	Millipede	0	0	0	0	0	0	0	0	0	0
Araneida		0	0	0	0	0	0	0	0	0	0
Nematoda		0	0	0	0	0	0	0	0	0	0
Trematoda		0	0	0	0	0	0	0	0	0	0
Mud, sand etc.		0	0	0	0	0	0	0	0	3	0

Table G10.26 cont'd: Dietary items of 79 brown trout captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Trout									
	Sample No	36	37	38	39	40	41	42	43	44	45
	Length group	1	3	3	3	3	3	3	3	2	3
	Fork Length (mm)	119	223	293	312	251	245	237	241	138	215
	Weight of fish (g)	21.2	150.4	>200	>200	194.2	>200	156.7	169.6	34.9	135.2
Plant material	Macrophytes	0	0	0	0	0	0	0	1	0	0
	Thistle seed	0	0	0	0	0	0	1	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1	1	1
	Total Plant Material	1	1	1	1	1	1	2	2	1	1
Fish	*P. parva*	0	0	0	0	0	0	1	0	2	0
	Indet. fish eggs	0	0	0	0	0	0	0	0	0	0
Tanypodae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	0	0	0	0
	Simulium ornatum larva	0	0	0	0	0	0	0	0	0	0
	Simulium spp	0	0	0	0	0	0	0	0	0	0
Indet. Chironomidae	pupae	0	0	0	0	0	0	0	0	0	1
	larvae	1	0	0	0	1	0	0	1	0	0
	adult	0	0	0	0	0	0	0	0	0	0
	other	1	0	0	0	1	0	0	1	0	1
Dicranota	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Athripsodes	larva	0	0	2	0	0	0	0	0	0	0
	larvae with case	0	1	0	1	0	0	0	0	0	0
Indet. Trichoptera	larvae	0	0	0	0	0	0	0	0	0	0
Mesovelidae		0	0	0	0	0	0	0	0	0	0
Paraleptophlebia	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Baetidae	larvae	1	0	0	0	2	0	0	0	0	0
	adult	0	0	0	0	1	0	0	0	0	0
Ephemera spp	larva	0	0	0	0	0	0	0	0	0	0
Ephemera spp	adult	0	0	0	1	0	0	0	0	0	0
other		0	0	0	0	0	0	0	0	0	0
Collembola		0	0	0	0	0	0	0	0	0	0
Sisyridae	larva	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Hemiptera	Corixidae	0	0	0	0	0	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0	0	0	0	0	0
Cyclopoidae		0	0	0	1	0	0	0	0	0	0
Astacidae	juvenile	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	1	0	0	1	7	0	0	0	0	0
Nematocera		0	1	3	0	51	5	5	0	9	0
Tipulidae		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Diptera	Diptera (fly)	0	0	0	0	0	3	0	0	0	0
	Diptera Wing (fly)	0	0	0	0	0	1	0	0	0	20
	Beetle	1	0	1	0	0	0	2	0	0	0
Curculionoidea	Weevil	0	0	0	0	0	0	2	0	0	0
Heteroptera		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Insects	insect head capsule	1	0	0	0	0	0	0	0	0	0
	insect cuticle fragment	0	0	0	0	0	0	0	3	1	20
	other	1	0	0	0	0	0	0	3	1	20
Total Aerial Insects		2	1	4	0	51	5	9	3	10	20
Isopoda	*Asellus* spp	3	0	0	0	1	0	0	0	0	0
Dermaptera	Earwig	0	0	0	0	0	0	0	0	0	0
Diplopoda	Millipede	0	0	0	0	0	0	0	0	1	0
Araneida		0	0	0	0	0	0	0	0	0	0
Nematoda		0	1	0	0	0	0	0	0	0	0
Trematoda		0	0	0	0	0	0	0	0	1	0
Mud, sand etc.		0	0	1	0	0	0	0	0	0	0

Table G10.26 cont'd: Dietary items of 79 brown trout captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Trout									
	Sample No	46	47	48	49	50	51	52	53	54	55
	Length group	3	2	1	4	3	4	3	4	4	3
	Fork Length (mm)	201	157	108	253	238	310	233	256	255	190
	Weight of fish (g)	99.5	49.1	11.5	>200	174.7	>200	149.1	>200	>200	78.2
Plant material	Macrophytes	0	0	0	0	0	1	0	1	0	1
	Thistle seed	0	0	0	0	0	0	0	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1	1	1
	Total Plant Material	1	1	1	1	1	2	1	2	1	2
Fish	*P. parva*	0	0	0	0	0	0	0	0	0	1
	Indet. fish eggs	0	0	0	0	0	0	0	0	0	0
Tanypodae	larvae	0	0	0	0	0	0	0	0	1	0
	adult	0	0	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	0	0	0	0
	Simulium ornatum larva	0	0	0	0	0	0	0	0	0	0
	Simulium spp	0	0	0	0	0	0	0	0	0	0
Indet. Chironomidae	pupae	0	2	0	0	0	0	0	0	1	0
	larvae	0	0	0	0	0	1	1	1	0	0
	adult	0	0	0	1	0	0	0	0	0	0
	other	0	2	0	1	0	1	1	1	1	0
Dicranota	larvae	0	0	0	0	0	0	0	1	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	1	1	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0	0	0	0	0	2
	larvae with case	0	0	0	0	0	0	0	4	1	0
	adult	0	0	0	0	0	0	0	0	0	0
Athripsodes	larva	0	1	0	0	0	0	0	0	11	2
	larvae with case	0	1	0	0	0	0	0	0	0	0
Indet. Trichoptera	larvae	0	0	0	0	0	0	0	0	0	0
Mesovelidae		0	0	0	0	0	0	1	1	1	0
Paraleptophlebia	larvae	0	0	0	0	0	0	0	0	10	0
	adult	0	0	0	0	0	0	0	0	0	0
Baetidae	larvae	0	0	0	14	0	1	0	1	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Ephemera spp	larva	0	0	0	0	0	0	0	0	0	0
Ephemera spp	adult	0	0	0	0	0	0	0	0	0	0
other		0	0	0	0	0	0	0	0	0	0
Collembola		0	0	0	0	0	0	0	0	0	0
Sisyridae	larva	0	0	0	0	0	0	1	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Hemiptera	Corixidae	0	0	0	0	0	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0	0	0	0	0	0
Cyclopoidae		0	0	0	0	1	0	0	0	0	0
Astacidae	juvenile	0	0	0	0	0	0	0	0	1	0
	adult	0	0	0	0	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	1	0	0	22	0	0	0	2	22	1
Nematocera		2	1	0	42	0	5	2	2	24	1
Tipulidae		0	0	0	0	0	2	1	0	0	0
Indet. Aerial Diptera	Diptera (fly)	0	0	0	0	0	0	0	0	0	0
	Diptera Wing (fly)	0	0	0	0	1	0	0	0	0	0
	Beetle	0	0	0	4	0	0	0	0	4	0
Curculionoidea	Weevil	0	0	0	0	0	0	0	0	0	0
Heteroptera		0	1	0	0	0	0	0	0	0	0
Indet. Aerial Insects	insect head capsule	0	1	0	0	0	0	0	0	0	0
	insect cuticle fragment	0	1	0	0	0	0	0	0	0	0
	other	0	2	0	0	0	0	0	0	0	0
Total Aerial Insects		2	4	0	46	0	7	3	2	28	1
Isopoda	*Asellus* spp	0	0	0	2	0	0	0	0	0	0
Dermaptera	Earwig	0	0	0	0	0	1	0	0	1	0
Diplopoda	Millipede	0	0	0	0	0	0	0	0	0	0
Araneida		0	0	0	0	1	0	0	1	0	0
Nematoda		0	0	0	0	1	0	0	0	0	0
Trematoda		0	0	1	0	0	0	0	0	0	0
Mud, sand etc.		0	0	0	0	0	0	0	0	0	1

Table G10.26 cont'd: Dietary items of 79 brown trout captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

						Trout					
	Sample No	56	57	58	59	60	61	62	63	64	65
	Length group	2	2	1	1	1	3	3	4	4	1
	Fork Length (mm)	139	165	129	123	134	249	221	289	272	135
	Weight of fish (g)	35	56.4	27.9	21.5	28.4	181.3	140.4	>200	>200	30.9
Plant material	Macrophytes	0	0	0	0	0	0	1	1	2	0
	Thistle seed	0	0	0	0	0	0	0	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1	1	1
	Total Plant Material	1	1	1	1	1	1	2	2	3	1
Fish	*P. parva*	0	0	0	0	0	0	1	2	0	0
	Indet. fish eggs	0	0	0	0	0	0	0	0	0	0
Tanypodae	larvae	0	0	1	0	0	1	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	0	2	0	0	1	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	1	0	1	0
	Simulium ornatum larva	2	0	0	0	0	0	0	0	0	0
	Simulium spp	2	0	0	0	0	0	1	0	1	0
Indet. Chironomidae	pupae	0	0	0	1	0	0	0	0	0	0
	larvae	1	0	0	0	0	0	0	0	0	0
	adult	1	0	1	0	0	0	0	0	1	0
	other	2	0	1	1	0	0	0	0	1	0
Dicranota	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	1	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Limnephiloida	larvae	1	0	1	0	0	0	0	0	0	0
	larvae with case	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Athripsodes	larva	1	0	1	0	0	0	0	0	0	0
	larvae with case	0	0	0	1	1	0	0	0	0	0
Indet. Trichoptera	larvae	0	0	0	0	0	0	0	0	0	0
Mesovelidae		0	0	0	0	0	0	0	0	0	0
Paraleptophlebia	larvae	6	0	0	0	0	0	0	0	1	0
	adult	0	0	0	0	0	0	0	0	0	0
Baetidae	larvae	7	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	1	0	0	0	0	0
Ephemera spp	larva	0	0	0	0	0	0	0	0	0	0
Ephemera spp	adult	0	0	0	0	0	1	0	0	0	0
other		0	0	0	0	0	0	0	0	0	0
Collembola		0	0	0	0	0	0	0	0	0	0
Sisyridae	larva	0	0	1	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Hemiptera	Corixidae	0	0	0	0	1	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0	0	0	0	0	0
Cyclopoidae		0	0	0	0	0	0	0	1	0	0
Astacidae	juvenile	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	7	1	0	1	12	1	1	0	0	0
Nematocera		6	2	4	0	2	0	0	0	0	0
Tipulidae		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Diptera	Diptera (fly)	0	0	0	0	0	1	0	0	4	0
	Diptera Wing (fly)	0	3	0	3	2	0	0	0	0	1
	Beetle	0	0	1	1	0	0	0	0	1	0
Curculionoidea	Weevil	0	0	2	0	0	0	0	0	0	0
Heteroptera		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Insects	insect head capsule	0	0	0	0	0	0	0	0	0	1
	insect cuticle fragment	0	0	0	0	0	0	0	0	0	0
	other	0	0	0	0	0	0	0	0	0	1
Total Aerial Insects		6	2	7	1	2	0	0	0	1	1
Isopoda	*Asellus* spp	2	0	1	0	0	0	0	0	0	0
Dermaptera	Earwig	0	0	0	0	0	0	0	0	0	0
Diplopoda	Millipede	0	0	1	0	0	0	0	0	0	0
Araneida		1	0	0	0	0	0	0	0	0	0
Nematoda		0	0	0	0	0	0	0	0	0	0
Trematoda		0	0	0	0	0	3	0	0	0	0
Mud, sand etc.		0	0	0	0	0	0	0	0	0	1

Table G10.26 cont'd: Dietary items of 79 brown trout captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Trout									
	Sample No	66	67	68	69	70	71	72	73	74	75
	Length group	1	2	1	1	3	4	4	3	3	3
	Fork Length (mm)	124	162	121	119	243	272	290	246	235	216
	Weight of fish (g)	22.7	59.9	26.5	19.0	168.1	>200	>200	187	159.8	133.3
Plant material	Macrophytes	0	0	3	0	0	0	0	0	0	1
	Thistle seed	0	0	1	0	0	0	0	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1	1	1
	Total Plant Material	1	1	5	1	1	1	1	1	1	2
Fish	*P. parva*	1	1	0	0	1	0	0	1	1	1
	Indet. fish eggs	0	0	0	0	0	0	0	0	0	0
Tanypodae	larvae	1	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	1	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	0	0	0	0
	Simulium ornatum larva	0	0	0	0	0	0	0	0	0	0
	Simulium spp	0	0	0	0	0	0	0	0	0	0
Indet. Chironomidae	pupae	0	0	0	0	0	0	0	0	0	0
	larvae	0	0	0	1	0	0	0	0	0	0
	adult	4	0	0	0	0	0	0	0	0	0
	other	4	0	0	1	0	0	0	0	0	0
Dicranota	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Athripsodes	larva	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	0	0	1	0	0	0	0	0	0
Indet. Trichoptera	larvae	0	1	0	0	0	0	0	0	0	0
Mesovelidae		0	0	0	0	0	0	0	0	0	0
Paraleptophlebia	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Baetidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Ephemera spp	larva	0	0	0	0	0	0	0	0	0	0
Ephemera spp	adult	0	0	0	0	0	0	0	0	0	0
other		0	0	0	0	0	0	0	0	0	0
Collembola		1	0	0	0	0	0	0	0	0	0
Sisyridae	larva	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Hemiptera	Corixidae	0	0	0	0	0	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0	0	0	0	0	0
Cyclopoidae		0	0	0	0	0	0	0	0	0	0
Astacidae	juvenile	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	0	1	0	0	0	0	0	0	0	0
Nematocera		0	0	0	0	0	0	0	0	0	0
Tipulidae		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Diptera	Diptera (fly)	1	1	1	0	0	0	0	0	0	0
	Diptera Wing (fly)	0	0	1	0	0	0	0	0	1	0
	Beetle	0	0	0	0	0	0	0	0	0	0
Curculionoidea	Weevil	0	0	0	0	0	0	0	0	0	0
Heteroptera		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Insects	insect head capsule	0	1	0	0	0	0	0	0	0	1
	insect cuticle fragment	0	0	0	0	1	0	0	1	0	1
	other	0	1	0	0	1	0	0	1	0	2
Total Aerial Insects		0	1	0	0	1	0	0	1	0	2
Isopoda	*Asellus* spp	0	0	0	0	0	0	0	0	0	0
Dermaptera	Earwig	0	0	0	0	0	0	0	0	0	0
Diplopoda	Millipede	0	0	0	0	0	0	0	0	0	0
Araneida		1	0	0	0	0	0	0	0	0	0
Nematoda		0	0	0	0	0	0	0	0	0	0
Trematoda		0	1	0	0	0	0	0	0	0	0
Mud, sand etc.		0	0	0	0	0	0	0	0	0	0

Table G10.26 cont'd: Dietary items of 79 brown trout captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Trout				
	Sample No	76	77	78	79	76
	Length group	2	2	1	1	2
	Fork Length (mm)	138	174	130	123	138
	Weight of fish (g)	31.6	61.3	47.3	23.4	31.6
Plant material	Macrophytes	0	0	0	0	0
	Thistle seed	0	0	0	0	0
	Debris and detritus	1	1	1	1	1
	Total Plant Material	1	1	1	1	1
Fish	*P. parva*	1	0	0	0	1
	Indet. fish eggs	0	0	0	0	0
Tanypodae	larvae	0	0	0	0	0
	adult	0	0	0	0	0
Orthocladinae	larvae	0	0	0	0	0
	adult	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0
	Simulium ornatum larva	0	0	0	0	0
	Simulium spp	0	0	0	0	0
Indet. Chironomidae	pupae	0	1	0	0	0
	larvae	0	0	0	0	0
	adult	0	0	0	0	0
	other	0	1	0	0	0
Dicranota	larvae	0	0	0	0	0
	adult	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0
	adult	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0
	larvae with case	0	0	0	0	0
	adult	0	0	0	1	0
Athripsodes	larva	0	0	0	0	0
	larvae with case	0	0	0	0	0
Indet. Trichoptera	larvae	0	0	0	0	0
Mesovelidae		0	0	0	0	0
Paraleptophlebia	larvae	0	0	0	0	0
	adult	0	0	0	0	0
Baetidae	larvae	0	0	0	0	0
	adult	0	1	0	0	0
Ephemera spp	larva	0	0	0	0	0
Ephemera spp	adult	0	0	0	0	0
other		0	0	0	1	0
Collembola		0	0	0	0	0
Sisyridae	larva	0	0	0	0	0
	adult	0	0	0	1	0
Hemiptera	Corixidae	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0
Cyclopoidae		0	0	0	0	0
Astacidae	juvenile	0	0	0	0	0
	adult	0	0	0	0	0
Gammaridae	*Gammarus pulex*	0	0	0	0	0
Nematocera		0	3	0	2	0
Tipulidae		0	1	0	0	0
Indet. Aerial Diptera	Diptera (fly)	0	0	0	0	0
	Diptera Wing (fly)	1	0	0	0	1
	Beetle	0	0	0	1	0
Curculionoidea	Weevil	0	0	0	0	0
Heteroptera		0	0	0	0	0
Indet. Aerial Insects	insect head capsule	0	0	0	1	0
	insect cuticle fragment	0	0	0	0	0
	other	0	0	0	1	0
Total Aerial Insects		0	4	0	4	0
Isopoda	*Asellus* spp	0	0	0	0	0
Dermaptera	Earwig	0	0	0	1	0
Diplopoda	Millipede	0	0	0	1	0
Araneida		0	0	0	0	0
Nematoda		0	1	0	0	0
Trematoda		0	0	0	0	0
Mud, sand etc.		0	0	0	0	0

Table G10.27: Dietary items of 63 chub captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

					Chub				
				Sample No	1	2	3	4	5
				Length group	1	1	1	1	1
				Fork Length (mm)	149	146	133	165	164
				Weight of fish (g)	49.1	34.5	31.4	55.6	55.3
Plant material				Macrophytes	0	0	0	1	0
				Thistle seed	0	0	0	0	0
				Debris and detritus	1	1	1	1	1
				Total Plant Material	1	1	1	2	1
Fish				*P. parva*	0	1	0	1	1
				Indet. fish eggs	0	0	0	0	0
Aquatic Insects	Diptera	Chironomidae	Tanypodae	larvae	0	0	0	0	0
				adult	0	0	0	0	0
			Orthocladinae	larvae	0	0	0	0	0
				adult	0	0	0	0	0
			Simuliidae	*Simulium vernum* gp	0	0	0	0	0
				Simulium ornatum larva	0	0	0	0	0
				Simulium spp	0	0	0	0	0
			Indet. Chironomidae	pupae	0	0	0	0	0
				larvae	0	0	0	0	3
				adult	0	0	0	0	0
				other	0	0	0	0	3
		Tipulidae	Dicranota	larvae	0	0	0	0	0
				adult	0	0	0	0	0
	Coleoptera	Gyrinidae		larvae	0	0	0	0	0
				adult	0	0	0	0	0
	Trichoptera	Limnephilidae	Limnephiloida	larvae	0	0	0	0	0
				larvae with case	0	0	0	0	0
				adult	0	0	0	0	0
		Leptoceridae	Athripsodes	larva	0	0	0	0	0
				larvae with case	2	0	0	1	0
			Indet. Trichoptera	larvae	0	0	0	0	0
	Hemiptera	Gerroidea	Mesovelidae		0	0	0	0	0
	Ephemeroptera	Leptophlebidae	Paraleptophlebia	larvae	0	0	0	0	0
				adult	0	0	0	0	0
		Baetidae		larvae	0	0	0	0	0
				adult	0	0	0	0	0
		Ephemeridae	Ephemera spp	larva	0	0	0	0	2
			Ephemera spp	adult	0	0	0	0	0
			other		0	0	0	0	0
	Apterygota		Collembola		0	0	0	0	0
	Neuroptera	Sisyridae		larva	0	0	0	0	0
				adult	0	0	0	0	0
	Exopterygota	Hemiptera	Corixidae		0	0	0	0	0
				Indet. Aquatic Insects	0	0	0	0	0
Aquatic Crustaceans		Copepoda	Cyclopoidae		0	0	0	0	0
		Decapoda	Astacidae	juvenile	0	0	0	0	0
				adult	0	0	0	0	0
		Amphipoda	Gammaridae	*Gammarus pulex*	2	0	0	0	0
Aerial Insects		Diptera	Nematocera		0	0	1	2	0
			Tipulidae		0	0	0	0	0
		Indet. Aerial Diptera		Diptera (fly)	0	0	0	0	0
				Diptera Wing (fly)	1	0	0	0	0
		Coleoptera		Beetle	0	0	0	0	0
			Curculionoidea	Weevil	1	0	0	0	0
		Hemiptera	Heteroptera		0	0	0	0	0
			Indet. Aerial Insects	insect head capsule	0	0	0	1	0
				insect cuticle fragment	0	0	0	0	0
				other	0	0	0	1	0
			Total Aerial Insects		1	0	1	3	0
Terrestrial Insects		Crustacea	Isopoda	*Asellus* spp	0	2	0	0	0
		Dermaptera		Earwig	0	0	0	0	0
		Arthropoda	Diplopoda	Millipede	0	0	0	0	0
			Araneida		0	0	0	0	0
			Nematoda		0	0	0	0	0
			Trematoda		0	0	0	0	0
Mud, sand etc.			Mud, sand etc.		0	0	0	0	0

Table G10.27 cont’d: Dietary items of 63 chub captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Chub									
	Sample No	6	7	8	9	10	11	12	13	14	15
	Length group	1	1	2	1	1	1	1	1	1	1
	Fork Length (mm)	182	170	194	167	126	131	129	136	135	143
	Weight of fish (g)	98.4	83.1	112.2	56.4	26.7	31.1	27.8	29.5	35.4	35.9
Plant material	Macrophytes	1	1	1	1	0	1	0	0	0	0
	Thistle seed	0	0	0	0	0	0	0	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1	1	1
	Total Plant Material	2	2	2	2	1	2	1	1	1	1
Fish	*P. parva*	1	0	1	0	0	0	0	0	0	0
	Indet. fish eggs	0	0	0	0	0	0	0	0	0	0
Tanypodae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	0	0	0	0
	Simulium ornatum larva	0	0	0	0	0	0	0	0	0	0
	Simulium spp	0	0	0	0	0	0	0	0	0	0
Indet. Chironomidae	pupae	0	0	0	0	0	0	0	0	0	0
	larvae	0	0	2	1	0	2	2	0	0	1
	adult	0	0	0	0	0	0	0	0	0	0
	other	0	0	2	1	0	2	2	0	0	1
Dicranota	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Athripsodes	larva	0	0	0	0	1	0	0	0	0	0
	larvae with case	0	1	0	0	0	0	0	1	0	0
Indet. Trichoptera	larvae	0	0	3	0	0	0	2	0	1	0
Mesovelidae		0	0	0	0	0	0	0	0	0	0
Paraleptophlebia	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Baetidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Ephemera spp	larva	0	0	1	0	1	0	1	0	0	0
Ephemera spp	adult	0	0	0	1	0	0	0	0	0	0
other		0	0	0	0	0	0	0	0	0	0
Collembola		0	0	0	0	0	0	0	0	0	0
Sisyridae	larva	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Hemiptera	Corixidae	0	0	0	0	0	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0	0	0	0	0	0
Cyclopoidae		0	0	0	0	0	0	0	0	0	0
Astacidae	juvenile	0	1	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	2	3	0	2	3	1	1	0	1	2
Nematocera		3	1	2	1	1	0	1	0	1	0
Tipulidae		0	0	0	0	0	1	0	0	0	0
Indet. Aerial Diptera	Diptera (fly)	0	0	0	0	1	0	0	0	0	0
	Diptera Wing (fly)	0	0	0	0	0	0	0	0	0	0
	Beetle	0	0	0	0	0	0	0	0	0	0
Curculionoidea	Weevil	0	0	0	0	0	0	0	0	0	0
Heteroptera		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Insects	insect head capsule	0	0	0	0	0	0	0	0	0	0
	insect cuticle fragment	0	0	0	0	0	0	0	0	0	0
	other	0	0	0	0	0	0	0	0	0	0
Total Aerial Insects		3	1	2	1	1	1	1	0	1	0
Isopoda	*Asellus* spp	0	0	0	0	0	1	0	0	0	1
Dermaptera	Earwig	0	0	0	0	0	0	0	0	0	0
Diplopoda	Millipede	0	0	0	0	0	0	0	0	0	0
Araneida		0	0	0	0	0	0	0	0	0	0
Nematoda		0	0	0	0	0	0	0	0	0	0
Trematoda		0	0	0	0	0	0	0	0	0	0
Mud, sand etc.		1	0	0	0	0	0	0	0	0	0

Table G10.27 cont'd: Dietary items of 63 chub captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Chub									
	Sample No	16	17	18	19	20	21	22	23	24	25
	Length group	1	1	1	1	2	1	1	1	1	2
	Fork Length (mm)	131	158	144	165	180	159	158	165	171	185
	Weight of fish (g)	39.9	49.3	44.3	93.4	89.4	61.4	55.3	59	59.5	101.5
Plant material	Macrophytes	1	1	1	0	0	1	1	0	0	0
	Thistle seed	0	0	0	0	0	0	0	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1	1	1
	Total Plant Material	2	2	2	1	1	2	2	1	1	1
Fish	*P. parva*	0	0	0	1	2	0	0	1	2	1
	Indet. fish eggs	0	0	0	0	0	0	0	0	0	0
Tanypodae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	0	0	0	0
	Simulium ornatum larva	0	0	0	0	0	0	0	0	0	0
	Simulium spp	0	0	0	0	0	0	0	0	0	0
Indet. Chironomidae	pupae	0	0	0	0	0	0	0	0	0	0
	larvae	1	3	0	2	0	2	0	2	4	0
	adult	0	0	0	0	0	0	0	0	0	0
	other	1	3	0	2	0	2	0	2	4	0
Dicranota	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Athripsodes	larva	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	0	0	0	0	0	0	0	0	0
Indet. Trichoptera	larvae	0	1	0	0	0	0	0	0	0	1
Mesovelidae		0	0	0	0	0	0	0	0	0	0
Paraleptophlebia	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Baetidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Ephemera spp	larva	1	0	0	0	0	0	0	0	0	0
Ephemera spp	adult	0	0	0	0	0	0	0	0	0	0
other		0	0	0	0	0	0	0	0	0	0
Collembola		0	0	0	0	0	0	0	0	0	0
Sisyridae	larva	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Hemiptera	Corixidae	0	0	0	0	0	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0	1	1	0	0	0
Cyclopoidae		0	0	0	0	0	0	0	0	0	0
Astacidae	juvenile	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	0	0	7	0	1	0	2	0	0	0
Nematocera		0	0	0	0	2	0	0	0	0	0
Tipulidae		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Diptera	Diptera (fly)	0	0	0	0	0	0	0	0	0	0
	Diptera Wing (fly)	0	0	0	0	0	0	0	0	0	0
	Beetle	0	0	0	0	0	0	0	0	0	0
Curculionoidea	Weevil	0	0	0	0	0	0	0	0	0	0
Heteroptera		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Insects	insect head capsule	1	0	1	0	0	0	0	0	0	0
	insect cuticle fragment	0	0	0	0	0	0	0	0	0	0
	other	1	0	1	0	0	0	0	0	0	0
Total Aerial Insects		1	0	1	0	2	0	0	0	0	0
Isopoda	*Asellus* spp	0	0	0	0	0	0	0	0	0	0
Dermaptera	Earwig	0	0	0	0	0	0	0	0	0	0
Diplopoda	Millipede	0	0	0	0	0	0	0	0	0	0
Araneida		0	0	0	0	0	0	0	0	0	0
Nematoda		0	0	0	0	0	0	0	0	0	0
Trematoda		0	0	0	0	0	0	0	0	0	0
Mud, sand etc.		0	0	0	0	0	1	0	0	0	0

Table G10.27 cont'd: Dietary items of 63 chub captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Chub									
	Sample No	26	27	28	29	30	31	32	33	34	35
	Length group	1	1	1	2	1	1	1	1	1	1
	Fork Length (mm)	178	171	182	186	162	122	139	142	164	141
	Weight of fish (g)	63.9	55.5	90.4	93.9	55.3	59.3	33	31	61.5	33.4
Plant material	Macrophytes	0	0	0	0	0	0	2	0	0	0
	Thistle seed	0	0	0	0	0	0	0	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1	1	1
	Total Plant Material	1	1	1	1	1	1	3	1	1	1
Fish	*P. parva*	0	0	1	0	0	0	0	0	1	0
	Indet. fish eggs	0	0	0	0	0	0	0	0	0	0
Tanypodae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	0	0	1	0
	Simulium ornatum larva	0	0	0	0	0	0	0	0	0	0
	Simulium spp	0	0	0	0	0	0	0	0	1	0
Indet. Chironomidae	pupae	0	0	0	0	0	0	2	0	1	0
	larvae	0	1	1	0	2	1	0	0	4	0
	adult	0	0	0	0	0	0	0	0	0	0
	other	0	1	1	0	2	1	2	0	5	0
Dicranota	larvae	0	0	0	0	0	0	1	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	0	0	0	0	0	0	0	1	0
	adult	0	0	0	0	0	0	0	0	0	0
Athripsodes	larva	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	0	0	0	0	1	2	13	13	0
Indet. Trichoptera	larvae	0	1	0	0	0	1	0	0	0	0
Mesovelidae		0	0	0	0	0	0	0	0	0	0
Paraleptophlebia	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Baetidae	larvae	2	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Ephemera spp	larva	0	0	0	0	0	0	0	0	0	0
Ephemera spp	adult	0	0	0	0	0	0	0	0	0	0
other		0	0	0	0	0	0	0	0	0	0
Collembola		0	0	0	0	0	0	0	0	0	0
Sisyridae	larva	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	1	0
Hemiptera	Corixidae	0	0	0	0	0	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0	0	0	0	0	0
Cyclopoidae		0	0	0	0	0	0	0	0	1	0
Astacidae	juvenile	0	0	0	0	0	0	1	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	2	3	2	0	1	0	7	0	1	0
Nematocera		28	19	0	0	7	0	23	27	18	28
Tipulidae		1	0	0	0	0	0	0	0	0	0
Indet. Aerial Diptera	Diptera (fly)	0	0	0	0	0	0	3	0	0	0
	Diptera Wing (fly)	0	0	0	0	2	1	1	0	0	14
	Beetle	0	0	0	0	0	0	0	0	0	0
Curculionoidea	Weevil	0	0	0	0	0	0	0	0	0	0
Heteroptera		0	0	0	0	0	0	0	0	1	0
Indet. Aerial Insects	insect head capsule	1	0	0	0	0	0	0	0	0	1
	insect cuticle fragment	0	0	0	0	0	0	1	0	0	0
	other	1	0	0	0	0	0	1	0	0	1
Total Aerial Insects		30	19	0	0	7	0	24	27	19	29
Isopoda	*Asellus* spp	0	0	0	0	0	0	0	0	0	0
Dermaptera	Earwig	0	0	0	0	0	0	0	0	0	0
Diplopoda	Millipede	0	0	0	0	0	0	0	0	0	0
Araneida		0	0	0	0	0	0	0	0	0	0
Nematoda		0	0	0	0	0	0	0	0	0	0
Trematoda		0	0	0	0	0	0	0	0	0	0
Mud, sand etc.		0	0	0	0	0	0	0	0	0	0

Table G10.27 cont'd: Dietary items of 63 chub captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Chub									
	Sample No Trout	36	37	38	39	40	41	42	43	44	45
	Length group	1	1	1	1	1	1	1	1	1	1
	Fork Length (mm)	133	141	149	122	134	135	156	138	148	142
	Weight of fish (g)	29.5	34.5	44.3	25.9	29	37.5	55.7	43.5	44.3	41.6
Plant material	Macrophytes	0	0	0	0	0	0	0	1	0	1
	Thistle seed	0	0	0	0	0	0	0	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1	1	1
	Total Plant Material	1	1	1	1	1	1	1	2	1	2
Fish	*P. parva*	1	0	0	0	0	0	0	0	1	0
	Indet. fish eggs	0	0	0	0	0	0	0	0	0	0
Tanypodae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	0	0	0	0
	Simulium ornatum larva	0	0	0	0	0	0	0	0	0	0
	Simulium spp	0	0	0	0	0	0	0	0	0	0
Indet. Chironomidae	pupae	0	0	0	0	0	0	0	0	0	0
	larvae	0	2	0	0	0	0	0	0	1	2
	adult	0	0	0	0	0	0	0	0	0	0
	other	0	2	0	0	0	0	0	0	1	2
Dicranota	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	0	0	0	0	0	0	0	0	0
	adult	0	0	1	0	0	0	0	0	0	0
Athripsodes	larva	0	0	0	1	0	0	0	0	0	0
	larvae with case	2	0	3	2	0	0	1	0	0	0
Indet. Trichoptera	larvae	0	1	0	0	0	0	0	0	0	0
Mesovelidae		0	0	0	0	0	0	0	0	0	0
Paraleptophlebia	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Baetidae	larvae	0	0	2	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Ephemera spp	larva	0	0	0	0	0	0	0	0	1	0
Ephemera spp	adult	1	0	0	0	0	0	0	0	0	0
other		1	0	1	0	0	0	0	0	0	0
Collembola		0	0	0	0	0	0	0	0	0	0
Sisyridae	larva	1	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Hemiptera	Corixidae	0	0	0	0	0	0	0	0	0	0
	Indet. Aquatic Insects	0	0	1	0	0	0	0	0	0	0
Cyclopoidae		0	0	0	0	0	0	0	0	0	0
Astacidae	juvenile	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	0	0	5	2	0	0	0	1	0	5
Nematocera		4	15	5	2	1	0	0	0	0	0
Tipulidae		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Diptera	Diptera (fly)	0	0	0	1	0	0	0	0	0	0
	Diptera Wing (fly)	3	0	0	3	3	0	0	0	0	0
	Beetle	0	0	0	0	0	0	0	0	0	0
Curculionoidea	Weevil	0	0	0	0	0	0	0	0	0	0
Heteroptera		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Insects	insect head capsule	0	0	0	0	2	0	0	0	0	0
	insect cuticle fragment	0	0	1	0	2	0	0	0	0	0
	other	0	0	1	0	4	0	0	0	0	0
Total Aerial Insects		4	15	6	2	5	0	0	0	0	0
Isopoda	*Asellus* spp	0	0	0	0	0	0	0	0	0	0
Dermaptera	Earwig	0	0	0	0	0	0	0	0	0	0
Diplopoda	Millipede	0	0	0	0	0	0	0	0	0	0
Araneida		0	0	0	0	0	0	0	0	0	0
Nematoda		0	0	0	0	0	0	0	0	0	0
Trematoda		0	0	0	0	0	0	0	0	0	0
Mud, sand etc.		0	0	0	0	0	0	0	0	0	0

Table G10.27 cont'd: Dietary items of 63 chub captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Chub									
	Sample No	46	47	48	49	50	51	52	53	54	55
	Length group	1	1	1	1	1	1	1	1	1	1
	Fork Length (mm)	148	170	173	155	176	129	135	123	142	148
	Weight of fish (g)	43.3	82.3	84.1	59.3	84.1	21.5	32.5	22.0	40.8	45.1
Plant material	Macrophytes	0	0	0	0	0	0	0	0	0	0
	Thistle seed	0	0	0	0	0	0	0	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1	1	1
	Total Plant Material	1	1	1	1	1	1	1	1	1	1
Fish	*P. parva*	0	0	0	0	0	0	0	1	2	1
	Indet. fish eggs	0	0	0	0	0	0	0	0	0	0
Tanypodae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	0	0	0	0
	Simulium ornatum larva	0	0	0	0	0	0	0	0	0	0
	Simulium spp	0	0	0	0	0	0	0	0	0	0
Indet. Chironomidae	pupae	0	0	0	0	0	0	0	0	0	0
	larvae	2	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
	other	2	0	0	0	0	0	0	0	0	0
Dicranota	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Athripsodes	larva	0	0	0	0	0	0	0	0	0	0
	larvae with case	0	2	3	0	0	1	0	4	2	0
Indet. Trichoptera	larvae	0	0	0	0	0	1	0	0	0	0
Mesovelidae		0	0	0	0	0	0	0	0	0	0
Paraleptophlebia	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Baetidae	larvae	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Ephemera spp	larva	0	0	0	0	0	1	0	0	0	0
Ephemera spp	adult	0	0	0	0	0	0	0	0	0	0
other		0	0	0	0	0	0	0	0	0	0
Collembola		0	0	0	0	0	0	0	0	0	0
Sisyridae	larva	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Hemiptera	Corixidae	0	0	0	0	0	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0	0	0	0	0	0
Cyclopoidae		0	0	0	0	0	0	0	0	0	0
Astacidae	juvenile	0	0	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	1	0	0	0	0	0	2	0	0	0
Nematocera		7	3	0	2	0	0	5	10	0	0
Tipulidae		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Diptera	Diptera (fly)	0	0	0	0	0	0	0	0	0	0
	Diptera Wing (fly)	0	0	0	0	0	0	0	0	0	0
	Beetle	0	0	0	0	0	0	0	0	0	0
Curculionoidea	Weevil	0	0	0	0	0	0	0	0	0	0
Heteroptera		0	0	0	0	0	0	0	0	0	0
Indet. Aerial Insects	insect head capsule	0	0	0	0	0	0	1	0	0	0
	insect cuticle fragment	0	0	0	0	0	0	0	0	0	0
	other	0	0	0	0	0	0	1	0	0	0
Total Aerial Insects		7	3	0	2	0	0	6	10	0	0
Isopoda	*Asellus* spp	0	0	0	0	0	0	0	0	0	0
Dermaptera	Earwig	0	0	0	0	0	0	0	0	0	0
Diplopoda	Millipede	0	0	0	0	0	0	0	0	0	0
Araneida		0	0	0	0	0	0	0	0	0	0
Nematoda		0	0	0	0	0	0	0	0	0	0
Trematoda		0	0	0	0	0	0	0	0	0	0
Mud, sand etc.		0	0	0	0	0	0	0	0	0	0

Table G10.27 cont'd: Dietary items of 63 chub captured on 28 April, 10 and 16 May 2005 at Tadburn Lake stream.

		Chub							
	Sample No	56	57	58	59	60	61	62	63
	Length group	1	1	1	1	1	1	1	1
	Fork Length (mm)	171	164	145	134	157	147	135	133
	Weight of fish (g)	55.9	57.9	45	39.1	49.9	44.3	30	30.3
Plant material	Macrophytes	0	1	1	1	0	0	0	0
	Thistle seed	0	0	0	0	0	0	0	0
	Debris and detritus	1	1	1	1	1	1	1	1
	Total Plant Material	1	2	2	2	1	1	1	1
Fish	*P. parva*	1	0	0	1	0	0	0	0
	Indet. fish eggs	0	0	0	0	0	0	0	0
Tanypodae	larvae	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0
Orthocladinae	larvae	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0
Simuliidae	*Simulium vernum* gp	0	0	0	0	0	0	0	0
	Simulium ornatum larva	0	0	0	0	0	0	0	0
	Simulium spp	0	0	0	0	0	0	0	0
Indet. Chironomidae	pupae	0	0	0	0	0	0	0	0
	larvae	0	3	1	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0
	other	0	3	1	0	0	0	0	0
Dicranota	larvae	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0
Gyrinidae	larvae	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0
Limnephiloida	larvae	0	0	0	0	0	0	0	0
	larvae with case	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0
Athripsodes	larva	0	0	0	0	0	0	0	0
	larvae with case	2	1	0	0	0	0	0	0
Indet. Trichoptera	larvae	0	0	0	0	0	0	0	0
Mesovelidae		0	0	0	0	0	0	0	0
Paraleptophlebia	larvae	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0
Baetidae	larvae	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0
Ephemera spp	larva	0	1	0	0	0	0	1	0
Ephemera spp	adult	0	0	1	0	0	0	0	0
other		0	0	0	0	0	0	0	0
Collembola		0	0	0	0	0	0	0	0
Sisyridae	larva	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0
Hemiptera	Corixidae	0	0	0	0	0	0	0	0
	Indet. Aquatic Insects	0	0	0	0	0	1	0	0
Cyclopoidae		0	0	0	0	0	0	0	0
Astacidae	juvenile	0	0	0	0	0	0	0	0
	adult	0	0	0	0	0	0	0	0
Gammaridae	*Gammarus pulex*	0	0	4	1	0	0	1	0
Nematocera		4	0	0	0	0	5	0	0
Tipulidae		0	0	0	0	0	0	0	0
Indet. Aerial Diptera	Diptera (fly)	0	0	0	0	0	0	0	0
	Diptera Wing (fly)	0	0	0	0	0	0	0	0
	Beetle	0	0	1	0	0	0	0	0
Curculionoidea	Weevil	0	0	0	0	0	0	0	0
Heteroptera		0	0	0	0	0	0	0	0
Indet. Aerial Insects	insect head capsule	0	0	0	0	0	0	1	0
	insect cuticle fragment	0	0	0	0	0	0	0	0
	other	0	0	0	0	0	0	1	0
Total Aerial Insects		4	0	1	0	0	5	1	0
Isopoda	*Asellus* spp	0	0	0	0	0	0	0	0
Dermaptera	Earwig	0	0	0	0	0	0	0	0
Diplopoda	Millipede	0	0	0	0	0	0	0	0
Araneida		0	0	0	0	0	0	0	0
Nematoda		0	0	0	0	0	0	0	0
Trematoda		0	0	0	0	0	0	0	0
Mud, sand etc.		0	0	0	0	0	1	0	0

Appendix H
Results of statistical analyses for diet in chub and brown trout at Tadburn Lake stream.

Table H10.28 Comparison of the diet between length groups of trout using non-parametric statistics

Kruskal-Wallis Test: Trout Length Groups versus Fish eggs

Fish eggs	N	Median	Ave Rank	Z
0	78	2.00	39.8	-0.70
14	1	3.00	56.0	0.70
Overall	79		40.0	

H = 0.49 DF = 1 P = 0.483
H = 0.53 DF = 1 P = 0.466 (adjusted for ties)

Kruskal-Wallis Test: Topmouth gudgeon (TMG) versus Trout Length Groups

Length groups	N	Median	Ave Rank	Z
1	26	0.00	35.2	-1.31
2	19	0.00	43.7	0.81
3	21	0.00	45.0	1.18
4	13	0.00	36.1	-0.67
Overall	79		40.0	

H = 3.04 DF = 3 P = 0.385
H = 4.41 DF = 3 P = 0.220 (adjusted for ties)

Kruskal-Wallis Test: Indeterminate Chironomidae Total versus Trout Length Groups

Length groups	N	Median	Ave Rank	Z
1	26	0.00	42.9	0.79
2	19	0.00	37.1	-0.64
3	21	0.00	35.1	-1.13
4	13	0.00	46.3	1.09
Overall	79		40.0	

H = 2.66 DF = 3 P = 0.446
H = 4.12 DF = 3 P = 0.249 (adjusted for ties)

Kruskal-Wallis Test: Macrophytes versus Trout Length Groups

Length groups	N	Median	Ave Rank	Z
1	26	0.00	37.7	-0.62
2	19	0.00	39.1	-0.20
3	21	0.00	40.3	0.08
4	13	0.00	45.3	0.92
Overall	79		40.0	

H = 0.99 DF = 3 P = 0.803
H = 2.26 DF = 3 P = 0.520 (adjusted for ties)

Kruskal-Wallis Test: Total Plant Material versus Trout Length Groups

Length groups	N	Median	Ave Rank	Z
1	26	1.000	37.3	-0.75
2	19	1.000	38.6	-0.31
3	21	1.000	41.7	0.39
4	13	1.000	44.9	0.84
Overall	79		40.0	

H = 1.15 DF = 3 P = 0.766
H = 2.47 DF = 3 P = 0.481 (adjusted for ties)

Kruskal-Wallis Test: Tanypodinae Larvae versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	41.0	0.28
2	19	0.00	38.0	-0.44
3	21	0.00	39.9	-0.03
4	13	0.00	41.0	0.18
Overall	79		40.0	

H = 0.22 DF = 3 P = 0.974
H = 1.56 DF = 3 P = 0.669 (adjusted for ties)

Kruskal-Wallis Test: Tanypodinae Adults versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	40.0	0.00
2	19	0.00	40.0	0.00
3	21	0.00	40.0	0.00
4	13	0.00	40.0	0.00
Overall	79		40.0	

H = 0.00 DF = 3 P = 1.000

Kruskal-Wallis Test: Mud, sand etc. versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	40.6	0.16
2	19	0.00	37.5	-0.54
3	21	0.00	41.2	0.28
4	13	0.00	40.5	0.09
Overall	79		40.0	

H = 0.31 DF = 3 P = 0.959
H = 1.73 DF = 3 P = 0.630 (adjusted for ties)

Kruskal-Wallis Test: Trematoda versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	39.5	-0.14
2	19	0.00	42.1	0.46
3	21	0.00	40.0	-0.01
4	13	0.00	38.0	-0.34
Overall	79		40.0	

H = 0.27 DF = 3 P = 0.965
H = 1.88 DF = 3 P = 0.598 (adjusted for ties)

Kruskal-Wallis Test: Orthocladinae Larvae versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	40.1	0.02
2	19	0.00	40.6	0.12
3	21	0.00	40.4	0.08
4	13	0.00	38.5	-0.26
Overall	79		40.0	

H = 0.07 DF = 3 P = 0.995
H = 0.65 DF = 3 P = 0.884 (adjusted for ties)

Kruskal-Wallis Test: Orthocladinae Adults versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	40.0	0.00
2	19	0.00	40.0	0.00
3	21	0.00	40.0	0.00
4	13	0.00	40.0	0.00
Overall	79		40.0	

H = 0.00 DF = 3 P = 1.000

Kruskal-Wallis Test: Simulium V versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	39.0	-0.27
2	19	0.00	39.0	-0.22
3	21	0.00	40.9	0.21
4	13	0.00	42.0	0.35
Overall	79		40.0	

H = 0.22 DF = 3 P = 0.974
H = 2.96 DF = 3 P = 0.398 (adjusted for ties)

Kruskal-Wallis Test: Simulium o L versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	39.5	-0.14
2	19	0.00	41.6	0.34
3	21	0.00	39.5	-0.12
4	13	0.00	39.5	-0.09
Overall 79	40.0			

H = 0.12 DF = 3 P = 0.990
H = 3.16 DF = 3 P = 0.368 (adjusted for ties)

Kruskal-Wallis Test: Simulium spp versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	38.5	-0.41
2	19	0.00	40.6	0.14
3	21	0.00	40.4	0.08
4	13	0.00	41.5	0.26
Overall	79		40.0	

H = 0.19 DF = 3 P = 0.980
H = 1.70 DF = 3 P = 0.638 (adjusted for ties)

Kruskal-Wallis Test: Baetidae Larvae versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	36.9	-0.83
2	19	0.00	44.0	0.87
3	21	0.00	37.4	-0.60
4	13	0.00	44.5	0.78
Overall	79		40.0	

H = 1.81 DF = 3 P = 0.612
H = 5.96 DF = 3 P = 0.113 (adjusted for ties)

Kruskal-Wallis Test: Baetidae Adult versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	40.0	0.01
2	19	0.00	40.6	0.13
3	21	0.00	40.4	0.09
4	13	0.00	38.5	-0.26
Overall	79		40.0	

H = 0.07 DF = 3 P = 0.995
H = 0.67 DF = 3 P = 0.880 (adjusted for ties)

Kruskal-Wallis Test: Ephemera Larvae versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	40.0	0.00
2	19	0.00	40.0	0.00
3	21	0.00	40.0	0.00
4	13	0.00	40.0	0.00
Overall	79		40.0	

H = 0.00 DF = 3 P = 1.000

Kruskal-Wallis Test: Ephemera Adults versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	39.0	-0.27
2	19	0.00	39.0	-0.22
3	21	0.00	42.8	0.64
4	13	0.00	39.0	-0.17
Overall	79		40.0	

H = 0.41 DF = 3 P = 0.937
H = 5.60 DF = 3 P = 0.133 (adjusted for ties)

Kruskal-Wallis Test: Ephemeridae versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	40.0	0.01
2	19	0.00	40.6	0.13
3	21	0.00	40.4	0.09
4	13	0.00	38.5	-0.26
Overall	79		40.0	

H = 0.07 DF = 3 P = 0.995
H = 0.67 DF = 3 P = 0.880 (adjusted for ties)

Kruskal-Wallis Test: Collembola versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	41.0	0.28
2	19	0.00	39.5	-0.11
3	21	0.00	39.5	-0.12
4	13	0.00	39.5	-0.09
Overall	79		40.0	

H = 0.08 DF = 3 P = 0.995
H = 2.04 DF = 3 P = 0.564 (adjusted for ties)

Kruskal-Wallis Test: Sisyridae Larvae versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	40.5	0.14
2	19	0.00	39.0	-0.22
3	21	0.00	40.9	0.21
4	13	0.00	39.0	-0.17
Overall	79		40.0	

H = 0.11 DF = 3 P = 0.991
H = 1.42 DF = 3 P = 0.701 (adjusted for ties)

Kruskal-Wallis Test: Total Indet Aerial Diptera versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	40.0	0.00
2	19	0.00	40.0	0.00
3	21	0.00	40.0	0.00
4	13	0.00	40.0	0.00
Overall	79		40.0	

H = 0.00 DF = 3 P = 1.000

Kruskal-Wallis Test: Total Aerial Insects versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	1.00	31.9	-2.19
2	19	4.00	49.0	1.96
3	21	1.00	38.6	-0.32
4	13	2.00	45.3	0.91
Overall	79	40.0		

H = 6.89 DF = 3 P = 0.076
H = 7.17 DF = 3 P = 0.067 (adjusted for ties)

Kruskal-Wallis Test: Araneida versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	38.0	-0.54
2	19	0.00	40.7	0.14
3	21	0.00	38.4	-0.38
4	13	0.00	45.6	0.97
Overall	79		40.0	

H = 1.09 DF = 3 P = 0.779
H = 4.51 DF = 3 P = 0.212 (adjusted for ties)

Kruskal-Wallis Test: Indet. Aquatic Insects versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	40.0	0.00
2	19	0.00	40.0	0.00
3	21	0.00	40.0	0.00
4	13	0.00	40.0	0.00
Overall	79		40.0	

H = 0.00 DF = 3 P = 1.000

Kruskal-Wallis Test: Mud, sand etc. versus Trout Length Groups

Length Groups	N	Median	Ave Rank	Z
1	26	0.00	40.6	0.16
2	19	0.00	37.5	-0.54
3	21	0.00	41.2	0.28
4	13	0.00	40.5	0.09
Overall	79		40.0	

H = 0.31 DF = 3 P = 0.959
H = 1.73 DF = 3 P = 0.630 (adjusted for ties)

Table H10.29 Comparison of the diet between sampling dates (1, 28 April 2005; 2, 10 May 2005; 3, 16 May 2005) of trout using non-parametric statistics

Kruskal-Wallis Test: Mud, sand etc. versus Date

Date	N	Median	Ave Rank	Z
1	8	0.00	37.5	-0.33
2	40	0.00	40.5	0.19
3	31	0.00	40.0	0.01
Overall	79		40.0	

H = 0.11 DF = 2 P = 0.945
H = 0.63 DF = 2 P = 0.728 (adjusted for ties)

Kruskal-Wallis Test: Fork length (FL) versus Date

Date	N	Median	Ave Rank	Z
1	8	20.50	44.2	0.54
2	40	19.40	38.7	-0.51
3	31	21.60	40.6	0.19
Overall	79		40.0	

H = 0.42 DF = 2 P = 0.812
H = 0.42 DF = 2 P = 0.812 (adjusted for ties)

Kruskal-Wallis Test: Indet Chironomidae Total versus Date

Date	N	Median	Ave Rank	Z
1	8	0.00	32.7	-0.95
2	40	0.00	38.9	-0.42
3	31	0.00	43.3	1.02
Overall	79		40.0	

H = 1.53 DF = 2 P = 0.465
H = 2.37 DF = 2 P = 0.306 (adjusted for ties)

Kruskal-Wallis Test: Gammarus versus Date

Date	N	Median	Ave Rank	Z
1	8	0.00	33.3	-0.88
2	40	0.00	41.7	0.66
3	31	0.00	39.6	-0.13
Overall	79		40.0	

H = 0.92 DF = 2 P = 0.633
H = 1.22 DF = 2 P = 0.544 (adjusted for ties)

Kruskal-Wallis Test: Total Aerial Insects versus Date

Date	N	Median	Ave Rank	Z
1	8	1.00	26.7	-1.73
2	40	2.50	47.0	2.76
3	31	1.00	34.4	-1.76
Overall	79		40.0	

H = 8.33 DF = 2 P = 0.016
H = 8.67 DF = 2 P = 0.013 (adjusted for ties)

Kruskal-Wallis Test: Indet. Aquatic Insects versus Date

Date	N	Median	Ave Rank	Z
1	8	0.00	40.0	0.00
2	40	0.00	40.0	0.00
3	31	0.00	40.0	0.00
Overall	79		40.0	

H = 0.00 DF = 2 P = 1.000

Kruskal-Wallis Test: Ephemeridae versus Date

Date	N	Median	Ave Rank	Z
1	8	0.00	43.4	0.45
2	40	0.00	39.5	-0.20
3	31	0.00	39.8	-0.07
Overall	79		40.0	

H = 0.20 DF = 2 P = 0.904
H = 1.85 DF = 2 P = 0.397 (adjusted for ties)

Kruskal-Wallis Test: Total Indet. Aerial Diptera versus Date

Date	N	Median	Ave Rank	Z
1	8	0.00	40.0	0.00
2	40	0.00	40.0	0.00
3	31	0.00	40.0	0.00
Overall	79		40.0	

H = 0.00 DF = 2 P = 1.000

Kruskal-Wallis Test: Total Aerial Insects versus Date

Date	N	Median	Ave Rank	Z
1	8	1.00	26.7	-1.73
2	40	2.50	47.0	2.76
3	31	1.00	34.4	-1.76
Overall	79		40.0	

H = 8.33 DF = 2 P = 0.016
H = 8.67 DF = 2 P = 0.013 (adjusted for ties)

Kruskal-Wallis Test: Tanypodinae Adult versus Date

Date	N	Median	Ave Rank	Z
1	8	0.00	40.0	0.00
2	40	0.00	40.0	0.00
3	31	0.00	40.0	0.00
Overall	79		40.0	

H = 0.00 DF = 2 P = 1.000

Kruskal-Wallis Test: Total Plant Material versus Date

Date	N	Median	Ave Rank	Z
1	8	1.50	51.8	1.53
2	40	1.00	35.4	-1.81
3	31	1.00	42.9	0.91
Overall	79		40.0	

H = 4.21 DF = 2 P = 0.122
H = 9.08 DF = 2 P = 0.011 (adjusted for ties)

Kruskal-Wallis Test: Simulium spp versus Date

Date	N	Median	Ave Rank	Z
1	8	0.00	38.5	-0.20
2	40	0.00	38.5	-0.59
3	31	0.00	42.3	0.72
Overall	79		40.0	

H = 0.52 DF = 2 P = 0.770
H = 4.77 DF = 2 P = 0.092 (adjusted for ties)

Kruskal-Wallis Test: Indet. Chironomidae Total versus Date

Date	N	Median	Ave Rank	Z
1	8	0.00	32.7	-0.95
2	40	0.00	38.9	-0.42
3	31	0.00	43.3	1.02
Overall	79		40.0	

H = 1.53 DF = 2 P = 0.465
H = 2.37 DF = 2 P = 0.306 (adjusted for ties)

Kruskal-Wallis Test: Total Ephemeroptera versus Date

Date	N	Median	Ave Rank	Z
1	8	0.00	35.9	-0.54
2	40	0.00	39.0	-0.38
3	31	0.00	42.3	0.72
Overall	79		40.0	

H = 0.65 DF = 2 P = 0.723
H = 1.22 DF = 2 P = 0.542 (adjusted for ties)

Table H10.30 Comparison of the diet between length groups of chub using non-parametric statistics

Kruskal-Wallis Test: Dermaptera (Earwig) versus Chub Length Groups

Length Groups	N	Median	Ave Rank	Z
1	59	0.00	32.0	0.00
2	4	0.00	32.0	0.00
Overall	63		32.0	

H = 0.00 DF = 1 P = 1.000

Kruskal-Wallis Test: Total Plant Mat versus Chub Length Groups

Length Groups	N	Median	Ave Rank	Z
1	59	1.00	32.1	0.08
2	4	1.00	31.3	-0.08
Overall	63		32.0	

H = 0.01 DF = 1 P = 0.933
H = 0.01 DF = 1 P = 0.913 (adjusted for ties)

Kruskal-Wallis Test: Topmouth gudgeon (TMG) versus Chub Length Groups

Length Groups	N	Median	Ave Rank	Z
1	59	0.00	31.0	-1.73
2	4	1.00	47.4	1.73
Overall	63		32.0	

H = 3.00 DF = 1 P = 0.083
H = 4.67 DF = 1 P = 0.031 (adjusted for ties)

Kruskal-Wallis Test: Fish eggs versus Chub Length Groups

Length Groups	N	Median	Ave Rank	Z
1	59	0.00	32.0	0.00
2	4	0.00	32.0	0.00
Overall	63		32.0	

H = 0.00 DF = 1 P = 1.000

Kruskal-Wallis Test: Total Aerial Insects versus Chub Length Groups

Length Groups	N	Median	Ave Rank	Z
1	59	1.00	32.2	0.39
2	4	1.00	28.5	-0.39
Overall	63		32.0	

H = 0.16 DF = 1 P = 0.693
H = 0.17 DF = 1 P = 0.678 (adjusted for ties)

Kruskal-Wallis Test: Araneida versus Chub Length Groups

Length Groups	N	Median	Ave Rank	Z
1	59	0.00	32.0	0.00
2	4	0.00	32.0	0.00
Overall	63		32.0	

H = 0.00 DF = 1 P = 1.000

Kruskal-Wallis Test: Coleoptera (Weevil) versus Chub Length Groups

Length Groups	N	Median	Ave Rank	Z
1	59	0.00	32.0	0.06
2	4	0.00	31.5	-0.06
Overall	63		32.0	

H = 0.00 DF = 1 P = 0.955
H = 0.07 DF = 1 P = 0.795 (adjusted for ties)

Kruskal-Wallis Test: Debris versus Chub Length Groups

Length Groups	N	Median	Ave Rank	Z
1	59	1.00	32.0	0.00
2	4	1.00	32.0	0.00
Overall	63		32.0	

H = 0.00 DF = 1 P = 1.000

Table H10.31 Comparison of the diet of chub between sampling dates (1, 28 April 2005; 2, 10 May 2005; 3, 16 May 2005) using non-parametric statistics

Kruskal-Wallis Test: Total Plant Material versus Date

Date	N	Median	Ave Rank	Z
1	13	1.000	37.8	1.28
2	33	1.00	31.3	-0.33
3	17	1.00	29.0	-0.80
Overall	63		32.0	

H = 1.82 DF = 2 P = 0.402
H = 3.06 DF = 2 P = 0.216 (adjusted for ties)

Kruskal-Wallis Test: Ephemeridae versus Date

Date	N	Median	Ave Rank	Z
1	13	0.00	31.0	-0.22
2	33	0.00	32.9	0.41
3	17	0.00	31.0	-0.26
Overall	63		32.0	

H = 0.17 DF = 2 P = 0.918
H = 1.85 DF = 2 P = 0.397 (adjusted for ties)

Kruskal-Wallis Test: Total Indet. Aerial Diptera versus Date

Date	N	Median	Ave Rank	Z
1	13	0.00	32.0	0.00
2	33	0.00	32.0	0.00
3	17	0.00	32.0	0.00
Overall	63		32.0	

H = 0.00 DF = 2 P = 1.000

Kruskal-Wallis Test: Mud, sand etc. versus Date

Date	N	Median	Ave Rank	Z
1	13	0.00	32.9	0.20
2	33	0.00	31.5	-0.25
3	17	0.00	32.4	0.09
Overall	63		32.0	

H = 0.07 DF = 2 P = 0.966
H = 0.50 DF = 2 P = 0.778 (adjusted for ties)

Kruskal-Wallis Test: Astacidae Adults versus Date

Date	N	Median	Ave Rank	Z
1	13	0.00	32.0	0.00
2	33	0.00	32.0	0.00
3	17	0.00	32.0	0.00
Overall	63		32.0	

H = 0.00 DF = 2 P = 1.000

Kruskal-Wallis Test: Total Aerial Insects versus Date

Date	N	Median	Ave Rank	Z
1	13	1.00	32.3	0.06
2	33	1.00	33.4	0.62
3	17	0.00	29.1	-0.75
Overall	63		32.0	

H = 0.60 DF = 2 P = 0.742
H = 0.66 DF = 2 P = 0.719 (adjusted for ties)

Kruskal-Wallis Test: Dermaptera (Earwig) versus Date

Date	N	Median	Ave Rank	Z
1	13	0.00	32.0	0.00
2	33	0.00	32.0	0.00
3	17	0.00	32.0	0.00
Overall	63		32.0	

H = 0.00 DF = 2 P = 1.000

Table H10.32 Comparison of the diet between species(1, Trout/2, Chub) using non-parametric statistics

Kruskal-Wallis Test: Macrophytes versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	68.7	-0.90
2	63	0.00E+00	75.0	0.90
Overall	142		71.5	

H = 0.82 DF = 1 P = 0.366
H = 1.59 DF = 1 P = 0.208 (adjusted for ties)

Kruskal-Wallis Test: Thistle versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.3	0.26
2	63	0.00E+00	70.5	-0.26
Overall	142		71.5	

H = 0.07 DF = 1 P = 0.796
H = 1.61 DF = 1 P = 0.205 (adjusted for ties)

Kruskal-Wallis Test: Debris versus Species

Species	N	Median	Ave Rank	Z
1	79	1.00	71.5	0.00
2	63	1.00	71.5	0.00
Overall	142		71.5	

H = 0.00 DF = 1 P = 1.000

Kruskal-Wallis Test: Total Plant Material versus Species

Species	N	Median	Ave Rank	Z
1	79	1.00	69.1	-0.78
2	63	1.00	74.5	0.78
Overall	142		71.5	

H = 0.60 DF = 1 P = 0.438
H = 1.14 DF = 1 P = 0.285 (adjusted for ties)

Kruskal-Wallis Test: Topmouth gudgeon (TMG) versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.8	0.41
2	63	0.00E+00	69.9	-0.41
Overall	142		71.5	

H = 0.17 DF = 1 P = 0.680
H = 0.25 DF = 1 P = 0.614 (adjusted for ties)

Kruskal-Wallis Test: Fish egg versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.9	0.13
2	63	0.00E+00	71.0	-0.13
Overall	142		71.5	

H = 0.02 DF = 1 P = 0.897
H = 0.80 DF = 1 P = 0.372 (adjusted for ties)

Kruskal-Wallis Test: Tanypodinae Larvae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.1	0.52
2	63	0.00E+00	69.5	-0.52
Overall	142		71.5	

H = 0.27 DF = 1 P = 0.605
H = 3.26 DF = 1 P = 0.071 (adjusted for ties)

Kruskal-Wallis Test: Tanypodinae Adults versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.5	0.00
2	63	0.00E+00	71.5	0.00
Overall	142		71.5	

H = 0.00 DF = 1 P = 1.000

Kruskal-Wallis Test: Orthocladinae Larvae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.7	0.39
2	63	0.00E+00	70.0	-0.39
Overall	142		71.5	

H = 0.15 DF = 1 P = 0.698
H = 2.43 DF = 1 P = 0.119 (adjusted for ties)

Kruskal-Wallis Test: Orthocladinae Adults versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.5	0.00
2	63	0.00E+00	71.5	0.00
Overall	142		71.5	

H = 0.00 DF = 1 P = 1.000

Kruskal-Wallis Test: Simulium V versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.8	0.10
2	63	0.00E+00	71.1	-0.10
Overall	142		71.5	

H = 0.01 DF = 1 P = 0.923
H = 0.15 DF = 1 P = 0.698 (adjusted for ties)

Kruskal-Wallis Test: Simulium o L versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.9	0.13
2	63	0.00E+00	71.0	-0.13
Overall	142		71.5	

H = 0.02 DF = 1 P = 0.897
H = 0.80 DF = 1 P = 0.372 (adjusted for ties)

Kruskal-Wallis Test: Simulium spp versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.2	0.23
2	63	0.00E+00	70.6	-0.23
Overall	142		71.5	

H = 0.05 DF = 1 P = 0.820
H = 0.63 DF = 1 P = 0.427 (adjusted for ties)

Kruskal-Wallis Test: Indet. Chironomidae P versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	74.8	1.09
2	63	0.00E+00	67.3	-1.09
Overall	142		71.5	

H = 1.18 DF = 1 P = 0.277
H = 4.72 DF = 1 P = 0.030 (adjusted for ties)

Kruskal-Wallis Test: Indet. Chironomidae Larvae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	62.7	-2.84
2	63	0.00E+00	82.5	2.84
Overall	142		71.5	

H = 8.09 DF = 1 P = 0.004
H = 15.17 DF = 1 P = 0.000 (adjusted for ties)

Kruskal-Wallis Test: Indet. Chironomidae Adults versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.5	0.65
2	63	0.00E+00	69.0	-0.65
Overall	142		71.5	

H = 0.42 DF = 1 P = 0.518
H = 4.10 DF = 1 P = 0.043 (adjusted for ties)

Kruskal-Wallis Test on Ind. Chironomidae Total versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	67.4	-1.34
2	63	0.00E+00	76.7	1.34
Overall	142		71.5	

H = 1.80 DF = 1 P = 0.180
H = 2.56 DF = 1 P = 0.109 (adjusted for ties)

Kruskal-Wallis Test: Dicranotra Larvae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.4	-0.03
2	63	0.00E+00	71.6	0.03
Overall	142		71.5	

H = 0.00 DF = 1 P = 0.974
H = 0.03 DF = 1 P = 0.872 (adjusted for ties)

Kruskal-Wallis Test: Dicranota Adults versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.9	0.13
2	63	0.00E+00	71.0	-0.13
Overall	142		71.5	

H = 0.02 DF = 1 P = 0.897
H = 0.80 DF = 1 P = 0.372 (adjusted for ties)

Kruskal-Wallis Test: Gyrinidae Larvae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.3	0.26
2	63	0.00E+00	70.5	-0.26
Overall	142		71.5	

H = 0.07 DF = 1 P = 0.796
H = 1.61 DF = 1 P = 0.205 (adjusted for ties)

Kruskal-Wallis Test: Gyrinidae Adults versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.5	0.00
2	63	0.00E+00	71.5	0.00
Overall	142		71.5	

H = 0.00 DF = 1 P = 1.000

Kruskal-Wallis Test: Limnephilidae Larvae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.1	0.52
2	63	0.00E+00	69.5	-0.52
Overall	142		71.5	

H = 0.27 DF = 1 P = 0.605
H = 3.26 DF = 1 P = 0.071 (adjusted for ties)

Kruskal-Wallis Test: Limnephilidae with case versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.4	0.62
2	63	0.00E+00	69.1	-0.62
Overall	142		71.5	

H = 0.38 DF = 1 P = 0.535
H = 2.73 DF = 1 P = 0.098 (adjusted for ties)

Kruskal-Wallis Test: Limnephilidae Adults

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.4	-0.03
2	63	0.00E+00	71.6	0.03
Overall	142		71.5	

H = 0.00 DF = 1 P = 0.974
H = 0.03 DF = 1 P = 0.872 (adjusted for ties)

Kruskal-Wallis Test: Athripsodes Larvae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.7	0.72
2	63	0.00E+00	68.7	-0.72
Overall	142		71.5	

H = 0.52 DF = 1 P = 0.470
H = 2.66 DF = 1 P = 0.103 (adjusted for ties)

Kruskal-Wallis Test: Athripsodes with case versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	70.8	-0.24
2	63	0.00E+00	72.4	0.24
Overall	142		71.5	

H = 0.06 DF = 1 P = 0.813
H = 0.08 DF = 1 P = 0.773 (adjusted for ties)

Kruskal-Wallis Test: Trichoptera Larvae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	67.4	-1.33
2	63	0.00E+00	76.7	1.33
Overall	142		71.5	

H = 1.78 DF = 1 P = 0.182
H = 9.06 DF = 1 P = 0.003 (adjusted for ties)

Kruskal-Wallis Test: Mesovelidae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.7	0.39
2	63	0.00E+00	70.0	-0.39
Overall	142		71.5	

H = 0.15 DF = 1 P = 0.698
H = 2.43 DF = 1 P = 0.119 (adjusted for ties)

Kruskal-Wallis Test on Paraleptophlebia Larvae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.7	0.39
2	63	0.00E+00	70.0	-0.39
Overall	142		71.5	

H = 0.15 DF = 1 P = 0.698
H = 2.43 DF = 1 P = 0.119 (adjusted for ties)

Kruskal-Wallis Test: Paraleptophlebia Adults versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.5	0.00
2	63	0.00E+00	71.5	0.00
Overall	142		71.5	

H = 0.00 DF = 1 P = 1.000

Kruskal-Wallis Test: Baetidae Larvae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	74.1	0.84
2	63	0.00E+00	68.3	-0.84
Overall	142		71.5	

H = 0.70 DF = 1 P = 0.403
H = 3.25 DF = 1 P = 0.071 (adjusted for ties)

Kruskal-Wallis Test: Baetidae Adults versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.7	0.39
2	63	0.00E+00	70.0	-0.39
Overall	142		71.5	

H = 0.15 DF = 1 P = 0.698
H = 2.43 DF = 1 P = 0.119 (adjusted for ties)

Kruskal-Wallis Test: Ephemera Larvae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	67.0	-1.46
2	63	0.00E+00	77.1	1.46
Overall	142		71.5	

H = 2.13 DF = 1 P = 0.144
H = 11.96 DF = 1 P = 0.001 (adjusted for ties)

Kruskal-Wallis Test on Ephemera Adults versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	70.8	-0.23
2	63	0.00E+00	72.4	0.23
Overall	142		71.5	

H = 0.05 DF = 1 P = 0.820
H = 0.51 DF = 1 P = 0.475 (adjusted for ties)

Kruskal-Wallis Test: Ephemeridae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.7	0.06
2	63	0.00E+00	71.3	-0.06
Overall	142		71.5	

H = 0.00 DF = 1 P = 0.949
H = 0.04 DF = 1 P = 0.842 (adjusted for ties)

Kruskal-Wallis Test: Collembola versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.9	0.13
2	63	0.00E+00	71.0	-0.13
Overall	142		71.5	

H = 0.02 DF = 1 P = 0.897
H = 0.80 DF = 1 P = 0.372 (adjusted for ties)

Kruskal-Wallis Test: Sisyridae Larvae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.8	0.10
2	63	0.00E+00	71.1	-0.10
Overall	142		71.5	

H = 0.01 DF = 1 P = 0.923
H = 0.15 DF = 1 P = 0.698 (adjusted for ties)

Kruskal-Wallis Test: Sisyridae Adults versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.4	-0.03
2	63	0.00E+00	71.6	0.03
Overall	142		71.5	

H = 0.00 DF = 1 P = 0.974
H = 0.03 DF = 1 P = 0.872 (adjusted for ties)

Kruskal-Wallis Test: Corixidae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.3	0.26
2	63	0.00E+00	70.5	-0.26
Overall	142		71.5	

H = 0.07 DF = 1 P = 0.796
H = 1.61 DF = 1 P = 0.205 (adjusted for ties)

Kruskal-Wallis Test: Indet. Aquatic Insects versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	69.5	-0.65
2	63	0.00E+00	74.0	0.65
Overall	142		71.5	

H = 0.42 DF = 1 P = 0.516
H = 5.12 DF = 1 P = 0.024 (adjusted for ties)

Kruskal-Wallis Test: Cyclopoidae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.0	0.48
2	63	0.00E+00	69.6	-0.48
Overall	142		71.5	

H = 0.23 DF = 1 P = 0.628
H = 1.93 DF = 1 P = 0.164 (adjusted for ties)

Kruskal-Wallis Test: Astacidae Juveniles versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.1	0.19
2	63	0.00E+00	70.8	-0.19
Overall	142		71.5	

H = 0.04 DF = 1 P = 0.847
H = 0.31 DF = 1 P = 0.580 (adjusted for ties)

Kruskal-Wallis Test: Astacidae Adults versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.9	0.13
2	63	0.00E+00	71.0	-0.13
Overall	142		71.5	

H = 0.02 DF = 1 P = 0.897
H = 0.80 DF = 1 P = 0.372 (adjusted for ties)

Kruskal-Wallis Test: *Gammarus pulex* versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	69.3	-0.73
2	63	0.00E+00	74.3	0.73
Overall	142		71.5	

H = 0.53 DF = 1 P = 0.467
H = 0.68 DF = 1 P = 0.410 (adjusted for ties)

Kruskal-Wallis Test: Nematocera versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.6	0.34
2	63	0.00E+00	70.2	-0.34
Overall	142		71.5	

H = 0.12 DF = 1 P = 0.732
H = 0.14 DF = 1 P = 0.709 (adjusted for ties)

Kruskal-Wallis Test: Tipulidae versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.3	0.59
2	63	0.00E+00	69.2	-0.59
Overall	142		71.5	

H = 0.34 DF = 1 P = 0.558
H = 1.92 DF = 1 P = 0.166 (adjusted for ties)

Kruskal-Wallis Test on Diptera Fly versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.8	0.42
2	63	0.00E+00	69.9	-0.42
Overall	142		71.5	

H = 0.18 DF = 1 P = 0.675
H = 0.89 DF = 1 P = 0.345 (adjusted for ties)

Kruskal-Wallis Test: Diptera Wing versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.7	0.71
2	63	0.00E+00	68.8	-0.71
Overall	142		71.5	

H = 0.50 DF = 1 P = 0.479
H = 1.18 DF = 1 P = 0.278 (adjusted for ties)

Kruskal-Wallis Test: Total Indet. Aerial Diptera versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.5	0.00
2	63	0.00E+00	71.5	0.00
Overall	142		71.5	

H = 0.00 DF = 1 P = 1.000

Kruskal-Wallis Test: Coleoptera Beetle versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	76.6	1.66
2	63	0.00E+00	65.1	-1.66
Overall	142		71.5	

H = 2.75 DF = 1 P = 0.098
H = 9.66 DF = 1 P = 0.002 (adjusted for ties)

Kruskal-Wallis Test: Coleoptera Weevil versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.2	0.23
2	63	0.00E+00	70.6	-0.23
Overall	142		71.5	

H = 0.05 DF = 1 P = 0.818
H = 0.64 DF = 1 P = 0.422 (adjusted for ties)

Kruskal-Wallis Test: Heteroptera versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.6	0.36
2	63	0.00E+00	70.1	-0.36
Overall	142		71.5	

H = 0.13 DF = 1 P = 0.722
H = 1.24 DF = 1 P = 0.266 (adjusted for ties)

Kruskal-Wallis Test: Insect Head Capsule versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	71.5	-0.01
2	63	0.00E+00	71.5	0.01
Overall	142		71.5	

H = 0.00 DF = 1 P = 0.993
H = 0.00 DF = 1 P = 0.989 (adjusted for ties)

Kruskal-Wallis Test: Insect Cuticle Fragment versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.2	0.55
2	63	0.00E+00	69.4	-0.55
Overall	142		71.5	

H = 0.30 DF = 1 P = 0.584
H = 1.40 DF = 1 P = 0.237 (adjusted for ties)

Kruskal-Wallis Test: Indet. Aerial Insects versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.7	0.40
2	63	0.00E+00	69.9	-0.40
Overall	142		71.5	

H = 0.16 DF = 1 P = 0.687
H = 0.37 DF = 1 P = 0.543 (adjusted for ties)

Kruskal-Wallis Test: Total Aerial Insects versus Species

Species	N	Median	Ave Rank	Z
1	79	1.000	76.4	1.59
2	63	1.000	65.4	-1.59
Overall	142		71.5	

H = 2.52 DF = 1 P = 0.113
H = 2.67 DF = 1 P = 0.102 (adjusted for ties)

Kruskal-Wallis Test on *Asellus* spp versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	74.0	0.81
2	63	0.00E+00	68.4	-0.81
Overall	142		71.5	

H = 0.65 DF = 1 P = 0.420
H = 2.60 DF = 1 P = 0.107 (adjusted for ties)

Kruskal-Wallis Test: Dermaptera Earwig versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.1	0.52
2	63	0.00E+00	69.5	-0.52
Overall	142		71.5	

H = 0.27 DF = 1 P = 0.605
H = 3.26 DF = 1 P = 0.071 (adjusted for ties)

Kruskal-Wallis Test: Diplopodae Millipede versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.1	0.52
2	63	0.00E+00	69.5	-0.52
Overall	142		71.5	

H = 0.27 DF = 1 P = 0.605
H = 3.26 DF = 1 P = 0.071 (adjusted for ties)

Kruskal-Wallis Test: Araneida versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	74.3	0.91
2	63	0.00E+00	68.0	-0.91
Overall	142		71.5	

H = 0.82 DF = 1 P = 0.365
H = 5.83 DF = 1 P = 0.016 (adjusted for ties)

Kruskal-Wallis Test: Nematoda versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.5	0.65
2	63	0.00E+00	69.0	-0.65
Overall	142		71.5	

H = 0.42 DF = 1 P = 0.518
H = 4.10 DF = 1 P = 0.043 (adjusted for ties)

Kruskal-Wallis Test: Trematoda versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	73.1	0.52
2	63	0.00E+00	69.5	-0.52
Overall	142		71.5	

H = 0.27 DF = 1 P = 0.605
H = 3.26 DF = 1 P = 0.071 (adjusted for ties)

Kruskal-Wallis Test: Mud, sand etc. versus Species

Species	N	Median	Ave Rank	Z
1	79	0.00E+00	72.0	0.17
2	63	0.00E+00	70.9	-0.17
Overall	142		71.5	

H = 0.03 DF = 1 P = 0.868
H = 0.17 DF = 1 P = 0.677 (adjusted for ties)

Appendix I

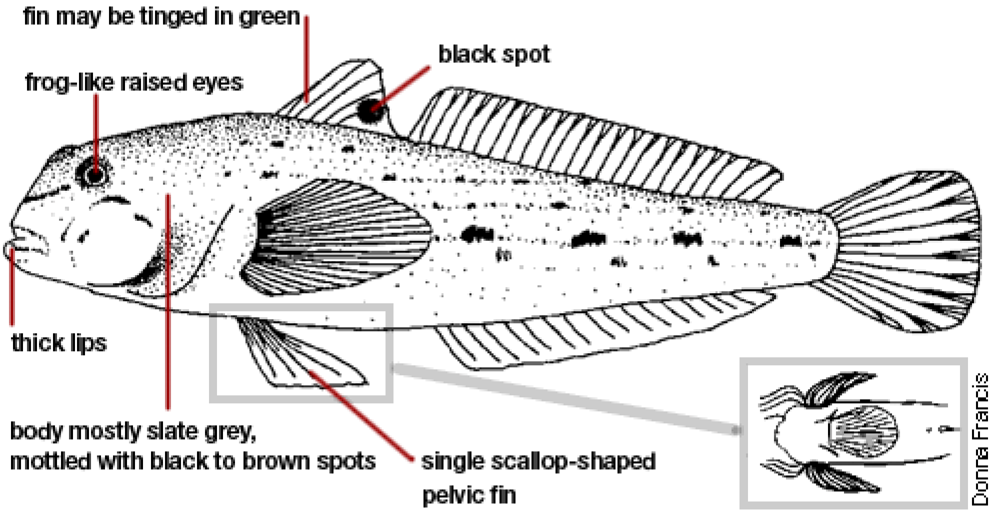
ID Card for Round Goby (*Neogobius melanostomus*) as prepared by the Minnesota Sea Grant (Minnesota Sea Grant, 2008)

Round Goby (*Neogobius melanostomus*)

The round goby may pose a serious threat to North American water ecosystems, with potential impacts on sport and commercial fishing. Since its discovery in the St. Clair River in 1990, this bottom-dwelling fish has rapidly spread to many areas of the Great Lakes. Once established, populations typically increase rapidly. The round goby can displace native fish, eat their eggs and young, take over optimal habitat, spawn multiple times a season, and survive in poor quality water — giving them a competitive advantage.

Anglers, commercial fishermen, and fishery professionals should know how to identify the round goby. Often, anglers are the first to discover round gobies because these aggressive fish are commonly caught by hook and line. Your help is vital to report new sightings and to prevent their spread.

Identify Round Goby



General Characteristics

1) No other native fish in the Great Lakes has the single pelvic fin
2) Young are solid slate gray
3) Usually 3-6 inches (7-15 cm) long, may be up to 10 inches (25 cm)

What You Can Do

1) Learn to identify the round goby
2) Always drain water from your boat, livewell, and bilge before leaving any water access
3) Always dispose of your unwanted bait on land
4) Never dip your bait bucket into a lake or river if it has water in it from another
5) Never dump live fish from one body of water into another
6) If you catch a round goby in the Great Lakes or other waters, kill it, freeze it, and call the MN Department of Natural Resources Invasive Species Program in St. Paul, 1-888-MINNDNR, or Doug Jensen of Minnesota Sea Grant. **Do not throw round gobies back alive!**

Know the Rules!

Round goby specimens are needed to confirm sightings, but many Great Lakes jurisdictions have different rules regarding possession and transport. Always contact your local resource management agency for instructions. Never transport a live round goby.