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The dynamics of larval and 0+ juvenile fish populations in lowland rivers

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ABSTRACT

THE DYNAMICS OF LARVAL AND 0+ JUVENILE FISH POPULATIONS IN LOWLAND RIVERS

Early development represents a critical period in the life cycle of fishes, with a wide range of biotic and abiotic factors influencing eventual recruitment to the adult populations. Despite their key importance in the sustainability of fish populations, however, there is a dearth of knowledge regarding the ecology of 0+ fish communities in lowland rivers. Thus, the factors affecting 0+ fish populations were studied in three lowland river catchments, namely the River Trent, the Warwickshire Avon and the Yorkshire Ouse, representing a range of topographical and biotopical characteristics. The 0+ fish populations were sampled monthly between May 1999 and October 2004 inclusive by micromesh seine netting and point abundance sampling by electric fishing. Captured fish were used to obtain information on 0+ fish community structure, growth, spawning periodicity, and the food and feeding relationships of larval and 0+ juvenile fish.

In the Trent and, particularly, the Avon, rheophilic fish species were heavily outnumbered by eurytopic species due to a lack of suitable spawning and nursery habitat for rheophilic species. Strictly rheophilic species were most abundant in the Ouse catchment where the habitat was characterised by fast-flowing water and a sand or gravel substratum. Almost all fish species used floodplain waterbodies at some point in their life history. For some species this use was transitional (rheophilic species) or facultative (eurytopic species), whereas for others it may be obligate (limnophilic species). Floodplain waterbodies also served as refugia for both 0+ and >0+ fish in winter, especially during floods.

Floodplain waterbodies provided enhanced feeding conditions for 0+ fish, with zooplankton diversity, size ranges and density being greater than in main river channels. For all fish species, ontogenetic shifts in resource use were identified. Young larvae had narrow diet spectra and the greatest interspecific diet overlap, with feeding diversity and the importance of species-specific traits increasing with development. There were significant, positive relationships between prey size and gape height for larvae, but not for juveniles. The majority of fish, however, consumed prey substantially smaller than the maximum theoretically possible inferred from their gape. Some taxa were consistently selected over others, irrespective of size, suggesting that taxa-specific, as well as size-specific prey characteristics, may be important in the selection process.

Chub and bleak, and to a lesser extent bream, gudgeon and minnow, adopted fractional or protracted spawning strategies, while dace, roach and perch spawned only once per season. Multiple spawning events are important for recruitment success as they disperse the mortality risk of the early developmental stages. In some years, therefore, relatively strong year classes may result, despite high mortality in early summer and smaller than average mean lengths, providing overwinter conditions are not severe.

Growth of 0+ fish was positively correlated with water temperature and negatively correlated with river discharge, while year-class strength (YCS) was positively correlated with 0+ fish growth and with the position of the Gulf Stream. River discharge (rather than water temperature) may be the key factor in determining YCS, however, either directly or indirectly. For example, a poor year class may be the result of elevated river flows causing high mortality during a critical period in the life history of a particular fish species, such as the larval period, or it may equally be the result of poor growth caused by a reduction in water temperature, discharge-associated increases in energy expenditure or a lack of suitable food. In most years it is likely that indirect effects will prevail over direct effects due to non-synchronicity of periods of elevated discharge and fish hatching, although this will differ between rivers. It could be that, in effect, water temperature determines potential YCS while discharge determines realised YCS.

CHAPTER ONE

GENERAL INTRODUCTION

1.1 THE IMPORTANCE OF LOWLAND RIVERS

Lowland rivers provide extremely important resources for industry, recreation and ecology. Many lowland rivers, for example, are used for potable water supply, abstraction for agriculture and industry, transport of freight, power generation and waste disposal (Cowx & Welcomme, 1998). In ecological terms, lowland rivers are important for a range of animal and plant species, and for ecosystem functioning as a whole. Lowland rivers, and particularly their floodplains, represent major spawning and nursery areas for fluvial fishes (Copp & Peňáz, 1988; Copp, 1989b; Junk *et al.*, 1989). A range of different habitats can be distinguished in lowland rivers: (1) the main river channel and its tributaries (eupotamon); (2) open, connected sidearms (parapotamon); (3) disconnected sidearms with ongoing terrestrification processes and a strong development of aquatic vegetation (plesiopotamon); and (4) strongly disconnected and fragmented waterbodies and wetlands (palaeopotamon) (Schiemer, 2000). The key attribute in the functioning of lowland rivers is the maintenance of hydrological connectivity between each of the habitat types (Schiemer, 2000).

1.2 THE LOWLAND RIVER ECOSYSTEM

The Flood Pulse Concept (Junk *et al.*, 1989) proposes that the pulsing of river discharge, the flood pulse that extends the river onto the floodplain, is the major force controlling biota in lowland rivers. Flood pulses control biota in three ways: (1) directly by facilitating migration of animals; (2) indirectly by enhancing primary production; and (3) by structuring habitats (Junk *et al.*, 1989). Depending upon magnitude, flood pulses connect main river channels to various parts of their floodplains. Floodplain inundation in natural rivers is thought to be beneficial, if not essential, for recruitment of many fish species by providing access to suitable spawning and nursery habitat (Copp, 1989b; Junk *et al.*, 1989; Cattanéo *et al.*, 2001; King *et al.*, 2003; Bonvechio & Allen, 2005). Many fish species spawn on flooded terrestrial vegetation in the floodplain, while others may migrate to or between floodplain waterbodies ordinarily isolated from the main river channel. Flood pulses may also liberate fish from isolated floodplain waterbodies, thereby increasing recruitment to the main river (Halačka *et al.*, 1998; Bartošová & Jurajda, 2001; Bartošová *et al.*, 2001; Grift *et al.*, 2001a, b; Jurajda *et al.*, 2004).

Lateral exchange processes during floods may expose food resources that were previously unattainable to fish in the main river channel (Schiemer, 2000). Floodplain waterbodies are often more productive than main river channels in terms of phytoplankton and zooplankton (Junk *et al.*, 1989), and receding water levels promote expulsion of these organisms to main river channels (Schiemer *et al.*, 2001b). Furthermore, flood pulses allow movement of nutrients and dead or live organic matter between rivers and their floodplains (Schiemer, 2000), and *vice versa*, with flood pulses frequently followed by peaks in primary production (Junk *et al.*, 1989).

On a longer time scale, flood pulses are also responsible for structuring habitats, for example by washing out sediment, aquatic vegetation and other organic matter, and creating gravel shoals, levees, secondary channels, backwaters and oxbow lakes. These processes maintain lowland rivers in a state of 'dynamic equilibrium', since floodplain habitats may variously be in stages of rejuvenation (via erosion) or terrestrialisation (via sedimentation), accounting for the high habitat and, thus, biotic diversity of lowland rivers (Junk *et al.*, 1989).

1.3 THE ICHTHYOFAUNA OF LOWLAND RIVERS

Fish communities in lowland rivers are characterised by high diversity, which reflects the structural diversity and habitat richness of inshore zones and connected floodplains (Schiemer, 2000). The fish of lowland rivers have evolved to utilise the various habitats in a number of ways and, indeed, can be classified into guilds according to their reproductive strategies (Schiemer & Waidbacher, 1992). Rheophilic fish species require flowing water to spawn and, as such, are usually found in fast-flowing, well-oxygenated stretches of river where the substratum is characterised by gravel or sand. Limnophilic species, on the other hand, require still water and prolific aquatic vegetation to deposit their eggs upon and, as such, are most abundant in isolated floodplain waterbodies or backwaters and oxbow lakes. Eurytopic species have less strict requisites for spawning, and are thus able to establish populations in a wider range of waterbodies than less adaptable species. Reproductive strategies can be further classified according to where particular species preferentially deposit their eggs (Balon, 1975a). Lithophilic species, for instance, deposit their eggs on gravel, while phytophils use aquatic vegetation as a substrate, phytolithophils use either vegetation or gravel, and psammophils use sand. In natural floodplain systems, this diversity in spawning requirements often leads to lateral zonation of fish reproduction, with a sequence of rheophilic-to-eurytopic-to-limnophilic fish species corresponding with a lotic-to-lentic succession of habitat (Copp & Peňáz, 1988; Copp, 1989b; Copp *et al.*, 1991, 1994).

1.4 THE STATUS OF LOWLAND RIVERS IN EUROPE

The majority of lowland rivers in Europe have been modified to some extent (Cowx & Welcomme, 1998). Typical examples include impoundment and embankment of stretches of river for flood defence or hydroelectric power generation. Such modifications inevitably reduce connectivity, either longitudinally or laterally, and detrimental impacts upon fish populations are universal (e.g. Peňáz *et al.*, 1995; Scheidegger & Bain, 1995; Guti, 1998; Humphries *et al.*, 1999, 2002; Humphries & Lake, 2000; Buijse *et al.*, 2002; Černý *et al.*, 2003; Holcík, 2003; Bartl & Keckeis, 2004; Pilcher *et al.*, 2004). Anadromous and rheophilic fish species, for example, may be unable to migrate to their spawning grounds due to loss of longitudinal connectivity, while loss of lateral (horizontal) connectivity may prevent limnophilic species from gaining access to their spawning habitats in the floodplain. As such, a common symptom of river modification is the loss or reduction of specialised (stenotopic) fish species in favour of a small number of eurytopic species. For example, 30 of the 52 fish species that occur in the River Danube are considered vulnerable or endangered due to the impacts of river modification (Schiemer & Waidbacher, 1992), and similar shifts in community structure have been reported in the rivers Rhine, Rhône, Warta, Pilica, Meuse and Morava in mainland Europe, and the River Great Ouse in the UK (Copp, 1990a, 1992a, b; Jurajda, & Peňáz, 1994; Jurajda, 1995, 1999; Penczak & Kruk, 2000, 2005; Jurajda *et al.*, 2001; Grift *et al.*, 2001b, 2003; Kruk & Penczak, 2003; Aarts *et al.*, 2004; Kruk, 2004; Penczak, 2004).

1.5 THE IMPORTANCE OF 0+ FISH

Fish are good indicators of the ecological integrity of lowland rivers because the various guilds integrate a wide range of conditions over their life cycles that are linked to the habitat requirements of particular species and ontogenetic stages (Copp, 1989b; Schiemer *et al.*, 1991, 2001b, 2003; Schiemer, 2000; Schmutz *et al.*, 2000). Larvae and 0+ juveniles may be particularly applicable in this respect as tolerable habitat conditions are often much narrower for such fish compared with older (larger) individuals, owing to the strict physical and energetic constraints imposed upon young fishes (Copp *et al.*, 1991; Schiemer *et al.*, 1991, 2001a, b; Schiemer & Waidbacher, 1992; Schiemer & Weiser, 1992). Furthermore, whereas adult fish may occur in a particular location for reasons other than reproduction, the presence of 0+ fish is a clear indication of the reproductive function of the area (Copp, 1989b).

Morphological and behavioural limitations often restrict early developmental stages of fish to specific habitats (Copp, 1992b) and, owing to the small size and fragility of such fish, the availability of suitable habitat during this period may thus be of considerable importance to their survival (Lightfoot & Jones, 1996; Mann *et al.*, 1997; Jurajda, 1999). For a fish population to persist within a given waterbody there must be habitat available, in sufficient quality and quantity, to all stages of development, for the range of activities undertaken by fish, such as feeding, spawning and resting, and as refuge from predators and elevated river flows. Implicit with this statement is that fish must be able to migrate between areas of habitat according to ontogenetic or temporal requirements. When this is not the case, a habitat bottleneck can occur, and fish population size and structure may be restricted.

1.6 THE CURRENT STUDY

To understand the importance and functional ecology of lowland river ecosystems with regard to fish life histories, information is required on the abundance, distribution, ichthyomass, production and population dynamics of the larval and juvenile fish populations (Welcomme, 1985, *fide* Copp & Peňáz, 1988). Despite their key importance in the sustainability of fish populations, there is still a dearth of knowledge regarding the ecology of 0+ fish communities in lowland rivers. This can be partly attributed to difficulties associated with the study of fish which undergo considerable changes in morphology and behaviour during early development. However, recent advances in identification of fish larvae (e.g. Pinder, 2001) have allowed interrogation of this issue. Thus, the 0+ fish populations were studied in three lowland river catchments, namely the River Trent, the Warwickshire Avon and the Yorkshire Ouse, representing a range of topographical and biotopical characteristics. The overall aim of the study was to examine a range of factors influencing the dynamics of the 0+ fish populations in these rivers, and to ascertain the causes of any differences in their respective fish communities. To this end, the study was divided into key topics which are addressed in Chapters 3 to 6. Specific objectives and hypotheses are provided at the start of each chapter.

Chapter 3 investigates the comparative 0+ fish populations of three lowland river catchments, with particular emphasis placed upon the species compositions, community structures, growth and spawning strategies of the fish populations therein. Parts of this chapter have already been published in Nunn *et al.* (2002, 2003b) (see Publications).

Chapter 4 investigates the availability of zooplankton to 0+ fish in lowland rivers and floodplain waterbodies, with particular emphasis placed upon on the species composition and density of key zooplankton groups in main river channels and floodplain areas.

Chapter 5 investigates the food and feeding relationships of larval and 0+ juvenile fish in lowland rivers and floodplain waterbodies, with particular emphasis placed upon spatial, interspecific and ontogenetic variations in diet composition and the mechanisms of prey selection.

Chapter 6 investigates the factors affecting the recruitment success of riverine fish populations, with particular emphasis placed upon the relationships between water temperature, river discharge, the position of the Gulf Stream and 0+ fish growth. Parts of this chapter have already been published in Nunn *et al.* (2003a) (see Publications).

Chapter 7 integrates the knowledge gained from the Chapters 3 to 6, and provides recommendations for further study.

CHAPTER TWO

GENERAL MATERIALS AND METHODS

2.1 STUDY AREAS

The study was carried out on three lowland river catchments, namely the River Trent, the Warwickshire Avon and the Yorkshire Ouse, representing a range of topographical and biotopical characteristics (Table 2.1). The River Trent and Yorkshire Ouse both flow to the Humber Estuary, and between them drain approximately one fifth of the area of England (Edwards *et al.*, 1997; Jarvie *et al.*, 1997). The Trent catchment includes a number of significant conurbations and has a history of severe pollution (Lester, 1975), while the Ouse drains a predominantly rural catchment and water quality is generally good (Jarvie *et al.*, 1997; Robson & Neal, 1997; Neal & Robson, 2000). The Warwickshire Avon is a major tributary of the River Severn, which flows in to the Bristol Channel, and suffered water quality problems similar to, though less severe than, those in the River Trent.

All three catchments have been modified to some extent. The lower Trent has been channelised in many areas and impounded by a number of large weirs and sluices, such as at Beeston, Stoke Bardolph, Holme Pierrepont and Cromwell lock. Water depths are artificially maintained for the transport of freight and pleasure craft by periodic dredging, and much of the floodplain has been claimed for urban development. Overbank flooding occurs relatively infrequently due to the regulated nature of the river. The Ouse and a number of its larger tributaries, such as the River Wharfe, are impounded by a succession of large weirs, whereas others (e.g. the River Nidd) have larger numbers of much smaller weirs or are largely unregulated (e.g. the River Swale). The Ouse itself is flanked by high embankments along much of its length, but overbank flooding occurs routinely in the winter due to rapid run-off from the Pennines. The Avon is also punctuated by weirs, such as those at Nafford and Pershore. Compared with the Trent and Ouse, the Avon is relatively unembanked, but much of the floodplain has been drained for agriculture. Overbank flooding occurs with intermediate frequency compared with the Trent and Ouse.

Table 2.1 Physical and chemical characteristics of the River Trent, Warwickshire Avon and Yorkshire Ouse catchments (Neal & Robson, 2000; Hilton *et al.*, 2002; Bowes *et al.*, 2005).

	Trent	Avon	Ouse
Physical			
River length (km)	274	179	200
Catchment size (km^2)	10 500	2 900	10 000
Mean river discharge (m^{3}s^{-1})	84	17	50
Mean water temperature (°C)	12.14	12.09	10.97
Chemical			
Mean SS (mg L^{-1})	18.86	25.31	21.90
Mean BOD (mg L^{-1})	6	3	2
Mean NO_3-N (mg L^{-1})	8.35	10.2	3.37
Mean PO_4-P (mg L^{-1})	1.13	2.05	0.12
Mean Cl (mg L^{-1})	118	60	30
Mean Ca (mg L^{-1})	105	113	62

2.1.1 The River Trent

The River Trent (Fig. 2.1) is 274 km long from its source on Biddulph Moor in north Staffordshire to its confluence with the Yorkshire Ouse at Trent Falls (Table 2.1; Cowx, 1991). The Trent is the third largest river in England and Wales, with a catchment area (10 500 km^2) that is comparable with those of the rivers Severn and Thames.

The Trent catchment is composed predominantly of Triassic Bunter Sandstones and Keuper Marls, with Jurassic Limestones and Clays to the south east of the catchment and Carboniferous rocks in the north Midlands (Jarvie *et al.*, 1997). The Trent rises from Carboniferous Coal Measures to the south-west of the Pennines, and flows in a southerly direction through Stoke-on-Trent to the confluence of the River Tame at Wychnor, before adopting a north-easterly course through Burton-on-Trent (Lester, 1975). Further downstream, the Trent is joined by the rivers Dove and Derwent from the north and the Soar and Anker from the south. The Dove and Derwent rise from the Carboniferous Millstone Grit of the Peak District, and drain an area of Carboniferous Limestone before flowing onto the Triassic Keuper Marl of the Trent valley (Lester,

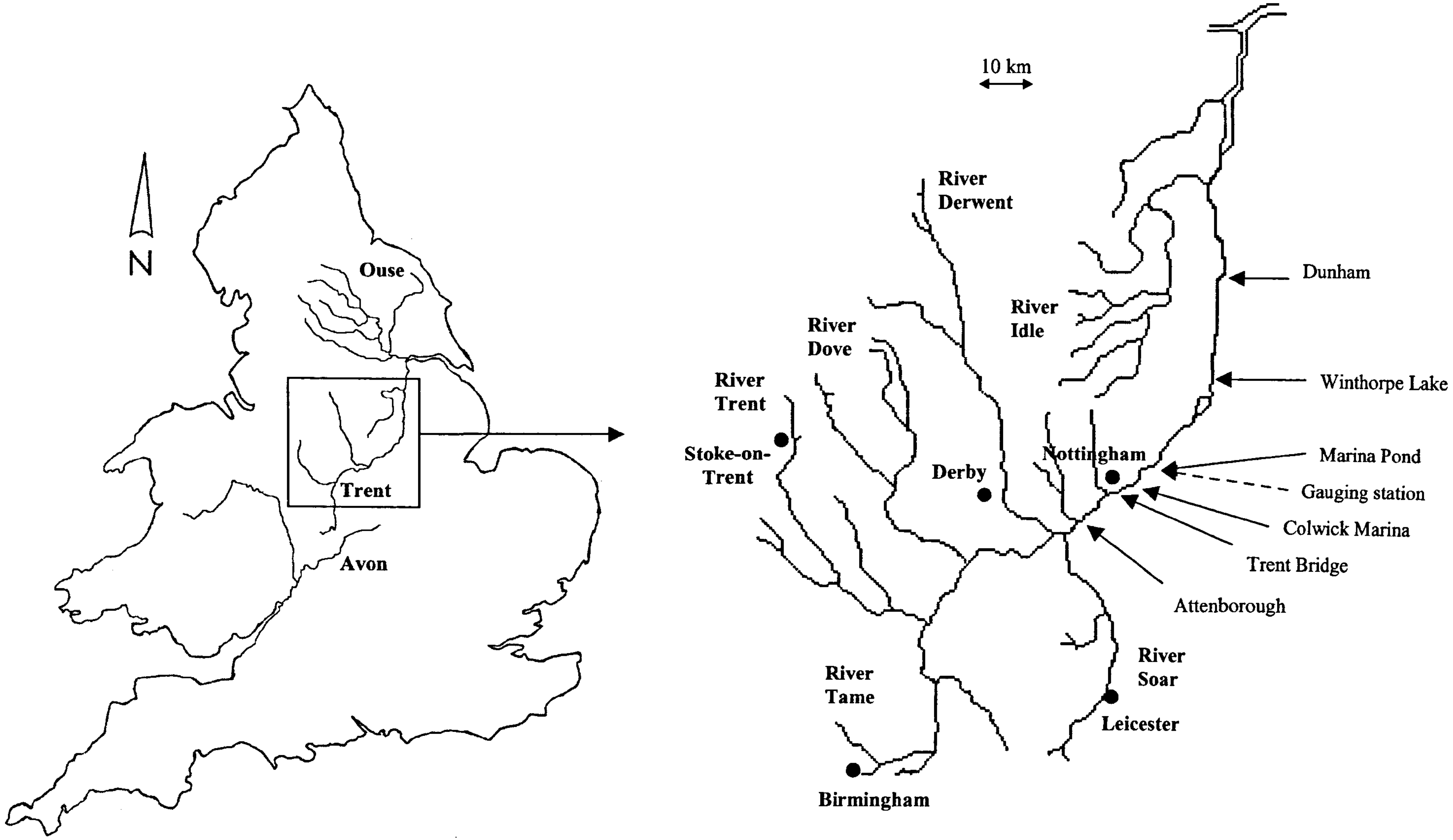

Fig. 2.1 Location of the River Trent catchment relative to the Warwickshire Avon and Yorkshire Ouse catchments, and River Trent site locations.

1975; Jarvie *et al.*, 1997, 2000). The rivers Soar and Anker drain the Triassic Keuper Marl and Carboniferous Coal Measures of Warwickshire and Leicestershire.

Through its tributaries, the Trent drains a number of large conurbations, including Birmingham, Leicester, Derby, Stoke-on-Trent and Nottingham. The intense industrialisation and urbanisation associated with these areas following the industrial revolution led to a deterioration in the water quality of the Trent (Mann, 1989; Jacklin, 1996). The upper reaches of the Trent receive the industrial and domestic effluents of Stoke-on-Trent, while effluents from Birmingham and the Black Country enter via the River Tame (Cowx & Broughton, 1986). Downstream of Burton-on-Trent, the River Soar (draining Leicester) and the River Erewash (draining several industrial towns in Nottinghamshire and Derbyshire) join the river. The city of Nottingham is situated on the Trent itself, but thereafter only two major towns, Newark-on-Trent and Scunthorpe, affect water quality before it reaches the Humber Estuary (Jacklin, 1996).

Fish populations of the River Trent

Prior to the industrial revolution, the Trent had diverse and prolific fish stocks, and supported salmon (*Salmo salar* L.) and eel (*Anguilla anguilla* (L.)) fisheries (Jacklin, 1996). However, with the expansion of industry, the fishery began to decline, and by 1920 the Tame was devoid of fish. Water quality reached its lowest level in the 1950s, and long stretches of the Trent suffered from a lack of dissolved oxygen and fish until the 1970s (Mann, 1989; Jacklin, 1996).

The imposition of pollution control measures by the Trent River Authority and its successors, Severn-Trent Water Authority, the National Rivers Authority and the Environment Agency, have resulted in improvements in the water quality of the River Trent (Cowx & Broughton, 1986; Mann, 1989). The diversion of industrial effluents to sewer, improved sewage treatment, introduction of biodegradable detergents and the cessation of coal gasification have all contributed to the progressive improvement in water quality (Jacklin, 1996). This, in turn, has resulted in a resurgence of the fish populations of the river (Mann, 1989). In the 1980s, the Trent was renowned as one of the premier river fisheries in the country, with catches usually dominated by roach (*Rutilus rutilus* (L.)) (Lyons, 1998). Since then, continued improvement in water quality has caused a shift in fish community structure, with a decline in the dominance of roach coinciding with an increase in the numbers of chub (*Leuciscus cephalus* (L.)) and bream (*Abramis brama* (L.)) (Cowx, 1991). Currently, the fish community of the lower Trent is characterised by roach, bream, chub, perch (*Perca fluviatilis* L.), bleak (*Alburnus alburnus* (L.)), dace (*Leuciscus leuciscus* (L.)) and gudgeon (*Gobio gobio* (L.)), although species such as barbel (*Barbus barbus* (L.)) and carp (*Cyprinus carpio* L.) are increasing in importance (Cooper & Wheatley, 1981; Cowx & Broughton, 1986; Mann, 1989; Cowx, 1991; Lyons & Lucas, 2002).

2.1.2 The Warwickshire Avon

The Warwickshire Avon (Fig. 2.2) is approximately 179 km long from its source near Naseby on the Northamptonshire and Leicestershire borders to its confluence with the River Severn at Tewkesbury, with a catchment that drains the majority of Warwickshire, and parts of Worcestershire, Gloucestershire, Oxfordshire, Leicestershire and Northamptonshire (Table 2.1; Bowes *et al.*, 2005).

The geology of the Avon catchment is dominated by Triassic Keuper Marl in the north-west, with an area of Carboniferous Coal Measures between Kenilworth, Tamworth and Nuneaton, while Jurassic Lower Lias Clays are present to the south and east. The Avon flows in an approximately south-westerly direction for the majority of its course, first passing through the town of Rugby before being joined by its first major tributary, the River Sowe, which drains Coventry. The river then passes through the conurbations of Leamington Spa and Warwick where it is joined by the River Leam. The River Stour joins the Avon below Stratford-upon-Avon, while the confluence of the River Arrow is approximately half way between Stratford-upon-Avon and Evesham. The river then meanders west towards Pershore, before turning south-west towards Tewkesbury.

Fish populations of the Warwickshire Avon

Although predominantly rural, there is a history of industrial activity in the catchment and, as a consequence, the Avon suffered from poor water quality until the 1950s (Environment Agency, 2000). As with the Trent, the reductions in water quality lead to an impoverished fish fauna. Since then, however, and particularly since the 1980s, large declines in BOD, ammonia, phosphate and nitrate loading have occurred, following the

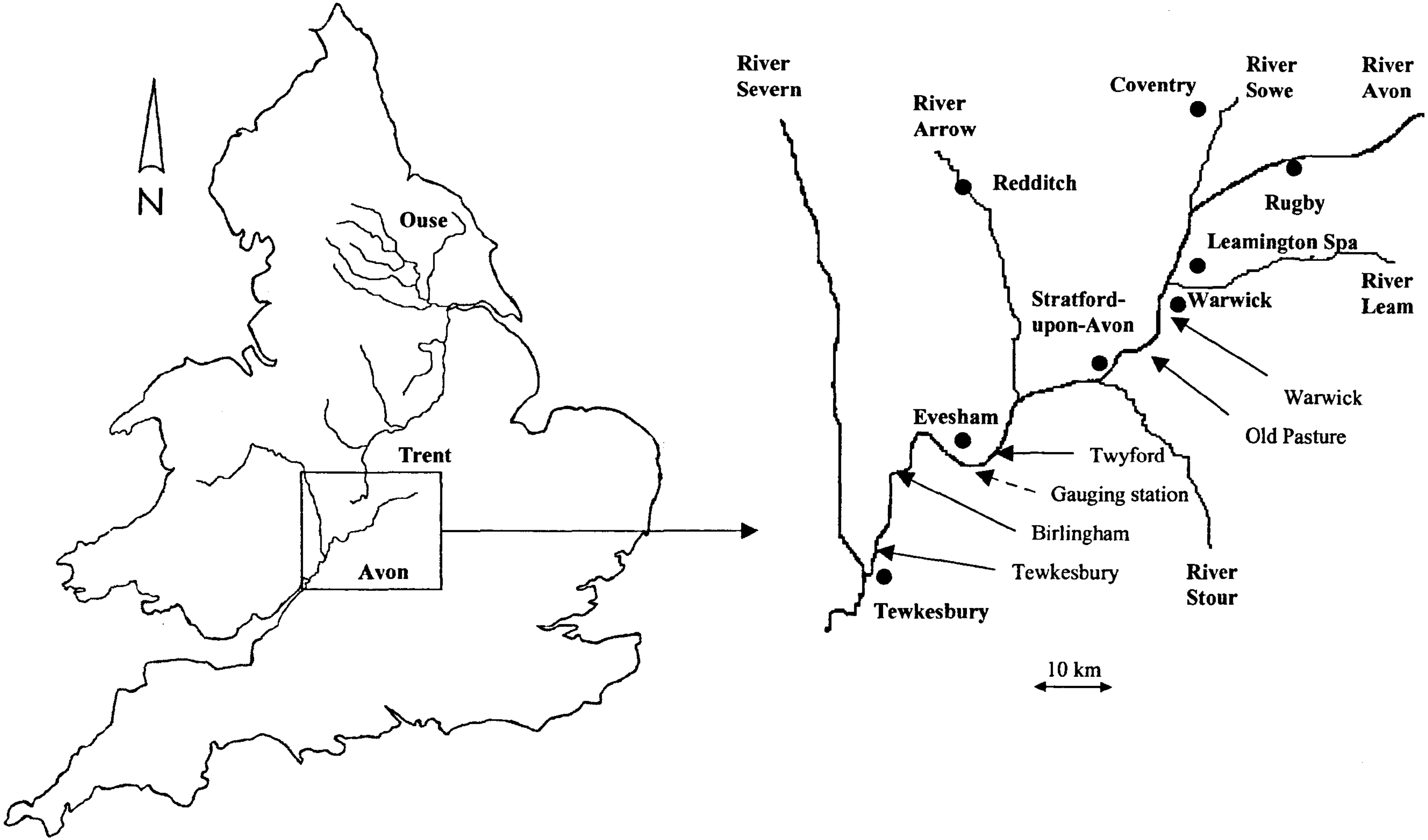

Fig. 2.2 Location of the Warwickshire Avon catchment relative to the River Trent and Yorkshire Ouse catchments, and Warwickshire Avon site locations.

diversion of industrial effluents to sewer and improved sewage treatment, and there has been a resurgence of the fish populations of the river (Environment Agency, 2000). In the 1970s and 1980s, the Avon was renowned as one of the premier river fisheries in the country, with catches usually dominated by roach and chub (Environment Agency, 2000). A range of fish species currently inhabits the Warwickshire Avon, with roach, chub, perch, bleak and bream the most abundant, while dace and barbel are also important in some reaches (Environment Agency, 2000).

2.1.3 The Yorkshire Ouse catchment

The Yorkshire Ouse (Fig. 2.3) is approximately 200 km long from its source near Hawes to its confluence with the River Trent at Trent Falls, and is the fourth largest river catchment in England and Wales, draining an area of over 10 000 km^2 (Table 2.1; Law *et al.*, 1997).

The Ouse (known as the River Ure in its upper reaches) rises in the Pennines and is formed by the combination of several small becks. The river flows east to Leyburn before turning towards Ripon and Boroughbridge. After its confluence with the River Swale (~3 km downstream of Boroughbridge), the river flows south-east and, at the confluence of Ouse Gill Beck, becomes known as the Ouse (Law *et al.*, 1997). The river then flows south to Nun Monkton where it is joined by the River Nidd. From this point, the river flows south-east towards the city of York and then south to Naburn weir, below which the river is tidal. After the confluence of the River Wharfe, the Ouse adopts a south-easterly course and is joined by the River Derwent at Barmby on the Marsh, the River Aire at Airmyn and the River Don at Goole, before its confluence with the River Trent at Trent Falls. Water quality is good upstream of York, but deteriorates downstream due to the impact of urban drainage, combined sewer overflows, Naburn sewage treatment works and inputs from the rivers Don, Aire and Foss (Lucas *et al.*, 1998).

Three Ouse tributaries, namely the rivers Swale, Nidd and Wharfe, are included in this study. The River Swale originates as a series of small becks in the northern Pennines. The river initially flows south before turning east towards Grinton. The river passes through Richmond and Catterick, and adopts a south-easterly course past Northallerton

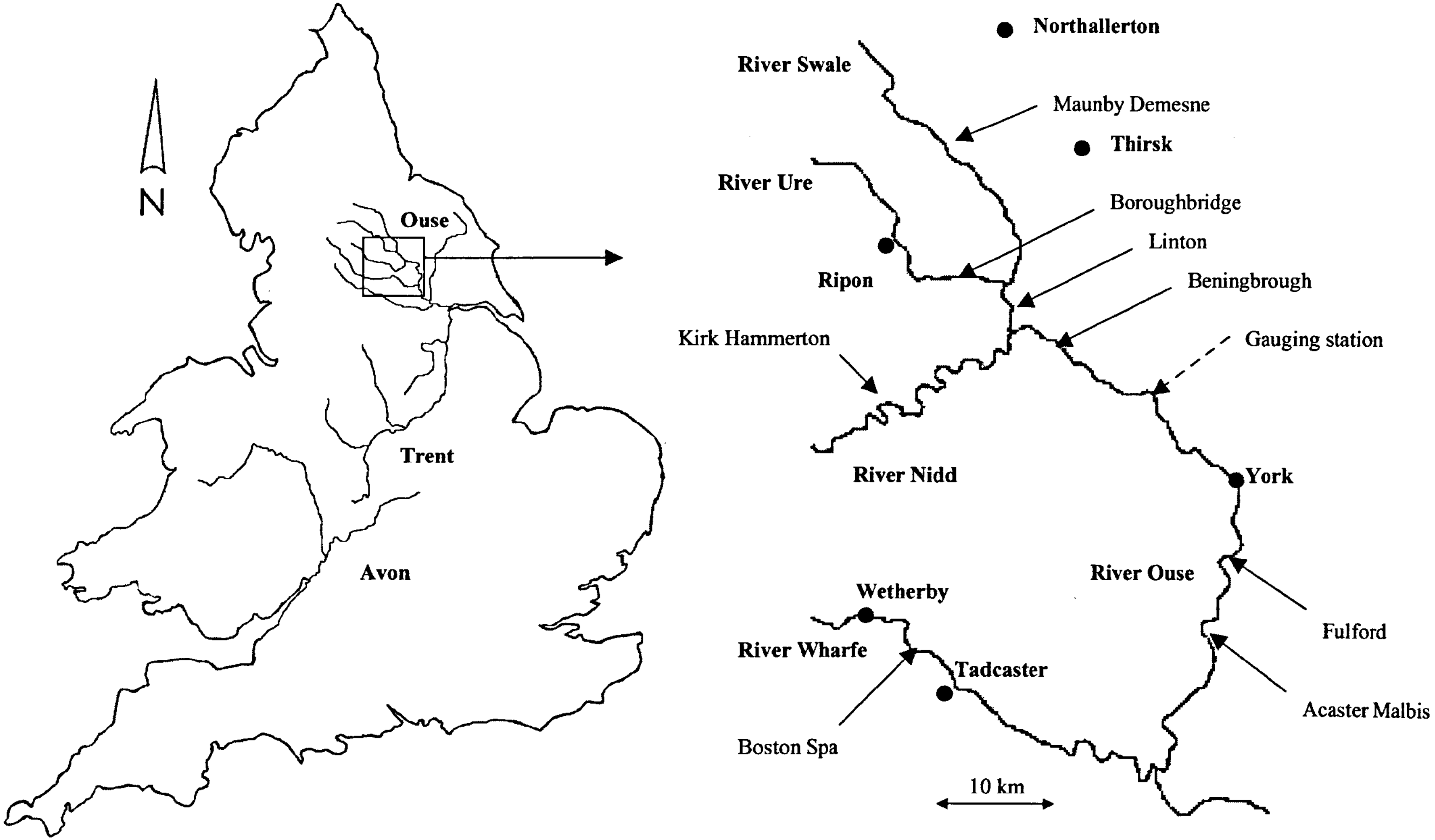

Fig. 2.3 Location of the Yorkshire Ouse catchment relative to the River Trent and Warwickshire Avon catchments, and Yorkshire Ouse site locations.

and Thirsk. The river then passes through a largely rural landscape before joining the Ouse (still known as the Ure at this point) near Boroughbridge, a total journal of approximately 100 km.

The River Nidd rises to the east of Great Whernside, and flows in a south-easterly direction past Pateley Bridge, Harrogate and Knaresborough. The river then turns north-east and flows through a predominantly rural landscape towards to its confluence with the Ouse at Nun Monkton, a total journey of approximately 97 km (Lucas & Batley, 1996; Lucas & Frear, 1997). The upper reaches of the Nidd have moderate gradients and are characterised by riffle-pool progressions with sections of faster, turbulent water and a boulder and cobble bed (Lucas *et al.*, 1998). The lower 30 km of the Nidd are highly convoluted, typically 10-15 m wide and 0.8-1.5 m deep (Lucas *et al.*, 1998, 2000; Lucas, 2000), with an average daily flow of approximately 8 $m^3.s^{-1}$ (Lucas & Batley, 1996).

The River Wharfe rises on the eastern flank of Peny-Ghent in the Pennines, and initially flows south-east through a steep-sided valley towards Grassington. The river turns south towards Addingham, and then flows east through Ilkley, Otley and Wetherby. From here, the Wharfe follows a south-easterly course through Boston Spa and Tadcaster, before joining the tidal Ouse near Cawood, a total journey of approximately 110 km.

The geology of the Ouse catchment is characterised by the Carboniferous Millstone grits and Carboniferous Limestone of the Pennines (Jarvie *et al.*, 1997; Law *et al.*, 1997). These are flanked by Coal Measures, which in the east give way to a north to south ridge of Magnesian Limestone (Law *et al.*, 1997). The rivers Swale, Ure, Nidd and Wharfe flow in a broadly eastwards direction, cutting across the Carboniferous rocks of the Pennines and the Triassic Sandstones of the Vale of York (Jarvie *et al.*, 1997).

Fish populations of the Yorkshire Ouse catchment

Compared to many UK rivers, the Yorkshire Ouse system possesses a relatively diverse fish fauna (Whitton & Lucas, 1997). The upper reaches, including those of the Swale, Ure, Nidd and Wharfe, have fish communities dominated by brown trout (*Salmo trutta* L.), salmon and grayling (*Thymallus thymallus* (L.)), with rheophilic cyprinids, such as chub, barbel, gudgeon and dace, replacing them downstream (Lucas *et al.*, 1998). Percids and eurytopic cyprinids such as roach are more abundant in the slower, deeper Ouse. Brook lamprey (*Lampetra planeri* (Bloch)) are common throughout the upper and middle reaches of the tributaries of the Ouse, while river lamprey (*Lampetra fluviatilis* (L.)) are relatively common in the Swale, Ure, Nidd, Wharfe and Ouse, but sea lamprey (*Petromyzon marinus* (L.)) are rarer (Whitton & Lucas, 1997).

2.2 SAMPLING SITE LOCATIONS

2.2.1 The River Trent

The lower reaches of the River Trent were surveyed at six sites (Table 2.2, Fig. 2.1) between Attenborough and Dunham, a river distance of approximately 60 km.

Attenborough

The river at Attenborough has a mean width of 100 m and a depth of 3-4 m in the main channel. The sampling site is situated adjacent to Attenborough Nature Reserve on the left hand bank, approximately 20 m downstream of the River Erewash confluence. Water depths in the sampling site vary from centimetres to approximately 1.2 m, and the gradient is slight. The substratum composition varies along a gradient from sand/silt in the margins to gravel in the main channel. There are extensive beds of helophytes (Table 2.2), but no submerged vegetation. Riparian vegetation mainly consists of grasses (Gramineae) and herbaceous plants, with a number of white willow (*Salix alba* L.) and osier (*Salix viminalis* L.) also present. Flow in the immediate sampling area is negligible, but increases with distance from the bank.

Trent Bridge

The river at Trent Bridge has a width of approximately 75 m and a depth of 3-4 m in the main channel. The sampling site is located on the right hand bank, immediately downstream of Trent Bridge. Water depths in the sampling area range from centimetres in the margins to approximately 1.2 m, with the gradient initially being slight before dropping off suddenly beyond the sampling area approximately 5 m from the bank. The substratum consists primarily of mud and silt, and frequently smells of sewage. No aquatic vegetation was recorded at Trent Bridge during the study period, probably due to

Table 2.2 Details of sites in the Trent, Warwickshire Avon and Yorkshire Ouse catchments.

Site name	Abbrev.	Catchment	NGR	Substratum	Key aquatic macrophytes
Attenborough	ATT	Trent	SK 520 335	Sand/gravel	*Acorus calamus* L., *Glyceria maxima* (Hartm.), *Sparganium erectum* L.
Trent Bridge	TB	Trent	SK 582 383	Mud/silt	–
Colwick Marina	CM	Trent	SK 610 393	Concrete	*A. calamus*, *Elodea canadensis* Michx., *G. maxima*, *Lemna minor* L., *S. erectum*
Marina Pond	MP a	Trent	SK 632 396	Gravel	*Potamogeton pectinatus* L. (little), *Zannichellia palustris* L. (little)
	MP b	Trent	SK 627 396	Gravel	–
Winthorpe Lake	WIN	Trent	SK 802 579	Sand/silt	*A. calamus*, *Butomus umbellatus* L., *E. canadensis*, *G. maxima*, *S. erectum*
Dunham	DUN	Trent	SK 820 745	Gravel/mud	*P. pectinatus* (little)
Warwick	WAR	Avon	SP 280 631	Mud/silt	*A. calamus*, *Alisma plantago-aquatica* L., *B. umbellatus*, *G. maxima*, *Nuphar lutea* (L.), *Nymphaea alba* L., *S. erectum*
Old Pasture	OP	Avon	SP 245 564	Mud/silt	*B. umbellatus*, *E. canadensis*, *G. maxima*, *Schoenoplectus lacustris* (L.), *S. erectum*
Twyford	TWY	Avon	SP 048 460	Mud/silt	*Callitriche* spp., *E. canadensis*, *L. minor*, *Lemna polyrhiza* L., *N. lutea*, *P. pectinatus*, *Sagittaria sagittifolia* L., *S. erectum*
Birlingham	BIRL	Avon	SO 941 419	Mud/silt	*B. umbellatus*, *G. maxima*, *N. lutea*, *Phragmites australis* Trin., *Polygonum amphibium* L., *S. lacustris*, *S. erectum*
Tewkesbury	TEWK	Avon	SO 892 326	Mud/silt	*G. maxima*, *N. lutea*, *P. amphibium*
Maunby Demesne	MAUN	Ouse	SE 337 876	Sand	*P. pectinatus* (little)
Boroughbridge	BORO a	Ouse	SE 395 672	Gravel/silt	*E. canadensis*, *Myriophyllum verticillatum* L., *P. pectinatus*, *Potamogeton perfoliatus* L., *Ranunculus fluitans* Lam., *S. lacustris*
	BORO b	Ouse	SE 395 672	Pebble/mud	*P. pectinatus* (little)
Kirk Hammerton	KHAM	Ouse	SE 469 546	Sand	*A. plantago-aquatica*, *B. umbellatus*, *Potamogeton crispus* L., *Potamogeton natans* L., *P. pectinatus*, *R. fluitans*, *S. erectum*
Boston Spa	BSPA	Ouse	SE 432 458	Gravel	*S. erectum* (little)
Linton	LINT	Ouse	SE 494 602	Sand/clay	*P. pectinatus*
Beningbrough	BEN	Ouse	SE 528 577	Sand/clay	*P. pectinatus*
Fulford	FUL	Ouse	SE 608 488	Mud/silt	*P. pectinatus*
Acaster Malbis	ACA	Ouse	SE 591 448	Concrete	–

the engineered nature of the river in that area and the presence of large numbers of mute swan (*Cygnus olor* L.) and Canada goose (*Branta canadensis* L.). Riparian vegetation is also sparse, consisting of typical pioneer species, and is mown periodically. Flow in the immediate sampling area is negligible, but increases towards the main channel. Areas of slack water are present downstream of the bridge stanchions.

Colwick Marina

Colwick Marina (surface area ~1 ha) is located on the left hand bank of the River Trent approximately 300 m upstream of Holme sluices, and is connected to the main river by a 30 m long channel of 20 m width. The sampling site is located on a boat slipway in the south-eastern corner of the marina. Water depths in the sampling area vary from centimetres in the margins to approximately 1.2 m towards the end of the slipway, and the gradient is steady (approximately 1:10). The substratum consists of imprinted concrete, with an ephemeral covering of silt and filamentous algae, with gravel and silt to the left and right of the slipway, respectively. Vegetation (mostly emergent) is present either side of the slipway (Table 2.2). Riparian vegetation is limited to typical pioneer species and is mown periodically, although a number of small sallow (*Salix caprea* L.), osier and alder (*Alnus glutinosa* (L.)) are present. Directional water movement within the marina is negligible.

Marina Pond

Marina Pond (surface area ~3 ha) is located on the right hand bank of the River Trent, and is connected to the main river by a 40 m long channel of 5-10 m width and 1 m depth. The pond is surveyed at two locations, one in the channel connecting the pond to the river (MP a) and the other at the upstream end of the pond (MP b, furthest from the river). Water depths in the sampling areas range from centimetres in the margins to approximately 1.2 m, and the substratum at both locations consists mostly of gravel. No aquatic vegetation is present in the pond itself, and only small amounts exist in the connecting channel (Table 2.2). Riparian vegetation consists mostly of grasses, although some sallow, osier, white willow and crack willow (*Salix fragilis* L.) are also present. Directional water movement in the pond itself is negligible, but can be substantial through the connecting channel. In November 2003, however, the channel was blocked, thereby disconnecting the pond from the river (except for during periods of elevated river levels).

Winthorpe Lake

Winthorpe Lake (surface area ~5 ha) is located on the right hand bank of the River Trent, and is connected to the main river by a 50 m long channel of 3-5 m width and 1-1.5 m depth. The sampling site is located at the lake-ward end of the connecting channel in the north-western corner of the lake. The substratum consists of sand and silt. Vegetation (mostly emergent) is present along the margins of the connecting channel (Table 2.2), while riparian vegetation consists mostly of grasses. Directional water movement through the connecting channel can be substantial, but is generally negligible.

Dunham

The river at Dunham is tidal and has a width of approximately 75 m and a depth of 3-4 m in the main channel. The sampling site is located on the left hand bank, immediately downstream of Dunham Toll Bridge. Water depths range from centimetres in the margins to approximately 1.2 m near the main channel, with the gradient being slight. The substratum consists primarily of mud in the margins and gravel in the main channel. Little aquatic vegetation is ever present (Table 2.2), probably due to the fluctuating water levels, while riparian vegetation consists of grasses, which are mown periodically, except for a narrow strip along the top of the river bank. Flow in the immediate sampling area is negligible, but increases towards the main channel.

2.2.2 The Warwickshire Avon

The lower reaches of the Warwickshire Avon were surveyed at five sites (Table 2.2, Fig. 2.2) between Warwick and Tewkesbury, a river distance of approximately 50 km.

Warwick

The river downstream of Warwick has a width of approximately 40 m and a depth of 2-3 m in the main channel. The sampling site is located on the left hand bank, immediately upstream of a bridge. Water depths in the sampling area range from centimetres in the margins to approximately 2 m, with the gradient being steep. The substratum consists largely of mud and silt, with woody debris usually also present. The whole area has extensive marginal vegetation (Table 2.2). There is little riparian vegetation, however, due to the shading effect of a number of large sycamore (*Acer pseudoplatanus* L.), pedunculate oak (*Quercus robur* L.), alder, black poplar (*Populus nigra* L.) and yew (*Taxus baccata* L.). Flow in the immediate sampling area is negligible, but increases towards the main channel.

Old Pasture

The river at Old Pasture has a width of approximately 40 m and a depth of 2 m in the main channel. The sampling site is situated on the right hand bank, on the outside of a bend. Water depths in the sampling area range from 0.5 m in the margins to approximately 2 m, with the gradient being steep. The substratum consists largely of mud and silt, and contains large quantities of allochthonous material and filamentous algae. The area has extensive marginal vegetation, plus submerged macrophytes during the summer (Table 2.2). Riparian vegetation consists of grasses and herbaceous plants, with a few alder downstream of the site. Flow in the immediate sampling area is negligible, but increases towards the main channel.

Twyford

The site at Twyford is situated on the right hand bank of the Warwickshire Avon, in a backwater of approximately 100 m length, 25 m width and 1-3 m depth. The area is surveyed approximately half way along the backwater, where water depths are approximately 2 m. The substratum consists of mud and silt, and flow in the backwater is negligible. The whole backwater has extensive aquatic vegetation (Table 2.2). Riparian vegetation consists of grasses and herbaceous plants, with a number of crack willow, alder and field maple (*Acer campestre* L.) also present.

Birlingham

The river at Birlingham has a width of approximately 40 m and a depth of 2-3 m in the main channel. The sampling site is situated on the right hand bank, approximately 100 m upstream of Nafford weir. Water depth is approximately 2 m throughout the sampling site, and the substratum consists of mud and silt. The area has extensive marginal vegetation (Table 2.2). Riparian vegetation consists primarily of grasses and herbaceous plants, with a number of alder and crack willow also present. Flow is negligible in the immediate sampling area, but increases towards the main river channel.

Tewkesbury

The river at Tewkesbury has a width of approximately 40 m and a depth of 2-3 m in the main channel. The sampling site is located on the left hand bank, where water depths range from 0.5 m in the margins to approximately 2 m, with the gradient being steep. The substratum consists largely of mud and silt, with woody debris usually also present. The area has extensive marginal vegetation (Table 2.2), while riparian vegetation consists mostly of grasses, with a few crack willow also present. Flow in the immediate sampling area is negligible, but increases towards the main channel.

2.2.3 The Yorkshire Ouse catchment

The Yorkshire Ouse catchment was surveyed at eight sites (Table 2.2, Fig. 2.3), with four located on the Yorkshire Ouse itself and the remainder located on the rivers Swale, Ure, Nidd and Wharfe.

Maunby Demesne (River Swale)

The river at Maunby Demesne has a width of approximately 25 m and a depth of 2-3 m in the main channel. The sampling site is located on the left hand bank, on the inside of a bend. Water depths range from centimetres in the margins to approximately 1.2 m, with the gradient being steady. The substratum largely consists of sand. The area has little aquatic vegetation (Table 2.2), probably due to the dynamic nature of the river. Riparian vegetation primarily consists of nettles (*Urtica* spp.), with a few crack willow, osier and alder present downstream. Water velocity in the immediate sampling area is generally slow, but increases substantially towards the main channel.

Boroughbridge (River Ure)

The river at Boroughbridge has a width of approximately 50 m and a depth of 1 m in the main channel. The area is surveyed at two locations, one in the main river (BORO a) and the other in an adjacent bypass canal (BORO b). The site in the river is situated on the left hand bank, approximately 50 m upstream of Boroughbridge bridge, while the site in the canal is located immediately upstream of a roundabout. Water depths at both sites range from centimetres in the margins to approximately 1 m, and the gradient is steady. The substratum in the river consists of gravel with small patches of silt, while that in the canal consists of pebble and mud, with a number of large boulders also present. Emergent and submerged macrophytes are present in the main river, but are scarce in the canal (Table 2.2). Riparian vegetation consists of grasses and herbaceous plants, with crack willow and osier also present. Flow in the river sampling area is slow, but rapidly increases with distance from the bank, while flow is negligible in the canal.

Kirk Hammerton (River Nidd)

The river at Kirk Hammerton has a width of approximately 20 m and a depth of 1.5 m in the main channel. The sampling site is located on the left hand bank, approximately 40 m downstream of Mill Farm weir. Water depths vary from centimetres in the margins to approximately 1.2 m, and the gradient is steady. The substratum consists mostly of sand, with an area of allochthonous material usually also present. Emergent and submerged macrophytes are present in the sampling area (Table 2.2). Riparian vegetation is dominated by Himalayan balsam (*Impatiens glandulifera* Royle), with a large number of crack willow, white willow and osier also present. Flow is slow in the sampling area, but increases towards the right hand bank.

Boston Spa (River Wharfe)

The river at Boston Spa has a width of approximately 40 m and a depth of 1.5 m in the main channel. The sampling site is situated on the left hand bank, immediately downstream of Thorp Arch bridge. Water depths in the sampling site range from centimetres in the margins to approximately 1.2 m, and the gradient is shallow. The substratum consists mostly of gravel, with a number of large boulders also present. Little aquatic vegetation is present in the sampling area (Table 2.2). Riparian vegetation is dominated by Himalayan balsam, with a number of large sycamore also present. Flow is slow in the sampling area, but increases with distance from the bank.

Linton (River Ouse)

The river at Linton has a width of approximately 50 m and a depth of 3-4 m in the main channel. The sampling site is located on the left hand bank, immediately beneath some electricity pylons. Water depths in the sampling site range from centimetres in the margins to approximately 1.2 m, and the gradient is shallow. The substratum consists of sand and clay, and submerged vegetation is present in the summer (Table 2.2). Riparian vegetation consists primarily of grasses, with a number of small osier, purple willow (*Salix purpurea* L.), white willow and alder also present. Flow is negligible in the sampling area, but increases with distance from the bank.

Beningbrough (River Ouse)

The river at Beningbrough has a width of approximately 50 m and a depth of 3-4 m in the main channel. The sampling site is located on the left hand bank, approximately 200 m downstream of Moor Monkton pumping station. Water depths in the sampling site range from centimetres in the margins to approximately 1.2 m, and the gradient is initially shallow before depths increase suddenly 4 m from the bank. The substratum consists of sand and clay, and submerged vegetation is present in the summer (Table 2.2). Riparian vegetation consists primarily of grasses, with a number of osier also present. Flow is negligible in the sampling area, but increases with distance from the bank.

Fulford (River Ouse)

The river at Fulford has a width of approximately 50 m and a depth of 3-4 m in the main channel. The sampling site is situated on the left hand bank, on the outside of a bend. Water depths in the sampling site range from centimetres in the margins to approximately 1.5 m, and the gradient is initially shallow before depths increase suddenly approximately 5 m from the bank. The substratum consists of mud and silt, with woody debris usually also present, and submerged vegetation is present in the summer (Table 2.2). Riparian vegetation consists primarily of grasses, with a number of large osier and crack willow also present. Flow is negligible in the sampling area, but increases with distance from the bank.

Acaster Malbis (River Ouse)

The river at Acaster Malbis has a width of approximately 50 m and a depth of 2-3 m in the main channel. The sampling site is located on a boat slipway on the right hand side of the river, approximately 200 m upstream of Naburn weir. Water depths in the sampling site range from centimetres in the margins to approximately 1.5 m, and the gradient is steady (approximately 1:10). The substratum consists of imprinted concrete, with an ephemeral covering of mud and allochthonous material. No aquatic or riparian vegetation is present in the immediate vicinity of the site, except for a large crack willow upstream. Flow is negligible in the sampling area, but increases with distance from the bank.

2.3 DATA COLLECTION

2.3.1 Fish surveys

Seine netting

Fish were surveyed approximately monthly from May 1999 to October 2004 inclusive in daylight hours, using a micromesh seine net. The main exceptions were: (1) between November and March in 1999/2000 and 2000/2001 when no sampling was undertaken; (2) in 2001 when sampling was restricted at many sites (Ouse catchment worst affected) due to an outbreak of foot and mouth disease; and (3) the Trent in 2003 where, between March and July inclusive, sampling was carried out fortnightly. The micromesh seine net was 25 m long by 3 m deep, with a 6 mm hexagonal mesh size, and was set in a rectangle parallel to the bank either by wading (Trent and Ouse) or from an inflatable dinghy (Avon). The net was fished to the bank in the usual manner for a beach seine and captured fish were transferred to large water-filled containers prior to analysis. In all cases, sampling was restricted to the margins in water ≤2 m deep, where water velocity is slowest and where 0+ fish tend to aggregate (Copp & Garner, 1995). Trent data from 1999 were obtained from Harvey *et al.* (1999).

In addition to the single seine net, between May and October inclusive 2002, a quantitative, double seine netting technique (Cowx *et al.*, 2001) was employed at key sites (Trent Bridge and Colwick Marina) for comparison with point abundance sampling (PAS) by electric fishing (see below). The technique involves setting two identical nets simultaneously, one inside the other, ensuring that the same area is sampled by both. First, the inside net is fished to the bank in the usual manner, and the process is then repeated for the second net. Theoretically, a proportion of the fish escaping the first net are caught in the second net. Catches one and two are kept separate for analysis.

Point abundance sampling (PAS) by electric fishing

Point abundance sampling (PAS) by electric fishing (Copp & Peňáz, 1988) was developed to address the problems of sampling small fishes (Garner, 1997c). Many authors (e.g. Bain *et al.*, 1985; Copp, 1989a; Persat & Copp, 1990; Baras, 1995; Baras *et al.*, 1995; Copp & Garner, 1995; Perrow *et al.*, 1996; Garner, 1997c; Scholten, 2003) have advocated PAS as an efficient and cost-effective method for assessing fish abundance and population structure. The method requires numerous, small sampling points, chosen randomly, to be taken at each sampling station (Copp, 1989a), and is intended to address the contagious distributions of 0+ fish. The theory behind PAS is that data from large numbers of small samples are more statistically robust than those from small numbers of large samples (Copp, 1990c). As long as sufficient samples are taken from a range of habitats, size distributions in catches will be representative of the target population(s), and the variance about mean density estimates should be small (Copp, 1989a; Persat & Copp, 1990; Copp & Garner, 1995; Perrow *et al.*, 1996; Garner, 1997c). Thus, PAS can be used to produce data pertaining to fish population parameters, such as size structure, density estimates and cohort strengths, comparable with seine netting (Garner, 1997c).

Between May and October inclusive 2002, PAS was conducted monthly at Trent Bridge and Colwick Marina using a purpose built framework in which the effective volume of the electric field was known (Harvey, 1996; Cowx *et al.*, 2001). PAS was carried out within a day of the seine netting surveys. A delimiting cathode frame was constructed from 12, 0.7-m-lengths of lightweight aluminium Dexion (140), which were bolted together in the form of a cube. The anode was a copper sphere (0.1 m diameter) suspended centrally within the cathode framework using non-conductive string. Power was supplied by a 2 kVA generator producing alternating current at 240 volts, which was transformed into pulsed direct current (100 Hz) by an electric fishing control box (Millstream: 2 anode, 25 A, pulsed DC model). The electric fishing control box was connected to the generator via an industrial waterproof, DIN plug (4 pin) and an appropriate cable. The anode and cathode cables were connected to the control box via industrial waterproof, lockable DIN plugs (3 pin) and the terminal ends were bolted to the anodic copper sphere and cathodic framework, respectively. A deadman's safety foot switch was connected to the control box via an industrial waterproof, DIN plug (2 pin) and a blanking plug was fixed to the second anode port on the control box.

Thirty point samples were taken at both sites, in each sampling period during daylight hours. Sampling points were selected randomly at each site from a map containing grid squares. Each sampling point was approached as discreetly as possible by wading in an upstream direction. The framework was positioned on the riverbed at the selected point, and left for approximately five minutes to allow recolonisation by fish (Cowx *et al.*, 2001; Janáč & Jurajda, 2005). A netsman then took position within viewing distance of the framework, taking care not to disturb any fish, and the system was energised for five seconds. Once the energising time had elapsed, the netsman removed immobilised fish using a fine mesh (280 μm), wooden-handled net. Samples were placed in separate water-filled containers for analysis.

Sample processing

All fish were, where possible, identified to species (Pinder, 2001) and measured (fork length, nearest mm) in the field. When identification was not immediately possible, fish were fixed in 4% formalin and returned to the laboratory. On occasions when excessively large numbers of fish were caught, a random sub-sample of known percentage of the total catch was processed. Details of data analyses are provided in the relevant sections in Chapters 3, 5 and 6.

2.3.2 Zooplankton surveys

Zooplankton samples were collected monthly at ten sites (Table 2.3) between June 2001 and October 2003 in daylight hours. The exceptions were between November 2001 and March 2002 when no samples were collected, and from the beginning of March to the end of July 2003 when the Trent was sampled fortnightly. A plankton net (100 μm mesh size) was used to assess availability of zooplankton to 0+ fish via three replicate horizontal trawls (10 m trawl length), as recommended for rivers by De Barnardi (1984). Sampling was restricted to the river margins since it is there that 0+ fish tend to aggregate and feed (Copp & Garner, 1995). Whilst the mesh size of the net likely underestimates the densities of the smallest rotifers (Bottrell *et al.*, 1976; Bass *et al.*, 1997a), it was considered satisfactory for the sizes eaten by 0+ fish. Each zooplankton sample was fixed in the field using 4% formalin solution, and later stained with 'Rose Bengal' to facilitate observation of small, transparent organisms in the laboratory. Details of processing and analysis of zooplankton samples are provided in Chapter 4.

Table 2.3 Zooplankton sampling sites in the Trent, Avon and Ouse catchments.

Site name	**Abbrev.**	**Catchment**	**Habitat**
Trent Bridge	TB	Trent	Main river
Colwick Marina	CM a	Trent	Floodplain (marina)
	CM b	Trent	Main river
Marina Pond	MP a	Trent	Floodplain (transition zone)
	MP b	Trent	Floodplain (pond)
Twyford	TWY	Avon	Floodplain (backwater)
Tewkesbury	TEWK	Avon	Main river
Boroughbridge	BORO a	Ouse	Main river
	BORO b	Ouse	Floodplain (canal)
Acaster Malbis	ACA	Ouse	Main river

2.3.3 Phytoplankton surveys

Samples of river water were collected from just below the water surface using one litre polyethylene bottles from the same sites that were sampled for zooplankton (Table 2.3) in daylight hours. Samples were kept in the dark until returning to the laboratory where they were either analysed immediately or kept in a refrigerator overnight. Details of processing and analysis of phytoplankton samples are provided in Chapter 4.

2.4 DATA ANALYSIS

A number of standard statistical techniques are used throughout this thesis. To avoid repetition, their general application is described here, with variations on the theme highlighted in the relevant sections. All data were tested for normality and homogeneity of variances using one-sample Kolmogorov-Smirnov and Levene tests, respectively (Dytham, 2003). Where these assumptions were violated, attempts were made to transform the data. Average values were compared by either one-way Analysis of Variance (ANOVA) or Kruskal-Wallis (Dytham, 2003). Differences in mean values were identified by either Scheffé (variances equal) or Games-Howell (variances not equal) *post hoc* tests, the latter of which were further supported with individual Mann-Whitney *U*-tests (Dytham, 2003). All statistical analyses were carried out using SPSS version 11.

CHAPTER THREE

COMPARATIVE 0+ FISH POPULATIONS OF THREE LOWLAND RIVER CATCHMENTS

3.1 INTRODUCTION

A range of factors determine the structure of 0+ fish communities, with availability of spawning and nursery areas among the most important (Jurajda & Peňáz, 1994; Jurajda, 1995). While some fish species are able to flourish in a wide range of habitat types, others have stricter habitat requirements. As such, species composition varies both within and between river catchments.

Species richness, diversity and density are usually highest where habitat heterogeneity is greatest, since such areas provide the necessary variety of resources for all life stages of a range of fish species. Larval and juvenile fish are particularly vulnerable to environmental perturbations owing to the strict physical, behavioural and energetic constraints imposed upon young fishes (Schiemer & Weiser, 1992) and, as such, are good indicators of ecosystem integrity (Schiemer *et al.*, 1991, 2001a; Schiemer, 2000). Rivers that have been heavily modified are typically characterised by a dominance of a small number of eurytopic species, with specialists such as rheophilic and limnophilic species often absent or rare.

Although studies of 0+ fish have become more numerous in recent years, there is still a dearth of knowledge regarding the ecology of 0+ fish communities in lowland rivers. The aim of the present chapter was to investigate the comparative 0+ fish populations in three lowland river catchments. Specifically, the objectives were to investigate: (1) the species composition of the 0+ fish communities from the River Trent, Warwickshire Avon and Yorkshire Ouse catchments; (2) spatial and temporal variations in 0+ fish community structure; (3) spatial and temporal variations in growth; (4) the comparative sampling characteristics of micromesh seine netting and point abundance sampling (PAS) by electric fishing; and (5) inter- and intraspecific differences in spawning periodicity. The hypothesis was that variations in habitat availability between catchments would be reflected in the structure of their respective 0+ fish communities.

3.2 MATERIALS AND METHODS

3.2.1 Sample processing

In the laboratory, fish were identified to species (Pinder, 2001) and measured (nearest 0.1 mm) using either a binocular microscope equipped with a stage micrometer (fish ≤10 mm) or a pair of vernier calipers (fish >10 mm). Standard length (SL) was the chosen measure of fish length since it is the most suitable for use throughout early development (Copp, 1990b). Fork length (FL) is unapplicable as a forked, homocercal tail does not begin to develop until larval step 4, and is not complete until larval step 5 (Tong, 1986; Copp, 1990c; Peňáz, 2001). Total length (TL) is also to be avoided as the finfolds of young larvae are easily damaged and may, thus, render measurements of TL inaccurate (Copp, 1990b). Field measurements of FL were therefore converted to SL using the linear regression relationships in Table 3.1. No significant spatial differences were found in the relationships between SL and FL (ANCOVA, $P>0.05$), so sites were combined to produce a single relationship for each fish species. Furthermore, the relationships were not affected by fixation in formalin (ANCOVA, $P>0.05$), therefore measurements of FL were converted to SL using relationships determined from fixed fish. These relationships compare favourably with those derived by Kubečka (1994) and Carter & Reader (2000).

Table 3.1 Linear regression relationship between standard length (*SL*, mm) and fork length (*FL*, mm) for eight species of fish.

Species	**Relationship**	***P***	r^2	***n***
Bleak	$SL = (FL - 0.88) / 1.06$	0.000**	0.99	21
Bream	$SL = (FL - 0.69) / 1.08$	0.000**	1	58
Chub	$SL = (FL - 0.10) / 1.12$	0.000**	1	107
Dace	$SL = (FL - 0.45) / 1.09$	0.000**	1	187
Gudgeon	$SL = (FL + 0.17) / 1.12$	0.000**	1	157
Minnow	$SL = (FL + 0.03) / 1.12$	0.000**	0.99	46
Perch	$SL = (FL + 0.21) / 1.13$	0.000**	1	142
Roach	$SL = (FL - 0.42) / 1.10$	0.000**	1	156

**$P<0.01$

Collections of 0+ fish often cannot be processed immediately after capture and so must be fixed or preserved to minimise *post mortem* degeneration (Smith & Walker, 2003). The effects of fixation and preservation on fish are well documented (e.g. Anderson & Gutreuter, 1983; Snyder, 1983; Treasurer, 1992; Takizawa *et al.*, 1994; Peterson & VanderKooy, 1996; Sagnes, 1997; Fey, 1999; Ajah & Nunoo, 2003; Smith & Walker, 2003; Paulet & Kaiser, 2004), with shrinkage a universal phenomenon. Nevertheless, length measurements were not corrected for the effects of formalin since, for the sizes of fish in this study and the minimal times for which fish were kept in formalin, absolute shrinkage would have been small (~1 mm maximum) (Treasurer, 1992; Smith & Walker, 2003). For the purposes of this study, fish were classified as 0+ from hatching until the end of the following March, with 0+ fish distinguished from >0+ fish using length distributions and, where necessary, from analysis of their scales (Bagenal & Tesch, 1978).

3.2.2 Data analysis

3.2.2.1 *Preliminary calculations*

Seine net catches were used to calculate frequency of occurrence, relative abundance and species-specific abundance of each fish species at each site (Hynes, 1950; Windell & Bowen, 1978; Hyslop, 1980; Bowen, 1983; Mohan & Sankaran, 1988; Amundsen *et al.*, 1996). The frequency of occurrence of a given species is defined as the number of surveys in which the species occurred, expressed as a frequency of the total number of surveys in which fish were captured. The relative abundance of a species is defined as the percentage of total catches (numbers) in all surveys comprised by the given species. Species-specific abundance is analogous to the prey-specific abundance of Amundsen *et al.* (1996), and is defined as the percentage a species comprises of all fish in only those surveys in which the particular species occurred. In mathematical terms, frequency of occurrence ($\%F_i$), relative abundance ($\%A_i$) and species-specific abundance ($\%P_i$) of species i can be described by the equations:

$$\%F_i = \frac{N_i}{N} \times 100 \tag{3.1}$$

$$\%A_i = \frac{\sum S_i}{\sum S_t} \times 100 \tag{3.2}$$

$$\%P_i = \frac{\sum S_i}{\sum S_{ti}} \times 100 \tag{3.3}$$

where N_i is the number of surveys that contained species i, N is the total number of surveys containing fish of any species, S_i is the sample content (number) composed by species i, S_t is the total content of all surveys in the entire sampling period, and S_{ti} is the total content in only those surveys containing species i (Amundsen *et al.*, 1996).

3.2.2.2 *Species composition*

Species composition of 0+ fish catches was analysed for all sites using the graphical method of Costello (1990), as modified by Amundsen *et al.* (1996). Although originally designed for fish diet analyses, this method can easily be adapted for investigations of fish community structure. In this method, species-specific abundance is plotted against frequency of occurrence. Interpretation of the output can be demonstrated by way of a schematic diagram (Fig. 3.1). Percent abundance, increasing along the diagonal from the lower left to the upper right corner, provides a measure of species importance, with dominant species at the upper, and rare species at the lower end. Species positioned in the upper part of the graph occurred in the largest numbers, while those positioned in the lower part occurred in smaller numbers. Points located at the upper left of the diagram indicate species that occurred infrequently but in large numbers (high between sample variation, BSV), and those in the upper right represent those that frequently occurred in large numbers. Points located in the lower right corner represent species that occurred in most surveys, but in only small numbers (low BSV).

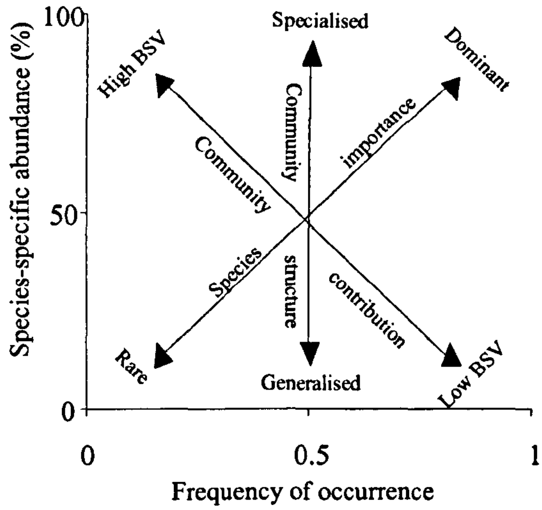

Fig. 3.1 Explanatory diagram of Costello plot for interpretation of 0+ fish community structure (see text for details).

3.2.2.3 *Spatial similarities in 0+ fish catches*

Numerous similarity indices have been applied in aquatic ecology (see Hurlbert, 1978; Wallace, 1981; Washington, 1984). Three in particular, Bray-Curtis (1957; syn. Czekanowski, 1913), Schoener (1970) and Zaret & Rand (1971), have been widely used in fisheries (e.g. Galat & Vucinich, 1983; Cowx *et al.*, 1984; Mark *et al.*, 1987; Garner, 1996b; Coelho *et al.*, 1997; Marshall & Elliott, 1997; Genner *et al.*, 1999; Vinni *et al.*, 2000). Trials demonstrated that Schoener and Bray-Curtis produced identical values of similarity, while those of Zaret & Rand were also similar. More importantly, the trends were the same. It was therefore decided that Bray-Curtis would be used since this method is included as part of the PRIMER (Plymouth Routines In Multivariate Ecological Research) statistical package (version 5.2), vastly reducing the amount of calculations that need be carried out manually. Thus, Bray-Curtis similarity matrices were calculated using frequency of occurrence data (Section 3.2.2.1) and presented as dendrograms using hierarchical agglomerative clustering (group average linkage) to investigate spatial similarities in 0+ fish catches. The Bray-Curtis similarity index (C_z) represents the overall similarity between each pair of samples, taking the occurrence of all species into consideration, and is calculated as follows:

$$C_z = \frac{2W}{(a+b)} \tag{3.4}$$

where W is the sum of the lesser percent frequency of occurrence value of each species common to the catches at two sites (including tied values), and a and b are the sums of the percent frequency of occurrences of species in the catches at site a and b, respectively. The index ranges from 0 (no species in common) to 1 (identical samples), with an arbitrary value of 0.6 (60% similarity) frequently taken as a guide of when there is significant overlap between samples (e.g. Zaret & Rand, 1971; Wallace, 1981; Galat & Vucinich, 1983; Garner, 1996b).

3.2.2.4 *Diversity and evenness of 0+ fish catches*

The Shannon-Wiener (H') and Simpson (D) diversity indices are commonly used in aquatic ecology (Washington, 1984). Trials demonstrated that both indices produced similar trends, albeit with different absolute values. Thus, the more widely-used H' was applied, together with Pielou's measure of evenness (J), to investigate spatial variations (within and between catchments) in diversity and evenness of 0+ fish catches. H' and J are calculated as follows (Marshall & Elliott, 1997):

$$H' = -\sum P_i \ln P_i \tag{3.5}$$

$$J = \frac{H'}{H'_{\max}} \tag{3.6}$$

where P_i is the proportion of the observations found in category i and $H'_{\max} = \ln(k)$, the maximum possible diversity for a set of data of k categories.

3.2.2.5 *Density of 0+ fish communities*

Seine net data were used to calculate relative density (fish per m^2) of 0+ fish (all species combined) at each site for each sampling occasion. Species were combined to avoid repetition as species composition is addressed elsewhere (Section 3.2.2.2). Total numbers of 0+ fish were divided by the known area sampled by the net at each site (area calculated from direct *in situ* measurements of the study sites).

3.2.2.6 *Point abundance sampling (PAS) by electric fishing versus micromesh seine netting*

The species compositions, size distributions and densities of 0+ fish catches obtained from quantitative point abundance sampling (PAS) by electric fishing and double micromesh seine netting surveys were compared at Trent Bridge and Colwick Marina on the River Trent, over a six-month period.

Species composition

The percent abundance of each fish species was calculated for both methods and each sampling occasion. Similarity of catches between seine netting and PAS were investigated using the Bray-Curtis (1957) similarity index (Section 3.2.2.3), and the Shannon-Wiener (H') diversity index and Pielou's measure of evenness (J) were calculated (Section 3.2.2.4).

Size distribution

Mean lengths and length-frequency distributions of fish captured by seine netting and PAS were compared for each sampling occasion using independent samples *t*-tests and two-sample Kolmogorov-Smirnov tests, respectively (Dytham, 2003). Seine net and PAS catches were further compared using a linear index of selection (Strauss, 1979):

$$L = r_i - p_i \qquad (3.7)$$

where L is the linear index of selection, r_i the proportion of fish in length class i captured by seine netting and p_i the proportion of fish in length class i captured by PAS. Values range between -1 and +1, with a negative value indicating a selection bias by seine netting against a given length class, and a positive value indicating a selection bias by PAS against a given length class. A result of 0 indicates that the given length class comprised the same proportion of both seine net and PAS catches.

Density

Density (fish per m^2) of 0+ fish (all species combined) was estimated for each sampling occasion from seine net catches using the two-catch depletion procedure of Seber & LeCren (1967):

$$\tilde{n} = \frac{c_1^2}{(c_1 - c_2)} \tag{3.8}$$

$$s = \sqrt{\frac{(c_1^2 \times c_2^2)(c_1 + c_2)}{(c_1 - c_2)^4}} \tag{3.9}$$

where $\tilde{n}$ is the estimated population density, c_1 and c_2 are the density of fish in catches one and two, respectively, and s is the standard deviation of $\tilde{n}$. c_1 and c_2 were calculated by dividing the numbers of fish in catches one and two by the area sampled by the seine nets.

Estimates of 0+ fish density were made from PAS catches by dividing the number of fish immobilised within the effective field at each sampling point by the area of the electric fishing framework (0.49 m^2). Mean values of density were compared between the two methods via Mann-Whitney *U*-tests.

Growth of 0+ fish

Growth of 0+ fish was demonstrated for key species (Table 3.2) by changes in observed mean SL (mm ± SD) and by progression of modal groups using length-frequency histograms. Other species were captured too infrequently or in insufficient numbers for analysis.

Table 3.2 Fish species used for growth analysis in the Trent, Avon and Ouse catchments.

	Bleak	**Bream**	**Chub**	**Dace**	**Gudgeon**	**Minnow**	**Perch**	**Roach**
Trent	+	+	+	+	+	–	+	+
Avon	+	+	+	–	+	–	+	+
Ouse	+	–	+	+	+	+	+	+

+ indicates species used for growth analysis, – indicates species not used for growth analysis

Growth rates (G, mm.day^{-1}) over the summer were calculated as:

$$G = \frac{(\bar{L}_{t_n} - \bar{L}_{t_1})}{(t_n - t_1)} \qquad (3.10)$$

where $\bar{L}_{t_1}$ is the mean length at time t_1, $\bar{L}_{t_n}$ is the mean length at time t_n, t_1 is the time of first capture, and t_n is the time of last capture (i.e. October).

3.2.2.8 *Weight-length relationships of 0+ fish*

The relationship between wet weight (g) and SL (mm) was investigated for formalin-fixed roach, dace and perch captured from Trent Bridge and Colwick Marina on the River Trent in 2003. Each fish was dried of excess moisture using blotting paper, weighed (nearest 0.01 mg) using an electronic balance, and measured (nearest 0.1 mm) for SL. Fish were classified as either larvae or juveniles (Tong, 1986; Copp, 1990c; Hensel, 1999; Peňáz, 2001; Urho, 2002), and wet weight-SL relationships were calculated using natural logarithm-transformed data. No significant differences were found in the relationships between sites (ANCOVA, P>0.1), so data were combined for each species.

3.2.2.9 *Spawning periodicity*

Spawning periodicity was investigated via recruitment patterns in length distributions. Multiple spawning events could be identified *a posteriori* either by bimodality/asymmetry in the initial cohort of 0+ fish or by the appearance of a discrete second cohort. In situations where fish hatch in small numbers over a protracted period, negative bilateral asymmetry may result, whereas if larger, intermittent batches are produced, positive skewness or non-overlapping modal distributions may form. Where there was evidence of multiple recruitment events, cohorts were separated via modal progression analysis (MPA) using Bhattacharya's method (Sparre & Venema, 1992) in FiSAT (FAO/ICLARM Stock Assessment Tools). Separation Indices of greater than 2 indicate significant separation of modal groups (Sparre & Venema, 1992).

3.3 RESULTS

3.3.1 Species composition

3.3.1.1 *Inter-catchment comparisons*

Almost 1 million specimens of 28 fish species were captured during the study period (Table 3.3). Of these, all were recorded in the River Trent, 21 were found in the Warwickshire Avon, and 19 were found in the Yorkshire Ouse catchment. In addition, one genus of lamprey (*Lampetra*) was captured, although it was not possible to identify the ammocoetes to species in the field (Gardiner, 2003). Overall, roach, dace, bream, bleak, gudgeon, chub, perch, minnow (*Phoxinus phoxinus* (L.)) and three-spined stickleback (*Gasterosteus aculeatus* L.) occurred most frequently in catches (Table 3.3). Other species, plus cyprinid hybrids (mostly roach × bream), were captured less often or in smaller numbers. Species richness was greatest in the Trent (Table 3.3, Fig. 3.2), with all species except river lamprey captured. Bitterling (*Rhodeus sericeus* (Pallas)), flounder (*Platichthys flesus* (L.)), common goby (*Pomatoschistus microps* (Krøyer)), thin-lipped grey mullet (*Liza ramada* (Risso)) and spined loach (*Cobitis taenia* L.) (Nunn *et al.*, 2003b) were unique to the Trent. The ichthyofauna of the Avon was similar to that of the Trent, but with a more pronounced dominance of eurytopic species (Table 3.3, Fig. 3.2). In relative terms, rheophilic species such as barbel, grayling, stone loach (*Barbatula barbatula* (L.)) and bullhead (*Cottus gobio* L.) were most abundant in the Yorkshire Ouse catchment, particularly in the tributaries (Table 3.3, Fig. 3.2). *Lampetra* ammocoetes were restricted to the Ouse catchment.

Sites were grouped by catchment on the basis of their fish fauna using the Bray-Curtis similarity index (Fig. 3.3a). Four main groups were differentiated, one comprising Trent sites, one containing Avon sites, another containing the Ouse tributaries and the most upstream Ouse sites, and the final group containing the lower Ouse sites plus Marina Pond on the Trent. The fish communities of the Trent and Avon were approximately 65% similar, whereas there was only 20% similarity with the majority of Ouse sites (Fig. 3.3a). The exceptions were the lower Ouse sites and the canal at Boroughbridge, which were dominated by roach (Section 3.3.1.2). Species associations could also be identified using the Bray-Curtis similarity index (Fig. 3.3b). Four main groups were identified, which corresponded approximately with the reproductive guild

Table 3.3 Frequency of occurrence of fish and lamprey species (all ages) captured from the River Trent, Warwickshire Avon and Yorkshire Ouse catchments.

Family			Reproductive	**River Trent catchment**						**Warwickshire Avon catchment**					**Yorkshire Ouse catchment**							
Species	Abbreviation	Vernacular name	guild[1]	ATT	TB	CM	MP	WIN	DUN	WAR	OP	TWY	BIRL	TEWK	MAUN	BORO	KHAM	BSPA	LINT	BEN	FUL	ACA
Anguillidae																						
Anguilla anguilla (L.)	*Ag*	Eel	Eurytopic	.	.	.	.	.	o	.	o	.	.	o	.	o	.	.	.	o	.	.
Balitoridae																						
Barbatula barbatula (L.)	*Bt*	Stone loach	Rheophilic A	o	○	○	.	○	o	o	o	.	o	.	❍	○	o	◯	○	o	.	.
Cobitidae																						
Cobitis taenia L.	*Ct*	Spined loach	Rheophilic B	○	○	o	o	○	o	.	.	.	.	.	.	.	.	.	.	.	.	.
Cottidae																						
Cottus gobio L.	*Cg*	Bullhead	Rheophilic A	○	◯	○	o	o	o	○	.	.	.	.	◯	o	o	o	.	○	.	o
Cyprinidae																						
Abramis bjoerkna (L.)	*Aj*	Silver bream	Eurytopic	○	○	.	o	○	o	.	.	○	o	o	.	o	.	.	o	o	.	.
Abramis brama (L.)	*Ab*	Bream	Eurytopic	⭘	◯	○	◯	◯	❍	◯	◯	⭘	◯	◯	.	○	.	o	○	o	◯	○
Alburnus alburnus (L.)	*Aa*	Bleak	Eurytopic	❍	◯	◯	○	❍	❍	○	⭘	⭘	⭘	◯	.	◯	○	.	◯	◯	◯	❍
Barbus barbus (L.)	*Bb*	Barbel	Rheophilic A	o	○	o	○	○	◯	.	.	o	o	.	◯	○	○	◯	◯	○	o	○
Cyprinus carpio L.	*Cc*	Carp	Eurytopic	o	.	o	○	○	.	.	.	o	.	o	.	.	.	.	.	.	.	.
Gobio gobio (L.)	*Gg*	Gudgeon	Rheophilic B	⭘	⭘	❍	◯	⭘	❍	❍	⭘	❍	○	◯	◯	○	❍	o	❍	❍	❍	❍
Leuciscus cephalus (L.)	*Lc*	Chub	Rheophilic A	❍	❍	◯	❍	⭘	⭘	◯	❍	❍	❍	o	◯	❍	◯	❍	❍	❍	❍	❍
Leuciscus leuciscus (L.)	*Ll*	Dace	Rheophilic A	◯	⭘	❍	❍	❍	❍	o	○	◯	◯	o	◯	❍	❍	❍	⭘	❍	◯	◯
Phoxinus phoxinus (L.)	*Pp*	Minnow	Rheophilic A	❍	◯	○	◯	⭘	❍	❍	⭘	⭘	◯	.	⭘	❍	❍	⭘	❍	◯	○	○
Rhodeus sericeus (Pallas)	*Rs*	Bitterling	Limnophilic	○	o	○	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rutilus rutilus (L.)	*Rr*	Roach	Eurytopic	⭘	⭘	❍	◯	❍	⭘	⭘	⭘	⭘	⭘	❍	○	◯	❍	○	❍	❍	❍	❍
Scardinius erythrophthalmus (L.)	*Se*	Rudd	Limnophilic	o	o	.	.	o	.	○	.	○	o	o	.	.	.	.	.	.	.	.
Tinca tinca (L.)	*Tt*	Tench	Limnophilic	o	o	.	.	.	o	.	○	◯	o	.	.	.	.	.	.	.	.	.
Esocidae																						
Esox lucius L.	*El*	Pike	Eurytopic	o	.	○	○	○	○	o	○	◯	o	○	.	○	○	○	○	○	o	.
Gasterosteidae																						
Gasterosteus aculeatus L.	*Ga*	Three-spined stickleback	Eurytopic	◯	❍	◯	o	○	❍	❍	⭘	❍	○	.	❍	○	○	◯	○	○	o	○
Pungitius pungitius (L.)	*Pg*	Ten-spined stickleback	Limnophilic	○	○	○	o	○	◯	.	o	.	.	.	o	o	.	.	o	○	o	○
Gobiidae																						
Pomatoschistus microps (Krøyer)	*Pm*	Common goby		.	.	.	.	.	◯	.	.	.	.	.	.	.	.	.	.	.	.	.
Mugilidae																						
Liza ramada (Risso)	*Lr*	Thin-lipped grey mullet		.	.	.	.	.	o	.	.	.	.	.	.	.	.	.	.	.	.	.
Percidae																						
Gymnocephalus cernuus (L.)	*Gc*	Ruffe	Eurytopic	○	○	o	○	◯	.	○	○	◯	o	○	.	○	o	○	◯	○	○	○
Perca fluviatilis L.	*Pf*	Perch	Eurytopic	❍	❍	❍	◯	⭘	◯	◯	○	⭘	○	❍	.	◯	○	○	○	○	◯	◯
Sander lucioperca (L.)	*Sl*	Zander	Eurytopic	o	o	.	○	o	.	○	o	○	.	○	.	.	.	.	.	.	.	.
Petromyzontidae																						
Lampetra spp.	*La*	River/brook lamprey	Rheophilic A	.	.	.	.	.	.	.	.	.	.	.	◯	○	○	○	o	o	.	.
Pleuronectidae																						
Platichthys flesus (L.)	*Pl*	Flounder	Rheophilic C	.	.	.	.	o	◯	.	.	.	.	.	.	.	.	.	.	.	.	.
Salmonidae																						
Salmo trutta L.	*St*	Brown/sea trout	Rheophilic A	.	.	.	.	.	o	.	.	.	.	.	.	o	.	.	.	.	.	.
Thymallus thymallus (L.)	*Ty*	Grayling	Rheophilic A	.	o	o	.	.	.	.	.	.	.	.	○	○	○	○	○	.	.	.

1 - classification according to Schiemer & Waidbacher (1992)

N.B. Site name abbreviations are the same as those in Table 2.2

Key (percent frequency of occurrence)

Dominant (>75%)	⭘
Abundant (51-75%)	❍
Frequent (26-50%)	◯
Occasional (6-25%)	○
Rare (1-5%)	o
Not captured	.

classifications of Schiemer & Waidbacher (1992). One cluster contained rheophilic species, another contained mostly limnophilic species, the majority of eurytopic species were grouped together, while the final cluster contained estuarine species. Similarity was greatest between the eurytopic species, emphasising their ubiquity. There was less similarity amongst the other guilds, due to the restricted distribution of those species and their irregular occurrence in catches.

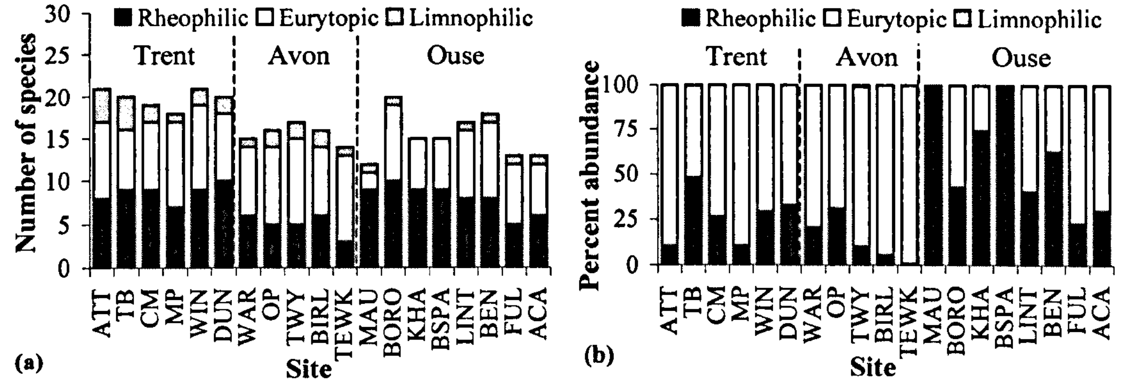

Fig. 3.2 Number (a) and percent abundance (b) of rheophilic, eurytopic and limnophilic species captured from each site in the Trent, Avon and Ouse catchments. Reproductive guild classification according to Schiemer & Waidbacher (1992). Site name abbreviations are the same as those in Table 2.2.

3.3.1.2 *Intra-catchment comparisons*

The River Trent

The River Trent was characterised by eurytopic species typical of lowland rivers (Table 3.3, Fig. 3.2). Roach accounted for 46% of Trent catches, with bream (17%), chub (8%), dace (8%), bleak (7%), gudgeon (7%) and perch (5%) also captured in substantial numbers. Strictly rheophilic species, such as barbel, bullhead and stone loach, were generally caught for only a short time after hatching, while limnophilic species were uncommon, even in floodplain waterbodies.

Attenborough was characterised by bream and roach, with these two species accounting for 53% and 29% of fish captured, respectively (Fig. 3.4). Chub, bleak, gudgeon, perch and minnow were captured in over 60% of surveys but in smaller numbers, as

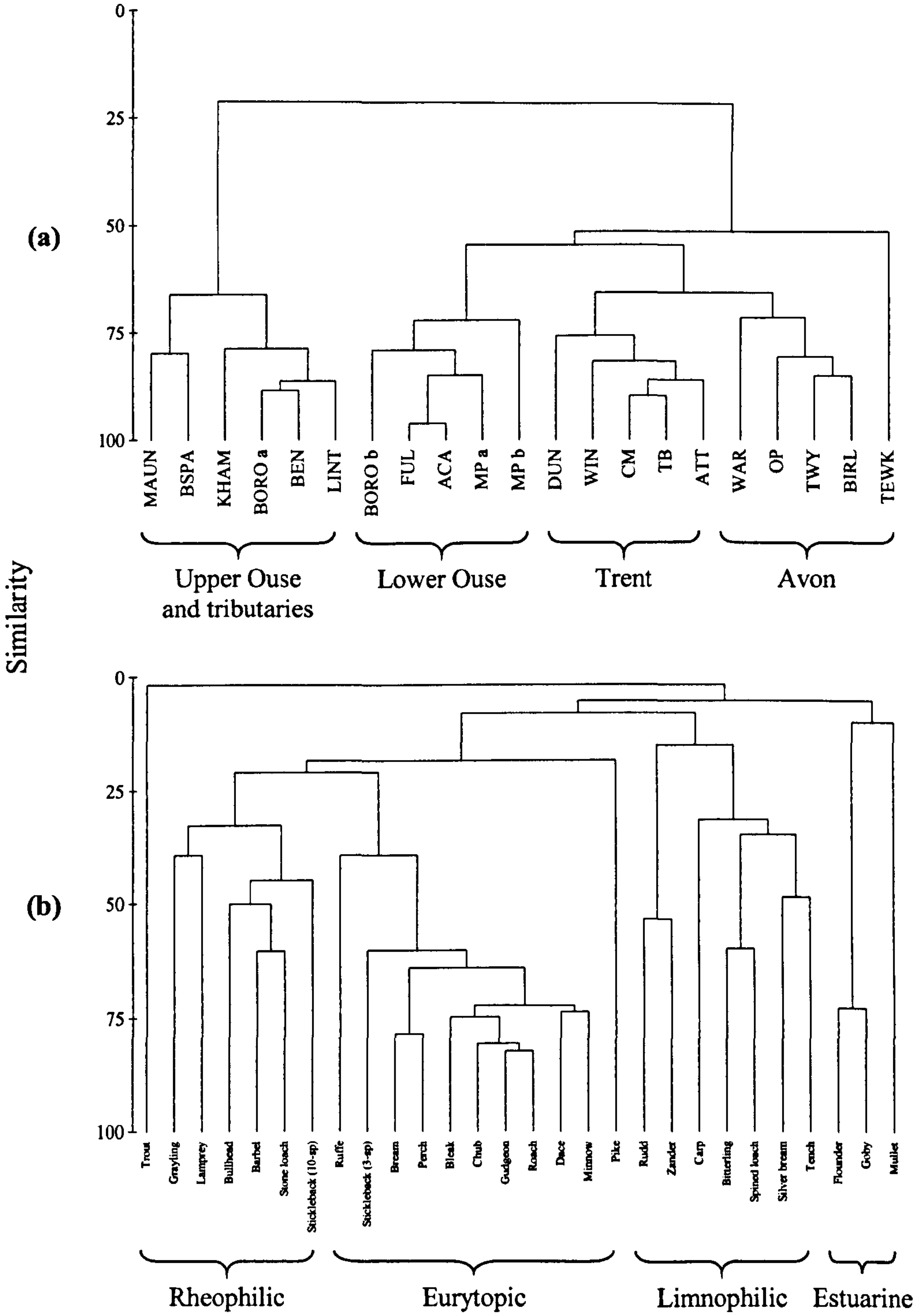

Fig. 3.3 Similarity in (a) fish species composition between sites and (b) spatial distribution between fish species. Site name abbreviations are the same as those in Table 2.2.

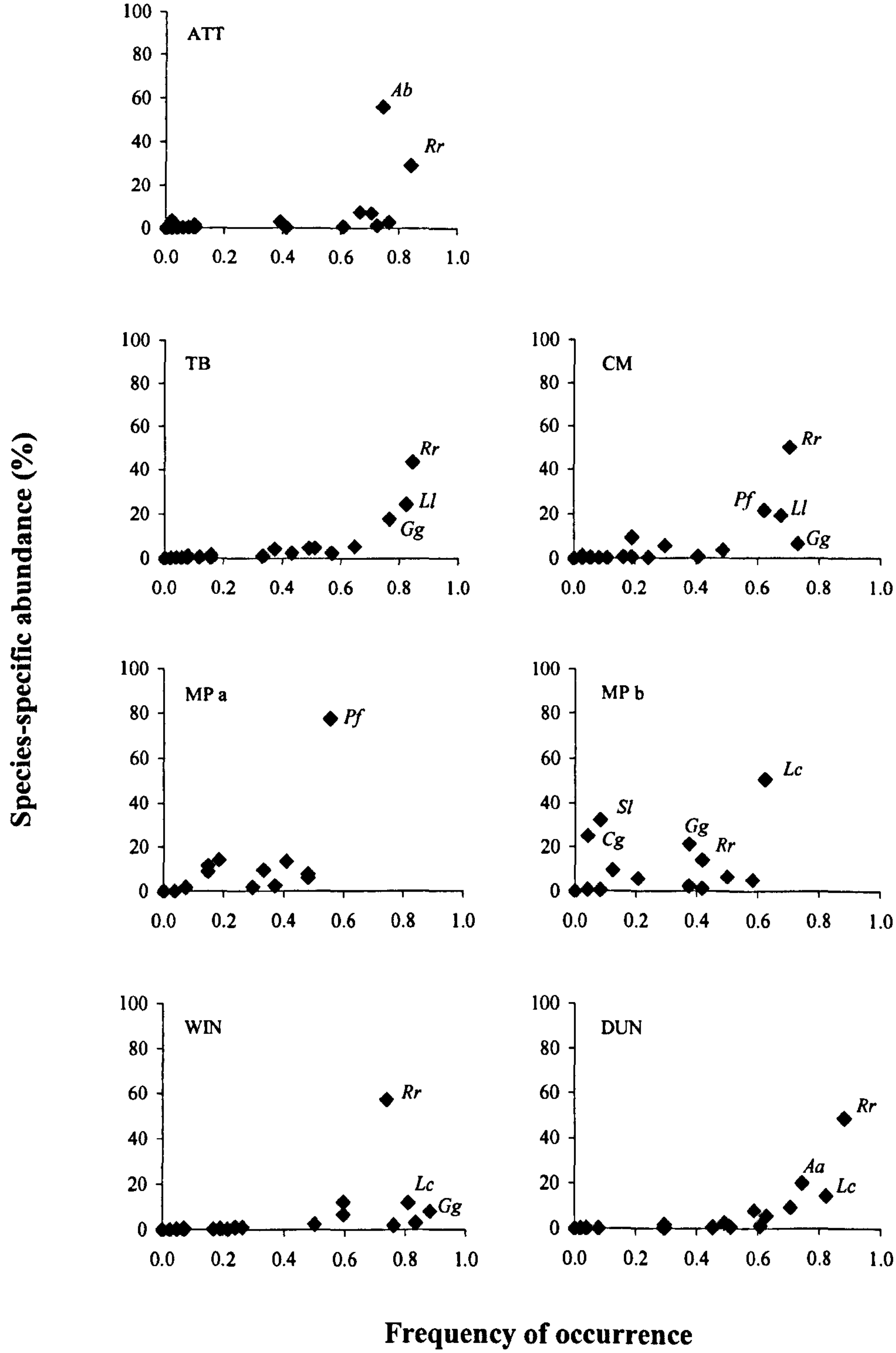

Fig. 3.4 Costello plots demonstrating 0+ fish community structure at seven sites on the River Trent. Site name abbreviations are the same as those in Table 2.2, species name abbreviations are the same as those in Table 3.3.

represented by the cluster of points towards the end of the abscissa (Fig. 3.4). Roach, dace and gudgeon were the three main species at Trent Bridge, accounting for 43%, 24% and 17% of catches, respectively, with a variety of other species frequently captured in smaller numbers (Fig. 3.4). Colwick Marina was characterised by roach, perch and dace, with these three species accounting for 49%, 21% and 19% of catches, respectively (Fig. 3.4). In addition, gudgeon occurred in 73% of surveys, but comprised only 7% of fish caught. Chub (48%) was the dominant species at Marina Pond, with gudgeon (17%) and roach (13%) the next most abundant (Fig. 3.4). Dace and perch were also captured in over 50% of surveys, but in smaller numbers. Zander (*Sander lucioperca* (L.)) and bullhead were rarely caught but comprised approximately 25% of catches when present, as demonstrated by their position along the ordinate. In contrast, the channel connecting Marina Pond with the Trent was dominated by perch (70%), with other species captured less often and in lesser numbers (Fig. 3.4). Winthorpe Lake was dominated by roach (57%), with smaller numbers of chub, bleak, gudgeon, dace, minnow, bream and perch also captured in over 50% of surveys (Fig. 3.4). Roach (49%) was also dominant at Dunham, with chub and bleak representing 14% and 13% of catches, respectively (Fig. 3.4). A further seven species were captured in over 40% of surveys.

The Warwickshire Avon

Similar to the River Trent, the Avon was characterised by eurytopic species (Table 3.3, Fig. 3.2). Roach (49%) dominated Avon catches, with bleak (13%), bream (13%) and perch (8%) the next most abundant species. Rheophilic and limnophilic species were generally uncommon, although the latter (i.e. rudd (*Scardinius erythrophthalmus* (L.)) and tench (*Tinca tinca* (L.))) were more prevalent than in the Trent (Table 3.3).

Warwick was dominated by roach, which accounted for 67% of catches (Fig. 3.5). Gudgeon (12%) was the other main species, with a number of others occurring in over 40% of surveys. Six species characterised catches at Old Pasture, with roach (35%), minnow (17%), bleak (17%) and three-spined stickleback (16%) the most abundant (Fig. 3.5). Chub and gudgeon also occurred in over 60% of surveys, but in smaller numbers. Roach (42%) was the most abundant species at Twyford, with bream (21%) and perch (13%) also captured in large numbers (Fig. 3.5). Bleak, minnow, chub and three-spined stickleback were also present in over 50% of surveys. Roach and bleak

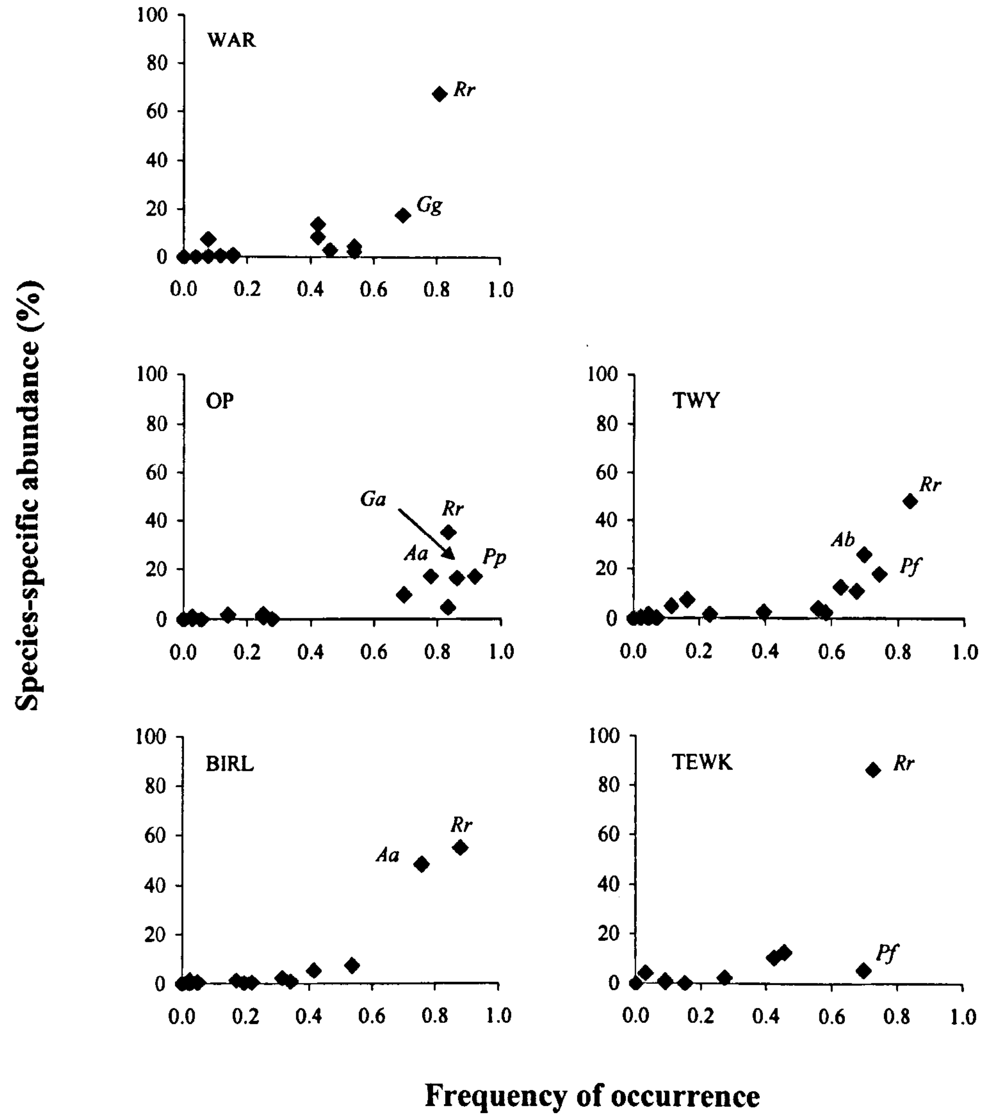

Fig. 3.5 Costello plots demonstrating 0+ fish community structure at five sites on the Warwickshire Avon. Site name abbreviations are the same as those in Table 2.2, species name abbreviations are the same as those in Table 3.3.

were characteristic of Birlingham, accounting for 55% and 37% of catches, respectively (Fig. 3.5). A variety of other species occurred intermittently, but never in large numbers. Tewkesbury was dominated by roach, accounting for 85% of all fish caught (Fig. 3.5). Bream, perch and bleak were also captured in over 40% of surveys, but accounted for less than 20% of catches.

The Yorkshire Ouse

The ichthyofauna of the Yorkshire Ouse catchment could be divided into two distinct categories. The tributaries (Swale, Ure, Nidd, Wharfe) were characterised by minnow (44%), roach (22%), chub (17%) and dace (11%), while the Ouse itself supported a fish community similar to those of the Trent and Avon, with roach (45%), chub (21%), gudgeon (14%), bleak (7%), bream (5%) and dace (5%) the most abundant species (Table 3.3, Fig. 3.2). The Ouse catchment supported a greater diversity and abundance of rheophilic species than the Trent and Avon, with barbel, grayling, brown trout and lamprey included among the species present.

Maunby Demesne was dominated by minnow, which accounted for 87% of all fish caught (Fig. 3.6), with a variety of other rheophilic species occurring in small numbers in over 35% of surveys. Grayling were captured on relatively few occasions, but accounted for more than 25% of catches when present. Boroughbridge was characterised by roach, chub and minnow, accounting for 53%, 20% and 14% of catches, respectively, and grayling contributed 55% to catches when present (Fig. 3.6). Roach (71%) dominated catches in the canal at Boroughbridge, with chub and perch also present in over 60% of surveys (Fig. 3.6). Minnow (28%), dace (27%), roach (15%), chub (12%) and bleak (10%) were the five main species at Kirk Hammerton, with grayling contributing 57% to catches when present (Fig. 3.6). Boston Spa was characterised by minnow (51%), chub (27%) and dace (17%), with other species captured less frequently and in smaller numbers (Fig. 3.6). Grayling accounted for 72% of catches when present. Roach was the most abundant species at Linton, accounting for 42% of catches, with chub (18%), gudgeon (14%), dace (6%) and a variety of other species captured less frequently and in smaller numbers (Fig. 3.6). Ten-spined stickleback (*Pungitius pungitius* (L.)) were rarely captured, but this species occupies a position half way along the ordinate as catches containing this species were small. Chub (33%), roach (30%) and gudgeon (23%) were the most abundant species at

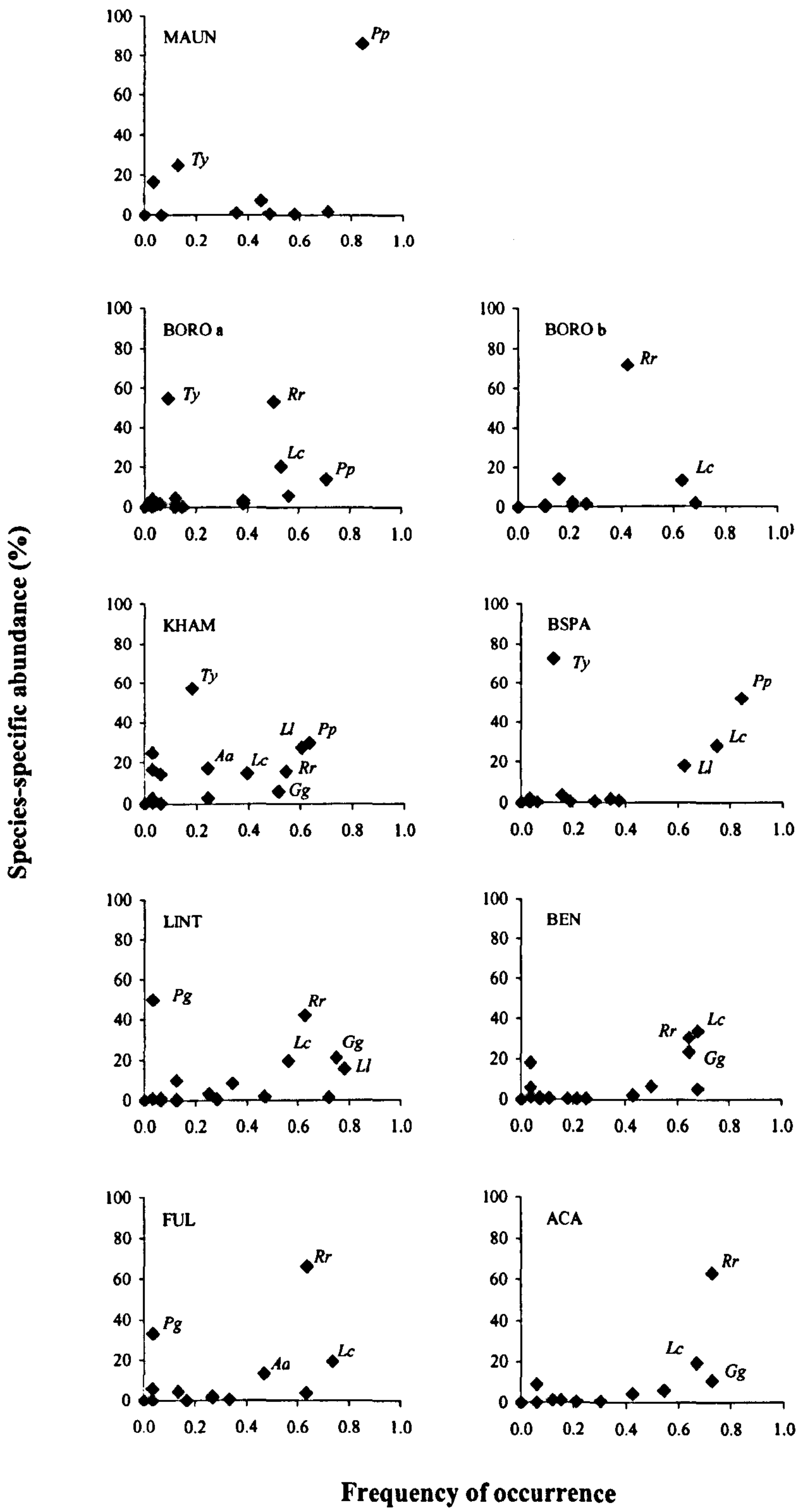

Fig. 3.6 Costello plots demonstrating 0+ fish community structure at nine sites in the Yorkshire Ouse catchment. Site name abbreviations are the same as those in Table 2.2, species name abbreviations are the same as those in Table 3.3.

Beningbrough, with bleak and dace also captured in over 50% of surveys (Fig. 3.6). Fulford was characterised by roach (64%), chub (18%) and bleak (10%) (Fig. 3.6). Gudgeon were also captured in over 60% of surveys, but accounted for only 4% of fish caught. Roach was also the dominant species at Acaster Malbis, accounting for 63% of fish caught, with chub (18%), gudgeon (10%) and a variety of other species captured in smaller numbers (Fig. 3.6).

3.3.2 Diversity and evenness

3.3.2.1 *Inter-catchment comparisons*

The ichthyofauna of the Trent was significantly (ANOVA, $P<0.05$) more diverse (mean H' of all surveys in Trent catchment = 0.95) than those of the Avon (0.79) and Ouse (0.72). The difference between the Avon and Ouse was not statistically significant (ANOVA, $P>0.05$). Mean evenness was highest in the Ouse ($J = 0.62$), followed by the Trent (0.60) and Avon (0.57), although the differences were not statistically significant (ANOVA, $P>0.05$).

3.3.2.2 *Intra-catchment comparisons*

The River Trent

In the Trent, Dunham had the highest mean value of diversity (mean H' of all surveys at Dunham = 1.13), followed by Winthorpe Lake (1.07) and Attenborough (1.04) (Fig. 3.7). The two lowest mean diversities were found at the Marina Pond sites (<0.7), while diversity at Trent Bridge (0.95) was similar to that at Colwick Marina (0.89). Mean diversity at Dunham was significantly greater than those at Marina Pond (ANOVA, $P<0.05$), but none of the other differences were statistically significant:

DUN WIN ATT TB CM MP b MP a

Evenness was highest at Colwick Marina and Marina Pond, and lowest at Trent Bridge and Winthorpe Lake (Fig. 3.7), although none of the differences were statistically significant (ANOVA, $P>0.05$).

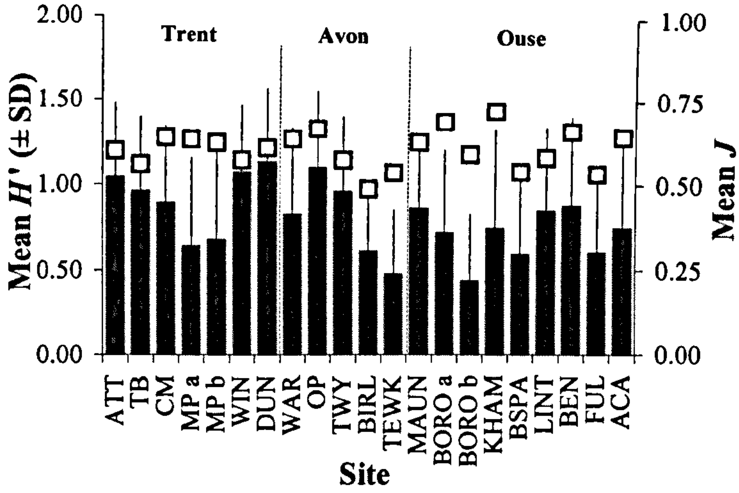

Fig. 3.7 Mean diversity (H', ■) and evenness (J, □) of 0+ fish communities at each site in the Trent, Avon and Ouse catchments. Site name abbreviations are the same as those in Table 2.2.

The Warwickshire Avon

In the Avon, mean diversity was greatest at Old Pasture (1.09), followed by Twyford (0.95) and Warwick (0.82), with the two lowest diversities at Birlingham (0.61) and Tewkesbury (0.47) (Fig. 3.7). Mean diversity was significantly greater at Old Pasture and Twyford than at Birlingham and Tewkesbury (ANOVA, P<0.05):

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There was a significant difference (ANOVA, P<0.05) in the mean evenness at Old Pasture (0.66) and Birlingham (0.49), but not between other sites (P>0.05) (Fig. 3.7).

The Yorkshire Ouse

In the Ouse catchment, the three greatest diversities of 0+ fish were found at Beningbrough (0.88), Maunby Demesne (0.86) and Linton (0.85), with the lowest in the canal at Boroughbridge (0.43) (Fig. 3.7). The river at Boroughbridge, Kirk Hammerton and Acaster Malbis had a similar diversity of fish fauna (0.70-0.80), while diversities at Boston Spa and Fulford were similar (0.59 and 0.60, respectively). None of the differences between sites were statistically significant (ANOVA, P>0.05). Evenness was highest at Kirk Hammerton (0.72), with the two lowest at Boston Spa (0.54) and Fulford (0.53) (Fig. 3.7), although none of the differences were statistically significant (ANOVA, P>0.05).

3.3.3 Density

3.3.3.1 *Inter-catchment comparisons*

Mean density of 0+ fish was highest in the Trent (26 fish per m^2), followed by the Ouse (8 fish per m^2) and Avon (5 fish per m^2) (Fig. 3.8), with the difference between the Trent and Ouse being significant (Mann-Whitney *U*-Test, $P<0.05$). The difference between the Trent and Avon, although substantial, was not statistically significant ($P>0.05$) due to high variance in the catches. Maximum densities were also highest in the Trent (2351 fish per m^2), followed by the Ouse (254 fish per m^2) and Avon (80 fish per m^2) (Fig. 3.8).

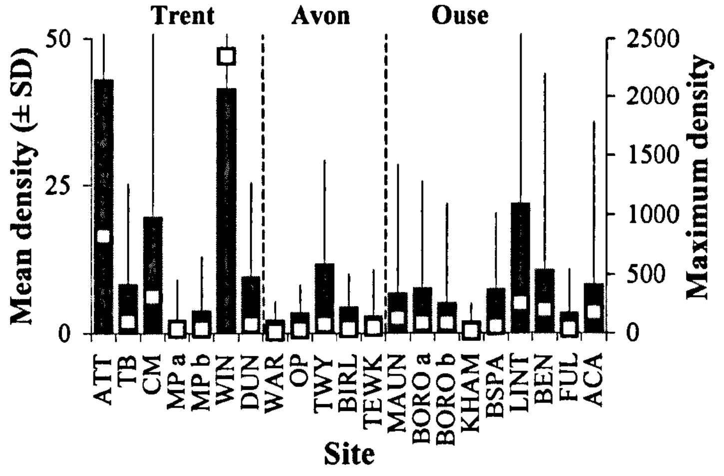

Fig. 3.8 Mean (■) and maximum (□) density (fish per m^2) of 0+ fish at each site in the Trent, Avon and Ouse catchments. The Winthorpe Lake mean estimate does not include the exceptional catch of 2351 fish per m^2 in November 2003. Site name abbreviations are the same as those in Table 2.2.

3.3.3.2 *Intra-catchment comparisons*

The River Trent

In the Trent, Attenborough (43 fish per m^2) and Winthorpe Lake (42 fish per m^2) had the two highest mean densities of 0+ fish, while the Marina Pond sites (<4 fish per m^2) had the two lowest densities (Fig. 3.8). Mean density was comparatively high at Colwick Marina (19 fish per m^2), although variance was also high due to low catches during the winter (Fig. 3.8). Mean density at Trent Bridge (8 fish per m^2) was similar to that at Dunham (10 fish per m^2), and with lower variance than at Colwick Marina (less drastically affected by season). Mean densities at Winthorpe Lake and Dunham were significantly greater than those at Marina Pond (Mann-Whitney *U*-Tests, $P<0.05$). There were no significant differences between other sites ($P>0.05$) due to the large variances associated with the mean density estimates. Maximum densities were at Winthorpe Lake (2351 fish per m^2) and Attenborough (821 fish per m^2), and the lowest at the Marina Pond sites (<40 fish per m^2) (Fig. 3.8). Maximum density at Colwick Marina was 309 fish per m^2, with Trent Bridge (100 fish per m^2) similar to Dunham (79 fish per m^2).

There were no consistent patterns in fish densities at the macrohabitat level, with floodplain sites (i.e. connected gravel pits) sometimes, but not always, supporting higher densities of fish than main river sites. Densities of all (not just rheophilic) species were negatively affected by the disconnection of Marina Pond from the river (Fig. 3.9). In the pond itself (MP b), mean density pre-disconnection was 6 fish per m^2 fish compared with 0.2 fish per m^2 post-disconnection (Mann-Whitney *U*-Test, $P<0.05$), while in the channel connecting Marina Pond to the river (MP a), mean density pre-disconnection was 3 fish per m^2 fish compared with 0.5 fish per m^2 post-disconnection ($P>0.05$).

The Warwickshire Avon

The greatest densities of 0+ fish in the Avon were found in the backwater at Twyford (mean 12 fish per m^2, Fig. 3.8). In addition, this site frequently supported high densities of >0+ fish, particularly in winter (maximum 111 >0+ fish per m^2, Fig. 3.10). Densities were substantially lower at the other sites, with Birlingham, Old Pasture, Tewkesbury and Warwick all supporting mean densities of <5 fish per m^2 (Fig. 3.8). There was a significant difference in the mean density of 0+ fish at Twyford compared with those at other Avon sites, with the exception of Birlingham (Mann-Whitney *U*-Tests, $P<0.05$):

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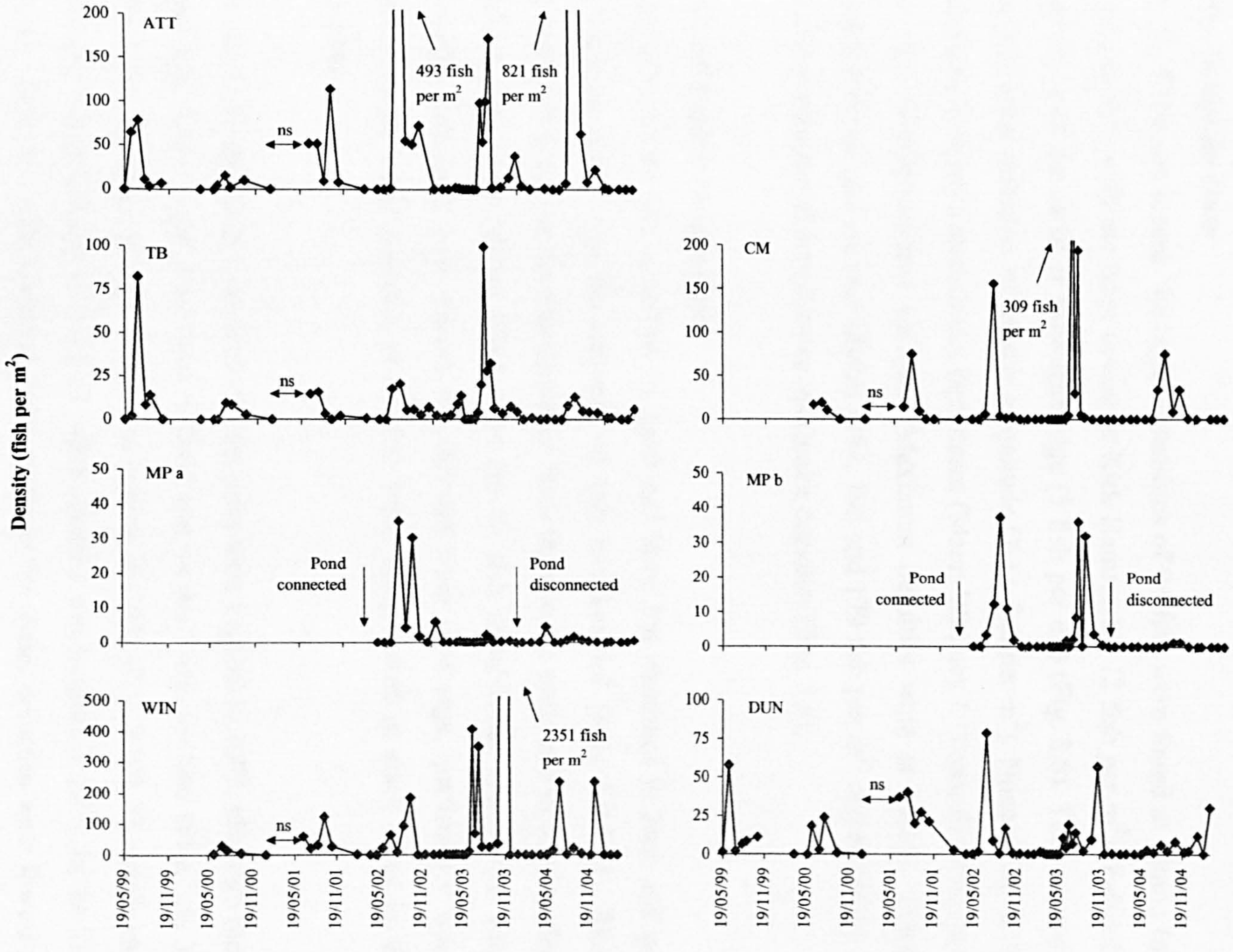


ns - No surveys conducted due to an outbreak of foot and mouth disease

Fig. 3.9 Temporal variations in density of 0+ fish at seven sites on the River Trent. Site name abbreviations are the same as those in Table 2.2.

Maximum densities were also found at Twyford (80 fish per m^2), with the lowest at Warwick (11 fish per m^2) (Fig. 3.8). Maximum densities were intermediate at Tewkesbury (49 fish per m^2), Birlingham (37 fish per m^2) and Old Pasture (27 fish per m^2).

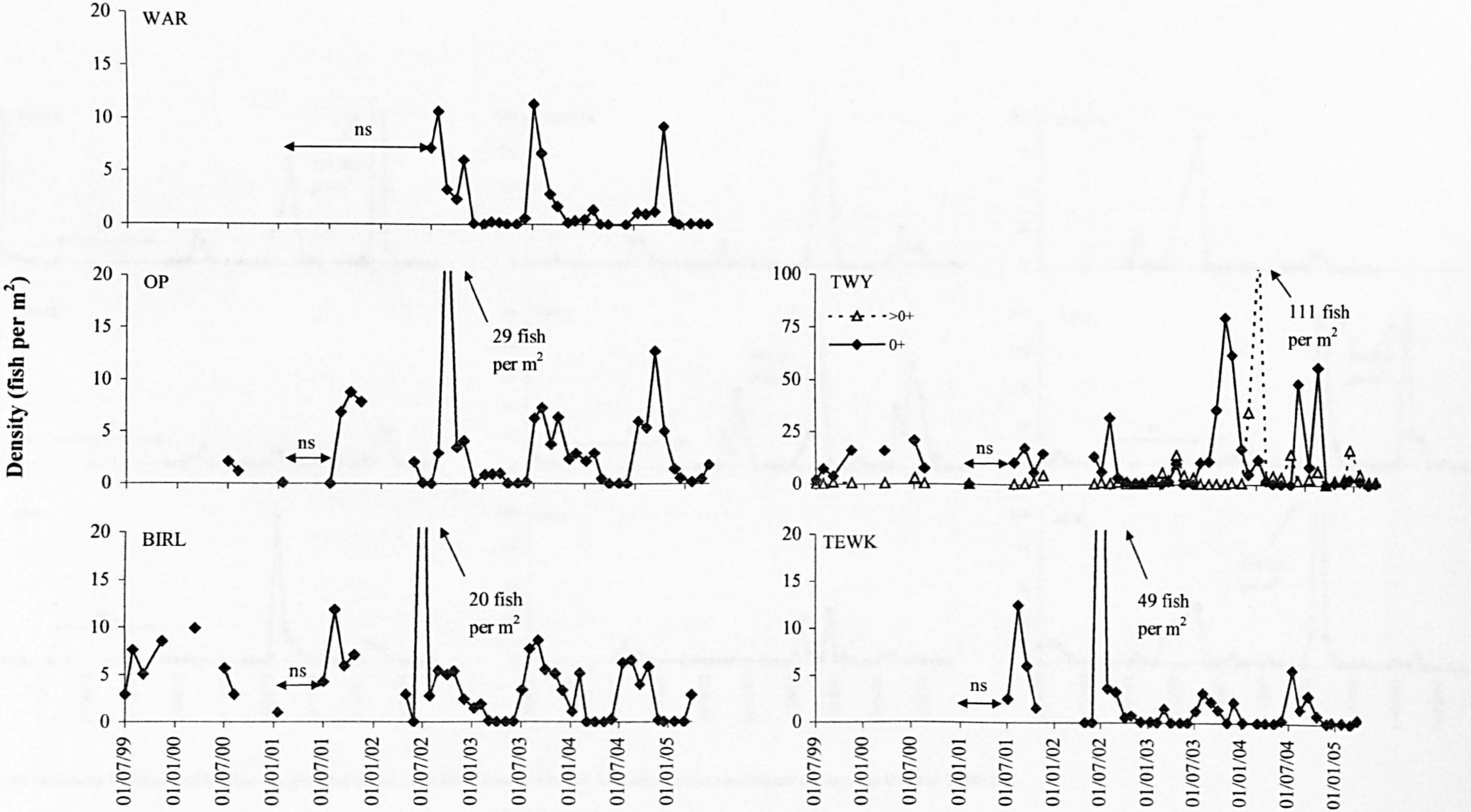
The Yorkshire Ouse

In the Ouse catchment, the highest densities of 0+ fish were found at Linton (mean 22 fish per m^2), with the three lowest at Kirk Hammerton (2 fish per m^2), Fulford (3 fish per m^2) and the canal at Boroughbridge (5 fish per m^2) (Fig. 3.8). The remaining sites all had mean densities of similar magnitude (7-11 fish per m^2). None of the differences between sites were statistically significant (Mann-Whitney *U*-Tests, $P>0.05$), partly due to high between-sample variance. Maximum densities were at Linton, followed by Beningbrough and Acaster Malbis (254, 196 and 179 fish per m^2, respectively). Fulford and the tributary sites had lower maximum densities (Fig. 3.8).

3.3.3.3 *Temporal variations*

Densities of 0+ fish were low in April and May, but increased in June and generally peaked in July, once the majority of fish had hatched (Figs 3.9-3.11). Thereafter, densities declined as the fish dispersed from the nursery areas and as density-dependent and -independent factors acted upon the 0+ fish populations. Occasional exceptions usually coincided with periods of elevated river discharge, particularly during the winter, with large numbers of 0+ fish often congregated in slack areas in the river margins.

In the Trent and Ouse, densities at most sites were highest in 2003, although there were also high densities at some sites in 2004 and, in the Trent, in 2002 (Figs 3.9, 3.11). In the Avon, densities at most sites were highest in 2002 (Fig. 3.10). The main exception was the backwater site at Twyford, where density was highest in 2003. In the Trent and Avon, densities were lowest in 2000, while in the Ouse, densities were lowest in 2000 and 2002.



ns - No surveys conducted due to an outbreak of foot and mouth disease

Fig. 3.10 Temporal variations in density of 0+ fish at five sites on the Warwickshire Avon. Site name abbreviations are the same as those in Table 2.2.

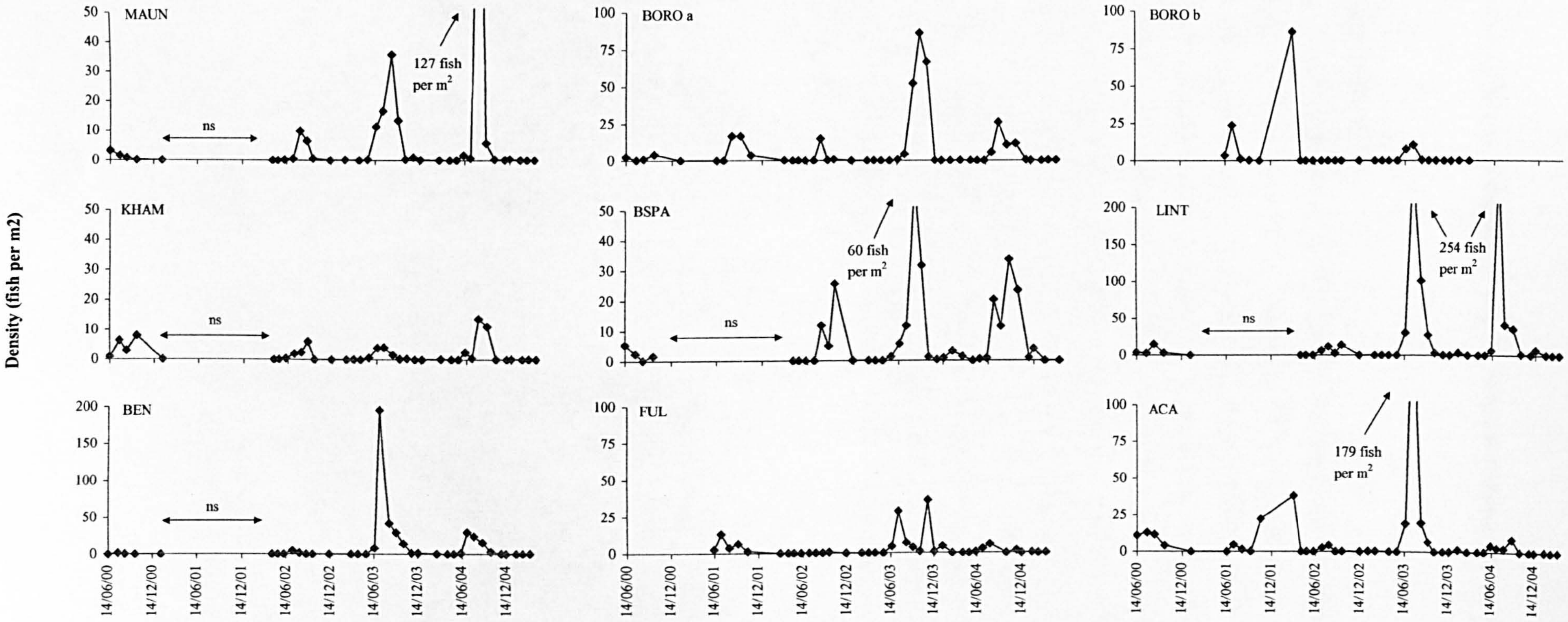


Fig. 3.11 Temporal variations in density of 0+ fish at eight sites in the Yorkshire Ouse catchment. Site name abbreviations are the same as those in Table 2.2.

3.3.4 Point abundance sampling (PAS) by electric fishing versus micromesh seine netting

3.3.4.1 *Species composition*

A total of 2 282 individuals of 16 fish species was captured by double seine netting, compared with 791 individuals of 12 species by PAS, between May and October 2002 inclusive. Seine net catches at Trent Bridge were characterised by dace in June and July, and dace, roach and gudgeon from August to October (Fig. 3.12). At Colwick Marina, seine net catches were characterised by dace in June, dace and roach in July, dace and gudgeon in August, and bleak and roach in September and October (Fig. 3.12). Dace also dominated June PAS samples at Trent Bridge, while stone loach was the most abundant species in July. Gudgeon and roach dominated the catches in August, with September and October samples characterised by perch and roach (Fig. 3.12). At Colwick Marina, dace was dominant in June, and again in July along with perch (Fig. 3.12). Roach dominated catches from August to October, with perch and gudgeon also captured in numbers.

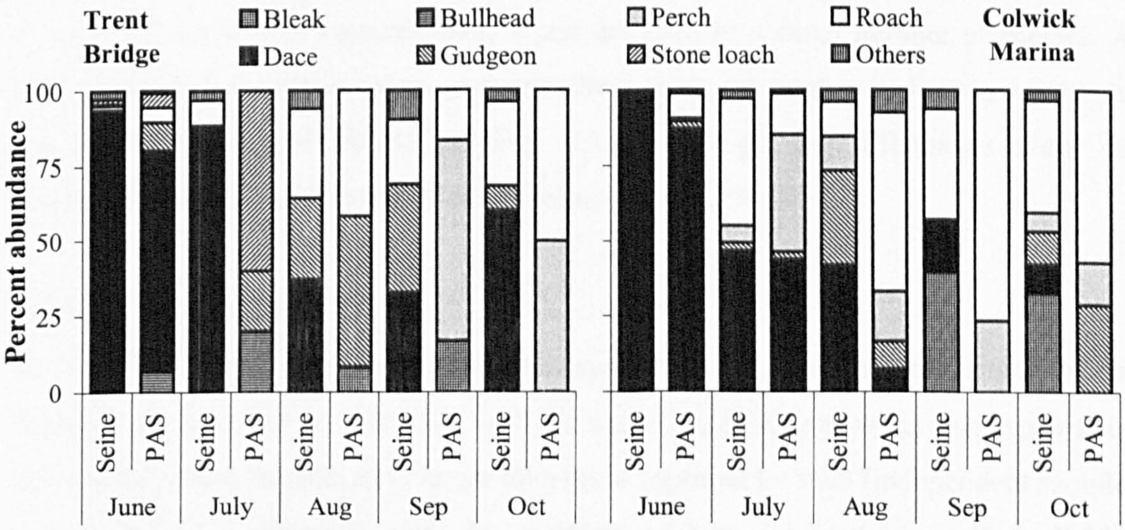


Fig 3.12 Species composition of seine net and PAS catches from Trent Bridge and Colwick Marina.

In terms of percent abundance, species composition of seine net and PAS catches were similar (≥60%) at both sites in June, and at Colwick Marina in July (Table 3.4). For the rest of the sampling period, species composition between the two methods was dissimilar (Table 3.4). Seine netting appeared to be relatively more effective than PAS at capturing mid-water cyprinids such as dace and roach, whereas PAS appeared relatively more effective at capturing benthic species and perch (Fig. 3.15).

Table 3.4 Similarity (Bray-Curtis) in species composition between seine net and PAS catches.

Site	June	July	Aug	Sep	Oct
Trent Bridge	**0.77**	0.02	0.57	0.17	0.28
Colwick Marina	**0.87**	**0.67**	0.43	0.37	0.55

Values in bold type designate significant overlap (≥0.60).

3.3.4.2 *Diversity and evenness*

Diversity and evenness of seine net catches increased from a minimum in June to a more balanced community thereafter as fish species hatched (Fig. 3.13). A similar trend was apparent in PAS catches at Colwick Marina, with the exception of September when diversity was low due to a dominance of roach (Fig. 3.13). Diversity and evenness in PAS catches at Trent Bridge were remarkably constant throughout the study period (Fig. 3.13), a result of approximately equal densities of a small number of species. At both sites, PAS catches were more diverse than seine net catches in June and July, but the situation reversed thereafter (Fig. 3.13), although the differences were not statistically significant overall (Mann-Whitney *U*-Test, $P>0.05$).

3.3.4.3 *Size distribution*

At Trent Bridge, no significant differences were found between the mean lengths of fish captured by seine netting and PAS, with the exception of August when fish captured by seine netting were significantly larger than those captured by PAS (independent samples *t*-test; Table 3.5). However, with the exception of June, PAS catches at Trent Bridge were small, possibly reducing the reliability of mean length estimates. The length distribution of the seine net catch in June was significantly different (two-sample Kolmogorov-Smirnov test, $P<0.05$) from that of PAS (Fig. 3.14). With the exception of September, however, there were no significant differences thereafter ($P>0.05$), although sample sizes for PAS were small (Fig. 3.14). Significant differences were found between the mean lengths of fish captured by the two methods at Colwick Marina (independent samples *t*-tests; Table 3.5). There was no consistent pattern in the differences, with seine net fish being larger in June and August, and PAS fish being larger in July and September. There was no significant difference in October, although catches were small. There was no significant difference in the length distributions of seine net and PAS catches in June, September and October (two-sample Kolmogorov-Smirnov tests, $P>0.05$), but there was in July and August ($P<0.01$) (Fig. 3.14).

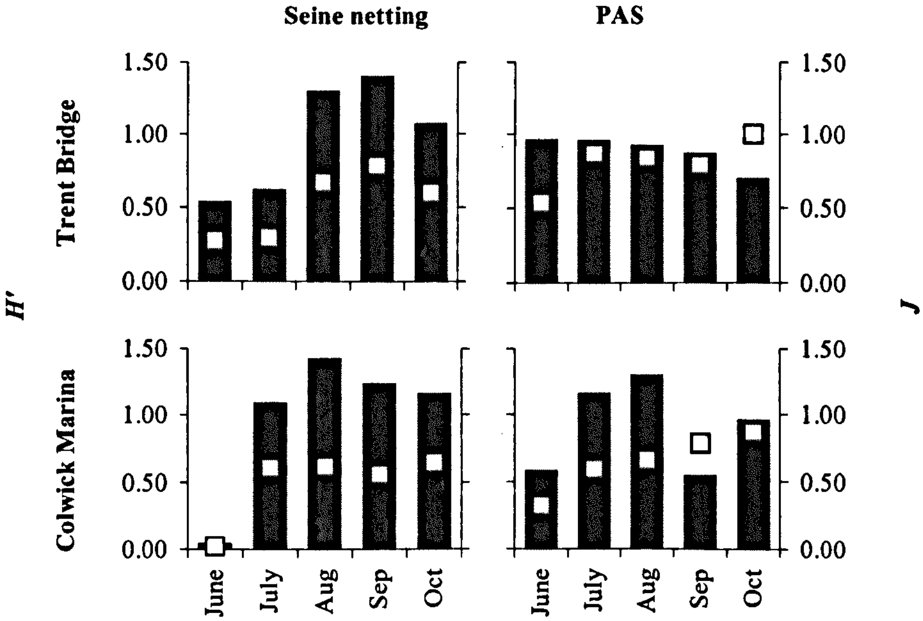


Fig. 3.13 Diversity (*H'*, ■) and evenness (*J*, □) of seine net and PAS catches from Trent Bridge and Colwick Marina.

Table 3.5 Mean SL (mm ± SD) of fish captured by seine net and PAS at Trent Bridge and Colwick Marina (sample sizes are provided in Fig. 3.14).

Site	Method	June	July	Aug	Sep	Oct
Trent Bridge	Seine	17.97	27.35	33.55*	41.41	42.83
		(3.96)	(8.27)	(5.91)	(8.23)	(6.96)
	PAS	17.62	25.80	29.75*	46.50	47.50
		(8.20)	(5.93)	(7.16)	(18.91)	(16.26)
Colwick Marina	Seine	22.15*	28.56**	35.07**	36.41*	34.84
		(6.67)	(5.56)	(7.70)	(9.47)	(11.13)
	PAS	19.95*	32.06**	31.16**	40.71*	35.79
		(3.49)	(6.51)	(8.85)	(13.54)	(14.09)

Asterisks indicate significant differences between seine net and PAS; $^*P<0.05$, $^{**}P<0.01$

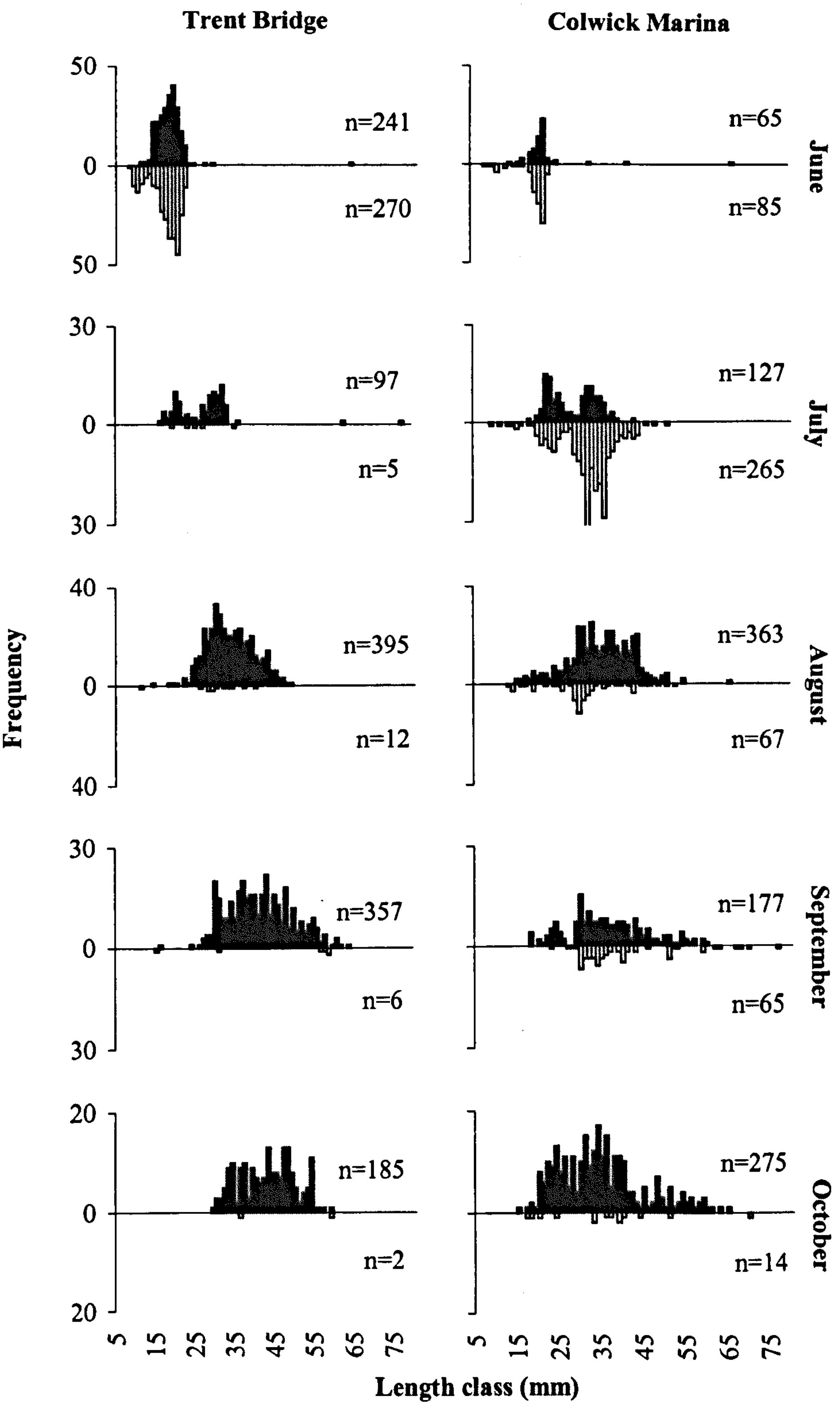


Fig. 3.14 Comparative length-frequency distributions of catches by seine net (filled bars) and PAS (clear bars) over a five month period.

The selection indices further demonstrate the inequality in size distribution between seine net and PAS catches (Fig. 3.15). The maximum deviation in the selection index was -0.46 (Fig. 3.15), indicating avoidance of the 10-19 mm length class by seine netting at Trent Bridge. In contrast, positive selection indices were found for the 30-39 and 40-49 mm length classes, indicating a positive selection bias for these length classes by seine netting. Larger length classes, and the smallest length class, contained relatively few fish, and so their selection indices were small. There was less difference in the seine net and PAS catches at Colwick Marina, perhaps due to larger sample sizes.

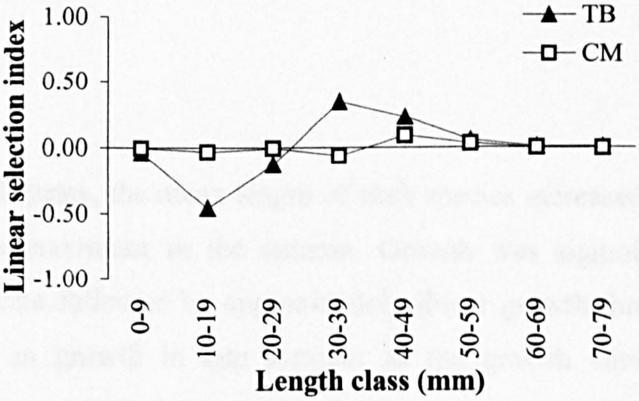


Fig. 3.15 Linear selection index (Strauss) of seine net and PAS catches from Trent Bridge (TB) and Colwick Marina (CM).

3.3.4.4 *Density*

No 0+ fish were captured by either seine netting or PAS at Trent Bridge and Colwick Marina in May. Total fish density calculated from seine net and PAS catches peaked in June (Trent Bridge) and July (Colwick Marina), before declining steadily thereafter (Fig. 3.16). With the exception of Colwick Marina in August, seine netting produced higher densities of 0+ fish than PAS, although the differences were not statistically significant (Mann-Whitney *U*-Tests, $P > 0.05$) (Fig. 3.16).

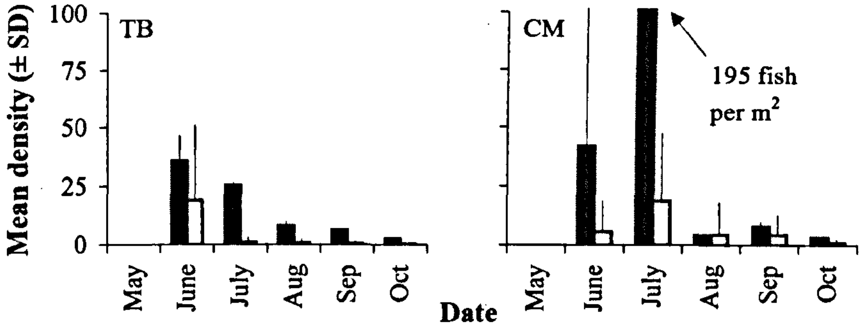


Fig. 3.16 Mean density (fish per m^2) of 0+ fish derived from seine net (■) and PAS (□) catches at Trent Bridge (TB) and Colwick Marina (CM).

3.3.5 Growth

At all sites and in all years, the mean length of each species increased from a minimum upon hatching to a maximum in the autumn. Growth was sigmoidal, with a rapid increase in growth rate followed by approximately linear growth through the summer, before a reduction in growth in late summer as the growth curve approached its asymptote. Due to space restrictions and for clarity, growth curves (Figs 3.17-3.19) and length-frequency histograms (Figs 3.20-3.39) are displayed for examples of each species, in each catchment, for a single year.

3.3.5.1 *Inter-catchment comparisons*

Absolute growth

Fish of all species grew significantly larger in the Trent than in the Ouse (Kruskal-Wallis tests, $P<0.01$), while fish in the Trent were larger than those in the Avon in 77% of cases. The main exception was in 1999, when roach, gudgeon, bream and perch were larger in the Avon than in the Trent. Avon fish were larger than Ouse fish in 67% of cases, with the main exception being gudgeon which were often larger in the Ouse.

Growth rates

There were notable differences in growth rates between catchments. With the exception of perch, all species grew faster in the Trent than in the Avon and Ouse (Table 3.6), while growth rates in the Avon were similar to those in the Ouse.

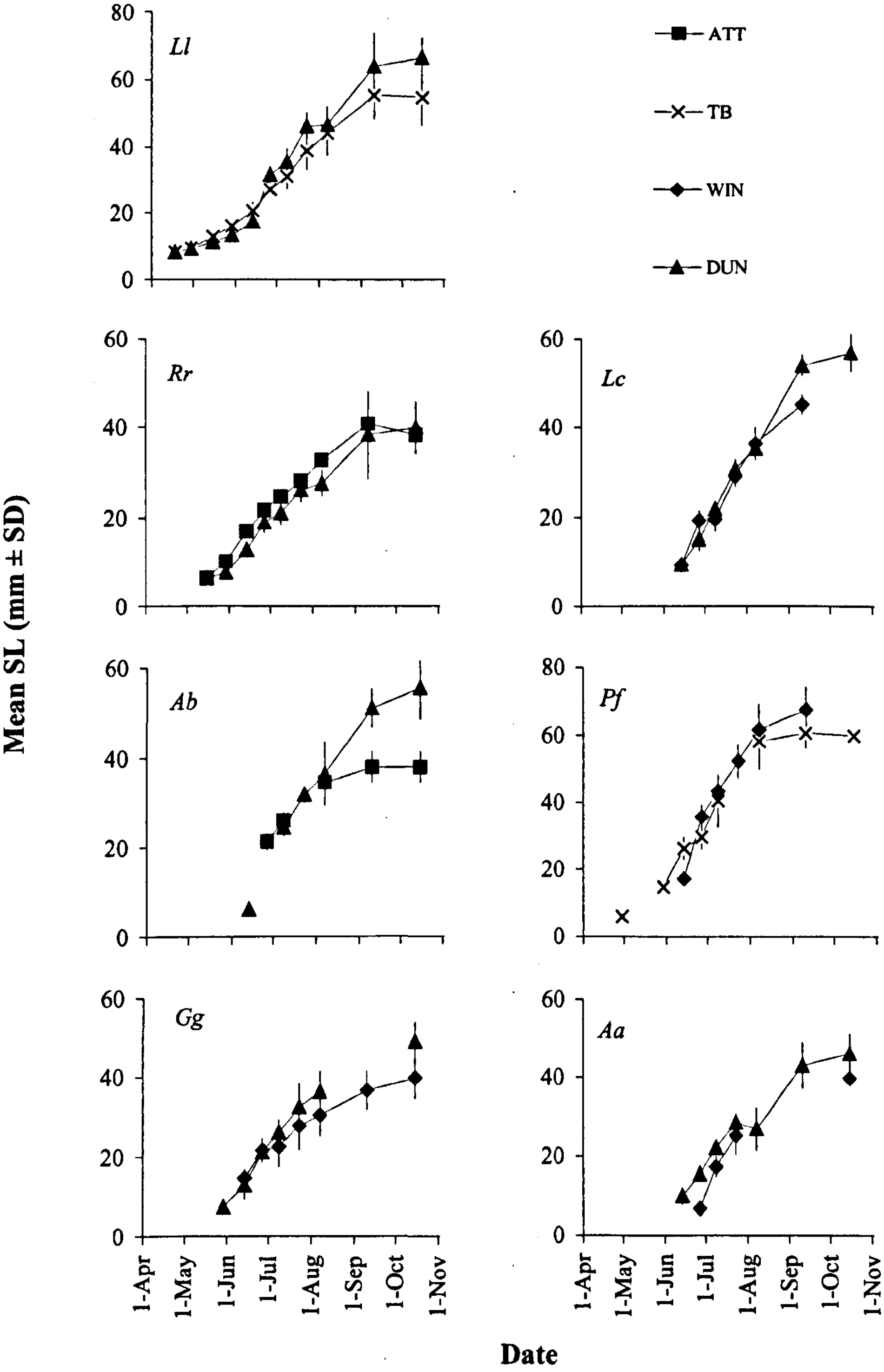


Fig. 3.17 Growth curves for seven species of 0+ fish at selected sites in the River Trent, 2003. Site name abbreviations are the same as those in Table 2.2, species name abbreviations are the same as those in Table 3.3.

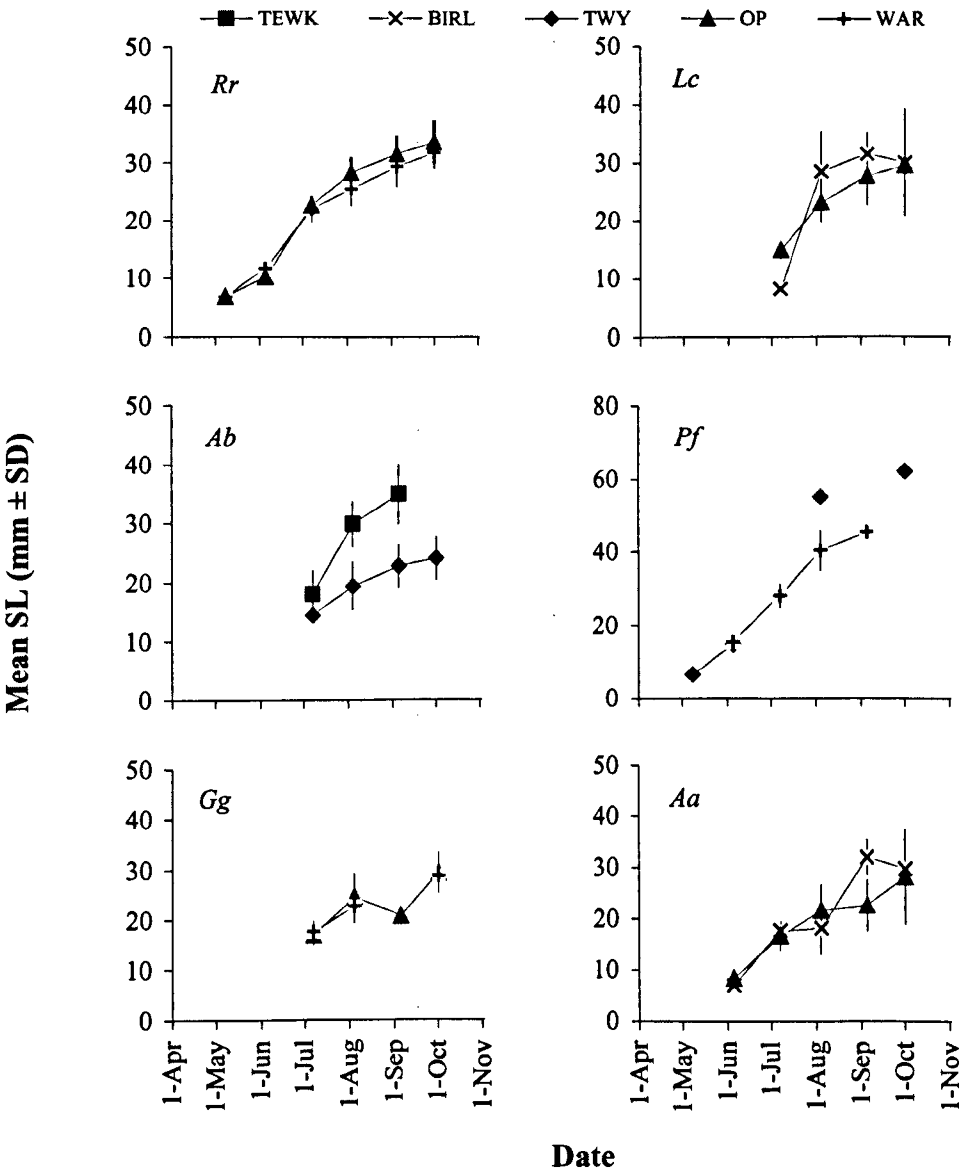


Fig. 3.18 Growth curves for six species of 0+ fish at selected sites in the Warwickshire Avon, 2003. Site name abbreviations are the same as those in Table 2.2, species name abbreviations are the same as those in Table 3.3.

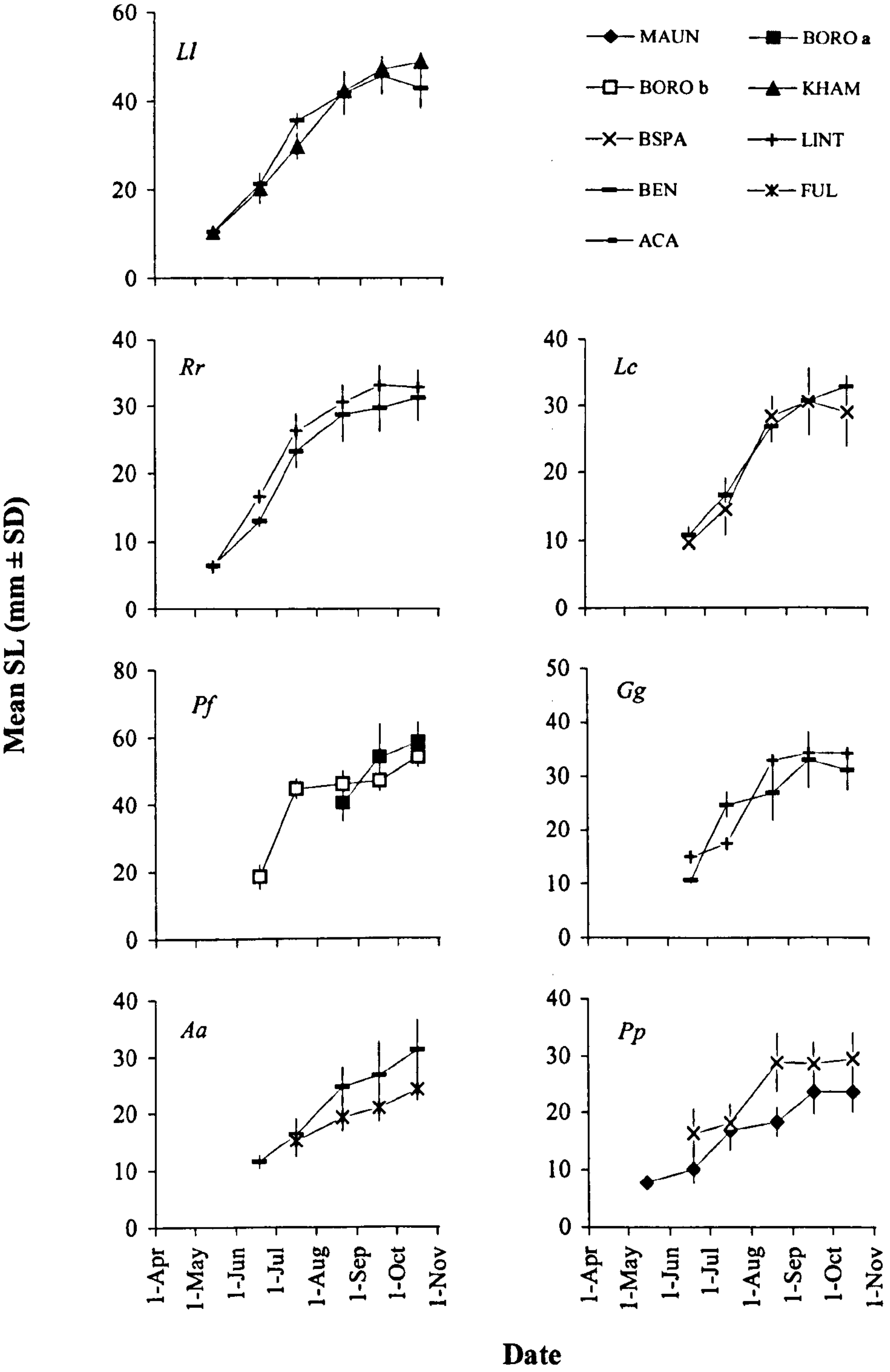


Fig. 3.19 Growth curves for seven species of 0+ fish at selected sites in the Yorkshire Ouse catchment, 2003. Site name abbreviations are the same as those in Table 2.2, species name abbreviations are the same as those in Table 3.3.

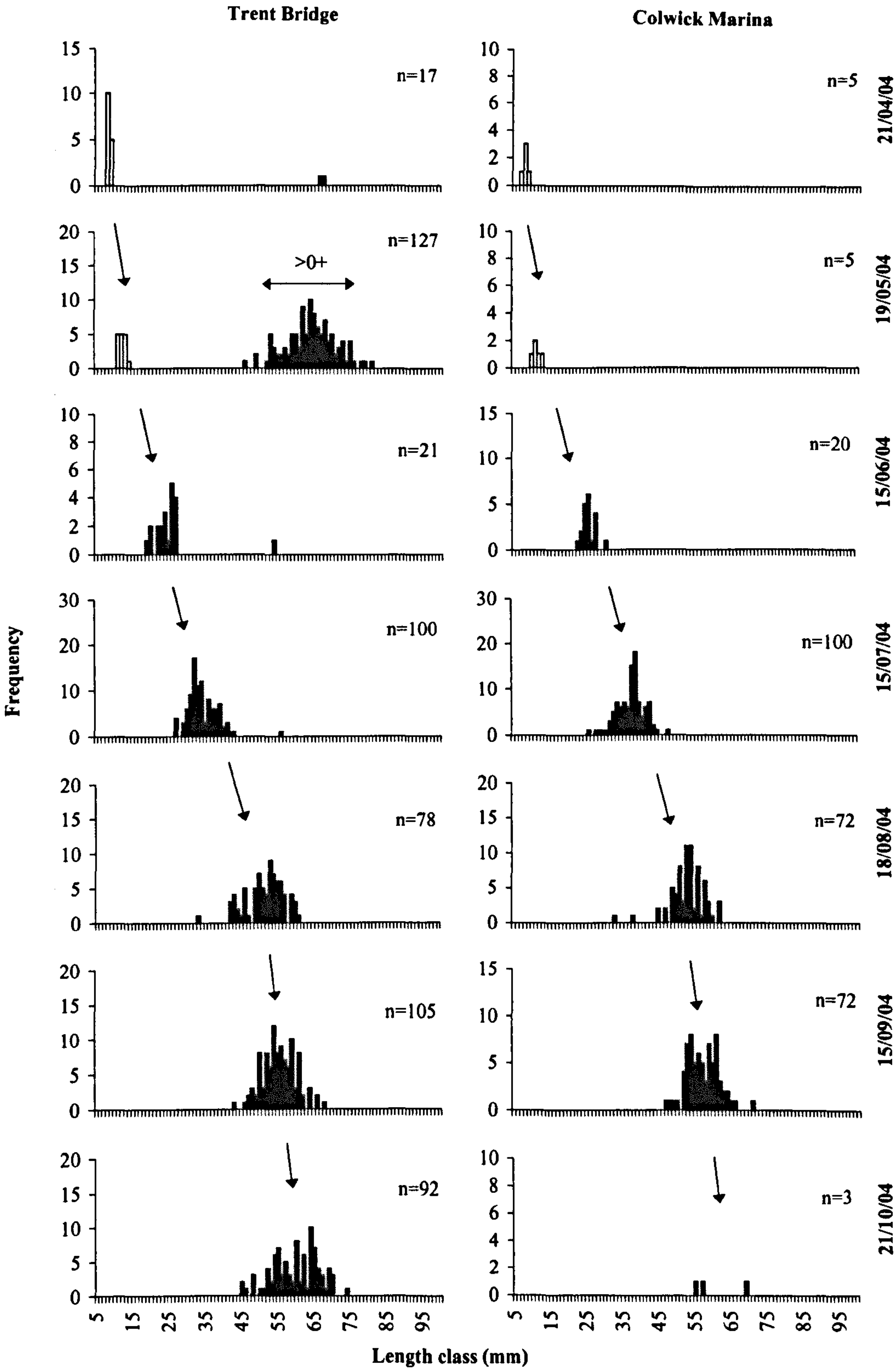


Fig. 3.20 Length-frequency distributions of dace captured by seine net from the River Trent, April to October 2004. Clear bars indicate fish captured by hand-net.

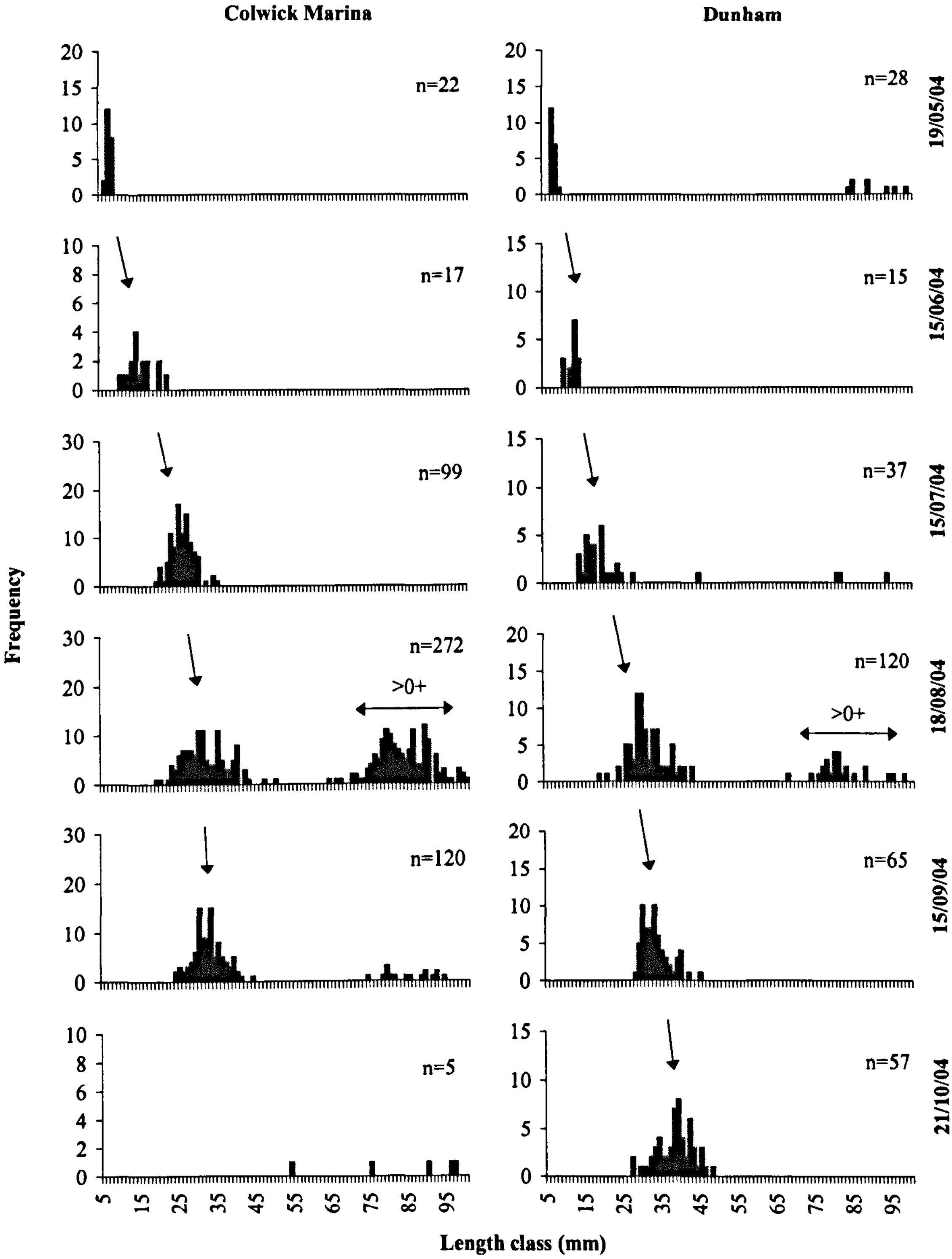


Fig. 3.21 Length-frequency distributions of roach captured by seine net from the River Trent, May to October 2004.

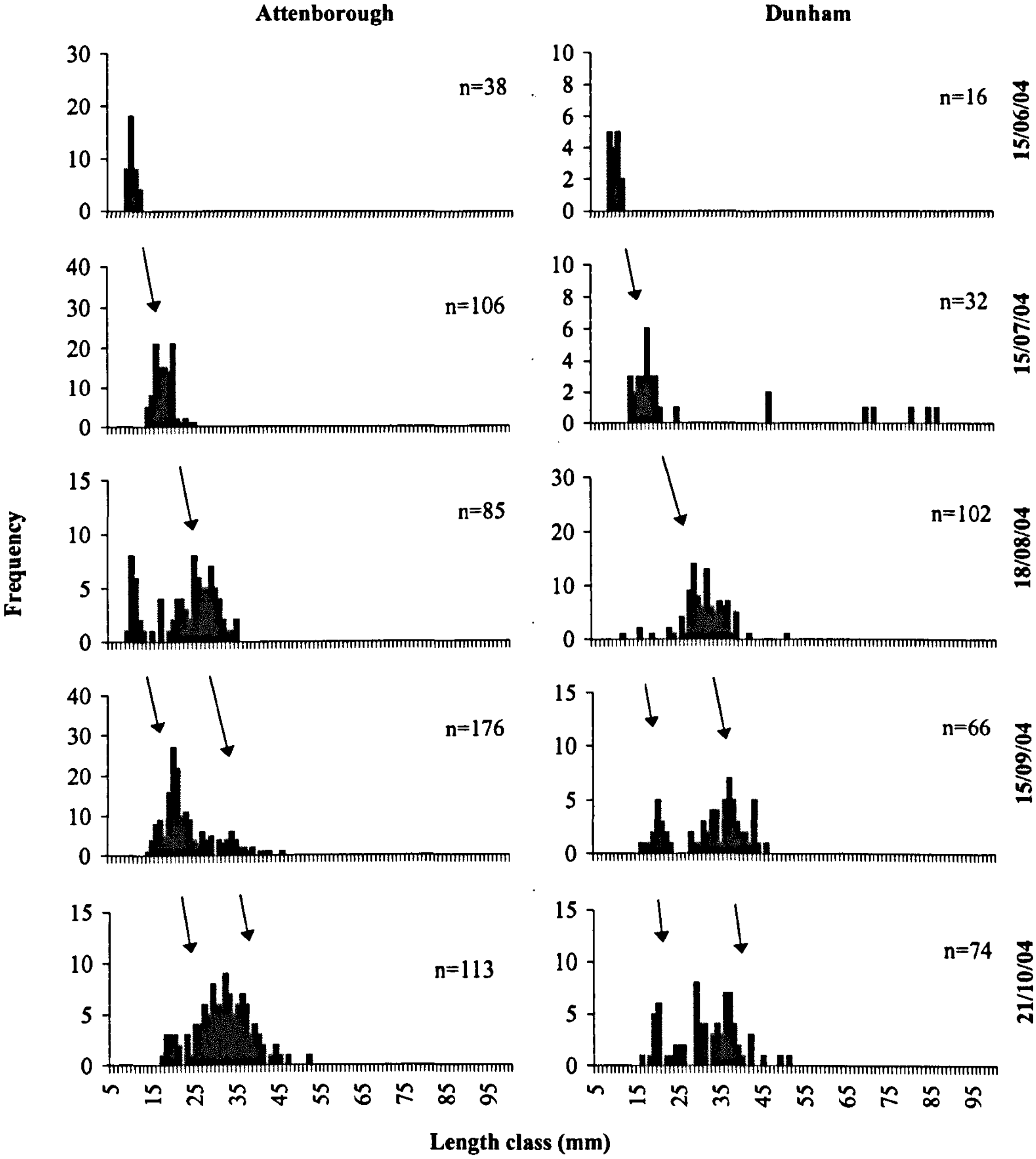


Fig. 3.22 Length-frequency distributions of chub captured by seine net from the River Trent, June to October 2004.

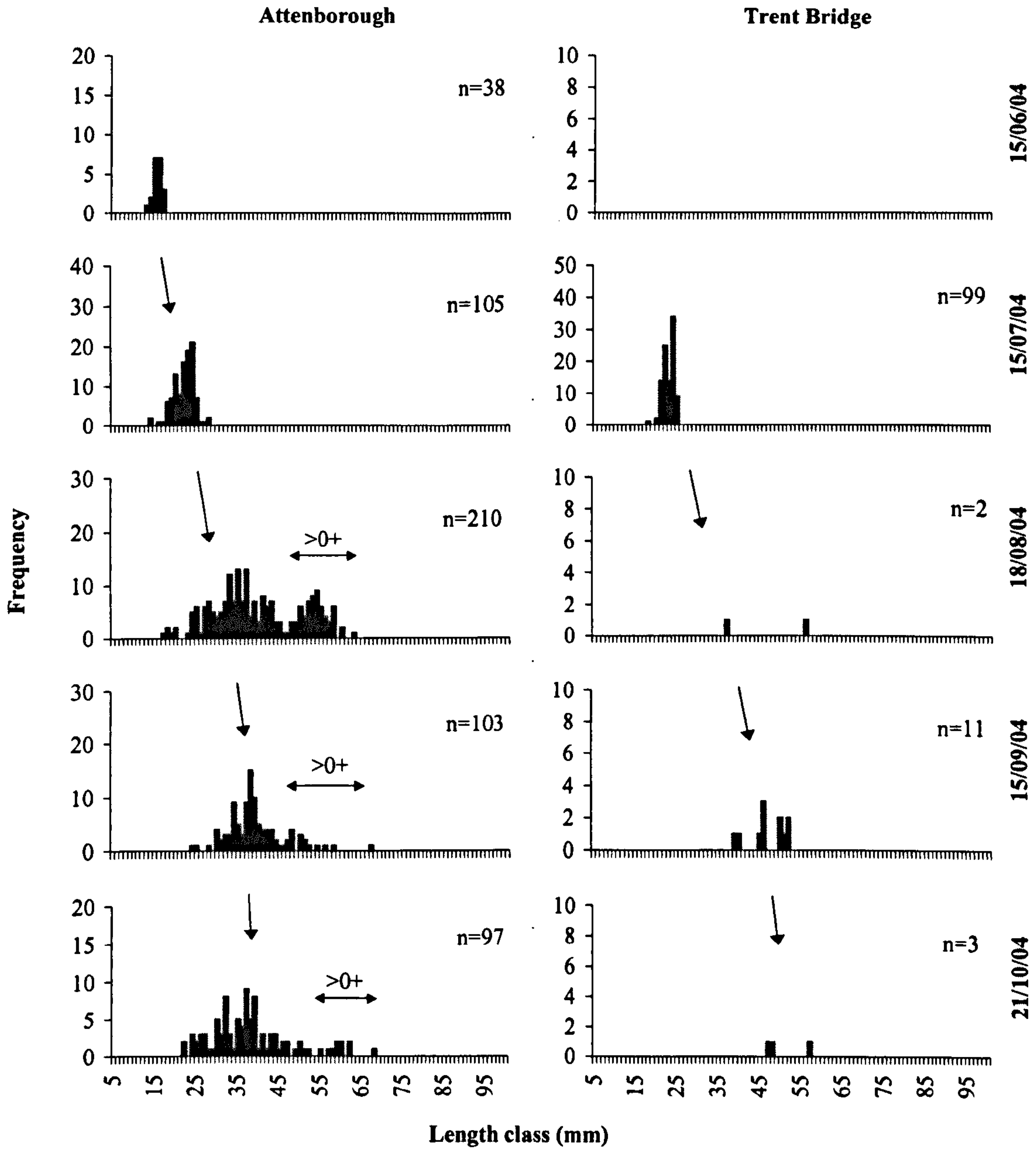


Fig. 3.23 Length-frequency distributions of bream captured by seine net from the River Trent, June to October 2004.

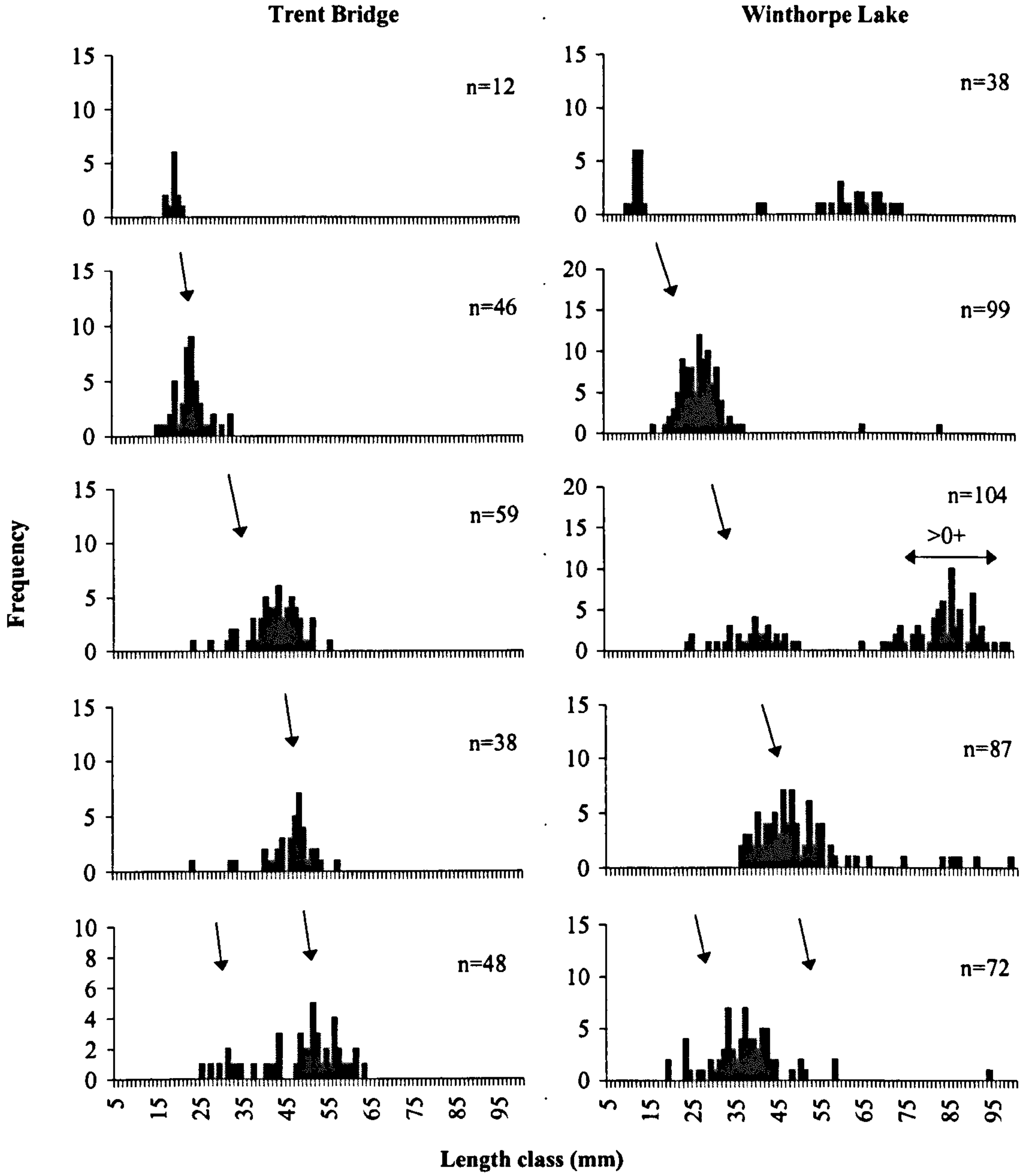


Fig. 3.24 Length-frequency distributions of gudgeon captured by seine net from the River Trent, June to October 2004.

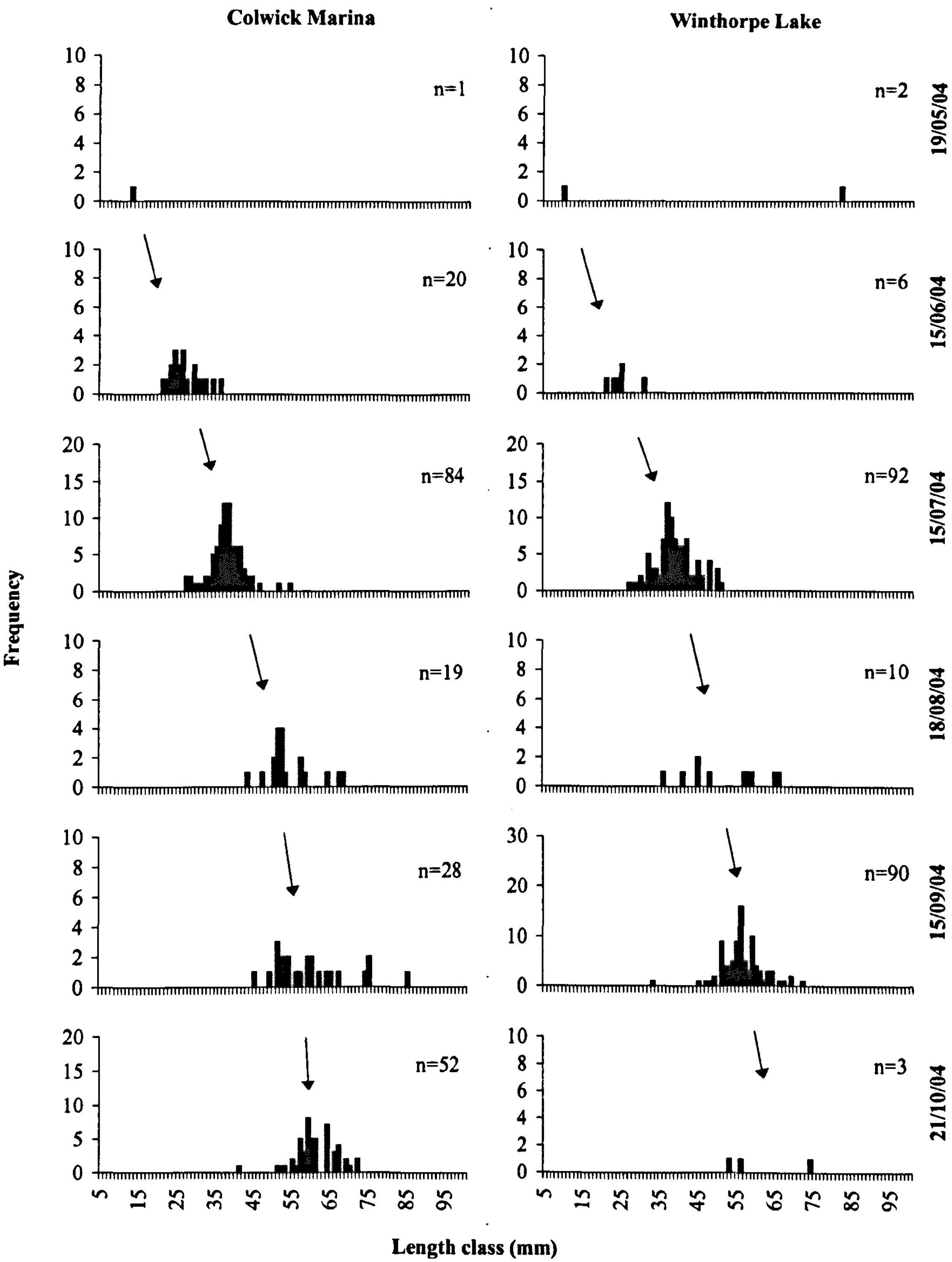


Fig. 3.25 Length-frequency distributions of perch captured by seine net from the River Trent, May to October 2004.

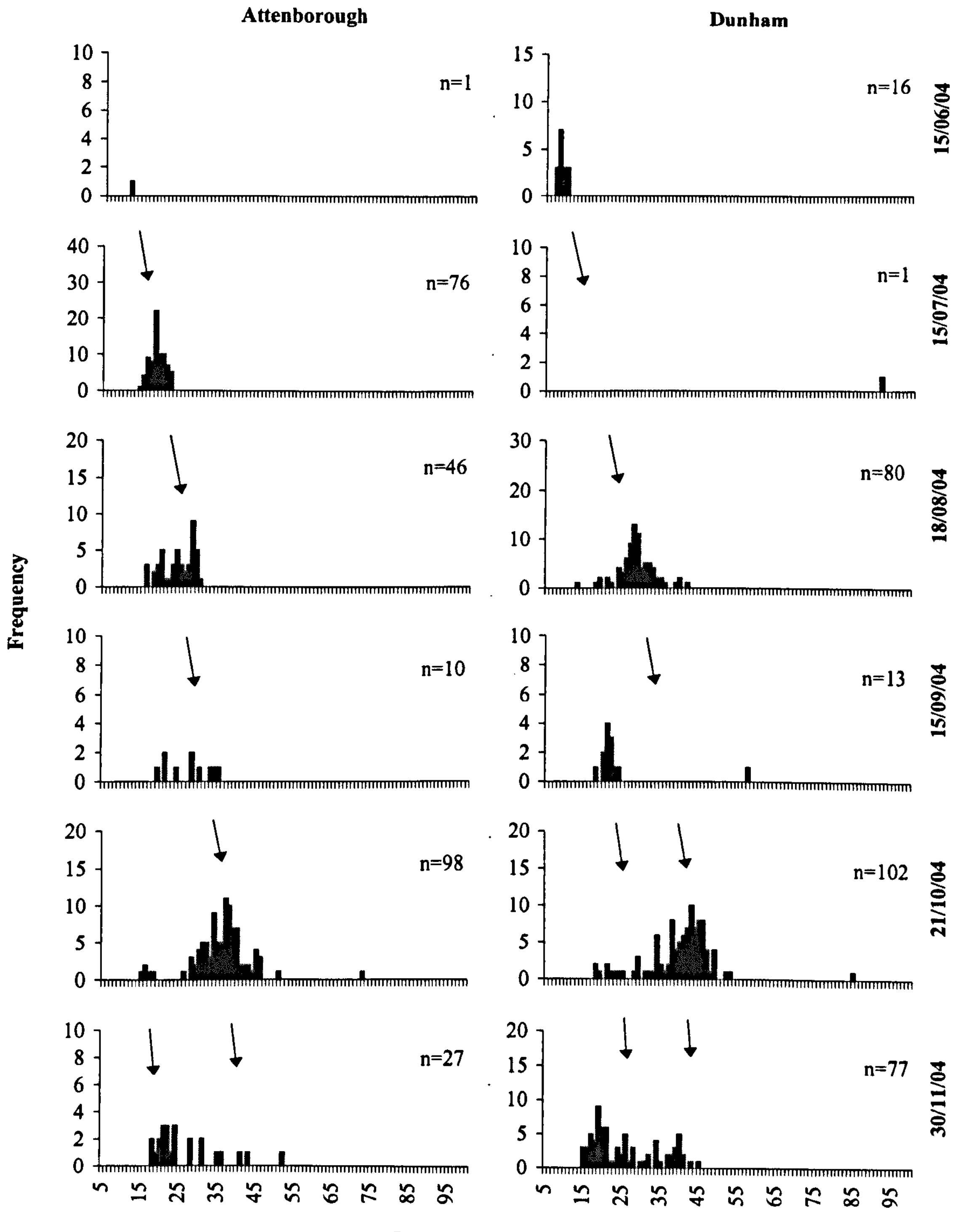


Fig. 3.26 Length-frequency distributions of bleak captured by seine net from the River Trent, June to November 2004.

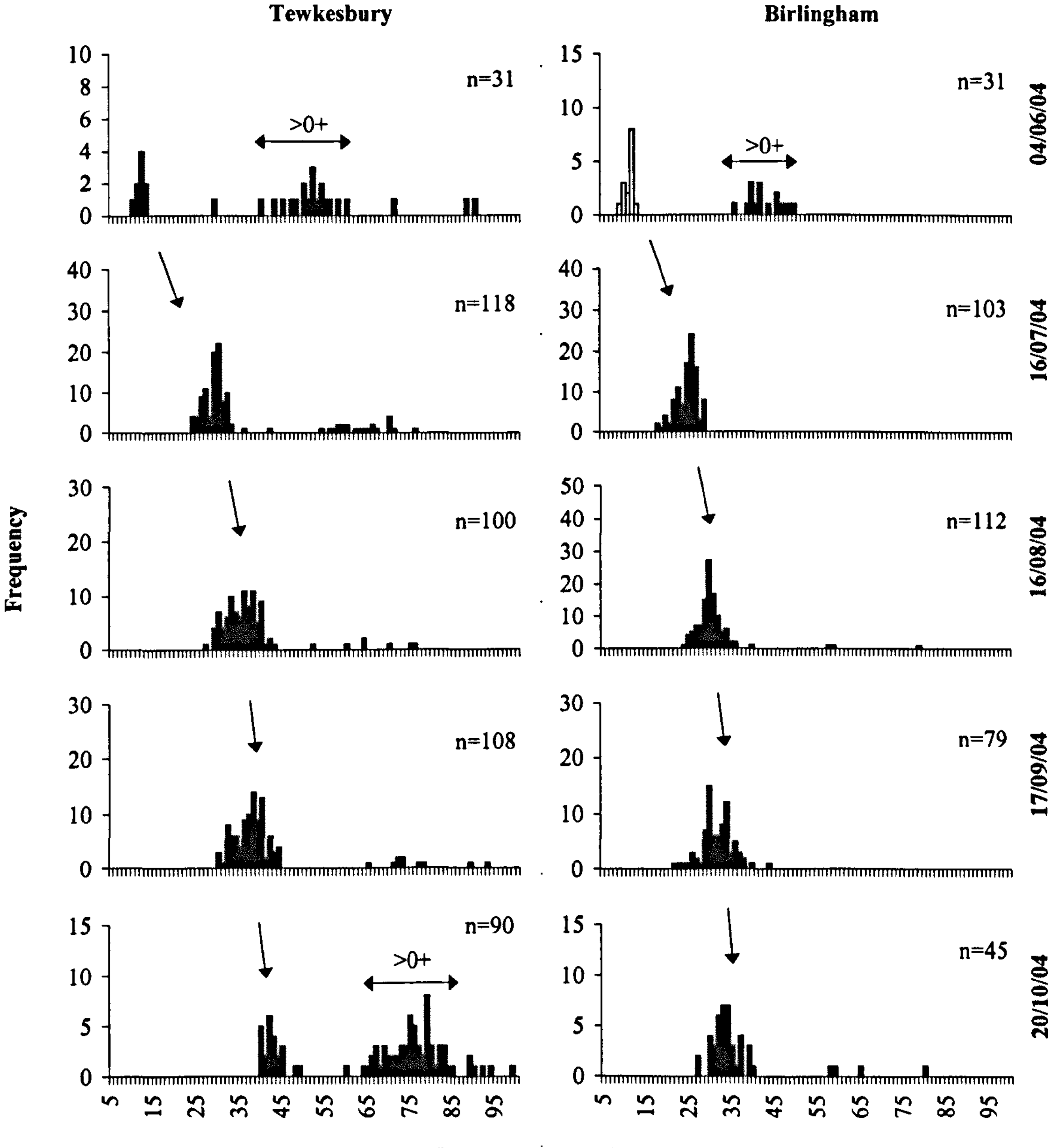


Fig. 3.27 Length-frequency distributions of roach captured by seine net from the Warwickshire Avon, June to October 2004. Clear bars indicate fish captured by hand-net.

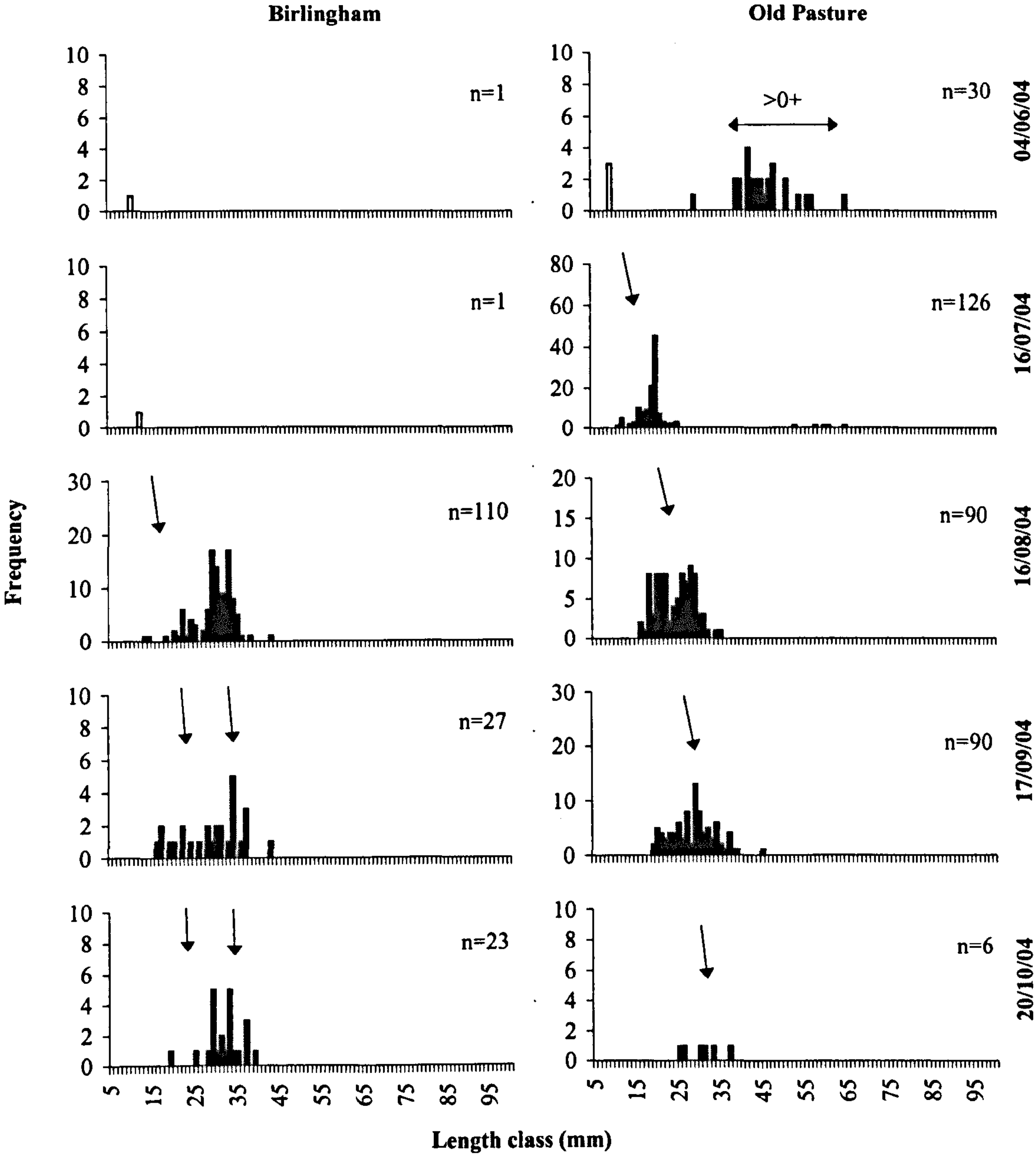


Fig. 3.28 Length-frequency distributions of chub captured by seine net from the Warwickshire Avon, June to October 2004. Clear bars indicate fish captured by hand-net.

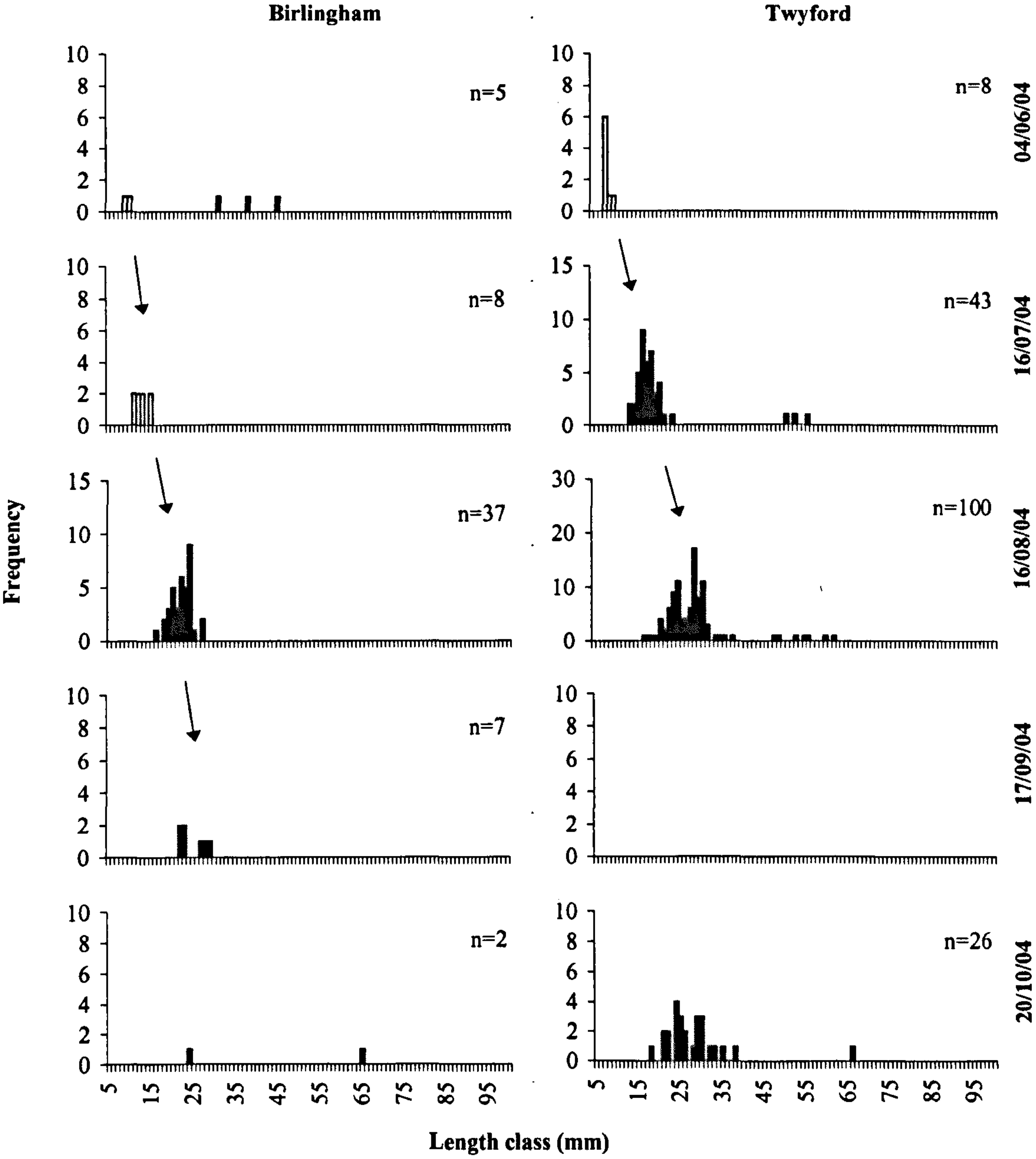


Fig. 3.29 Length-frequency distributions of bream captured by seine net from the Warwickshire Avon, June to October 2004. Clear bars indicate fish captured by hand-net.

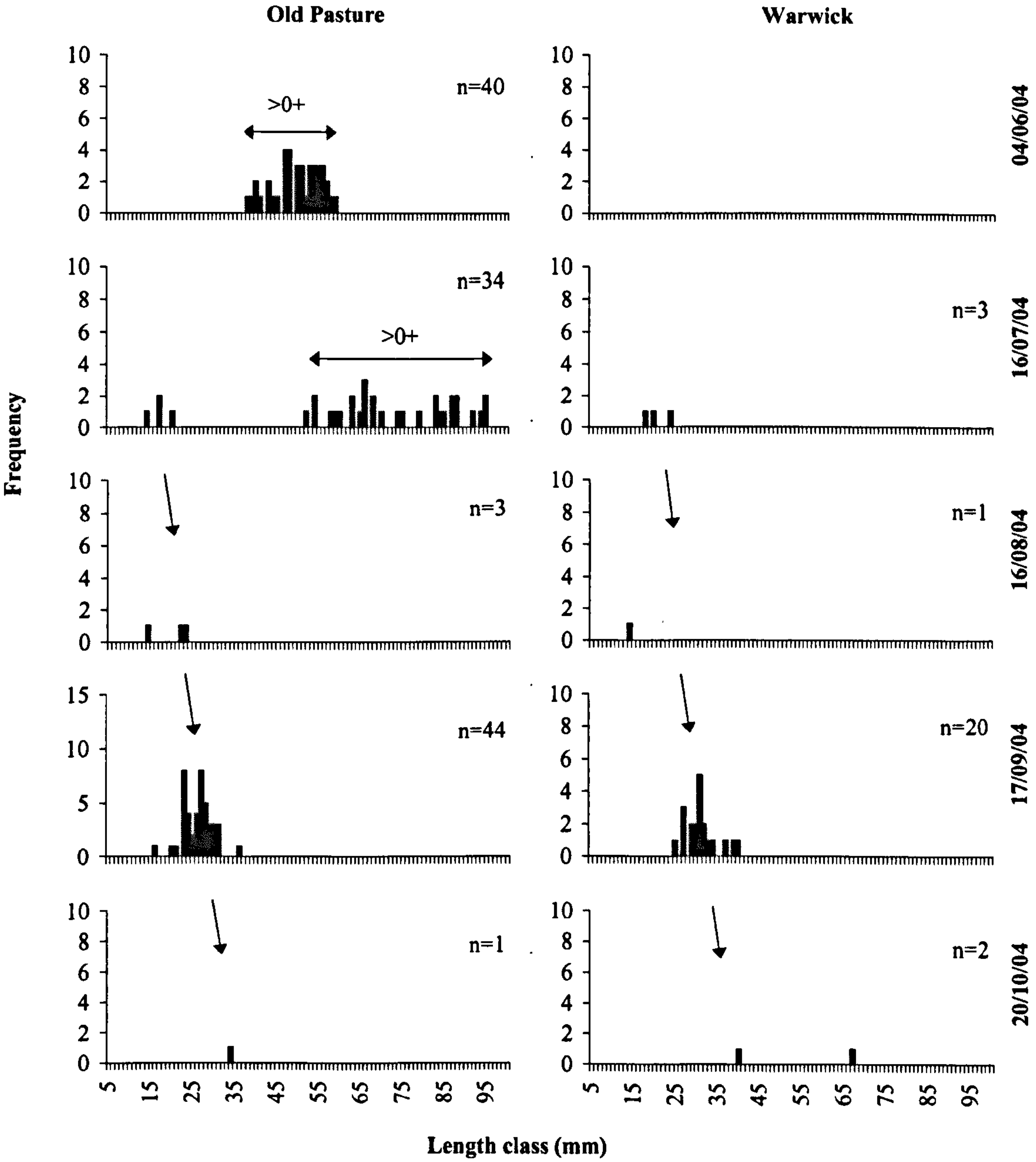


Fig. 3.30 Length-frequency distributions of gudgeon captured by seine net from the Warwickshire Avon, June to October 2004.

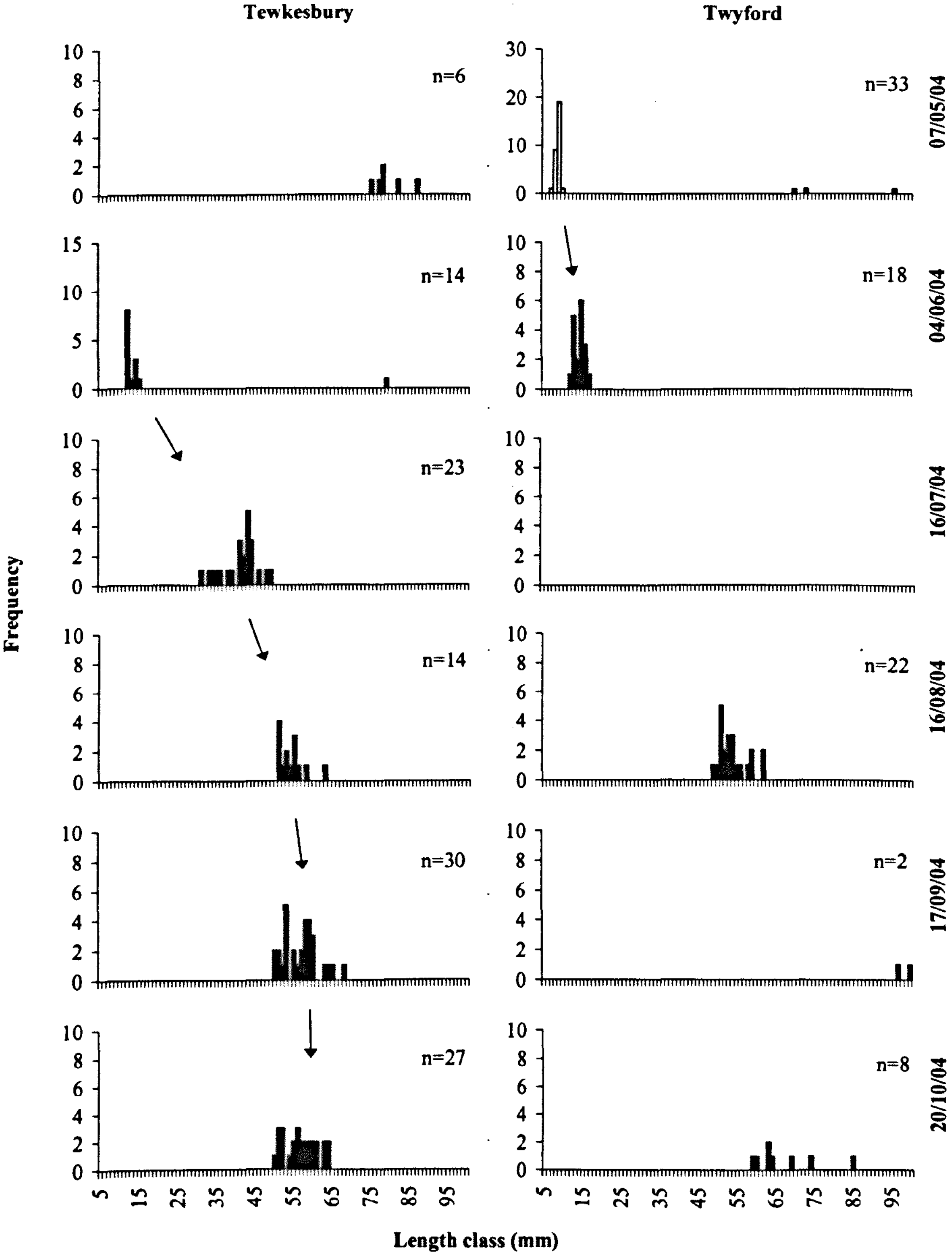


Fig. 3.31 Length-frequency distributions of perch captured by seine net from the Warwickshire Avon, May to October 2004. Clear bars indicate fish captured by hand-net.

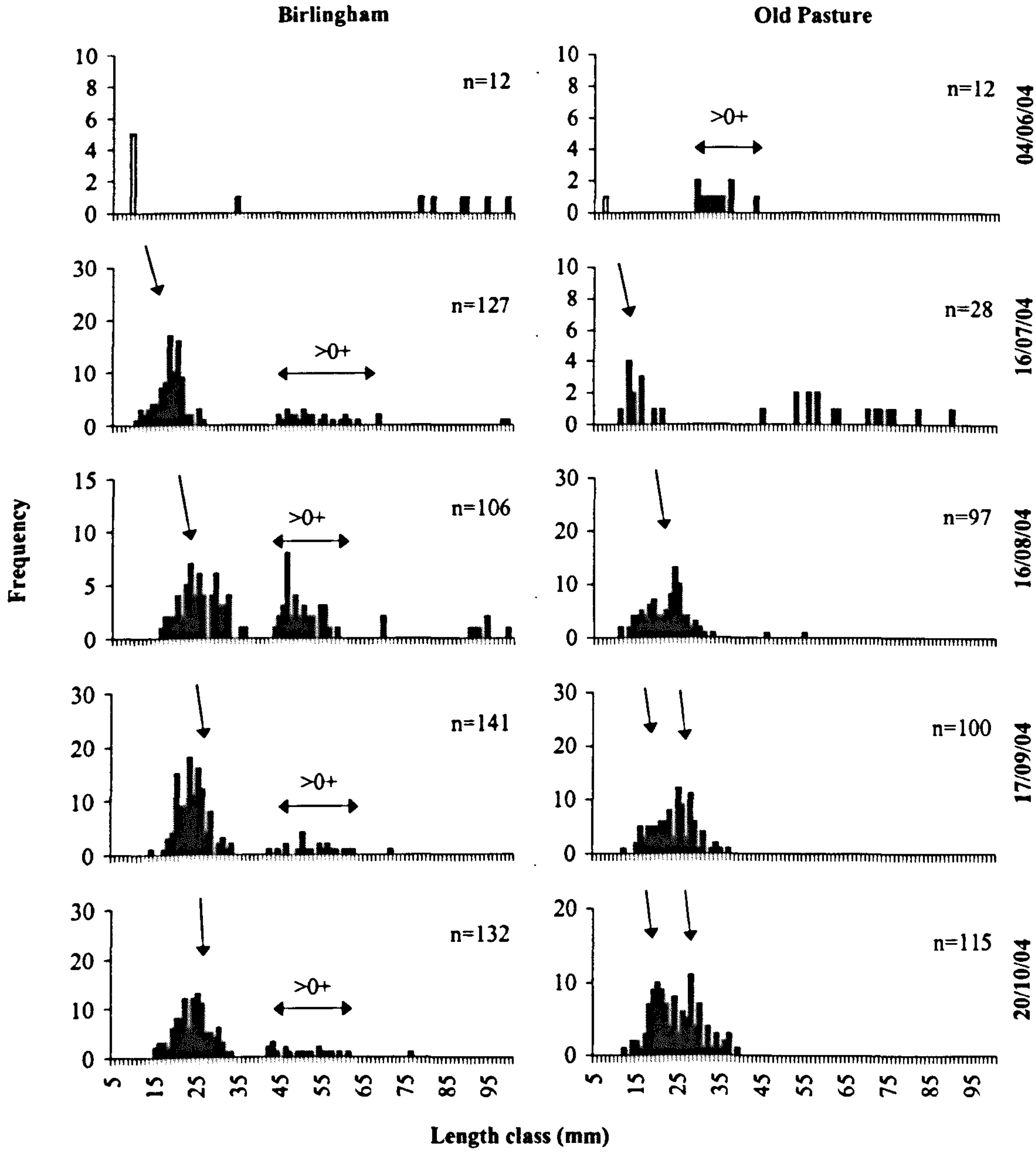


Fig. 3.32 Length-frequency distributions of bleak captured by seine net from the Warwickshire Avon, June to October 2004. Clear bars indicate fish captured by hand-net.

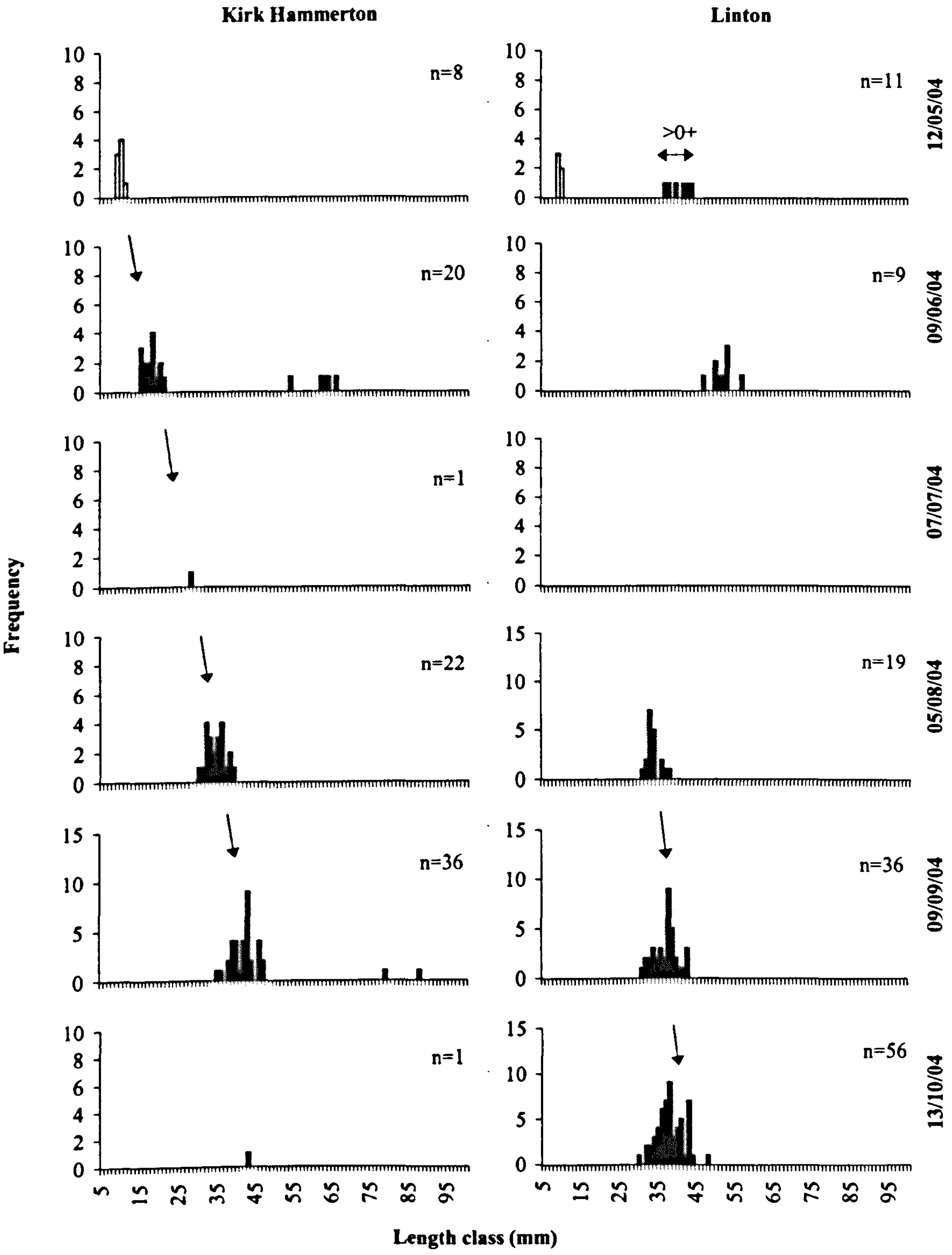


Fig. 3.33 Length-frequency distributions of dace captured by seine net from the Yorkshire Ouse catchment, May to October 2004. Clear bars indicate fish captured by hand-net.

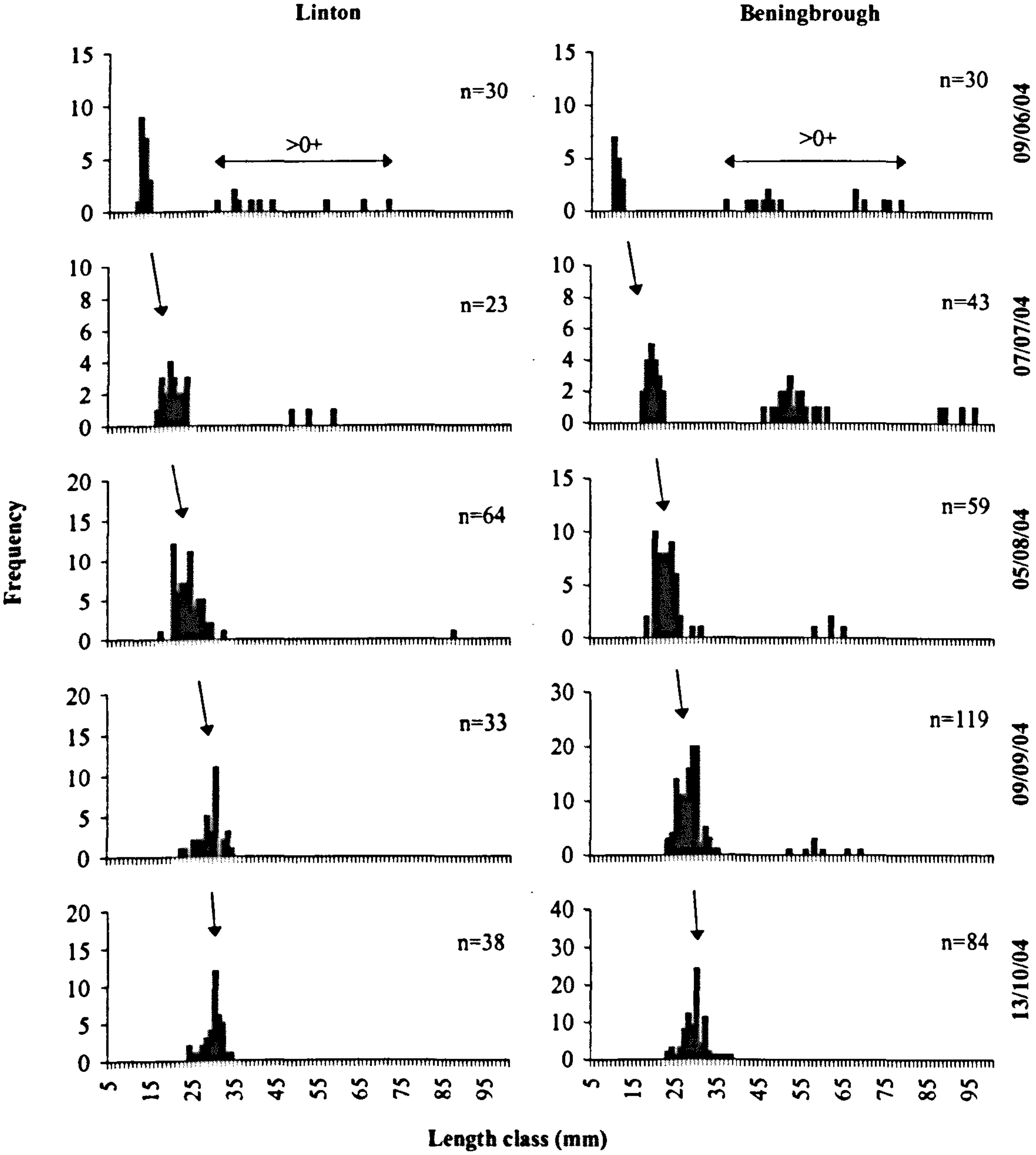


Fig. 3.34 Length-frequency distributions of roach captured by seine net from the Yorkshire Ouse catchment, June to October 2004.

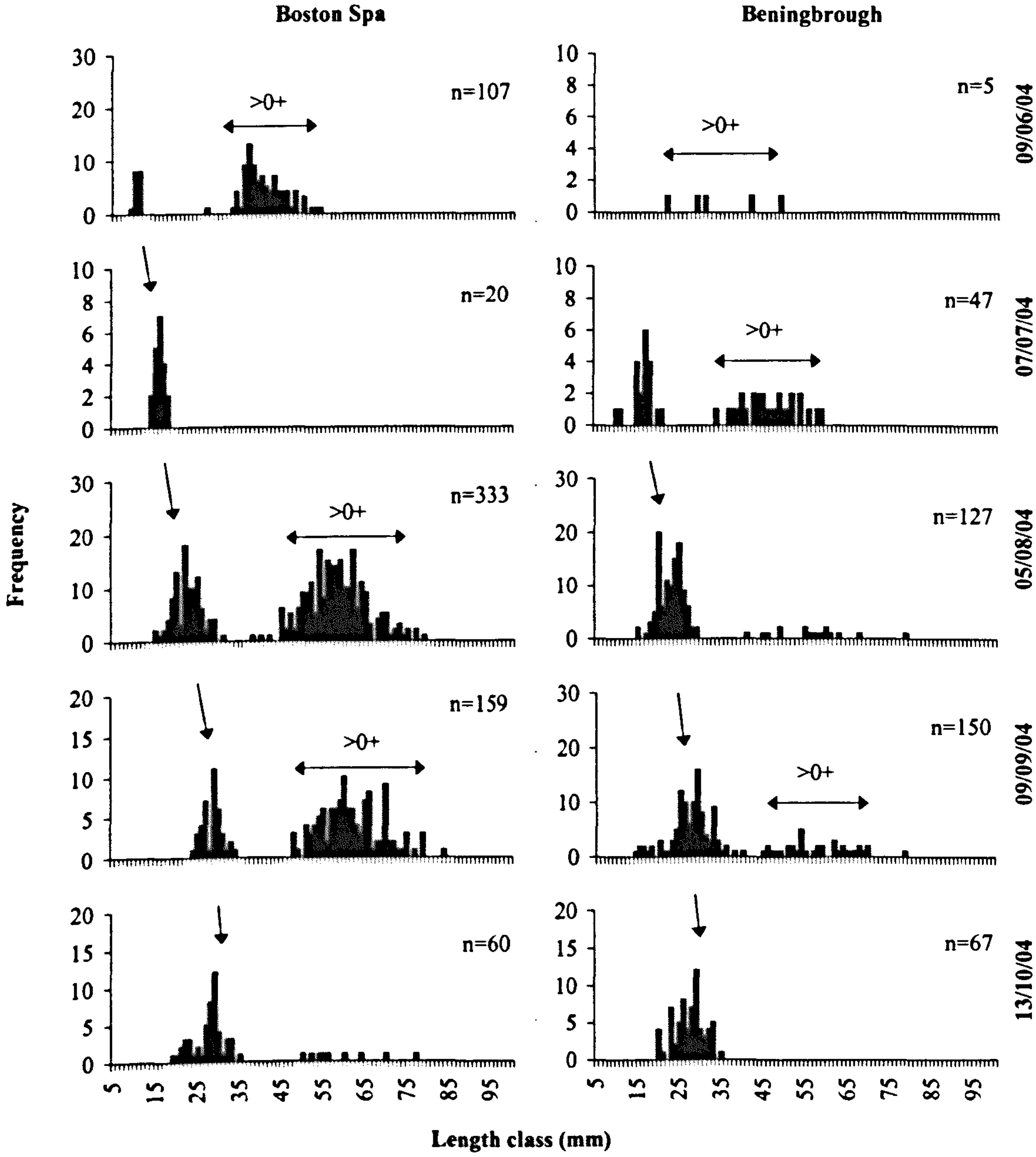


Fig. 3.35 Length-frequency distributions of chub captured by seine net from the Yorkshire Ouse catchment, June to October 2004.

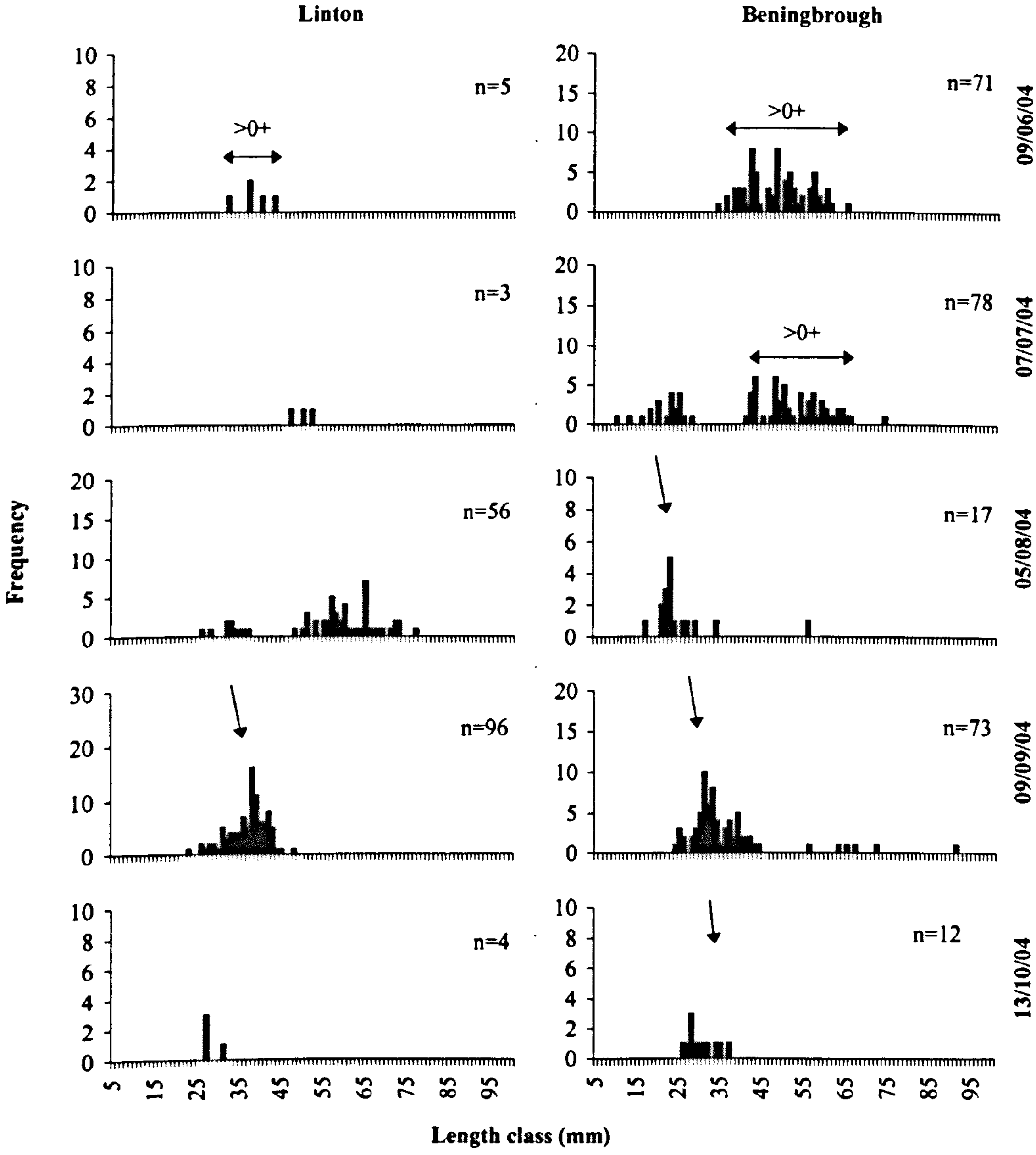


Fig. 3.36 Length-frequency distributions of gudgeon captured by seine net from the Yorkshire Ouse catchment, June to October 2004.

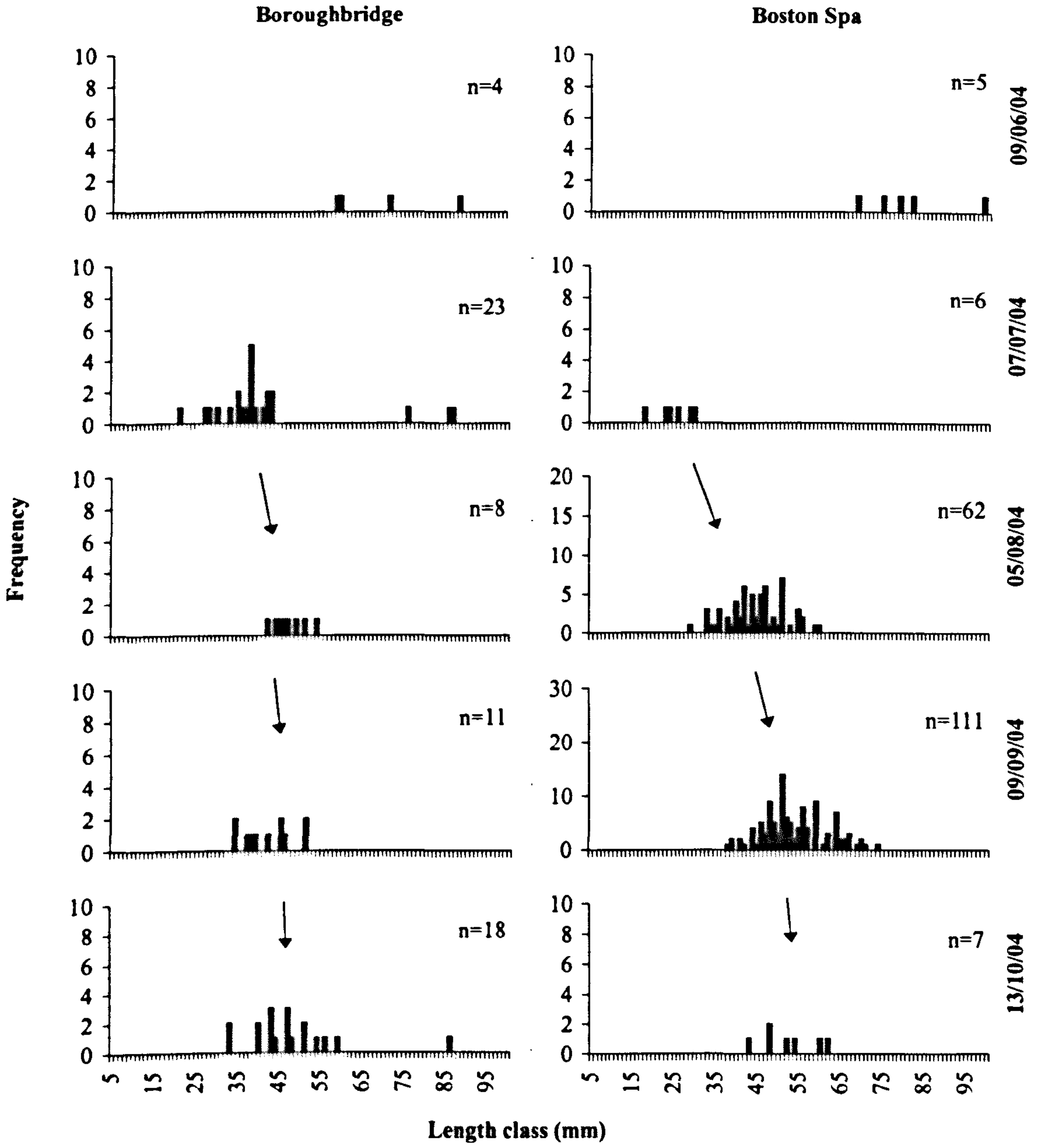


Fig. 3.37 Length-frequency distributions of perch captured by seine net from the Yorkshire Ouse catchment, June to October 2004.

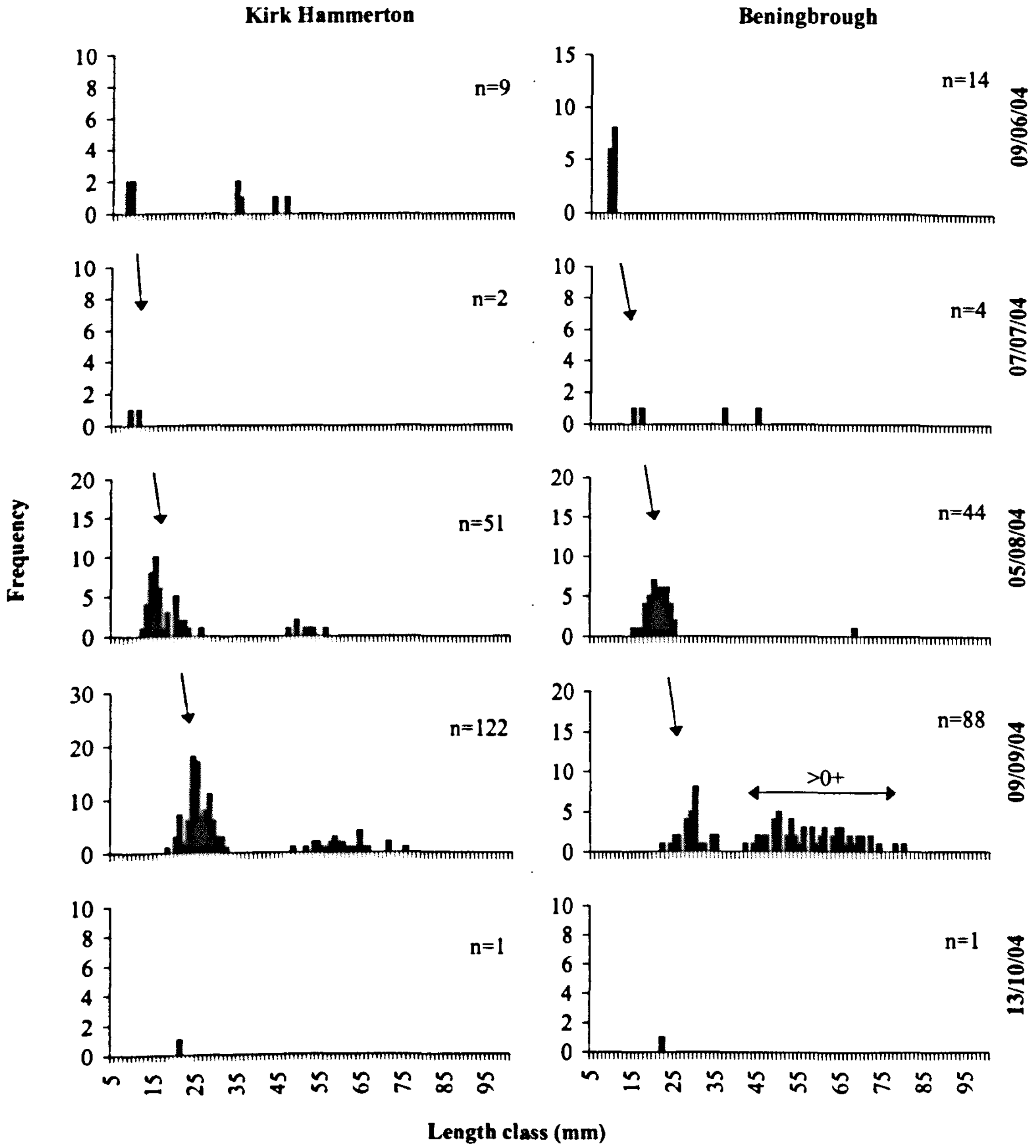


Fig. 3.38 Length-frequency distributions of bleak captured by seine net from the Yorkshire Ouse catchment, June to October 2004.

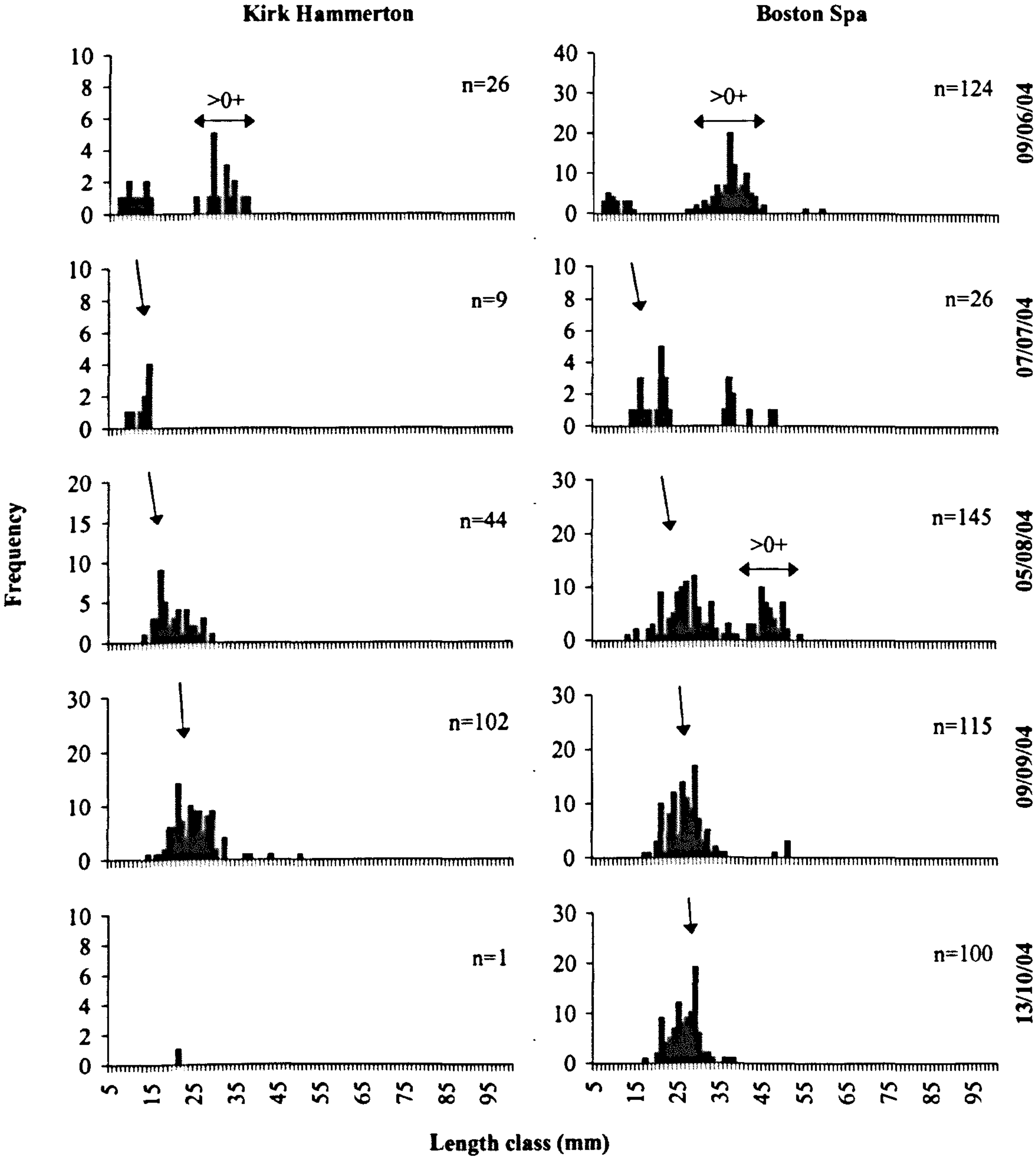


Fig. 3.39 Length-frequency distributions of minnow captured by seine net from the Yorkshire Ouse catchment, June to October 2004.

Table 3.6 Mean (all sites and years, ± SD) growth rates (mm.day^{-1}) of 0+ fish in the Trent, Avon and Ouse catchments.

	Bleak	**Bream**	**Chub**	**Dace**	**Gudgeon**	**Minnow**	**Perch**	**Roach**
Trent	0.24	0.20	0.25	0.32	0.24	–	0.34	0.22
	(0.10)	(0.08)	(0.08)	(0.07)	(0.05)		(0.10)	(0.04)
Avon	0.16	0.17	0.18	–	0.15	–	0.36	0.18
	(0.07)	(0.06)	(0.04)		(0.03)		(0.08)	(0.07)
Ouse	0.15	–	0.18	0.27	0.20	0.16	0.30	0.18
	(0.05)		(0.05)	(0.06)	(0.05)	(0.05)	(0.02)	(0.05)

3.3.5.2 *Intra-catchment comparisons*

The River Trent

There were a number of spatial patterns in the growth of 0+ fish in the Trent. Dace, for example, were frequently smallest at Trent Bridge, while roach were usually largest at Winthorpe Lake and Trent Bridge, and smallest at Attenborough and Dunham. End of summer catches of perch were irregular but, when captured, perch were largest at Marina Pond. Bream and gudgeon were generally smallest at Attenborough, with the largest often recorded at Dunham and Trent Bridge, respectively. The largest bleak were found at Winthorpe Lake and Dunham, but there were no consistent patterns for chub.

There were no consistent patterns in the growth of fish from the main channel of the Trent and those in the floodplain waterbodies, although identification of any such patterns would be complicated by the likely migration of fish between the two areas. Fish were often larger in Marina Pond than elsewhere, but unfortunately small catches prevented detailed analysis.

The Warwickshire Avon

Roach grew consistently larger at Tewkesbury than at other sites on the Avon (Kruskal-Wallis tests, $P<0.05$). Patterns were difficult to differentiate for bleak, with no one site consistently producing larger than average fish. Similarly, patterns were difficult to identify for chub, although those at Twyford were often largest. Catches of perch, bream and gudgeon were not sufficient to enable spatial differences in growth to be identified.

The Yorkshire Ouse

Dace from the tributary rivers (Swale, Ure, Nidd, Wharfe) were generally larger than those from the Ouse itself, with dace at Linton consistently smaller than at other sites. Roach were invariably largest in the Ouse, although there was no apparent ranking of sites. Perch, gudgeon and bleak were not captured in sufficient numbers of facilitate observation of spatial variations in growth, and no consistent patterns could be identified for chub and minnow.

3.3.5.3 *Temporal variations*

For all species and in each catchment, there was a general trend of good growth in 2003 and 2004, intermediate growth in 1999 and 2001, and poor growth in 2000 and 2002. This subject is dealt with extensively in Chapter 6, and so is not addressed further here.

3.3.5.4 *Weight-length relationships of 0+ fish*

Dace, perch and roach exhibited a significant (ANCOVA, $P<0.05$) shift from allometric (regression coefficient $b>3$) towards isometric growth ($b \approx 3$) at the transition from the larval to the juvenile period (Table 3.7), indicated by a flexion point in the weight-length relationships. Solving each species pair of simultaneous equations indicated that this transition occurred at a SL of 18.7 mm, 19.2 mm and 16.1 mm in dace, perch and roach, respectively. Similar shifts were found in the same species elsewhere, and also in carp, bleak, bream, silver bream (*Abramis bjoerkna* (L.)), gudgeon, rudd and chub (Guma'a, 1978b; Tong, 1986; Rheinberger *et al.*, 1987; Copp & Peňáz, 1988; Szlamińska *et al.*, 1989; Prokeš, 1993, 1995; Garner & Copp, 1997).

Table 3.7 Linear regression relationship between the natural logarithm (ln) of wet weight (W, g) and standard length (SL, mm) for the larvae and juveniles of three species of fish.

Species	Period	Relationship	P	r^2	n
Dace	Larval	$\ln W = (4.13 \times \ln SL) - 14.43$	0.000**	0.99	152
	Juvenile	$\ln W = (2.99 \times \ln SL) - 11.09$	0.000**	0.99	240
Perch	Larval	$\ln W = (3.50 \times \ln SL) - 12.50$	0.000**	0.99	62
	Juvenile	$\ln W = (3.22 \times \ln SL) - 11.65$	0.000**	0.99	184
Roach	Larval	$\ln W = (4.21 \times \ln SL) - 14.46$	0.000**	0.90	42
	Juvenile	$\ln W = (3.13 \times \ln SL) - 11.46$	0.000**	0.98	225

**$P<0.01$

3.3.6 Spawning periodicity

Investigations into spawning periodicity were restricted to dace, roach, perch, chub, bleak, bream, gudgeon and minnow. Other species were captured too infrequently or in insufficient numbers to enable identification of recruitment patterns. Due to space restrictions and for clarity, examples are displayed for each species.

3.3.6.1 *Single spawning fish species*

Dace

Recruitment of dace appeared to be based upon a single spawning event (Figs 3.20, 3.33). In the Trent, dace hatched between the third week of April (2003) and the first week of May (2002), whereas in the Ouse catchment larvae appeared three or four weeks later. Comparatively few dace were captured from the Avon, but they appeared to hatch about one week later than in the Trent.

Roach

Recruitment of roach also appeared to be based upon a single spawning event (Figs 3.21, 3.27, 3.34). In the Trent, roach hatched between the end of April (2003) and the beginning of June (2002), but usually in the third and fourth weeks of May. Roach in the Avon hatched at approximately the same time as those in the Trent, whereas those in the Ouse catchment hatched two or three weeks later. There were possible cases of multiple spawning at Winthorpe Lake in 2002 and 2004, where newly hatched roach were captured approximately one month apart and which became manifest in bimodality in subsequent length distributions (Fig. 3.40). This may have been caused by interruption of spawning activity for some reason, or it could perhaps be an artefact of asynchronous spawning by lake and river fish or migration of fish from elsewhere.

Perch

Similar to dace and roach, recruitment of perch was based upon a single spawning event (Figs 3.25, 3.31, 3.37). In the Trent and Avon, perch hatched at approximately the same time as roach, between the end of April (2003) and the middle of May (all other years). Too few newly hatched perch were captured from the Ouse to identify hatching dates.

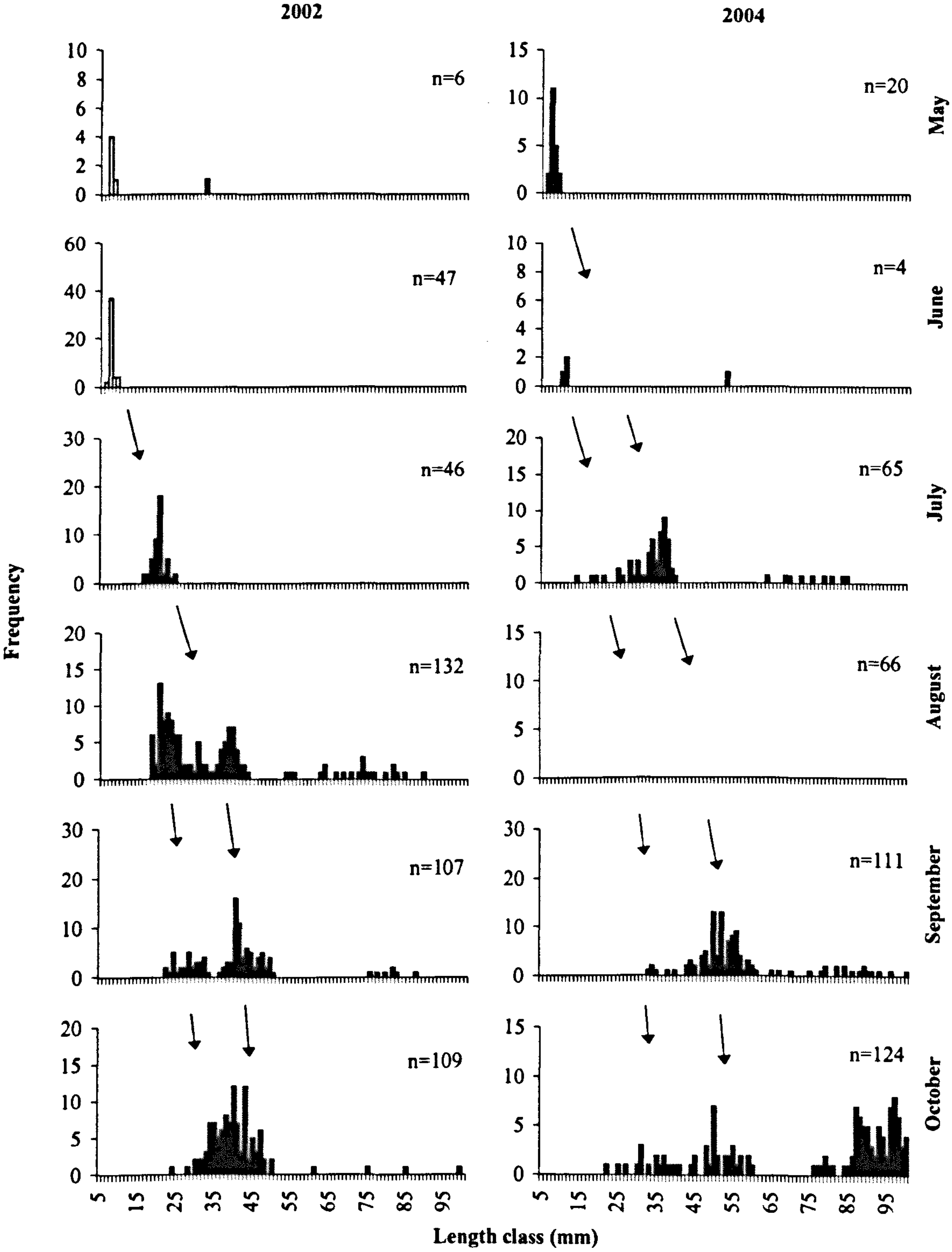


Fig. 3.40 Length-frequency distributions of roach captured by seine net from Winthorpe Lake (River Trent), May to October 2002 and 2004. Clear bars indicate fish captured by hand-net.

3.3.6.2 *Multiple spawning fish species*

Chub

There was evidence of multiple spawning events in chub. In the Trent, initial hatching took place between mid June and mid July, with successive batches appearing at intervals thereafter. At Winthorpe Lake, for example, young chub larvae were captured on five consecutive sampling occasions (spanning 8 weeks) between 13 June and 7 August 2003, encompassing possibly three or more batches (Fig. 3.41). A similar pattern was apparent at other sites. Although sampling was less frequent in 1999-2002 and 2004 (monthly) than in 2003 (fortnightly), multiple recruitment events were still readily apparent, particularly in 2004 (Fig. 3.22). Bimodal length distributions rarely persisted into the autumn, because initially discrete cohorts merged to form one homogeneous length distribution. Where necessary, polymodal distributions were analysed using Bhattacharya's method (all Separation Indices >3).

Multiple spawning of chub in the Avon and Ouse catchments appeared to be less prevalent than in the Trent. Initial hatching took place between early June and early August, with subsequent batches invariably small (Figs 3.28, 3.42). At many sites in the Ouse catchment, there was evidence of bimodality in the length distributions between July and October 2003, and chub larvae as small as 12 mm SL were captured in September and October 2002. In July 2003, there was evidence of bimodality at Boston Spa, Beningbrough, Acaster Malbis and Fulford, which was still apparent at Beningbrough and Fulford in August (Fig. 3.42). In the Avon, discrimination of recruitment patterns was complicated by small and infrequent catches. Nonetheless, multiple spawning events could be inferred by modal progression in the length distributions, the presence of chub larvae throughout the summer and from the wide length ranges of 0+ chub in the autumn. Where necessary, polymodal distributions were analysed using Bhattacharya's method (all Separation Indices >2).

Bleak

Bleak also appeared to adopt multiple spawning strategies. In the Trent, the initial hatching period was between mid June and mid July, with successive batches appearing at intervals thereafter. Small numbers of bleak larvae were found at the entrance to Marina Pond on four consecutive sampling occasions (spanning almost 6 weeks)

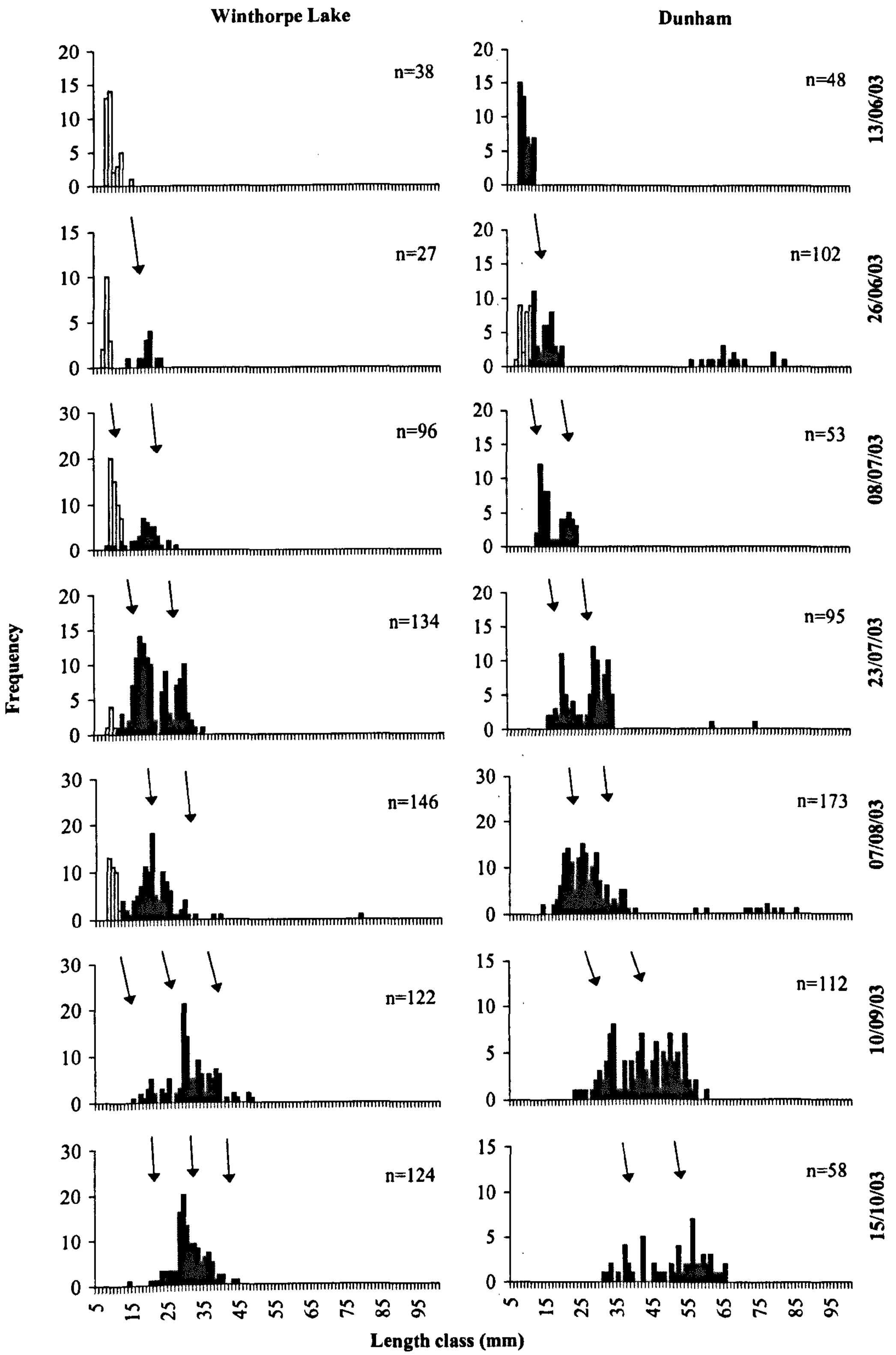


Fig. 3.41 Length-frequency distributions of chub captured by seine net from the River Trent, June to October 2003. Clear bars indicate fish captured by hand-net. N.B. Sampling frequency shifts from fortnightly to monthly after July.

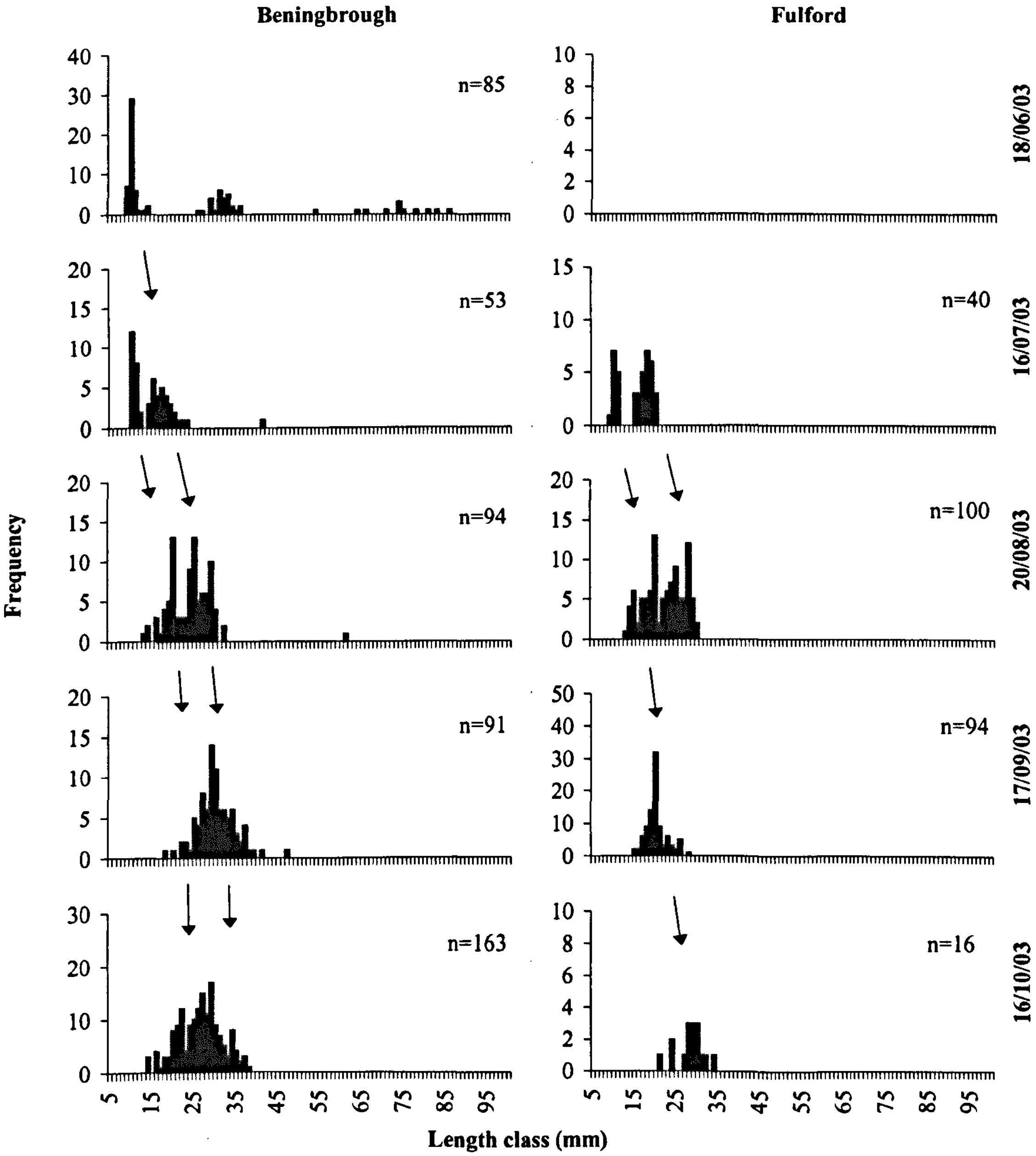


Fig. 3.42 Length-frequency distributions of chub captured by seine net from the Yorkshire Ouse, June to October 2003.

between 13 June and 23 July 2003, and similar patterns were found elsewhere. Where newly hatched bleak were not captured, multiple spawning events could be inferred by modal progression in the length distributions, the presence of larvae throughout the summer and from the wide length ranges of 0+ bleak in the autumn. Multiple recruitment events occurred in all years, but were most evident in 2002 and, especially, 2004 when there was bimodality or asymmetry in the length distributions at many sites (Figs 3.26, 3.43). All Separation Indices were >3.

Bleak in the Avon hatched at approximately the same time as those in the Trent. There was evidence of multiple spawning in most years, with progeny from later spawnings merging with the initial cohorts. A typical example is at Old Pasture in August 2003, where a positive skew in the length distributions was apparent (Fig. 3.44). Bleak in the Ouse catchment hatched between early June and early July, but there was no clear evidence for multiple spawning events, although catches were usually small and infrequent. All Separation Indices were >2.

Bream

In the Trent, there were suggestions of occasional multiple spawning events in bream. The main hatching period occurred around the second week of June, concordant with spawning of bream at the end of May (*pers. obs.*; Adámek *et al.*, 2004). Smaller batches appeared at intervals thereafter, with the majority of hatching complete by mid July. Where newly hatched bream were not captured, multiple spawning events could be inferred by modal progression in the length distributions and from the wide length ranges of 0+ bream in the autumn. Progeny from later spawnings merged with the initial cohorts, causing a positive skew in some of the length distributions, a typical example being Attenborough in October 1999 (Fig. 3.45). Bream in the Avon hatched at approximately the same time as those in the Trent, but there was no evidence of multiple spawning events, and too few bream were captured from the Ouse catchment to identify hatching dates reliably. All Separation Indices were >3.

Gudgeon

There was some evidence of multiple spawning events in gudgeon. In the Trent, the main hatching period was between late May and mid June, with smaller numbers of fish from later spawnings appearing as a more-or-less continual influx rather than in distinct

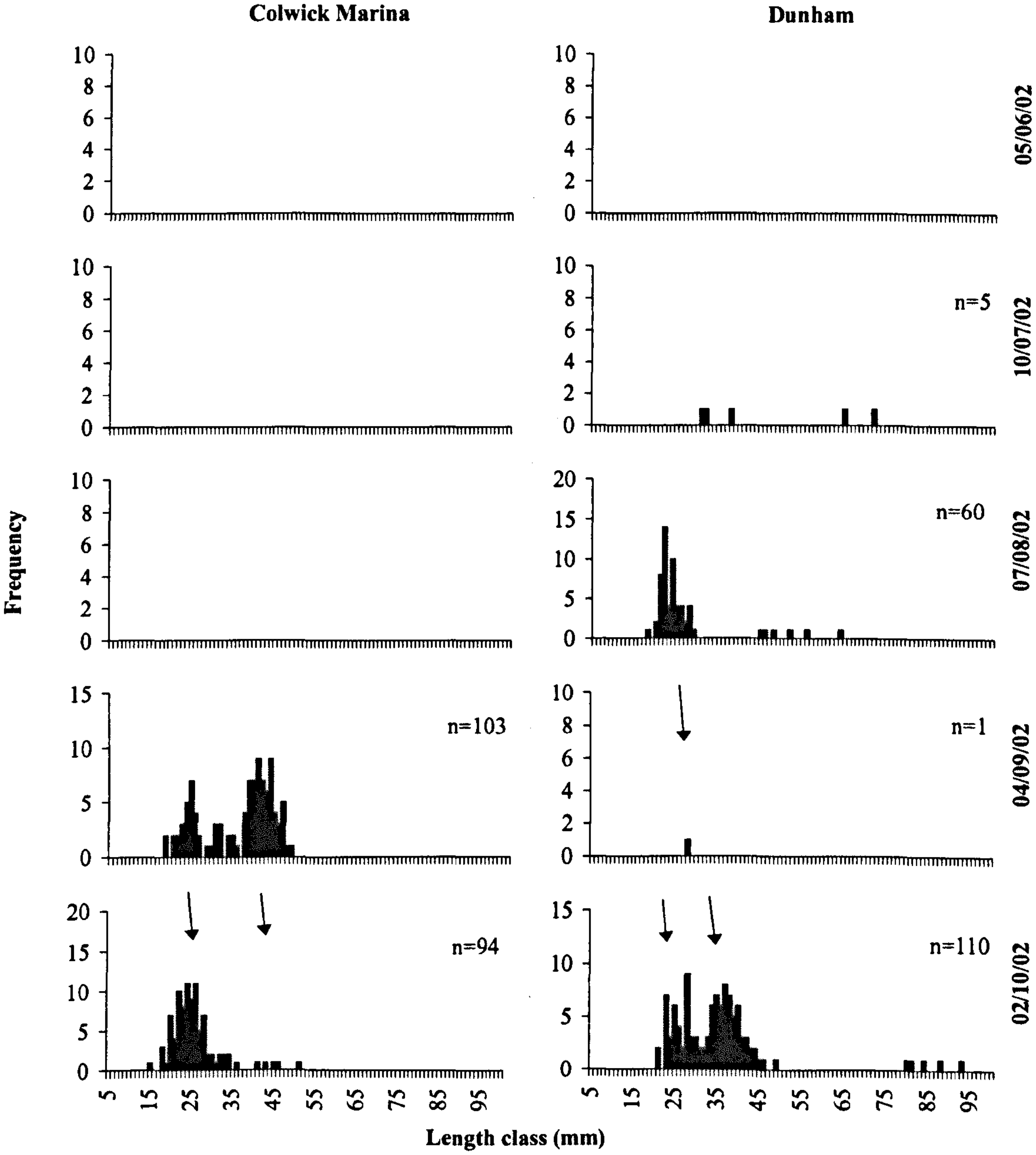


Fig. 3.43 Length-frequency distributions of bleak captured by seine net from the River Trent, June to October 2002.

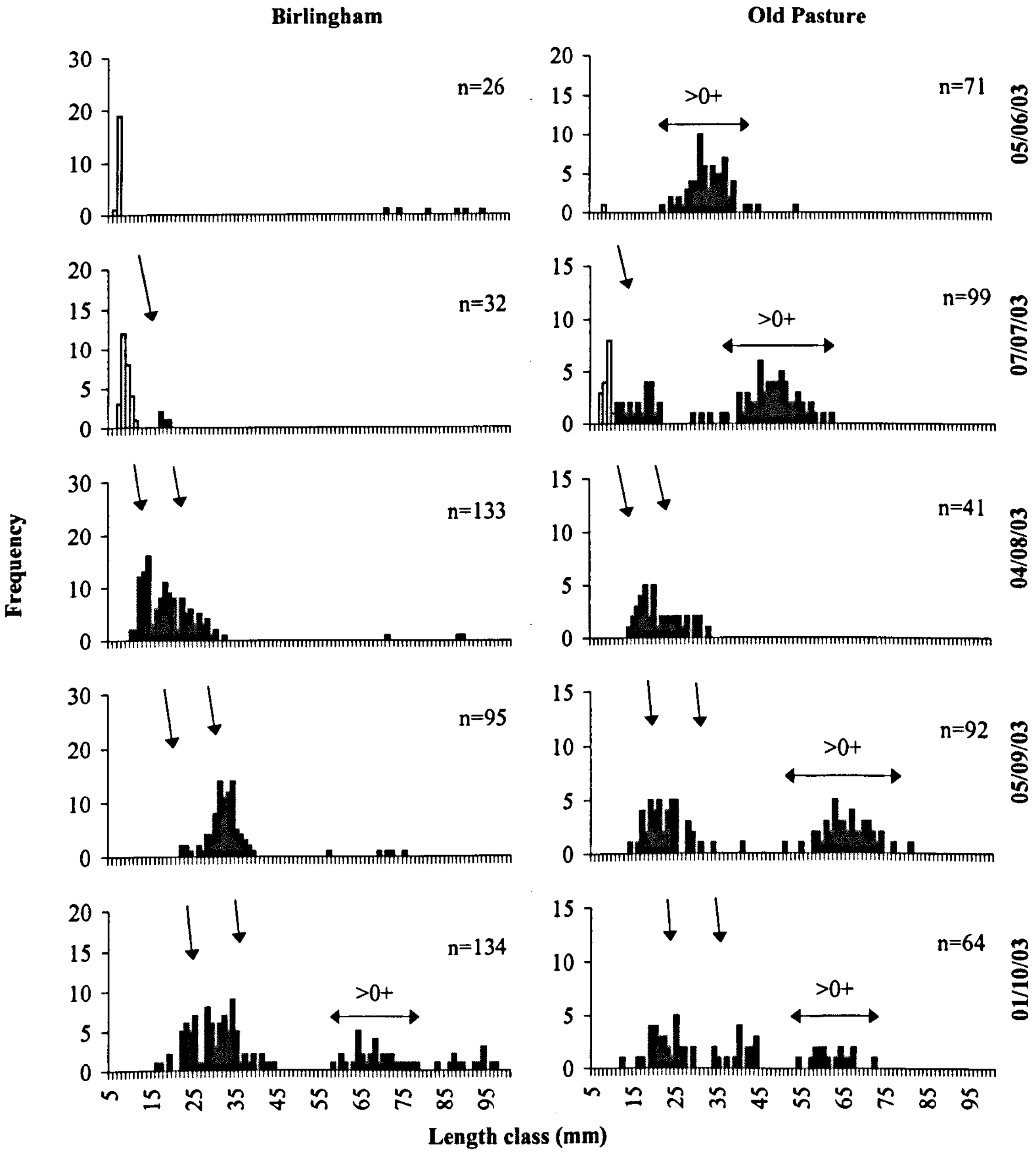


Fig. 3.44 Length-frequency distributions of bleak captured by seine net from the Warwickshire Avon, June to October 2003. Clear bars indicate fish captured by hand-net.

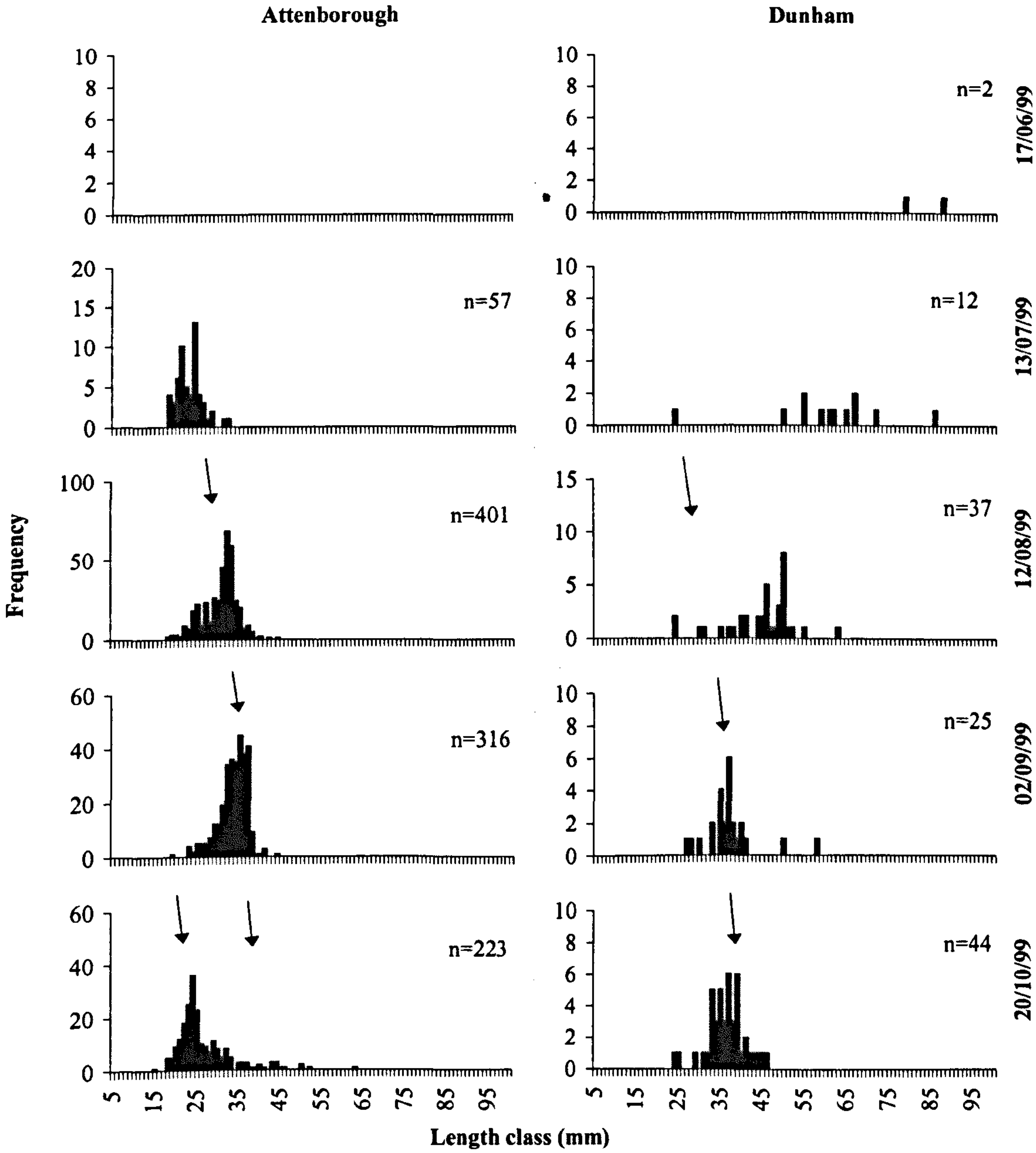


Fig. 3.45 Length-frequency distributions of bream captured by seine net from the River Trent, June to October 1999.

batches (Fig. 3.24). As with the other species, where newly hatched gudgeon were not captured multiple spawning events could be inferred by modal progression in the length distributions and from the wide length ranges of 0+ gudgeon in the autumn. In the Ouse catchment, the majority of gudgeon hatched in June. Fish from later spawnings occasionally appeared in small numbers throughout the summer, although multiple recruitment was not as apparent as in the Trent. Insufficient gudgeon were captured from the Avon to determine recruitment patterns. All Separation Indices were >3.

Minnow

In the Ouse catchment, there was evidence of multiple spawning events in minnow. The main hatching period was around early June, with fish from later spawnings appearing sporadically in small numbers thereafter. An example is Boston Spa in 2002, where the original cohort was joined by a second, causing bimodality from August to October (Fig. 3.46). A similar pattern was apparent at Maunby Demesne. Minnow were caught too infrequently and in insufficient numbers to identify recruitment patterns in the Trent and Avon. All Separation Indices were >3.

3.4 DISCUSSION

3.4.1 Structure of 0+ fish communities

A range of factors determine the structure of 0+ fish communities, with availability of spawning and nursery areas among the most important (Jurajda & Peňáz, 1994; Jurajda, 1995). Tolerable habitat conditions are considerably narrower for 0+ individuals than for older conspecifics owing to the strict physical, behavioural and energetic constraints imposed upon young fishes (Schiemer & Weiser, 1992; Schiemer *et al.*, 2001b). For a fish population to persist within a given waterbody, therefore, there must be habitat available, in sufficient quality and quantity, to all stages of development, for the range of activities undertaken by fish, such as feeding, spawning and resting, and as refuge from predators and elevated river flows (Mann, 1995).

While some fish species are able to flourish in a wide range of habitat types, others have stricter requirements. As such, species composition varies both within and between river catchments. Species richness, diversity, evenness and density are usually highest where

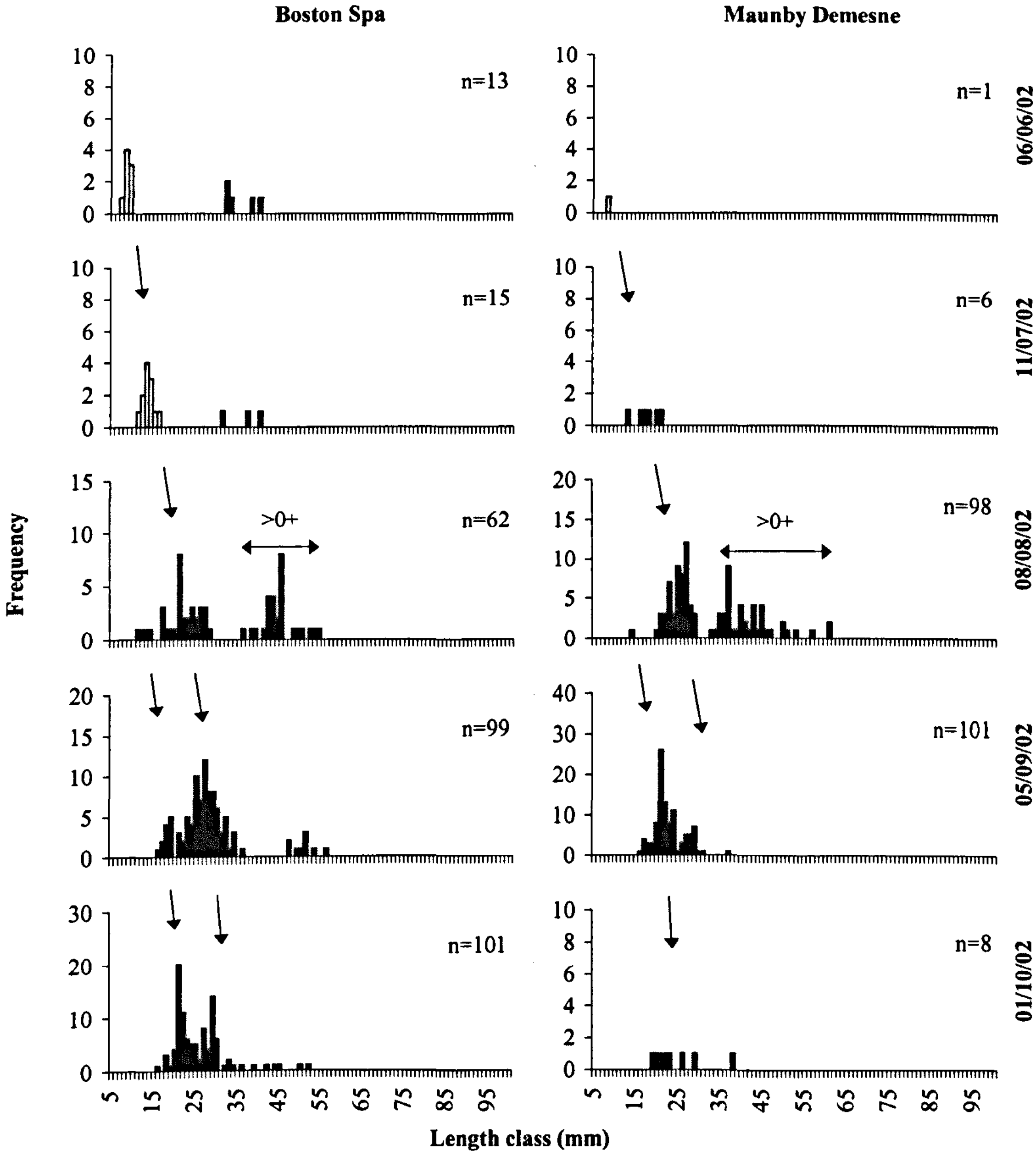


Fig. 3.46 Length-frequency distributions of minnow captured by seine net from the Yorkshire Ouse catchment, June to October 2002. Clear bars indicate fish captured by hand-net.

habitat heterogeneity is greatest, since such areas provide the necessary variety of resources for all life stages of a range of fish species. The abundance of 0+ eurytopic species at many of the sampling sites in the present study, particularly where habitat diversity was low, reflects the ability of these species to occupy a range of habitat types. Roach, for example, was ubiquitous in the Trent, Avon and Ouse, but rare in the rivers Swale and Wharfe. Less tolerant species have more specific habitat requirements, and are generally most abundant where conditions resemble their 'preferred' biotope (Cowx, 1988). Barbel, for instance, inhabit shallow bays as larvae and young juveniles before moving to gravel banks and riffles (Bischoff & Scholten, 1996; Baras & Nindaba, 1999a; Bischoff & Freyhof, 1999), while tench usually occur in the greatest densities in lentic backwater areas with prolific macrophyte growth (Copp, 1993a; Copp & Mann, 1993). In the Avon, species such as dace, chub, gudgeon and minnow were most abundant at Old Pasture, where the river flow was fastest. Strictly rheophilic species, such as barbel, grayling and river lamprey, were most abundant in the rivers Swale, Ure, Nidd and Wharfe, where the habitat was characterised by fast-flowing water and a sand or gravel substratum. Sea lamprey, brook lamprey and Atlantic salmon are also present (Whitton & Lucas, 1997), but were not captured in this study. By contrast, densities of strictly rheophilic species in the Trent were low, and such species were virtually absent from the Avon.

Initially, 0+ fish are restricted to the area surrounding the spawning site (Copp, 1989b), but active selection of habitat may occur with development (Garner, 1997a, c; Baras & Nindaba, 1999a, b) (Fig. 3.47). Copp (1997b) found that the larvae of gudgeon select cooler than average, shallow waters at weak/medium sloped banks where gravel substrata dominate, avoiding dense duckweed (Lemnaceae) and submerged vegetation. In contrast, roach larvae favour dense submerged vegetation or ligneous debris in warmer than average, lentic waters of medium depth (0.5-1 m) over silty sand/gravel (Copp, 1990c, 1997b). The transition from the larval to the juvenile period often coincides with a shift in habitat use (Copp, 1990c; Garner, 1996b). Roach, for example, move to cooler and shallower (<0.5 m) than average, lentic waters over silty sand/gravel at the littoral interface, with (Garner, 1995) or without (Copp, 1990c, 1997b) vegetation and ligneous debris. Chub are positively associated with emergent macrophytes and algae during both day and night (Garner, 1996b) while, unlike most other species, juvenile bleak often exploit deeper areas with steep banks (Copp, 1992b; Garner,

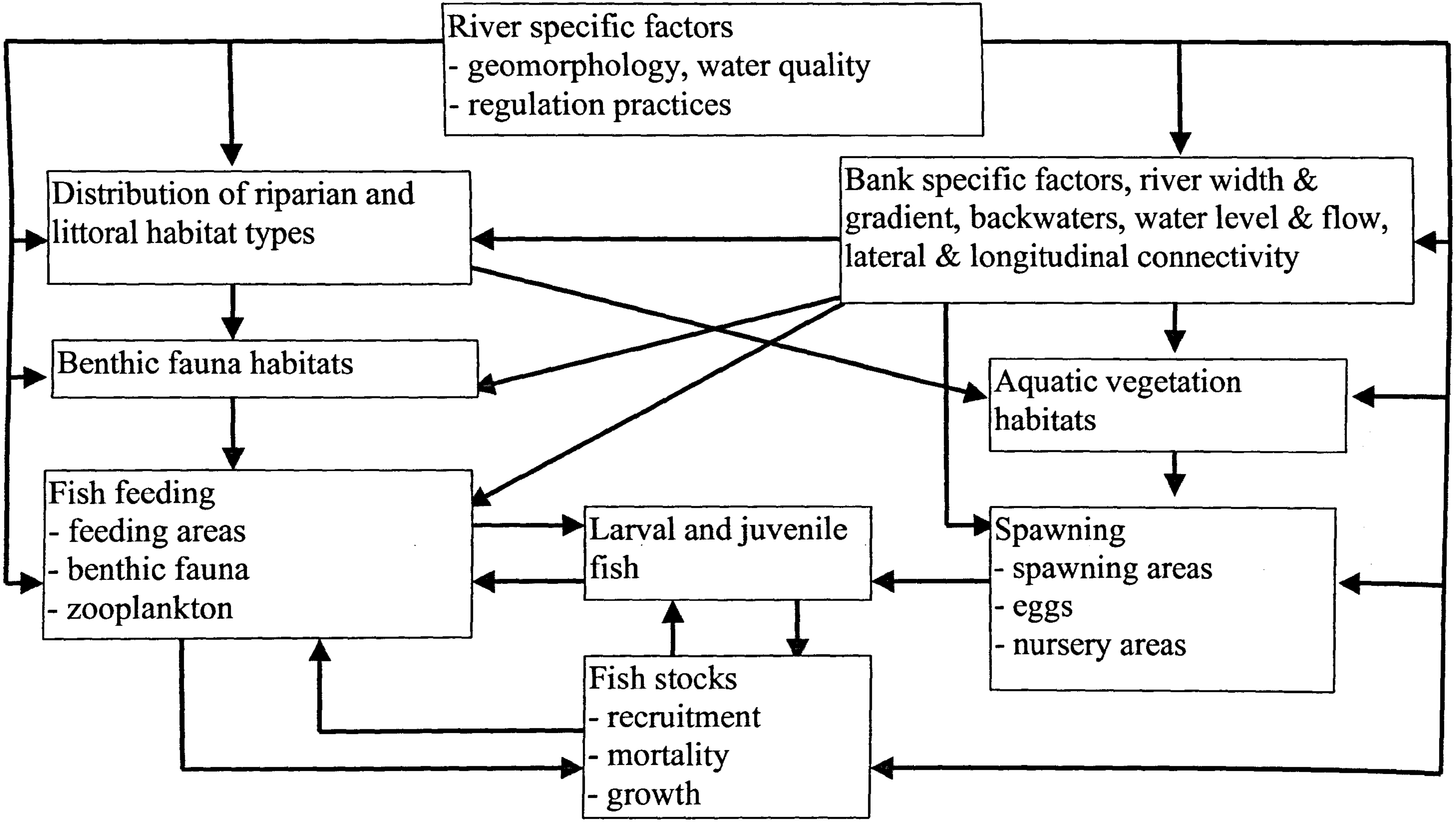


Fig. 3.47 Habitat requirements (simplified) of riverine fish populations (Cowx, unpublished).

1996b). Other species exhibit similar ontogenetic shifts in habitat use (Copp, 1992b, 1993a, 1997b; Garner, 1996b).

Optimal habitat conditions offer increased growth rates, reduced predation risk and increased food abundance to 0+ fish species (Garner, 1995, 1996a). Larval and juvenile fish are most often associated with areas of shallow, slow-flowing water in the littoral zone and, where present, in close proximity of aquatic macrophytes. Indeed, many species select areas with emergent or submerged macrophytes, even though they are not truly phytophilic or limnophilic (Copp, 1992a, 1993a, b; Watkins *et al.*, 1997; Jurajda, 1999). Aquatic vegetation provides refuge from water currents and predators for both fish (Dolinsky, 1983; Scott, 1987; Rozas & Odum, 1988; Lightfoot & Jones, 1996; Mann & Bass, 1997; Grenouillet *et al.*, 2000, 2001b, 2002; Duncan *et al.*, 2001; Grenouillet & Pont, 2001; Okun & Mehner, 2005a, b; Okun *et al.*, 2005) and their prey items (Northcott, 1979; Garner *et al.*, 1996; Mann *et al.*, 1997; Gozlan *et al.*, 1998). The selection by 0+ fish of areas containing macrophytes is therefore likely to be in response to elevated prey densities associated with macrophytes (Garner, 1996a) and predator avoidance (Garner *et al.*, 1996).

The function of floodplain waterbodies

It has been widely purported that floodplain waterbodies enhance recruitment of riverine fish populations via provision of refuge from floods (Copp, 1997a; Pinder *et al.*, 1997a) and by increased availability of food resources (Bass *et al.*, 1997a; Mann, 1997; Marker & Collett, 1997; see Chapter 4). Unfortunately, the engineered nature of many lowland rivers has deemed that such waterbodies are often scarce, although marinas and other boat-mooring facilities may compensate to some extent (Copp, 1997a; Pinder, 1997; Pinder *et al.*, 1997a). Such areas are found at intervals along the rivers Trent, Avon and Ouse, in addition to a number of floodplain waterbodies that have been connected to the main river channels. Few studies have provided empirical evidence of any benefits of reconnecting floodplain waterbodies to the parent river, mainly due to the great difficulty associated with demonstrating the existence of a causal relationship between the availability of such waterbodies and fish recruitment success. Nonetheless, the benefits of floodplain waterbodies can be inferred by virtue of their use by fish and the availability of food resources (Chapter 4).

There is no doubt that many fish species use floodplain waterbodies at various points in their life history (Bouvet *et al.*, 1985; Sabo & Kelso, 1991; Molls & Neumann, 1994; Neumann *et al.*, 1994, 1996; Staas & Neumann, 1994; Nicolas & Pont, 1995, 1997; Kurmayer *et al.*, 1996; Tales *et al.*, 1996; Schropp & Bakker, 1998; Molls, 1999; Hohausová, 2000; Penczak *et al.*, 2000, 2003, 2004; Berrebi-dit-Thomas *et al.*, 2001; Grift *et al.*, 2001a, b, 2003; Lusk *et al.*, 2001, 2003; Simons *et al.*, 2001; Borcherding *et al.*, 2002; Hohausová *et al.*, 2003; King *et al.*, 2003; Horák *et al.*, 2004; King, 2004b). For some species this use is transitional (rheophilic species) or facultative (eurytopic species), whereas for others it may be obligate (limnophilic species). In the present study, the function of many of the floodplain waterbodies as spawning areas was confirmed by direct observation of spawning activity (e.g. carp and bream at Colwick Marina and Winthorpe Lake) or collection of eggs (e.g. pike (*Esox lucius* L.) at Twyford). After hatching, nearly all fish species remain in their spawning areas and use them as nurseries (Copp & Peňáz, 1988; Copp, 1989b). For many species, therefore, the use of floodplain waterbodies as spawning areas could be inferred by the presence of newly hatched larvae. For example, newly hatched roach, bream, bleak and carp were captured from all floodplain sites, with the exception of the canal at Boroughbridge. In addition, newly hatched perch were captured in small numbers at Marina Pond, Colwick Marina and Twyford, and gravid perch were captured during an adult fish survey at another floodplain waterbody not included in this study (Bingham's Pond, River Trent).

In the current study, almost all species, including those that are strictly rheophilic, used floodplain waterbodies as nursery areas. Young chub and dace larvae were captured from Winthorpe Lake and Marina Pond, but only where they join the River Trent, suggesting that spawning takes place in the river and that the larvae disperse into the floodplain after hatching. Similarly, these two species were rarely captured as young larvae from Colwick Marina, although they were present in the adjacent river, but were abundant as old larvae and 0+ juveniles. Barbel and gudgeon larvae were captured from all of the Trent floodplain sites, with the largest catches coming from the channel that connects Winthorpe Lake with the main river.

Floodplain waterbodies are particularly important for limnophilic species due to their requirement for lentic areas with prolific macrophyte growth. Tench were regularly captured from the backwater at Twyford, although only as 0+ juveniles and adults, since the larvae occupy dense vegetation and so are unlikely to be captured by seine nets. This species was not captured from floodplain sites in the Trent, however, and larvae of rudd, ten-spined stickleback and bitterling were rare. One possible explanation for the rarity of limnophilic species is the lack of (especially submerged) vegetation at many of the floodplain sites. Marina Pond in particular supports populations of Canada goose, coot (*Fulica atra* L.), moorhen (*Gallinula chloropus* L.) and mute swan which are known to damage aquatic vegetation (Moss *et al.*, 1996), whilst Winthorpe Lake suffers from extensive wave action and, as such, vegetation is restricted to a small number of sheltered bays.

Natural river systems have a buffering capacity against flood events whereby excess water spills out of the main river channel (the eupotamon) onto the floodplain and associated waterbodies which are connected to the main channel (the parapotamon) or become connected to the river during flood (the pseudopotamon). During floods, fish and other aquatic organisms find shelter in these areas until water levels recede. The backwater at Twyford is a good example of this, with large numbers of 0+ and adult fish, particularly roach, bleak and pike, overwintering there, especially during floods. Other floodplain sites are also likely to be important refuge areas, but could not be sampled as effectively as Twyford due to their larger size. Indeed, exceptional numbers of 0+ fish were occasionally captured from the channels connecting Winthorpe Lake and Marina Pond to the Trent during flood. Conversely, floods may be essential for the liberation of fish from floodplain waterbodies to the main river (Halačka *et al.*, 1998; Bartošová & Jurajda, 2001; Bartošová *et al.*, 2001; Grift *et al.*, 2001a, b; Jurajda *et al.*, 2004). In the present study, there is a possibility that the carp, tench and bitterling captured from the Trent at Attenborough may have originated from the complex of gravel pits adjacent to the river, since the River Erewash flows through them to its confluence with the Trent immediately upstream of the sampling site (Sayer & Roberts, 2001).

Unfortunately, the importance of floodplain sites may only become apparent following their isolation from the main river channel. Regulation and engineering of lowland rivers is usually associated with a reduction in habitat heterogeneity, notably of natural backwaters and side channels (Jurajda, 1999). For many lowland rivers, therefore, potential spawning and nursery areas are limited to the main channel, since fish are no longer able to undertake lateral migrations. In the River Great Ouse, such activities have been linked to low recruitment of some species of fish (Copp, 1990a, 1991, 1997b). Obligate rheophilic and limnophilic species are likely to be most severely affected by river engineering, while eurytopic species subsist or may increase in abundance in the absence of interspecific competition for resources (Copp, 1992a; Jurajda, 1995, 1999; Jurajda *et al.*, 2001). In the current study, loss of connectivity between Marina Pond and the River Trent had a marked impact on the 0+ fish assemblages of the pond. Most noticeable was a dramatic decline in densities of all fish species, not just those classified as rheophilic. This agrees with Jurajda *et al.* (2004), who found that flooded borrow pits supported greater densities of fish than non-flooded pits. Similarly, Kruk & Penczak (2003) found that all species, including facultative riverine species, were negatively affected by dam construction.

3.4.2 Point abundance sampling (PAS) by electric fishing versus micromesh seine netting

Validation of the efficacy of sampling methods may be achieved either by testing the chosen method against a population of known density and size distribution, or via direct comparison between data sets collected using different sampling methods (Bohlin & Cowx, 1990). Theoretically, if both seine netting and PAS sample fish from the same population(s), and without bias, they should provide density and mean length estimates, and length distributions that are not significantly different from each other (Cowx *et al.*, 2001).

The present study illustrates some of the limitations of both PAS and micromesh seine netting. Differences were observed between species composition, diversity and evenness, mean lengths and densities, and length distributions derived from seine net and PAS catches. In early summer, the seine nets were relatively less efficient than PAS at capturing fish smaller than ~15 mm length, which implies that the two methods were not sampling the same populations equally. It is likely that seine netting greatly underestimates 0+ fish density and overestimates mean length during spring and early summer. By contrast, owing to small sample size, it is likely that PAS underestimates 0+ fish density in late summer.

In early summer, when 0+ fish are restricted to shallow water and mobility is low, PAS is likely to produce estimates of mean length, length distributions and density which more accurately reflect those of the actual 0+ fish populations than seine netting. However, as fish increase in size through the summer and develop an escape response, investigator bias becomes an issue. The situation is exacerbated if a small number of samples is taken. Persat & Copp (1990) and Copp (1990c) noted that with only 25 point samples, a stable image of taxocenose structure can be obtained. However, Garner (1997b) suggested that great care should be taken when interpreting data collected by PAS, with 50 point samples being the minimum required for reliable estimates of fish density. Thus, although the numbers of fish caught by PAS in this study were sufficient for determinations of mean length and length distribution (Garner, 1997b), a larger number of point samples may have been advisable to obtain accurate estimates of density.

In practicable terms, the reliability of PAS for estimates of fish density is questionable since the method frequently suffers from small catches, although reliable estimates of mean 0+ length can be obtained without considerable effort. Furthermore, if estimates of recruitment to older age groups are desired, reliability will be greater in late summer, when the effectiveness of seine netting at capturing representative samples of the fish community is greater than PAS. Nonetheless, there is great potential for specially designed PAS gear in the study of small fish which, either for morphometric or habitat (e.g. narrow streams, debris, water velocity, macrophyte density) restrictions, cannot be effectively sampled by conventional techniques.

3.4.3 Growth of 0+ fish

The preferential allocation of energy to growth is an essential feature of the early life history of fish (Keckeis & Schiemer, 1992). Fish survival is positively related to body size, with growth in the first few weeks after hatching an important determinant of recruitment success (Keast & Eadie, 1984; Mills & Mann, 1985; Mann & Mills, 1986; Kubečka, 1994; Kirjasniemi & Valtonen, 1997a, b; Chapter 6). Species or individuals that grow fast may, therefore, gain an advantage over others and, as a consequence, strong selective pressures must exist for an effective growth strategy in young fish (Keast & Eadie, 1984).

There are three main growth phases in 0+ fish from temperate latitudes: (1) accelerated growth after hatching; (2) approximately linear growth over summer, when most of the first-year growth is completed; and (3) decreasing growth associated with autumn (Keast & Eadie, 1984; Kubečka, 1994). A range of factors, such as food availability, water temperature, oxygen, salinity and social interactions, exert influence upon the growth of 0+ fish (Wootton, 1990). Of these, water temperature and food availability are the most important regarding growth patterns in the field (Keckeis & Schiemer, 1992). Temperature controls the rate of food consumption and metabolism and, thus, growth (Wootton, 1990). As such, many studies have reported a positive relationship between fish growth and water temperature (e.g. Brown, 1973, 1979; Broughton & Jones, 1978; Sadler, 1980; Mills & Mann, 1985; Wieser *et al.*, 1988; Holmes & Henderson, 1990; Mooij & van Tongeren, 1990; Mooij *et al.*, 1994; Karås, 1996; Donald, 1997; Kucharczyk *et al.*, 1997, 1998; Slavík & Bartoš, 1997; Mooij & van Nes, 1998; Cowx, 2000; Grenouillet *et al.*, 2001a; Kjellman *et al.*, 2001, 2003; see Chapter 6).

In all cases, fish in the Trent grew larger than those in the Ouse. This is in part due to the longer growing season experienced by fish in the Trent, afforded by an earlier increase in water temperatures in the spring, earlier hatching times and a later decline of water temperatures in the autumn. Notwithstanding, there were also differences in growth rates between catchments, with those in the Trent higher than those in the Avon and Ouse. For the Trent and Ouse, this may be partly explained by differences in temperature regime (Chapter 6). The Ouse is naturally a cooler river than the Trent due to its more northerly latitude and the topography of its catchment. In addition, the Trent receives warm water inputs from power stations, albeit less so than in previous decades (Sadler, 1980; Cowx, 1991). The reasons for the differences between the Trent and Avon are less apparent, however, since both experience similar temperature regimes and both appear to be similarly productive in terms of phytoplankton and zooplankton (Chapter 4). It may simply be that growth rates in the two rivers are fixed genetically, or by a combination of extrinsic factors that has yet to be determined. Alternatively, although the overall temperature regimes of the Trent and Avon are similar, there may be important differences at the microhabitat scale. Whereas the Trent has an appreciable littoral zone for much of its length, the Avon lacks the very shallow, warmer water in the river margins that fish larvae preferentially inhabit (Garner *et al.*, 1998). The implication is that fish in the Trent grow faster than their counterparts in the Avon and Ouse, irrespective of differences in hatching dates or length of growing season. Conversely, this suggests that the larger size of fish in the Avon than in the Ouse may be largely due to earlier hatching dates and longer growing season (see Chapter 6), since a larger absolute size is achieved despite similar growth rates.

Intra-catchment variations in growth may also be of considerable importance (Cowx, 2001). In the Hampshire Avon, Ladle (1991) found that 0+ dace at downstream sites were significantly larger than their counterparts upstream, which he attributed to the temperature gradient in the river. Similarly, Mann (1997) noted that growth rates of roach in the River Great Ouse were highest at the most downstream sites. In contrast, observations from the Yorkshire Ouse suggested that 0+ fish are often smallest downstream, perhaps due to flow rates whereby the smallest fish are washed downstream (Cowx, 2001). In the current study, it was observed that dace from the Ouse tributary rivers (Swale, Ure, Nidd, Wharfe) were generally larger than those from the Ouse itself, most likely due to the differences in habitat characteristics described above (Section 3.4.1). Although catches were irregular, fish from Marina Pond (Trent) and Tewkesbury (Avon) were invariably larger than their counterparts from elsewhere. For Marina Pond, the explanation may be the great availability of zooplankton (Chapter 4), the relatively low densities of fish (Section 3.3.3), possible differences in water temperature between floodplain waterbodies and main river channels (Schiemer *et al.*, 2001c), or a combination of factors. Tewkesbury also supported relatively low fish densities (Section 3.3.3), which together with other factors, such as inputs of organic matter and nutrients from the conurbation of Tewkesbury and agriculture upstream, may explain the increased growth of 0+ fish there.

3.4.4 Spawning periodicity

While some fish species shed a single batch of eggs in a short spawning period, others ripen successive batches within a season (fractional spawning) or spawn a single batch over an extended period (protracted spawning). Species that adopt fractional or protracted spawning strategies are likely to have a greater size range of young at the end of the growing season than those that do not, since progeny from later spawnings have less time in which to grow before water temperatures decline in autumn than those from earlier spawning events (Lowerre-Barbieri *et al.*, 1998). Such spawning strategies expose young fish to variable environmental conditions (Durham & Wilde, 2005), with fish from later spawnings generally less likely to survive the winter than larger siblings (Miller *et al.*, 1988; Johnson & Evans, 1990, 1996; Thompson *et al.*, 1991; Griffiths & Kirkwood, 1995; Hurst & Conover, 1997; Kirjasniemi & Valtonen, 1997a, b; Copeland & Carline, 1998; Garvey *et al.* 1998; Post *et al.*, 1998; Lappalainen *et al.*, 2000; McCollum *et al.*, 2003; Eckmayer & Margraf, 2004; Pangle *et al.*, 2004; Curry *et al.*, 2005).

The results of the current study corroborate observations of adult spawning behaviour and reproductive development. Chub and bleak, and to a lesser extent bream, gudgeon and minnow, adopted fractional or protracted spawning strategies, while dace, roach and perch spawned only once per season. Dace and perch shed a single batch of eggs in a two to three week spawning period (Kennedy, 1969; Mann, 1978; Mills, 1980; Mann & Mills, 1985, 1986; Cowx, 1990; Mills, 1991; Lobón-Cerviá *et al.*, 1996) and roach usually spawn once within a two to four day period (Mackay & Mann, 1969; Diamond, 1985a; Mark *et al.*, 1987; Rheinberger *et al.*, 1987; Rinchard & Kestemont, 1996, 2003; Rinchard *et al.*, 1997). Chub are known to adopt fractional spawning strategies (White & Williams, 1978; Libosvárský & Sterba, 1981; Rheinberger *et al.*, 1987; Poncin *et al.*, 1989; Economou *et al.*, 1991; Vriese *et al.*, 1994; Çalta, 2000) with eggs scattered in up to three spawnings (Libosvárský, 1979; Mark *et al.*, 1987). Gametes from the anal end of both ovaries and testes have been shown to be the first to ripen and be shed, compared with other species in which the entire gonad ripens at one time (Mann, 1976). Fractional spawning has also been reported in bleak (Mackay & Mann, 1969; Bíró, 1980; Rinchard & Kestemont, 1996, 2003; Kestemont *et al.*, 2001), gudgeon (Prokeš & Peňáz, 1979; Mann, 1980; Mann *et al.*, 1984), bream (Matěna, 1995a, b, 1998; Grift *et al.*, 2001b; Hladík & Kubečka, 2003) and minnow (Frost, 1943; Mills, 1987), with two or three batches of eggs produced. For bleak, this has subsequently been supported by evidence of up to four size groups of eggs in the ovary prior to spawning (Barus & Prokeš, 1996). With the exception of chub and bream, fractional spawning is probably a consequence of small body size which permits only relatively small numbers of eggs per fish to be produced (Cowx, 2001). It has been suggested that small fish compensate for this by extending the spawning period and producing successive batches of eggs (Heins & Bresnick, 1975; Gale & Gale, 1977; Keast & Eadie, 1984).

Many studies, however, failed to differentiate between multiple spawning at the individual and population levels. Poncin *et al.* (1996), for example, observed that bream spawned in two batches approximately two weeks apart, but did not specify whether the same fish spawned on both occasions or whether two different sub-populations were involved. Similarly, Peňáz *et al.* (1978, *fide* Fredrich *et al.*, 2003) observed chub at spawning grounds on three occasions, but did not state whether they were repeat spawners. In contrast, Fredrich *et al.* (2003) tagged individual chub and obtained definitive evidence that individual fish spawned at least twice in one season. In the present study, although there was no direct evidence of multiple spawning events, such activities could be identified *a posteriori* either by bimodality/asymmetry in the initial cohort of 0+ fish or by the appearance of a discrete second cohort. It was not possible, however, to ascertain whether the patterns were a result of *actual* multiple spawning by individual fish or *apparent* multiple spawning by sub-populations that delay their spawning activities. It may be, for example, that younger individuals of some species spawn at different times to older conspecifics. Alternatively, flooding or other environmental perturbations may interrupt or delay spawning activity under some circumstances (e.g. L'Abée-Lund & Vollestad, 1987), potentially culminating in bimodality in the 0+ population. In addition, drift of small individuals from upstream (Pavlov *et al.*, 1977; Gale & Mohr, 1978; Peňáz *et al.*, 1992; Pavlov, 1994; Johnston *et al.*, 1995; Jurajda, 1998; Carter & Reader, 2000; Reichard *et al.*, 2001, 2002a, b, 2004; Copp *et al.*, 2002a; Oesmann, 2003; White & Harvey, 2003; Peterka *et al.*, 2004; Reichard & Jurajda, 2004; Zitek *et al.*, 2004a, b), active dispersal of larger individuals away from the sampling areas and other factors may complicate the situation. However, drift is generally restricted to the first few weeks of life (Araujo-Lima & Oliveira, 1998; Carter & Reader, 2000), and this phenomenon does not explain the presence of young larvae throughout the summer. Furthermore, the patterns observed for chub, bleak, bream, gudgeon and minnow were not observed for roach, dace and perch.

The current study has identified spatial and temporal variations in multiple spawning events. Multiple spawning was much more prevalent in the Trent than in the Avon and Ouse, although the reasons for this are uncertain. This was especially the case with chub, with batches easily identified in the Trent in most years. Even when catches were too small for detailed analysis, particularly in the Avon and Ouse, multiple spawning events could be tentatively inferred by virtue of a complete lack of growth (mean length) over time. Kennedy & Fitzmaurice (1968) stated that bream are more likely to spawn more than once a year towards the south of its range, and only once in the north. Certainly, the growing season is longer in the Trent compared with the Ouse (see Chapter 6), but this does not explain the differences between the Trent and Avon. There were also differences in intensity between years. There was no apparent pattern regarding these differences, however, with warm and dry years not noticeably different from cold and wet years.

A possible implication of multiple spawning events is that fish hatching in late summer may not develop scales before the winter or that scales may be very small. In most species there is usually some reabsorption of scales over the winter, and it is possible that the smallest scales may be reabsorbed to such an extent (perhaps completely) that the first annulus may be missed (or missing) in later attempts to age the fish. Indeed, this phenomenon has been observed in minnow (Mills, 1987), and Atlantic salmon and brown trout (Jensen & Johnsen, 1982). This could subsequently impact upon calculations of growth, survival, year-class strength and, ultimately, fishery management decisions based upon them.

Multiple spawning events are important for recruitment success as they disperse the mortality risk of the early developmental stages (Begg & Marteinsdottir, 2000; Fuiman *et al.*, 2005). It has been suggested that multiple spawning may act as an 'insurance policy' against discharge-induced mortality in early summer (Nunn *et al.*, 2003a). In some years, therefore, relatively strong year-classes may result, despite high mortality in early summer and smaller than average mean lengths, providing overwinter conditions are not severe. Knowledge regarding fractional and protracted spawning events remains limited, however, and should be supplemented by further, more detailed studies to further assess the causes and significance of temporal (within and between years) and spatial (within and between catchments) variations in spawning strategies adopted by fish species or populations (Nunn *et al.*, 2002). That large numbers of fish from late summer spawnings do survive the winter in some years is evident, but it has still to be ascertained empirically what the significance of multiple spawning events is with respect to recruitment success.

CHAPTER FOUR

ZOOPLANKTON AVAILABILITY TO 0+ FISH IN LOWLAND RIVERS AND FLOODPLAIN WATERBODIES

4.1 INTRODUCTION

Zooplankton are the most important food items of the larvae and 0+ juveniles of a wide range of fish species (Whiteside *et al.*, 1985; Wanzenböck & Schiemer, 1989; Mehner & Winfield, 1997; Mehner & Thiel, 1999; Mehner *et al.*, 1997; see Chapter 5) and, as such, zooplankton availability is a key factor regulating growth and survival of 0+ fish (Miller *et al.*, 1988; Schiemer *et al.*, 1989; Bass *et al.*, 1997a; Mann, 1997; Mann *et al.*, 1997; Romare, 2000; Graeb *et al.*, 2004). Floodplain waterbodies are reputed to enhance recruitment of riverine fish populations due to increased availability of food resources compared with main river channels (Bass *et al.*, 1997a; Mann, 1997; Marker & Collett, 1997). Few studies have provided empirical evidence of such benefits, however, largely due to the great difficulty associated with demonstrating the existence of a causal relationship between the availability of floodplain waterbodies and fish recruitment success. Nonetheless, the benefits of floodplain waterbodies can be inferred by virtue of the increased availability of food resources compared with river channels and their use by fish (Chapter 3). Phytoplankton and zooplankton populations often exceed and persist for longer than those in lotic environments (Bass *et al.*, 1997a; Marker & Collett, 1997), and may therefore provide suitable feeding conditions for 0+ fish after resources have been diminished in main river channels (Mann, 1997).

The aim of this chapter was to investigate the availability of zooplankton to 0+ fish in lowland rivers and floodplain waterbodies. Specifically, the objectives were to investigate: (1) the composition of the zooplankton at main river and floodplain sites; (2) differences in diversity and evenness of the zooplankton between main river and floodplain sites; (3) differences in the density of key zooplankton groups at main river and floodplain sites; (4) differences in phytoplankton biomass at main river and floodplain sites; (5) the influence of river discharge on phytoplankton and zooplankton populations; (6) the relationships between phytoplankton biomass and density of zooplankton; and (7) the relationships between the densities of zooplankton and 0+ fish.

The hypothesis was that floodplain waterbodies enhance recruitment of riverine fish populations by provision of increased availability of food resources compared with main river channels.

4.2 MATERIALS AND METHODS

4.2.1 Zooplankton processing

Each zooplankton sample was made up to 100 mL with 4% formalin solution and thoroughly mixed before withdrawing a 500 μL sub-sample with a wide-bore, automatic pipette. The sub-sample was emptied into a Sedgewick Rafter counting chamber, and all organisms were identified to appropriate taxonomic groups (Johnson, 1952; Scourfield & Harding, 1966; Harding & Smith, 1974; Pontin, 1978; Fitter & Manuel, 1986) and enumerated using a binocular microscope. Cladocerans, for example, were identified to either species or genus, while other taxa were typically identified to lower levels of taxonomic resolution. The numbers of organisms enumerated always fell within the range recommended by Bottrell *et al.* (1976) and Prepas (1984), with the exception of during winter when zooplankton were scarce. Three sub-samples were analysed for each zooplankton sample. The volume of water filtered by the zooplankton trawl (V) was determined by assuming that the net filtered the volume of the column of water traversed by the net:

$$V = \pi \times r^2 \times d \qquad (4.1)$$

where r is the radius of the aperture of the net and d is the distance the net was towed (Bottrell *et al.*, 1976; De Bernardi, 1984). The absence of a standing wave immediately in front of the net was taken as an indication that flow into the net was not being impeded by clogging (Carter & Reader, 2000). The number of each taxon in each sub-sample was used to calculate mean (± SD) density (plankters L^{-1}) for each sampling occasion.

4.2.2 Chlorophyll *a* concentration

Concentration of chlorophyll *a* is a reliable and commonly used proxy of phytoplankton biomass (Kelly & Whitton, 1998; Skidmore *et al.*, 1998; Pápista *et al.*, 2002; Gregor &

Maršálek, 2004; van de Bund *et al.*, 2004). Determinations of chlorophyll *a* concentration from phytoplankton were made according to the method of Jespersen & Christoffersen (1987). Replicate 500 mL samples of well-mixed river water were filtered through 7 cm Whatman GF/C glass fibre filters under vacuum. The filters were transferred to plastic centrifuge tubes with 10 mL of absolute ethanol and boiled in a water bath at 70°C for five minutes to extract the chlorophyll. The filters were removed and squeezed dry, and the tubes were centrifuged at 3000 rpm for ten minutes. The samples were then transferred to 1 cm path-length cuvettes and the absorptions were measured at 665 and 750 nm using a spectrophotometer. The second wavelength is used to account for any turbidity in the samples. Concentration of chlorophyll *a* $[Chl]$ was calculated using:

$$[Chl] = \frac{A_{665} - A_{750}}{83.4} \times 10^6 \times \frac{10}{V} \qquad (4.2)$$

where A_{665} and A_{750} are the mean absorptions at 665 and 750 nm, respectively, V is the volume of river water filtered, and 83.4 $L.g^{-1}.cm^{-1}$ is the specific absorption coefficient for chlorophyll *a* in ethanol.

4.2.3 Data analysis

4.2.3.1 *Similarity*

Similarity in zooplankton composition between sites was investigated using the Bray-Curtis (1957; syn. Czekanowski, 1913) similarity index in PRIMER (version 5.2). The merits of this index are detailed in Chapter 3 (Section 3.2.2.3). Bray-Curtis similarity matrices were calculated using percent abundance data (Section 3.2.2.1) and presented as dendrograms using hierarchical agglomerative clustering (group average linkage) to investigate spatial similarities in zooplankton structure.

4.2.3.2 *Diversity and evenness*

The diversity and evenness of the zooplankton at each site was assessed using the Shannon-Wiener (H') diversity index and Pielou's evenness index (J), respectively. The merits of these indices are detailed in Chapter 3 (Section 3.2.2.4).

4.2.3.3 *River discharge, phytoplankton, zooplankton and 0+ fish*

Mean daily river discharge data were obtained from the Environment Agency gauging stations at Holme Pierrepont (River Trent), Evesham (Warwickshire Avon) and Skelton (Yorkshire Ouse) (Figs 2.1-2.3). River discharge, chlorophyll *a* concentration, zooplankton density and 0+ fish density data were tested for normality using one-sample Kolmogorov-Smirnov tests, and subsequently submitted to natural logarithm transformations (Dytham, 2003). A series of Pearson product-moment correlations was performed to test for associations between each of the variables (Dytham, 2003).

4.3 RESULTS

4.3.1 Composition of the zooplankton

A total of 30 zooplankton taxa was identified during the study period (Table 4.1). Of these, all were recorded in the River Trent, 22 were found in the Warwickshire Avon, and 20 were found in the Yorkshire Ouse catchment. Overall, rotifers and copepod nauplii occurred most frequently in zooplankton samples, with cyclopoid copepods, *Bosmina longirostris* (Müller), *Alona* and *Chydorus* spp. also prevalent (Table 4.1). *Camptocercus rectirostris* Schödler, *Leydigia* spp., *Daphnia cucullata* Sars, *Daphnia galeata* Sars, *Daphnia magna* Straus, *Daphnia obtusa* Kurz, *Daphnia pulex* (L.) and *Polyphemus pediculus* (L.) were restricted to the Trent, with *Daphnia hyalina* Leydig also more prevalent than in the Avon and Ouse. The zooplankton of the Avon was similar to that of the Ouse, with non-planktonic cladocerans (especially chydorids) more prevalent than planktonic taxa such as *Daphnia* spp. Primarily benthic or phytophilic invertebrates such as ostracods, water mites (Hydracarina), simulid and chironomid larvae, dispersal phases of vorticellids, bryozoan statoblasts and testate amoebae were occasionally found, but were not considered zooplankton.

Sites were grouped on the basis of their zooplankton using the Bray-Curtis similarity index. All sites had very similar zooplankton overall (>75% similarity; Fig. 4.1a), due mainly to the predominance of rotifers (typically *Euchlanis*, *Brachionus*, *Keratella*, *Polyarthra* or *Asplanchna* spp.). Exclusion of this taxon allowed differentiation of two main groups, with one comprising floodplain sites (including the Marina Pond transitional site) and the other containing the main river sites, plus Colwick Marina (Fig.

Table 4.1 Frequency of occurrence of zooplankton taxa in the River Trent, Warwickshire Avon and Yorkshire Ouse catchments.

PHYLUM	CLASS ORDER	Family *Species*	Trent TB	 CM a	 CM b	 MP a	 MP b	Avon TWY	 TEWK	Ouse BORO a	 BORO b	 ACA
CRUSTACEA	BRANCHIOPODA											
	CLADOCERA	**Bosminidae**										
		Bosmina longirostris (Müller)	○	◯	◯	◯	◯	○	○	◦	⚬	○
		Chydoridae										
		Acroperus harpae (Baird)	·	◦	·	◦	·	◦	·	·	◦	·
		Alona spp. Baird	⚬	○	○	○	⚬	○	◯	◦	⚬	⚬
		Camptocercus rectirostris Schödler	◦	◦	◦	·	∘	·	·	·	·	·
		Chydorus spp. Leach	○	○	⚬	◯	○	○	◯	⚬	○	◯
		Disparalona rostrata (Koch)	◦	◦	⚬	◦	·	·	⚬	∘	·	·
		Eurycercus lamellatus (Müller)	·	◦	◦	·	◦	∘	∘	·	◦	·
		Graptoleberis testudinaria (Fischer)	·	∘	∘	·	·	⚬	⚬	·	·	·
		Leydigia spp. Kurz	·	∘	·	·	∘	·	·	·	·	·
		Peracantha truncata (Müller)	·	∘	·	·	·	◦	·	·	·	·
		Pleuroxus spp. Baird	◦	⚬	◦	⚬	⚬	⚬	⚬	·	∘	∘
		Daphniidae										
		Ceriodaphnia spp. Dana	·	⚬	◦	⚬	⚬	◦	⚬	◦	◦	∘
		Daphnia cucullata Sars	·	∘	·	∘	◦	·	·	·	·	·
		Daphnia galeata Sars	∘	◦	◦	◦	◦	·	·	·	·	·
		Daphnia hyalina Leydig	◦	⚬	⚬	⚬	◯	∘	◦	∘	∘	·
		Daphnia magna Straus	·	∘	·	·	·	·	·	·	·	·
		Daphnia obtusa Kurz	·	·	·	∘	◦	·	·	·	·	·
		Daphnia pulex (L.)	·	◦	·	·	·	·	·	·	·	·
		Scapholeberis mucronata (Müller)	·	◦	·	◦	∘	∘	◦	∘	⚬	◦
		Simocephalus exspinosus (DeGeer)	·	◦	∘	◦	◦	◦	◦	◦	◦	◦
		Simocephalus vetulus (Müller)	·	◦	·	∘	·	∘	·	·	·	·
		Macrothricidae										
		Ilyocryptus sordidus (Liévin)	◦	◦	◦	◦	◦	◦	◦	∘	·	∘
		Macrothrix spp. Baird	·	·	·	◦	∘	·	∘	·	∘	◦
		Polyphemidae										
		Polyphemus pediculus (L.)	·	◦	∘	·	·	·	·	·	·	·
		Sididae										
		Sida crystallina (Müller)	·	∘	◦	∘	·	·	⚬	·	◦	◦
	COPEPODA											
	CALANOIDA	spp.	∘	◯	⚬	○	○	◦	∘	∘	·	◦
	CYCLOPOIDA	spp.	◯	◯	◯	◯	◯	◯	◯	○	○	◯
	HARPACTICOIDA	spp.	⚬	⚬	⚬	⚬	◦	⚬	⚬	∘	◦	∘
	nauplii[1]	spp.	◯	◯	◯	◯	◯	◯	◯	○	◯	◯
ROTIFERA[2]		spp.	◯	◯	◯	◯	◯	◯	◯	◯	◯	◯

Key (percent frequency of occurrence)	
Dominant (>75%)	◯
Abundant (51-75%)	○
Frequent (26-50%)	⚬
Occasional (6-25%)	◦
Rare (1-5%)	∘
Not captured	·

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1 - copepod nauplii not identified to order

2 - mostly *Brachionus*, *Euchlanis*, *Keratella* (all Brachionidae), *Asplanchna* (Asplanchnidae) and *Polyarthra* (Synchaetidae) spp.

N.B. Site name abbreviations are the same as those in Table 2.3.

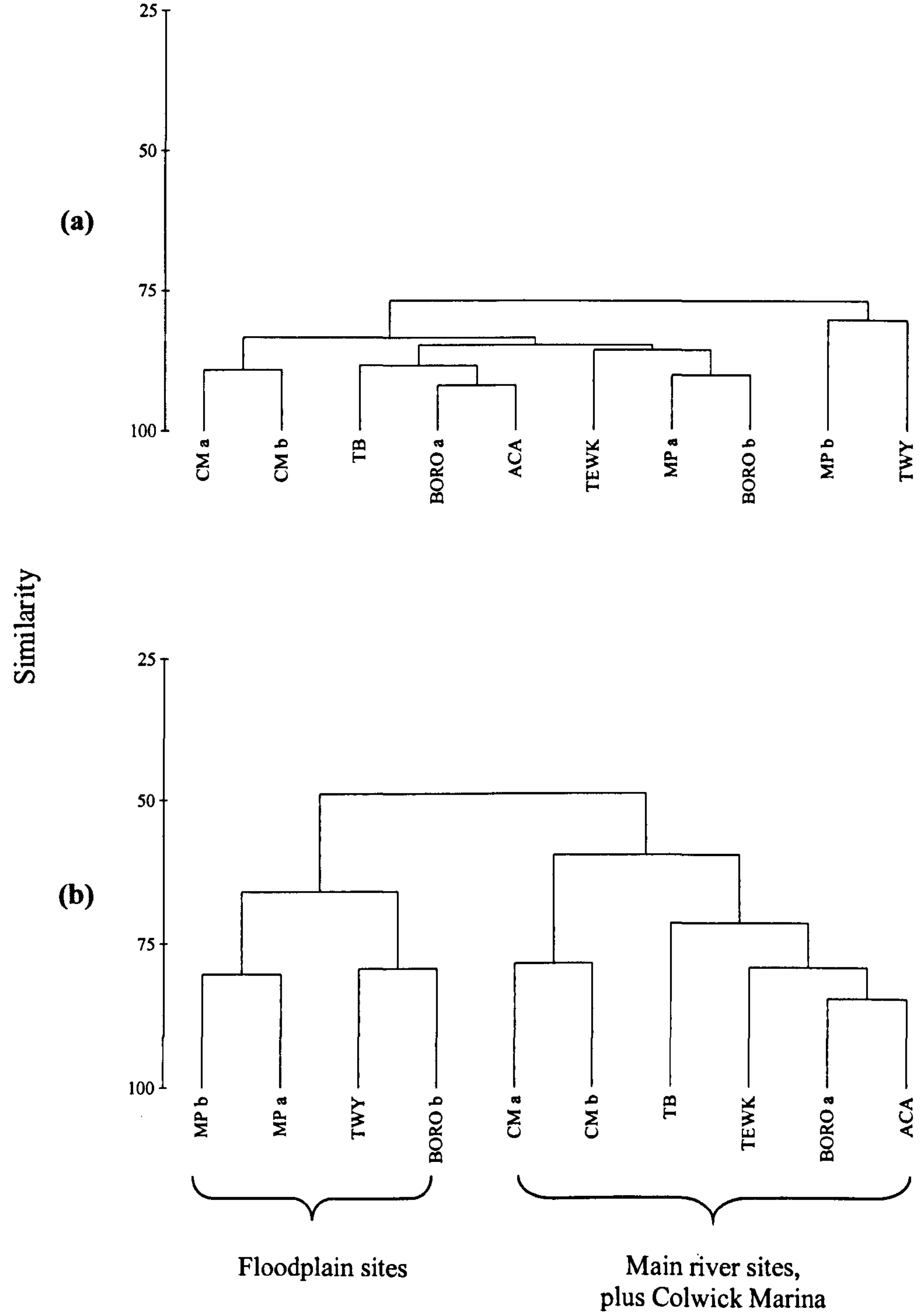


Fig. 4.1 Similarity in (a) all zooplankton and (b) zooplankton excluding rotifers between sites. Site name abbreviations are the same as those in Table 2.3.

4.1b). Zooplankton composition at main river sites was approximately 50% similar to that at floodplain sites (Fig. 4.1b).

4.3.1.1 *Main river sites*

Main river sites were characterised by an overwhelming (numerical) dominance of rotifers (Fig. 4.2). Other taxa such as cyclopoid copepods, copepod nauplii and small cladocerans (e.g. *Bosmina*, *Alona* spp. and *Chydorus* spp.) were frequently present, but generally comprised only a small percentage of the zooplankton. Benthic taxa such as harpacticoid copepods, small chydorids and macrothricids were relatively more abundant in main river than floodplain samples, but this was probably due to their presence in the drift rather than higher densities *per se*. Large and planktonic taxa were generally rare, probably due to low shoreline sinuosity and, consequently, poor inshore retention. The site in the river adjacent to Colwick Marina had a greater richness of taxa than the other main river sites, probably due to its location immediately downstream of the marina entrance, while Tewkesbury had a greater prevalence of phytophilic taxa, such as *Sida crystallina* (Müller), *Simocephalus exspinosus* (DeGeer) and *Ceriodaphnia* spp., than other main river sites due to the presence of water lilies (Table 4.1).

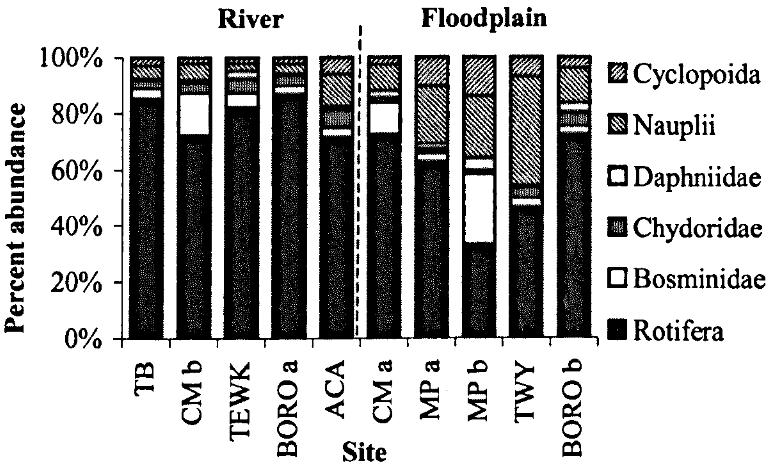


Fig. 4.2 Percent abundance of key zooplankton groups at main river and floodplain sites. Site name abbreviations are the same as those in Table 2.3.

4.3.1.2 *Floodplain sites*

Floodplain sites were also dominated by rotifers, but zooplankton composition differed markedly from main river sites due to a greater richness of cladoceran taxa (Table 4.1;

Fig. 4.2). Colwick Marina had a diverse range of chydorid species including the large *Eurycercus lamellatus* (Müller) and *Camptocercus rectirostris* which, although accounting for only a small percentage of the zooplankton, were abundant in close proximity to aquatic vegetation (*pers. obs.*). Colwick Marina also had a diverse range of planktonic and non-planktonic daphnid species (Table 4.1), but these were generally present for only a relatively short time period in spring and early summer. The same was true for *Polyphemus pediculus*, although this species was able to persist within helophyte beds after it had disappeared from the pelagial. The general zooplankton composition at Twyford and Boroughbridge was broadly similar to that at Colwick Marina, but with greater emphasis on non-planktonic cladocerans which, at Twyford, is likely to be due to an abundance of submerged vegetation (Table 4.1). Zooplankton in general was sparse at Boroughbridge, probably due to its close proximity to the fast-flowing River Ure. In contrast with the other floodplain sites, Marina Pond was characterised by planktonic copepods and cladocerans, such as *Bosmina* and *Daphnia* spp. Non-planktonic species were comparatively rare, probably due largely to the lack of macrophytes at this site (Table 4.1).

4.3.2 Diversity and evenness

There was no significant difference in the mean diversity of the zooplankton at main river and floodplain sites (ANOVA, $P>0.05$). Furthermore, there was only one statistically significant difference between individual sites, with zooplankton at Marina Pond (floodplain) more diverse than at Boroughbridge (river) (Mann-Whitney *U*-Test, $P<0.05$; Fig. 4.3). Evenness was significantly greater at main river sites than at floodplain sites (Mann-Whitney *U*-Test, $P<0.05$; Fig. 4.3) since, despite their greater species richness, floodplain sites were, for the most part, largely dominated by the same key taxa as main river sites, but with more extreme differences in abundance between the taxa.

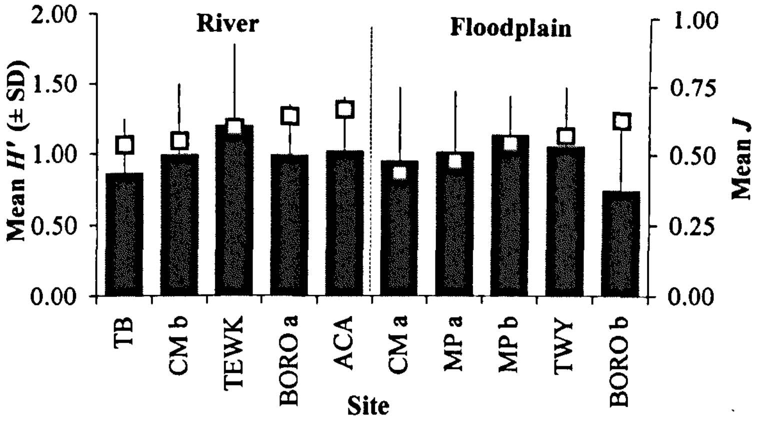


Fig. 4.3 Mean diversity (*H'*) and evenness (*J*) of zooplankton at main river and floodplain sites. Site name abbreviations are the same as those in Table 2.3.

4.3.3 Density

Densities were calculated for key zooplankton groups, namely Rotifera, Bosminidae, Chydoridae, Daphniidae, Cyclopoida and copepod nauplii. Overall, mean densities of all groups were significantly higher at floodplain sites than at main river sites (Mann-Whitney *U*-Tests, $P<0.01$; Fig. 4.4). It should be noted that even when zooplankton densities in floodplain waterbodies were low, they were still higher than the majority of maximal densities in the main river channels. The main exception was Boroughbridge, which had zooplankton densities that were comparable with the lowest found at the main river sites (Fig. 4.4). There were few statistically significant differences in the densities of the key zooplankton groups between individual sites, probably because of a large amount of temporal variation in densities.

4.3.3.1 *Rotifera*

Both at main river and floodplain sites, densities of rotifers increased abruptly to a peak in April or May each year, before declining equally as rapidly by June (Fig. 4.5). Densities in the main river generally remained low thereafter until the following spring, although small increases in density were observed at many river sites in late summer 2003. In contrast, a number of additional, smaller peaks in density sometimes occurred at floodplain sites, particularly in the Trent (Fig. 4.5). Densities of rotifers at main river sites never exceeded 200 L^{-1}, and were between 2 (Acaster Malbis) and 20 L^{-1} (Tewkesbury) on average (Figs 4.4, 4.5). Rotifers attained substantially higher densities at floodplain sites than in the main river channels, with a maximum of over 3400 L^{-1} at

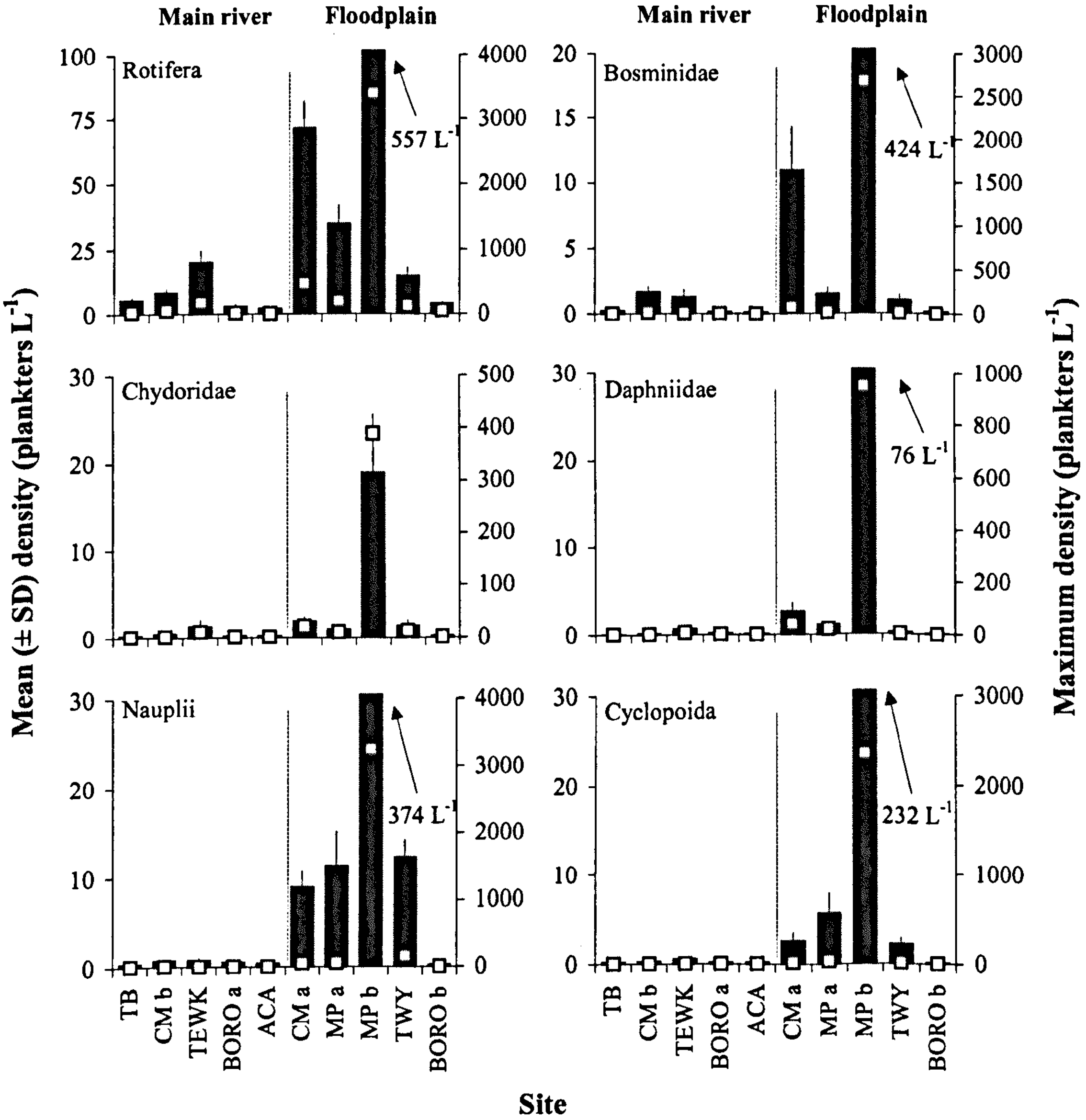


Fig. 4.4 Mean (filled bars) and maximum (clear bars) density of six key zooplankton groups at main river and floodplain sites. Site name abbreviations are the same as those in Table 2.3.

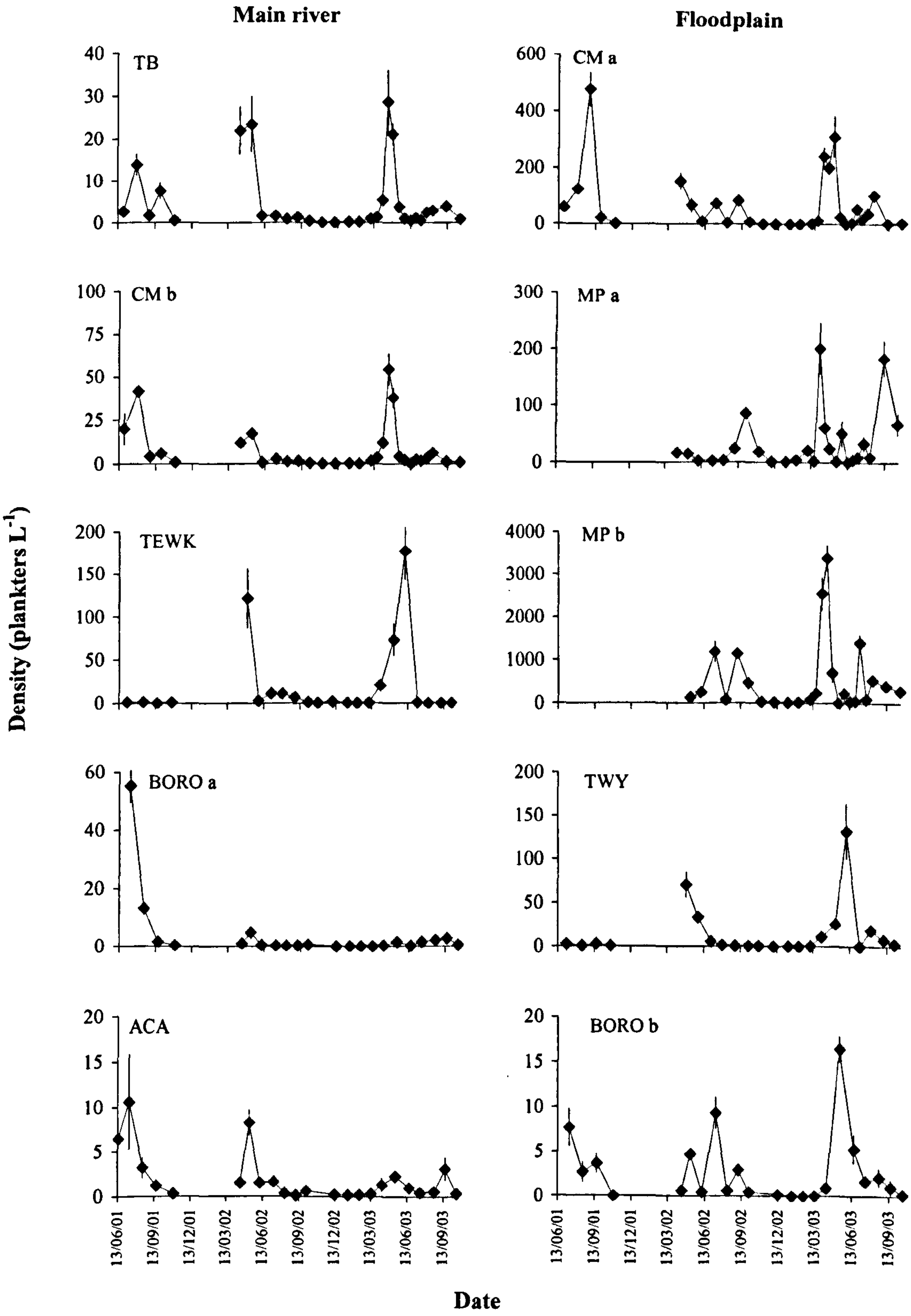


Fig. 4.5 Temporal variations in density (± SD) of Rotifera at main river and floodplain sites. Site name abbreviations are the same as those in Table 2.3.

Marina Pond. Mean densities at floodplain sites ranged between 3 (Boroughbridge) and 557 L^{-1} (Marina Pond).

4.3.3.2 *Bosminidae*

Seasonal trends in *Bosmina* densities were more variable than for rotifers. At both main river and floodplain sites, peak densities invariably occurred between May and July, and densities generally remained low thereafter until the following spring (Fig. 4.6). There were some variations on this general sequence, however, especially in the Trent where there was an additional peak in late summer/early autumn at many sites (Fig. 4.6). Densities of *Bosmina* at main river sites never exceeded 20 L^{-1}, and were less than 2 L^{-1} on average (Figs 4.4, 4.6). Bosminids attained substantially higher densities at floodplain sites, with a maximum of almost 2700 L^{-1} at Marina Pond. Mean densities at floodplain sites ranged between <1 (Boroughbridge) and 424 L^{-1} (Marina Pond).

4.3.3.3 *Chydoridae*

Seasonal trends in chydorid abundance at riverine sites were similar to those of *Bosmina*, with peak densities typically occurring in June or July, followed by low densities thereafter (Fig. 4.7). Trends at lacustrine sites differed slightly from those in the main river channels in that the majority of peak densities occurred during May, rather than in June or July (Fig. 4.7). In common with main river sites, there were no clear secondary peaks as were observed for a number of the other zooplankton groups. Densities of chydorids at main river sites never exceeded 12 L^{-1}, and were less than 2 L^{-1} on average (Figs 4.4, 4.7). Chydorids attained substantially higher densities at floodplain sites, with a maximum of almost 400 L^{-1} at Marina Pond. Mean densities at floodplain sites ranged between <1 (Boroughbridge) and 18 L^{-1} (Marina Pond).

4.3.3.4 *Daphniidae*

Seasonal patterns in daphnid abundance were difficult to discern at main river sites due to low densities. Nonetheless, peak densities generally occurred around July, with abundance very low for the remainder of the year (Fig. 4.8). At floodplain sites, peak daphnid densities occurred around May in the Trent, whereas they occurred in June or July in the Avon and Ouse (Fig. 4.8). This is largely due to differences in daphnid species composition between the rivers, with planktonic *Daphnia* spp. most abundant in the Trent compared with non-planktonic daphnids in the Avon and Ouse.

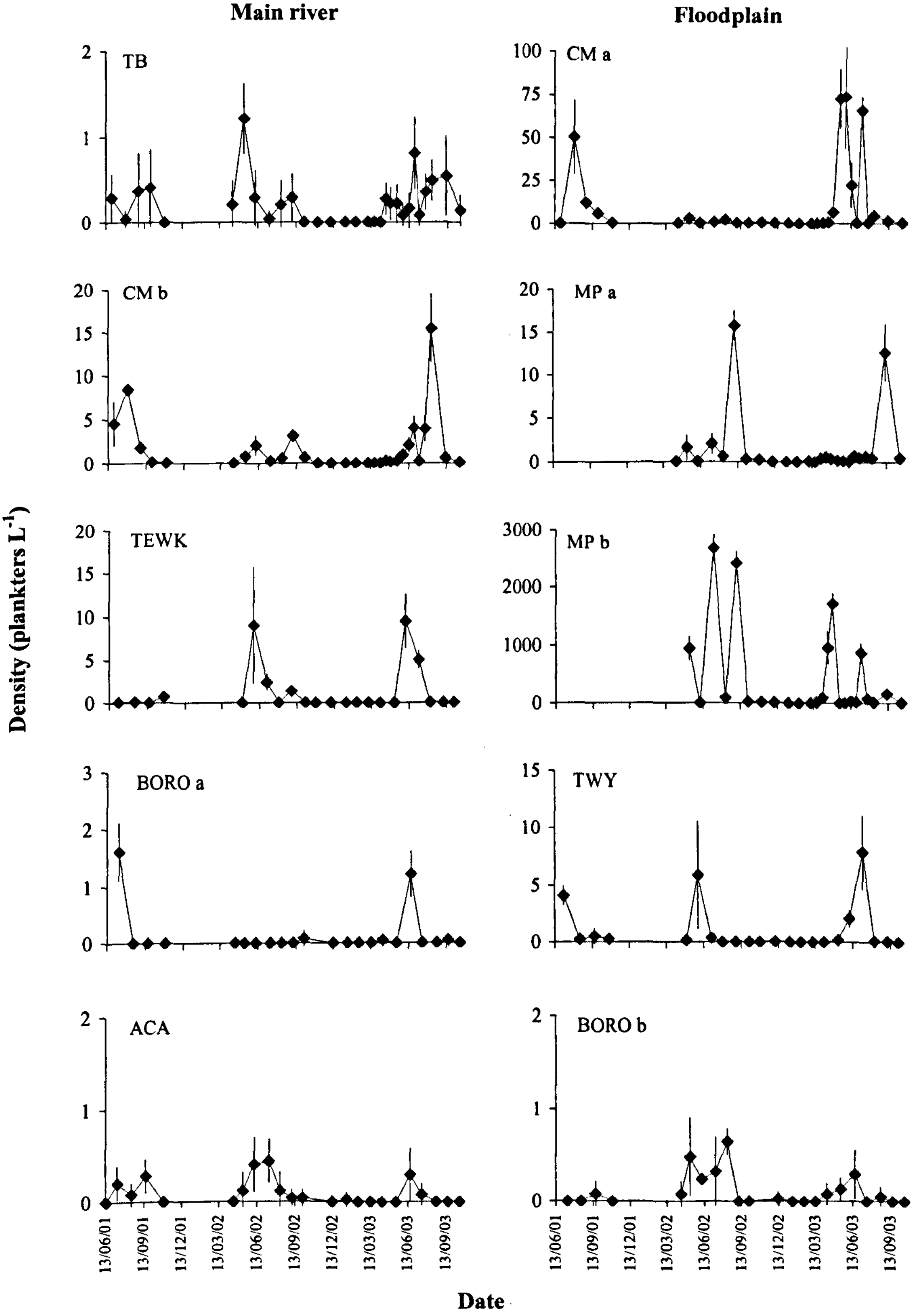


Fig. 4.6 Temporal variations in density (± SD) of Bosminidae at main river and floodplain sites. Site name abbreviations are the same as those in Table 2.3.

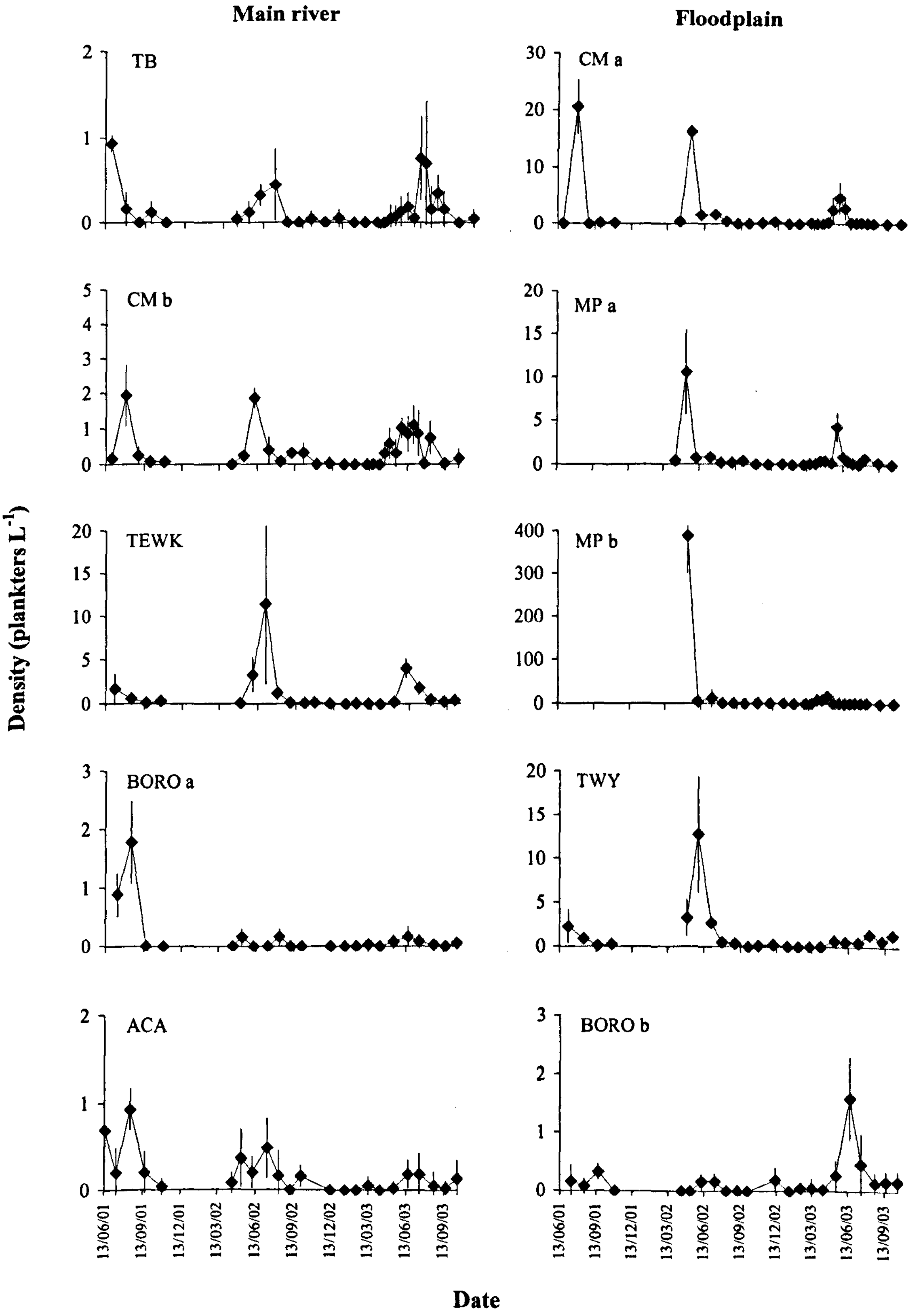


Fig. 4.7 Temporal variations in density (± SD) of Chydoridae at main river and floodplain sites. Site name abbreviations are the same as those in Table 2.3.

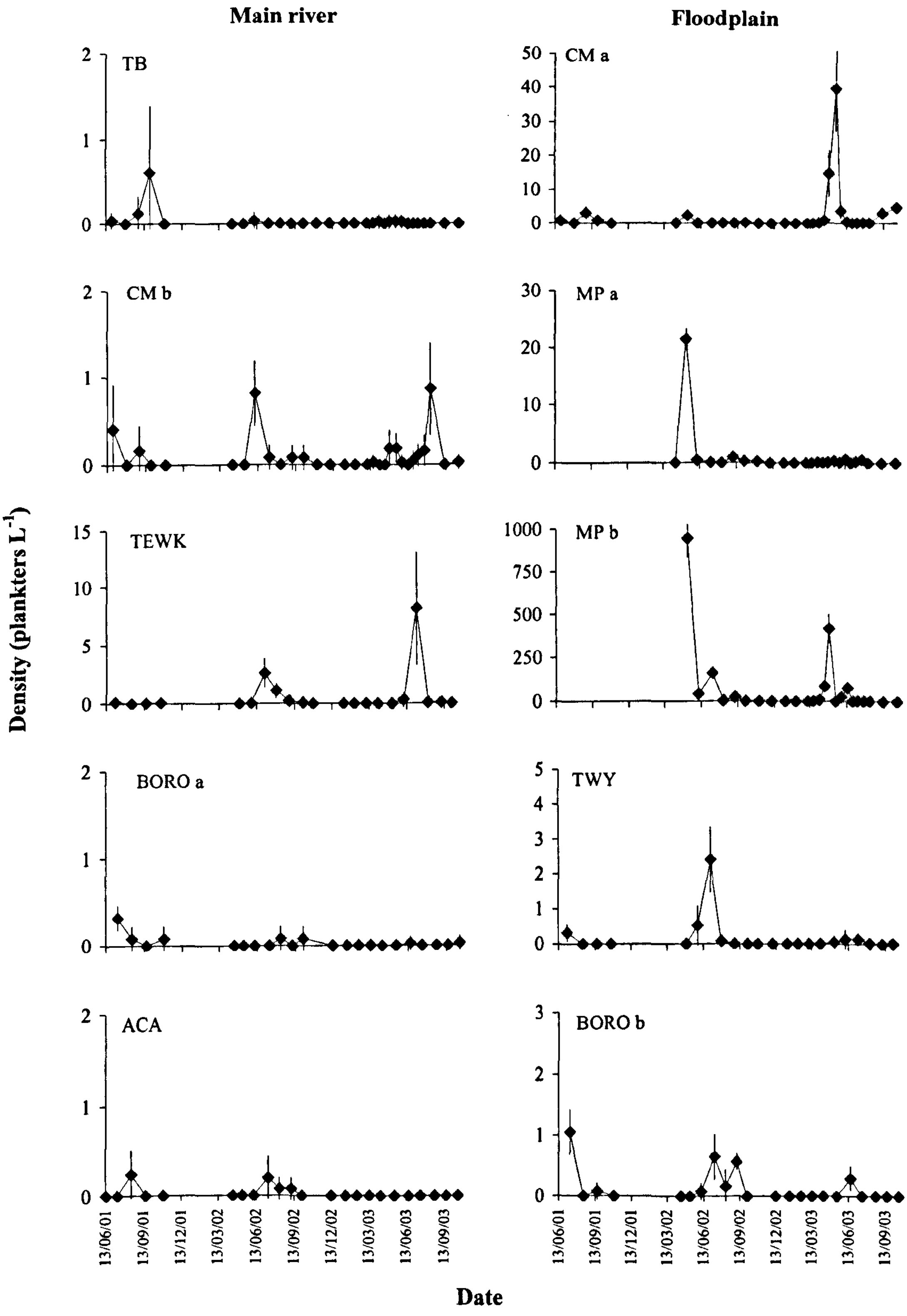


Fig. 4.8 Temporal variations in density (± SD) of Daphniidae at main river and floodplain sites. Site name abbreviations are the same as those in Table 2.3.

Notwithstanding, densities rapidly declined after the initial peak and remained low until the following year. Densities of daphnids at main river sites never exceeded 10 L^{-1}, and were less than 1 L^{-1} on average (Figs 4.4, 4.8). Daphnids attained substantially higher densities at floodplain sites, with a maximum of over 900 L^{-1} at Marina Pond. Mean densities at floodplain sites ranged between <1 (Boroughbridge) and 76 L^{-1} (Marina Pond).

4.3.3.5 *Copepod nauplii*

Peak densities of copepod nauplii usually occurred in April or May at riverine sites (Fig. 4.9). Fluctuations in abundance in general were more prevalent than for other zooplankton groups, and additional peaks were occasionally observed in late summer (Fig. 4.9). At floodplain sites, peak densities usually occurred in May (Trent and Avon) or June (Ouse), with an additional peak frequently observed in late summer (Fig. 4.9). Densities of copepod nauplii at main river sites never exceeded 3 L^{-1}, and were less than 1 L^{-1} on average (Figs 4.4, 4.9). Copepod nauplii attained substantially higher densities at floodplain sites, with a maximum of over 3250 L^{-1} at Marina Pond. Mean densities at floodplain sites ranged between <1 (Boroughbridge) and 374 L^{-1} (Marina Pond).

4.3.3.6 *Cyclopoida*

At both main river and floodplain sites, cyclopoid copepods followed a similar seasonal pattern of abundance to copepod nauplii, but with a greater amount of variation in the timing of peak densities (Fig. 4.10). Generally there were two main peaks in density, one in the spring and one in late summer. Densities of cyclopoid copepods at main river sites never exceeded 2 L^{-1}, and were less than 1 L^{-1} on average (Figs 4.4, 4.10). Cyclopoid copepods attained substantially higher densities at floodplain sites, with a maximum of over 2350 L^{-1} at Marina Pond. Mean densities at floodplain sites ranged between <1 (Boroughbridge) and 232 L^{-1} (Marina Pond).

4.3.4 Chlorophyll *a* concentration

At the majority of sites and in most years, chlorophyll *a* concentration began to increase around March and peaked in April or May (Fig. 4.11). In addition, there was frequently a second, smaller peak in late summer/early autumn in the Trent, but not in the Avon. Patterns were less easily identified in the Ouse, since sampling could not commence

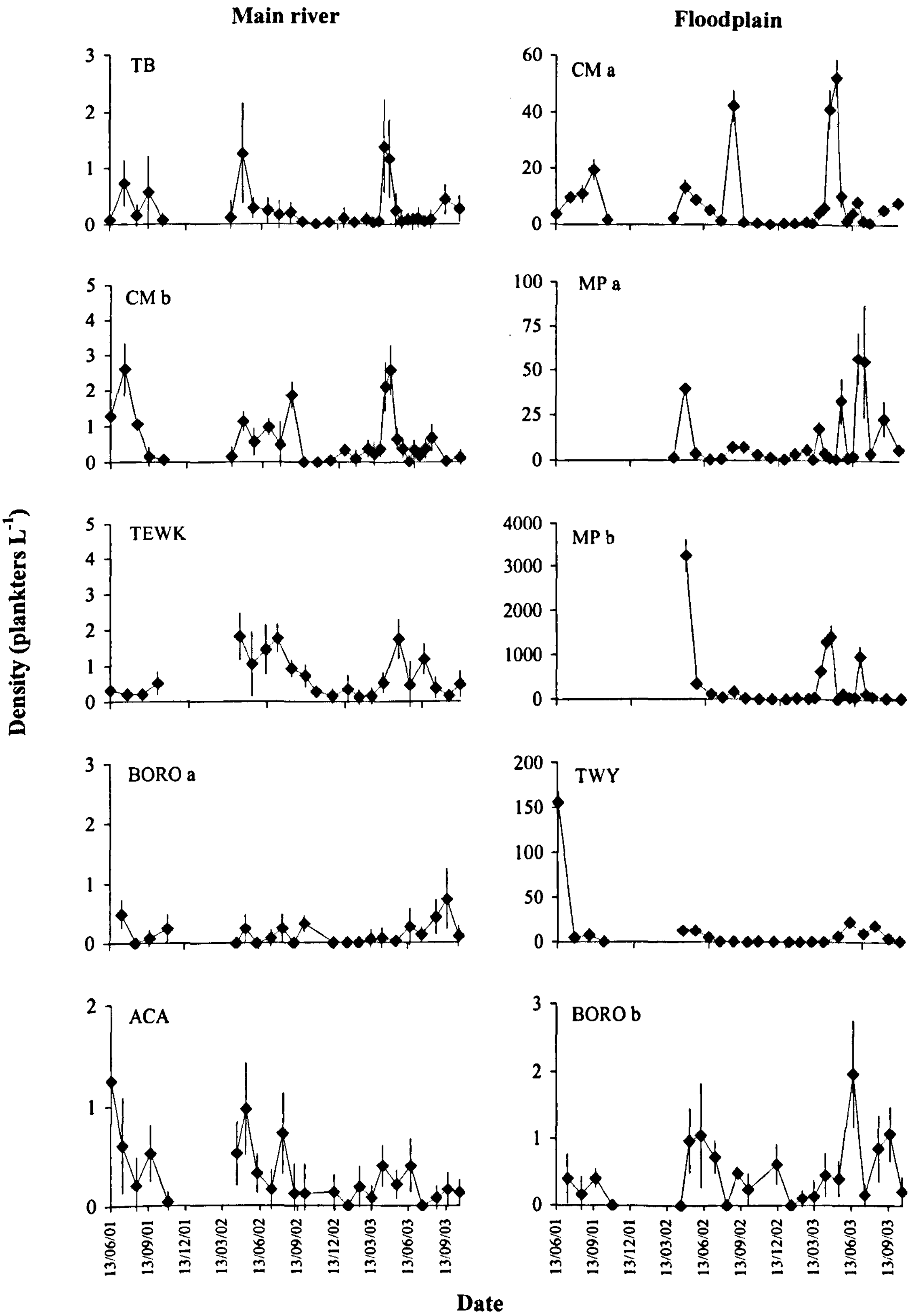


Fig. 4.9 Temporal variations in density (± SD) of copepod nauplii at main river and floodplain sites. Site name abbreviations are the same as those in Table 2.3.

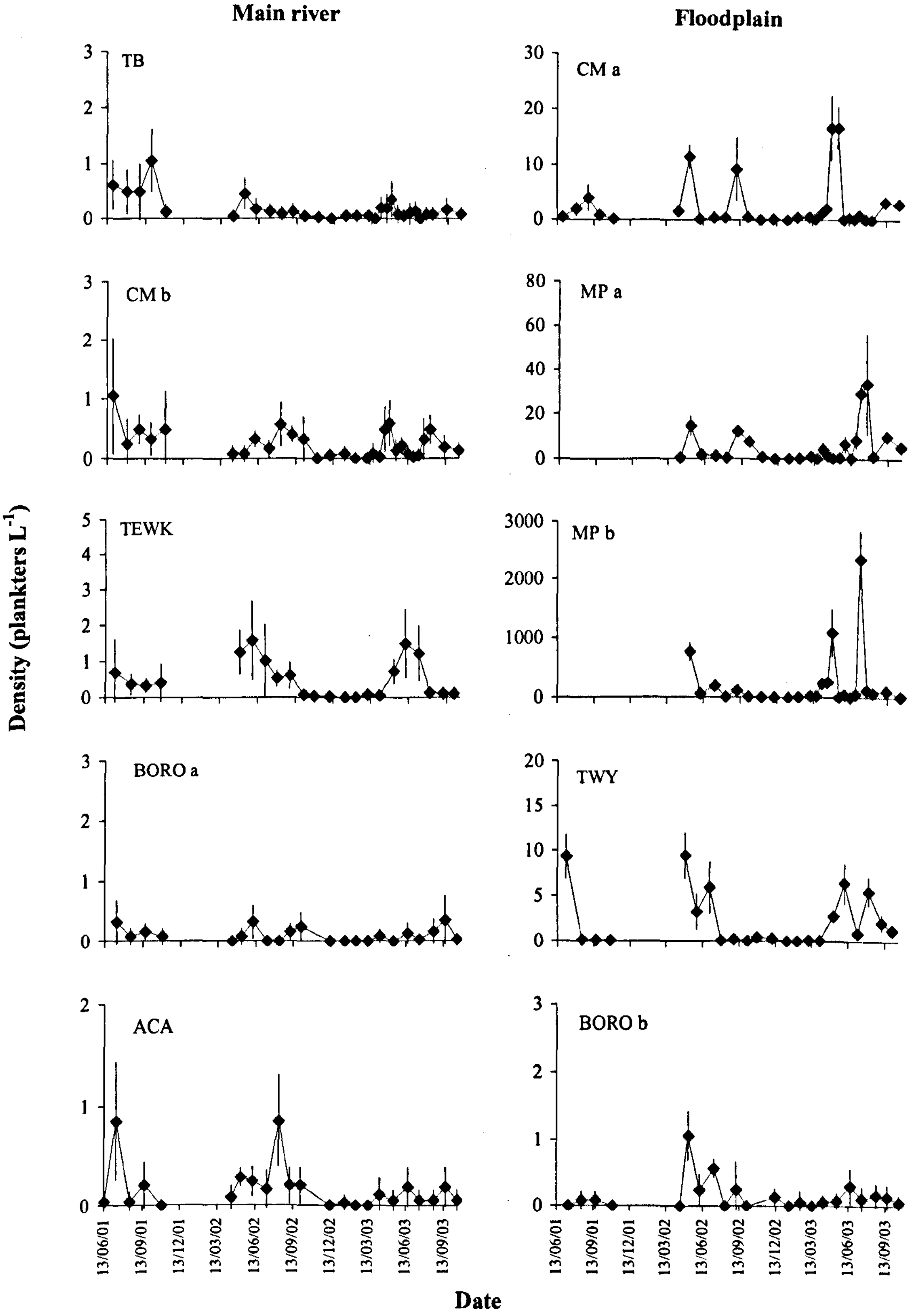


Fig. 4.10 Temporal variations in density (± SD) of Cyclopoida at main river and floodplain sites. Site name abbreviations are the same as those in Table 2.3.

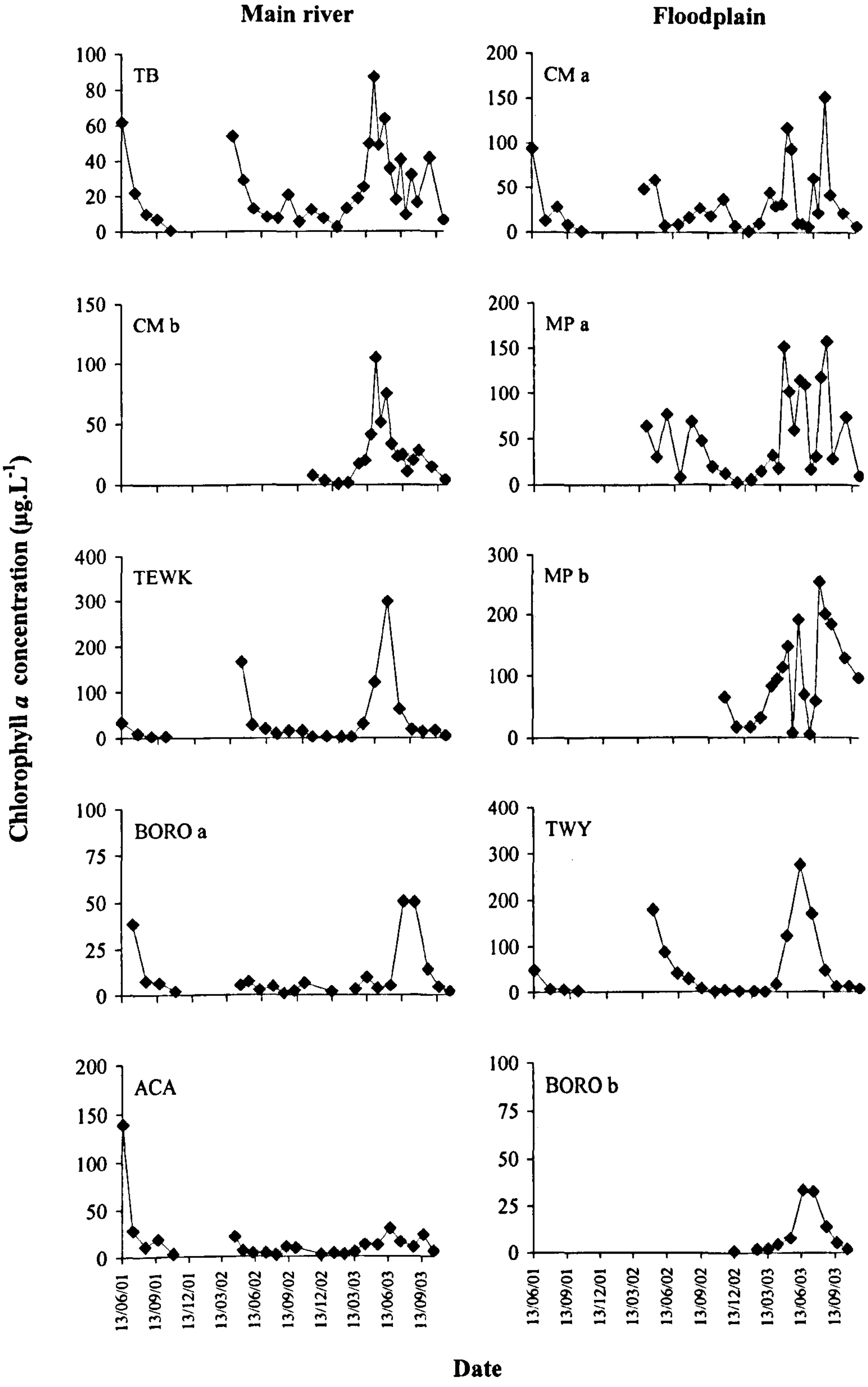


Fig. 4.11 Temporal variations in chlorophyll *a* concentration at main river and floodplain sites. Site name abbreviations are the same as those in Table 2.3.

until June in 2001 due to an outbreak of foot and mouth disease, and because no substantial populations of phytoplankton developed in 2002, probably due to intermittent periods of elevated river discharge. Chlorophyll *a* concentrations peaked in June in 2003, although there was a spate in March and two in May which may have delayed development of phytoplankton populations.

There were considerable spatial differences in chlorophyll *a* concentration. Overall, mean chlorophyll *a* concentration was significantly higher at floodplain sites than at main river sites (Mann-Whitney *U*-Test, $P<0.01$). In the Trent, floodplain sites almost always had higher concentrations of chlorophyll *a* than main river sites (Fig. 4.11). Maximum chlorophyll *a* concentrations in the main river channel at Trent Bridge and Colwick were 87 and 105 $\mu g.L^{-1}$, respectively, compared with 152 in Colwick Marina, and 255 and 158 $\mu g.L^{-1}$ at the pond and transitional sites at Marina Pond (Fig. 4.11).

There was less of a difference between the main channel (Tewkesbury, maximum 298 $\mu g.L^{-1}$) and the floodplain site (Twyford, maximum 275 $\mu g.L^{-1}$) on the Avon (Fig. 4.11), probably partly due to the high degree of connectivity of the latter site with the main river. In addition, this site supports dense beds of aquatic macrophytes (Table 2.2), which may reduce phytoplankton biomass, either directly via competition for nutrients and/or allelopathy or indirectly by virtue of the filter feeding activities of macrophyte-associated invertebrates and shading. There was no significant difference between mean chlorophyll *a* concentration in the main river at Boroughbridge and the adjacent bypass canal (Mann-Whitney *U*-Test, $P>0.05$), although standing stock in general was substantially lower than in the Trent and Avon (Fig. 4.11).

4.3.5 Influence of river discharge on phytoplankton and zooplankton

Development of phytoplankton may be delayed or suppressed by increases in river discharge (Marker & Collett, 1997). Such a situation may have arisen in the Ouse in 2002, where no distinct peak in chlorophyll *a* concentration was observed (Fig. 4.11). Similarly, river discharge can influence zooplankton, both through its impacts on phytoplankton and directly via wash-out. No relationships were found between river discharge and chlorophyll *a* concentration or zooplankton densities (Pearson product-moment correlations, $P>0.05$), partly because sampling was too infrequent, and partly because of the complicating influences of various biotic and abiotic factors (Marker & Collett, 1997).

4.3.6 Relationships between phytoplankton and zooplankton

Concentration of chlorophyll *a* and rotifer density were significantly, positively correlated at all sites (Pearson product-moment correlations, $P<0.05$, Fig. 4.12), with the exception of Marina Pond (floodplain) and Boroughbridge (river) where no significant relationships were found for any of the zooplankton groups. At Marina Pond (transition zone) and Acaster Malbis, an improved relationship was obtained between chlorophyll *a* and density of copepod nauplii, while at Boroughbridge (canal) the best correlation was with density of cladocerans. Relationships were weaker or non-existent for other zooplankton groups, probably because of their ephemeral presence or low densities in the zooplankton.

4.3.7 Relationships between zooplankton and fish

Only two significant relationships were found between zooplankton and fish densities, partly because the time intervals between samples were inevitably longer than the generation times of the key zooplankton taxa. Notwithstanding, 0+ fish density at Colwick Marina was positively correlated with cladoceran density (Pearson product-moment correlations, $P<0.05$), while 0+ fish density at Twyford was negatively correlated with copepod density ($P<0.05$).

4.4 DISCUSSION

4.4.1 Composition of the zooplankton

Riverine zooplankton communities are invariably dominated by rotifers and small crustaceans throughout the year, with no marked development of large-bodied cladoceran and copepod populations (Basu & Pick, 1996; Viroux, 1997; Kim & Joo, 2000; Kim *et al.*, 2001). The dominance of small organisms is often attributed to the selective predation of large zooplankton by fish, and the short generation times of smaller organisms which allow their *in situ* reproduction, in spite of short water residence times (Pourriot *et al.*, 1997; Jack & Thorp, 2002). Areas of reduced flow, either within the main river channel or in backwaters, exert a considerable influence on riverine plankton dynamics (Spaink *et al.*, 1998). Such areas, owing to increased water

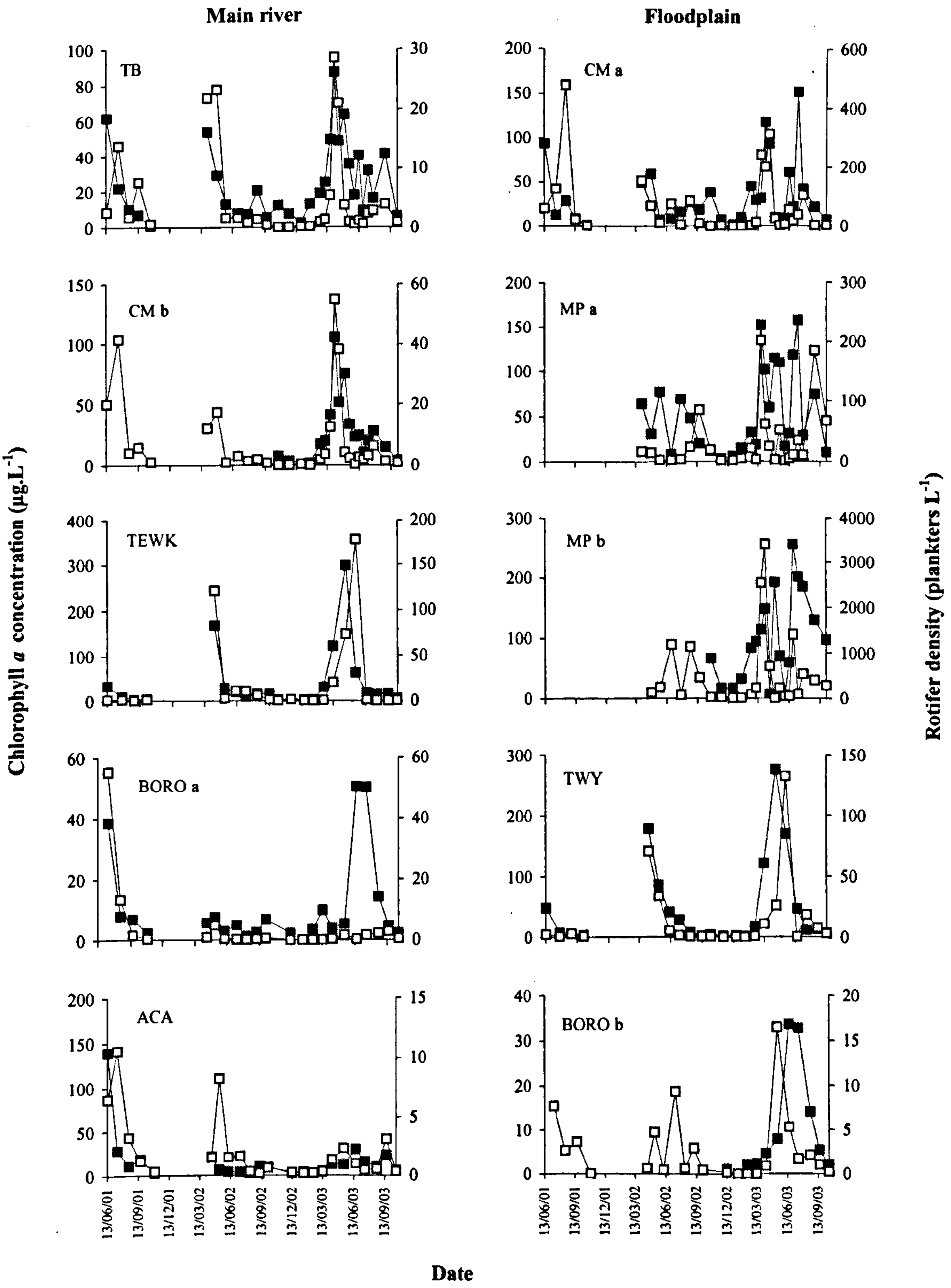


Fig. 4.12 Relationship between chlorophyll *a* concentration (filled bars) and Rotifera density (clear bars) at main river and floodplain sites. Site name abbreviations are the same as those in Table 2.3.

retention time, frequently provide superior conditions for plankton development than main river channels, and are important sources of drifting material which may, under suitable conditions, colonise the main river channels (Bass *et al.*, 1997a; Walks & Cyr, 2004).

In addition to increased water retention time, floodplain waterbodies frequently support substantial populations of aquatic macrophytes (van Geest *et al.*, 2003), which provide habitat for phytophilic zooplankton (Garner *et al.*, 1996; Bass *et al.*, 1997b; Scheffer, 1999; Nurminen *et al.*, 2001; Balayla & Moss, 2003, 2004) and refuge for planktonic species from fish predation (Schriver *et al.*, 1995; Stansfield *et al.*, 1997; Bertolo *et al.*, 1999; Perrow *et al.*, 1999; Burks *et al.*, 2001). Furthermore, plants invariably support larger numbers of animals, greater ranges of body size and greater numbers of species than areas of open water (Northcott, 1979; Whiteside *et al.*, 1985). In the current study, main river sites were characterised by an overwhelming dominance of rotifers, with other taxa such as cyclopoid copepods, copepod nauplii and small cladocerans (e.g. *Bosmina*, *Alona* and *Chydorus* spp.) also frequently present in small numbers. Floodplain sites were also dominated by rotifers, but zooplankton composition differed markedly from main river sites due to a greater richness of cladoceran taxa. Most floodplain sites, especially Colwick Marina, were characterised by a range of planktonic and non-planktonic cladoceran species which were most abundant in close proximity to aquatic vegetation (*pers. obs.*) and were important in the diets of 0+ fish (Chapter 5). In contrast, Marina Pond was characterised by planktonic copepods and cladocerans, such as *Bosmina* and *Daphnia* spp. Non-planktonic species were comparatively rare, probably due largely to the lack of macrophytes at this site.

4.4.2 Density of zooplankton

Zooplankton populations exhibit seasonal cycles in abundance, with peak densities frequently occurring during spring and early summer, followed by population 'crashes' in mid summer (Hülsmann & Mehner, 1997; Mehner *et al.*, 1998b; Hülsmann *et al.*, 1999; Benndorf *et al.*, 2001; Voigt & Hülsmann, 2001; Hülsmann, 2003; Wagner *et al.*, 2004). In the current study, for example, there was a shift in dominance from *Daphnia* spp. to cyclopoid copepods and/or *Bosmina* at Marina Pond each summer. Reasons mooted for the initiation of such population declines include predation by fish (especially 0+) (Gliwicz, 1994; Ślusarczyk, 1997; Mehner & Thiel, 1999), predation by invertebrates (Hoffman *et al.*, 2001; Riccardi *et al.*, 2002; Liljendahl-Nurminen *et al.*, 2003; Wojtal *et al.*, 2004), starvation (Gliwicz, 1985) or combinations of factors.

Studying the River Great Ouse, Bass *et al.* (1997a) found maximum rotifer densities were usually around 2000 to 3000 L^{-1}, but observed a peak of over 15 000 L^{-1} in one year. Copepods were recorded at consistently lower densities (maxima, 20 to 125 L^{-1}), while cladocerans never exceeded 10 L^{-1}. Similarly, Lair & Reyes-Marchant (1997) recorded peak rotifer densities of 5800 L^{-1}, while May & Bass (1998) found densities up to 4160 L^{-1} in the River Thames. In the current study, rotifer densities at main river sites never exceeded 200 L^{-1}, compared with a maximum of over 3400 L^{-1} at floodplain sites. These are underestimates of total rotifer abundance, however, because of the large mesh size (100 μm) of the zooplankton trawl (Bottrell *et al.*, 1976; Bass *et al.*, 1997a). Notwithstanding, the difference in rotifer densities between main river and floodplain sites is readily apparent.

Bass *et al.* (1997a) found that whilst zooplankton populations declined after mid summer in the main river, in an adjacent marina high populations of rotifers and microcrustaceans persisted later into the year. In the current study, mean densities of all zooplankton groups were significantly higher at floodplain sites than in the main river channels. Daphnids, for example, were recorded at maximum densities of over 900 L^{-1} at floodplain sites, compared with <10 L^{-1} in main river channels. This is in agreement with Spaink *et al.* (1998) who found that the total zooplankton biovolume in a backwater was over 100 times higher than in the main river channel. Similar results were obtained by Tans *et al.* (1998) and Aoyagui & Bonecker (2004).

The explanation for the exceptional densities of zooplankton at Marina Pond compared with Colwick Marina may partly be due to differences in hydrological regime. Marina Pond is influenced by the adjacent River Trent, with water usually either flowing in or out of the pond. In contrast, water movement in and out of Colwick Marina is less obvious due to its wider and deeper connection with the river, and its location upstream of some sluice gates. Timms & Moss (1984), Moss & Balls (1989) and Moss *et al.* (1991) found that waterbodies characterised by high flushing rates favour small and rapidly growing phytoplankters, rather than colonial forms. Small phytoplankters are much more readily ingested by zooplankton, compared with colonial and filamentous taxa that impede feeding activity and blue-green algae that may produce toxins (Gliwicz & Siedlar, 1980; Gliwicz & Lampert, 1990). Although no specific microscopic studies of the composition of the phytoplankton were undertaken, a difference was observed when processing zooplankton samples between the phytoplankton communities of the two waterbodies. Between March and April each year, Colwick Marina was characterised by *Tabellaria* spp. and solitary diatoms (Bacillariophyta), after which taxa such as *Pediastrum*, *Closterium*, *Eudorina* (Chlorophyta) and *Surirella* spp. (Bacillariophyta) appeared. From July to September, the blue-green algae *Microcystis* and *Oscillatoria* spp. (Cyanophyta) dominated the plankton, indicative of stable conditions (Jacoby *et al.*, 2000). In contrast, very few algae were found in Marina Pond zooplankton samples, despite the high chlorophyll *a* concentrations, suggesting that the phytoplankton was dominated by taxa that were too small to be retained in the zooplankton net. Thus, despite there being comparable biomasses of phytoplankton at Colwick Marina and Marina Pond, greater densities of zooplankton may have been supported at the latter site by virtue of a dominance of small, coccal phytoplankters over colonial and filamentous forms.

4.4.3 Phytoplankton biomass

The size of riverine phytoplankton populations is determined by the differential rates of production, controlled by temperature, light and concentration of inorganic nutrients, and loss resulting from grazing, sedimentation, respiration and hydraulic flushing (Skidmore *et al.*, 1998). In the current study, chlorophyll *a* concentrations began to increase around March and peaked in April or May, with maximum concentrations in the Trent and Ouse corresponding closely with the findings of Pinder *et al.* (1997b), Skidmore *et al.* (1998) and Uncles *et al.* (1998). Phytoplankton biomass then fell dramatically and remained comparatively low until the following spring. In the Trent and Ouse, the spring bloom is usually dominated by diatoms (especially *Cyclotella* and *Stephanodiscus* spp.), while any late summer peaks are usually of Chlorophyceae and Cyanophyta (Skidmore *et al.*, 1998).

In contrast with the main channel of the River Great Ouse, Marker & Collett (1997) observed that the crash in phytoplankton biomass did not occur in an adjacent marina, where high chlorophyll concentrations occurred in mid to late summer. A similar situation was observed in this study, with phytoplankton biomass at floodplain waterbodies fluctuating around means that were substantially higher than main river sites. Although standing crop of phytoplankton does not necessarily equate to production or turnover rate, the high biomass of phytoplankton at floodplain sites compared with the main river channels is reflected in the higher zooplankton densities (Section 4.4.2).

4.4.4 Influence of river discharge on phytoplankton and zooplankton

The hydrology of a river is a key factor in controlling the extent and timing of phytoplankton and, hence, zooplankton populations (Ferrari *et al.*, 1989; Pace *et al.*, 1992; van Dijk & van Zanten, 1995; Basu & Pick, 1996; Kobayashi *et al.*, 1998a, b; Tans *et al.*, 1998; Ietswaart *et al.*, 1999; Kim & Joo, 2000; Reynolds, 2000; Speas, 2000; Kim *et al.*, 2001; Viroux, 1999, 2002; Leland, 2003; Limberger *et al.*, 2004). Retention zones play an important role in the development of potamoplankton (Lair & Reyes-Marchant, 1997; Keckeis *et al.*, 2003), with such areas promoting faster population growth of phytoplankton (Reynolds *et al.*, 1991; Marker & Collett, 1997) and zooplankton (Reckendorfer *et al.*, 1999; Baranyi *et al.*, 2002) than main river channels.

In the current study, no relationships were found between river discharge and phytoplankton biomass or zooplankton density. As illustrated above (Section 4.4.2), the influence of hydrology on phytoplankton and zooplankton can be subtle, and it is likely that the influences of various biotic (predation, disease, starvation) and abiotic (light, temperature, nutrients) factors complicate matters. For example, Marker & Collett (1997) noted that, in the River Great Ouse, peaks in phytoplankton biomass frequently occurred during periods of relatively high discharge (in the spring), and that the crash of phytoplankton populations occurred despite seemingly good or better conditions in the summer (i.e. increased retention time, lower turbidity). They (*ibid.*) therefore postulated that either the specific growth rates of the phytoplankton were lower in the summer than the spring, or the loss processes (wash-out, sedimentation, grazing) were greater.

4.4.5 Relationships between phytoplankton and zooplankton

The relationships between phytoplankton and zooplankton have been studied extensively, especially in still waters (e.g. Timms & Moss, 1984; Lampert *et al.*, 1986; Kerfoot *et al.*, 1988; Grigorszky *et al.*, 1989; Bothár & Kiss, 1990; Dawidowicz, 1990;

Gosselain *et al.*, 1994, 1998a, b; Beklioğlu & Moss, 1995, 1996; Fussman, 1996; George & Reynolds, 1997; Gasiūnaitė & Olenina, 1998; Sarvala *et al.*, 1998; Kim *et al.*, 2000; Wilk-Woźniak *et al.*, 2001; Talling, 2003; Tõnno *et al.*, 2003). According to the size-efficiency hypothesis (Brooks & Dodson, 1965), large-bodied zooplankters are more efficient grazers of phytoplankton than smaller-bodied species and, in the absence of severe predation, dominate the zooplankton. Grazing by zooplankton may influence phytoplankton communities in terms of both biomass and species composition (Irvine *et al.*, 1989; Schriver *et al.*, 1995). The algal groups that are generally reduced by zooplankton grazing are small, coccal forms, and their suppression allows larger, slower growing taxa to develop. Where filamentous or colonial algae are abundant, small zooplankters frequently dominate the plankton due to mechanical interference of feeding activity of larger zooplankters.

Many studies have reported positive relationships between phytoplankton biomass and zooplankton (especially rotifer) density (e.g. van Dijk & van Zanten, 1995; Bass *et al.*, 1997a; Lair & Reyes-Marchant, 1997; Kobayashi *et al.*, 1998a, b; May & Bass, 1998). The present study corroborates this observation. The positive relationship between rotifer density and phytoplankton biomass is likely a consequence of the relatively short generation times of rotifers which allow them to adapt to rapidly-changing food conditions. Moreover, this suggests either that phytoplankton turnover rate exceeds rates of loss by grazing, or that grazing by rotifers is of only minor importance with respect to the dynamics of algal communities (Vakkilainen *et al.*, 2004).

The large-bodied crustaceans identified as the key grazers of phytoplankton in still waters are rarely abundant in rivers. In the present study, relationships between phytoplankton biomass and density of cladocerans were weak or non-existent, even at floodplain sites, partly due to the ephemeral presence and low densities of cladocerans in the zooplankton. Similarly, few other studies have identified significant relationships between phytoplankton and crustaceans in rivers, although unionid and dreissenid mussels may be important grazers (Basu & Pick, 1997; Welker & Walz, 1999; Descy *et al.*, 2003; Thorp & Casper, 2003).

4.4.6 Relationships between zooplankton and fish

It has long been recognised that planktivorous fish are a major factor influencing the species and size composition of zooplankton in freshwater ecosystems (e.g. Hrbáček *et al.*, 1961; Brooks & Dodson, 1965; Bohl, 1982; Mills & Forney, 1983; Vanni, 1986, 1987; Post & McQueen, 1987; Whiteside, 1988; Salo *et al.*, 1989; Luecke *et al.*, 1990; Mehner *et al.*, 1995, 1996, 1997; Mehner, 1996, 2000; Dettmers & Stein, 1996; Jeppesen *et al.*, 1996, 2004; Kurmayer & Wanzenböck, 1996; Korponai *et al.*, 1997; Post & Kitchell, 1997; Węgleńska *et al.*, 1997; Kubečka *et al.*, 1998; Moss *et al.*, 1998; Bergman & Bergstrand, 1999; Chappaz *et al.*, 1999; Romare & Bergman, 1999; Romare *et al.*, 1999, 2003; Declerck & De Meester, 2003; Vašek *et al.*, 2003; Chang *et al.*, 2004; Hansson *et al.*, 2004; Mátyás *et al.*, 2004; Vašek & Kubečka, 2004). Phenomena frequently attributed to heavy fish predation include suppressed zooplankton biomass, small individual size of plankters, and reduced representation of vulnerable (typically larger) species (Cryer *et al.*, 1986). Selection for large species and individuals by fish can therefore cause a shift in the species composition of the cladoceran community, as well as a reduction in the mean size of individuals of large species and in the assemblage as a whole (Perrow & Irvine, 1992).

The midsummer decline of large cladocerans (especially *Daphnia* spp.) has frequently been attributed to strong predation by newly hatched fish in June and July (Mills & Forney, 1983; Cryer *et al.*, 1986; Whiteside, 1988). In the current study, however, very few significant relationships were found between densities of zooplankton and 0+ fish. Indeed, the population crashes of *Daphnia* spp. each year occurred before the majority of 0+ fish had hatched, and certainly before they were capable of ingesting such prey (see Chapter 5). Furthermore, the time intervals between surveys were inevitably longer than the generation times of many of the key zooplankton taxa, such that the impacts of any population fluctuations caused by fish predation may have been missed in subsequent surveys. Fish larvae are now thought to exert only minor impacts on small zooplankton such as rotifers, copepodids and cladocerans (Mehner & Thiel, 1999). In contrast, 0+ juveniles have the potential to depress populations of large cladocerans and copepods, especially during late summer and autumn. Cryer *et al.* (1986), for example, observed that in years when 0+ roach were abundant, the summer zooplankton became sparse and was dominated by copepods and rotifers, with cladocerans being very much reduced in density. Moreover, a number of studies (e.g. Cryer *et al.*, 1986; Perrow &

Irvine, 1992; Dettmers & Wahl, 1999) have demonstrated a causal link between fish recruitment and zooplankton dynamics, with abundant 0+ fish sometimes showing poor growth as a result of depression of their prey populations.

Apart from the direct (lethal) impacts of fish predation on zooplankton demography, indirect impacts may also occur via shifts in life history (e.g. changes in birth rates, fecundity, size and age at maturity, a switch from parthenogenetic to sexual reproduction, diapause), morphology (e.g. cyclomorphosis) or behaviour (e.g. diel vertical and horizontal migration). Although such changes may be induced in the absence of fish by changes in temperature, turbulence and starvation, fish kairomones produce similar responses (Stibor & Luning, 1994; Pijanowska & Stolpe, 1996; Ślusarczyk, 1997; Hanazato *et al.*, 2001; Hülsmann *et al.*, 2004). Shifts in life history in particular may mask the impacts of fish predation. Gliwicz (2001) and Gliwicz *et al.* (2004), for example, found that the species-specific density level of particular zooplankton did not depend upon reproduction rate, since neither increased birth rates nor reproductive effort coincided with an increase in population density; a clear indication that larger numbers of prey were being harvested by fish at the time of increased reproduction. Furthermore, fish may select ephippial or egg-bearing females, due to their increased visibility compared with non-ephippial and non-egg-bearing individuals, and thereby influence zooplankton recruitment potential. For example, Gliwicz *et al.* (2004) revealed strong selection by smelt (*Osmerus eperlanus* (L.)) for later instars and females with greater clutches of *Daphnia* spp. and *Bosmina* sp.

The impacts of fish predation on zooplankton may therefore be both direct and indirect. Large-bodied cladocerans are generally not abundant in rivers, and so the impacts of fish predation upon them are not easily observed. Notwithstanding, the high densities of large-bodied cladocerans at floodplain sites compared with main river channels, combined with the presence of substantial populations of 0+ fish (Chapter 3) and the importance of cladocerans in their diets (Chapter 5), suggests that floodplain waterbodies may enhance recruitment of riverine fish populations.

CHAPTER FIVE

THE FOOD AND FEEDING RELATIONSHIPS OF LARVAL AND 0+ JUVENILE FISH IN LOWLAND RIVERS AND FLOODPLAIN WATERBODIES

5.1 INTRODUCTION

Feeding success during the first weeks of life is critical in determining survival and ultimate year-class strength of fishes (DeVries *et al.*, 1998), with the transition to exogenous feeding the decisive threshold (Balon, 1984). Larval fish can be highly susceptible to fluctuations in prey availability (Hoxmeier *et al.*, 2004), and knowledge of how such fluctuations influence growth and survival of larval fish is imperative to understand recruitment processes (Welker *et al.*, 1994). Many fish species are zooplanktivorous at the onset of exogenous feeding (Whiteside *et al.*, 1985; Wanzenböck & Schiemer, 1989; Mehner & Winfield, 1997; Mehner & Thiel, 1999), and the growth, survival and, ultimately, recruitment of such fish during their early life history is often strongly linked with zooplankton availability (Miller *et al.*, 1988; Schiemer *et al.*, 1989; Mann, 1997; Mann *et al.*, 1997; Graeb *et al.*, 2004). Early in fish ontogeny, food intake may be strictly governed by morphological and behavioural constraints (Mark *et al.*, 1987; Bremigan & Stein, 1994). Food particles must therefore be available in both sufficient quantity and the correct size (Mills & Mann, 1985; Bass *et al.*, 1997a; King, 2004a), with a decline in abundance of appropriately-sized prey potentially causing either slow growth or starvation (Hoxmeier *et al.*, 2004).

The food and feeding relationships of adult fish have been investigated extensively (e.g. Frost, 1943, 1950; Hartley, 1948; Thomas, 1962; Maitland, 1965; Mann & Orr, 1969; Hellawell, 1971, 1972, 1974; Mann, 1973, 1974, 1976; Bohl, 1980, 1982; Haberlehner, 1988; Specziár *et al.*, 1997, 1998; García-Berthou, 1999, 2001b). However, fewer studies have examined the food and, particularly, the feeding relationships of larval and 0+ juvenile fish in lowland rivers. To date, most studies have been conducted in lakes and reservoirs in the USA on centrarchid, percid, coregonid and clupeid species. With the notable exception of Garner (1996a, b, 1998), there have been few comprehensive studies of the ontogenetic aspects of 0+ fish community feeding ecology in lowland rivers, and few have addressed the complex relationships between 0+ fish and their prey, or the function of floodplain waterbodies with respect to the abundance and diversity of food resources.

The aim of this chapter was to investigate the food and feeding relationships of larval and 0+ juvenile fish in the lower reaches and floodplain waterbodies of the River Trent. Specifically, the objectives were to investigate: (1) the diet composition of each of the fish species from three contrasting macrohabitats and identify ontogenetic shifts in resource use; (2) ontogenetic, interspecific and spatial differences in diversity and evenness of the diet; (3) synchronous and non-synchronous, intra- and interspecific similarities in diet composition; (4) the relative importance of taxa- and size-specific prey selection; and (5) the influence of fish gape size on the sizes of prey consumed. The hypothesis was that level of development would be the key factor influencing initial diet spectra, with differences in food availability and species-specific traits increasing in importance with development.

5.2 MATERIALS AND METHODS

5.2.1 Introduction

According to the theory of saltatory ontogeny, during their first year of life, fishes with indirect development (i.e. those with a larval period) pass through a sequence of developmental steps characterised by biochemical, physiological, morphological, ethological and ecological traits that result in important shifts in resource use (Balon, 1975b, 1979, 1984, 1999). With respect to the foraging ability of 0+ fish, the key attributes are those pertaining to enhanced swimming performance, namely development of the fins, and improved vision (Wanzenböck & Schiemer, 1989). Once fins are fully developed, associated improvements in manoeuvrability allow a broadening and diversification of diet spectra due to an increased ability to capture more agile and evasive prey. Similarly, improved vision increases the search volumes of 0+ fish, effectively increasing prey availability (Schiemer *et al.*, 1989; Wanzenböck & Schiemer, 1989; Keckeis & Schiemer, 1990, 1992; Flore *et al.*, 2000; Gliwicz, 2001). It can be misleading to classify 0+ fish based solely on length, because individuals of similar length may display great differences in development (Balinsky, 1948, *fide* Copp, 1990b). For this reason, fish were separated into a series of categories based upon development rather than size. The key characteristics of the seven developmental steps are as follows (Tong, 1986; Copp, 1990c; Gozlan *et al.*, 1999; Peňáz, 2001):

Larval step 1 (L1) begins at the onset of exogenous feeding, and is characterised by a reduction of the yolk sac, a straight notochord, a rudiment of a swim bladder in percids, a single gas-filled chamber in the swim bladder of cyprinids, and development of objective vision and vaguely defined anal, dorsal and caudal finfolds.

Larval step 2 (L2) commences upon complete resorption of the yolk (transition to exclusively exogenous feeding), and is characterised by ossification of the vertebral bodies, further differentiation of the finfolds, a terminal closable mouth, increased diameter of the intestine, filling of the swim bladder in percids, and enlargement of the swim bladder in cyprinids.

Larval step 3 (L3) begins with development of the hypurals and mesenchymal lepidotrichia formation in the dorsal and anal finfolds, and is characterised by the posterior end of the notochord bending upwards at an obtuse angle, continued differentiation of the finfolds, formation of the first rays in the slightly heterocercal caudal fin, and the appearance of teeth in the jaws of percids.

Larval step 4 (L4) is characterised by the posterior end of the notochord bending sharply upwards so that the hypurals and caudal fin rays point backwards, ossification of the caudal fin rays, appearance of rays in the dorsal and anal finfolds, anlagen of pelvic fins, a two-chambered swim bladder in cyprinids, and development of the upper field of vision.

Larval step 5 (L5) is characterised by ossification of the rays of the dorsal and anal fins, formation of mesenchymal rays in the pectoral and pelvic fins, pelvic fins nearing the edge of the preanal finfold, and a deeply incised caudal fin which changes from trilobate to homocercal.

Larval step 6 (L6) is characterised by full development of rays in all fins, atrophy of the preanal finfold such that the pelvic fins of cyprinids surpass its margin, a marked increase in intestine length and development of the first pair of intestinal loops, and flexion of the myomeres into a zigzag formation.

The juvenile period (J) begins with disappearance of any remnants of the preanal finfold, complete differentiation of the fins, bifurcation of most fin rays, differentiation of the nasal orifice and the onset of squamation.

5.2.2 The food of larval and 0+ juvenile fish

To permit comparisons with food availability, analyses of the food and feeding relationships of larval and 0+ juvenile fish were carried out at sites where the zooplankton was investigated (Chapter 4), namely Trent Bridge, Colwick Marina and Marina Pond; hereafter referred to as the 'main river', 'marina' and 'pond' macrohabitats, respectively. Fish used in diet analyses were captured by seine netting as described in Chapter 2, between April and October 2003 inclusive, and fixed in 4% formalin. Additional samples of the smallest larvae were collected using a hand-net. In the laboratory, fish were identified to species (Pinder, 2001) and developmental step (Tong, 1986; Copp, 1990c; Gozlan *et al.*, 1999; Peňáz, 2001), and measured for standard length (nearest 0.1 mm). Maximum gape height was measured (nearest 0.1 mm) for each fish by fully opening the mouth with a pair of watchmaker's forceps, and measuring the maximum dorsoventral gape from the anterior-most tip of the premaxilla to the anterior-most tip of the mandible using a binocular microscope equipped with a stage micrometer.

For each sampling occasion, the contents of the entire gastrointestinal tract were removed from up to ten representatives of each developmental step of each species, from each site. Discrete food items were identified to the highest practicable taxonomic level using various keys (e.g. Scourfield & Harding, 1966; Fitter & Manuel, 1986) and enumerated. Cladocerans, for example, were identified to either species or genus, while other taxa were typically identified to lower levels of taxonomic resolution. Numerical data were considered more appropriate than weight and volume data, since 0+ fish are largely zooplanktivorous and consume their prey whole. Furthermore, numerical data are not influenced by stage of digestion, unlike weight or volume data. Aufwuchs (the amorphous organic matrix often covering underwater surfaces) and associated meiofauna (e.g. bryozoan statoblasts, testate amoebae) was recorded as percent volume and converted to 'number' using the relationship between percent volume of aufwuchs and the number and percent volume of 'non-aufwuchs':

$$N_{aufwuchs} = \frac{N_{non\text{-}aufwuchs}}{V_{non\text{-}aufwuchs}} \times V_{aufwuchs} \tag{5.1}$$

where N and V are the number and percent volume, respectively, of aufwuchs and non-aufwuchs in each fish.

This method was considered more satisfactory than those reported in the literature where aufwuchs and algae were assigned an index (typically between 0 and 3) based upon their contribution to the diet (e.g. Garner, 1996b; Garner *et al.*, 1996; Mann *et al.*, 1997), since such indices are precluded from any subsequent calculations without prior standardisation of the data sets. Simply disregarding these food categories, as condoned by some authors, is similarly unsatisfactory due to their high importance in the diets of some fish.

Dietary data were used to calculate frequency of occurrence, relative abundance and prey-specific abundance (Hynes, 1950; Windell & Bowen, 1978; Hyslop, 1980; Bowen, 1983; Mohan & Sankaran, 1988; Amundsen *et al.*, 1996). The frequency of occurrence of a given prey type is defined as the number of fish in which that prey occurs, expressed as a frequency of the total number of fish in which prey are present. The relative abundance of a given prey type is defined as the percentage of total gut contents (numbers) in all fish comprised by that given prey. The prey-specific abundance is defined as the percentage a prey taxon comprises of all prey items in only those fish in which the particular prey occurs. In mathematical terms, frequency of occurrence ($\%F_i$), relative abundance ($\%A_i$) and prey-specific abundance ($\%P_i$) of prey type i can be described by:

$$\%F_i = \frac{N_i}{N} \times 100 \tag{5.2}$$

$$\%A_i = \frac{\sum S_i}{\sum S_t} \times 100 \tag{5.3}$$

$$\%P_i = \frac{\sum S_i}{\sum S_{ti}} \times 100 \tag{5.4}$$

where N_i is the number of fish that have eaten prey type i, N is the total number of fish that have eaten prey of any type, S_i is the gut content (number) composed by prey i, S_t is the total gut content of all guts in the entire sample, and S_{ti} is the total gut content in only those fish that have eaten prey type i (Amundsen *et al.*, 1996).

The Costello (1990) method, as modified by Amundsen *et al.* (1996), combines prey-specific abundance and frequency of occurrence, and allows prey importance, feeding strategy and the inter- and intra-individual components of niche width to be explored (Fig. 5.1). Percent abundance, increasing along the diagonal from the lower left to the upper right corner, provides a measure of prey importance, with dominant prey at the upper, and rare or unimportant prey at the lower end. The feeding strategy of the fish in terms of specialisation or generalisation is represented by the vertical axis. Fish specialised on prey positioned in the upper part of the graph, whereas prey positioned in the lower part were eaten less frequently. Prey points located at the upper left of the diagram indicate specialisation by individual fish (high between-phenotype component, BPC), and those in the upper right represent specialisation of the fish population. Prey points located in the lower right corner represent those that have been eaten by most fish but in only small numbers (high within-phenotype component, WPC). The sum of the between- and within-phenotype components combines to form the total niche width (Giller, 1984, *fide* Amundsen *et al.*, 1996). In the present study, plots were produced for each developmental step of each species, from each site.

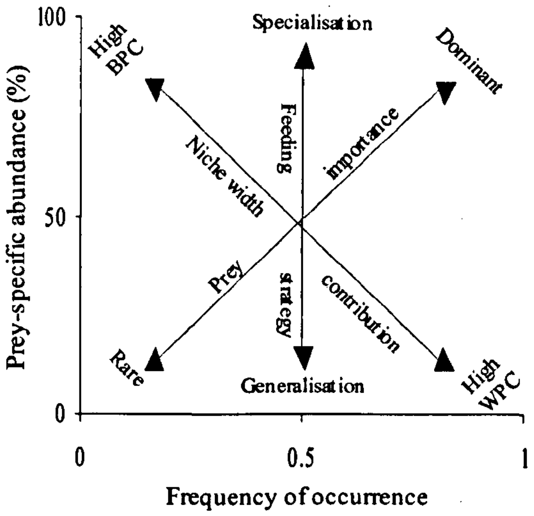


Fig. 5.1 Explanatory diagram for interpretation of feeding strategy, niche width contribution and prey importance (see text for details).

5.2.3 Diversity and evenness of the diet

Ontogenetic, interspecific and spatial variations in diversity and evenness of the diet were investigated by applying the Shannon-Wiener diversity index (*H'*) and Pielou's evenness index (*J*), respectively, to each developmental step of each fish species, from each site. The merits of these indices are detailed in Chapter 3 (Section 3.2.2.4).

5.2.4 Intra- and interspecific diet similarity

Fish can sometimes be grouped as functional guilds or 'ecospecies' on the basis of their morphology and behaviour (Copp, 1990c). Garner (1996b) grouped cyprinids in larval steps L1-L3 as young larvae and those in steps L4-L6 as old larvae, representing the transition from 'finfold' to 'finformed' larvae (Balon, 1999), while 0+ juveniles were grouped as a third ecospecies. In the current study, similarity of diet within and between species was investigated using the Bray-Curtis (1957; syn. Czekanowski, 1913) similarity index in PRIMER (version 5.2). The merits of this index are detailed in Chapter 3 (Section 3.2.2.3). Bray-Curtis similarity matrices were calculated using percent abundance data (Section 3.2.2.1) and presented as dendrograms using hierarchical agglomerative clustering (group average linkage) to investigate synchronous and non-synchronous, intra- and interspecific similarities in diet composition, and to ascertain whether the transition from finfold to finformed larvae, and from the larval to the juvenile period coincided with shifts in the diet.

5.2.5 Selection

The diet of freshwater fish in their first few weeks of life can include both an increase in prey size and changes in prey species as the fish grow and develop (Ghan & Sprules, 1993). Selection indices can be used to measure the utilisation of particular types or sizes of food in relation to their abundance or availability in the environment (Lechowicz, 1982). Selection was calculated for four size classes (<0.25, 0.25-0.49, 0.5-1, >1 mm) within each of five zooplankton groups (rotifers, planktonic cladocerans (*Bosmina longirostris*, *Daphnia* spp.), unidentified copepod nauplii, planktonic copepods (mostly cyclopoids), non-planktonic crustaceans (mostly chydorids, plus harpacticoids, macrothricids, *Sida crystallina*, *Polyphemus pediculus*, *Ceriodaphnia* spp., *Simocephalus* spp., *Scapholeberis mucronata* (Müller))). Calculations were restricted to these key groups since abundances and lengths of benthic macroinvertebrates were not known, and to avoid potential bias caused by inclusion of rare zooplankton taxa (Lechowicz, 1982).

Where available, the lengths of at least 30 individuals of each taxa from both diet and zooplankton samples were measured (nearest 0.023 mm) using a compound microscope equipped with an ocular micrometer, according to the methods of Bottrell *et al.* (1976), McCauley (1984) and Ghan & Sprules (1993). Thus, cladocerans were measured from the top of the head to the point of insertion of the tail spine (where present). For globular rotifers such as *Asplanchna* spp., the longest dimension from the corona to the opposite end of the body was measured, and for spined rotifers such as *Keratella* spp., the maximum linear dimension of the body core was measured, excluding spines. Copepods (adult and copepodite stages) were measured from the anterior of the cephalothorax to the base of the caudal rami, while the maximum linear dimension of the body core was measured for copepod nauplii. Estimates of zooplankton availability were made from samples collected concurrently with the fish samples, as described in Chapter 4.

Selection was calculated using the relativised electivity index (E^*) of Vanderploeg & Scavia (1979b). Lechowicz (1982) reviewed the sampling characteristics of a range of electivity indices, including those of Ivlev (1961), Jacobs (1974), Chesson (1978), Paloheimo (1979), Strauss (1979) and Vanderploeg & Scavia (1979a, b), and concluded that Vanderploeg & Scavia's E^* provides the single most useful index. E^* is calculated as:

$$E_i^* = \frac{W_i - \left(\frac{1}{n}\right)}{W_i + \left(\frac{1}{n}\right)} \tag{5.5}$$

where n is the number of prey types available and W_i is estimated by

$$W_i = \frac{\left(\frac{r_i}{p_i}\right)}{\sum\left(\frac{r_i}{p_i}\right)} \tag{5.6}$$

where r_i and p_i are the percentage of prey type i in the diet and in the environment, respectively. E^* ranges from −1 to +1, with negative values indicating avoidance, positive values indicating selection, and 0 representing no preference.

Occasionally a prey category occurred in the diet but not in the corresponding plankton samples. When such prey composed ≥5% of the diet, their electivities were set at +1 since they were ingested despite not being detected in the environment (Ghan & Sprules, 1993; H. A. Vanderploeg, *pers. comm.*). When the relative proportion of such categories in the diet was less than 5%, electivity was set at 0.

5.2.6 The influence of gape on the sizes of prey consumed

Mouth gape has often been identified as a key morphological trait limiting prey size of fish that swallow prey whole (e.g. Dąbrowski & Bardega, 1984; DeVries *et al.*, 1998; Mehner *et al.*, 1998a; Krebs & Turingan, 2003; Truemper & Lauer, 2005) and, since gape varies both within and between species, it may serve as a predictor of prey choice (Bremigan & Stein, 1994). The relationships between maximum gape height and SL, and maximum prey (zooplankton) length consumed and maximum gape height were determined for each fish species at each site via linear regression, and compared using ANCOVA (García-Berthou, 2001a; Dytham, 2003).

5.3 RESULTS

5.3.1 The food of larval and 0+ juvenile fish

A total of 1313 fish were used for diet analyses. The species examined were dace, roach, chub, perch, gudgeon, bream, bleak, minnow, barbel, carp, bullhead, stone loach, three-spined stickleback, zander and ruffe (*Gymnocephalus cernuus* (L.)).

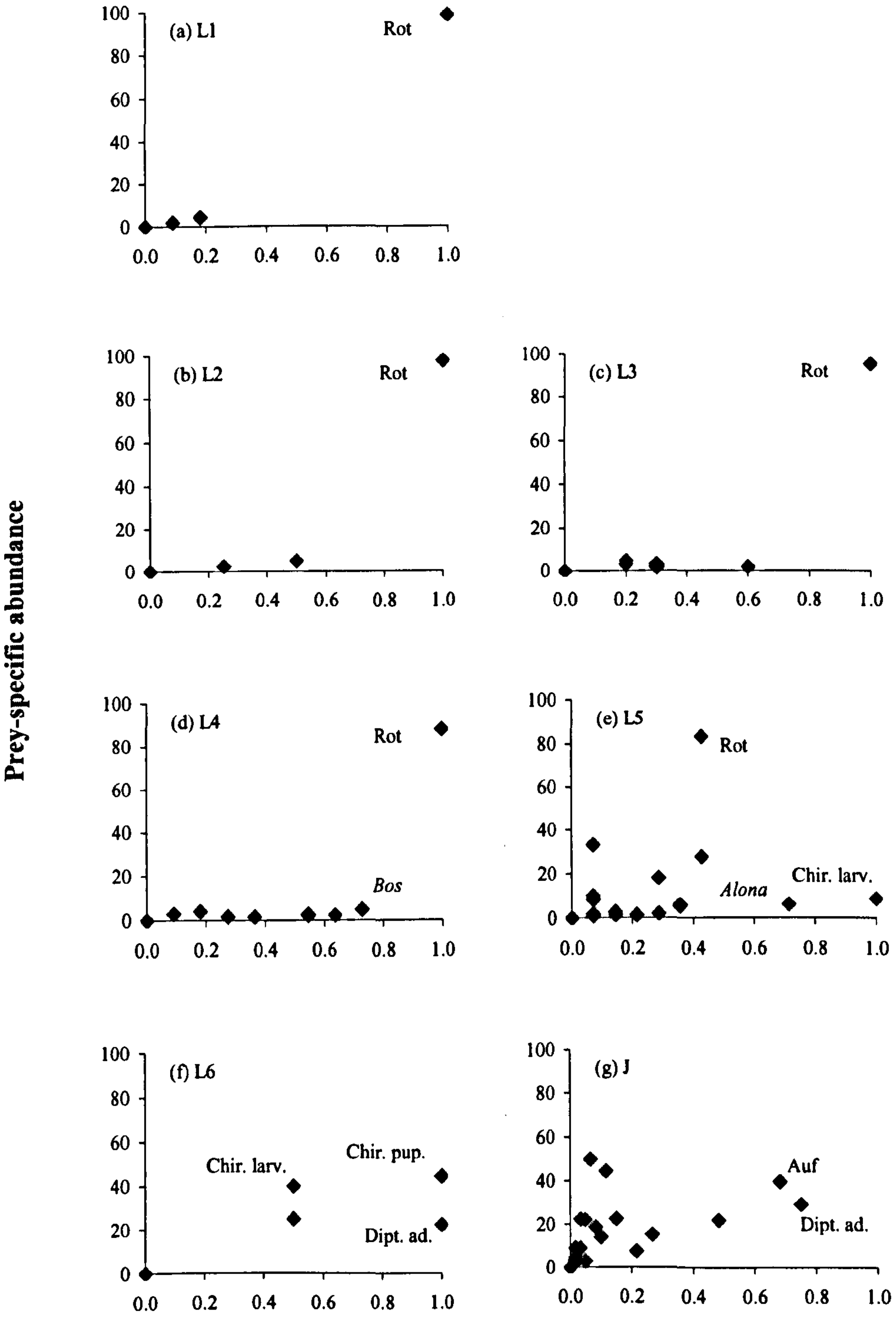
Young larvae had narrow diet spectra, with small numbers of taxa accounting for the majority of the diet, as demonstrated by the location of points in the top right corner of the Costello plots (e.g. Fig. 5.2a). In contrast, older larvae and juveniles had less specialised diets than younger individuals, with a range of prey eaten in small proportions located along the abscissae (e.g. Fig. 5.2e). Prey taxa are abbreviated as in Table 5.1.

In all three macrohabitats, the diets of the majority of young (L1-L3) dace larvae were dominated by rotifers (primarily *Brachionus*, *Euchlanis*, *Keratella* spp.) (Figs 5.2-5.4). In the main river, some first-feeding dace also consumed small numbers of algae (*Closterium*, *Navicula* spp.) (Fig. 5.2a), while in the marina copepod nauplii were eaten by some L1-L2 fish (Figs 5.3a, b). Rotifers and copepod nauplii continued to be the most frequent food items during step L3 in the marina, with small cladocerans (especially chydorids and *Polyphemus pediculus*) also occurring in the diet of many fish (Fig. 5.3c). In the main river, small numbers of cladocerans such as *Bosmina*, *Ilyocryptus sordidus* (Liévin) and chydorids were also eaten by many fish during steps L2-L4 (particularly L4), along with early instar chironomid larvae, harpacticoid copepods and copepod nauplii (Figs 5.2b-d). In the marina, L4 dace consumed *Polyphemus pediculus* extensively, plus *Bosmina*, *Alona* spp. and rotifers (Fig. 5.3d), while in the pond they fed predominantly on rotifers (Fig. 5.4b). In step L5, dace in the main river mostly consumed rotifers, chironomids (larvae, pupae) and *Alona* spp. (Fig. 5.2e), while the oldest (L6) larvae preyed upon chironomids (larvae, pupae, adults)

Table 5.1 Taxa consumed by 0+ fish, and abbreviations used in Costello plots.

Taxa	**Abbrev.**	**Taxa**	**Abbrev.**
Acroloxus sp.	*Acrol*	Filamentous algae	Fil. alg.
Acroperus sp.	*Acrop*	*Gammarus* sp.	*Gamm*
Alona spp.	*Alona*	Glossiphoniidae	Gloss
Arcella spp.	*Arcella*	*Graptoleberis testudinaria*	*Grapto*
Argulus sp.	*Argulus*	Harpacticoida	Harp
Asellus sp.	*Asellus*	*Hydra* spp.	*Hydra*
Aufwuchs	Auf	Hydracarina	Hydrac
Bosmina sp.	*Bos*	Hydrobiidae	Hydrob
Bryozoa (statoblast)	Bryo	Hymenoptera	Hym
Calanoida	Calan	*Ilyocryptus* sp.	*Ilyo*
Camptocercus sp.	*Campto*	Lemnaceae	Lemna
Centropyxis spp.	*Centro*	*Leuciscus cephalus*	*Lc*
Ceratopogonidae	Cerato	*Leydigia* sp.	*Leydigia*
Ceriodaphnia spp.	*Cerio*	*Lymnaea* spp.	*Lymnaea*
Chironomidae (larvae)	Chir. larv.	*Macrothrix* spp.	*Macro*
Chironomidae (pupae)	Chir. pup.	*Microcystis* spp.	*Micro*
Chydorus spp.	*Chyd*	Microturbellaria	Microturb
Cladophora sp.	*Cladoph*	*Navicula* spp.	*Navicula*
Closterium spp.	*Clost*	Nematoda	Nemat
Coleoptera (adult)	Coleop. ad.	Nematomorpha	Nematom
Coleoptera larvae	Coleop. larv.	Odonata	Odon
Collembola	Collem	Oligochaeta	Oligo
Copepod nauplii	Naup	Ostracoda	Ostrac
Corixidae	Corix	*Pediastrum* spp.	*Ped*
Cyclopoida	Cyclop	*Peracantha* spp.	*Pera*
Daphnia cucullata	*D. cucullata*	*Piscicola geometra* (L.)	*Pisci*
Daphnia ephippia	Ephipp	*Pisidium* spp.	*Pisidium*
Daphnia galeata	*D. galeata*	Planorbidae	Planorb
Daphnia hyalina	*D. hyalina*	Plecoptera	Plecop
Daphnia magna	*D. magna*	*Pleuroxus* spp.	*Pleuro*
Daphnia obtusa	*D. obtusa*	*Polyphemus pediculus*	*Poly*
Daphnia pulex	*D. pulex*	Rotifera	Rot
Diatoma spp.	*Diatoma*	*Rutilus rutilus*	*Rr*
Dictyosphaerium spp.	*Dictyo*	*Scapholeberis mucronata*	*Scaph*
Diptera (adult)	Dipt. ad.	*Sida crystallina*	*Sida*
Disparalona sp.	*Dispar*	*Simocephalus* spp.	*Simo*
Dreissena polymorpha (Pallas)	*Dreiss*	*Surirella* spp.	*Surirella*
Ephemeroptera	Ephem	*Tabellaria* spp.	*Tabell*
Erpobdellidae	Erpob	Trichoptera	Trichop
Eudorina spp.	*Eudorina*	Tricladida	Triclad
Eurycercus lamellatus	*Eury*	*Valvata* sp.	*Valvata*

and cyclopoid copepods (Fig. 5.2f). The predominant prey of L5-L6 dace in the marina were chironomid larvae and a variety of non-planktonic cladocerans (Figs 5.3e, f). At all three sites, juvenile dace mainly ate chironomids (larvae, adults) and aufwuchs (Figs 5.2g, 5.3g, 5.4d), although some fish consumed high proportions of non-planktonic cladocerans and *Daphnia* ephippia, and cyclopoid copepods and ephemeropteran larvae in the main river and marina, respectively.



Frequency of occurrence

Fig. 5.2 Costello plots demonstrating diet and feeding strategy of seven developmental steps (six larval, one juvenile) of 0+ dace from the main river.

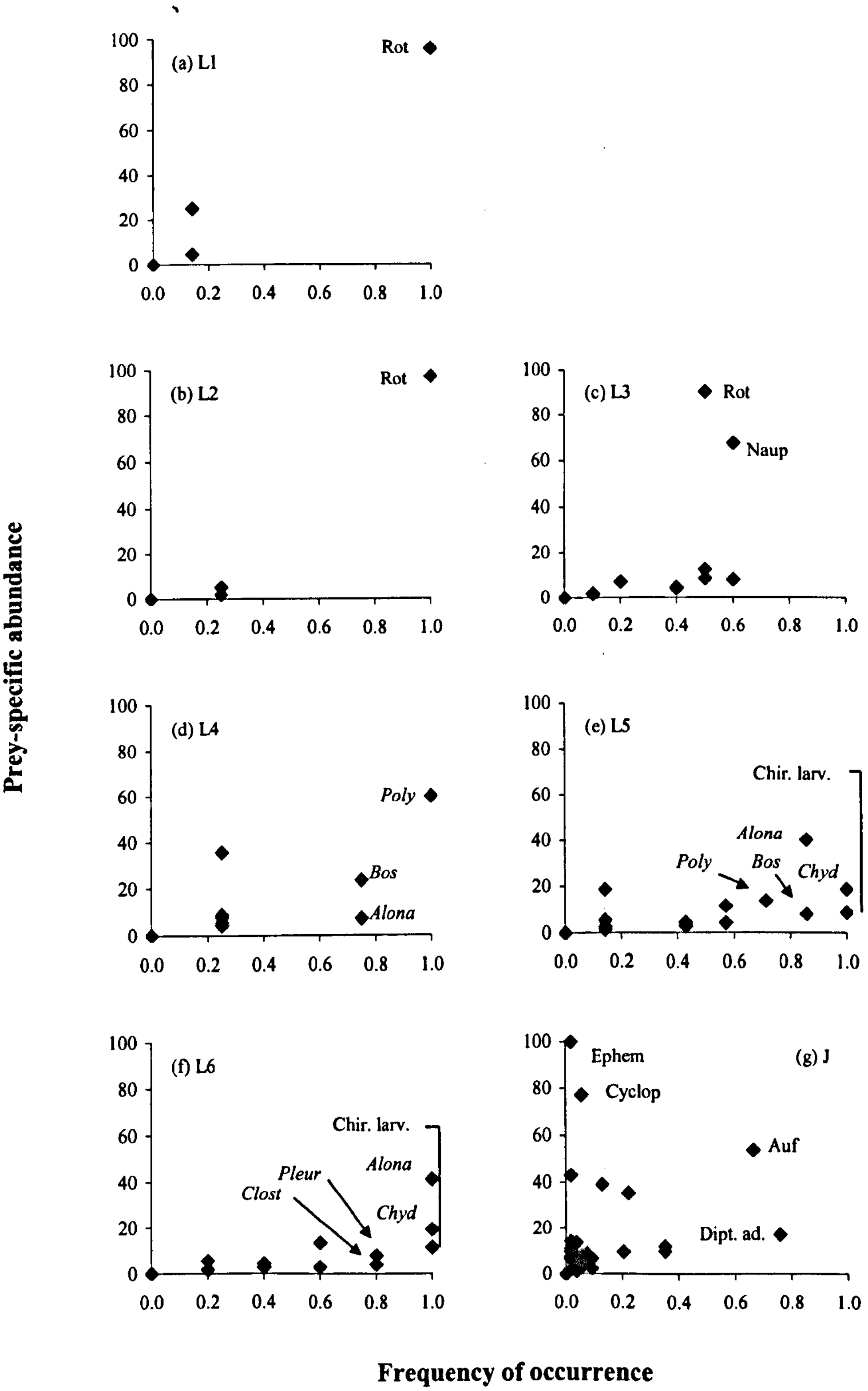


Fig. 5.3 Costello plots demonstrating diet and feeding strategy of seven developmental steps (six larval, one juvenile) of 0+ dace from the marina.

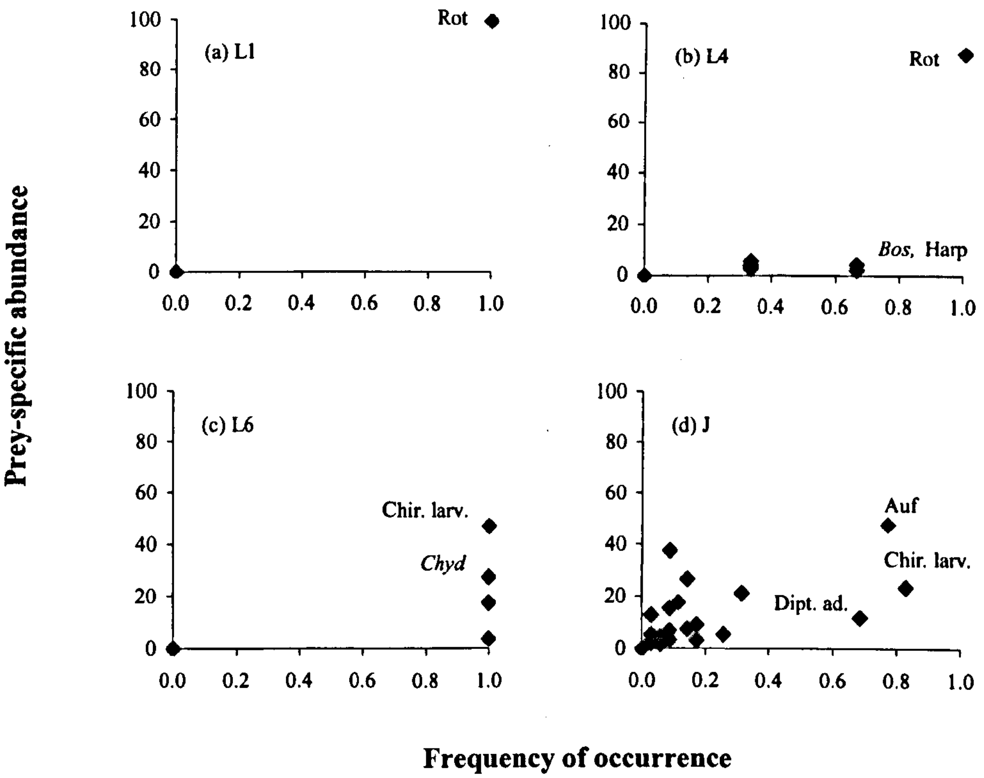


Fig. 5.4 Costello plots demonstrating diet and feeding strategy of four developmental steps (three larval, one juvenile) of 0+ dace from the pond.

In all three macrohabitats, young (L1-L3) roach larvae consumed rotifers extensively, with copepod nauplii the main other prey (Figs 5.5-5.7). In the main river, the majority of L4 roach mainly consumed rotifers and *Bosmina*, although some fish had specialised on aufwuchs (Fig. 5.5d), while in the marina they ate copepod nauplii and *Bosmina*, with smaller numbers of desmids (*Closterium* spp.) and non-planktonic cladocerans also eaten by many fish (Fig. 5.6d). In the pond, old (L5-L6) larvae preyed upon *Alona* spp., *Daphnia hyalina*, *Bosmina*, cyclopoid copepods and chironomid larvae (Figs 5.7c, d). Aufwuchs was the dominant food group of juvenile roach in both the main river (Fig. 5.5e) and the marina (Fig. 5.6f), although some individuals had consumed large numbers of *Bosmina* and, at the latter site, small green algae (*Eudorina* spp.). In contrast, juvenile roach in the pond mostly consumed either *Bosmina*, cyclopoid copepods or aufwuchs, with some fish consuming high proportions of adult dipterans (Fig. 5.7e). Generally, at all three sites the importance of planktonic cladocerans (*Bosmina*) declined and that of aufwuchs increased over the summer.

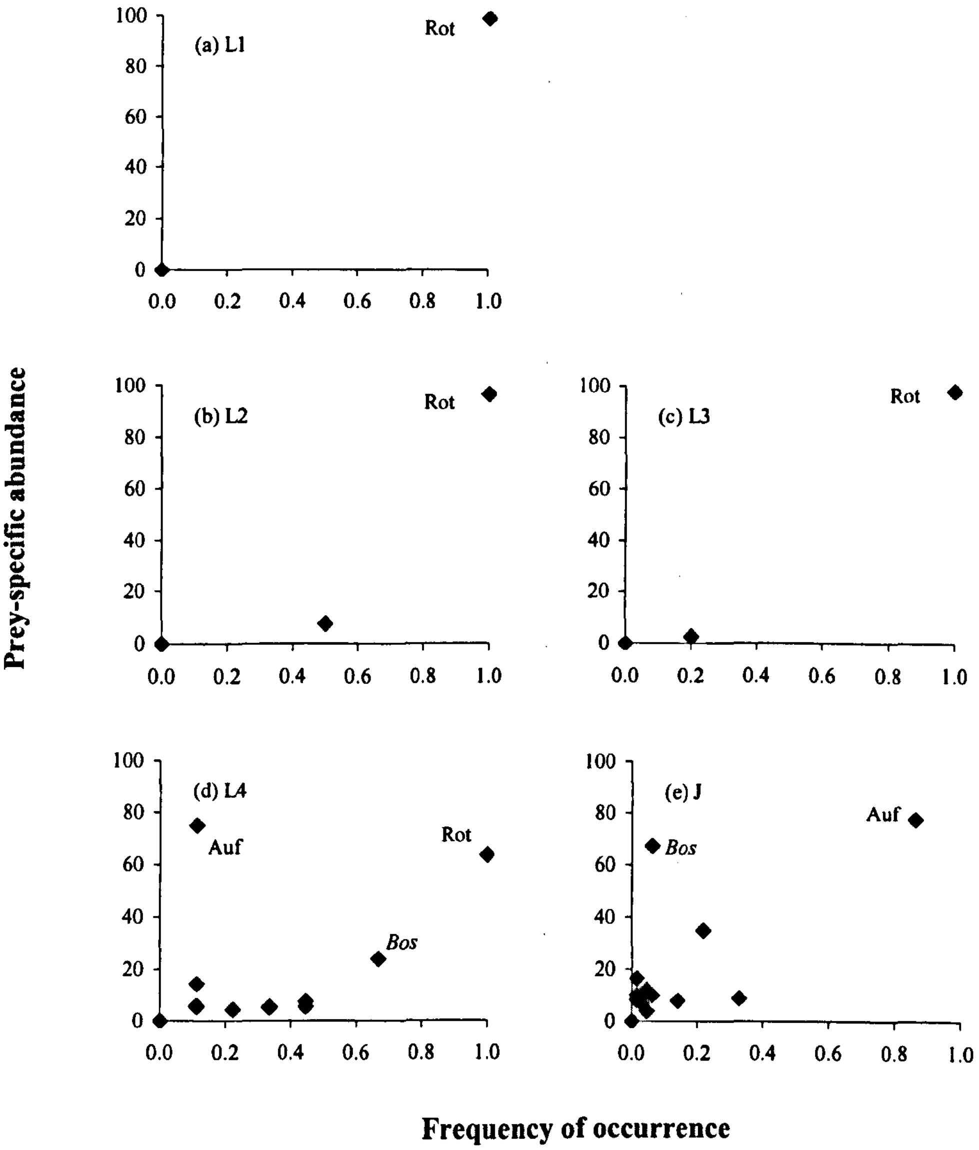


Fig. 5.5 Costello plots demonstrating diet and feeding strategy of five developmental steps (four larval, one juvenile) of 0+ roach from the main river.

Rotifers were the prey most frequently consumed by first-feeding chub in the main river, although algae (*Pediastrum* spp.) and chironomid larvae were also eaten (Fig. 5.8a). Rotifers were also the main prey of first-feeding chub in the pond, with copepod nauplii the only other prey taken (Fig. 5.10a). During steps L2 and L3, rotifers, algae (*Closterium*, *Navicula*, *Pediastrum* spp.) and early instar chironomid larvae were the most common food items of chub in the main river, although small cladocerans (mainly *Alona* spp.) were also eaten, especially during step L3 (Figs 5.8b, c). In the pond, chub in step L2 consumed rotifers, copepod nauplii and chironomid larvae (Fig. 5.10b), and the same was true for chub in steps L3-L6, with the addition of cyclopoid copepods (Figs 5.10c-f). In the main river, L4-L5 chub mostly consumed *Alona* spp. and chironomid larvae (Figs 5.8d, e). In the marina, chub in steps L4-L6 had varied but

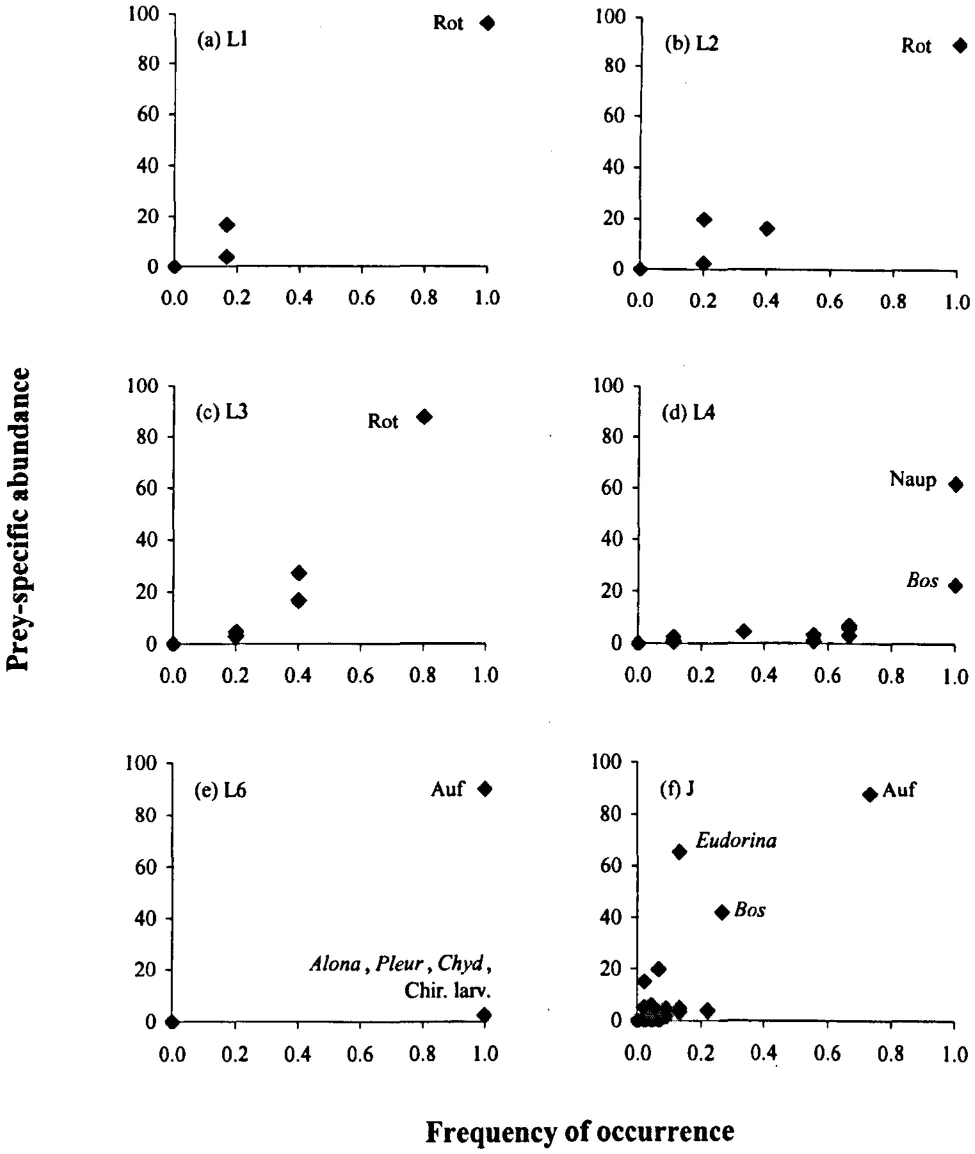


Fig. 5.6 Costello plots demonstrating diet and feeding strategy of six developmental steps (five larval, one juvenile) of 0+ roach from the marina.

broadly similar diets comprising chironomid larvae, small cladocerans (*Scapholeberis mucronata*, *Polyphemus pediculus*, *Bosmina*, *Chydorus*, *Pleuroxus*, *Alona* spp.), copepod nauplii, cyclopoid copepods, rotifers, testate amoebae and adult dipterans (particularly L6), with a small number of the oldest larvae consuming high proportions of *Eurycercus lamellatus* (Figs 5.9a-c). In both the main river and the marina, juvenile chub mostly consumed chironomids (larvae, adults) and aufwuchs, although at the latter site some fish had eaten large numbers of *Scapholeberis mucronata* (Figs 5.8f, 5.9d). In the pond, juvenile chub mostly consumed cyclopoid copepods, with chironomid larvae, corixids, adult dipterans and aufwuchs eaten in lesser amounts (Fig. 5.10g).

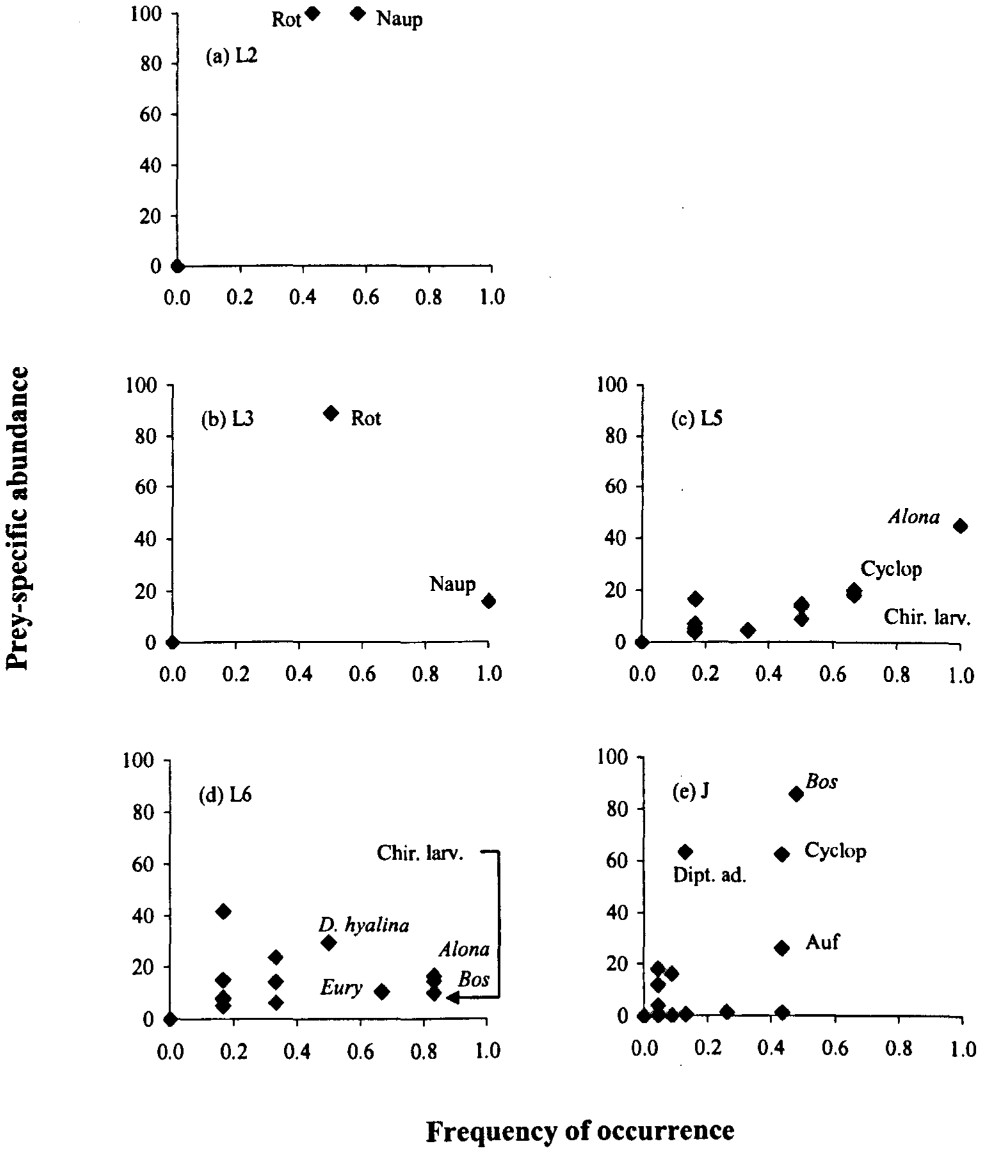


Fig. 5.7 Costello plots demonstrating diet and feeding strategy of five developmental steps (four larval, one juvenile) of 0+ roach from the pond.

On 29 April 2003, two newly hatched perch were captured from the main river and the marina, but they had not commenced exogenous feeding. In the pond, L2-L5 perch consumed cyclopoid copepods almost exclusively, with only L4-L5 fish also consuming small numbers of *Daphnia hyalina* (Figs 5.13a-d). In the marina, L3 perch consumed cyclopoid copepods extensively, although *Daphnia hyalina* and copepod nauplii were also taken (Fig. 5.12a), while older (L4-L6) larvae mostly consumed *Bosmina*, with smaller numbers of non-planktonic cladocerans (mainly *Eurycercus lamellatus*, *Alona* spp.), *Daphnia hyalina* and cyclopoid copepods also eaten (Figs 5.12b-d). In the main river, L6 perch mostly consumed *Bosmina*, cyclopoid copepods and *Daphnia hyalina*,

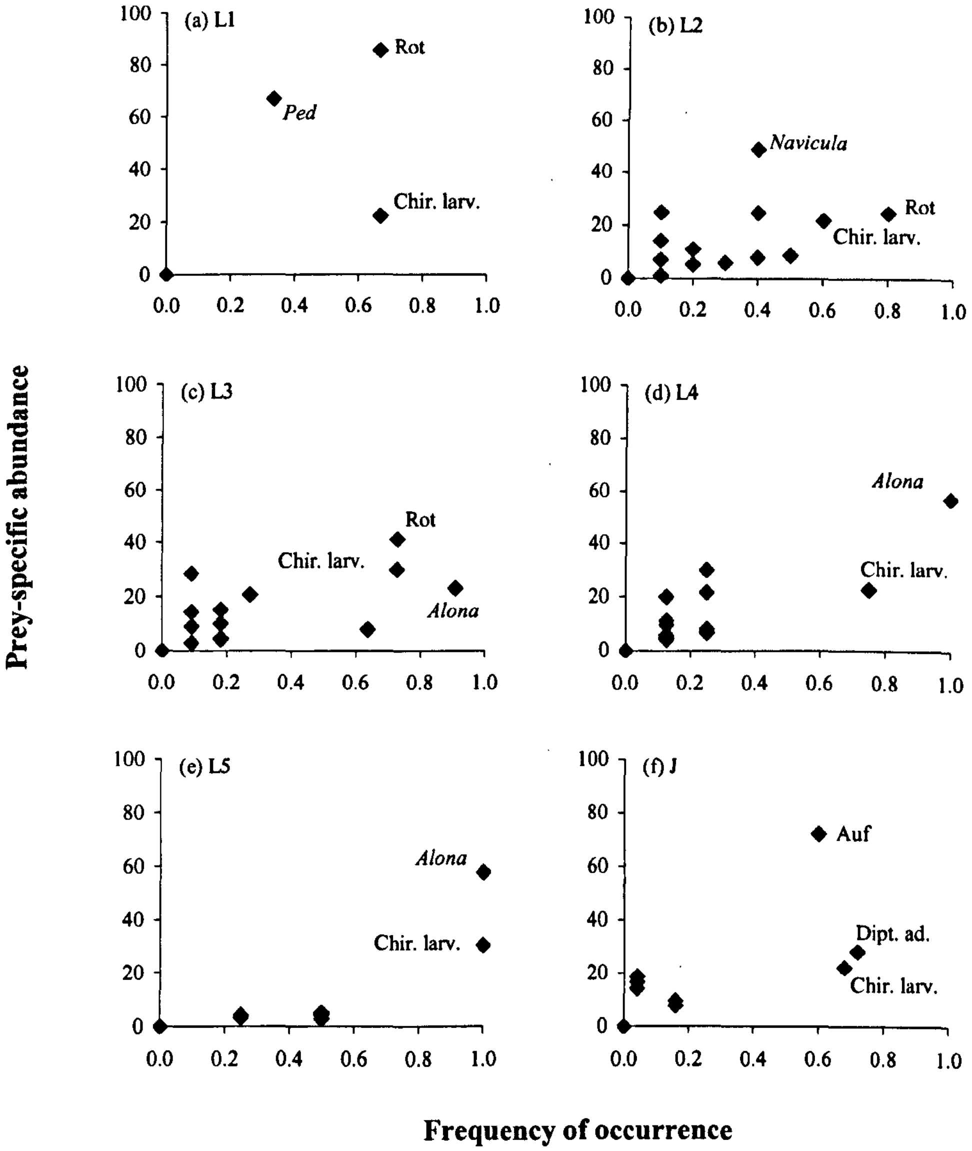


Fig. 5.8 Costello plots demonstrating diet and feeding strategy of six developmental steps (five larval, one juvenile) of 0+ chub from the main river.

although some fish specialised on chironomid pupae (Fig. 5.11a). Juvenile perch consumed a diverse range of food items, but in the main river their diet essentially comprised planktonic cladocerans (*Daphnia hyalina*, *Bosmina*) in June, non-planktonic cladocerans (chydorids) and cyclopoid copepods in July, and chironomid larvae, cyclopoid copepods and ephemeropteran larvae from August to October (Fig. 5.11b). *Bosmina*, cyclopoid copepods, chironomid larvae, ephemeropteran larvae and non-planktonic cladocerans (*Eurycercus lamellatus*, *Camptocercus rectirostris*, *Acroperus harpae* (Baird), *Simocephalus*, *Pleuroxus* spp.) were the food items most frequently eaten by juvenile perch in the marina (Fig. 5.12e), with cladocerans decreasing and copepods and macroinvertebrates increasing in importance through the summer.

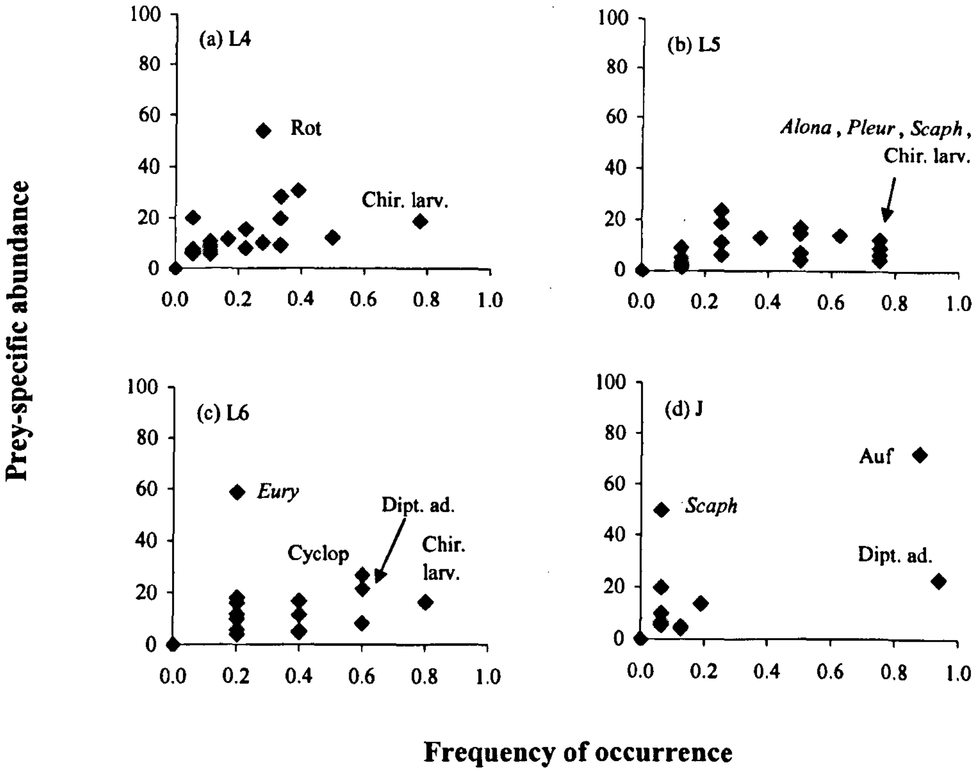


Fig. 5.9 Costello plots demonstrating diet and feeding strategy of four developmental steps (three larval, one juvenile) of 0+ chub from the marina.

Juvenile perch in the pond consumed cyclopoid copepods extensively, along with lesser numbers of *Bosmina* and *Daphnia hyalina* in mid summer and chironomids (larvae, pupae, adults) in the autumn (Fig. 5.13e). In addition, one fish (60 mm SL) in the main river had eaten a chub, and three fish (40-57 mm SL) in the marina had eaten two chub and two roach between them.

Few larval gudgeon were captured from any of the three macrohabitats. In the main river and the marina, L6 gudgeon mainly consumed *Alona* spp., copepod nauplii, chironomid larvae (main river) and *Closterium* spp. (marina) (Figs 5.14a, 5.15a). Old larvae (L5-L6) and juveniles in the pond mainly ate cyclopoid copepods, chironomid larvae and non-planktonic crustaceans, although some L6 fish consumed high proportions of aufwuchs (Figs 5.16a-c). In the main river, the diet of juvenile gudgeon remained fairly constant throughout the summer until sampling ceased in October, with chironomid larvae, non-planktonic cladocerans (especially *Alona* spp.) and aufwuchs the predominant taxa in the diet (Fig. 5.14b). Juvenile gudgeon in the marina consumed a wide range of prey

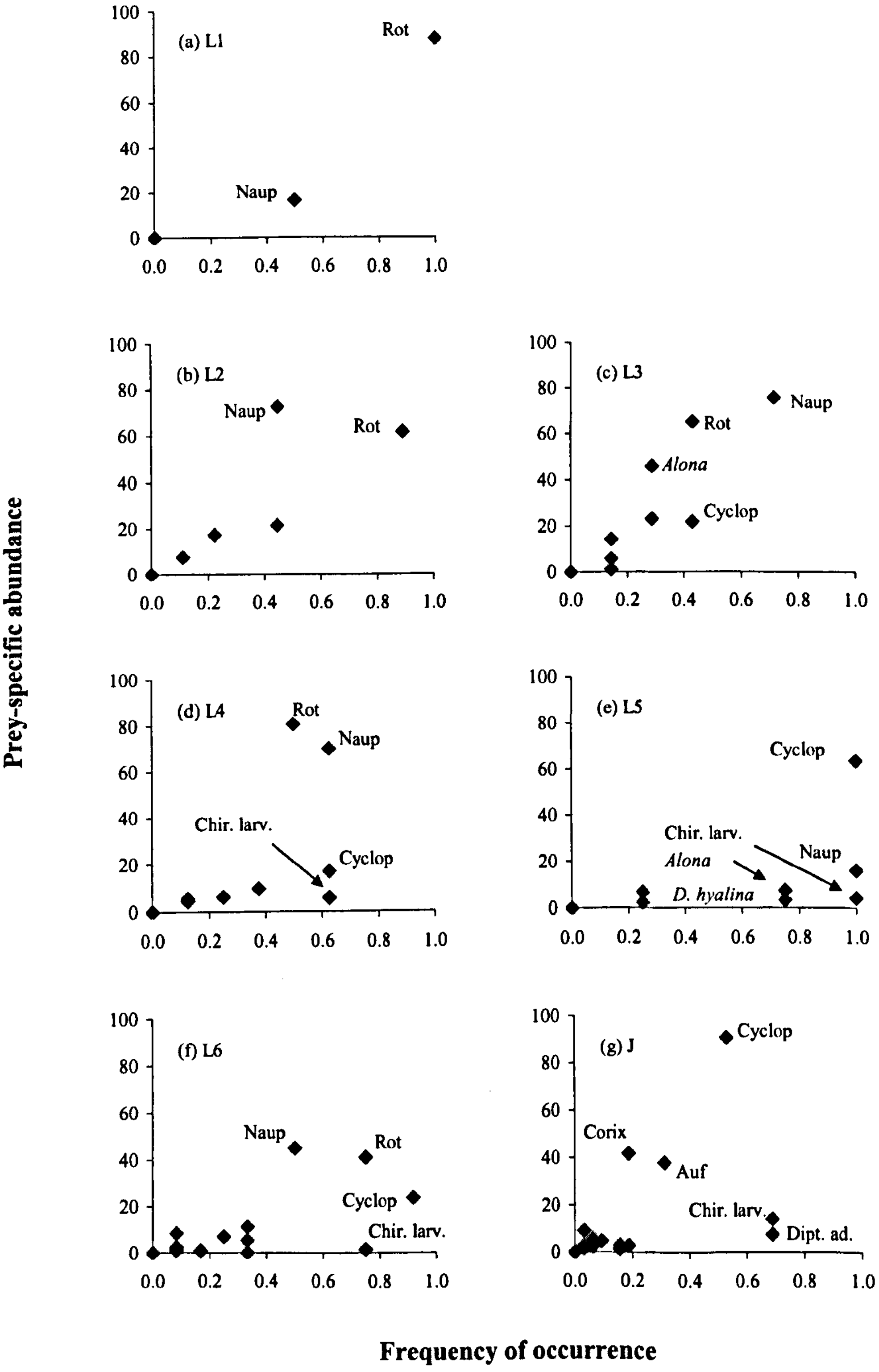


Fig. 5.10 Costello plots demonstrating diet and feeding strategy of seven developmental steps (six larval, one juvenile) of 0+ chub from the pond.

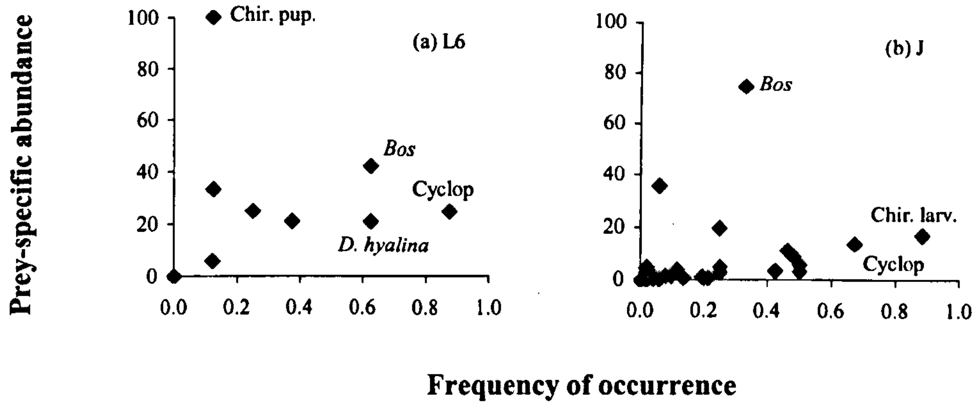


Fig. 5.11 Costello plots demonstrating diet and feeding strategy of two developmental steps (one larval, one juvenile) of 0+ perch from the main river.

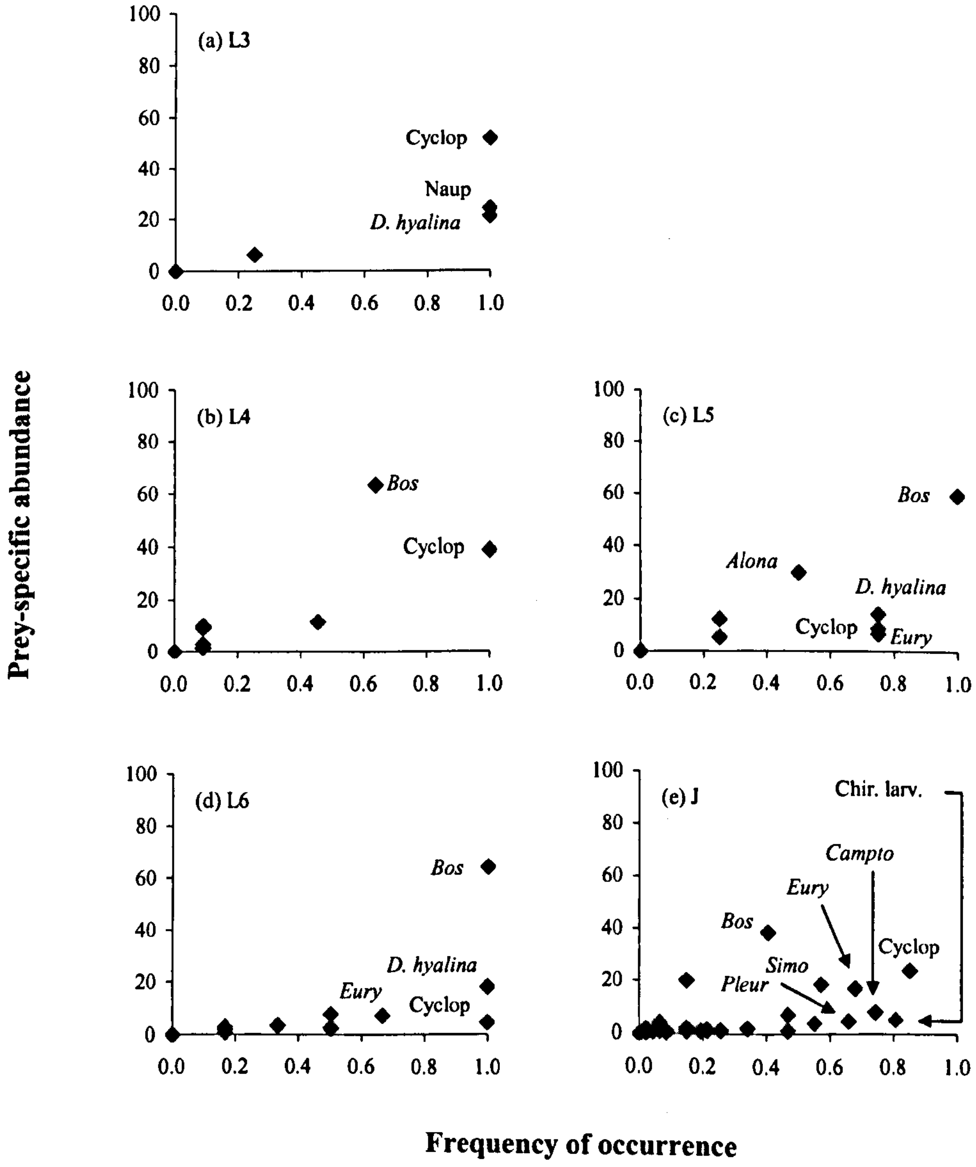


Fig. 5.12 Costello plots demonstrating diet and feeding strategy of five developmental steps (four larval, one juvenile) of 0+ perch from the marina.

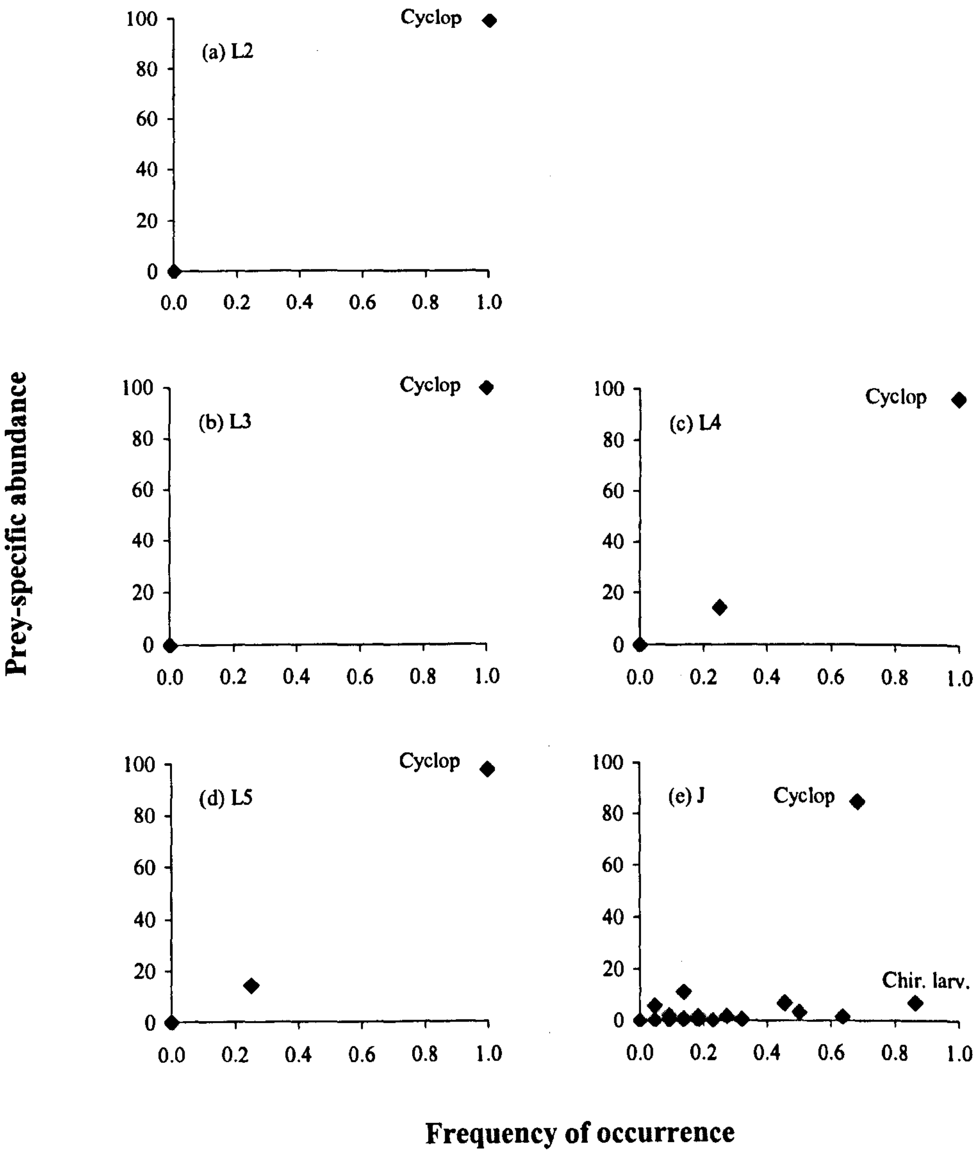


Fig. 5.13 Costello plots demonstrating diet and feeding strategy of five developmental steps (four larval, one juvenile) of 0+ perch from the pond.

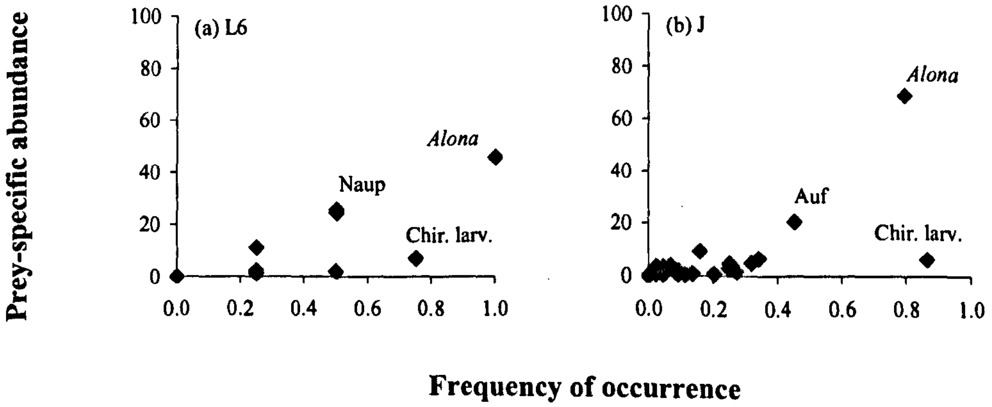


Fig. 5.14 Costello plots demonstrating diet and feeding strategy of two developmental steps (one larval, one juvenile) of 0+ gudgeon from the main river.

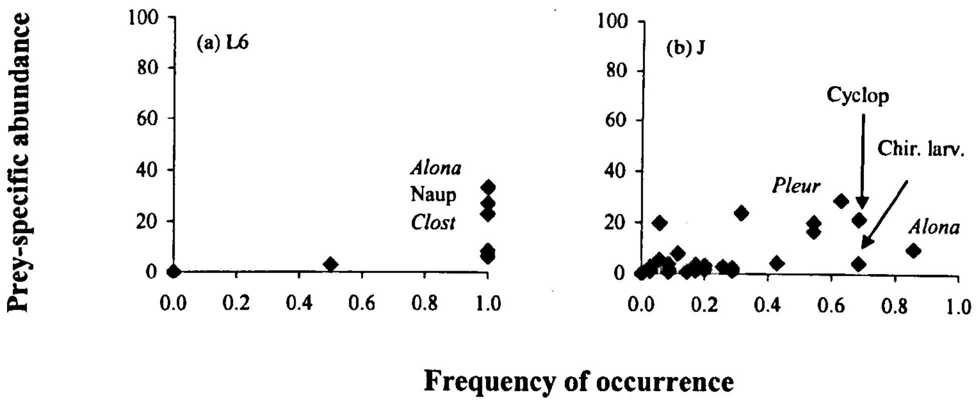


Fig. 5.15 Costello plots demonstrating diet and feeding strategy of two developmental steps (one larval, one juvenile) of 0+ gudgeon from the marina.

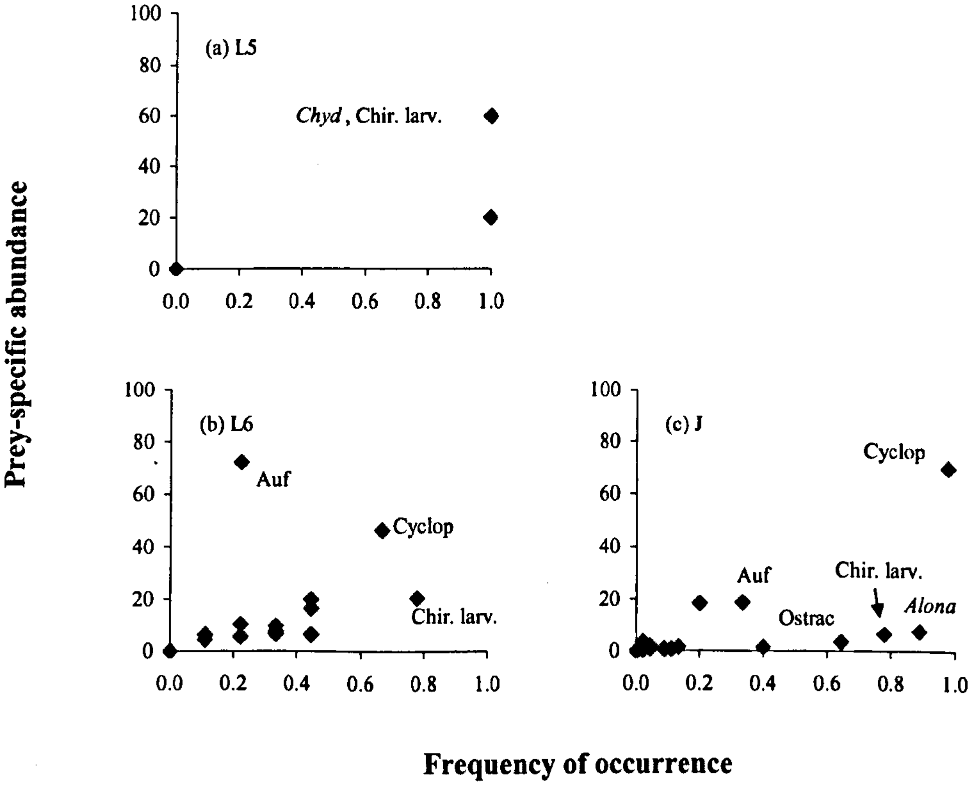


Fig. 5.16 Costello plots demonstrating diet and feeding strategy of three developmental steps (two larval, one juvenile) of 0+ gudgeon from the pond.

items, with chironomid larvae, cyclopoid copepods, ostracods, aufwuchs, *Alona* and *Pleuroxus* spp. most frequently eaten (Fig. 5.15b).

No young larval bream were caught from either the main river or the marina, despite spawning taking place in close proximity to the latter site (*pers. obs.*). In the pond,

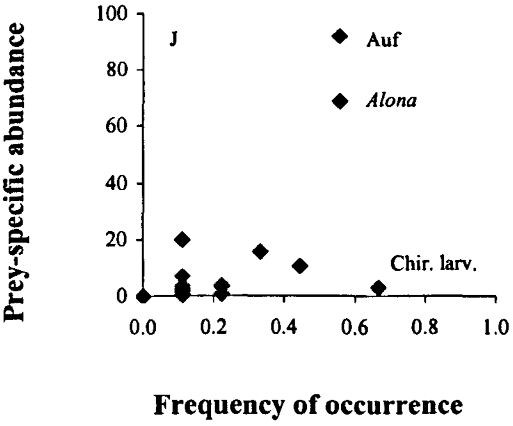


Fig. 5.17 Costello plot demonstrating diet and feeding strategy of one developmental step (juvenile) of 0+ bream from the main river.

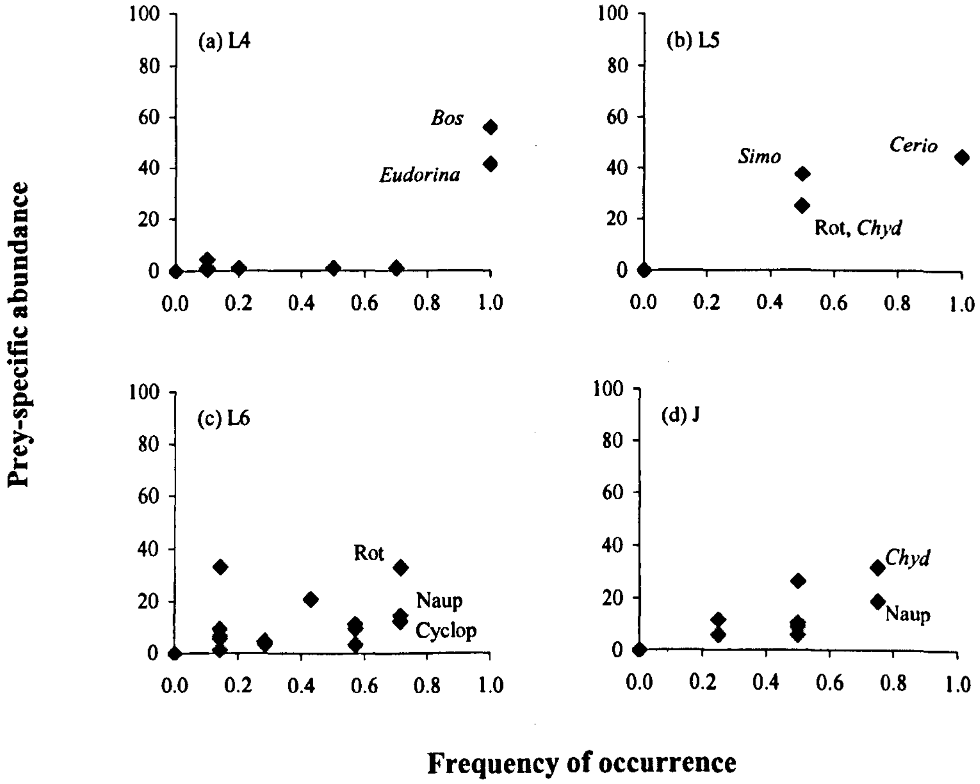


Fig. 5.18 Costello plots demonstrating diet and feeding strategy of four developmental steps (three larval, one juvenile) of 0+ bream from the marina.

bream in steps L2-L4 preyed upon copepod nauplii and rotifers extensively (Figs 5.19a-c), while L4 bream in the marina mainly consumed *Bosmina* and small green algae (*Eudorina* spp.) (Fig. 5.18a). L5 bream in the marina consumed non-planktonic cladocerans (*Chydorus*, *Ceriodaphnia*, *Simocephalus* spp.) and rotifers (Fig. 5.18b),

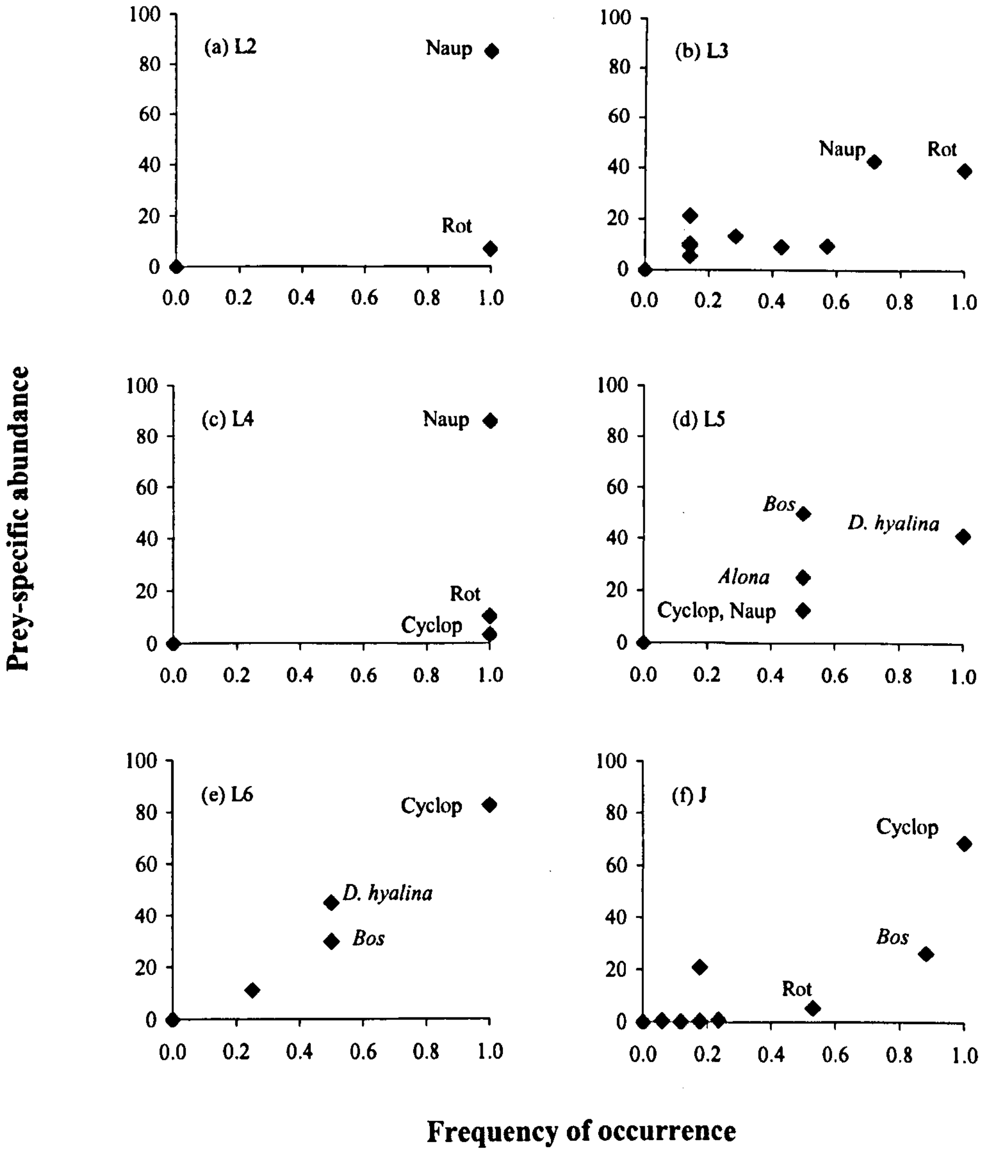


Fig. 5.19 Costello plots demonstrating diet and feeding strategy of six developmental steps (five larval, one juvenile) of 0+ bream from the pond.

while rotifers, *Bosmina*, cyclopoid copepods, copepod nauplii, chironomid larvae and non-planktonic cladocerans (*Ceriodaphnia*, *Chydorus* spp.) were the most frequent prey of the oldest (L6) larvae (Fig. 5.18c). In the pond, L5-L6 bream mostly consumed cyclopoid copepods, *Bosmina*, *Daphnia hyalina* and *Alona* spp. (Figs 5.19d, e), while cyclopoid copepods and *Bosmina* were the most frequent prey of juvenile bream (Fig. 5.19f). The digestive tracts of juveniles in the main river were often empty, with *Alona* spp. and aufwuchs comprising the majority of the diet of the remaining fish (Fig. 5.17). In the marina, juvenile bream consumed copepod nauplii and non-planktonic cladocerans (*Ceriodaphnia*, *Chydorus* spp.), plus small numbers of other zooplankters (Fig. 5.18d).

First-feeding bleak in the pond consumed only rotifers (Fig. 5.21a). Rotifers were also the most frequent prey of bleak in steps L2-L3, with early instar chironomid larvae and copepod nauplii also featuring in the diet (Figs 5.21b, c). In the marina, both young (L2) and old (L4) larvae consumed small algae (*Eudorina* spp.) almost exclusively, with only very small numbers of *Bosmina*, copepod nauplii and early instar chironomid larvae also eaten (Figs 5.20a, b). In the pond, bleak in step L4 mainly consumed rotifers and chironomid larvae (Fig. 5.21d), while older (L5-L6) larvae and juveniles preyed upon copepod nauplii, rotifers and *Bosmina* (Figs 5.21e-g).

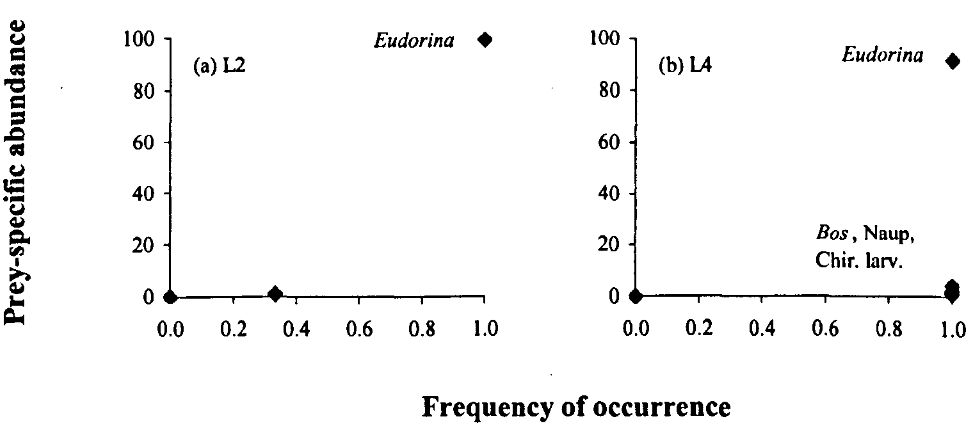


Fig. 5.20 Costello plots demonstrating diet and feeding strategy of two developmental steps (both larval) of 0+ bleak from the marina.

No first-feeding minnow were captured from any of the three macrohabitats. In the pond, minnow in step L2 mostly consumed rotifers and copepod nauplii, with small numbers of algae (*Closterium*, *Pediastrum* spp.) and early instar chironomid larvae also taken (Fig. 5.24a), while minnow in steps L3-L5 preyed upon copepod nauplii, rotifers, chironomid larvae and *Alona* spp. (Figs 5.24b-d). In the marina, all larvae captured (L3-L6) consumed rotifers almost exclusively, with chironomid larvae the only other food items (Figs 5.23a-d). In the main river, old (L4-L5) larvae mostly consumed rotifers, chironomid larvae and aufwuchs (Figs 5.22a, b), while the diet of juvenile minnow mostly comprised chironomid larvae, *Alona* spp. and aufwuchs (Fig. 5.22c). Juvenile minnow in the marina consumed chironomid larvae, cyclopoid copepods, non-planktonic cladocerans and aufwuchs (Fig. 5.23e), while in the pond the oldest (L6)

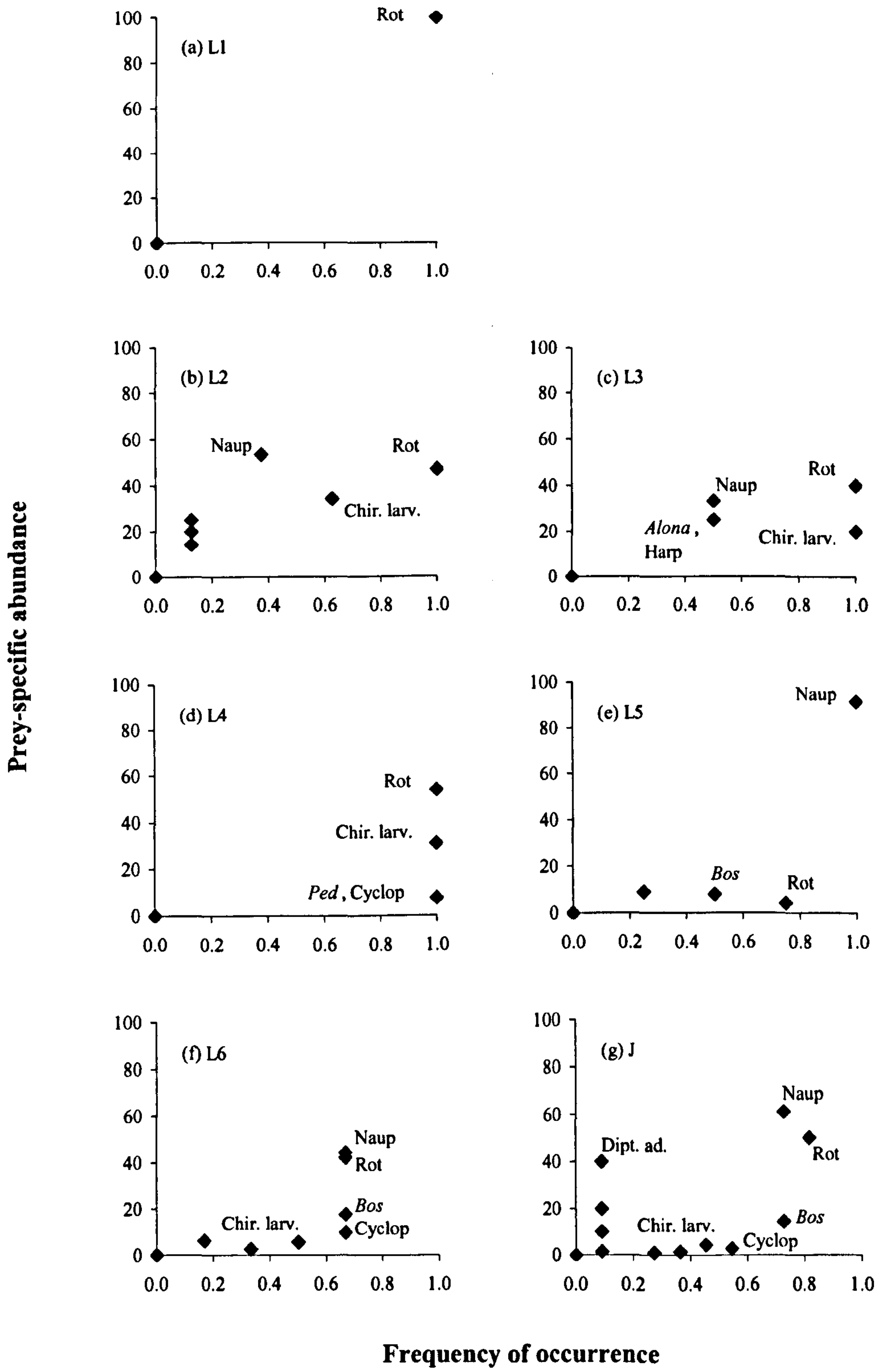


Fig. 5.21 Costello plots demonstrating diet and feeding strategy of seven developmental steps (six larval, one juvenile) of 0+ bleak from the pond.

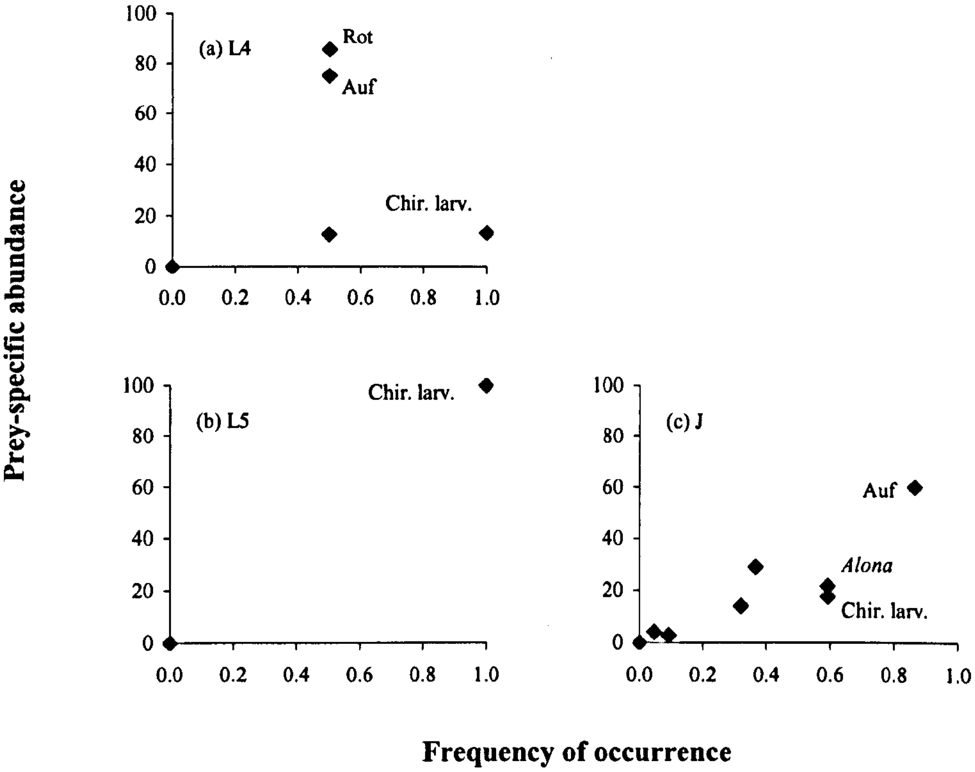


Fig. 5.22 Costello plots demonstrating diet and feeding strategy of three developmental steps (two larval, one juvenile) of 0+ minnow from the main river.

larvae and juveniles mostly consumed cyclopoid copepods, chironomid larvae and *Bosmina* (Figs 5.24e, f).

No young barbel larvae were encountered at any of the three macrohabitats. In the marina, old (L4-L5) larvae mostly consumed chironomid larvae, non-planktonic cladocerans (*Scapholeberis mucronata*, *Acroperus harpae*, *Alona*, *Pleuroxus* spp.), cyclopoid copepods, copepod nauplii and rotifers (Figs 5.26a, b). Chironomid larvae, *Alona* spp. and cyclopoid copepods were the predominant prey of L5-J barbel in the main river (Figs 5.25a-c), while old (L4-L6) larvae and juveniles in the pond consumed cyclopoid copepods almost exclusively, with other prey eaten in only small numbers (Figs 5.27a-d).

In the marina, L3 carp larvae mostly preyed upon non-planktonic cladocerans (especially *Simocephalus* spp., plus *Polyphemus pediculus*, *Eurycercus lamellatus* and *Ceriodaphnia* spp.) (Fig. 5.28), while in the pond they predominantly consumed copepod nauplii and *Scapholeberis mucronata* (Fig. 5.29a). L4 carp in the pond preyed

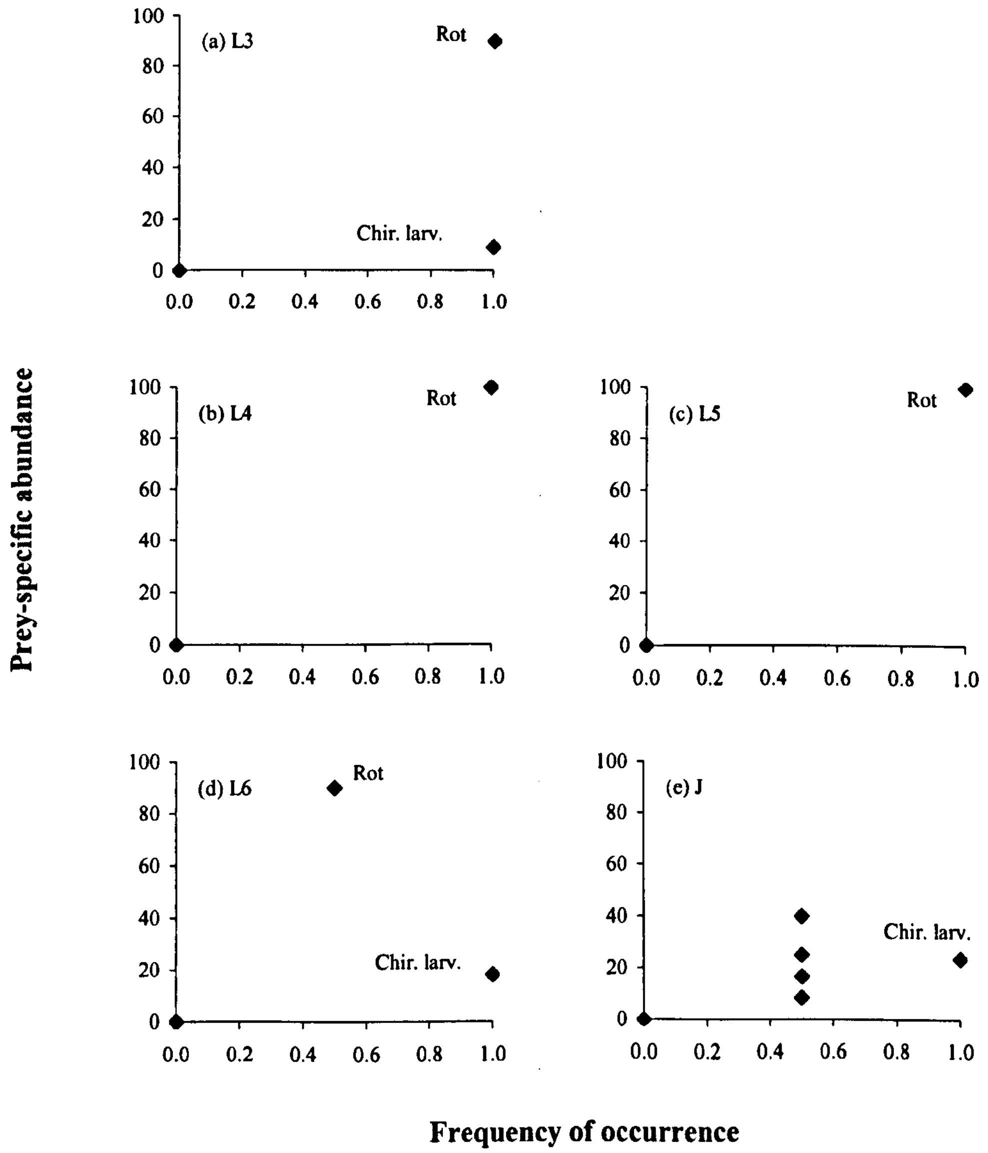


Fig. 5.23 Costello plots demonstrating diet and feeding strategy of five developmental steps (four larval, one juvenile) of 0+ minnow from the marina.

upon *Eurycercus lamellatus*, *Daphnia hyalina*, *Scapholeberis mucronata*, *Simocephalus* spp. and cyclopoid copepods (Fig. 5.29b), while the diet of juvenile carp consisted almost entirely of cyclopoid copepods, with other animals such as chydorids, daphnids, chironomid larvae, ostracods and corixids eaten in lesser numbers (Fig. 5.29c).

No larval bullhead were encountered at any of the three macrohabitats. The diet of juvenile bullhead in the main river mostly consisted of chironomid larvae, with cyclopoid copepods and aufwuchs also featuring in the diet (Fig. 5.30a), while in the

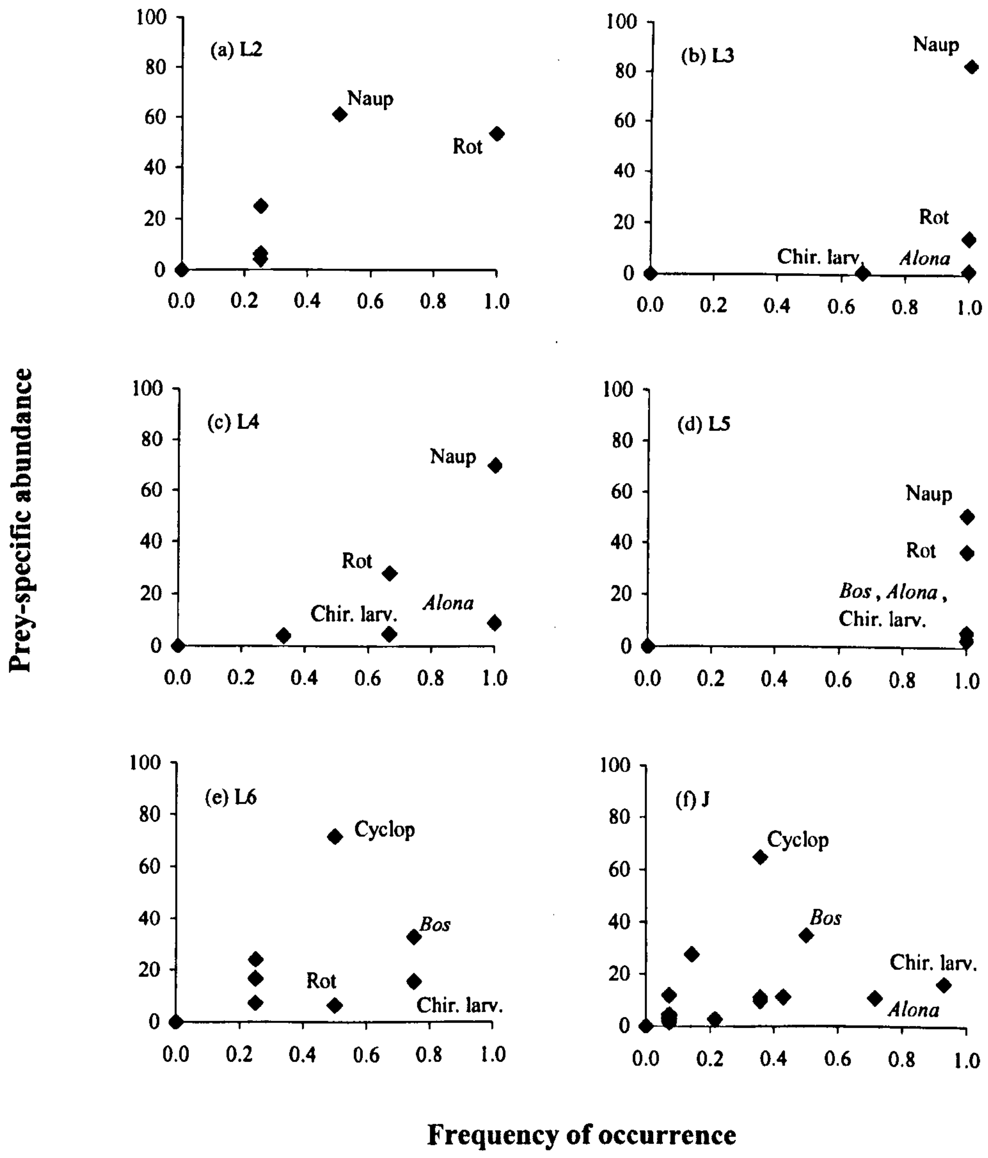


Fig. 5.24 Costello plots demonstrating diet and feeding strategy of six developmental steps (five larval, one juvenile) of 0+ minnow from the pond.

marina they mostly consumed cyclopoid copepods, with non-planktonic cladocerans and aufwuchs eaten in smaller amounts (Fig. 5.30b).

One newly hatched stone loach that had not commenced exogenous feeding was captured from the main river on 29 April 2003, but no other young larvae were caught subsequently from any of the three macrohabitats. Old (L6) larvae in the main river mostly consumed *Alona* spp., cyclopoid copepods and copepod nauplii (Fig. 5.31a), while juveniles also consumed *Alona* spp. and cyclopoid copepods, plus chironomid larvae and aufwuchs (Fig. 5.31b).

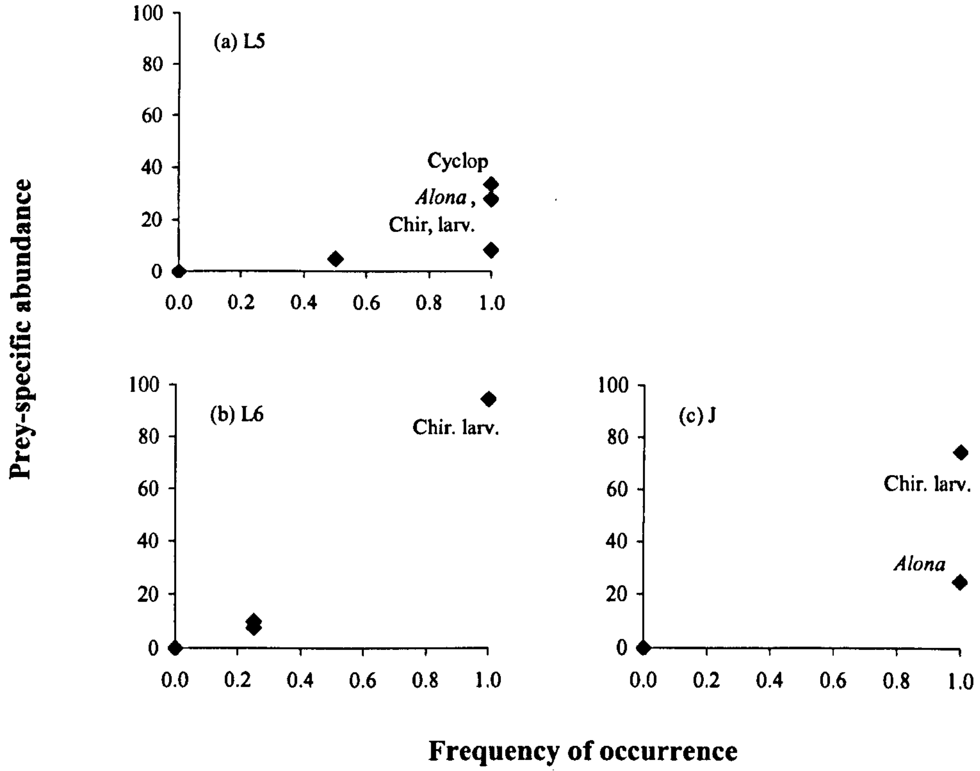


Fig. 5.25 Costello plots demonstrating diet and feeding strategy of two developmental steps (one larval, one juvenile) of 0+ barbel from the main river.

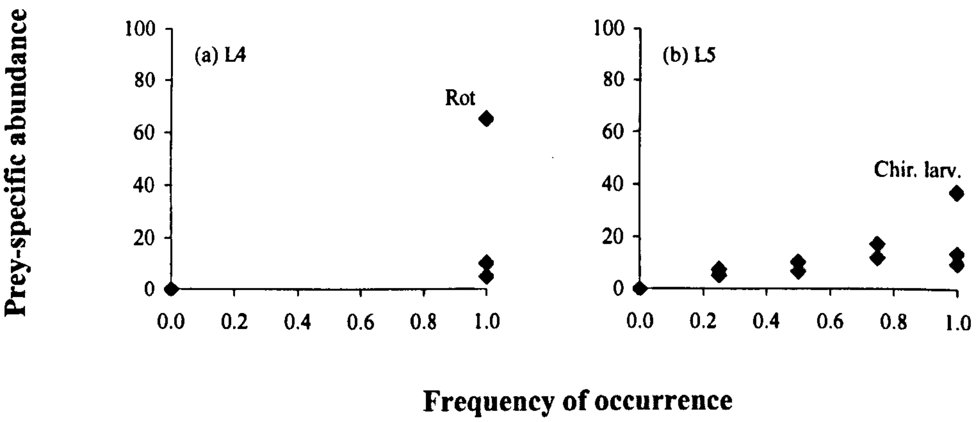


Fig. 5.26 Costello plots demonstrating diet and feeding strategy of two developmental steps (both larval) of 0+ barbel from the marina.

No young three-spined stickleback, zander or ruffe larvae were captured from any of the three macrohabitats. In the main river, old (L6) stickleback larvae preyed upon rotifers, cyclopoid copepods and chironomid larvae (Fig. 5.32a), while juveniles mostly consumed *Bosmina* and chironomids (larvae, pupae) (Fig. 5.32b). In the pond, L5-L6 zander larvae consumed only cyclopoid copepods and *Daphnia hyalina* (Figs 5.33a, b), while old (L6) ruffe larvae and juveniles consumed cyclopoid and calanoid

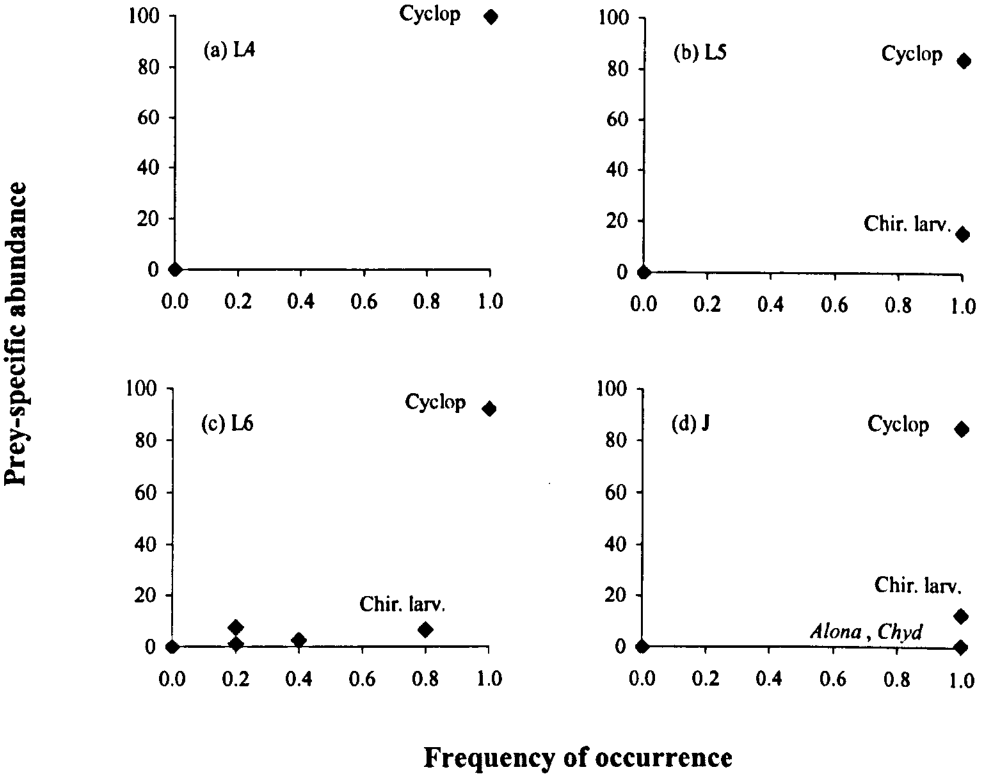


Fig. 5.27 Costello plots demonstrating diet and feeding strategy of four developmental steps (three larval, one juvenile) of 0+ barbel from the pond.

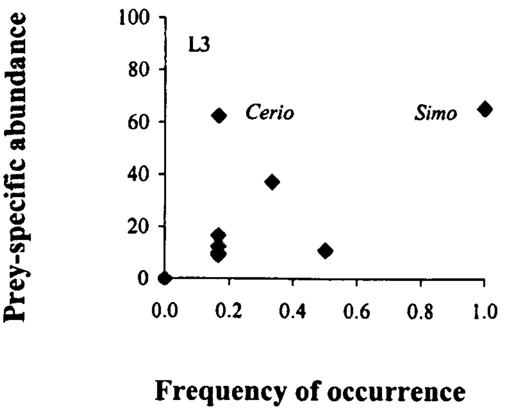


Fig. 5.28 Costello plot demonstrating diet and feeding strategy of one developmental step (larval) of 0+ carp from the marina.

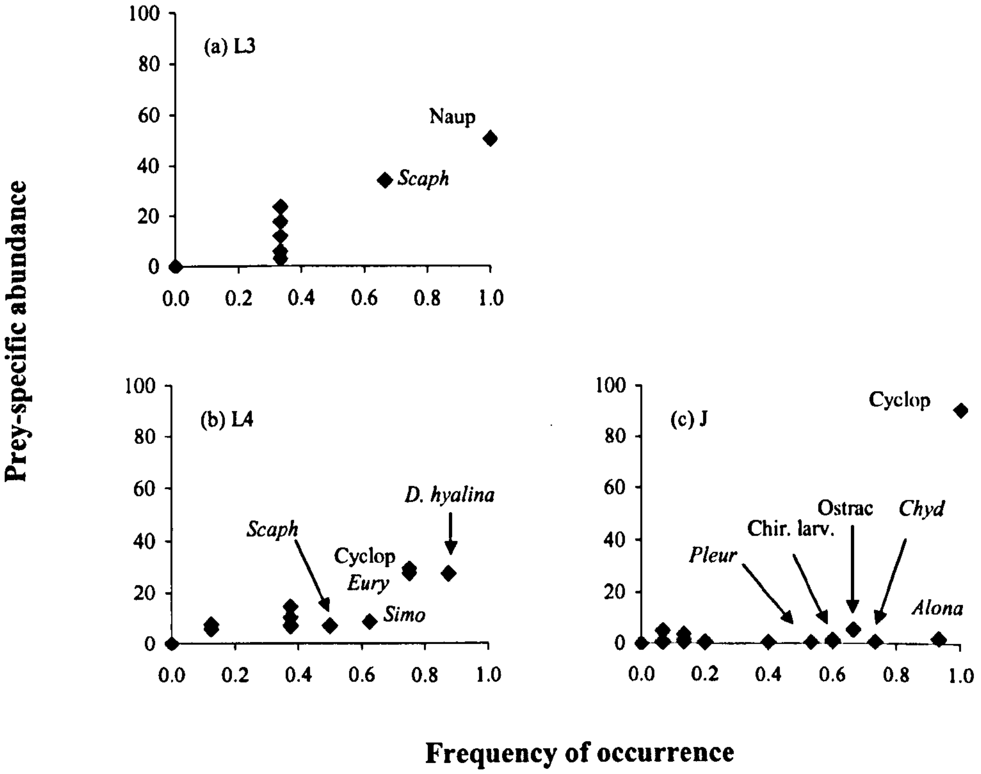


Fig. 5.29 Costello plots demonstrating diet and feeding strategy of three developmental steps (two larval, one juvenile) of 0+ carp from the pond.

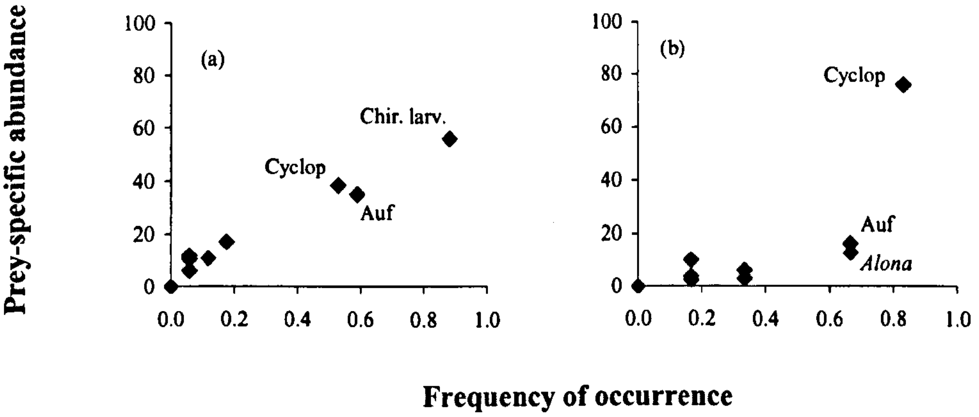


Fig. 5.30 Costello plots demonstrating diet and feeding strategy of one developmental step (juvenile) of 0+ bullhead from (a) the main river and (b) the marina.

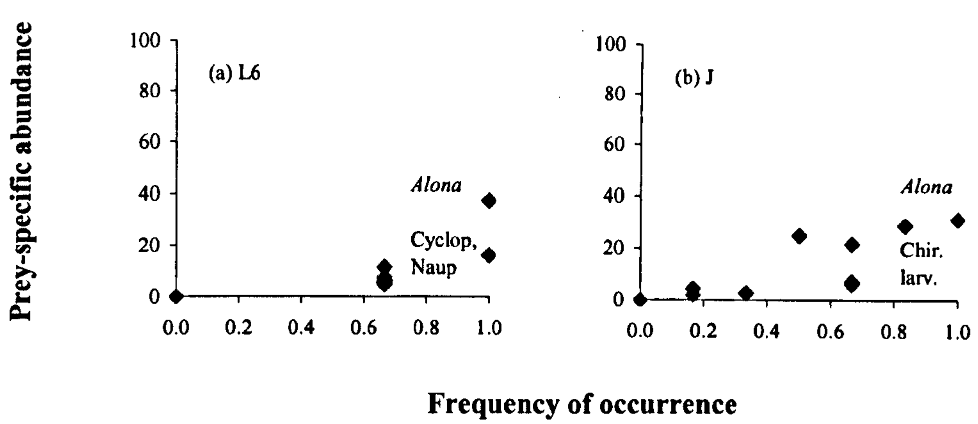


Fig. 5.31 Costello plots demonstrating diet and feeding strategy of two developmental steps (one larval, one juvenile) of 0+ stone loach from the main river.

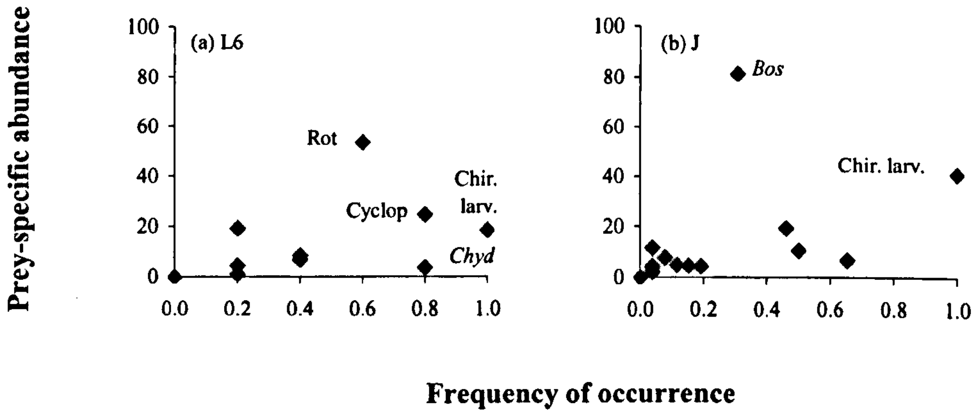


Fig. 5.32 Costello plots demonstrating diet and feeding strategy of two developmental steps (one larval, one juvenile) of 0+ three-spined stickleback from the main river.

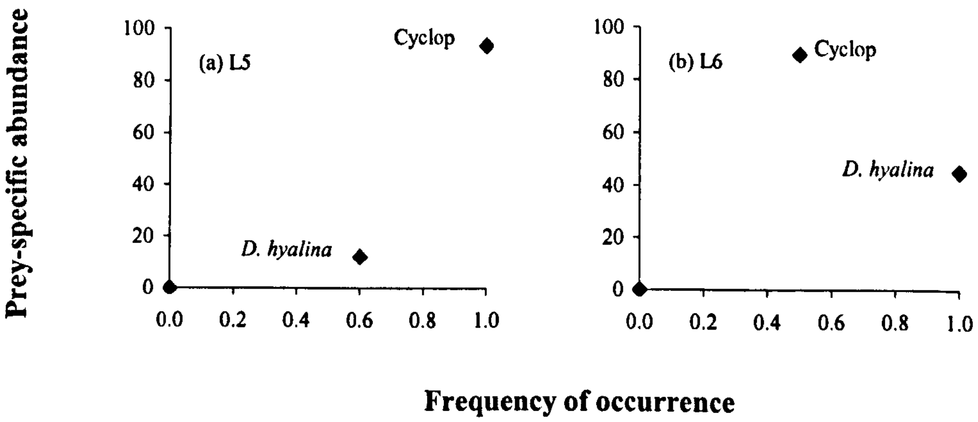


Fig. 5.33 Costello plots demonstrating diet and feeding strategy of two developmental steps (both larval) of 0+ zander from the pond.

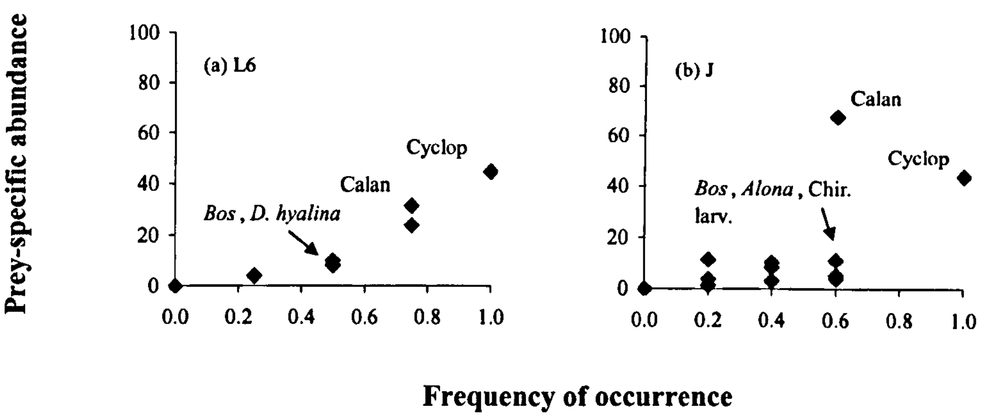


Fig. 5.34 Costello plots demonstrating diet and feeding strategy of two developmental steps (one larval, one juvenile) of 0+ ruffe from the pond.

copepods, with smaller numbers of cladocerans and chironomid larvae also eaten (Figs 5.34a, b).

5.3.2 Diversity and evenness of diet

Ontogenetic variations in diversity and evenness of diet

Ontogenetic variations in diet diversity and evenness could only be observed in species for which sufficient developmental steps were captured, namely roach, dace, chub and perch. In these species, feeding diversity was lowest in first-feeding larvae and increased with development (Fig. 5.35), although increases in feeding diversity between contiguous developmental steps were gradual rather than saltatory, and few were statistically significant. In the cyprinids there was a reduction in feeding diversity in the juvenile period (Fig. 5.35). This may in part be an artefact of the identification of zooplankton to higher levels of taxonomic resolution than other invertebrates, thereby artificially increasing the number of taxa consumed by zooplanktivorous fish (i.e. larval and juvenile perch, larval cyprinids). There were no clear ontogenetic patterns in evenness of diet (Fig. 5.35).

Interspecific variations in diversity and evenness of diet

It was rare for any particular species to have either significantly more or less diverse diets than all other species present. Where there were interspecific differences in feeding diversity, chub and roach consistently had some of the most and least diverse diets, respectively (Fig. 5.35). Such differences did not materialise until complete resorption

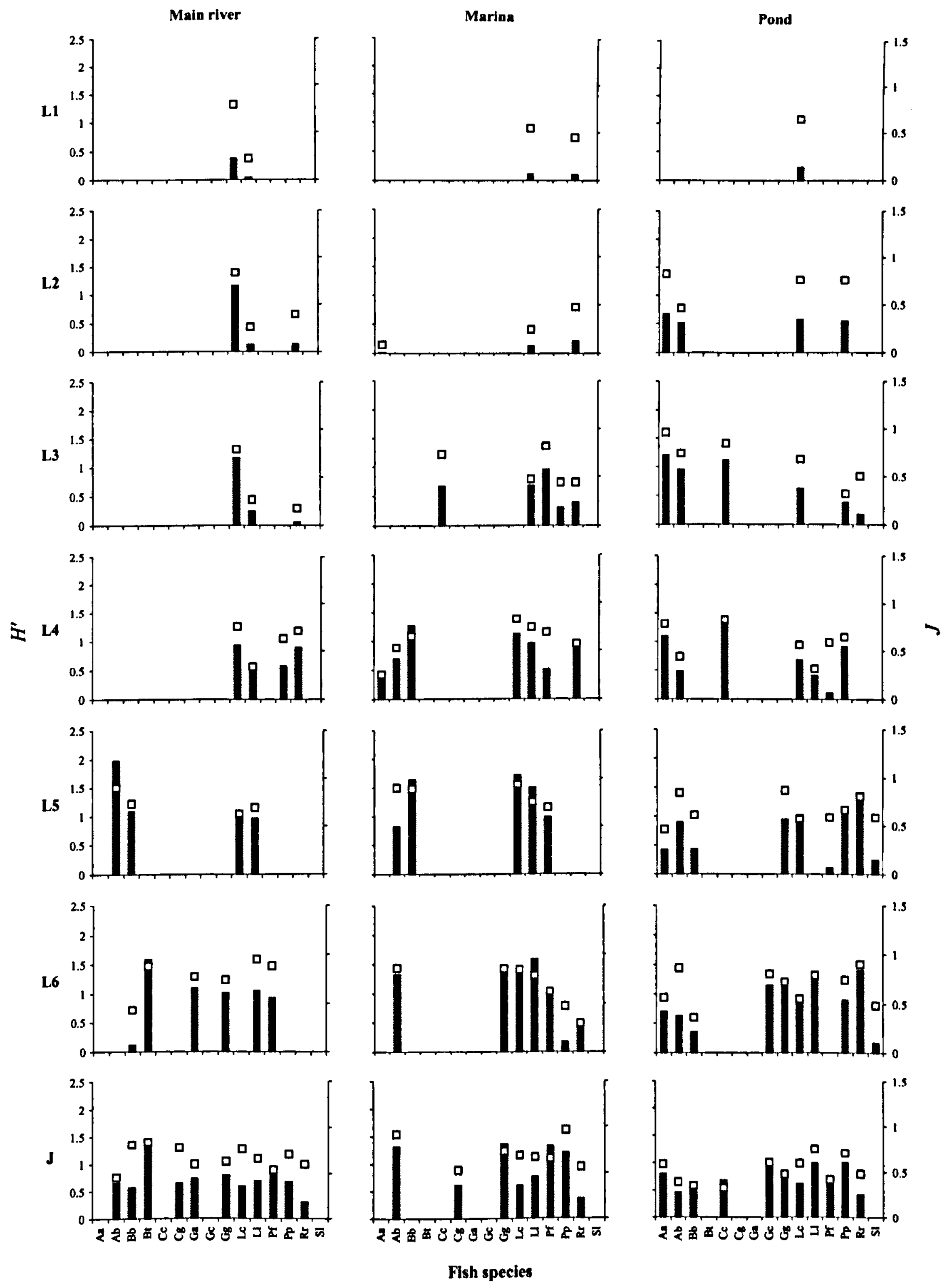


Fig. 5.35 Diversity (*H'*, ■) and evenness (*J*, □) of diet of seven developmental steps of 15 species of fish from main river, marina and pond macrohabitats. Species name abbreviations are the same as those in Table 3.3.

of the yolk sac. Thus, there were no significant interspecific variations in diet diversity of first-feeding individuals (Mann-Whitney *U*-Tests, $P>0.05$). During larval steps L2 and L3, chub and roach had the most and least diverse diets, respectively, in the main river ($P<0.05$). In the marina, no L2-L3 chub were caught, and there were no significant differences between the other species investigated ($P>0.05$). In the pond, roach had the least diverse diet during larval step L2 ($P<0.05$), while there were no differences between the feeding diversities of other species, nor between any species in step L3 ($P>0.05$). Only carp from the pond had significantly more diverse diets than other species during step L4 ($P<0.05$). That case excepted, chub once again had the most diverse diets at all sites (Fig. 5.35). In both the marina and the pond, chub also had the most diverse diets during step L5 ($P<0.05$), while in the main river there were no interspecific differences (Fig. 5.35). Stone loach had the most diverse diet of fish in step L6 in the main river (although chub in this developmental step were not captured), while there were no significant interspecific differences in the marina and the pond (Fig. 5.35). During the juvenile period, there were no significant interspecific differences in feeding diversity in the main river and the pond ($P>0.05$), while in the marina, gudgeon and perch had the most diverse diets (Fig. 5.35). At all three sites, roach had the least diverse diets during the juvenile period (Fig. 5.35). Of the species for which sufficient developmental steps were captured, chub frequently had the highest values of evenness for a given developmental step (Fig. 5.35).

Spatial variations in diversity and evenness of diet

Fish from the marina invariably had more diverse diets than conspecifics of the same developmental step from the main river and the pond (Fig. 5.35), although the differences were often not statistically significant. No spatial variations were found in the diet diversity of first-feeding individuals of any species (Mann-Whitney *U*-Tests, $P>0.05$). In addition, there were no statistically significant spatial variations in diet diversity of dace larvae in steps L2-L4 ($P>0.05$). The diets of the oldest dace larvae (L5-L6) were more diverse in the marina than at the other sites ($P<0.05$), whereas juvenile dace in the pond had more diverse diets than those from the main river (but not the marina). Chub in steps L2 and L3 had more diverse diets in the main river than their counterparts in the pond ($P<0.05$; no L2-L3 chub caught from the marina), whereas there were no statistically significant spatial differences in the feeding diversities of older (L4-J) chub ($P>0.05$). No spatial variations were found in the feeding diversity of roach of any developmental step ($P>0.05$). Perch in steps L3-L5 from the marina had greater feeding diversities than their counterparts from the pond ($P<0.05$), whereas there were no spatial differences between the feeding diversity of the oldest (L6) perch larvae ($P>0.05$). Juvenile perch and gudgeon from the marina had significantly more diverse diets than those from the main river and the pond ($P<0.01$). Fish from the pond frequently had the lowest values of evenness for a given species and developmental step (Fig. 5.35).

5.3.3 Intra- and interspecific diet similarity

Fish in steps L1-L3, L4-L6 and J could be grouped on the basis of their diet (e.g. Fig. 5.36). Thus, ontogenetic diet changes corresponded with the shifts in habitat use identified by Copp (1990c) and Garner (1996b). For the cyprinids, the likely explanation for the unanimous separation of larvae from juveniles is the lack of rotifers in the diets of juveniles and the lack of aufwuchs in the diets of larvae. The shifts were not as clear for perch due to their continued consumption of zooplankton into the juvenile period and their avoidance of rotifers and copepod nauplii.

Non-synchronous diet overlap

Due to good inter-replicate similarity and the large number of fish analysed, non-synchronous diet overlap was investigated via the Bray-Curtis similarity index using mean percent abundance values of each prey taxa, for each developmental step of each species, from each site. Moreover, dendrograms produced using mean values formed the same basic groups as those produced using all fish, but with improved clarity. Percent abundance data were used rather than raw abundance to avoid potential bias related to fish size.

In general, ecologically similar ecospecies had similar diets. The initial division separated young larvae from the majority of old larvae and juveniles, with the diets of fish in the two clusters being almost completely dissimilar (Fig. 5.37). Division of the young larvae cluster separated roach and dace, irrespective of site, and minnow from the marina from the other species (Fig. 5.37), with the diets of the former group dominated by rotifers. Another group contained young larvae of various species and bleak of all

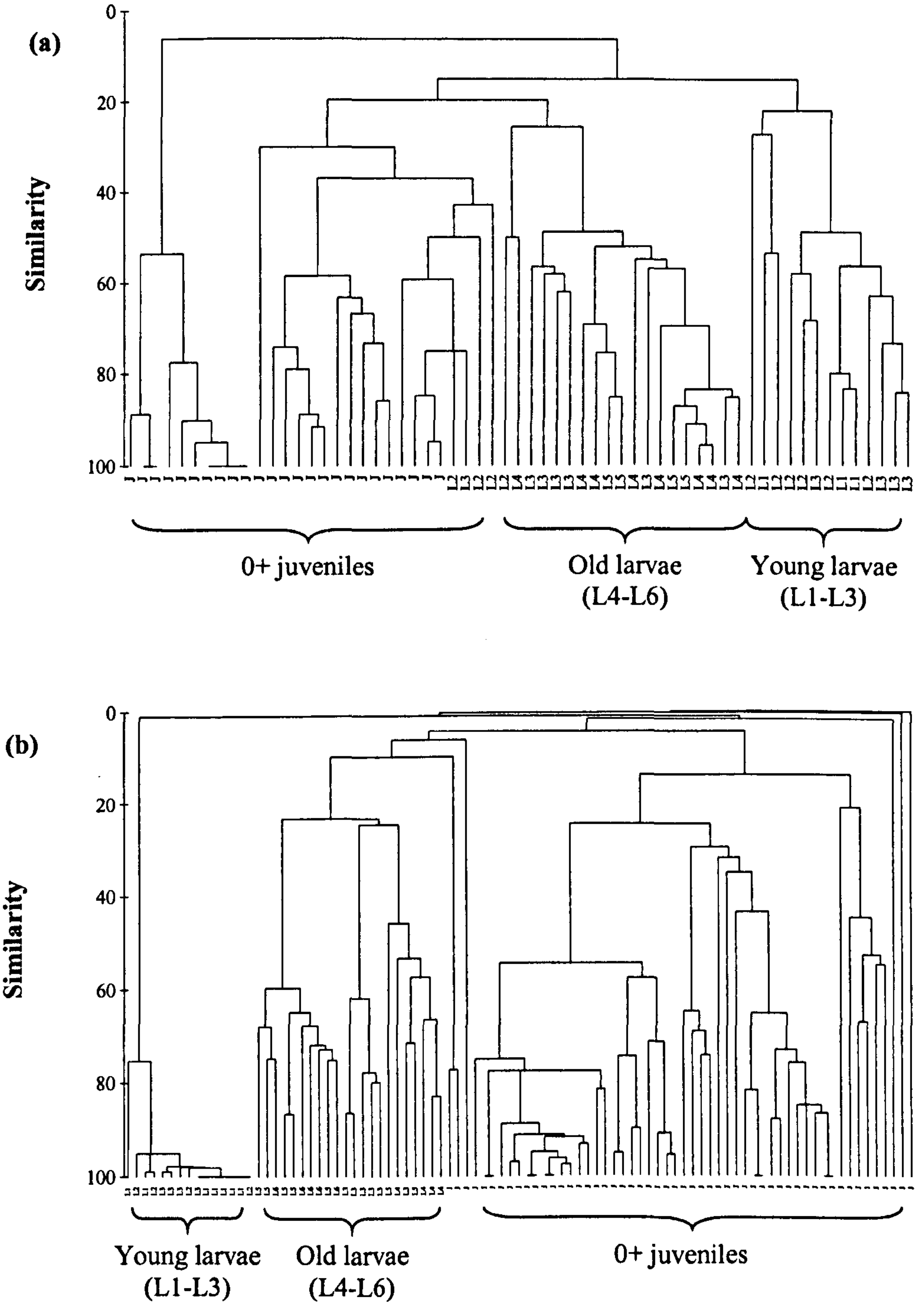


Fig. 5.36 Similarity in diet composition between developmental steps of (a) chub in the main river and (b) dace in the marina. Each sample represents an individual fish.

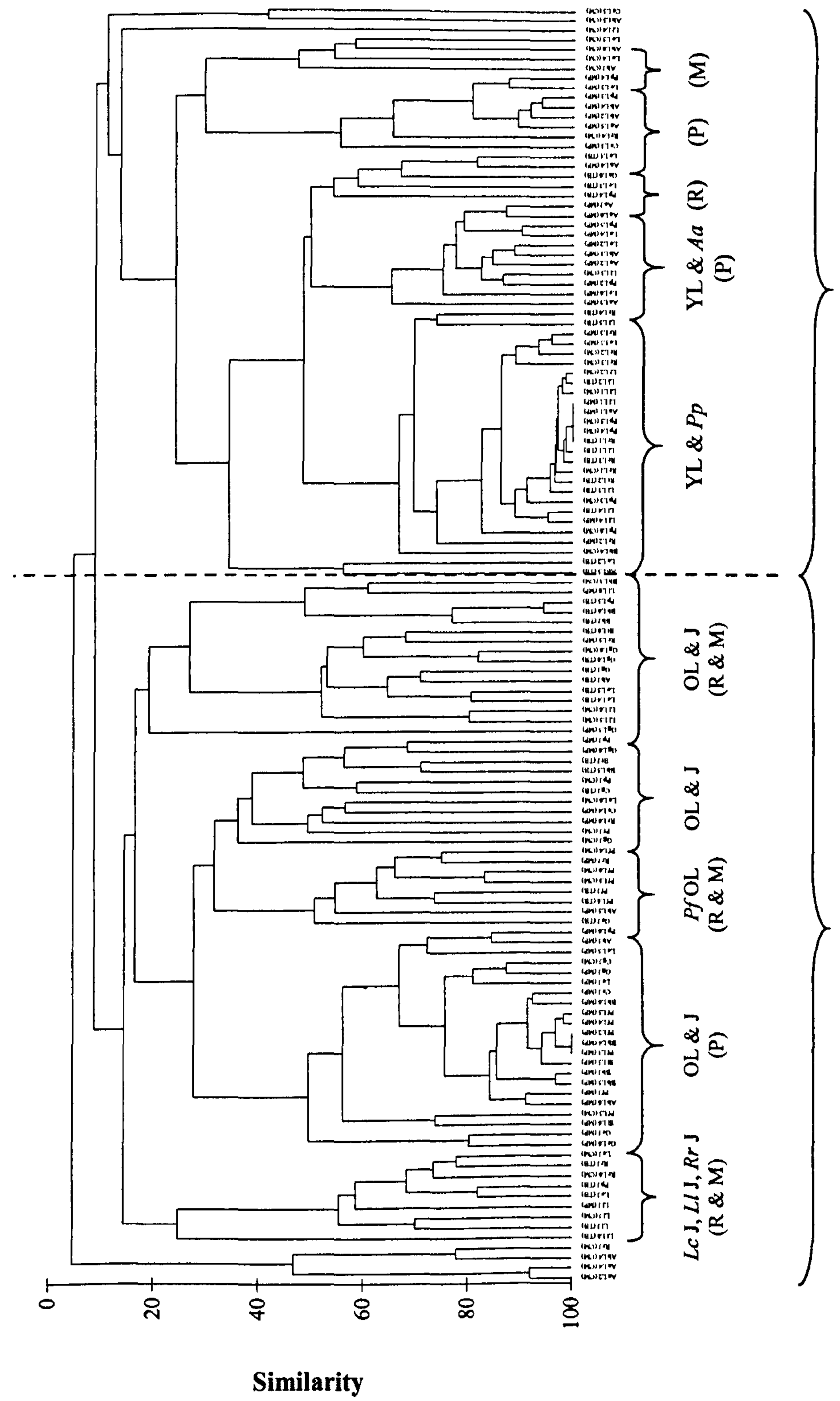


Fig. 5.37 Similarity in diet composition between seven developmental steps of 15 fish species from main river (R), marina (M) and pond (P) macrohabitats. Species name abbreviations (italics) are the same as those in Table 3.3. YL = young larvae, OL = old larvae, J = 0+ juveniles. Each sample represents an individual fish.

developmental steps from the pond (Fig. 5.37), with the diets of these fish characterised by copepod nauplii. Three smaller groups of lesser similarity contained young and old larvae from the main river, marina and pond, respectively. There was, however, no obvious aggregation of species or developmental steps within these groups. Interspecific overlap was greatest in the young larval steps although, unfortunately, young larvae were caught for relatively few species. The young larvae (L1-L3) of dace and roach had the most similar diets (>95% similarity), while the diets of older (L4-L5) dace and roach were also comparable to those of the young larvae (Fig. 5.37). In contrast with dace and roach, there was less similarity of diet within larval steps for chub which, consequently, were grouped irrespective of developmental step. Distinct clusters of particular developmental steps were difficult to discern, and may have been exacerbated by the presence of many developmental steps over extended time periods (of differing food conditions) due to multiple spawning events (see Chapter 3). Unfortunately, however, insufficient data were available to test for overlap between cohorts. Chub appeared to be grouped more by site than developmental step, perhaps a reflection of the constraints of site-specific food availability rather than those of ontogenetic foraging capability. Of the commoner species, only perch and bleak had diets that differed from those of other young larvae. All perch were grouped in the old larvae/juvenile cluster while bleak were either grouped in the young larvae cluster or on their own (Fig. 5.37), since perch rarely consumed rotifers and bleak nearly always consumed rotifers.

The old larvae/juvenile cluster was divided into five main groups (Fig. 5.37). Percids (perch, zander, ruffe) and benthic feeders (especially barbel) from the pond were grouped together (Fig. 5.37), with their diets characterised by copepods. Perch from the marina and the main river were grouped together, as were most juvenile dace, roach and chub. The two remaining groups of lesser similarity contained predominantly benthic feeders (gudgeon, barbel, bullhead, stone loach) and old dace, roach and chub larvae (Fig. 5.37). Within each species, the majority of old larvae were separated from the juveniles, although this was obscured when plotting all species together. Fish from the pond had the most similar diets, irrespective of species or developmental step, with the majority of diets >70% similar (Fig. 5.37). Whereas fish from the main river and the marina were grouped first by ecospecies, then species (or functional guild), the high availability of food in the pond appeared to override the effects of these factors, with all species sharing similar diets (Fig. 5.37).

Synchronous diet overlap

Although the diets of the young larvae of many species were similar, they did not necessarily compete for food resources since many of them did not overlap spatially or temporally. For example, dace hatched approximately two months earlier than chub, by which time all dace were juveniles. Dace and chub larvae, therefore, did not overlap temporally and so could not compete for resources.

In the main river, the diets of L3-L5 dace overlapped with those of L1-L3 roach (Fig. 5.38), while the diets of older roach (L4), dace (L5-L6), perch (L6) and stone loach (L6-J) were unique (Fig. 5.39). In mid June, the majority of dace (J), perch (J), chub (L2), gudgeon (L6-J) and three-spined stickleback (L6-J) had unique diets, while most juvenile minnow were clustered with juvenile roach (Fig. 5.40). Another cluster contained mostly benthic feeders (i.e. barbel, bullhead, stone loach). In late June, juvenile dace, roach, chub and minnow overlapped, L3-L4 chub and juvenile gudgeon overlapped, and juvenile perch and three-spined stickleback overlapped (Fig. 5.41). In early July, juvenile dace and three-spined stickleback had unique diets, while juvenile roach and minnow were similar (Fig. 5.42). Most juvenile gudgeon were grouped together, as were juvenile perch. In late July, juvenile dace, roach, chub and gudgeon all overlapped (Fig. 5.43). In August, most juvenile dace, chub, perch, roach and gudgeon were grouped together, with the remaining roach and dace overlapping with bream (Fig. 5.44). In September, roach and dace overlapped, while perch had separate diets (Fig. 5.45), whereas in October dace and chub were grouped together, and gudgeon and roach had separate diets (Fig. 5.46).

In the marina, young dace larvae (L1-L3) shared similar diets to first-feeding roach (Fig. 5.47), whereas in both early and late May, roach, perch and dace had separate diets (Figs 5.48-5.49). In early June, bleak, roach (J) and bream (L4) shared diets, and most carp were grouped with perch, while chub, barbel, gudgeon, dace and bullhead had separate diets (Fig. 5.50). In late June and early July, perch, dace, roach, chub and bream had separate diets (Figs 5.51-5.52). In late July, juvenile roach, dace and chub were grouped

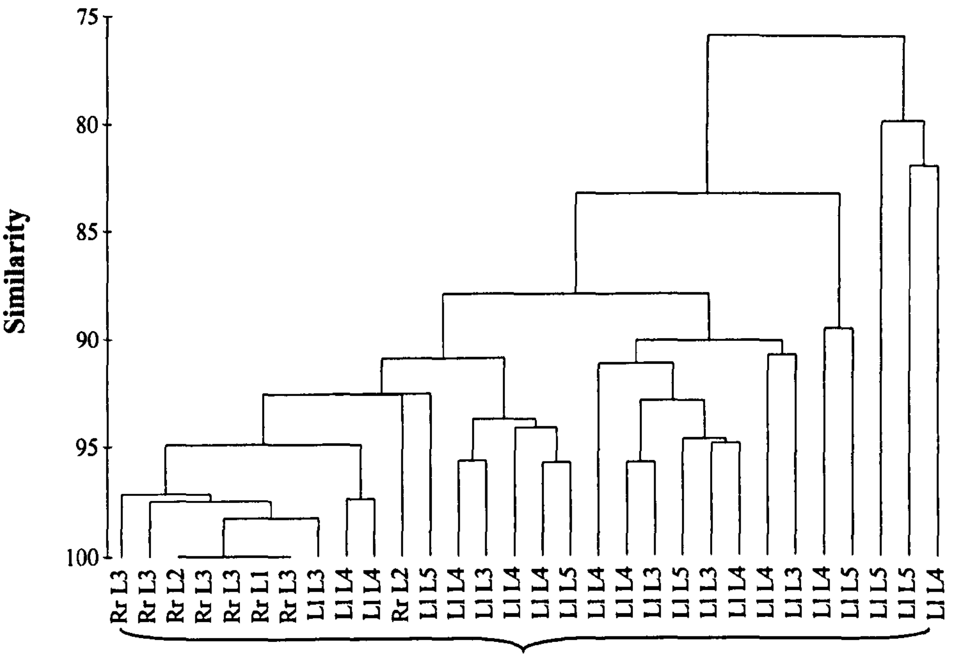


Fig. 5.38 Similarity in diet composition of 0+ fish in the main river, 15 May 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

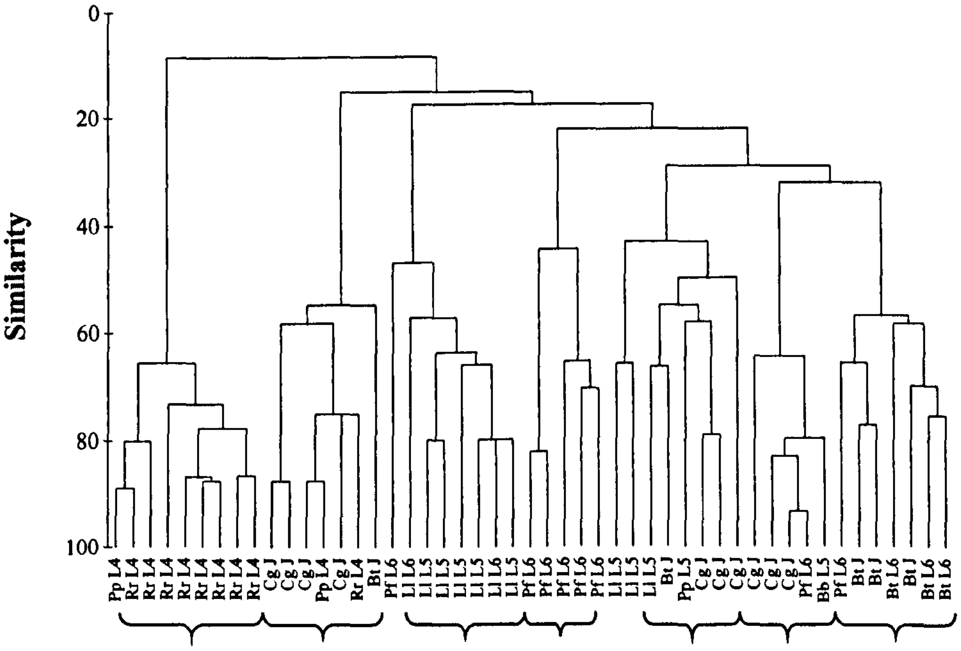


Fig. 5.39 Similarity in diet composition of 0+ fish in the main river, 29 May 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

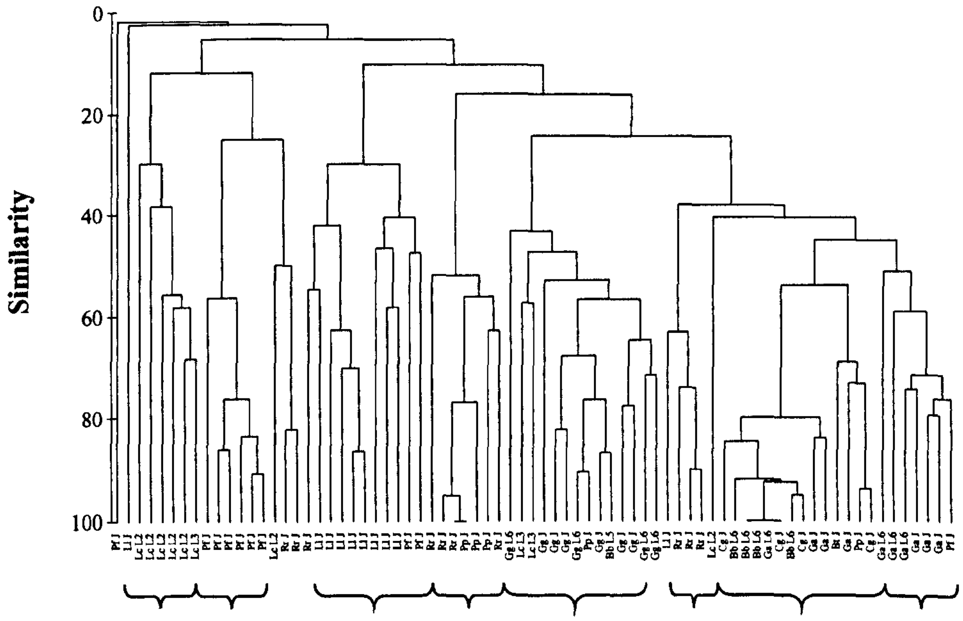


Fig. 5.40 Similarity in diet composition of 0+ fish in the main river, 13 June 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

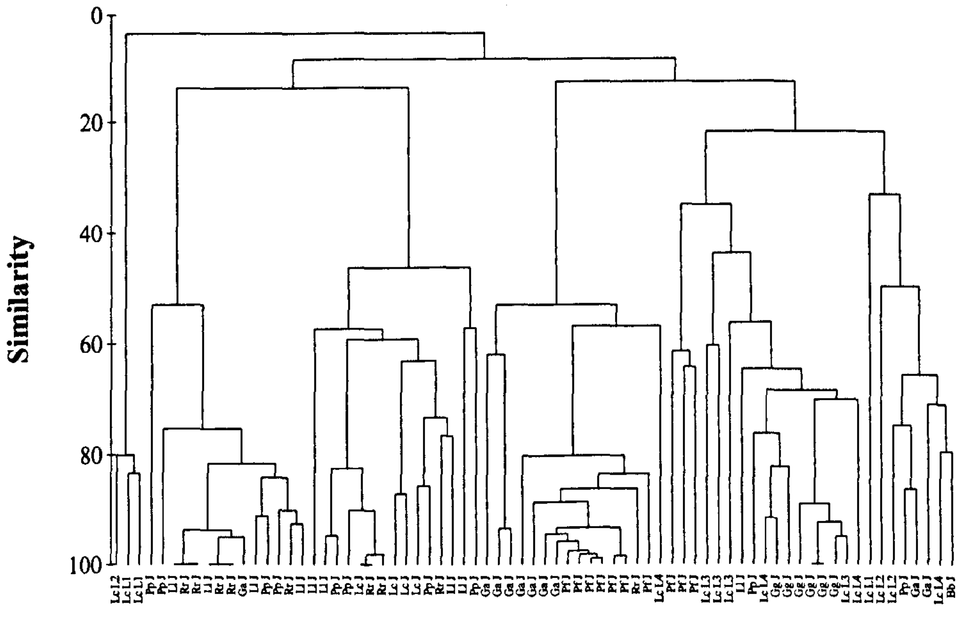


Fig. 5.41 Similarity in diet composition of 0+ fish in the main river, 26 June 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

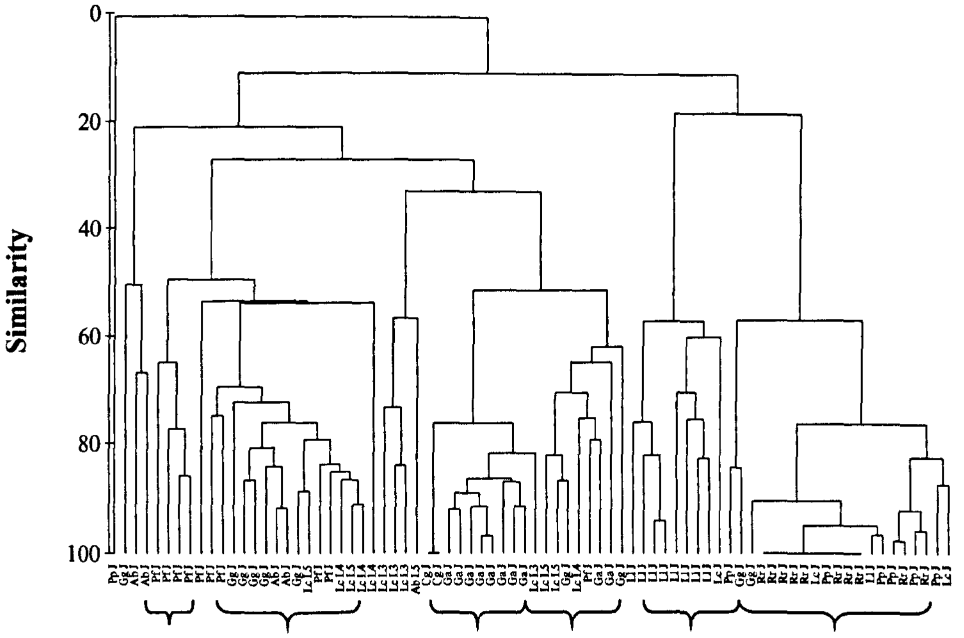


Fig. 5.42 Similarity in diet composition of 0+ fish in the main river, 8 July 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

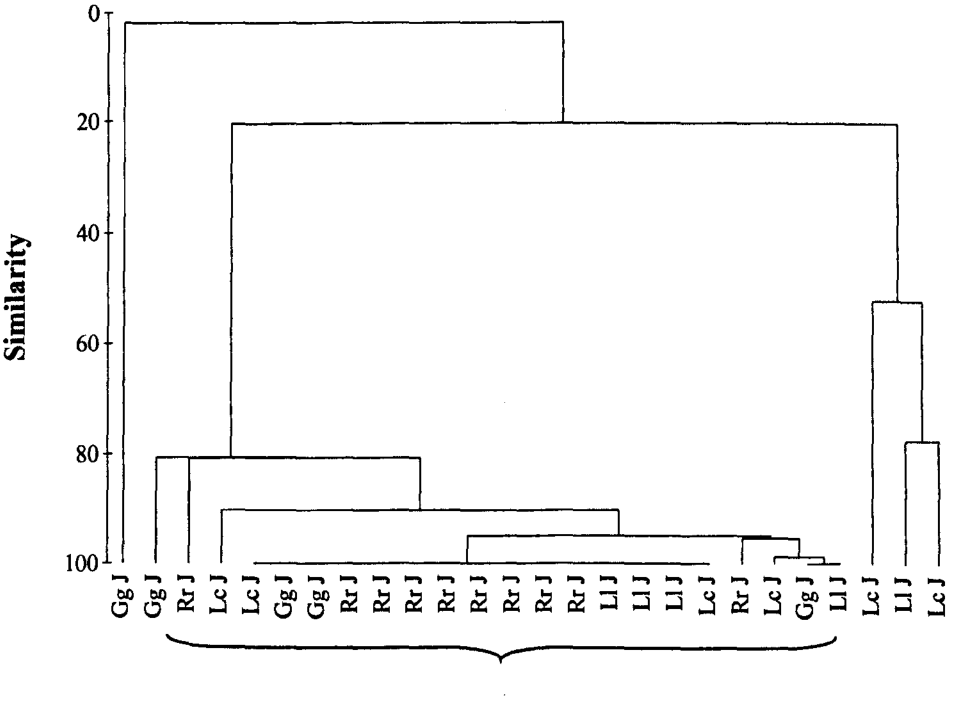


Fig. 5.43 Similarity in diet composition of 0+ fish in the main river, 23 July 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

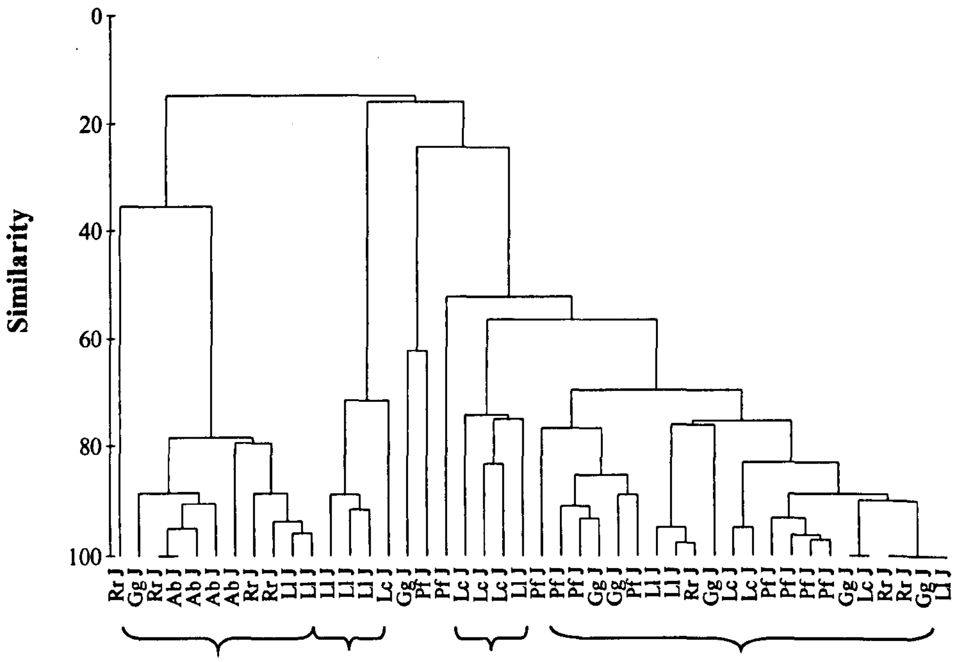


Fig. 5.44 Similarity in diet composition of 0+ fish in the main river, 7 August 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

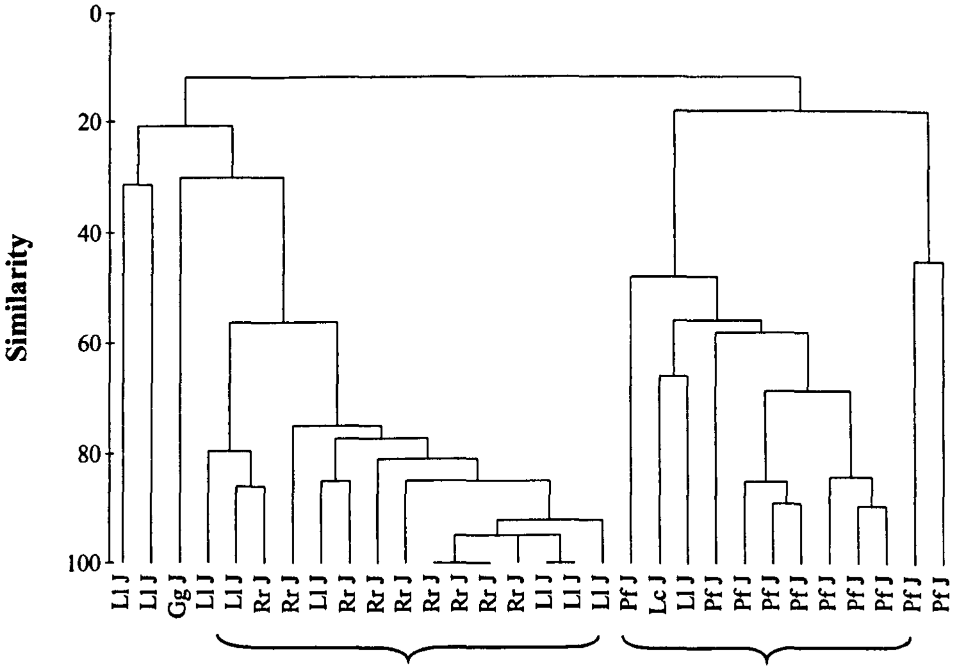


Fig. 5.45 Similarity in diet composition of 0+ fish in the main river, 10 September 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

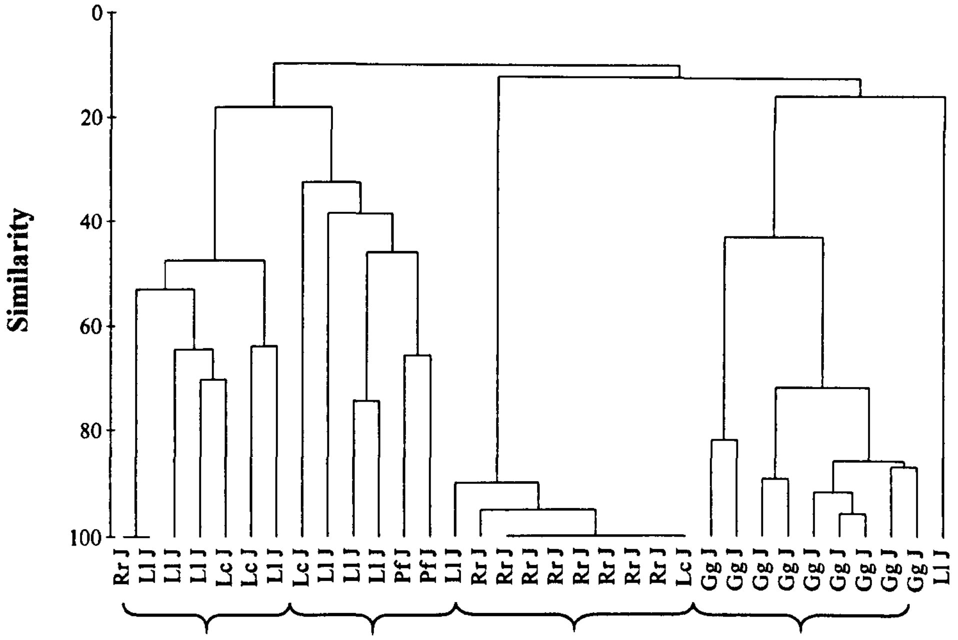


Fig. 5.46 Similarity in diet composition of 0+ fish in the main river, 15 October 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

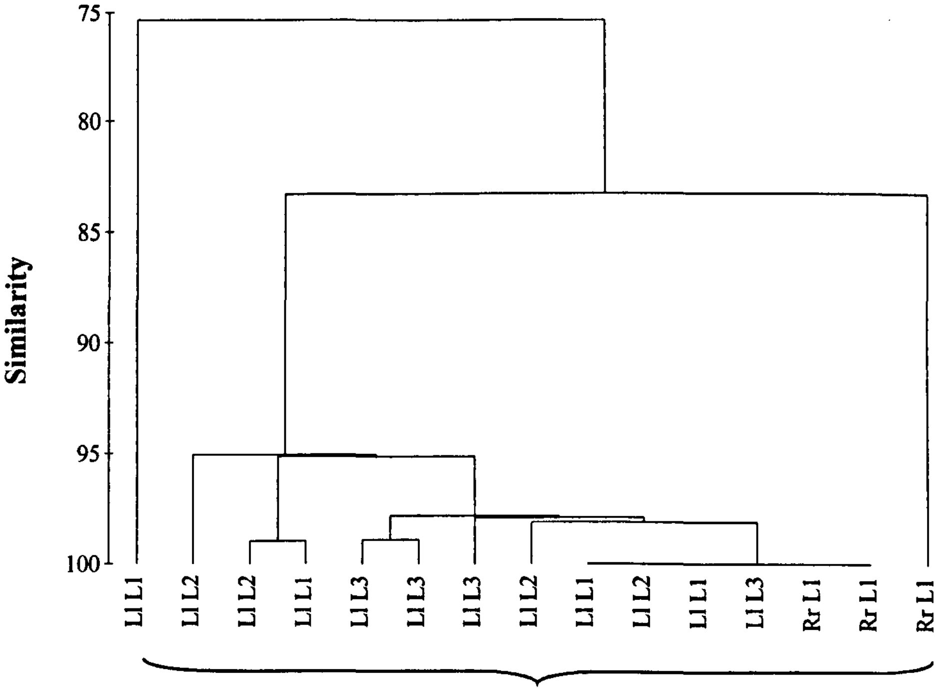


Fig. 5.47 Similarity in diet composition of 0+ fish in the marina, 29 April 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

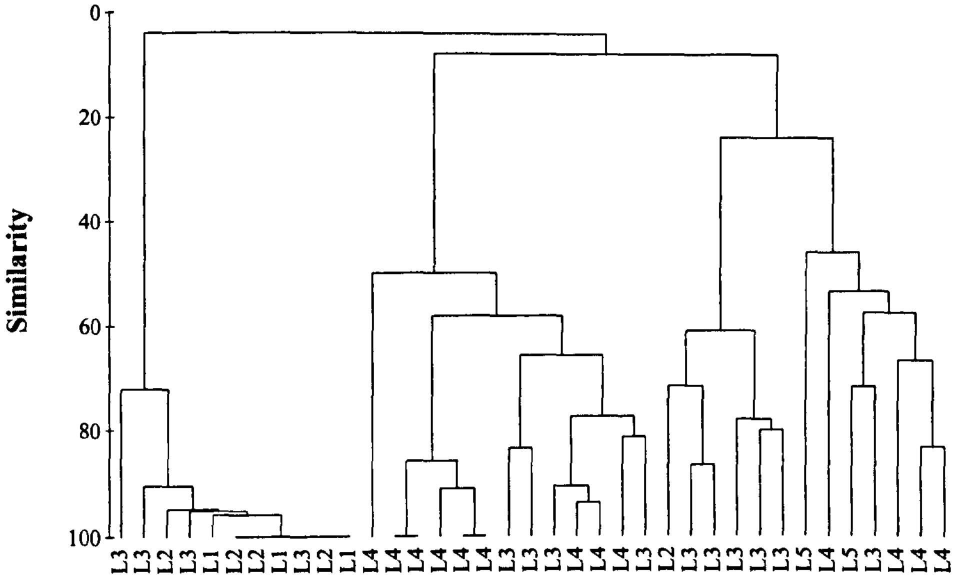


Fig. 5.48 Similarity in diet composition of 0+ fish in the marina, 15 May 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

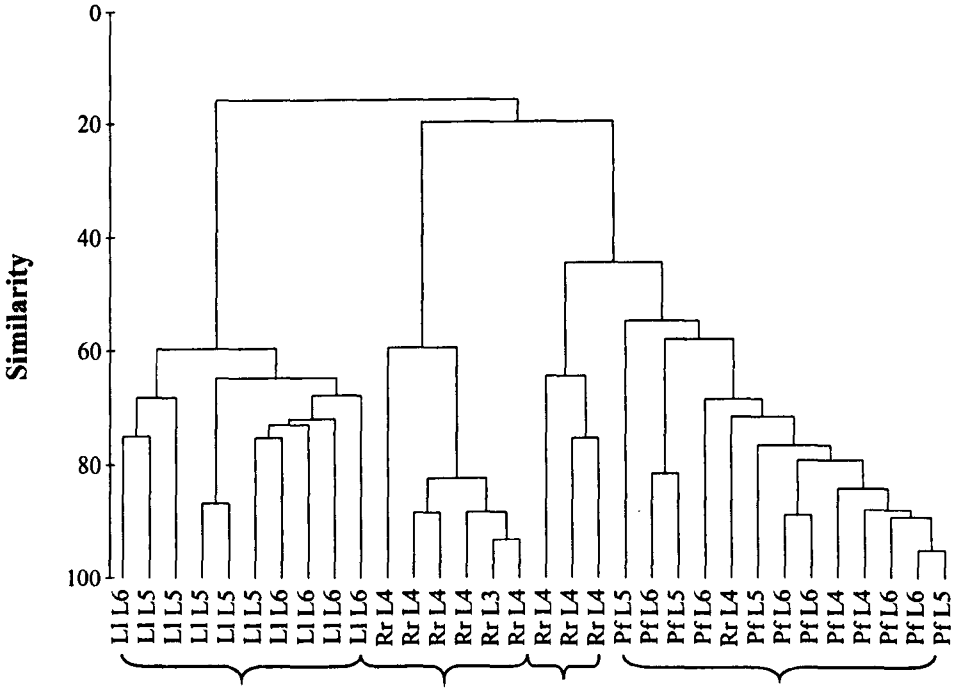


Fig. 5.49 Similarity in diet composition of 0+ fish in the marina, 29 May 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

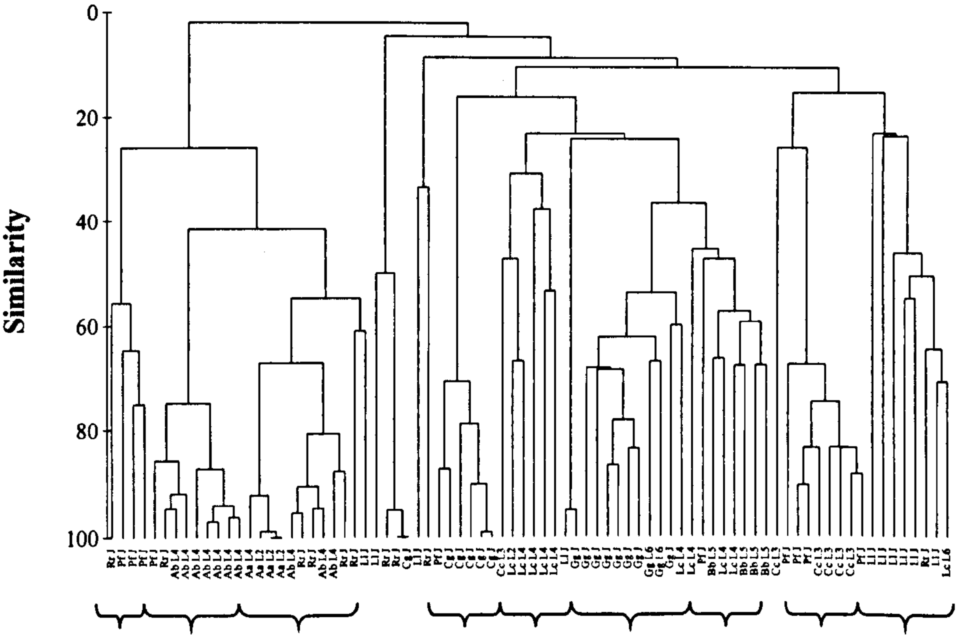


Fig. 5.50 Similarity in diet composition of 0+ fish in the marina, 13 June 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

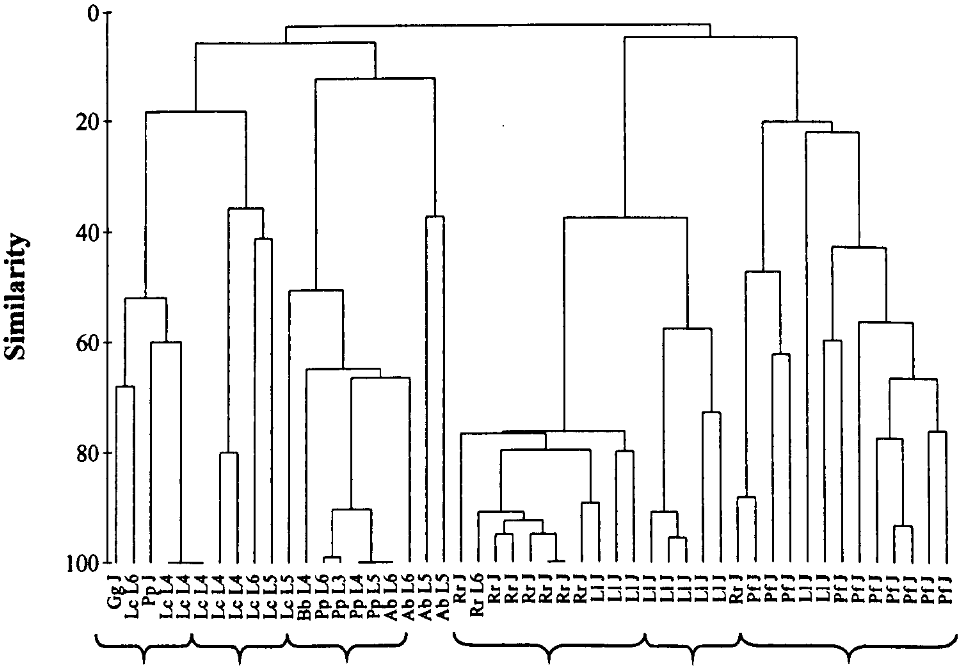


Fig. 5.51 Similarity in diet composition of 0+ fish in the marina, 26 June 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

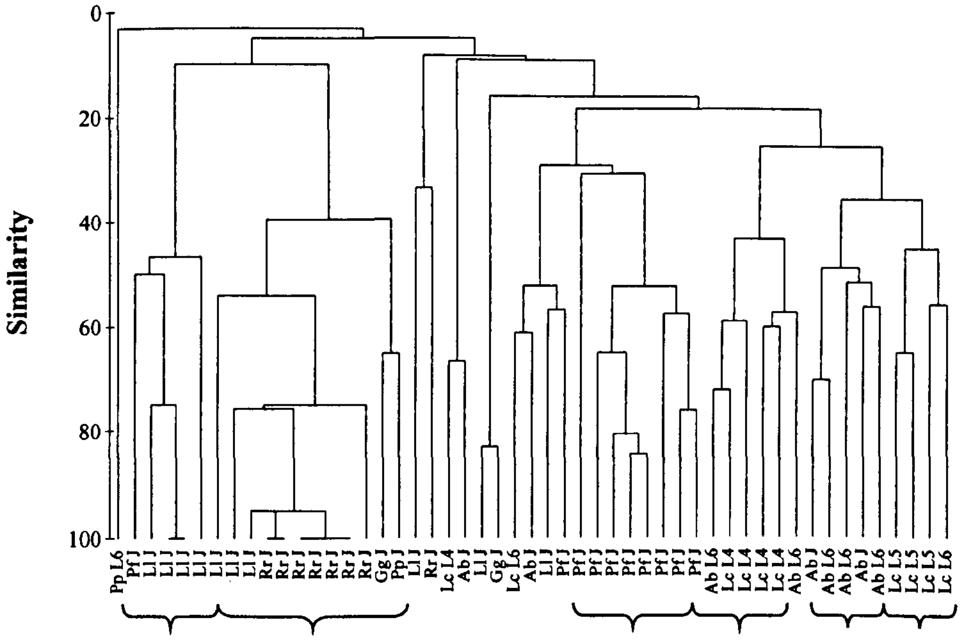


Fig. 5.52 Similarity in diet composition of 0+ fish in the marina, 8 July 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

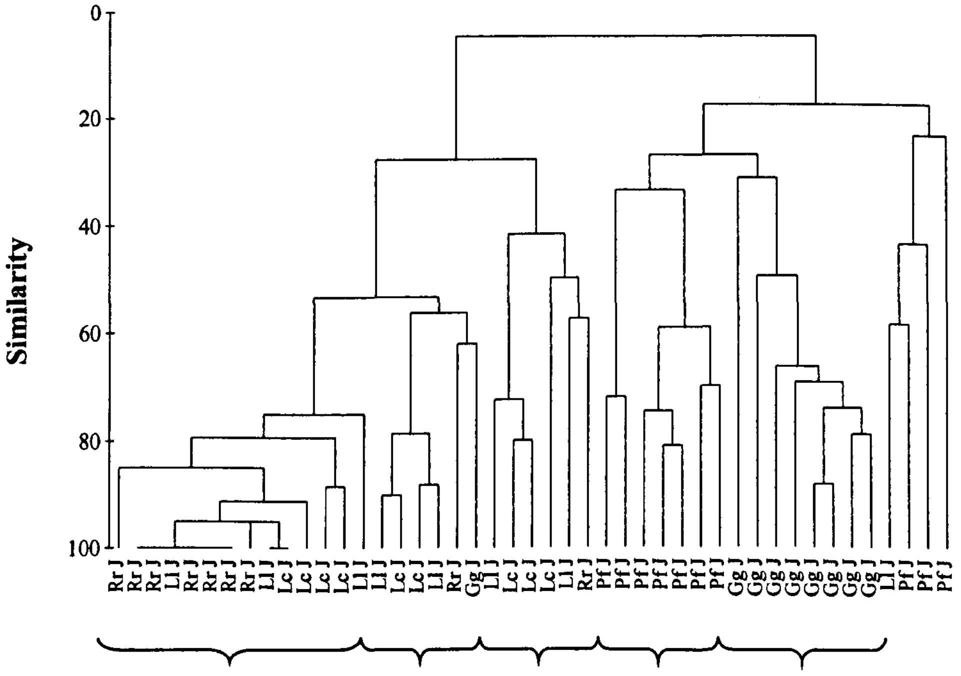


Fig. 5.53 Similarity in diet composition of 0+ fish in the marina, 23 July 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

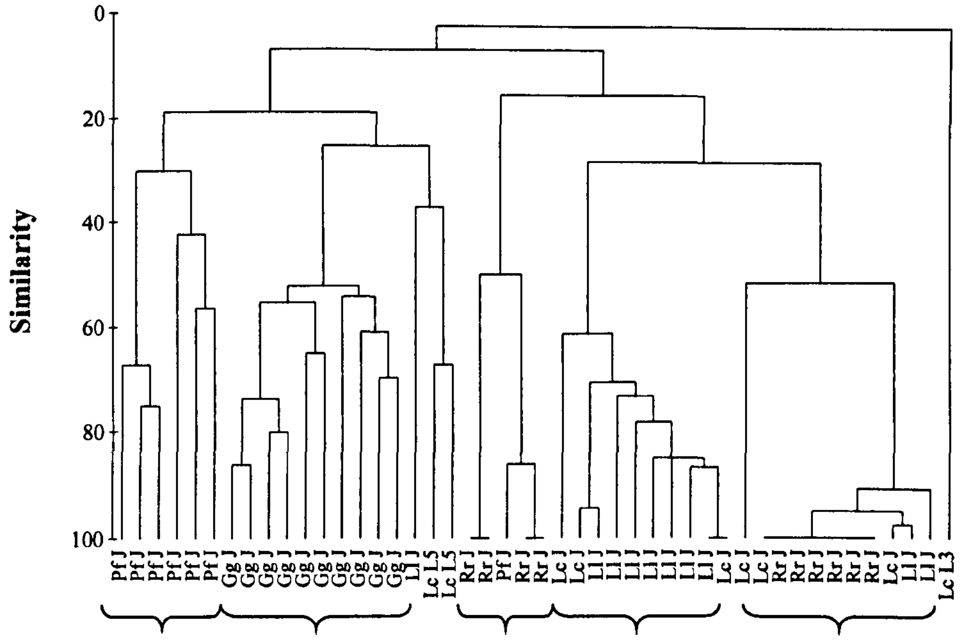


Fig. 5.54 Similarity in diet composition of 0+ fish in the marina, 7 August 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

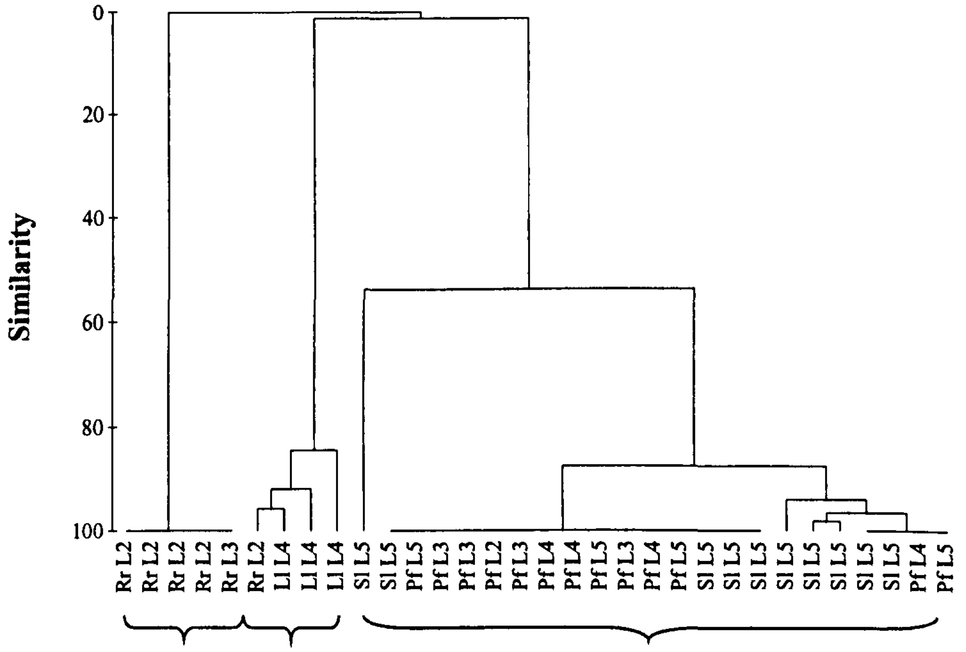


Fig. 5.55 Similarity in diet composition of 0+ fish in the pond,15 May 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

together, while juvenile gudgeon and perch had distinct diets (Fig. 5.53). In August, juvenile perch, roach, dace and gudgeon had separate diets (Fig. 5.54).

In the pond, perch (L2-L5) and zander (L5) had almost identical diets, while roach (L2-L3) and dace (L4) had separate diets (Fig. 5.55). Few fish were captured in late May but, nonetheless, dace (L6), zander (L6), roach (L2-L3) and bream (L3) had separate diets (Fig. 5.56). In early June, ruffe, carp, roach, chub, bleak and dace had separate diets (Fig. 5.57), while in late June, bleak overlapped with minnow (L2-L5), and carp, gudgeon and the majority of older (L4-J) chub were grouped together (Fig. 5.58). Young (L1-L3) chub and juvenile minnow had separate diets. Patterns were difficult to discern in early July, with only larval chub having separate diets (Fig. 5.59). Patterns were again difficult to discern in late July, although the majority of juvenile chub, gudgeon and bream overlapped (Fig. 5.60). In August, the majority of chub and dace had separate diets, while bream and gudgeon were clustered together (Fig. 5.61). In September, perch and gudgeon had separate diets (Fig. 5.62).

5.3.4 Selection

The general sequence of ontogenetic shifts in food consumption identified in Section 5.3.1 was reflected in the electivity indices (e.g. Fig. 5.63). Rotifers and the <0.25 mm food category were most highly selected by young larvae, with electivity indices declining and becoming negative with development. A similar pattern was often apparent for copepod nauplii, although electivity indices were rarely positive. Electivity indices for planktonic cladocerans and copepods, and 0.25-0.49 mm prey were highest, albeit usually negative, in the intermediate (small planktonic cladocerans) and late larval and juvenile steps (large planktonic cladocerans and planktonic copepods). In contrast with rotifers and copepod nauplii, non-planktonic crustaceans and ≥0.5 mm zooplankters were avoided in the early larval steps, with electivity indices typically increasing with development.

L1 and L2 dace selected <0.25 mm rotifers but avoided similar-sized copepod nauplii and all larger prey (including rotifers), the exception being in the pond where 0.25-0.49 mm rotifers were selected by L1 fish (Fig. 5.63). In the main river and the pond, L3-L4 dace selected <0.25 mm rotifers over other similar-sized and larger prey, whereas in the

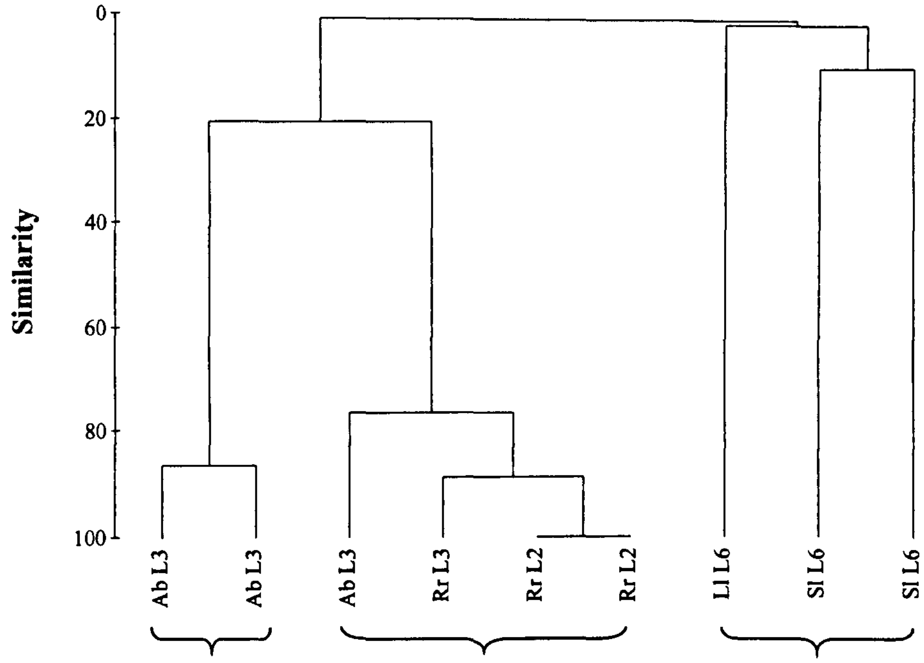


Fig. 5.56 Similarity in diet composition of 0+ fish in the pond, 29 May 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

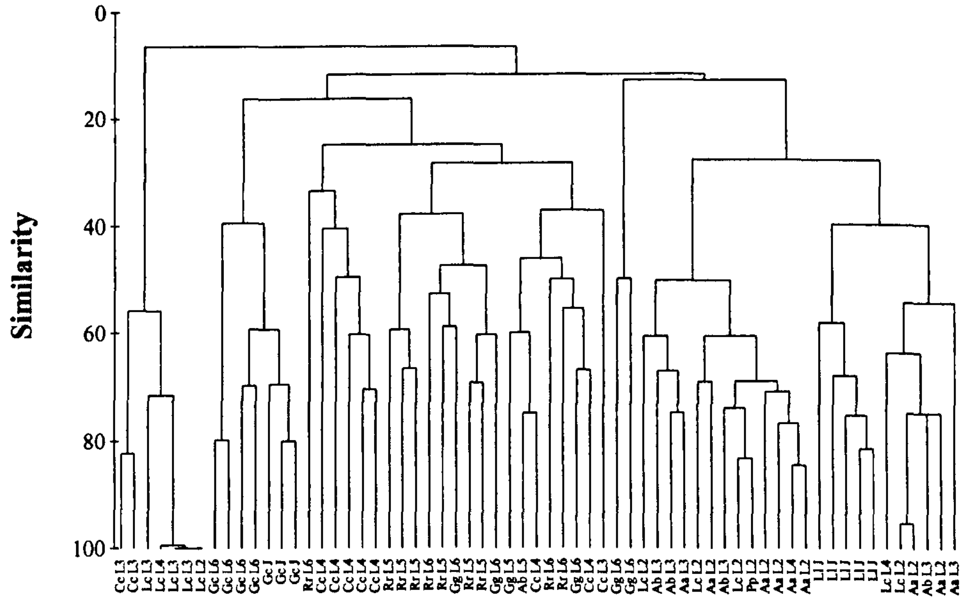


Fig. 5.57 Similarity in diet composition of 0+ fish in the pond, 13 June 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

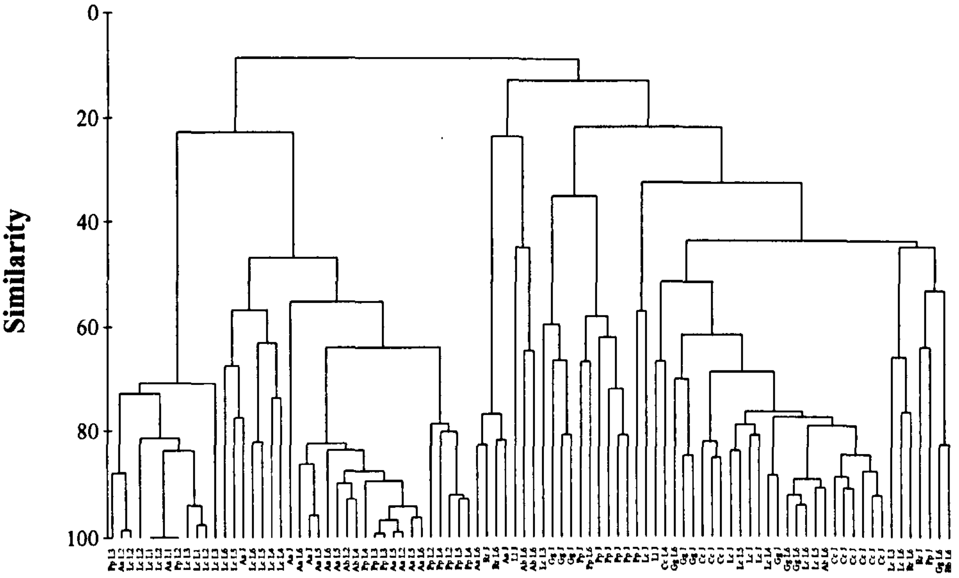


Fig. 5.58 Similarity in diet composition of 0+ fish in the pond, 26 June 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

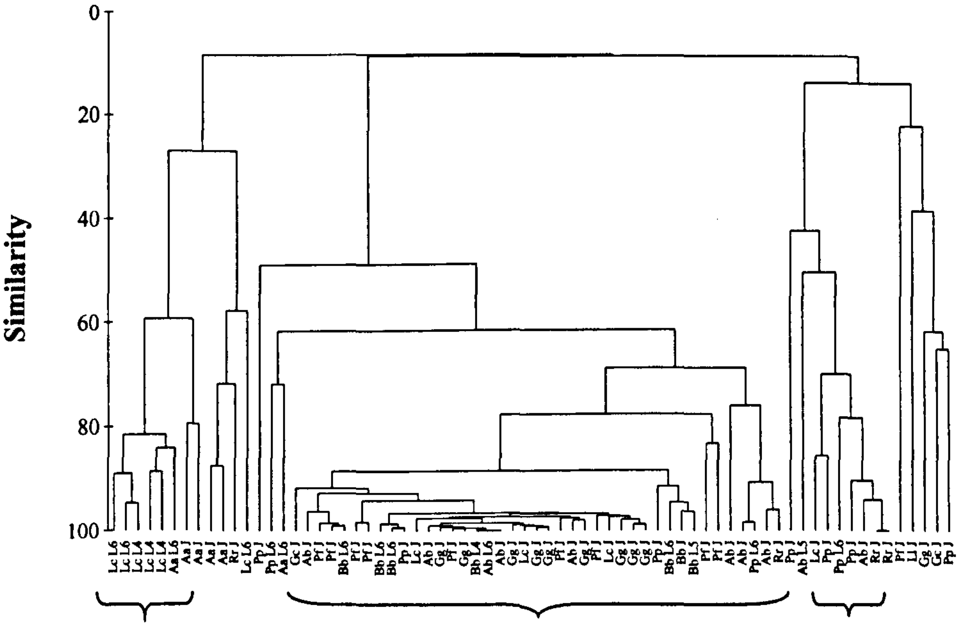


Fig. 5.59 Similarity in diet composition of 0+ fish in the pond, 8 July 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

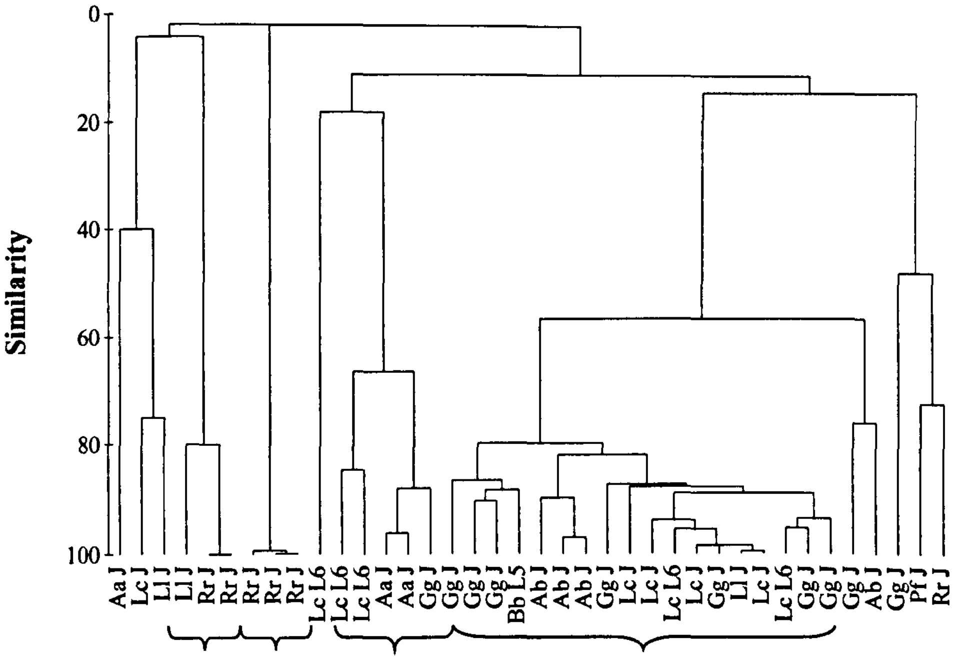


Fig. 5.60 Similarity in diet composition of 0+ fish in the pond, 23 July 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

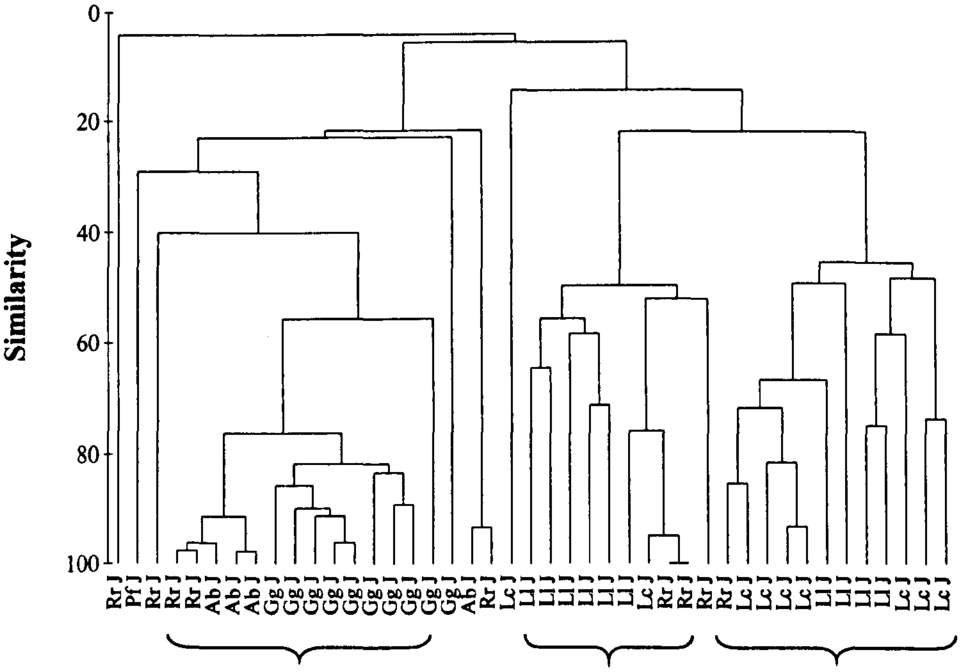


Fig. 5.61 Similarity in diet composition of 0+ fish in the pond, 7 August 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

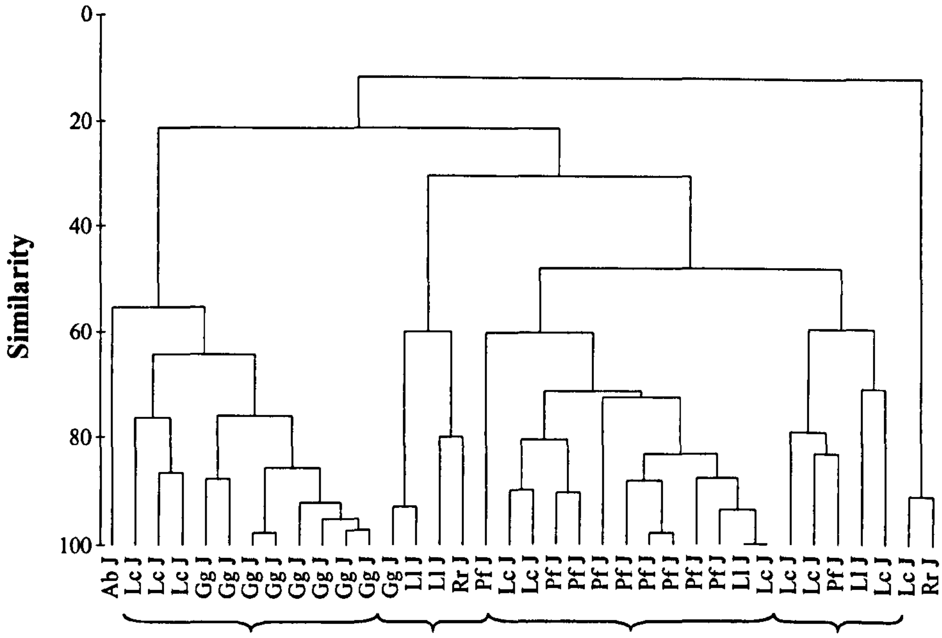


Fig. 5.62 Similarity in diet composition of 0+ fish in the pond, 10 September 2003. Species name abbreviations are the same as those in Table 3.3. Each sample represents an individual fish.

marina 0.25-1 mm non-planktonic crustaceans were favoured (Fig. 5.63). No <0.25 mm prey were selected from L5-J, with ≥0.25 mm non-planktonic crustaceans selected over other zooplankton. Electivity indices for <0.25 mm rotifers declined and became negative with development, with rotifers of all sizes avoided by dace from step L5. All sizes of copepod nauplii, planktonic copepods and planktonic cladocerans were generally avoided by dace of all developmental steps, the main exceptions being in the pond where juveniles selected 0.5-1 mm planktonic copepods and ≥0.5 mm planktonic cladocerans (Fig. 5.63). Electivity indices for non-planktonic crustaceans were generally positive and, particularly for those ≥0.25 mm, greater than those of other zooplankton.

L1-L3 roach selected <0.25 mm rotifers but avoided copepod nauplii of similar size and most larger prey, although 0.25-0.49 mm rotifers were selected by L2-L3 roach in the marina and L3 roach in the main river and the pond (Fig. 5.64). L4-L6 roach favoured ≥0.25 mm non-planktonic crustaceans, while 0.25-1 mm planktonic cladocerans and copepods were also selected to a lesser extent by L5-L6 roach in the pond (Fig. 5.64). Juvenile roach selected 0.25-0.49 mm planktonic cladocerans and ≥0.5 mm non-planktonic crustaceans (Fig. 5.64). Electivity indices for <0.25 mm rotifers declined and

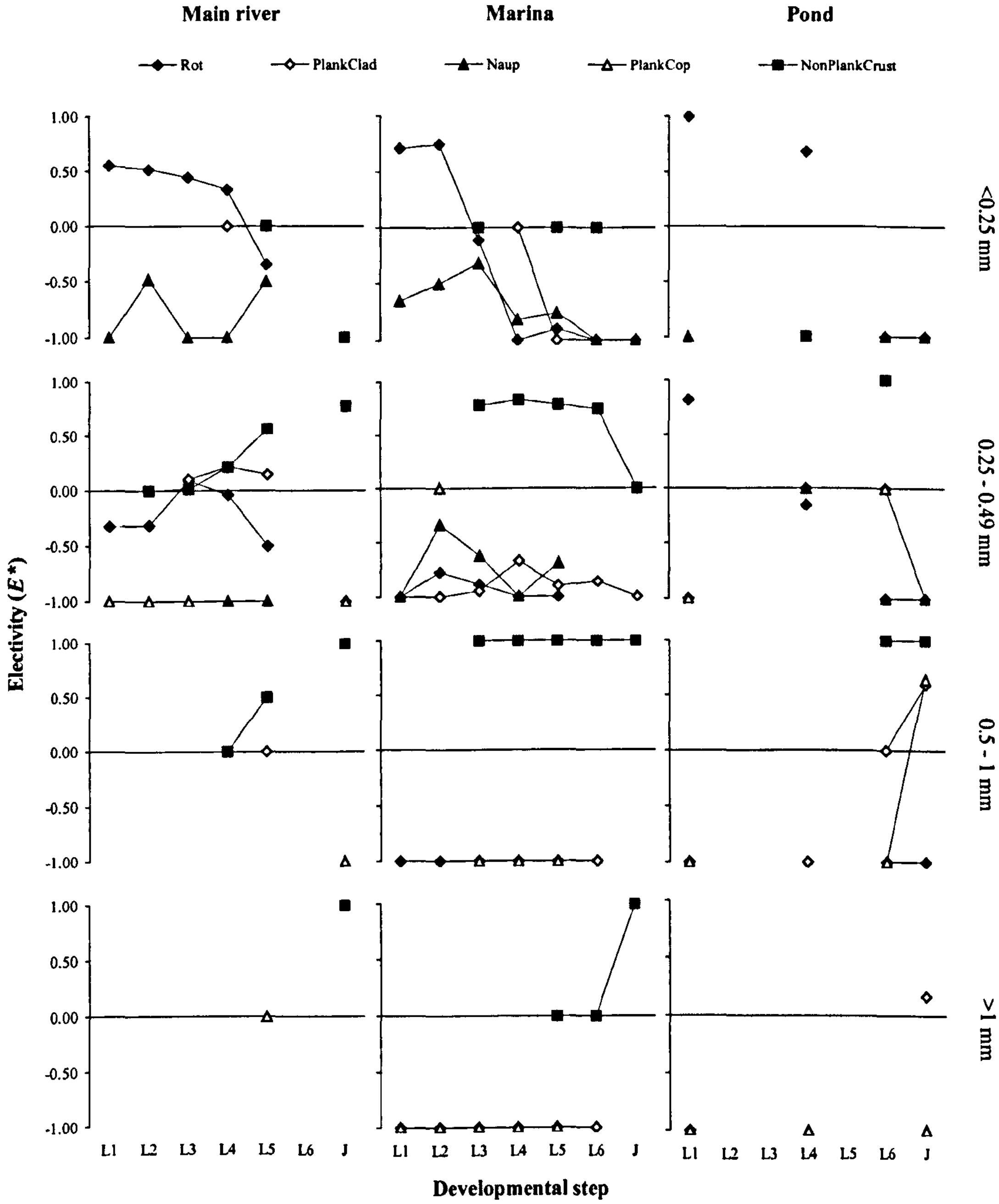


Fig. 5.63 Electivity indices for dace for four size classes of five zooplankton groups at main river, marina and pond macrohabitats.

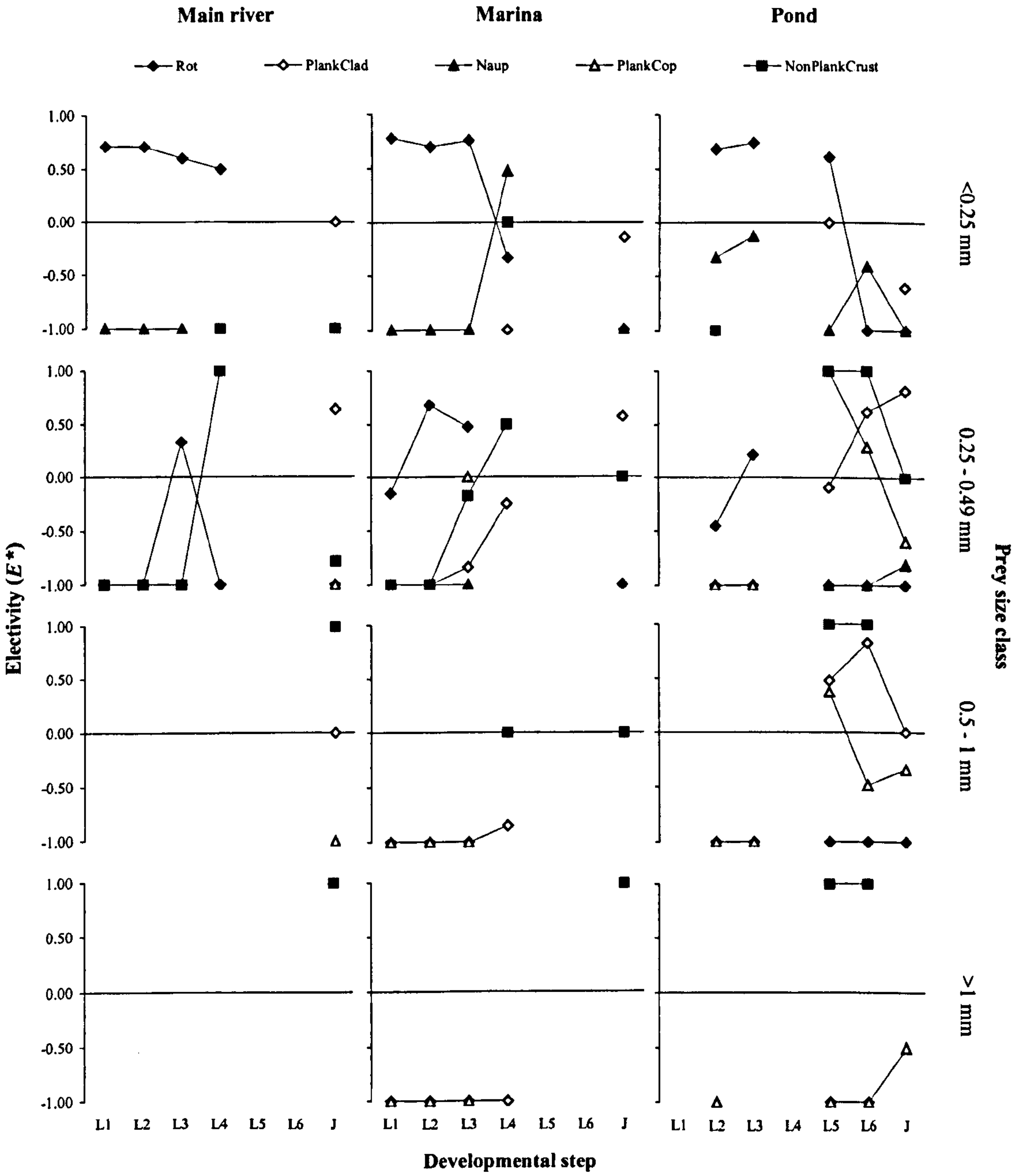


Fig. 5.64 Electivity indices for roach for four size classes of five zooplankton groups at main river, marina and pond macrohabitats.

became negative with development, with rotifers of all sizes avoided by roach from step L6. Planktonic cladocerans of all sizes were avoided by young larvae, but electivity indices, particularly of 0.25-1 mm prey, increased with development and became positive in late larval steps and the juvenile period. Copepod nauplii of all sizes were invariably avoided by roach of all developmental steps, and the same was broadly true for planktonic copepods, with the main exception being in the pond where 0.25-1 mm individuals were selected by L5 roach (Fig. 5.64). Non-planktonic crustaceans of all sizes were avoided by young larvae but, with the exception of the <0.25 mm size class, electivity values increased with development, and generally became positive in the late larval steps when they were selected over similar-sized rotifers, planktonic cladocerans and copepod nauplii.

L1 chub selected <0.25 mm rotifers over similar-sized copepod nauplii and planktonic cladocerans, and larger zooplankton (Fig. 5.65). L2 chub also selected <0.25 mm rotifers plus, along with L3-J chub, 0.25-1 mm non-planktonic crustaceans (Fig. 5.65). In the pond, L5-L6 and juvenile chub also displayed strong selection for 0.5-1 mm and >1 mm planktonic cladocerans, respectively (Fig. 5.65). Electivity indices for <0.25 mm rotifers declined and became negative with development, with larger rotifers also avoided by all developmental steps. Planktonic cladocerans <0.25 mm were avoided by all developmental steps, while electivity indices for 0.25-0.49 mm and ≥0.5 mm planktonic cladocerans were generally greatest in the middle, and late larval and juvenile steps, respectively. Copepod nauplii of all sizes were invariably avoided by chub of all developmental steps, the exception being in the pond where L3-L6 chub selected <0.25 mm nauplii over other taxa of similar size (Fig. 5.65). Planktonic copepods were generally avoided in the main river, whereas they were selected by L5-L6 chub in the marina. In the pond, planktonic copepods were completely avoided by L1 and L2 chub, but electivity indices, particularly for 0.25-1 mm prey, increased with development and became positive in the late larval steps and juvenile period. Non-planktonic crustaceans <0.25 mm were generally avoided by chub of all developmental steps, whereas those ≥0.25 mm were frequently selected over other taxa of similar sizes.

Perch of all developmental steps avoided <0.25 mm zooplankton, and most also avoided 0.25-0.49 mm animals. L3 and L4 perch selected 0.5-1 mm planktonic copepods (Fig.

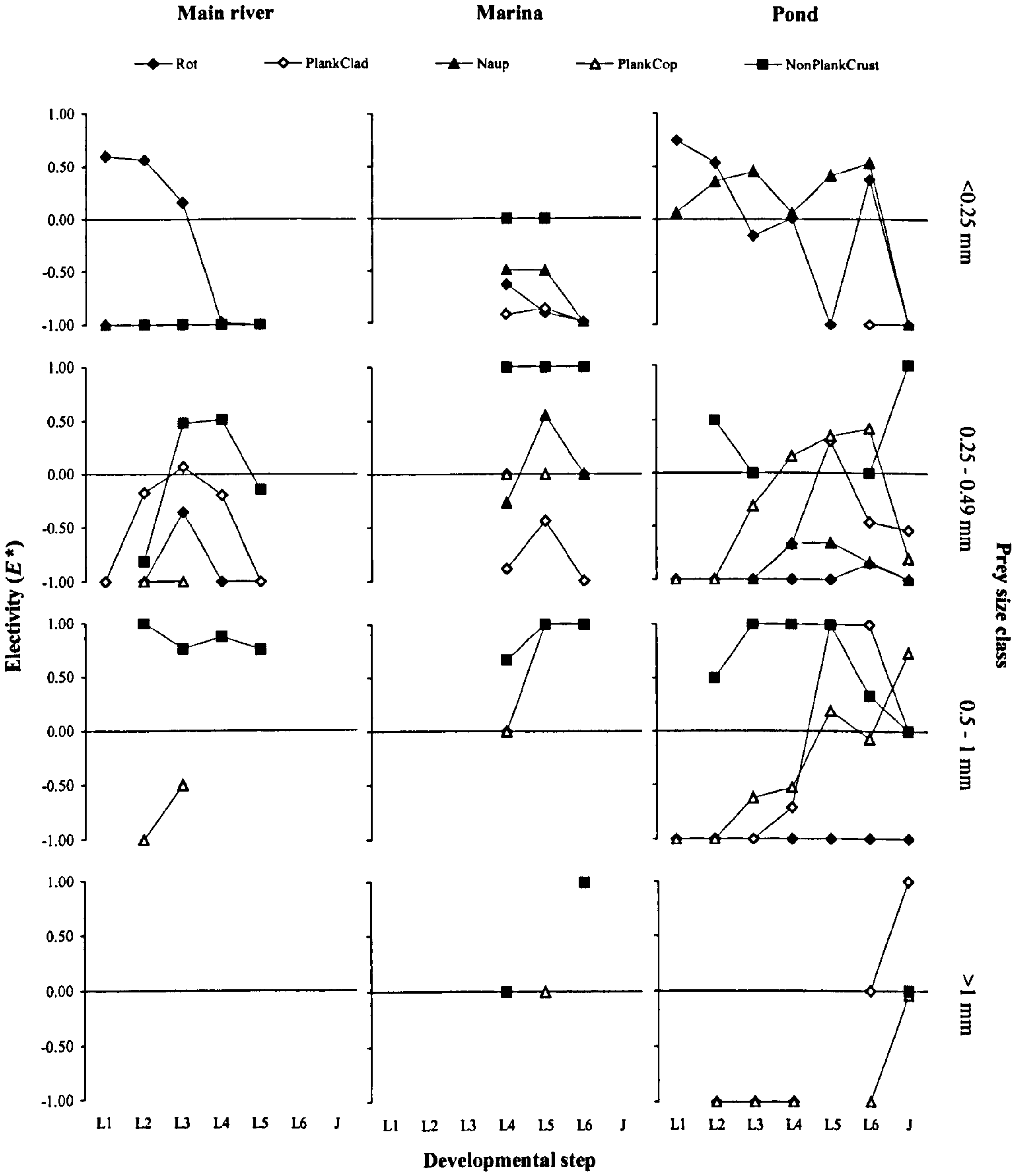


Fig. 5.65 Electivity indices for chub for four size classes of five zooplankton groups at main river, marina and pond macrohabitats.

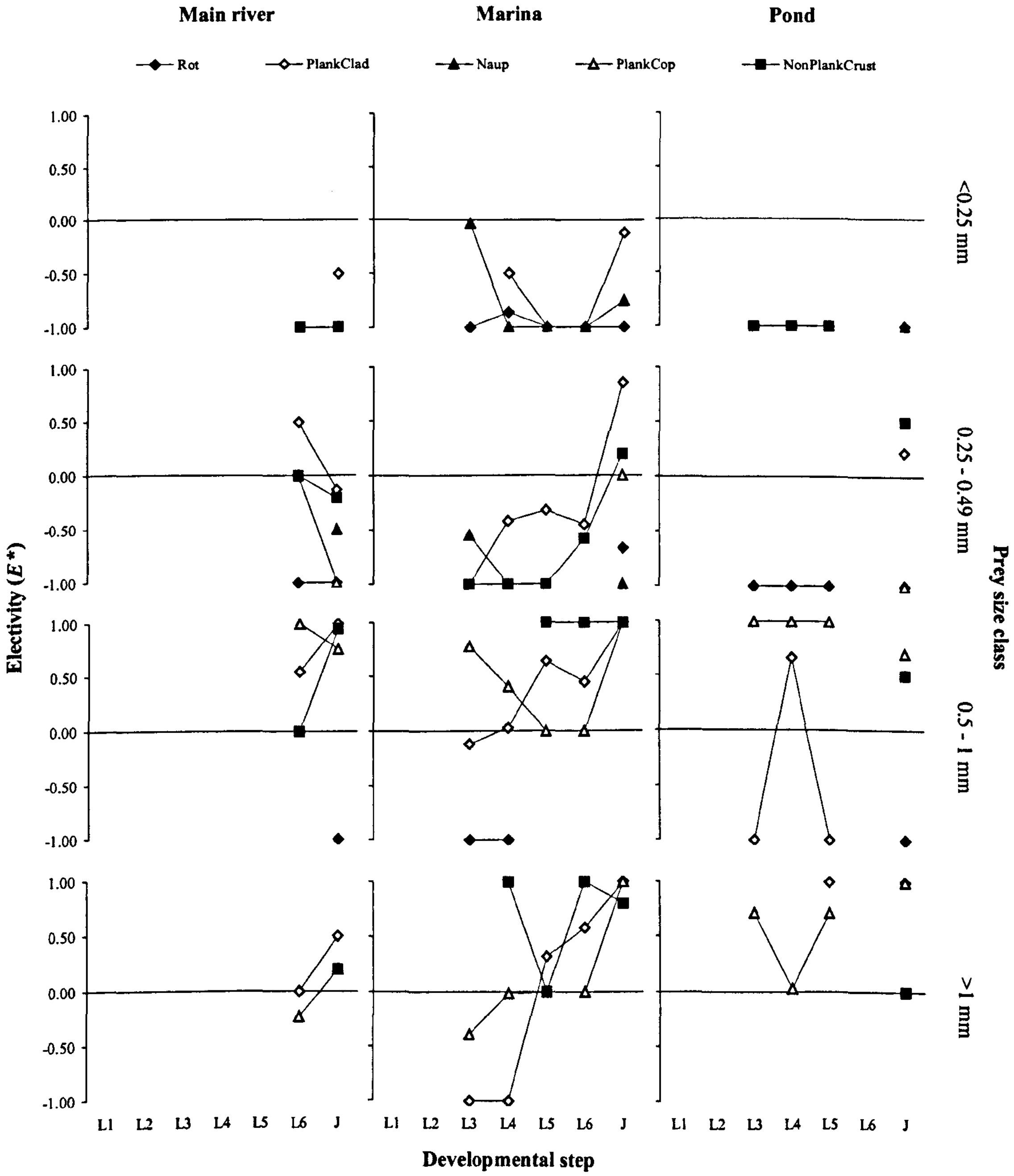


Fig. 5.66 Electivity indices for perch for four size classes of five zooplankton groups at main river, marina and pond macrohabitats.

5.66). In the marina, L4 perch also displayed strong selection for >1 mm non-planktonic crustaceans, while in the pond they also selected 0.5-1 mm planktonic cladocerans (Fig. 5.66). In the marina, L5-L6 perch selected ≥0.5 mm planktonic cladocerans and non-planktonic crustaceans, while L5 perch in the pond favoured ≥0.5 mm planktonic copepods and >1 mm planktonic cladocerans (Fig. 5.66). L6 perch in the main river selected 0.25-1 mm planktonic cladocerans and 0.5-1 mm planktonic copepods (Fig. 5.66). At all sites, juveniles selected ≥0.25 mm planktonic cladocerans and non-planktonic crustaceans, and ≥0.5 mm planktonic copepods (Fig. 5.66). All size classes of rotifers and copepod nauplii were avoided. Electivity indices for ≥0.25 mm planktonic cladocerans increased with development, with ≥0.5 mm prey particularly favoured. Planktonic copepods were frequently selected, especially those in the 0.5-1 mm size class. Non-planktonic crustaceans <0.5 mm were generally avoided, whereas those ≥0.5 mm were selected.

In the pond, L2 bream selected <0.25 mm copepod nauplii but avoided similar-sized rotifers and larger zooplankton, while electivity indices for L3 bream predating on <0.25 mm rotifers and copepod nauplii were approximately equal (Fig. 5.67). L4 bream in the pond selected <0.25 mm copepod nauplii, whereas their counterparts in the marina selected 0.25-0.49 mm planktonic cladocerans (Fig. 5.67). L5 bream selected ≥0.25 mm non-planktonic crustaceans and ≥0.5 mm planktonic cladocerans, while L6 fish selected ≥0.5 mm planktonic cladocerans and 0.5-1 mm planktonic copepods (Fig. 5.67). Juveniles in the main river selected 0.25-1 mm non-planktonic cladocerans, with other prey avoided, whereas their counterparts in the pond selected 0.25-0.49 mm planktonic cladocerans and 0.25-1 mm planktonic copepods (Fig. 5.67).

L1 bleak selected <0.25 mm rotifers but avoided copepod nauplii of similar size and all larger zooplankters (Fig. 5.68). L2 and L3 bleak selected <0.25 mm rotifers and copepod nauplii and 0.25-0.49 mm non-planktonic crustaceans, while L4 bleak selected <0.25 mm rotifers and 0.5-1 mm planktonic copepods (Fig. 5.68). L5 bleak selected <0.25 mm copepod nauplii over 0.25-0.49 mm planktonic cladocerans and avoided other prey, while L6 bleak selected <0.25 mm copepod nauplii and 0.25-0.49 mm planktonic cladocerans and copepods (Fig. 5.68). Juveniles selected <0.25 mm rotifers and 0.25-0.49 mm planktonic cladocerans (Fig. 5.68). The majority of developmental

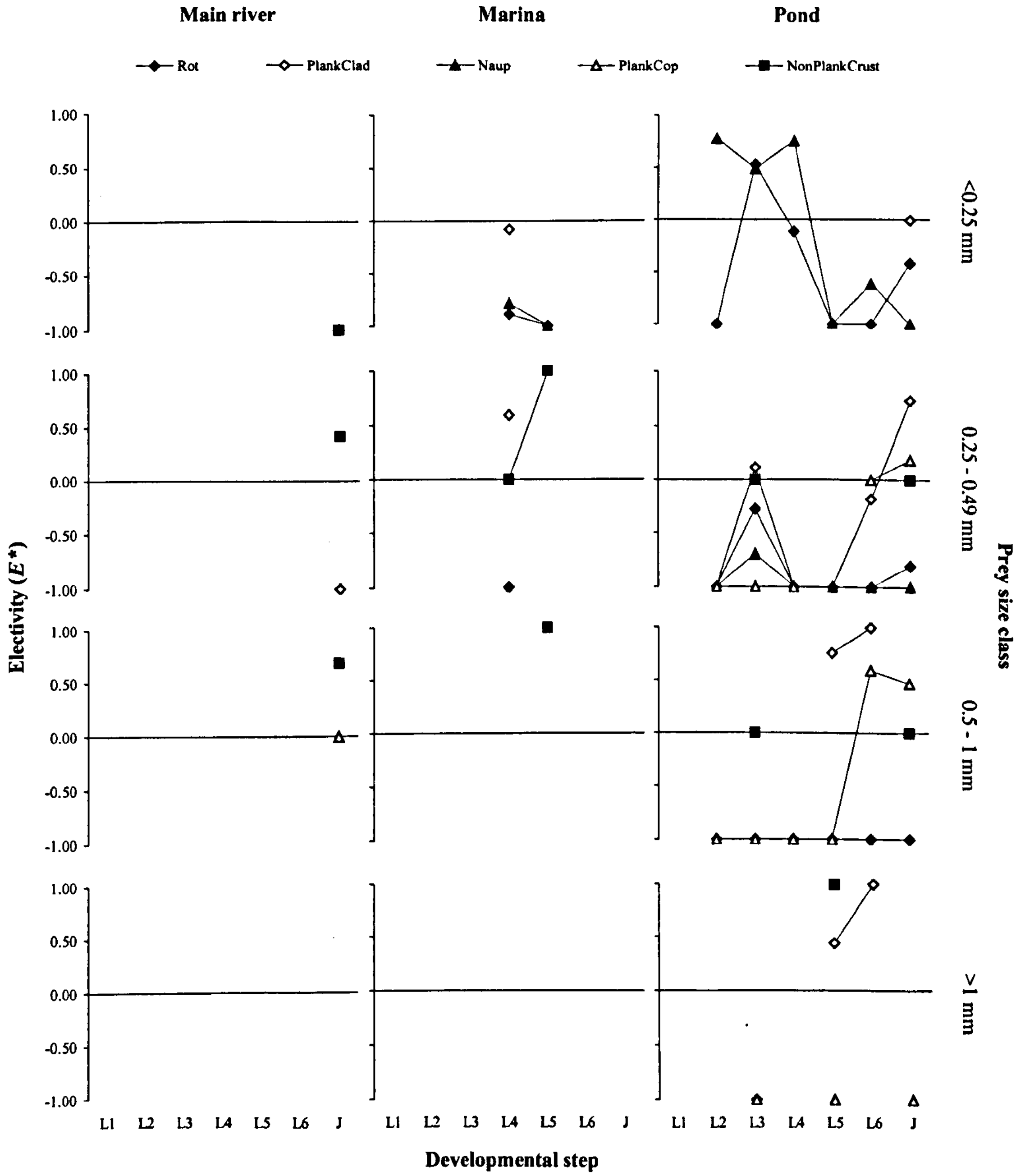


Fig. 5.67 Electivity indices for bream for four size classes of five zooplankton groups at main river, marina and pond macrohabitats.

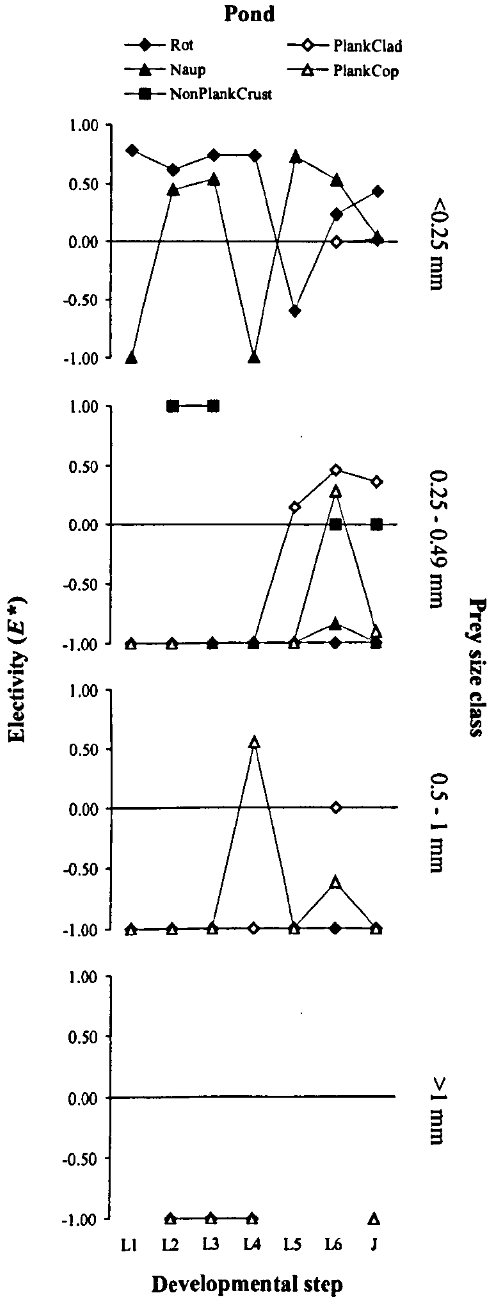


Fig. 5.68 Electivity indices for bleak for four size classes of five zooplankton groups at the pond macrohabitat.

steps had positive electivity indices for <0.25 mm rotifers and, to a lesser extent, copepod nauplii. Small (<0.25 mm) prey were invariably selected over larger zooplankton, even in the late larval steps and the juvenile period.

5.3.5 The influence of gape on the sizes of prey consumed

The relationship between maximum gape height and SL was investigated for species for which sufficient developmental steps were captured, namely dace, roach, chub, perch, bream and bleak. There were no significant spatial differences in the relationships between maximum gape height and SL (ANCOVA, $P>0.05$), so sites were combined to produce a single relationship for each fish species. For all species, gape height increased linearly with SL (Fig. 5.69), although there were significant differences in the relationship between species ($P<0.05$). Thus, perch had the largest gape for a given body length, followed by chub, dace, roach, bleak and bream, although the differences between roach and bleak, and bleak and bream were not statistically significant ($P>0.05$). There were no significant interspecific differences in the intercepts ($P>0.05$).

Maximum prey (zooplankton) length consumed was plotted against maximum gape height for each species at each site. Sites were kept separate due to differences in their zooplankton assemblages. The majority of fish consumed zooplankton substantially smaller than the maximum theoretically possible inferred from their maximum gape height, as demonstrated by the distribution of data points below the line of equality (prey length = gape height; Fig. 5.70). The main exceptions to this were larval chub and roach, many of which had consumed zooplankton that were longer than their gape was high. It should be noted, however, that some fish (particularly juvenile perch) had consumed large benthic invertebrates (especially ephemeropteran larvae), although the sizes of these food items were not measured since comparable data from the benthos were not available.

There were significant, positive relationships between maximum prey length and maximum gape height for larvae, but not for juveniles (Table 5.2). Thus, larvae were gape-limited, whereas (zooplanktivorous) juveniles were not. The main exception was larval roach, although this was probably due to the lack of gape measurements for the youngest larvae and the narrow length ranges occupied by older larvae. In contrast with

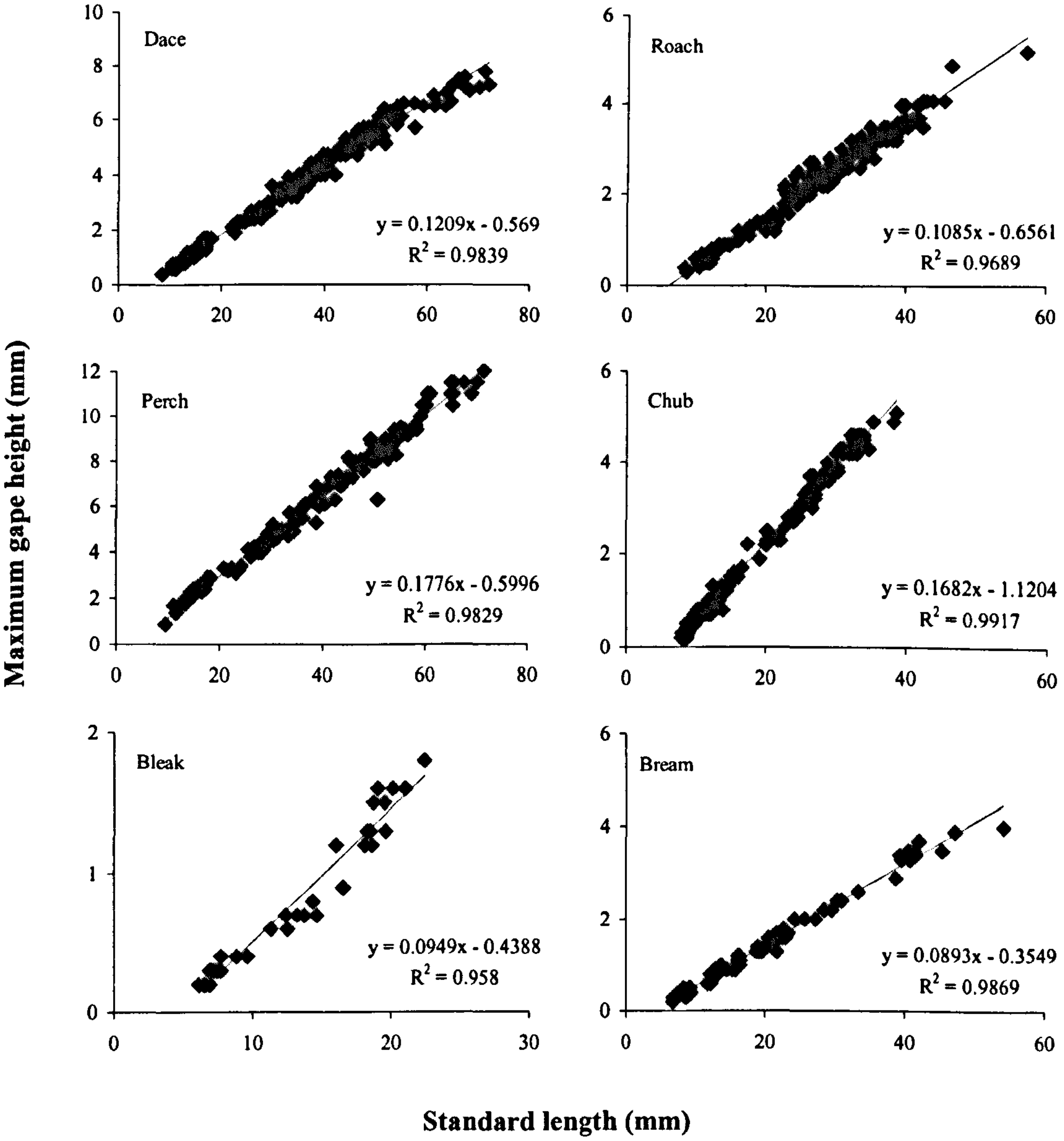


Fig. 5.69 Gape height-standard length relationships for six species of fish in the River Trent.

the cyprinids, perch larvae were not gape-limited in the main river or the pond, probably due to their relatively larger mouths, combined with the restricted size range of zooplankton available in the main river and the high abundance of copepods in the pond. Conversely, perch larvae did appear to be gape-limited in the marina, possibly as a consequence of the greater availability of large non-planktonic cladocerans (Chapter 4). The mean maximum prey length of larvae was 58% of gape height in dace, 103% in roach, 98% in chub, 73% in perch, 89% in bream and 66% in bleak.

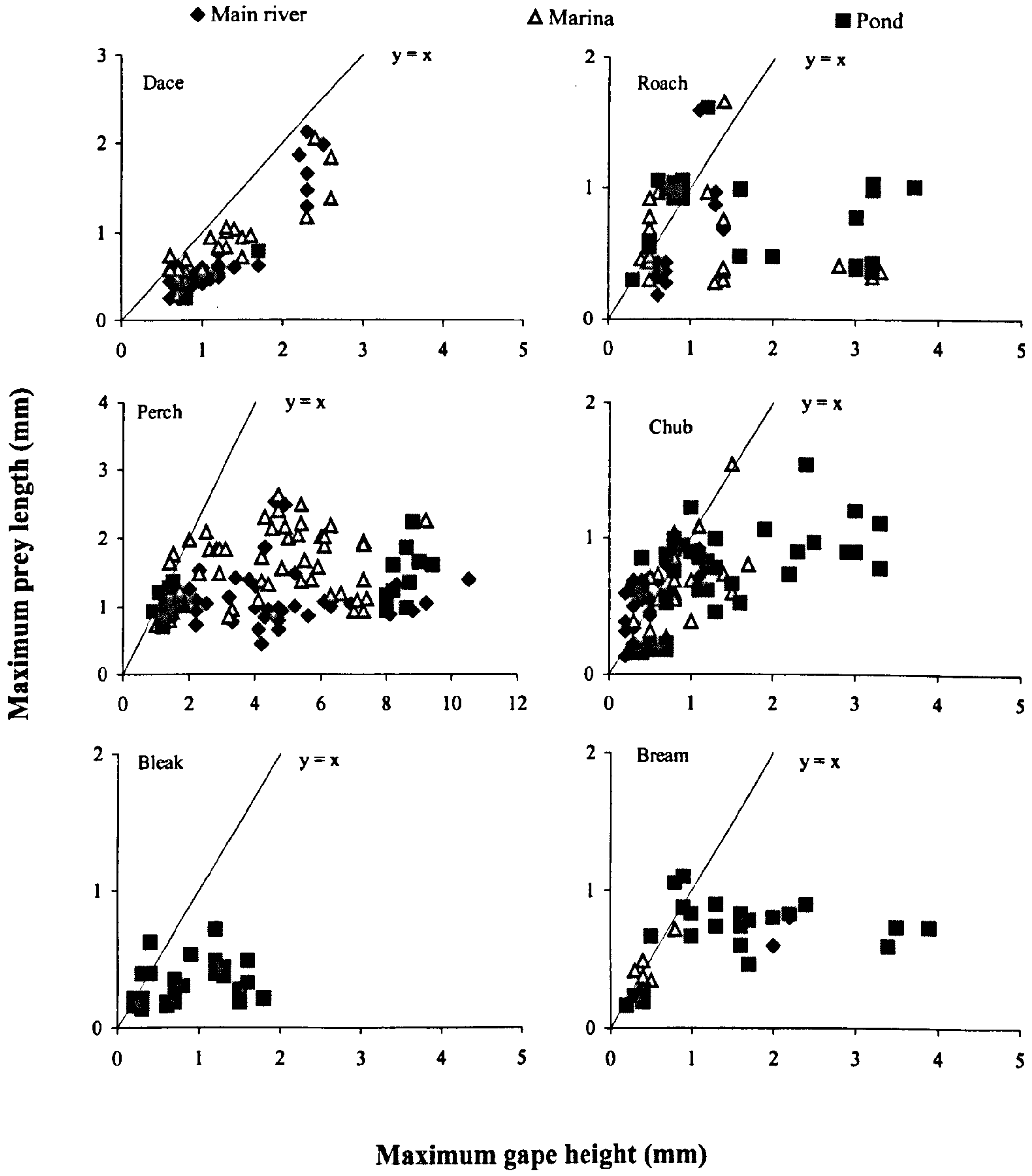


Fig. 5.70 Relationships between maximum prey length and maximum gape height for six species of fish in the River Trent.

5.4 DISCUSSION

5.4.1 Ontogenetic shifts in the diets of 0+ fish

First-feeding is considered a critical period in the early life of fish (Kamler, 2002), with zooplankton serving as a vital food resource for the survival of newly hatched fish of many species (Whiteside *et al.*, 1985; Wanzenböck & Schiemer, 1989). Poor feeding

Table 5.2 Linear regression relationships between maximum prey length and maximum gape height for dace (*Ll*), chub (*Lc*), roach (*Rr*), perch (*Pf*), bream (*Ab*) and bleak (*Aa*) larvae (L) and juveniles (J) in the main river, marina and pond.

Linear regression	***P***	r^2	***n***
$\mathit{Prey\ length}_{Ll\ \mathrm{L\ river}} = 0.386(\mathit{Gape\ height}_{Ll\ \mathrm{L\ river}}) + 0.083$	0.000**	0.564	28
$\mathit{Prey\ length}_{Ll\ \mathrm{J\ river}} = 0.766(\mathit{Gape\ height}_{Ll\ \mathrm{J\ river}}) - 0.043$	0.649	0.057	6
$\mathit{Prey\ length}_{Ll\ \mathrm{L\ marina}} = 0.451(\mathit{Gape\ height}_{Ll\ \mathrm{L\ marina}}) + 0.276$	0.000**	0.599	21
$\mathit{Prey\ length}_{Ll\ \mathrm{J\ marina}} = 0.652(\mathit{Gape\ height}_{Ll\ \mathrm{J\ marina}}) - 0.003$	0.759	0.058	4
$\mathit{Prey\ length}_{Ll\ \mathrm{L\ pond}} = 0.511(\mathit{Gape\ height}_{Ll\ \mathrm{L\ pond}}) - 0.081$	0.033*	0.935	4
$\mathit{Prey\ length}_{Lc\ \mathrm{L\ river}} = 0.636(\mathit{Gape\ height}_{Lc\ \mathrm{L\ river}}) + 0.278$	0.000**	0.589	27
$\mathit{Prey\ length}_{Lc\ \mathrm{L\ marina}} = 0.447(\mathit{Gape\ height}_{Lc\ \mathrm{L\ marina}}) + 0.287$	0.006**	0.295	24
$\mathit{Prey\ length}_{Lc\ \mathrm{L\ pond}} = 0.436(\mathit{Gape\ height}_{Lc\ \mathrm{L\ pond}}) + 0.235$	0.002**	0.279	33
$\mathit{Prey\ length}_{Lc\ \mathrm{J\ pond}} = -0.045(\mathit{Gape\ height}_{Lc\ \mathrm{J\ pond}}) + 1.128$	0.800	0.009	10
$\mathit{Prey\ length}_{Rr\ \mathrm{L\ river}} = -0.222(\mathit{Gape\ height}_{Rr\ \mathrm{L\ river}}) + 0.493$	0.669	0.028	9
$\mathit{Prey\ length}_{Rr\ \mathrm{L\ marina}} = 2.550(\mathit{Gape\ height}_{Rr\ \mathrm{L\ marina}}) - 0.662$	0.131	0.294	9
$\mathit{Prey\ length}_{Rr\ \mathrm{J\ marina}} = -0.177(\mathit{Gape\ height}_{Rr\ \mathrm{J\ marina}}) + 0.917$	0.264	0.136	11
$\mathit{Prey\ length}_{Rr\ \mathrm{L\ pond}} = 1.248(\mathit{Gape\ height}_{Rr\ \mathrm{L\ pond}}) - 0.004$	0.000**	0.834	12
$\mathit{Prey\ length}_{Rr\ \mathrm{J\ pond}} = 0.068(\mathit{Gape\ height}_{Rr\ \mathrm{J\ pond}}) + 0.510$	0.623	0.032	10
$\mathit{Prey\ length}_{Pf\ \mathrm{L\ river}} = -0.028(\mathit{Gape\ height}_{Pf\ \mathrm{L\ river}}) + 1.170$	0.976	0.000	6
$\mathit{Prey\ length}_{Pf\ \mathrm{J\ river}} = -0.005(\mathit{Gape\ height}_{Pf\ \mathrm{J\ river}}) + 1.182$	0.920	0.000	29
$\mathit{Prey\ length}_{Pf\ \mathrm{L\ marina}} = 0.546(\mathit{Gape\ height}_{Pf\ \mathrm{L\ marina}}) + 0.341$	0.000**	0.554	20
$\mathit{Prey\ length}_{Pf\ \mathrm{J\ marina}} = -0.008(\mathit{Gape\ height}_{Pf\ \mathrm{J\ marina}}) + 1.737$	0.904	0.000	35
$\mathit{Prey\ length}_{Pf\ \mathrm{L\ pond}} = 0.205(\mathit{Gape\ height}_{Pf\ \mathrm{L\ pond}}) + 0.777$	0.403	0.064	13
$\mathit{Prey\ length}_{Pf\ \mathrm{J\ pond}} = 0.462(\mathit{Gape\ height}_{Pf\ \mathrm{J\ pond}}) - 2.483$	0.123	0.270	10
$\mathit{Prey\ length}_{Ab\ \mathrm{L\ marina}} = 0.681(\mathit{Gape\ height}_{Ab\ \mathrm{L\ marina}}) + 0.079$	0.011*	0.530	11
$\mathit{Prey\ length}_{Ab\ \mathrm{L\ pond}} = 1.020(\mathit{Gape\ height}_{Ab\ \mathrm{L\ pond}}) - 0.053$	0.002**	0.724	10
$\mathit{Prey\ length}_{Ab\ \mathrm{J\ pond}} = -0.029(\mathit{Gape\ height}_{Ab\ \mathrm{J\ pond}}) + 0.820$	0.455	0.041	16
$\mathit{Prey\ length}_{Aa\ \mathrm{L\ pond}} = 0.329(\mathit{Gape\ height}_{Aa\ \mathrm{L\ pond}}) + 0.126$	0.004**	0.381	20
$\mathit{Prey\ length}_{Aa\ \mathrm{J\ pond}} = -0.257(\mathit{Gape\ height}_{Aa\ \mathrm{J\ pond}}) + 0.714$	0.121	0.273	10

*$P<0.05$; **$P<0.01$

success of first-feeding larvae may result from low density of small, non-elusive/evasive prey (Krebs & Turingan, 2003). After hatching, the larvae of fish grow rapidly, their mode of swimming changes and so does their food spectrum (Mark *et al.*, 1987). Although many fish species are zooplanktivorous at the onset of exogenous feeding, distinct shifts in their foraging biology may occur during development (Wanzenböck & Schiemer, 1989). A general sequence of ontogenetic shifts in resource use often exists for the first weeks after hatching (Mark *et al.*, 1987; Garner, 1996b; Mann *et al.*, 1997). Newly hatched individuals of many fish species prey mainly upon pelagic rotifers and phytoplankton, owing to their inability to catch and handle larger prey (Mark *et al.*, 1987, 1989; Treasurer, 1992), with microcrustaceans and chironomid larvae becoming more frequent in the diet as the fish develop (Broughton & Jones, 1978; Garner, 1996b; Lightfoot & Jones, 1996; Mann *et al.*, 1997).

The results of the present study corroborate this general sequence. Fish in steps L1-L3, L4-L6 and J were grouped as distinct ecospecies on the basis of their diet, corresponding with the transition from 'finfold' to 'finformed' larvae, and from the larval to the juvenile period (Balon, 1999). The diets of the majority of young dace, roach, chub, bream, bleak and minnow larvae were dominated by rotifers (predominantly *Keratella*, *Brachionus* and *Euchlanis* spp.), with smaller numbers of algae (mainly *Closterium* and *Pediastrum* spp.), copepod nauplii and early instar chironomid larvae also eaten.

As they develop, dace larvae begin to feed upon cladocerans, copepods and chironomid larvae (Mills *et al.*, 1985; Mann & Mills, 1986), with aerial insects, chironomid pupae and tubificids occurring in the diet towards the end of the larval period (Weatherley, 1987). Roach feed upon phytophilous and periphytic organisms (Matěna, 1995a, b) or small planktonic cladocerans (Peirson, 1983), with daphnids ingested after reaching a length of approximately 12-15 mm (Mehner *et al.*, 1997), while bream feed upon small planktonic and non-planktonic cladocerans from a length of approximately 10 mm (Kennedy & Fitzmaurice, 1968; Peirson, 1983). In the present study, bleak and bream continued to consume rotifers extensively towards the end of the larval period, with planktonic and non-planktonic cladocerans, cyclopoid copepods, copepod nauplii and chironomid larvae also consumed by older bream larvae.

Unlike many of the other cyprinids in this study, chub were not restricted solely to rotifers, copepod nauplii and algae at the onset of exogenous feeding. Indeed, Mark *et al.* (1987) found that chub larvae rarely consumed rotifers and copepod nauplii at all, but preyed upon small crustaceans, adult copepods and chironomid larvae immediately after hatching. In addition, chub appeared to be grouped more by site than developmental step, perhaps a reflection of the constraints of site-specific food availability rather than those of ontogenetic foraging capability. Perhaps as a result of their precocious feeding habits, chub had more diverse diets than other cyprinid species, with older larvae consuming a range of prey, including chironomid larvae, *Scapholeberis*, *Polyphemus*, *Bosmina*, *Eurycercus*, *Chydorus*, *Pleuroxus*, *Alona*, copepod nauplii, cyclopoid copepods, rotifers and adult dipterans.

Perch larvae subsist on the yolk sac until the mouth becomes terminal (Spanovskaya & Grygorash, 1977), whereupon rotifers and copepod nauplii are the initial food items (Treasurer, 1990; Mehner *et al.*, 1997; Skrzypczak *et al.*, 1998), with ciliates and algae eaten occasionally (Guma'a, 1978a). No rotifers or algae were eaten by perch in the present study, although first-feeding larvae were not encountered. Small cladocerans are eaten after perch larvae reach a length of approximately 7 mm (Skrzypczak *et al.*, 1998), while *Daphnia* become important in the diet after perch exceed 10-15 mm, and *Leptodora kindti* (Focke) and *Bythotrephes* spp. are taken by >15 mm larvae (Guma'a, 1978a; Mehner *et al.*, 1997). Copepods may also be common in the diet (Matěna, 1995b), and are sometimes favoured over cladocerans (Guma'a, 1978a). In the present study, perch larvae in the pond consumed cyclopoid copepods almost exclusively, whereas in the main river and marina a greater range of prey were eaten, including cyclopoid copepods, *Daphnia*, copepod nauplii, *Bosmina*, *Eurycercus* and *Alona*.

Species-specific dietary selection may become evident during the juvenile period (Garner, 1996b). As juveniles, roach feed primarily upon zooplankton before switching to aufwuchs (Weatherley, 1987; Garner, 1996b; Mann *et al.*, 1997). The proportion of aufwuchs in the diet typically increases through the summer (Weatherley, 1987; Matěna, 1995a, b), often coinciding with low availabilities of animal prey, particularly cladocerans (Persson, 1983; Mehner *et al.*, 1998a; Vinni *et al.*, 2000). It has been suggested that the high gut fullness yet relatively slow growth of roach feeding on aufwuchs indicates it is a poor food resource (Mann, 1997). Indeed, growth rates of fish feeding on aufwuchs and cyanobacteria have been shown to be lower than of those feeding on animal prey due to the poor digestibility and low nutritive value of the former food types (Persson, 1983; Sillah, 1983; Lemke & Bowen, 1998; Kamjunke &

Mehner, 2001; Kamjunke *et al.*, 2002a, b; Lewin *et al.*, 2003; Tomec *et al.*, 2003). Although catches were irregular, fish from the pond were invariably larger than their counterparts from elsewhere (Chapter 3). The explanation for this may be the great availability of zooplankton compared with other sites (Chapter 4) and the delayed shift to aufwuchs (Section 5.3.1), the relatively low densities of fish in the pond (Chapter 3), possible differences in water temperature between floodplain waterbodies and main river channels (Schiemer *et al.*, 2001c), or a combination of factors.

Mann *et al.* (1997) noted that the switch to aufwuchs did not occur in a marina habitat, where planktonic cladocerans dominated the diet. Similarly, Perrow & Irvine (1992) and Matěna (1995a, b) found that large planktonic cladocerans were the most important components of the diet of juvenile roach, while Northcott (1979) noted that *Ceriodaphnia*, *Bosmina* and *Sida* were the dominant prey. Townsend *et al.* (1986) observed that roach fed predominantly on planktonic cladocerans in late spring and summer, and non-planktonic cladocerans for the remainder of the year. As with the switch to aufwuchs observed elsewhere, the switch from planktonic to non-planktonic cladocerans coincided with low availabilities of planktonic prey (<40 plankters L^{-1}; Townsend *et al.*, 1986). Compared with the main river and marina, the switch to aufwuchs was delayed in the pond where large quantities of zooplankton (especially *Bosmina* and cyclopoid copepods) were available later into the summer. Significantly perhaps, all of the above examples are from still waters, since large-bodied cladocerans are rare in riverine environments (see Chapter 4).

Garner (1996b) found that, of the species he studied, only roach utilised aufwuchs. Bream undergo an ontogenetic diet shift similar to roach, but from zooplankton to benthic macroinvertebrates (Persson & Brönmark, 2002) or non-planktonic cladocerans (Garner, 1996b) rather than aufwuchs. Garner (1996b) hypothesised that the continued feeding of bream on cladocerans suggests they are either unable or unwilling to feed upon aufwuchs. Alternatively, they may be more capable than roach at feeding on low densities of zooplankton, as observed with bleak (Wanzenböck & Schiemer, 1989). Bream are reputed to be far more efficient than roach at feeding on elusive prey such as copepods (Winfield, 1983; Winfield *et al.*, 1983) and may feed on them extensively (Peirson, 1983). In the present study, while non-planktonic cladocerans comprised the majority of the diet of juvenile bream in the marina, cyclopoid copepods and *Bosmina* were the most frequent prey of fish in the pond, and aufwuchs was the dominant food of juvenile bream in the main river, reflecting the relative lack of zooplankton at the latter site.

Juvenile chub feed upon adult dipterans and chironomid larvae (Kokeš, 1979; Mark *et al.*, 1987), with the often small number of prey compensated for by their large size (Garner, 1996b). This was certainly the case in the main river and the marina, although aufwuchs was also consumed, whereas juvenile chub in the pond mostly fed upon cyclopoid copepods. In the River Dee, the diets of juvenile dace were dominated by blue-green algae and detritus (Weatherley, 1987), whereas in the present study, chironomids (larvae, adults) and aufwuchs were the main food. Unlike many other cyprinid species, bleak continue to be largely zooplanktivorous into the juvenile period (Schiemer *et al.*, 1989), with *Bosmina* the most frequent prey (Garner, 1996b; Alajärvi & Horppila, 2004), even in >0+ age classes (Politou *et al.*, 1993). The results of the present study agree with these observations, with juvenile bleak preying upon small planktonic prey such as *Bosmina*, copepod nauplii and rotifers.

Juvenile perch consume mainly planktonic cladocerans, especially *Daphnia*, *Bosmina* and *Leptodora* (Spanovskaya & Grygorash, 1977). Littoral forms such as *Sida* and *Chydorus* are of less importance, while copepods and chironomid larvae and pupae are more important than in larvae. The predominance of zooplankton, nekton or benthos in the diet of juvenile perch appears to be determined by the relative abundance of these items (Spanovskaya & Grygorash, 1977). A switch to benthic prey often occurs during the first summer, which invariably coincides with a substantial reduction in zooplankton availability (Guma'a, 1978a; Persson & Greenberg, 1990; Wu & Culver, 1992; Mehner *et al.*, 1995, 1996) although some fish, usually the largest, may become piscivorous (Brabrand, 1995, 2001; van Densen *et al.*, 1996; Borcherding *et al.*, 2000; Beeck *et al.*, 2002). In the main river and marina, there was a general shift in the diet from planktonic cladocerans, to non-planktonic cladocerans and cyclopoid copepods, to chironomid larvae, cyclopoid copepods and ephemeropteran larvae through the summer, analogous to the switch to aufwuchs in roach. There was no such trend in the pond, however, where cyclopoid copepods were consumed extensively.

Ontogenetic shifts in the diet may not be obvious in all species. Bischoff & Freyhof (1999), for example, detected no remarkable shifts in diet between larval and juvenile barbel, and Kokeš (1979) found that 0+ chub of all sizes (10-40 mm) consumed almost identical diets. In the present study, this appeared to be the case with benthic species, although comparatively few larvae were caught. Gudgeon mainly consumed benthic animals (e.g. chydorids, ostracods, chironomid larvae) and aufwuchs, although in the pond they also consumed cyclopoid copepods, as found by Garner (1996b) in the River Great Ouse. Barbel and stone loach also consumed benthic organisms, plus cyclopoid copepods, copepod nauplii and rotifers, irrespective of developmental step.

5.4.2 Intra- and interspecific diet similarity

Intra- and interspecific similarity in the diets of 0+ fish varies spatially, temporally and ontogenetically. Generally, resource requirements are likely to be most similar within rather than between populations and so, therefore, is diet composition (Wootton, 1990). High similarity in diet offers the potential for competition, with possible implications for 0+ fish growth, survival and recruitment success.

The results of the current study suggest that level of development is the key factor determining potential for dietary overlap. Intra- and interspecific overlap were greatest in the young larval steps, suggesting that the fish are still morphologically and behaviourally undifferentiated during this period (Garner, 1996b). Although the diets of the young larvae of many species were similar, they did not necessarily compete, since many of them did not overlap spatially or temporally. For example, dace hatched approximately two months earlier than chub, by which time all dace were juveniles. Dace and chub larvae, therefore, could not compete for resources. Similarly, rheophilic barbel larvae did not overlap spatially with limnophilic tench larvae, and overlap between benthivorous and planktivorous or neuston-feeding species is likely to have been limited.

Many cyprinid larvae form mixed species shoals in the littoral zone after hatching (Rheinberger *et al.*, 1986), and dietary overlap can be high (Matěna, 1998). In the current study, synchronous overlap in diet was generally greatest between ecologically similar species. The diets of dace larvae, for example, frequently overlapped with those of sympatric roach larvae. Similarly, the diets of juvenile dace, roach and chub often overlapped, while benthic fish species frequently shared similar diets. In the Římov Reservoir, Matěna (1998) found that the diets of juvenile perch, zander, ruffe, roach and bream overlapped significantly, resulting from high preference for *Daphnia*, and assumed strong interspecific competition for food resources. Synchronous overlap does not necessarily imply competition, however, since competition is 'the demand, typically at the same time, of more than one organism for the same resource of the environment in excess of immediate supply' (Zaret & Rand, 1971). Cowx (1989), for example, found that the overlap in diet between adult roach and dace in the River Exe was mainly of algae, macrophytes and detritus, which were not limited in availability. In the current study, dietary overlap was greatest among fish feeding upon rotifers and aufwuchs, which were invariably the most abundant food categories (Chapter 4). Similarly, in the pond, the diets of the majority of fish were over 70% similar, irrespective of species or level of development, with highly abundant cyclopoid copepods the common prey.

Interspecific competition often causes a narrowing of the niche widths of the competing species along one or more niche dimensions (Wootton, 1990). Zaret & Rand (1971), studying competition in tropical stream fishes, demonstrated a change from distinct food niches during the dry season (limited food supply) to widely overlapping niches in the wet season (abundant food supply). Similarly, in the absence of roach, 0+ perch feed mainly upon planktonic cladocerans, whereas in the presence of roach they consume copepods and macroinvertebrates, and have lower growth rates (Persson, 1987; Persson & Greenberg, 1990). Likewise, Cowx (1989) found that where roach and dace coexisted in the River Exe, growth rates of one or both species were reduced, possibly due to reductions in feeding diversity. Matěna (1995b) observed that resource partitioning was a characteristic feature in the littoral 0+ fish assemblages of the Římov Reservoir, with perch favouring pelagic copepods and roach consuming periphytic organisms such as chironomid larvae. The only significant overlap in diet occurred when *Polyphemus* was eaten, when it formed up to 90% of the diet of both roach and perch, in spite of its low abundance in the zooplankton.

Competitive effects on growth occur when behavioural interactions between fish cause an unequal distribution of a resource that is directly or indirectly related to growth (Wootton, 1990). A number of studies have demonstrated a negative relationship between fish growth and fish density (e.g. Persson & Greenberg, 1990; Byström & García-Berthou, 1999; Dettmers & Wahl, 1999; Cowan *et al.*, 2000; Feldlite & Milstein, 2000; Pivnička & Švátora, 2000; Romare, 2000). Grenouillet *et al.* (2001a) found that survival of roach in the first year of life was density-dependent, and stated that intraspecific competition within the 0+ cohort could influence recruitment to older age-classes. This may be of particular importance in years of good recruitment. Cryer *et al.* (1986) and Perrow & Irvine (1992), studying lacustrine populations of roach, demonstrated that abundant 0+ roach can sometimes show poor growth as a result of depression of their prey populations. Although catches were irregular, fish from the pond were invariably larger than their counterparts from elsewhere (Chapter 3). The explanation for this may be the great availability of zooplankton in the pond (Chapter 4), the relatively low densities of fish (Chapter 3), possible differences in water temperature between floodplain waterbodies and main river channels (Schiemer *et al.*, 2001c), or a combination of factors.

5.4.3 Selection and gape

The diet of freshwater fish in the first weeks of life can include both an increase in prey size and changes in prey species as the fish grow and develop (Werner & Gilliam, 1984; Ghan & Sprules, 1993). Optimal foraging theory predicts that predators should select prey that maximise the energetic gains available in relation to the energetic costs of capturing, ingesting and digesting the prey (Begon *et al.*, 1986; Gill & Hart, 1998). For a fish predator, the energetic content of a given prey type increases with prey size, but there is also an associated increase in handling time (Gill & Hart, 1994, 1996a, b, 1999). Handling times also vary between prey taxa, but few studies have succeeded in isolating the effects of taxa (e.g. morphology, behaviour) and size in prey selection by 0+ fish.

The small gape of 0+ fish limits their prey size, yet within constraints set by gape, food eaten influences growth and, ultimately, survival (Bremigan & Stein, 1994). Mayer & Wahl (1997) demonstrated that young walleye (*Sander vitreus* (Mitchill)) fed selectively and that, for at least some size classes, the selected prey conferred benefits in terms of greater growth or survival. Utilisation of cladocerans as a common food resource during the late larval and early juvenile periods of many fish species probably occurs as a result of their ease of capture compared with copepods (Hammer, 1985), even though the latter are often numerically abundant and of greater calorific value (Bass *et al.*, 1997a). 0+ juvenile roach and bream both find copepods more difficult to capture than cladocerans (Winfield, 1983; Winfield *et al.*, 1983; Matěna, 1998), since copepods are faster moving than cladocerans and have sensory hairs that enable them to detect the shock waves of approaching fish. Nevertheless, some studies, although almost exclusively of non-cyprinids, have reported a low importance of daphnids as food and a higher preference for copepods (e.g. Guma'a, 1978a; Furnass, 1979; Treasurer, 1990), perhaps because copepods, especially egg-bearing females, are more visible to young fish than cladocerans (Ghan & Sprules, 1993) or due to the small sizes of the fish investigated (Mehner *et al.*, 1998a).

In the current study, the general sequence of ontogenetic shifts in food consumption was reflected in the electivity indices. Electivity values for rotifers and copepod nauplii declined with development, whereas those of cladocerans and copepods generally increased. This can be largely attributed to the restrictions imposed by the gape of 0+ fish. However, certain taxa were consistently selected over others of the same size. For example, the majority of young cyprinid larvae selected rotifers over similar-sized copepod nauplii. Ghan & Sprules (1993) observed a similar phenomenon in young burbot (*Lota lota* (L.)) larvae, with the globular rotifer *Asplanchna* sp. selected over spined rotifers and copepod nauplii, perhaps due to differences in morphology or behaviour between taxa. Copepod nauplii, for instance, are faster moving than rotifers, while the protuberances of spined rotifers may hinder fish attempting to prey upon them and increase handling times. The apparent selection of non-planktonic crustaceans over other zooplankters by many late larval and 0+ juvenile fish may partly be explained by the relative ineffectiveness of the zooplankton trawl at capturing them, such that their abundance relative to other zooplankton groups was underestimated. Notwithstanding, the extensive consumption of non-planktonic crustaceans by many fish suggests they were preferentially feeding in the proximity of aquatic macrophytes or the benthos, rather than in open water.

The interactions between the relative importance of taxa and size of prey may be subtle. Gliwicz *et al.* (2004) found that, when studying smelt, selectivities were similar for small- and large-bodied prey, but lower for elongated- (*Daphnia*, *Diaphanosoma*) than for compact-bodied (*Bosmina*, *Chydorus*) species. Furthermore, smelt selected later instars and females with the greatest clutches, demonstrating that size distribution in a cladoceran *population* may be structured by fish predation in a similar way to that a cladoceran *community* is structured (see Chapter 4). Unfortunately, it was not possible to assess the clutch size of cladoceran prey in the current study as mastication/digestion or preservation had caused the eggs to be voided from the brood cavities.

There was evidence that cyprinid larvae were gape-limited, whereas (zooplanktivorous) 0+ juveniles were not. In contrast with the cyprinids, perch larvae were not gape-limited in the main river or the pond, probably due to their relatively larger mouths, combined with the restricted size range of zooplankton available. Conversely, perch larvae did appear to be gape-limited in the marina, possibly as a consequence of the greater availability of large, non-planktonic cladocerans (Chapter 4). Ghan & Sprules (1993) found that prey width rather than prey length limited the size of prey ingested, probably since large prey are orientated and swallowed 'head first'. This conclusion is supported by the current study with some fish consuming prey that were longer than their maximum gape was high.

Since the size distribution of zooplankton available to larval fishes influences their foraging success, growth and survival, an optimal prey size for larval fish may exist (Bremigan & Stein, 1994). In the current study, the majority of fish consumed zooplankton substantially smaller than the maximum theoretically possible inferred from their gape height. Similarly, Mehner *et al.* (1998a) found that modal lengths of *Daphnia* consumed by perch were substantially smaller than the fish were capable of consuming according to their gape size. Indeed, Scott (1987) found that juvenile dace and roach preferred prey approximately 60% of their maximum gape. A similar figure was obtained for dace and bleak in the current study. The preference for prey that are smaller than the maximum theoretically ingestible is probably due to the increased handling time required for large prey (Wanzenböck, 1995a, b).

The diets of 0+ fish therefore vary spatially, temporally and ontogenetically. Food availability determines the potential diets of 0+ fish while, due to restrictions of morphology and behaviour, level of development is the limiting factor regarding initial diet spectra. Thus, young larvae had the most interspecific diet overlap, with feeding diversity and the importance of species-specific traits increasing with development. Dietary overlap was generally greatest among ecologically similar species, with competition and resource partitioning most likely in the main river where zooplankton availability was lowest. The majority of fish consumed prey substantially smaller than the maximum theoretically possible inferred from their gape, probably due to the increased handling time required for large prey. Within the constraints determined by gape, certain prey taxa were consistently selected over others of the same size, demonstrating that taxa-specific as well as size-specific characteristics are important in the prey selection process. The greater availability and size ranges of zooplankton at floodplain sites compared with the main river provides suitable prey for all developmental steps of a range of fish species and may, thus, enhance recruitment success.

CHAPTER SIX

FACTORS AFFECTING RECRUITMENT SUCCESS OF FISH POPULATIONS IN LOWLAND RIVERS

6.1 INTRODUCTION

Early development represents a critical period in the life cycle of cyprinid fishes (Copp, 1990b, 1992b; Baras *et al.*, 1995; Garner, 1996a, b; Mann, 1997), and variations in mortality during this phase may be crucial in determining year-class strength (YCS) (Cowx, 2001). For a given fish species, mortality is generally inversely related to body size (Wootton, 1990), and the growth of many cyprinids in the first few weeks after hatching largely determines their survival over the first year and the subsequent strength of that year class (Mills & Mann, 1985; Mann & Mills, 1986; Bremigan & Stein, 1994; Kubečka, 1994; Kirjasniemi & Valtonen, 1997a, b; Grenouillet *et al.*, 2001a).

Since survival during the first weeks of life often determines recruitment success of freshwater fish, understanding what controls survival during this period will improve the ability to predict YCS (DeVries *et al.*, 1998; Claramunt & Wahl, 2000). In cyprinid populations, there are occasional large cohorts of adult fish (Mills & Mann, 1985; Nunn *et al.*, 2003a; Britton *et al.*, 2004), and a wide range of biotic (competition, predation, disease) and abiotic (e.g. physicochemical, physical habitat and water chemistry) factors influence eventual recruitment to the adult populations. In particular, the relationships between water temperature, fish growth and recruitment success have received considerable attention (e.g. Mann *et al.*, 1984; Mooij *et al.*, 1994). Temperature controls the rate of food consumption and metabolism and, thus, fish growth (Wootton, 1990). In many cases YCS appears to be determined by the growth of fish in the first year of life (Mills & Mann, 1985; Copp, 1990b; Mann, 1997; Cowx, 2001) and correlations with temperature indicate that, for cyprinid populations, large cohorts of adult fish often result from higher than average water temperature in the first summer of life (Mills & Mann, 1985; Cowx, 2000; Grenouillet *et al.*, 2001a).

The cumulative annual number of degree-days >12°C has therefore often been used as a predictor for subsequent YCS in cyprinids. Whilst temperature explains much of the variation in YCS it is not the only influential factor, however, since high water temperatures do not necessarily yield strong year classes. Furthermore, years in which a strong year class is prevalent in one species do not necessarily result in strong year classes in other coexisting species (Cowx, 2001), suggesting other biotic and abiotic factors can influence recruitment success.

Some evidence suggests that discharge rate plays an important role in recruitment dynamics, but as yet no definite relationship has been found, probably due to difficulties in separating the effects of discharge from those of other factors such as temperature and habitat availability (Crecco & Savoy, 1984; Spindler, 1995; Lucas *et al.*, 1998; Cowx, 2001; Pont & Nicolas, 2001). As mentioned above, water temperature exerts a considerable influence on YCS but it is also interlinked with river discharge. Periods of higher flow in summer often coincide with reduced water temperature, making it difficult to ascertain whether any resultant effects are due to one or the other. This chapter examines the relationships between water temperature, river discharge, the position of the Gulf Stream, 0+ fish growth and recruitment success in three species of cyprinid fish in the rivers Trent, Warwickshire Avon and Yorkshire Ouse. It aims to identify: (1) the key correlates of YCS; and (2) 'critical periods' in the first summer of life when fish may be particularly vulnerable to environmental perturbations. The hypothesis was that in some rivers, river discharge (rather than water temperature) may be the key factor that determines YCS.

6.2 MATERIALS AND METHODS

6.2.1 Adult fish data

Adult fish data were collected by the Environment Agency and its predecessors (the National Rivers Authority and Yorkshire Water Authority) from the Yorkshire Ouse around York by electric fishing from a boat (Electracatch WCF-7, 1.5-kW generator, 50 Hz pulsed direct current at 220 V, output approximately 1.5 A), between 1984 and 2004 inclusive. Adult fish surveys on the River Trent around Nottingham and the Warwickshire Avon around Evesham were carried out by Britton (1999) and the Environment Agency (unpublished data), respectively, by boom-boat electric fishing (Harvey & Cowx, 1996). Samples of scales were removed from captured fish for age determination (Bagenal & Tesch, 1978). Adult fish data were combined by catchment and used to calculate YCS for roach, chub and dace, according to the method of Cowx & Frear (2004):

(1) The number of fish in each cohort was used to determine the instantaneous mortality rate (*Z*) of the target population using the linear relationship between the natural logarithm of the number of fish in each age group (ln N_t) against age (t) according to:

$$Z = \frac{(\ln N_t - \log N_0)}{t} \tag{6.1}$$

(2) The number of fish at time zero (N_0) was calculated independently for each age group using:

$$N_0 = N_t \exp Zt \tag{6.2}$$

where N_t is the number of fish at age t;

(3) The mean number of fish in each age group (N) was determined as:

$$\frac{\sum t_{\max} N}{t_{\max}} \tag{6.3}$$

where t_{max} is the total number of age groups represented;

(4) YCS was determined for each age group by:

$$YCS = \frac{N_0}{\overline{N}} \times 100 \tag{6.4}$$

where N_0 is the number of fish determined at time t_0 for age group t, i.e. YCS, which is then related to the year of birth, is calculated as an index standardised against a value of 100. A value greater than 100 is a strong year class and a lower value a weak year class.

6.2.2 0+ fish data

The Yorkshire Ouse 0+ fish data used in this chapter were collected from Beningbrough in September each year by the Environment Agency and its predecessors, between 1984 and 2004 inclusive. River Trent and Warwickshire Avon 0+ fish surveys were carried out as described in Chapter 2. Data from seine net surveys were grouped by catchment and used to calculate mean fork length (mm ± SD) of 0+ roach, chub and dace at the end of the summer (September) in the Trent, Avon and Ouse (sample sizes are given on Figs 6.1-6.3). This was deemed to represent the maximum growth achieved by fish in their first year of life (Mann, 1973; Mills & Mann, 1985; Kubečka, 1994).

6.2.3 Environmental data

Water temperature data (1984-2004 inclusive) were obtained from the Environment Agency (Trent and Avon) and Yorkshire Water plc (Ouse). Mean daily water temperature was used to calculate the cumulative number of degree-days >12°C (April-September inclusive). Cumulative degree-days >12°C is believed to provide the best correlation with 0+ cyprinid growth (Mann, 1973; Mills & Mann, 1985; Grenouillet *et al.*, 2001a). For occasions when data were unavailable, water temperatures were calculated using the appropriate relationship between rivers in Table 6.1.

Table 6.1 Linear regression relationships between water temperature (cumulative degree-days >12°C, April-September inclusive) in the rivers Trent, Avon and Ouse.

Linear regression	***P***	r^2	***n***
Trent = *Ouse* (1.75) – 293.37	0.003**	0.68	10
Trent = *Avon* (1.39) – 398.59	0.000**	0.92	8
Avon = *Trent* (0.66) + 336.53	0.000**	0.92	8
Ouse = *Trent* (0.39) + 341.47	0.003**	0.68	10

**$P<0.01$. N.B. No relationships could be calculated between the Avon and Ouse due to limited temporal overlap of data sets.

Mean daily river discharge data (1984-2004 inclusive) were obtained from the Environment Agency gauging stations at Holme Pierrepont (Trent), Evesham (Avon) and Skelton (Ouse) (Figs 2.1-2.3). These data were used to calculate the cumulative number of discharge-days above the basal discharge rate (i.e. the long-term mean daily discharge calculated for each month using a 21-year data set), April to September inclusive. This is analogous to the cumulative number of degree-days used for water temperature.

Data on the position of the North Wall of the Gulf Stream (NWGS, 1984-2004 inclusive) were downloaded from the website of the Plymouth Marine Laboratory, UK (http://www.pml.ac.uk/gulfstream/data.htm). Positive values of this index indicate a displacement to the north of the long-term mean location of the NWGS, while negative values indicate a movement south.

All data were checked for normality using one-sample Kolmogorov-Smirnov tests (Dytham, 2003). A series of linear regressions was calculated to investigate the relationships between water temperature, river discharge, Gulf Stream position, 0+ fish growth and YCS of roach, chub and dace.

6.3 RESULTS

Comparisons of the annual trends in 0+ fish growth, YCS, water temperature and river discharge suggest covariation between each of the variables (Figs 6.1-6.3). The strongest year classes usually coincided with the greatest end of summer mean lengths which, in turn, tended to occur in years with the highest numbers of cumulative degree-days and lowest cumulative discharge-days. For example, 1993 and 1998 were poor year classes for roach, chub and dace, and these coincided with high river flows, relatively low water temperatures and poor growth. At the other extreme, 1989-1991 and 1995 were good years for 0+ fish growth, and coincided with strong year classes for all three species. Compared with 1993 and 1998, river discharge in 1989-1991 and 1995 was below average and ambient river temperature and mean length above average.

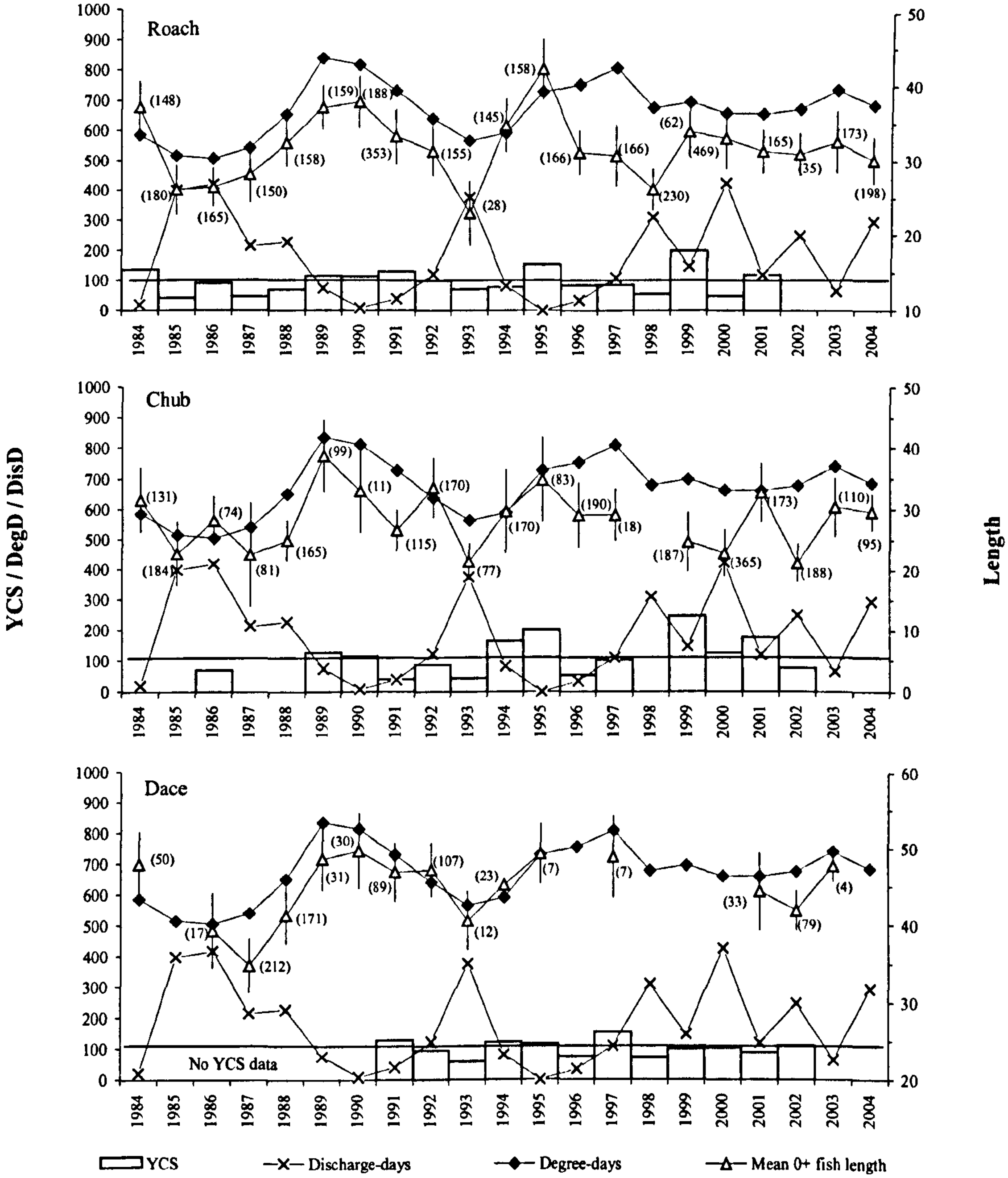


Fig. 6.1 Relationships between 0+ fish growth (mean fork length [mm ± SD] of roach, chub and dace in September), YCS, water temperature (cumulative degree-days >12°C, April-September inclusive) and river discharge (cumulative discharge-days above basal discharge rate [m^3s^{-1} x 10], April-September inclusive) in the Yorkshire Ouse, 1984 to 2004 inclusive. Numbers in parentheses refer to sample sizes used to calculate mean lengths. N.B. Y-axis abbreviations - YCS (year-class strength), DegD (cumulative degree-days), DisD (cumulative discharge-days).

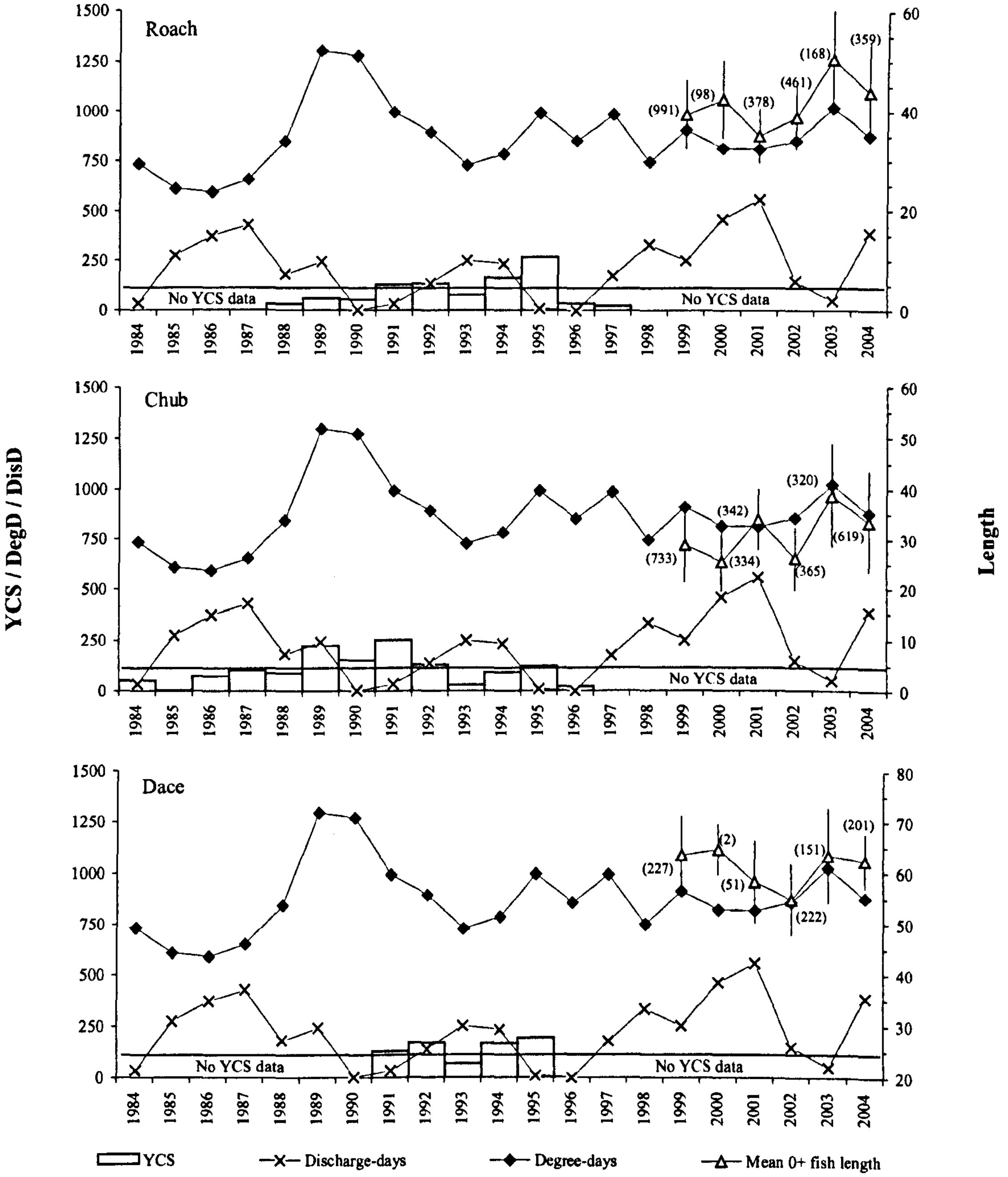


Fig. 6.2 Relationships between 0+ fish growth (mean fork length [mm ± SD] of roach, chub and dace in September), YCS, water temperature (cumulative degree-days >12°C, April-September inclusive) and river discharge (cumulative discharge-days above basal discharge rate [m^3s^{-1} x 10], April-September inclusive) in the River Trent, 1984 to 2004 inclusive. Numbers in parentheses refer to sample sizes used to calculate mean lengths. N.B. Y-axis abbreviations - YCS (year-class strength), DegD (cumulative degree-days), DisD (cumulative discharge-days).

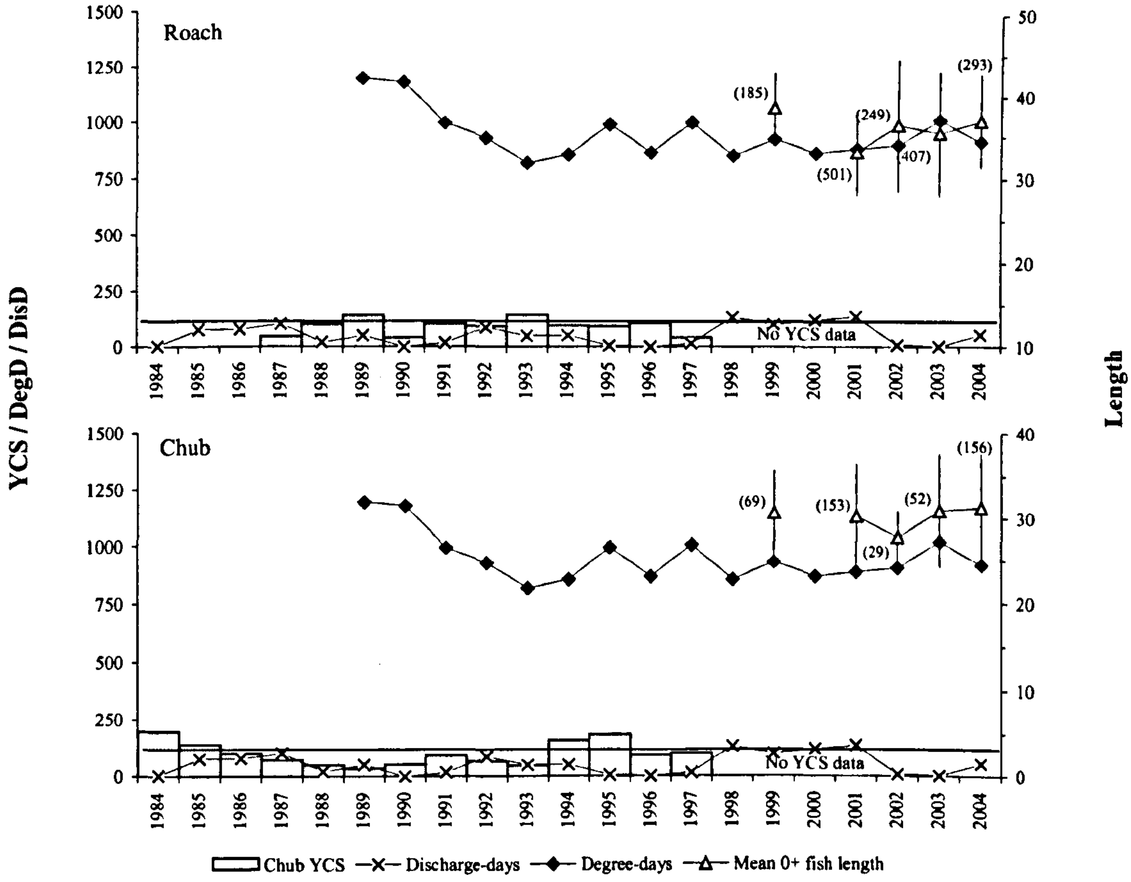


Fig. 6.3 Relationships between 0+ fish growth (mean fork length [mm ± SD] of roach and chub in September), YCS, water temperature (cumulative degree-days >12°C, April-September inclusive) and river discharge (cumulative discharge-days above basal discharge rate [m^3s^{-1} x 10], April-September inclusive) in the Warwickshire Avon, 1984 to 2004 inclusive. Numbers in parentheses refer to sample sizes used to calculate mean lengths. N.B. Y-axis abbreviations - YCS (year-class strength), DegD (cumulative degree-days), DisD (cumulative discharge-days).

6.3.1 Water temperature and river discharge

Temporal patterns in both water temperature and river discharge were broadly similar across all three catchments, with many of the extreme 'cold and wet' and 'warm and dry' years the same in all three rivers (Fig. 6.4a, b). For example, 1984, 1989-1991, 1995 and 2003 were warmer and drier than average in all three rivers, while 1986, 1993, 1998 and 2000 were colder and wetter than average. Some spatial differences were apparent; for example, 2001 was relatively dry in the Ouse, whereas it was the wettest year recorded in the Trent and Avon. In contrast, 2002 was relatively dry in the Trent and Avon, but comparatively wet in the Ouse (Fig. 6.4b). There was less spatial variation in water temperature patterns (Fig. 6.4a).

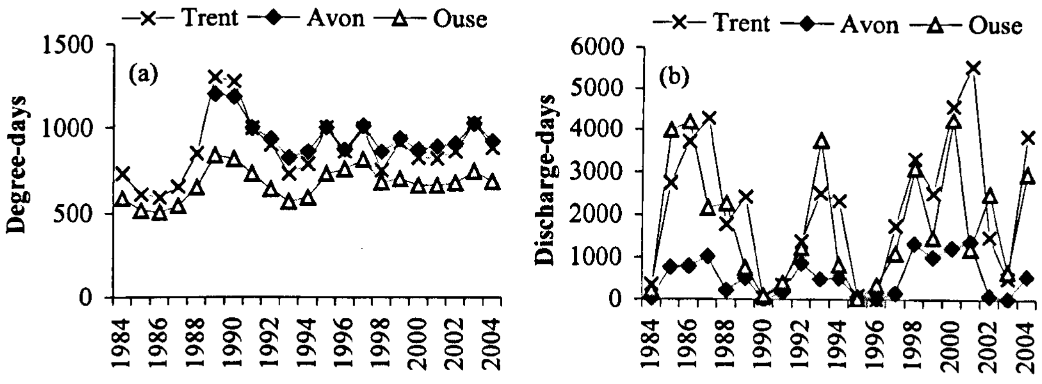


Fig. 6.4 Temporal patterns in (a) water temperature (cumulative degree-days >12°C) and (b) river discharge (cumulative discharge-days above basal discharge rate, m^3s^{-1}) in the rivers Trent, Avon and Ouse.

A significant negative relationship was found between water temperature (cumulative degree-days >12°C, April to September inclusive) and river discharge (cumulative discharge-days above basal discharge rate, April to September inclusive) in the Ouse and Trent, but not in the Avon (Table 6.2; equations 1-3). River discharge explained more of the variance in water temperature in the Ouse than the Trent, perhaps due to the nature of the Ouse catchment which is prone to large and rapid fluctuations in run-off. Note, the cumulative number of discharge-days above the basal rate is very similar for the Trent and Ouse (Fig. 6.4b), despite a substantial difference in the long-term mean daily discharge rate of the two rivers (Trent, 84 m^3s^{-1}; Ouse, 50 m^3s^{-1}).

6.3.2 0+ fish growth and water temperature/river discharge

Growth (September mean length) of 0+ roach, chub and dace in the Ouse was positively correlated with water temperature (cumulative degree-days >12°C) and negatively correlated with river discharge (cumulative discharge-days above basal discharge rate) (Table 6.2; equations 4-9, Fig. 6.1). There were also signs of covariation between the variables in the Trent and Avon (Figs 6.2-6.3), although the relationships were not statistically significant (Table 6.2; equations 10-19), probably due to small sample sizes (growth data were only available for six years in the Trent and five in the Avon).

Table 6.2 Linear regression relationships between water temperature, river discharge, Gulf Stream position, 0+ fish growth and YCS of roach, chub and dace (refer to text for details).

Eqn	Linear regression	P	r^2	n
1	$\mathit{Temperature}_{\mathrm{Ouse}} = -0.040(\mathit{Discharge}_{\mathrm{Ouse}}) + 740.58$	0.004**	0.37	21
2	$\mathit{Temperature}_{\mathrm{Trent}} = -0.052(\mathit{Discharge}_{\mathrm{Trent}}) + 983.36$	0.035*	0.21	21
3	$\mathit{Temperature}_{\mathrm{Avon}} = -0.097(\mathit{Discharge}_{\mathrm{Avon}}) + 1002.59$	0.094	0.19	16
4	$\mathit{Rr\ length}_{\mathrm{Ouse}} = 0.026(\mathit{Temperature}) + 14.284$	0.009**	0.31	21
5	$\mathit{Ll\ length}_{\mathrm{Ouse}} = 0.032(\mathit{Temperature}) + 23.269$	0.001**	0.57	15
6	$\mathit{Lc\ length}_{\mathrm{Ouse}} = 0.026(\mathit{Temperature}) + 10.678$	0.019*	0.27	20
7	$\mathit{Rr\ length}_{\mathrm{Ouse}} = -0.002(\mathit{Discharge}) + 36.000$	0.000**	0.56	21
8	$\mathit{Ll\ length}_{\mathrm{Ouse}} = -0.003(\mathit{Discharge}) + 48.824$	0.000**	0.64	15
9	$\mathit{Lc\ length}_{\mathrm{Ouse}} = -0.002(\mathit{Discharge}) + 32.262$	0.001**	0.44	20
10	$\mathit{Rr\ length}_{\mathrm{Trent}} = 0.054(\mathit{Temperature}) - 6.234$	0.055	0.64	6
11	$\mathit{Ll\ length}_{\mathrm{Trent}} = 0.017(\mathit{Temperature}) + 45.696$	0.488	0.13	6
12	$\mathit{Lc\ length}_{\mathrm{Trent}} = 0.043(\mathit{Temperature}) - 7.164$	0.164	0.42	6
13	$\mathit{Rr\ length}_{\mathrm{Trent}} = -0.002(\mathit{Discharge}) + 46.850$	0.210	0.36	6
14	$\mathit{Ll\ length}_{\mathrm{Trent}} = 0.000(\mathit{Discharge}) + 60.809$	0.922	0.00	6
15	$\mathit{Lc\ length}_{\mathrm{Trent}} = -0.001(\mathit{Discharge}) + 32.757$	0.703	0.04	6
16	$\mathit{Rr\ length}_{\mathrm{Avon}} = 0.005(\mathit{Temperature}) + 31.741$	0.840	0.02	5
17	$\mathit{Lc\ length}_{\mathrm{Avon}} = 0.011(\mathit{Temperature}) + 20.181$	0.512	0.16	5
18	$\mathit{Rr\ length}_{\mathrm{Avon}} = -0.001(\mathit{Discharge}) + 36.763$	0.695	0.06	5
19	$\mathit{Lc\ length}_{\mathrm{Avon}} = 0.001(\mathit{Discharge}) + 29.688$	0.610	0.10	5
20	$\mathit{Rr\ YCS}_{\mathrm{Ouse}} = 5.280(\mathit{Rr\ length}_{\mathrm{Ouse}}) - 70.594$	0.005**	0.39	18
21	$\mathit{Ll\ YCS}_{\mathrm{Ouse}} = 6.375(\mathit{Ll\ length}_{\mathrm{Ouse}}) - 180.779$	0.053	0.49	8
22a	$\mathit{Lc\ YCS}_{\mathrm{Ouse}} = 5.349(\mathit{Lc\ length}_{\mathrm{Ouse}}) - 60.155$	0.122	0.14	18
22b	$\mathit{Lc\ YCS}_{\mathrm{Ouse}} = 6.849(\mathit{Lc\ length}_{\mathrm{Ouse}}) - 113.055$	0.019*	0.32	17
23a	$\mathit{Rr\ YCS}_{\mathrm{Ouse}} = 8.473(\mathit{NWGS}_{\mathrm{annual\ mean}}) + 92.549$	0.496	0.03	18
23b	$\mathit{Rr\ YCS}_{\mathrm{Ouse}} = 25.388(\mathit{NWGS}_{\mathrm{annual\ mean}}) + 83.864$	0.004**	0.48	15
24a	$\mathit{Ll\ YCS}_{\mathrm{Ouse}} = 10.611(\mathit{NWGS}_{\mathrm{June\text{-}July}}) + 94.696$	0.112	0.23	12
24b	$\mathit{Ll\ YCS}_{\mathrm{Ouse}} = 12.596(\mathit{NWGS}_{\mathrm{June\text{-}July}}) + 87.948$	0.012*	0.52	11
25a	$\mathit{Lc\ YCS}_{\mathrm{Ouse}} = 33.372(\mathit{NWGS}_{\mathrm{annual\ mean}}) + 64.364$	0.121	0.14	19
25b	$\mathit{Lc\ YCS}_{\mathrm{Ouse}} = 45.516(\mathit{NWGS}_{\mathrm{annual\ mean}}) + 45.796$	0.013*	0.33	18
26	$\mathit{Rr\ YCS}_{\mathrm{Trent}} = 92.458(\mathit{NWGS}_{\mathrm{annual\ mean}}) + 29.939$	0.000**	0.92	12
27	$\mathit{Ll\ YCS}_{\mathrm{Trent}} = 90.995(\mathit{NWGS}_{\mathrm{April}}) + 90.485$	0.080	0.69	5
28a	$\mathit{Lc\ YCS}_{\mathrm{Trent}} = 17.538(\mathit{NWGS}_{\mathrm{June\text{-}July}}) + 98.364$	0.353	0.08	13
28b	$\mathit{Lc\ YCS}_{\mathrm{Trent}} = 45.597(\mathit{NWGS}_{\mathrm{May}}) + 102.283$	0.024*	0.42	12
29a	$\mathit{Rr\ YCS}_{\mathrm{Avon}} = 11.933(\mathit{NWGS}_{\mathrm{Nov}}) + 84.805$	0.194	0.18	11
29b	$\mathit{Rr\ YCS}_{\mathrm{Avon}} = 19.973(\mathit{NWGS}_{\mathrm{Nov}}) + 90.722$	0.039*	0.48	9
30	$\mathit{Lc\ YCS}_{\mathrm{Avon}} = 18.424(\mathit{NWGS}_{\mathrm{August}}) + 88.946$	0.046*	0.29	14
31	$\mathit{Rr\ YCS}_{\mathrm{Ouse}} = -0.031(\mathit{Discharge}_{\mathrm{June\text{-}Sep}}) + 125.786$	0.002**	0.45	18
32	$\mathit{Ll\ YCS}_{\mathrm{Ouse}} = -0.037(\mathit{Discharge}_{\mathrm{May}}) + 111.241$	0.104	0.24	12
33	$\mathit{Lc\ YCS}_{\mathrm{Ouse}} = -0.158(\mathit{Discharge}_{\mathrm{July}}) + 109.106$	0.030*	0.25	19
34	$\mathit{Rr\ YCS}_{\mathrm{Trent}} = -0.090(\mathit{Discharge}_{\mathrm{June\text{-}Aug}}) + 121.444$	0.045*	0.34	12
35	$\mathit{Ll\ YCS}_{\mathrm{Trent}} = -0.576(\mathit{Discharge}_{\mathrm{June}}) + 173.150$	0.010*	0.92	5
36	$\mathit{Lc\ YCS}_{\mathrm{Trent}} = -0.067(\mathit{Discharge}_{\mathrm{Aug\text{-}Sep}}) + 141.566$	0.024*	0.38	13
37	$\mathit{Rr\ YCS}_{\mathrm{Avon}} = -0.098(\mathit{Discharge}_{\mathrm{June}}) + 101.544$	0.137	0.23	11
38	$\mathit{Lc\ YCS}_{\mathrm{Avon}} = -0.029(\mathit{Discharge}_{\mathrm{May\text{-}July}}) + 115.442$	0.260	0.10	14

*$P<0.05$; **$P<0.01$

6.3.3 YCS and 0+ fish growth

A significant positive relationship was found between YCS and growth (September mean length) of 0+ roach in the Ouse (Table 6.2; equation 20, Fig. 6.5a). A near significant relationship was also found for dace (Table 6.2; equation 21, Fig. 6.5b), although sample size was small (paired YCS and length data only available for eight years). The relationship for chub was poor (Table 6.2; equation 22a), despite apparent covariation between the two variables (Fig. 6.5c). Omission of the extreme 1999 YCS data point substantially improved the relationship (Table 6.2; equation 22b). No paired YCS and 0+ fish growth data were available for the Trent and Avon, and so relationships could not be investigated for these rivers.

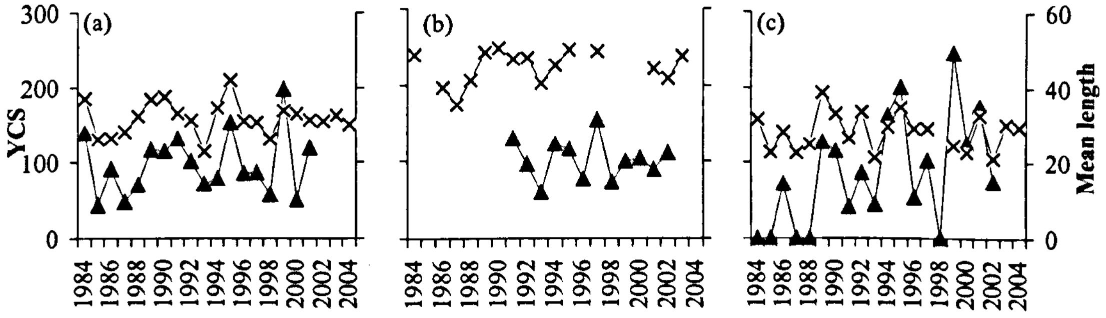


Fig. 6.5 Temporal patterns in year-class strength (YCS, ▲) and growth (September mean 0+ fish length, mm, ×) of (a) roach, (b) dace and (c) chub in the Yorkshire Ouse.

6.3.4 YCS and the position of the Gulf Stream

Comparisons of the yearly trends in YCS of roach, chub and dace and the position of the North Wall of the Gulf Stream (NWGS) suggested positive relationships between the two variables (Figs 6.6-6.8). In the Ouse, the best predictor of YCS of roach and chub was the annual mean position of the NWGS, while YCS of dace was best predicted by position of the NWGS in June and July (Table 6.2; equations 23-25). The relationships were weakened by a small number of outlying data points. For roach, exclusion of the extreme 1985, 1999 and 2000 YCS data points (Fig. 6.6a) greatly improved the amount of variance in YCS explained by the position of the NWGS (Table 6.2; equations 23b). Similarly, removal of the extreme dace and chub YCS values for 1997 (Fig. 6.6b) and 1999 (Fig. 6.6c), respectively, substantially improved their relationships (Table 6.2; equations 24b, 25b).

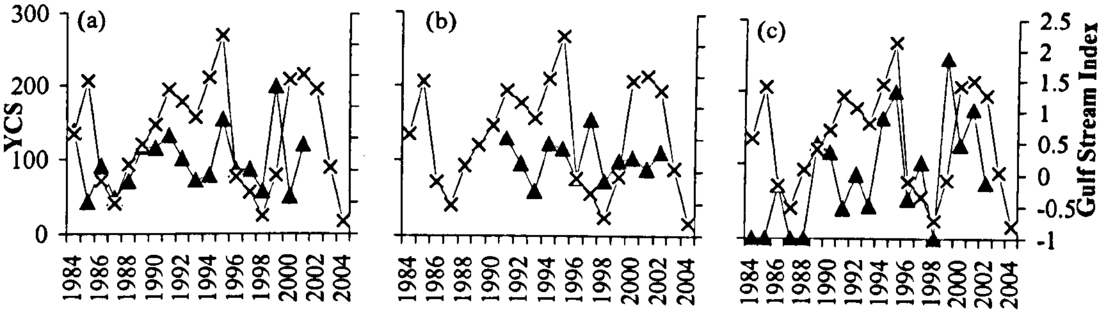


Fig. 6.6 Temporal patterns in year-class strength (YCS, ▲) of (a) roach, (b) dace and (c) chub in the Yorkshire Ouse and the annual mean position of the North Wall of the Gulf Stream (×).

In the Trent, YCS of roach was best predicted by the annual mean position of the NWGS (Table 6.2; equation 26, Fig. 6.7a). The position of the NWGS in April was the best predictor of dace YCS, although the relationship was not statistically significant due to small sample size (Table 6.2; equation 27). The position of the NWGS in June and July accounted for the greatest amount of variation in YCS of chub, although the relationship was not statistically significant (Table 6.2; equation 28a), despite apparent covariation in the variables (Fig. 6.7c). Removal of the extreme 1985 YCS value greatly improved the relationship and identified the position of the NWGS in May as the best descriptor (Table 6.1; equation 28b).

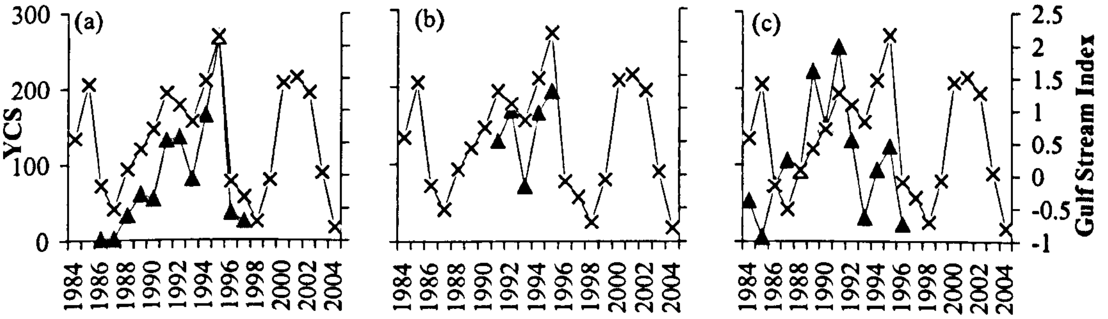


Fig. 6.7 Temporal patterns in year-class strength (YCS, ▲) of (a) roach, (b) dace and (c) chub in the River Trent and the annual mean position of the North Wall of the Gulf Stream (×).

In the Avon, the best predictor of YCS of roach was the position of the NWGS in November (Table 6.2; equation 29a). The relationship was weakened by the unexpectedly low (on theoretical grounds) 1990 and 1995 YCS data points (Fig. 6.8a), but their omission improved the relationship (Table 6.2; equation 29b). For chub, the position of the NWGS in August proved the most reliable predictor of YCS (Table 6.2; equation 30).

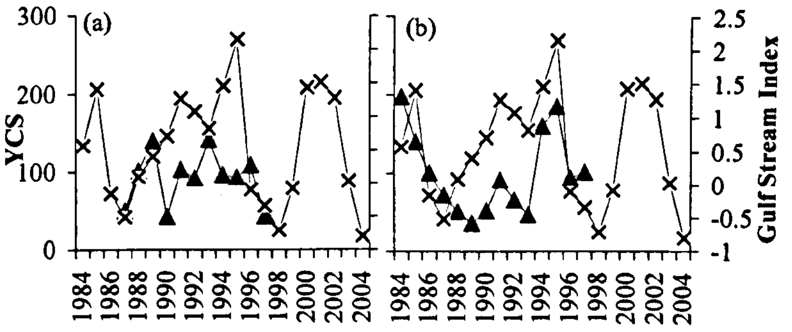


Fig. 6.8 Temporal patterns in year-class strength (YCS, ▲) of (a) roach and (b) chub in the Warwickshire Avon and the annual mean position of the North Wall of the Gulf Stream (×).

Multiple regressions did not account for more of the variance in YCS due to colinearity, i.e. a number of the variables were autocorrelated/confounded one another.

6.3.5 Identification of 'critical' life history periods

An attempt was made to identify any periods when each of the 0+ fish species may be more susceptible to the direct effects of increases in river discharge (i.e. discharge-induced mortality), and thereby identify key periods during which YCS is determined. Linear regressions were performed between YCS and river discharge (cumulative discharge-days above basal discharge rate) during a series of time periods.

In the Ouse, the strongest correlate of YCS of roach was discharge during the period from June to September inclusive (Table 6.2; equation 31), with July the best single month (Fig. 6.9a). The best relationship for YCS of dace was with discharge in May (Table 6.2; equation 32), followed by the period from April to May inclusive (Fig. 6.9b), although the relationships were not statistically significant partly due to the influence of the high YCS value for 1997. YCS of chub was most significantly related to discharge in July (Table 6.2; equation 33), with the period from July to August the next best predictor (Fig. 6.9c).

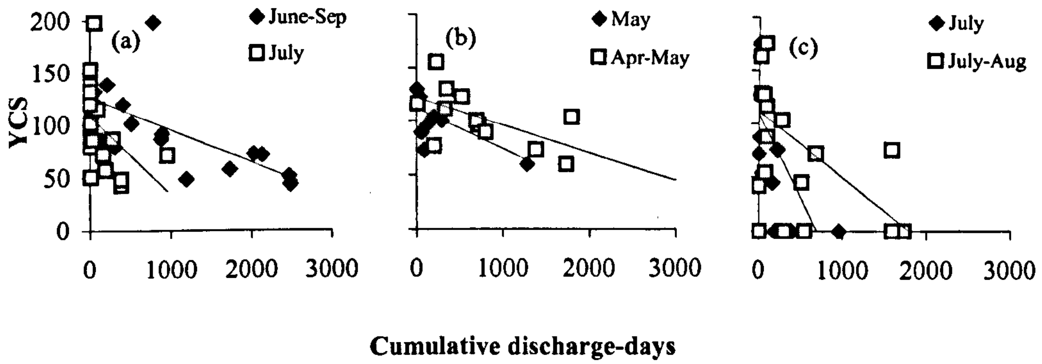


Fig. 6.9 Temporal patterns in year-class strength of (a) roach, (b) dace and (c) chub and river discharge (cumulative discharge-days above basal discharge rate, m^3s^{-1}) during 'critical periods' (see text for details) in the Yorkshire Ouse. N.B. Two best correlations only shown for each species (see Table 6.2 for associated statistics; equations 31-33).

In the Trent, the strongest correlate of YCS of roach was discharge during the period from June to August inclusive (Table 6.2; equation 34), with June the best single month (Fig. 6.10a). The best relationship for YCS of dace was with discharge in June (Table 6.2; equation 35), followed by the period from June to July inclusive (Fig. 6.10b). YCS of chub was most significantly related to discharge during the period from August to September inclusive (Table 6.2; equation 36), with September the best single month (Fig. 6.10c).

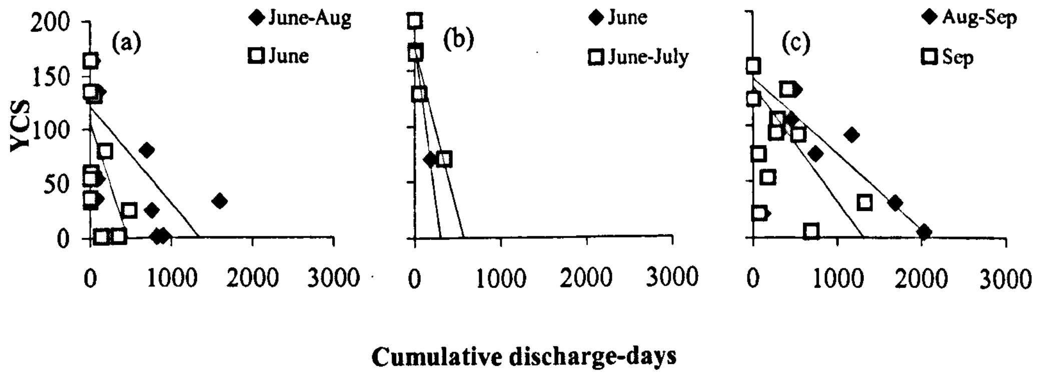


Fig. 6.10 Temporal patterns in year-class strength of (a) roach, (b) dace and (c) chub and river discharge (cumulative discharge-days above basal discharge rate, m^3s^{-1}) during 'critical periods' (see text for details) in the River Trent. N.B. Two best correlations only shown for each species (see Table 6.2 for associated statistics; equations 34-36).

In the Avon, the strongest correlate of YCS of roach was discharge in June (Table 6.2; equation 37), followed by the period from June to July (Fig. 6.11a), while YCS of chub was most significantly related to discharge during the period from May to July inclusive (Table 6.2; equation 38), with July the best single month (Fig. 6.11b). None of the relationships were statistically significant.

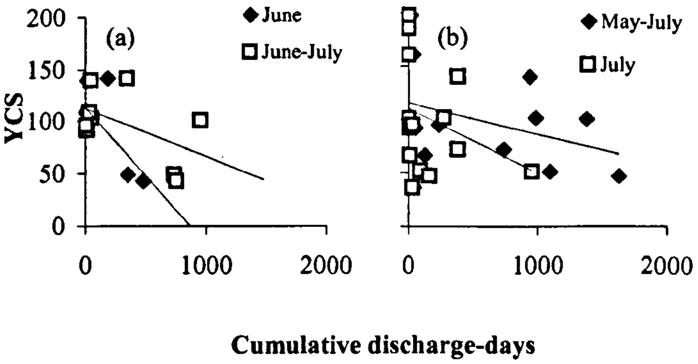


Fig. 6.11 Temporal patterns in year-class strength of (a) roach and (b) chub and river discharge (cumulative discharge-days above basal discharge rate, m^3s^{-1}) during 'critical periods' (see text for details) in the Warwickshire Avon. N.B. Two best correlations only shown for each species (see Table 6.2 for associated statistics; equations 37-38).

Inter-annual variations in river discharge relative to the timing of fish hatching are likely to mask the effects of river discharge on recruitment success. Furthermore, increases in river discharge need not necessarily be large to cause discharge-induced mortality if such events coincide with the emergence of newly hatched fish. Direct effects of river discharge (i.e. discharge-induced mortality) may not occur regularly in many rivers, with indirect effects prevailing in most years. Of the three rivers studied here, it is likely that the direct effects of discharge are most important in the Ouse due to its proportionally higher number of discharge-days relative to basal discharge rate and more prevalent large and rapid fluctuations in discharge.

Any direct causal relationship between river discharge and recruitment success may be overlooked if 'warm and dry' years are included in analyses. Unfortunately it was not possible to separate the direct and indirect effects of river discharge using conventional data analysis techniques. However, observation of the relative patterns in YCS and each of the predictive factors enabled a number of cases where discharge-induced mortality may potentially have been important to be identified. For example, although YCS of all three species was weak in 1998, dace were less affected than roach and chub (Fig. 6.1).

Mean daily discharge data revealed that discharge was lower than average in May (when dace in the Ouse hatch), but above average for the whole of June (when roach and chub hatch) (Fig. 6.12a). In addition, although discharge in the Ouse in 2000 was the highest recorded, YCS was high for chub, average for dace and low for roach (Fig. 6.1). Although 2000 was wet, the majority of discharge-days were accrued during April, before any of the three species had hatched, and early June, before chub had hatched but whilst roach were in their early larval steps and dace were nearing the end of the larval period or already juveniles (Fig. 6.12b). The rest of the summer was mostly drier than average until late September.

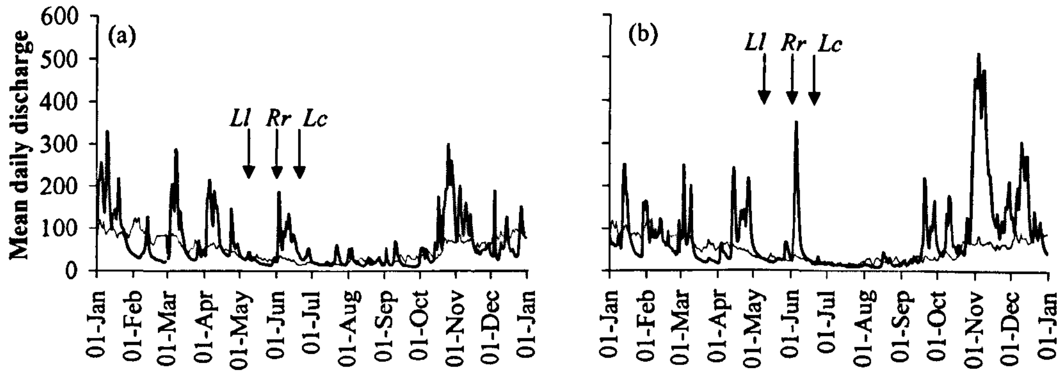


Fig. 6.12 Mean daily discharge (m^3s^{-1}) in the Yorkshire Ouse at Skelton in (a) 1998 and (b) 2000, compared with the long-term daily mean (smoother line). Arrows represent the approximate hatching dates of dace (*Ll*), roach (*Rr*) and chub (*Lc*).

6.4 DISCUSSION

Synchronous fluctuations in the abundance of several populations at a regional scale can be a sign of a climatic effect on their dynamics (Tedesco *et al.*, 2004). Indeed, such phenomena are increasingly being recognised as important factors causing interannual variability in organism abundances in aquatic ecosystems (e.g. George & Harris, 1985; George & Taylor, 1995; Reid *et al.*, 1998; George, 2000, 2005; George *et al.*, 2000, 2004; Irigoien *et al.*, 2000; Straile, 2000; Aprahamian & Aprahamian, 2001; Axenrot & Hansson, 2003; Nunn *et al.*, 2003a; Britton *et al.*, 2004; Ravier & Fromentin, 2004; Hays *et al.*, 2005). In cyprinid fish populations, strong year classes are often correlated with high water temperature during the first summer of life (Mills & Mann, 1985; Cowx, 2000; Grenouillet *et al.*, 2001a), and several studies have demonstrated that a major influence on summer water temperatures is the position of the North Wall of the

Gulf Stream (e.g. Taylor & Stephens, 1980; Willis *et al.*, 1995; Taylor, 1996). Any change in the position of the NWGS should, therefore, manifest itself in terms of a change in recruitment, with higher recruitment associated with a more northerly position of the NWGS (Aprahamian & Aprahamian, 2001). The present study corroborates these general observations. The exact mechanism by which this occurs probably differs between waterbodies, however, since the Gulf Stream influences a range of interlinked factors, all of which have varying impacts upon aquatic ecosystems.

Newly hatched cyprinids are weak swimmers, owing to their small size (usually <10 mm) and lack of fully-formed fins (Mann, 1995). Mann & Bass (1997) stated that the ability of 0+ roach and dace to hold station was positively related to fish length and water temperature, and negatively related to water velocity. The vulnerability of fish larvae to displacement by river currents dictates that they are usually confined to a narrow riparian zone with water velocities <2 cm s^{-1} (Mills & Mann, 1985; Mann & Mills, 1986; Lightfoot & Jones, 1996; Mann & Bass, 1997; Flore & Keckeis, 1998; Schiemer *et al.*, 2001b), and the possibility of recolonisation by displaced larvae may be precluded because survival after displacement by flood events is invariably low (Harvey, 1987). Stochastic, episodic increases in river discharge, therefore, can significantly influence survival of 0+ fish, and may cause the density, species richness and species composition of fish communities to fluctuate yearly (Schlosser, 1985; Schlosser & Angermeier, 1990; Pont & Nicolas, 2001). The impact of increased river discharge on eventual YCS may be determined by small differences in the timing of such events relative to vulnerable life history periods, as there is a rapid decline in susceptibility to displacement with increasing size in cyprinids (Harvey, 1987). The quicker fish grow during development, therefore, the sooner the risk of displacement by river current is reduced (Mann & Bass, 1997).

A small increase in discharge in early summer may be more severe in terms of 0+ fish mortality than a larger increase in late summer, especially for rivers where lateral connectivity has been lost. In the present study, the strongest relationships between YCS and discharge were often for periods when the respective fish species were in their larval stages. In the Yorkshire Ouse, for example, the strongest relationships between YCS of dace and chub were with discharge in May and July, respectively. Precise critical periods were not identified in all cases, probably due to inter-annual variations in river discharge relative to the timing of fish hatching. In the Ouse, for instance, the strongest relationship between YCS of roach was with discharge in the period from June to September inclusive. This may suggest (as is likely) that in most years it is the flow regime over the summer as a whole, rather than discharge in short specific time periods, that is most influential in determining YCS of this species, and that the main influence of discharge on YCS is indirect (i.e. reduced growth due to suppressed water temperatures, discharge-associated increases in energy expenditure and reduced food availability) rather than direct (i.e. discharge-induced mortality). However, it was possible in some instances to identify increases in discharge that coincided with the approximate hatching times of the fish and infer an effect to some degree.

The generally poorer relationships for chub may partly be because of the potential for populations of this species to spawn more than once a summer (Nunn *et al.*, 2002; Chapter 3), which may act as an 'insurance policy' against discharge-induced 0+ mortality in early summer (Nunn *et al.*, 2003a). In some years, therefore, relatively strong year classes of chub may result, despite high mortality in early summer and smaller than average mean lengths, providing overwinter conditions are not severe. Roach and dace, on the other hand, spawn only once per summer (Nunn *et al.*, 2002; Chapter 3). In addition, Garner (1999) found that chub are better able to locate slow flowing patches of water than either roach or dace throughout their early development, and so may be less susceptible to increases in river discharge than these latter species. Separation of 0+ cohorts may have improved the relationships for chub, but unfortunately this was not possible from the annual samples collected from the Ouse.

Increases in river discharge and floods appear to influence recruitment success of riverine fish populations in two opposing ways. As a rule, fish communities that inhabit rivers with naturally-developed floodplains are not negatively affected even by extreme floods (Schiemer *et al.*, 2001b; Lusk *et al.*, 2004). Moreover, floodplain inundation in such rivers is thought to enhance recruitment by providing suitable spawning and nursery habitat (Copp, 1989b; Junk *et al.*, 1989; Reimer, 1991; Cattanéo *et al.*, 2001; King *et al.*, 2003; Bonvechio & Allen, 2005). Furthermore, the larvae of many fish species use floods for dispersal, allowing movement from the spawning habitat to nursery areas (e.g. Pavlov *et al.*, 1977; Copp & Cellot, 1988; Peňáz *et al.*, 1992; Pavlov, 1994; Johnston *et al.*, 1995; Johnston, 1997; Araujo-Lima & Oliveira, 1998; Jurajda, 1998; Robinson *et al.*, 1998; Carter & Reader, 2000; Reichard *et al.*, 2001, 2002a, b, 2004; Copp *et al.*, 2002; Oesmann, 2003; Peterka *et al.*, 2004; Reichard & Jurajda, 2004; Zitek *et al.*, 2004a, b). Floods may also be necessary for the liberation of fish from isolated floodplain waterbodies, thereby increasing recruitment to the main river (Halačka *et al.*, 1998; Bartošová & Jurajda, 2001; Bartošová *et al.*, 2001; Grift *et al.*, 2001a, b; Jurajda *et al.*, 2004).

Many studies have reported negative impacts of increased discharge and floods on fish survival (e.g. Erman *et al.*, 1988; Spindler, 1995; Mion *et al.*, 1998; Jensen & Johnsen, 1999; Pyron & Lauer, 2004; Bonvechio & Allen, 2005). Whereas floods may enhance recruitment in natural rivers, 'wash-out' of 0+ fish from poorly structured or degraded habitats may be high (Pearsons *et al.*, 1992; Bischoff & Wolter, 2001; Schiemer *et al.*, 2001b), with limnophilic species likely to be most affected owing to their generally poor ability to withstand elevated river flows (Harvey, 1987; Bischoff & Wolter, 2001). Large cohorts of 0+ fish may be inconsequential to eventual YCS if overwinter survival is poor, and availability (i.e. lack) of overwintering habitat may restrict YCS of many fish species in some rivers, particularly during severe winters which experience prolonged periods of elevated flow. In homogeneous stretches of river, flow regulation may provide long-term refuge from mortality associated with high flows (Humphries *et al.*, 1999, 2002; Driver *et al.*, 2005).

Although discharge and water temperature account for a great deal of the variation in YCS, there are likely to be other complicating factors of varying importance. For example, in all three catchments, the 1994 year classes of all three species were stronger than those in 1996, despite conditions seemingly being more favourable in the latter year (i.e. water temperature was higher and river discharge was lower in 1996 than in 1994). In addition, the relatively poorer relationships between recruitment success and abiotic variables (especially discharge) in the Trent and Avon may suggest that, due to their more stable and predictable flow regimes, biotic factors such as competition, predation and disease may be of greater significance than in spate rivers such as the Ouse.

Whilst the influence of climatic forces such as the Gulf Stream on fish population dynamics may be regional, biotic influences necessarily occur at lower scales of geographic resolution governed by the distribution of sympatric organisms. A number of studies have demonstrated a negative relationship between fish growth and fish density (e.g. Persson & Greenberg, 1990; Byström & García-Berthou, 1999; Dettmers & Wahl, 1999; Cowan *et al.*, 2000; Feldlite & Milstein, 2000; Pivnička & Švátora, 2000; Romare, 2000). Grenouillet *et al.* (2001a) found that survival of roach in the first year of life was density-dependent, and stated that intraspecific competition within the 0+ cohort could influence recruitment to older age-classes. This may be of particular importance in years of good recruitment. Cryer *et al.* (1986) and Perrow & Irvine (1992), studying lacustrine populations of roach, demonstrated that abundant 0+ roach can sometimes show poor growth as a result of depression of their prey populations.

Variations in prey (zooplankton) abundance may influence the initial growth rates of fish larvae, and a switch in the diet of 0+ roach in late June from small invertebrates (Cladocera, Chironomidae) to one dominated by detritus may explain discrepancies between observed growth rates and those predicted from temperature growth models (Mann, 1997). Moreover, competition for food resources may influence 0+ overwinter mortality. Overwinter survival is positively related to fish length, although it is the condition (≈lipid content) of the fish (which is a function of length) that is the key factor (Miller *et al.*, 1988; Post & Evans, 1989; Johnson & Evans, 1990, 1991, 1996; Thompson *et al.*, 1991; Griffiths & Kirkwood, 1995; Hurst & Conover, 1998; Kirjasniemi & Valtonen, 1997a, b; Copeland & Carline, 1998; Garvey *et al.* 1998; Post *et al.*, 1998; Schindler, 1999; Lappalainen *et al.*, 2000; McCollum *et al.*, 2003; Eckmayer & Margraf, 2004; Pangle *et al.*, 2004; Curry *et al.*, 2005). It is also important, therefore, to consider the impacts of increased river flows on the food supply of 0+ fish, since discharge influences fish populations indirectly through its key role in controlling phytoplankton and, hence, zooplankton populations (Richardson, 1992; Bass *et al.*, 1997a; Lair & Reyes-Marchant, 1997; Marker & Collett, 1997; Reckendorfer *et al.*, 1999; Schiemer *et al.*, 2001c; Baranyi *et al.*, 2002).

Disease is known to impact upon 0+ fish populations (Brabrand *et al.*, 1994; Cooper, 1996; McKeown & Irwin, 1997; Bagge & Valtonen, 1999; Bartošová *et al.*, 1999; Molnár *et al.*, 2002; Ondračková *et al.*, 2002, 2004a, b, c; Longshaw *et al.*, 2003, 2005; Feist & Longshaw, 2005), although its importance regarding recruitment success is uncertain (Cowx, 2001). However, recent research by Longshaw *et al.* (submitted) suggests that parasites may be important factors in recruitment success of riverine fish populations. Some *Myxobolus* spp., for example, can be extremely pathogenic (Longshaw *et al.*, 2003), whereas other parasites, such as *Posthodiplostomum cuticola* (von Nordmann), rarely cause mortality (Ondračková *et al.*, 2002, 2004a, b). Although mass mortality caused by disease is rare (Cowx, 2001), parasites may nevertheless influence recruitment indirectly via alterations in host growth, swimming ability, predation risk or behaviour (Barber *et al.*, 2000; Barber, 2003; Ondračková *et al.*, 2004b, c).

Predation may be an important factor regulating 0+ fish survival (Paradis *et al.*, 1996), particularly in fresh waters (Myers *et al.*, 1997). Invertebrates, especially the larvae of Odonata, *Dytiscus* sp. and *Notonecta* spp., are known to predate upon fish larvae (Diamond, 1985b; Mills & Mann, 1985; Diamond & Wakefield, 1986; Mann & Mills, 1986; Le Louarn & Cloarec, 1997), although it is not known what their significance is regarding recruitment success. Similarly, proving empirically that predation by piscivorous fish has a significant impact of recruitment is difficult and, although it is known to occur (e.g. Frankiewicz *et al.*, 1996, 1999; Dörner *et al.*, 1999; Dörner & Benndorf, 2003), few studies have identified it as a major factor. An exception is Mooij *et al.* (1996) who found that predation by zander was the most important factor controlling YCS of bream in the shallow and highly eutrophic Lake Tjeukemeer.

The effects of river discharge on YCS of particular fish species may, therefore, be either direct or indirect. For example, a poor year class may be the result of elevated river flows causing high mortality during a critical period in the life history of a particular fish species, such as the larval period, or it may equally be the result of poor growth caused by a reduction in water temperature, discharge-associated increases in energy expenditure or a lack of suitable food. In most years it is likely that indirect effects will prevail over direct effects due to non-synchronicity of periods of elevated discharge and fish hatching, although this will differ between rivers. It was not possible in the present study to conclusively separate the roles of either. Whilst it is likely that water temperature is the limiting factor with respect to fish growth, river discharge may be the factor that ultimately controls YCS, either directly or indirectly. It could be that, in effect, water temperature determines potential YCS while discharge determines realised YCS.

CHAPTER SEVEN

GENERAL DISCUSSION

7.1 INTRODUCTION

In many fish populations, there are occasional large cohorts of adult fish, with a wide range of biotic and abiotic factors influencing recruitment success (Mills & Mann, 1985). The relationships between each of these factors can be illustrated by way of a flow diagram (Fig. 7.1). Habitat availability is the key factor controlling 0+ fish community structure in the Trent, Avon and Ouse catchments (Chapter 3). Habitat also influences the structure of phytoplankton and zooplankton communities (Chapter 4), which themselves determine the potential diets of 0+ fish (Chapter 5). The food eaten by 0+ fish has implications for growth (Chapter 3), which has further ramifications for recruitment success, as survival is positively related to fish body length (Chapter 6). Underlying all these interactions is the influence of water temperature (Chapter 6), which determines growth directly via its influence on food consumption and metabolism, but also indirectly via its influence on the dynamics of plankton populations. Water temperature itself may be influenced by river discharge, and both are controlled by the climate, which is governed by the position of the North Wall of the Gulf Stream (Chapter 6). The overall aim of this study was to examine the dynamics of larval and 0+ juvenile fish populations in lowland rivers. To this end, the study was divided into key topics which were addressed in Chapters 3 to 6. This chapter integrates the knowledge gained from the previous four chapters, and provides recommendations for further study.

7.2 ABIOTIC FACTORS

7.2.1 Climate

Chapter 6 explored the relationships between water temperature, river discharge, the position of the Gulf Stream, 0+ fish growth and year-class strength, and suggested that river discharge may be the factor that ultimately controls recruitment success. The effects of river discharge may be either direct or indirect. For example, a poor year class

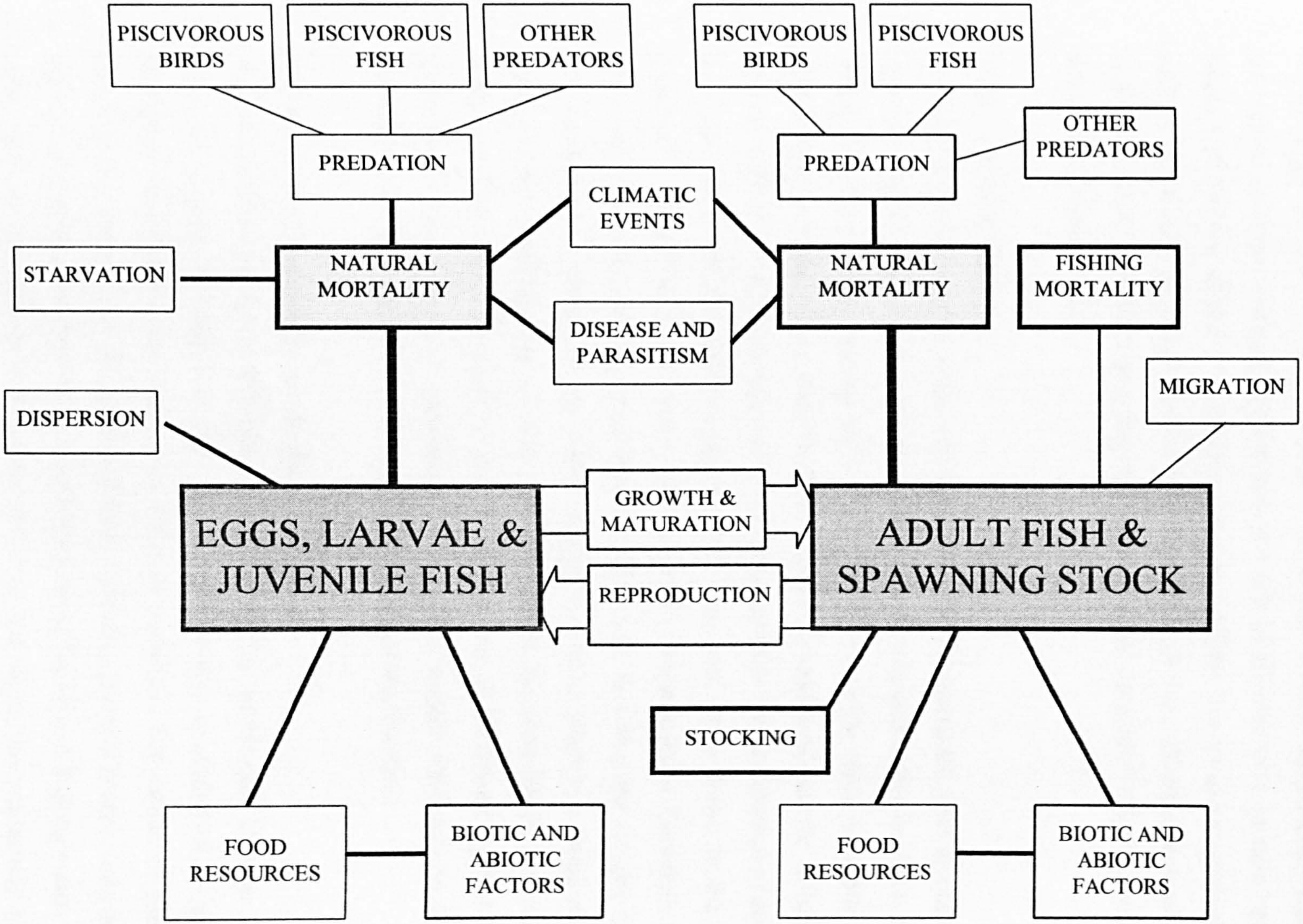


Fig. 7.1 Model to illustrate the complexity of the factors that influence fish populations in rivers (after Cowx, 2001).

may be the result of elevated river flows causing high mortality during a critical period in the life history of a particular fish species, such as the larval period, or it may equally be the result of poor growth caused by a reduction in water temperature, discharge-associated increases in energy expenditure or a lack of suitable food. In most years it is likely that indirect effects will prevail over direct effects due to non-synchronicity of periods of elevated discharge and fish hatching, although this will differ between rivers. It could be that, in effect, water temperature determines potential YCS while discharge determines realised YCS.

7.2.2 Physical habitat

A range of factors determine the structure of 0+ fish communities, with availability of spawning and nursery areas among the most important (Jurajda & Peňáz, 1994; Jurajda, 1995). While some fish species are able to flourish in a wide range of habitat types, others have stricter habitat requirements. Chapter 3 demonstrated the influence of habitat availability on the structure of 0+ fish communities. The dominance of eurytopic over rheophilic and limnophilic species in the Trent and Avon is due to the greater availability of spawning and nursery habitat for the former species. Eurytopic species are usually found in the largest numbers where habitat diversity and density of other fish species is low, reflecting the ability of these species to adapt to a range of habitat types. Strictly rheophilic species were most abundant in the rivers Swale, Ure, Nidd and Wharfe of the Ouse catchment where the habitat was characterised by fast-flowing water and a sand or gravel substratum. Limnophilic species were rare in all three catchments due to a lack of densely vegetated floodplain waterbodies.

The function of floodplain waterbodies

Where available, almost all fish species used floodplain waterbodies at some point in their life history. A number of fish species were proven or presumed to spawn in floodplain waterbodies, and most used them as nurseries. The larvae of rheophilic species were assumed to have dispersed from spawning grounds nearby since they are unlikely to reproduce in floodplain waterbodies due to the lack of flowing water. After a short time, species such as barbel emigrated from the floodplain and moved to faster flowing areas with a substratum characterised by gravel or sand. In contrast, eurytopic and, where present, limnophilic species resided in floodplain waterbodies for the whole of their first year. Floodplain waterbodies also served as refugia for both 0+ and >0+

fish in winter, especially during floods, and such areas invariably provided superior feeding conditions than main river channels (Chapters 4 and 5).

7.3 BIOTIC FACTORS

7.3.1 Growth

Growth of fish in the first summer of life was found to be a key correlate of recruitment success (Chapter 6). A range of factors exert influence upon the growth of 0+ fish, with water temperature and food availability the most important regarding growth patterns in the field (Keckeis & Schiemer, 1992). Differences in growth between the Trent and Ouse could be attributed to the longer growing season experienced by fish in the Trent (Chapter 6), afforded by an earlier increase in water temperatures in the spring, earlier hatching times (Chapter 3) and a later decline of water temperatures in the autumn. Reasons for differences between the Trent and Avon were less apparent, since both experience similar temperature regimes (Chapter 6) and both are similarly productive in terms of phytoplankton and zooplankton (Chapter 4). However, whereas the Trent has an appreciable littoral zone for much of its length, the Avon lacks the very shallow, warmer water in the river margins that fish larvae preferentially inhabit. Although, due to migration, it could not be proven that fish in floodplain waterbodies grew larger than fish in main river channels (Chapter 3), a benefit could nonetheless be inferred by virtue of the greater availability of zooplankton compared with the main river channels (Chapter 4).

7.3.2 Food and feeding

The diets of 0+ fish vary spatially, temporally and ontogenetically (Chapter 5). Food availability (Chapter 4) determines the potential diets of 0+ fish while, due to restrictions of morphology and behaviour, level of development is the limiting factor regarding initial diet spectra. Thus, young larvae had the most interspecific diet overlap, with feeding diversity and the importance of species-specific traits increasing with development. The majority of fish consumed prey substantially smaller than the maximum theoretically possible inferred from their gape, probably due to the increased handling time required for large prey. Within the constraints determined by gape, certain prey taxa were consistently selected over others of the same size, demonstrating that taxa-specific as well as size-specific characteristics are important in the prey selection process.

Zooplankton was the most important food of the larvae and 0+ juveniles of almost all fish species (Chapter 5). Chapter 4 demonstrated conclusively that floodplain waterbodies provide enhanced feeding conditions for 0+ fish, with zooplankton diversity, size ranges and density being greater than in main river channels. Thus, fish from floodplain waterbodies had correspondingly more diverse diets than fish from main river channels (Chapter 5). In particular, the higher densities of large-bodied cladocerans and copepods in floodplain waterbodies compared with main river channels is significant due to the higher energy intake per unit volume when feeding upon large prey (Gill & Hart, 1998) and the greater nutritional value of zooplankton over benthic macroinvertebrates (Persson, 1987; Persson & Greenberg, 1990). Furthermore, whilst phytoplankton and zooplankton populations typically decline after mid summer in main river channels, they may not in floodplain waterbodies, where biomass is often higher than in the main river and persists later into the year (Bass *et al.*, 1997a; Mann *et al.*, 1997; Marker & Collett, 1997).

7.3.3 Spawning periodicity

Chapter 3 examined the spawning periodicity of key fish species. Chub and bleak, and to a lesser extent bream, gudgeon and minnow, adopted fractional or protracted spawning strategies, while dace, roach and perch spawned only once per season. Multiple spawning events are important for recruitment success as they disperse the mortality risk of the early developmental stages (Begg & Marteinsdottir, 2000). In some years, therefore, relatively strong year classes of such species may result, despite high mortality in early summer and smaller than average mean lengths, providing overwinter conditions are not severe. It has still to be ascertained empirically, however, what the significance of multiple spawning events is with respect to recruitment success.

7.4 CONCLUSIONS AND RECOMMENDATIONS

Physical habitat

In the Trent and, particularly, the Avon, rheophilic fish species were heavily outnumbered by eurytopic species due to a lack of suitable spawning and nursery habitat for rheophilic species. **It is recommended that floodplain waterbodies (e.g. disused gravel quarries, disconnected oxbow lakes) should continue to be connected to the River Trent where appropriate, or purpose built habitats (e.g. flow-through secondary channels) created to provide suitable spawning and nursery habitat for rheophilic fish species.** Such activities should include investigations into the habitat requirements of the various developmental stages of key fish species. In general, floodplain waterbodies should be shallow, have complex shorelines with a high variability of flow velocities, and be located close to known spawning areas for key fish species. If possible, pre-connection data should be collected for comparative purposes. The Avon and Ouse would also benefit from an increase in lateral connectivity which, at present, is limited due to isolation of their floodplains.

Limnophilic fish species are rare in all three river catchments due to a lack of suitable habitat. **It is recommended that floodplain waterbodies should continue to be connected to the River Trent were appropriate, or purpose-built habitats created should land become available.** Such waterbodies should support dense populations of submerged macrophytes and, ideally, the degree of connectivity with the main river channel should be less than for rheophilic species. The causes for the lack of submerged vegetation in many of the existing floodplain waterbodies should be identified and, if possible, mitigation measures employed. For example, fencing could be used to discourage grazing waterfowl such as geese and swans, and destructive fish species, such as carp, could similarly be excluded until macrophyte populations have become established.

Almost all fish species utilised floodplain waterbodies at some point in their life history. **It is recommended that further floodplain waterbodies are investigated to facilitate identification of the key attributes (e.g. morphology, degree of connectivity, biotopic characteristics) of such waterbodies regarding their functions as spawning, nursery and refuge areas, so that the benefits for the various fish reproductive guilds can be maximised.** The use of floodplain waterbodies as spawning areas should be further assessed for species for which data are currently lacking via intense surveys of spawning activity, and supplemented by collection and rearing of spawned eggs to an identifiable life stage.

Fish were presumed to migrate from main river channels to floodplain waterbodies, and *vice versa*, to spawn, feed and shelter from floods. **It is recommended that traps or fish counters are installed at the entrance(s) of a selection of floodplain waterbodies to identify any seasonal, diel, species-specific and ontogenetic variations in use of floodplain waterbodies.** This could include an assessment of the factors influencing drift of larval fish, including between main river channels and lentic waterbodies, and tagging studies of adult fish. The outcomes of such investigations could clarify the extent of inter-population mixing, and assist in the identification of key spawning and overwintering areas.

Food and feeding

Floodplain waterbodies provide enhanced feeding conditions for 0+ fish, with zooplankton diversity, size ranges and density being greater than in main river channels. **It is recommended that further investigations are undertaken to assess the availability of planktonic and non-planktonic zooplankton to 0+ fish in a wider range of floodplain waterbodies.** Such investigations should include assessments of diel horizontal migration of zooplankton and be linked with patterns of fish distribution. The outcomes of such investigations should allude to the key times and areas used by foraging 0+ fish. Studies should also be undertaken to compare availability of benthic macroinvertebrates to 0+ fish between main river channels and floodplain waterbodies.

Zooplankton densities at Marina Pond were in excess of an order of magnitude higher than at other floodplain sites. **It is recommended that detailed studies are initiated to identify the causes for the high densities of zooplankton at Marina Pond.** These should include studies of zooplankton demography to assess the impacts of fish and invertebrate predation on the fecundity and birth and death rates of key zooplankton groups, assessments of nutrient availability, phytoplankton production (turnover rate), microscopic studies of phytoplankton composition or calculation of percentage ingestible carbon, and water residency times/flushing rates. The outcomes of such studies could potentially be utilised in the design of future floodplain waterbodies to maximise plankton production for 0+ fish.

Few relationships were found between densities of phytoplankton, zooplankton and fish. **It is recommended that sampling frequency is increased to once per week or**

more to ensure the time elapsed between surveys is shorter than the life cycles of the key phytoplankton and zooplankton groups. A higher frequency of surveys would permit a closer examination of the reactions of fish to changes in prey availability, and *vice versa*. Future studies of selection by fish should include a measure of gape and prey width, in addition to studies of selection of particular components, such as ephippial or egg-bearing females, of key zooplankton taxa.

Dietary overlap was greatest among ecologically similar fish species. **It is recommended that further studies are initiated to ascertain the implications of competition and resource partitioning on 0+ fish growth and, subsequently, recruitment success.** Such work should address the issue of resource limitation and consider the possibility of intraspecific competition between 0+ cohorts of multiple spawning fish.

Certain prey taxa were consistently selected over others of the same size. **It is recommended that further studies are undertaken to establish the relative importance of taxa- (e.g. morphology, movement) and size-specific characteristics in the prey selection process of 0+ fish.** Such research should consider potential selection for specific components of the zooplankton, such as egg-bearing or ephippial females, and attempt to quantify the direct and indirect impacts of fish predation upon zooplankton populations and communities. Such studies could provide information regarding the benefits accrued from selection of particular prey taxa over others, and the existence of feedback mechanisms on 0+ fish growth.

Spawning periodicity

Chub and bleak, and to a lesser extent bream, gudgeon and minnow, adopted fractional or protracted spawning strategies, while dace, roach and perch spawned only once per season. **It is recommended that temporal and spatial variations in overwinter survival of fish from late summer spawnings is investigated to assess the significance of multiple spawning events with respect to recruitment success.** This could perhaps be achieved via analysis of length distributions through the winter months and into the following spring. Such studies should also attempt to elucidate the reasons for, and consequences of, temporal and spatial differences in the prevalence and intensity of multiple spawning events.

It was not possible in the current study to ascertain whether recruitment patterns were a result of *actual* multiple spawning by individual fish or *apparent* multiple spawning by sub-populations that delay their spawning activities. **It is recommended that telemetry or tagging is used to confirm multiple spawning by individual fish.** Where necessary, an assessment of the reproduction bionomics of adult fish should be undertaken to clarify the reproductive sequences of key fish species. Genetic studies of 0+ fish from discrete spawning events may also facilitate identification of sub-populations of fish that adopt alternative reproductive strategies.

A possible implication of multiple spawning is that fish hatching in late summer may not develop scales before the winter or that scales may be very small, and that the first annulus may be missed (or missing) in later attempts to age the fish. **It is recommended that small 0+ fish surviving the winter are analysed to investigate the impacts of overwintering at such small sizes on the reliability of ageing from fish scales and, hence, the implications for calculations of growth, survival and year-class strength.** Such fish could be aged from daily growth increments on their otoliths and the error associated with scale reading calculated.

Growth and recruitment

Growth of fish in the first summer of life was found to be a key correlate of recruitment success. **It is recommended that studies are undertaken, perhaps implementing otolith microstructure, to further assess temporal and spatial differences in growth, particularly those that cannot not be fully explained by differences in water temperature regime.** Such studies should include assessments of primary and secondary production, and should also consider the possibility that spatial differences in growth are genetically fixed. The importance of the very shallow, warmer water in the river margins that fish larvae preferentially inhabit should also be investigated.

River discharge may be the factor that ultimately controls recruitment success, either directly (i.e. via discharge-induced mortality) or indirectly (i.e. via reduced growth due to suppressed water temperatures, discharge-associated increases in energy expenditure and reduced food availability). **It is recommended that the effects of river discharge on fish recruitment success are investigated further, specifically to address**

temporal and spatial variations in the relative importance of direct and indirect influences. This should be linked to river type and flow regimes, and could potentially be employed to minimise some of the detrimental impacts of river regulation on fish recruitment success.

Critical periods when fish may be particularly vulnerable to environmental perturbations (such as floods) were difficult to discern in some cases. **It is recommended that studies are undertaken, perhaps targeting extreme wet and dry years only or years for which hatching and flooding were synchronous, to identify incidences of discharge-induced mortality and the consequent implications for recruitment success.** Where applicable, the outcomes of such studies could be used to assess the mitigation effects of multiple spawning events following high discharge-associated mortality.

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Recruitment patterns of six species of cyprinid fishes in the lower River Trent, England

Nunn AD, Cowx IG, Harvey JP. Recruitment patterns of six species of cyprinid fishes in the lower River Trent, England.
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Abstract – Fisheries data were collected for six species of 0-group cyprinid fishes from eight sites in the lower reaches of the River Trent, England, between May and October 1999 inclusive, using a micromesh seine net. Recruitment and growth patterns were observed via monthly length–frequency histograms and estimations of mean length. In the cases of roach and dace, growth was approximately linear through the summer, before declining in September and October. In the cases of chub and gudgeon, and to a lesser extent bream and bleak, however, there were suggestions of multiple recruitment events. It is argued that some of the fish species examined in the present study adopt fractional or protracted spawning strategies in the lower River Trent.

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Key words: recruitment; juvenile growth; fractional spawning; protracted spawning; cyprinid fishes

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

The survival of many cyprinid fish species over the first year of life is largely determined by the amount of growth attained in the first few weeks after hatching, with the smaller, potentially weaker, fish least likely to survive (Keast & Eadie 1984; Mills & Mann 1985; Mann & Mills 1986; Kubečka 1994; Kirjasniemi & Valtonen 1997). Strong selective pressures must therefore exist for an effective growth strategy in young fish (Keast & Eadie 1984). Although some fish species shed a single batch of eggs in a short spawning period, others are known to have a capacity to ripen successive batches of eggs within a season (fractional spawning) or spawn a single batch over an extended period (protracted spawning). Species that adopt fractional or protracted spawning strategies are likely to have a greater size range of young at the end of the growing season than those that do not, as progeny from later spawnings have less time in which to grow before water temperatures decline in autumn than those from earlier spawning events. Consequently, survival of the fish from later spawnings (assuming size-dependent winter mortality [Kirjasniemi & Valtonen (1997)]), and their contribution to eventual year-class strengths, may largely be dependent upon environmental conditions during the winter.

In the past, much work (e.g. Hellawell 1972; Mann 1976; Hickley & Bailey 1982; Cowx 1988) has focused upon the growth of European freshwater fishes, but little attention appears to have been given to recruitment or growth patterns of the 0-group fishes, particularly in large, lowland rivers. The present study examines the recruitment and growth patterns of six species of 0-group cyprinid fishes in the lower River Trent, England. The existence of fractional and protracted spawning events in some of the fish species studied is investigated.

Materials and methods

The study was carried out at eight sites (Table 1) on the lower reaches of the River Trent between Thrumpton (NGR: SK 510,315), upstream of Nottingham, and Dunham (NGR: SK 820,745),

Table 1. Details of sampling sites on the River Trent.

Site name	National Grid Reference	Site characteristics
Thrumpton	SK 510,315	Natural bank with restricted littoral zone; mean river width approximately 60 m and depth 2–4 m in main channel
Attenborough	SK 520,335	Natural bank with macrophytes; mean river width approximately 60 m and depth 2–4 m in main channel
Beeston	SK 536,352	A refuge area (surface area approximately 400 m^2); pool with shallow gradient to maximum depth of 1.5 m
Embankment	SK 581,382	Artificial bank comprising concrete revetment; mean river width approximately 60 m and depth 4 m in main channel
Trent Bridge	SK 582,383	Natural bank without macrophytes; mean river width approximately 60 m and depth 2–4 m in main channel
Stoke Bardolph	SK 646,425	Natural bank with an area of slack water; mean river width approximately 60 m and depth 3 m in main channel
South Muskham	SK 803,565	Natural bank with a shallow bay; mean river width approximately 40 m and depth 2–3 m in main channel
Dunham	SK 820,745	Natural bank with a shallow bay; mean river width approximately 40 m and depth 2–4 m in main channel, tidal

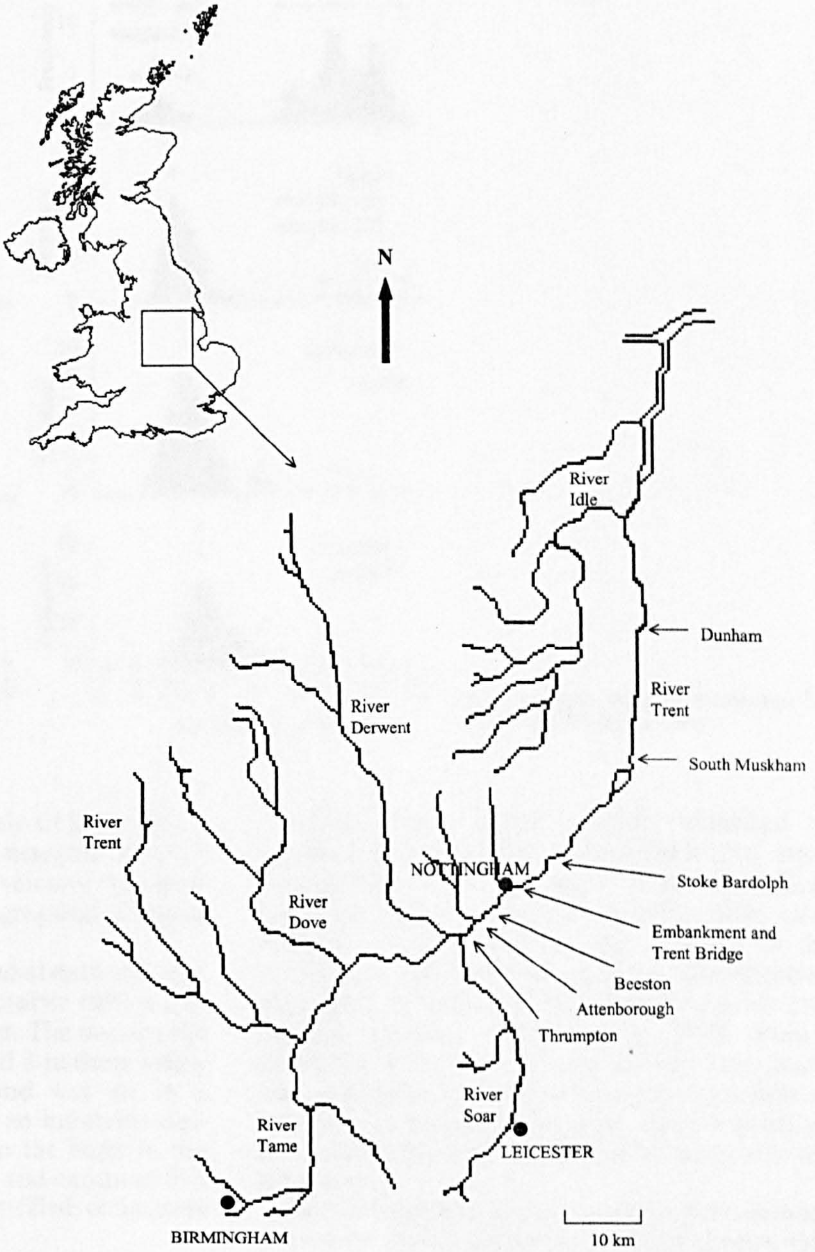

Fig. 1. The River Trent catchment and sampling site locations.

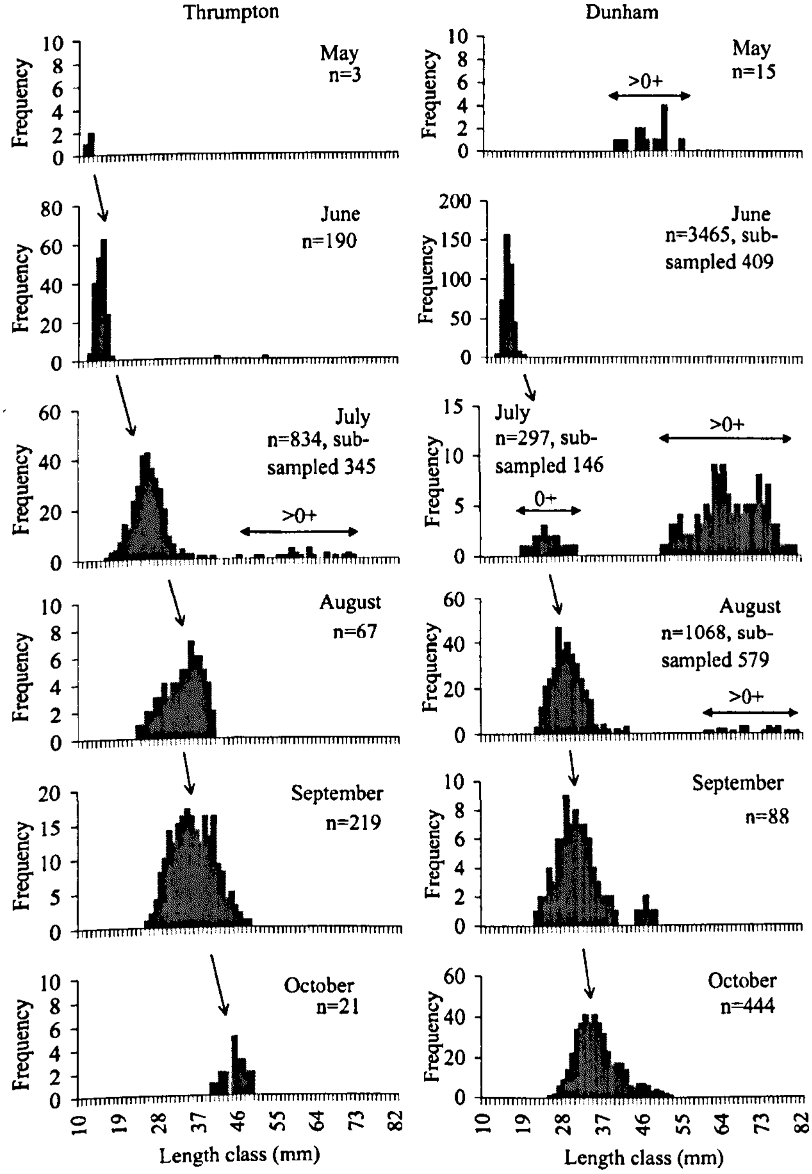

Fig. 2. Length-frequency histograms for roach from the River Trent.

a river distance of approximately 65 km (Fig. 1). Sampling was restricted to the margins in water <1.5-m deep, where the water velocity was slow and 0-group fishes tend to be aggregated (Copp & Garner 1995).

Fish populations were sampled at each site on a monthly basis, from May to October 1999 inclusive, using a micromesh seine net. The micromesh seine net used was 25-m long and 3-m deep with a 6-mm hexagonal mesh size, and was set in a semicircle from the bank using an inflatable dinghy. The net was then fished to the bank in the usual manner for a beach seine and captured fish were transferred to large water-filled containers prior to analysis.

All fish were, where possible, identified to species level and measured (standard length, nearest millimetre) in the field. When identification was not immediately possible, fish were preserved in 4% formalin and returned to the laboratory for analysis. Species identification was from species-specific morphological and meristic features (see Wheeler 1978; Pinder 2001). On occasions when excessively large numbers of fish were caught, a random subsample of known percentage of the total catch was either measured in the field or retained for analysis in the laboratory.

Recruitment and growth patterns were demonstrated by modal progression of size classes with

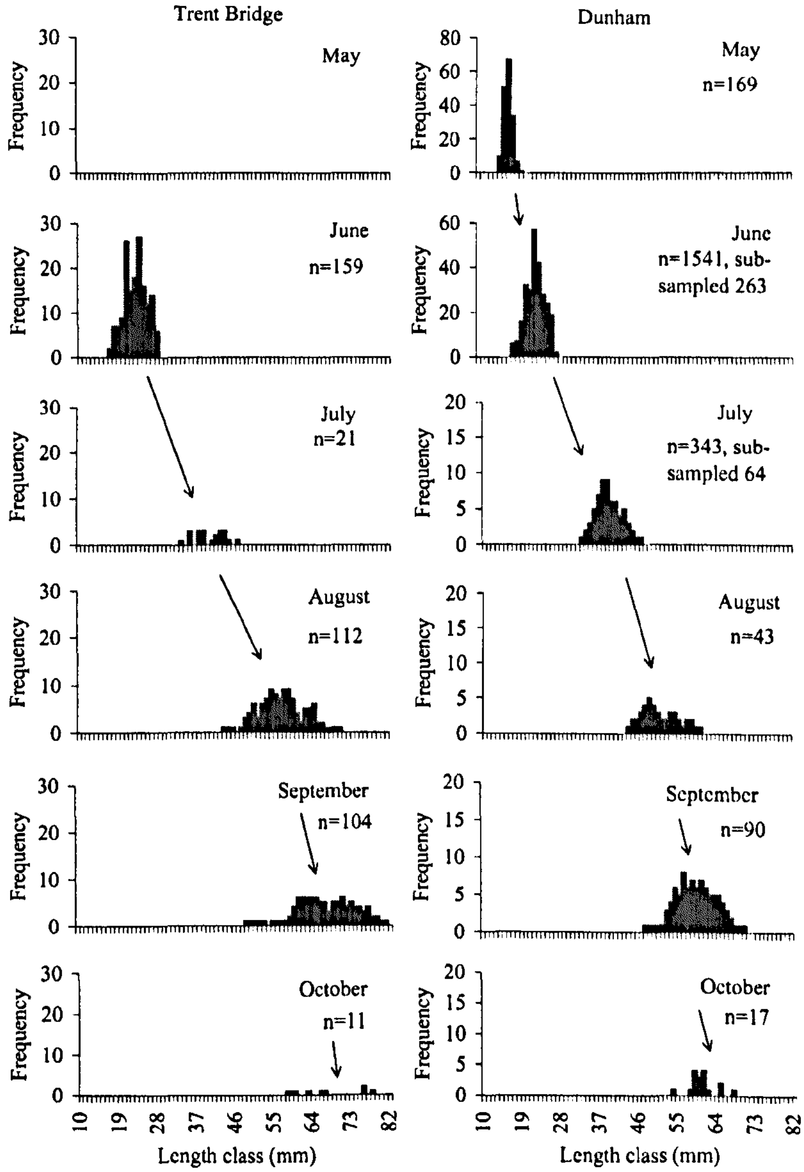

Fig. 3. Length-frequency histograms for dace from the River Trent.

time through the study period using length–frequency histograms, and by increases in mean standard length (mm ± SD) of 0-group fish over time. Where there was evidence of multiple spawning events, separate mean lengths were calculated for each 'batch' after verification of the separate modal distributions using Bhattacharya's method (Sparre & Venema 1992) in FiSAT (FAO/ICLARM Stock Assessment Tools), and mean lengths of fish from each batch were compared using *t*-tests.

Results

A total of 20 species of fish, plus hybrids of undetermined parentage, were captured during the study period. The main 0-group species captured, and upon which analyses were based, were roach (*Rutilus rutilus* (L.)), dace (*Leuciscus leuciscus* (L.)), chub (*L. cephalus* (L.)), bream (*Abramis brama* (L.)), gudgeon (*Gobio gobio* (L.)) and bleak (*Alburnus alburnus* (L.)). Owing to space restrictions and for clarity, the length–frequency histograms (Figs 2–7) and plots of mean lengths (±SD) (Fig. 8) were restricted to two examples of each species.

Single spawning fish species

Recruitment of roach and dace appeared to be based on a single spawning event (Figs 2 and 3). At all sites, mean standard lengths of both 0-group

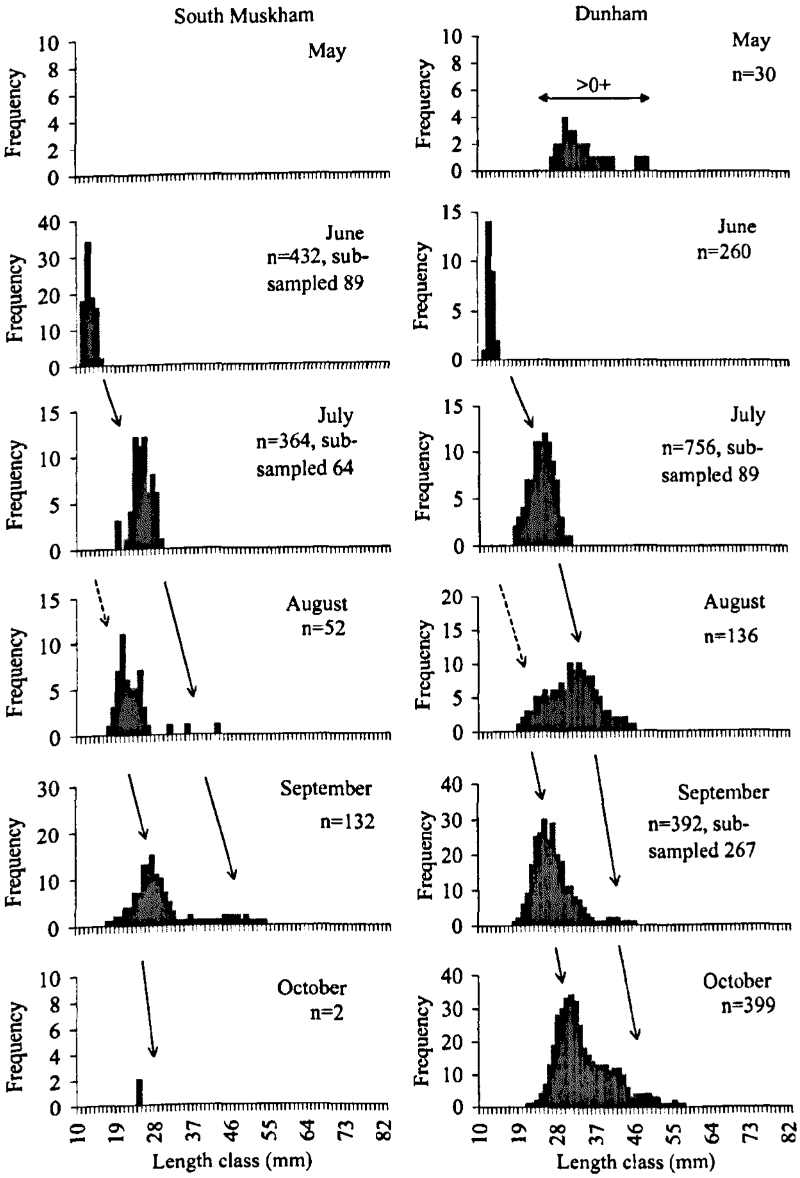

Fig. 4. Length–frequency histograms for chub from the River Trent.

roach and dace increased through the study period to a maximum in October, and growth was approximately linear (10–20 mm/month) through the summer before slowing in September and October (Fig. 8).

Multiple spawning fish species

Overall mean standard lengths of 0-group chub did not exhibit a steady increase with time as observed for roach and dace. At many sites there was no definite trend in the length–frequency distributions that described the growth of discrete cohorts of 0-group chub (Fig. 4). Initial spawning appeared to take place in June, but large numbers of small (<25 mm standard length) 0-group chub continued to feature in catches at all sites into late summer (Fig. 4). This was particularly evident in August and September, suggesting fractional spawning events may have occurred. Where necessary, polymodal distributions were analysed using Bhattacharya's method (all Separation Indices >2). Significant differences ($P < 0.05$) were found between the mean lengths of 0-group chub from separate modal distributions (Fig. 8).

At Attenborough, the mean standard length of 0-group bream increased through the study period to a maximum in September (Fig. 8), but showed a substantial drop in October, linked to the appearance of a large number of smaller

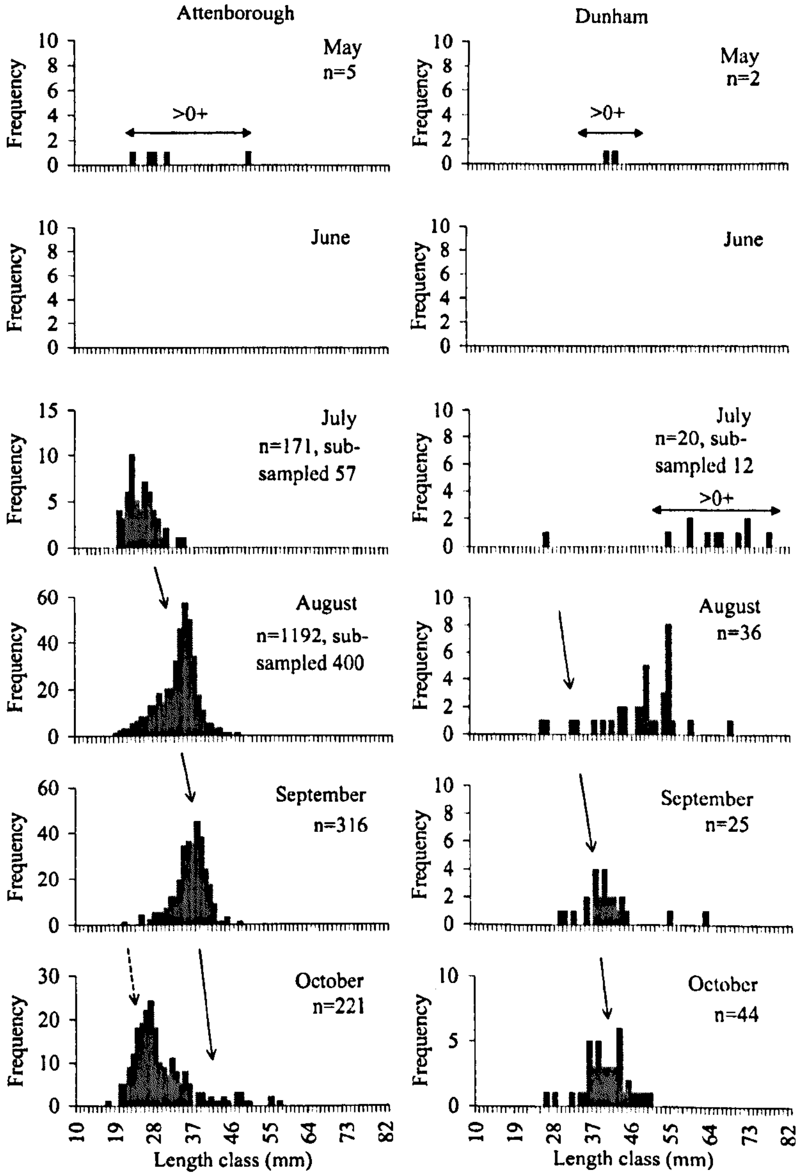

Fig. 5. Length–frequency histograms for bream from the River Trent.

individuals (Fig. 5). No clear pattern of growth or recruitment was observed at Dunham (Fig. 5), and at other sites, 0-group bream were caught too infrequently and in too few numbers to reveal any trends between sampling periods. Bhattacharya's method (Separation Index = 3.78) was used to analyse the length–frequency distribution at Attenborough in October, and a significant difference ($P < 0.01$) was found between the mean length of 0-group bream from the separate modal distributions (Fig. 8).

Although at some sites, mean standard length of 0-group gudgeon increased steadily through the study period to a maximum in October, at others there was no definite trend in the length–frequency distributions that described the growth of discrete cohorts of 0-group fish (Fig. 6). Initial spawning appeared to be in June, but at all sites small (<25 mm standard length) 0-group gudgeon featured in catches in late summer, with an infusion of smaller individuals in September at many sites (Fig. 6). Significant differences ($P < 0.01$) were found between the mean lengths of 0-group gudgeon from distinct modal distributions (Fig. 8) which, where necessary, were separated using Bhattacharya's method (all Separation Indices >2).

At none of the sites did mean standard length of 0-group bleak increase steadily through the study period to a maximum in the autumn, although growth and recruitment patterns were difficult to

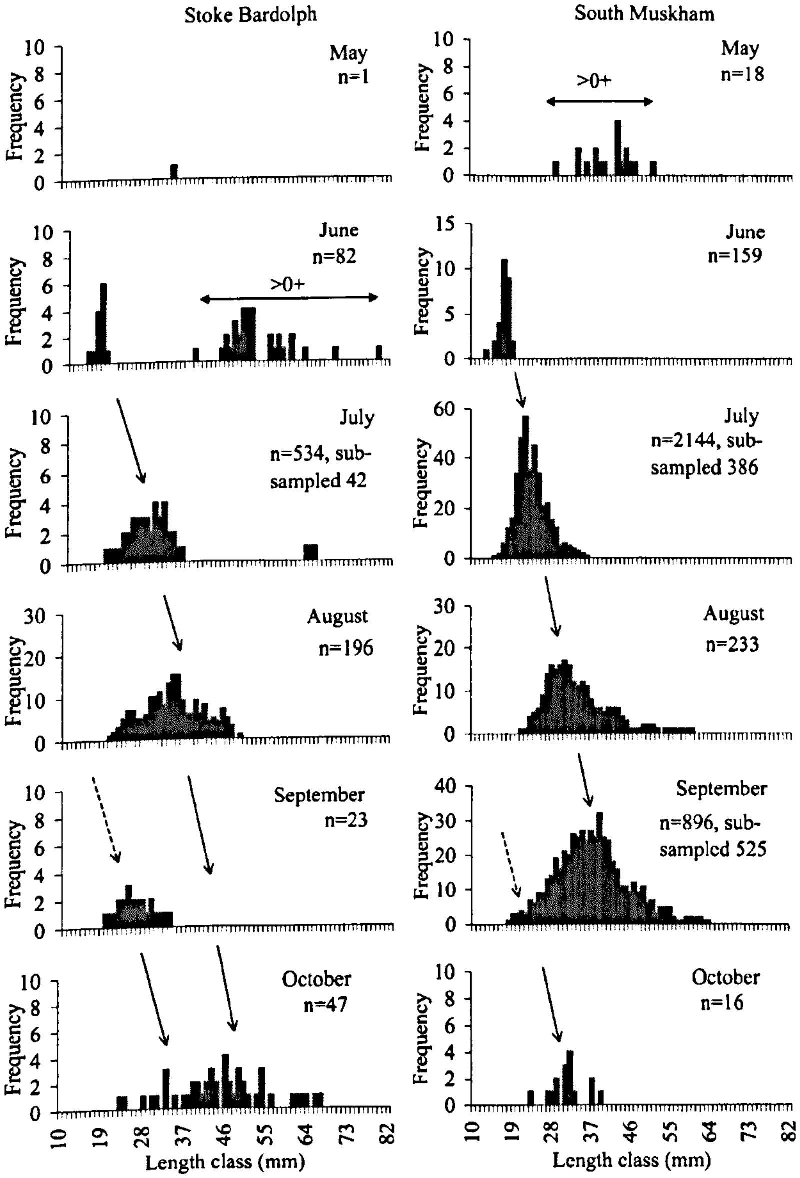

Fig. 6. Length–frequency histograms for gudgeon from the River Trent.

discern largely because of small and infrequent catches (Fig. 7). Nonetheless, some evidence of recruitment was found in June and July, although the main recruitment period seemed to be in late August or September. The October length–frequency distribution at Dunham was analysed using Bhattacharya's method (Separation Index = 4.14) and significant differences ($P < 0.01$) were found between the mean lengths of 0-group bleak from separate modal distributions (Fig. 8).

Discussion

Kubečka (1994) observed three main growth phases in 0-group fish from temperate latitudes: (1) accelerated growth after hatching; (2) approximately linear growth over summer, when most of the first-year growth is completed; and (3) decreasing juvenile growth associated with autumn. In the present study, the first of these phases was not observed, probably as sampling was too infrequent and as the seine net used was inefficient at capturing fish <15 mm in length (Cowx et al. 2001). Notwithstanding, in the majority of cases growth was approximately linear through the summer and slowed by October.

In some cases, however, there were suggestions of multiple recruitment events in the length–frequency distributions. Polymodality and, indeed, apparently distinct size-classes were observed in the length–frequency distributions of some species, and September/October mean lengths were

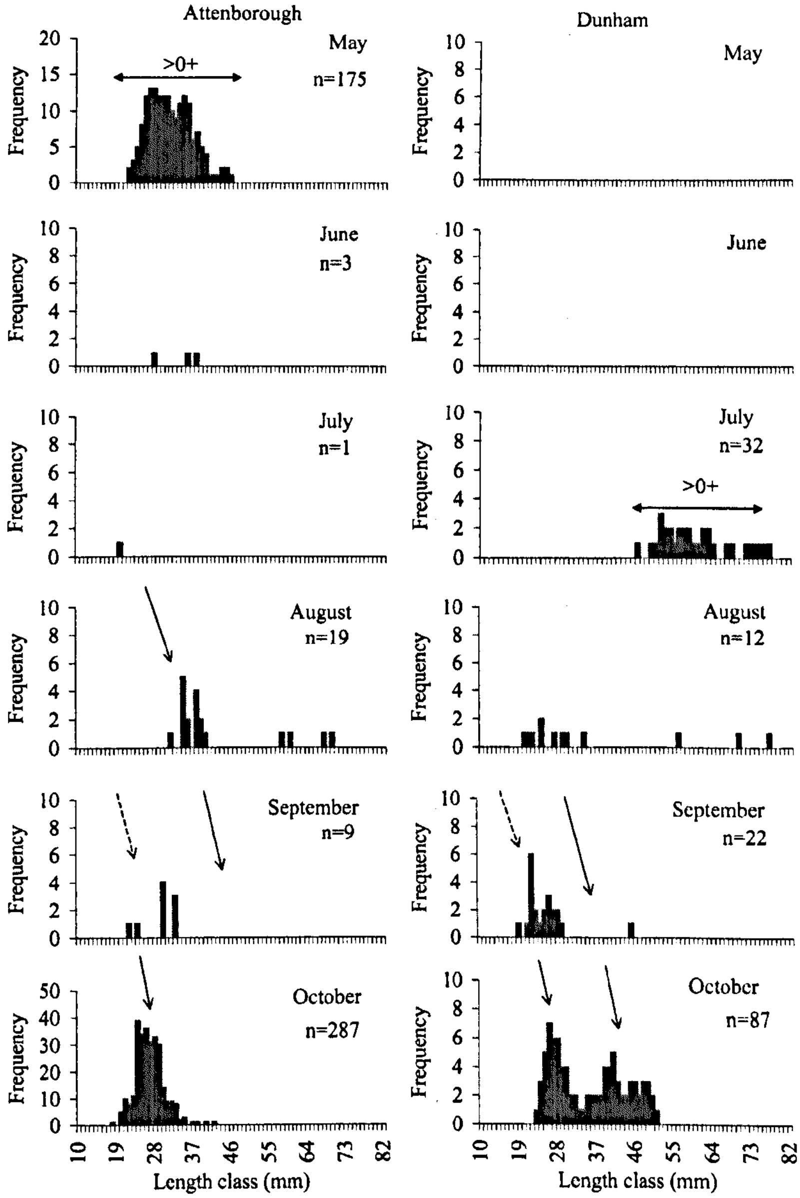

Fig. 7. Length-frequency histograms for bleak from the River Trent.

sometimes smaller than in August/September. This was particularly evident with chub, gudgeon, bream and bleak. Potential explanations for this include drift of small individuals from upstream (Jurajda 1998; Carter & Reader 2000), active dispersal of larger individuals away from the sampling areas, fractional/protracted spawning events (Mackay & Mann 1969; White & Williams 1978; Economou et al. 1991; Vriese et al. 1994) or a combination of these factors. However, May catches revealed the presence of small (<30 mm) >0+ chub, gudgeon, bream and bleak. Although the small size of these fish may simply have been a consequence of poor growth in the previous summer, the subsequent capture of small (<25 mm) 0-group individuals of these species throughout the study period suggests they were the offspring from the late summer spawnings which had less time to grow before water temperatures declined.

Chub and gudgeon, and to a lesser extent bream and bleak, appeared to exhibit fractional or protracted spawning, with batches being discharged possibly several months apart. Dace shed a single batch of eggs in a 2–3-week spawning period (Mann & Mills 1986; Mills 1991) and roach usually spawn once within a 2–4-day period (Mackay & Mann 1969). In contrast, chub are known to be capable of fractional spawning

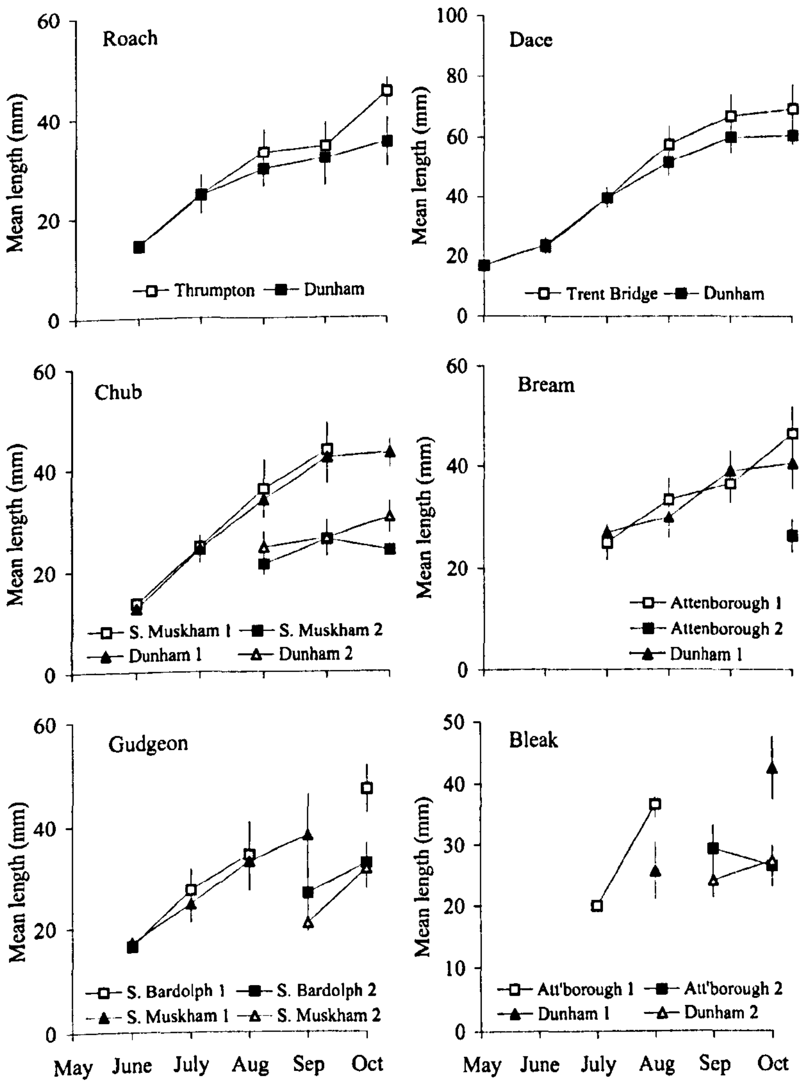

Fig. 8. Monthly mean lengths of six species of 0-group cyprinids from the River Trent (mean lengths (±SD) plotted separately for each spawning – see text for details).

(White & Williams 1978; Economou et al. 1991; Vriese et al. 1994) whose eggs may be scattered in up to three spawnings (Libosvarsky 1979). Gametes from the anal end of both ovaries and testes have been shown to be the first to ripen and be shed, compared to most other species in which the entire gonad ripens at one time (Mann 1976). Fractional spawning has also been reported in bleak (Mackay & Mann 1969) and gudgeon (Mann 1980) which, in the former, has subsequently been supported by evidence of up to four size groups of eggs in the ovary prior to spawning (Barus & Prokes 1996). Similarly, bream are known to occasionally have a protracted spawning period, particularly in suboptimum conditions (Cowx 2001). In the case of bleak and gudgeon, fractional spawning is probably a consequence of their small body size which permits them to produce only relatively small numbers of eggs per fish (see Cowx 2001). It has been suggested that small fish compensate for this by extending the spawning period and producing successive batches of eggs (Heins & Bresnick 1975; Gale & Gale 1977; Keast & Eadie 1984). However, it may also be possible that younger (smaller) individuals of some species adopt alternative (perhaps fractional or protracted) spawning strategies to older conspecifics.

Downstream drift of smaller 0-group individuals, including from tributaries, may distort or even mask the existence of fractional/protracted spawning strategies. Carter & Reader (2000) suggested that drift of 0-group fishes is probably part of a migratory cycle, and has the function of allowing movement from the spawning habitat to nursery areas. However, they (*op. cit.*) noted that drift of 0-group fish was mostly restricted to the first few weeks of life, and this phenomenon does not explain the presence of small (<25 mm) individuals of certain species throughout the summer. Furthermore, the patterns observed for chub, bream, gudgeon and bleak were not observed for roach or dace. This can only be explained by the existence of fractional or protracted spawning events.

Knowledge regarding fractional or protracted spawning events is, however, limited and should be supplemented by further, more detailed studies to assess the existence and significance of any temporal (within and between years), spatial (within and between catchments) or ontogenetic (i.e. age/size related) variation in spawning strategies adopted by fish species or populations. The overwinter survival of the smaller 0-group fish is largely stochastic (Mills & Mann 1985; Mann & Mills 1986; Kubečka 1994; Kirjasniemi & Valtonen 1997), particularly where the overwinter habitat may be limited, such as in the lower Trent (Harvey et al. 1999), primarily because of their inability to withstand elevated river flows (Mann & Mills 1986; Mann & Bass 1997). However, subsequent surveys on the River Trent and Warwickshire Avon (Nunn, Cowx and Harvey unpubl. data) have provided conclusive evidence that large numbers of offspring from late summer spawnings do survive the winter in some years. When this is the case, such fish may contribute substantially to year-class strengths and should be investigated further. Ultimately, fisheries management could potentially be tailored to enhance the survival of such fish, and hence augment recruitment to older age classes.

Resumen

1. Entre Mayo y Octubre del año 1999 (ambos inclusive), collectamos con redes de arrastre datos pesqueros de juveniles 0+ de seis especies de ciprínidos en ocho localidades de la region inferior del Río Trent (Inglaterra). Los patrones de crecimiento y reclutamiento fueron detectados analizando histogramas bi-mensuales de frecuencias de longitudes y estimando longitudes medias.

2. En los casos de *Rutilus rutilus* y *Leuciscus leuciscus* el crecimiento fue aproximadamente lineal a lo largo del verano, antes de declinar en Septiembre y Octubre. Sin embargo, los datos sugirieron eventos de reclutamiento multiples en los casos de *L. cephalus* y *Gobio gobio* y en menor medida, de *Abramis brama* y *Alburnus alburnus*. Se argumenta que algunas de las especies de peces examinadas en este estudio adoptan estrategias de puesta fraccionadas en la region.

Acknowledgements

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Is water temperature an adequate predictor of recruitment success in cyprinid fish populations in lowland rivers?

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SUMMARY

1. Higher than average ambient water temperature in the first year of life may be responsible for strong cohorts of adult cyprinid fish. Whilst temperature explains much of the variation in year-class strength (YCS), however, it is not the only influential factor as high temperature does not inevitably yield strong year-classes. Furthermore, years in which a strong year-class is prevalent in one species do not necessarily result in strong year-classes in other coexisting species, suggesting other biotic and abiotic factors are important in regulating recruitment success.
2. The relationships between water temperature, river discharge, the position of the Gulf Stream, 0-group fish growth and recruitment success (YCS) were examined in three cyprinid fish species in an English lowland river, using a 15-year data set.
3. Mean length of 0-group fish at the end of the summer was positively correlated with water temperature (cumulative degree-days >12 °C) and negatively correlated with river discharge (cumulative discharge-days above basal discharge rate). Water temperature was negatively correlated with river discharge.
4. YCS was positively correlated with mean 0-group fish length at the end of the summer and with the position of the North Wall of the Gulf Stream.
5. 'Critical periods' (i.e. periods in the first summer of life when fish may be more susceptible to increases in river discharge) were difficult to discern because of interannual variations in river discharge relative to the timing of fish hatching. YCS of roach and chub was most strongly correlated with discharge in the period from June to September inclusive, while YCS of dace was most significantly correlated with discharge in August.
6. River discharge (rather than water temperature) may be the key factor in determining YCS, either directly (through discharge-induced mortality) or indirectly (via reduced growth at lower water temperatures, discharge-associated increases in energy expenditure or reduced food availability). It could be that, in effect, water temperature determines potential YCS while discharge determines realised YCS.

Keywords: Gulf Stream, lowland rivers, recruitment, river discharge, water temperature, year-class strength (YCS)

Introduction

Early development represents a critical period in the life cycle of cyprinid fishes (Copp, 1990, 1992; Baras, Nindaba & Philippart, 1995; Garner, 1996a,b; Mann, 1997), and variations in mortality during this phase

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may be crucial in determining year-class strength (YCS) (Cowx, 2001). In general, mortality of fish is inversely related to fish body size (Wootton, 1990), and the growth of many cyprinids in the first few weeks after hatching largely determines their survival over the first year and the subsequent strength of that year-class (Mills & Mann, 1985; Mann & Mills, 1986; Kubečka, 1994; Kirjasniemi & Valtonen, 1997; Grenouillet *et al.*, 2001).

In cyprinid populations, there are occasional large cohorts of adult fish (Mills & Mann, 1985), and a wide range of biotic (competition, predation, disease) and abiotic (e.g. physicochemical, physical habitat and water chemistry) factors influence the eventual recruitment to the adult populations. In particular, the relationships between water temperature, fish growth and recruitment success have received considerable attention (e.g. Mann, Mills & Crisp, 1984). Temperature controls the rate of food consumption and metabolism and, thus, fish growth (Wootton, 1990). In many cases YCS appears to be determined by the growth of fish in the first year of life (Mills & Mann, 1985; Copp, 1990; Mann, 1997; Cowx, 2001) and correlations with temperature indicate that, for cyprinid populations, large cohorts of adult fish often result from higher than average water temperature in the first summer of life (Mills & Mann, 1985; Cowx, 2000; Grenouillet *et al.*, 2001).

The cumulative annual number of degree-days has therefore often been used as a predictor for subsequent YCS in cyprinids. Whilst temperature explains much of the variation in YCS, it is not the only influential factor, as high water temperature does not necessarily yield strong year-classes. Furthermore, years in which a strong year-class is prevalent in one species do not necessarily result in strong year-classes in other coexisting species (Cowx, 2001), suggesting other biotic and abiotic factors can regulate recruitment success.

Some evidence suggests that discharge rate plays an important role in recruitment dynamics, but as yet no definite relationship has been found, probably because of difficulties in separating the effects of discharge from those of other factors such as temperature and habitat availability (Lucas *et al.*, 1998; Cowx, 2001). As mentioned above, water temperature exerts a considerable influence on YCS but it is also interlinked with river discharge. Periods of higher flow in summer often coincide with reduced water temperature, making it difficult to ascertain whether any resultant effects are as a result of one or the other. This paper examines the relationships between water temperature, river discharge, the position of the Gulf Stream, 0-group fish growth and recruitment success in three species of cyprinid fish in a lowland river in northern England. It aims to identify (1) the key correlates of YCS, and (2) any 'critical periods' in the first summer of life when fish may be particularly vulnerable to environmental perturbations. The hypothesis was that river discharge (rather than water temperature) is the key factor that determines realised growth and ultimately, YCS.

Methods

The Yorkshire Ouse in north-east England has a catchment which includes much of the Yorkshire Dales and North York Moors (Fig. 1). Long-term mean summer flow is approximately 20 $m^3 s^{-1}$ when mean velocity rarely exceeds 0.05 ms^{-1} (Lucas *et al.*, 1998). Large and rapid fluctuations in run-off from the moorland catchment do occur, however, and have been exacerbated by changes in land management (such as land drainage and an increase in stocking density) in the Pennines since the 1980s. Fluctuations in fish recruitment and YCS are well known (Axford, 1978, 1991).

This study uses adult and 0-group fish data from unpublished reports of the Environment Agency (EA) and its predecessors, the National Rivers Authority (NRA) and Yorkshire Water Authority (YWA), for the period from 1984 to 1998 inclusive. Surveys of adult fish were carried out at six sites (each ~400 m long) by electric fishing (Electracatch WCF-7, 1.5-kW generator, 50 Hz pulsed direct current at 220 V, output approximately 1.5 A) using twin, hand-held anodes and a grid cathode from a boat. 0-group fish surveys were conducted at a site typical of the Yorkshire Ouse (Beningbrough; Fig. 1) in September each year using a micromesh seine net set in the margins of the river (single net during each survey, 25 m long by 3 m deep with a 6-mm hexagonal mesh size). This net effectively captures fish larger than ~15 mm long (Cowx, Nunn & Harvey, 2001). Adult fish data from each of the sites were combined and used to calculate YCS for roach (*Rutilus rutilus* (L)), chub (*Leuciscus cephalus* (L)) and dace (*Leuciscus leuciscus* (L)) (the three most abundant fish species in the Yorkshire Ouse) as follows:

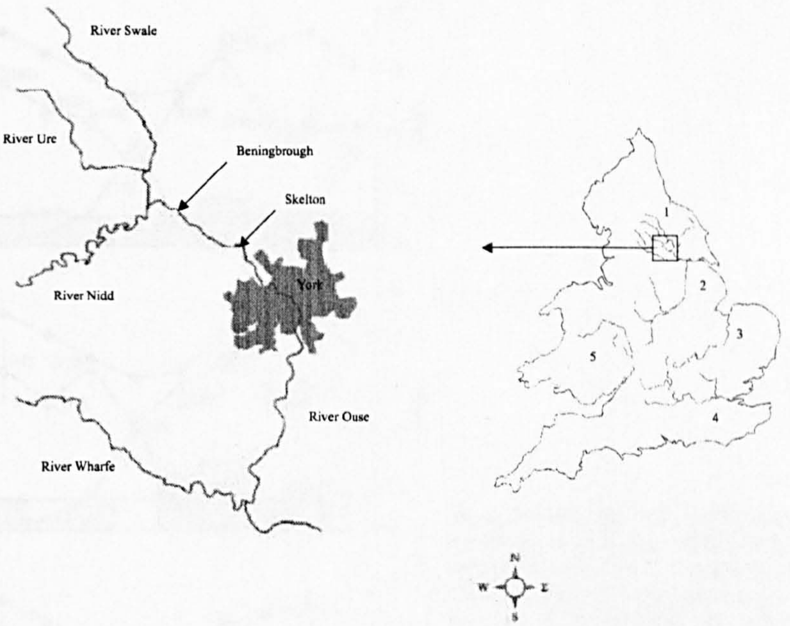

Fig. 1 Location of the River Yorkshire Ouse catchment relative to other river catchments, and site locations (numbers refer to river catchments: 1. Yorkshire Ouse, 2. Trent, 3. Great Ouse, 4. Thames, and 5. Severn).

1 The number of fish in each cohort was used to determine the instantaneous mortality rate (Z) of the target population using the linear relationship between the natural logarithm of the number of fish in each age group (ln N_t) against age (t) according to $Z = (\ln N_t - \log N_0)/t$;

2 The number of fish at time zero (N_0) was calculated independently for each age group using $N_0 = N_t \exp Zt$, where Nt is the number of fish at age t;

3 The mean number of fish in each age group (N) was determined as $\Sigma t_{\max} N / t_{\max}$, where $t_{\max}$ is the total number of age groups represented;

4 The YCS for each age group was determined by YCS at age $t = (N_0/N) \times 100$, where N_0 is the number of fish determined at time t_0 for age group t, i.e. YCS, which is then related to the year of birth, is calculated as an index standardised against a value of 100. A value greater than 100 is a strong year-class and a lower value a weak year-class.

Data from seine net surveys were used to calculate mean fork length (mm ± SD) of 0-group roach, chub and dace at the end of the summer (September) (sample sizes are given on Fig. 2). This was deemed to represent the maximum growth achieved by fish in their first year of life (Kubečka, 1994).

Daily water temperature data (1984–98 inclusive) were obtained from Yorkshire Water plc, with the exception of 1993 (when no data were available). For this missing year water temperature was calculated from air temperature using a linear regression between 15 years of water temperature and air temperature data (1-day lag, $P < 0.05$):

$$\textit{Water temperature}_t = 0.8714\,(\textit{Air temperature}_{t-1}) + 2.6154 \qquad r^2 = 0.74$$

Daily water temperature was used to calculate the cumulative number of degree-days >12 °C (April–September inclusive) for each year as a predictor of subsequent YCS in the populations of roach, chub and dace. Cumulative degree-days >12 °C is believed to provide the best correlation with 0-group cyprinid growth (Mills & Mann, 1985).

Daily river discharge data (1984–98 inclusive) were obtained from the EA multipath ultrasonic flow gauging station at Skelton (Fig. 1). These data were used to calculate the cumulative number of discharge-days above the basal discharge rate (i.e. long-term mean daily discharge calculated for each month using a 15-year data set), April to September inclusive.

Data on the position of the North Wall of the Gulf Stream (NWGS; 1984–98 inclusive) were downloaded from the Web Site of the Plymouth Marine Laboratory, UK (*http://www.pml.ac.uk/gulfstream/inetdat.htm*). Positive values of this index indicate a displacement to the north of the long-term mean location of the

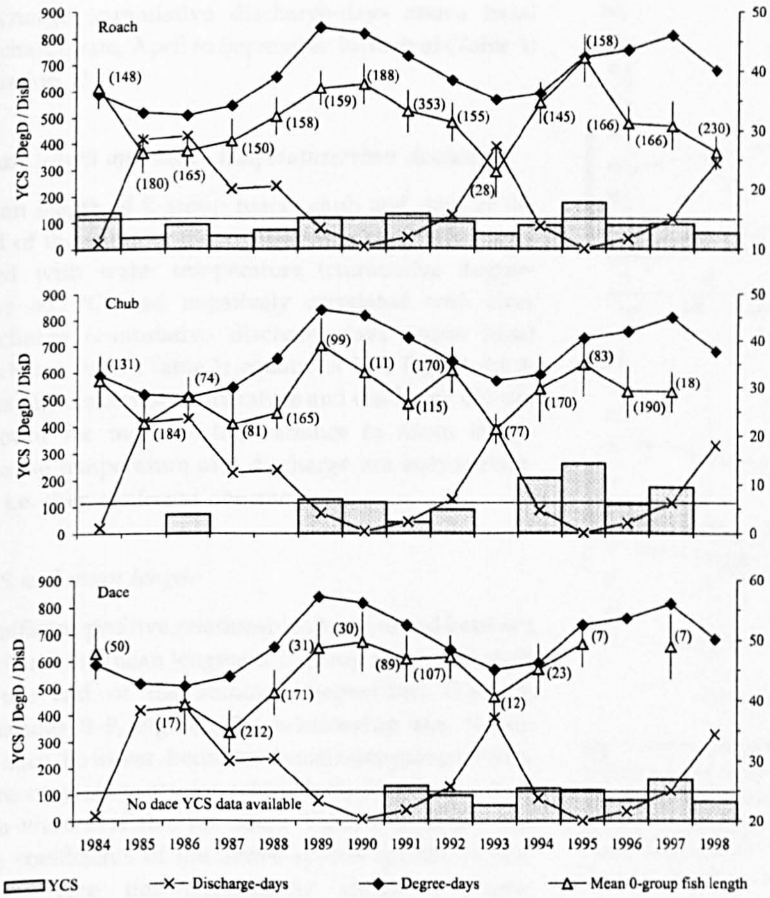

Fig. 2 Relationships between 0-group fish growth (mean ± SD fork length (mm) of roach, chub and dace in September), YCS, water temperature (cumulative degree-days >12 °C, April–September inclusive) and river discharge (cumulative discharge-days above basal discharge rate [$m^3\ s^{-1} \times 100$], April–September inclusive) in the Yorkshire River Ouse 1984–98 inclusive. Numbers in parentheses refer to sample sizes used to calculate mean lengths. N.B. *Y*-axis abbreviations – YCS: year-class strength; DegD: cumulative degree-days; DisD: cumulative discharge-days.

NWGS, while negative values indicate a movement south.

A series of linear regressions was calculated to investigate the relationships between water temperature, river discharge, Gulf Stream position, mean length and YCS of roach, chub and dace, and to identify the key correlates of YCS. All analyses were carried out using SPSS©.

Results

Comparisons of the yearly trends in mean 0-group fish length, YCS, cumulative degree-days and cumulative discharge-days suggest covariation between each of the variables (Fig. 2). The strongest year-classes usually coincided with the greatest mean lengths which, in turn, tended to occur in years with the highest numbers of cumulative degree-days and lowest cumulative discharge-days. For example 1993 and 1998 were poor year-classes for roach, chub and dace, and these coincided with high river flow and relatively low water temperature, and with poor growth. At the other extreme 1989–91 and 1995 were very good years for 0-group fish growth, and this coincided with strong year-classes for all three species. Compared with 1993 and 1998, river discharge in 1989–91 and 1995 was below average and ambient river temperature and mean lengths above average. There were occasions when various data were unavailable (e.g. no 0-group dace were captured in September 1998), thus the size of the data sets depended upon which combination of fish species and metrics were analysed. Sample sizes are given in Table 1.

Water temperature and river discharge

A significant negative relationship was found between water temperature (cumulative degree-days >12 °C, April to September inclusive) and river discharge (cumulative discharge-days above basal discharge rate, April to September inclusive) (Table 1; equation 1).

Mean length and water temperature/river discharge

Mean length of 0-group roach, chub and dace at the end of the summer (September) was positively correlated with water temperature (cumulative degree-days >12 °C) and negatively correlated with river discharge (cumulative discharge-days above basal discharge rate) (Table 1; equations 2–7, Fig. 3). Multiple regressions of temperature and discharge did not account for more of the variance in mean length because temperature and discharge are autocorrelated, i.e. they confound one another.

YCS and mean length

Significant positive relationships were found between YCS and the mean lengths of 0-group roach and chub at the end of the summer (September) (Table 1; equations 8–9, Fig. 4). The relationship was poorer for dace, however, because of small sample size (there were only six years for which both length and YCS data were available for dace) (Table 1; equation 10). The coefficients of the above species-specific regressions were not significantly different (*t*-tests, $P > 0.05$), i.e. the relationship between YCS and mean length is the same for roach, chub and dace.

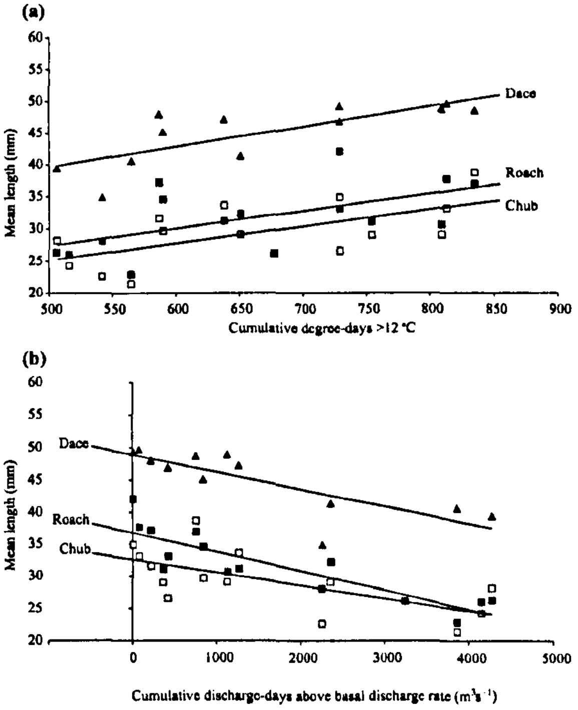

Fig. 3 Relationships between mean September 0-group fish lengths and (a) water temperature (cumulative degree-days >12 °C, April–September inclusive), and (b) river discharge (cumulative discharge-days above basal discharge rate, April–September inclusive) in the Yorkshire River Ouse. N.B. Roach ■, chub (□) and dace (▲).

Table 1 Results of linear regressions between water temperature, river discharge, Gulf Stream position, 0-group fish length and YCS of roach, chub and dace (refer to text for details)

Eqn no.	Linear regression	*P*	r^2	*n*
1	$Temperature = -0.049\ (Discharge) + 745.41$	0.005**	0.47	15
2	$Length_{roach} = 0.0268\ (Temperature) + 14.016$	0.03*	0.32	15
3	$Length_{chub} = 0.0261\ (Temperature) + 12.156$	0.016*	0.39	14
4	$Length_{dace} = 0.0322\ (Temperature) + 23.563$	0.004**	0.59	12
5	$Length_{roach} = -0.003\ (Discharge) + 36.773$	0.000**	0.75	15
6	$Length_{chub} = -0.002\ (Discharge) + 32.566$	0.013*	0.41	14
7	$Length_{dace} = -0.0027\ (Discharge) + 48.895$	0.002**	0.64	12
8	$YCS_{roach} = 5.875\ (Length_{roach}) - 92.147$	0.000**	0.73	15
9	$YCS_{chub} = 10.476\ (Length_{chub}) - 223.77$	0.025*	0.36	14
10	$YCS_{dace} = 8.0095\ (Length_{dace}) - 258.4$	0.063	0.62	6
11	$YCS_{roach} = 22.259\ (NWGS_{annual\ mean}) + 81.125$	0.052	0.26	15
12	$YCS_{chub} = 24.807\ (NWGS_{January}) + 53.109$	0.024*	0.34	15
13	$YCS_{dace} = 24.689\ (NWGS_{July}) + 87.743$	0.027*	0.59	8
14	$YCS_{roach} = 29.12\ (NWGS_{annual\ mean}) + 82.368$	0.006**	0.48	14
15	$YCS_{chub} = 25.734\ (NWGS_{January}) + 58.713$	0.018*	0.39	14
16	$YCS_{roach} = -0.0324\ (Discharge_{June - Sep}) + 123.71$	0.000**	0.66	15
17	$YCS_{chub} = -0.059\ (Discharge_{June - Sep}) + 131.89$	0.010*	0.41	15
18	$YCS_{dace} = -0.1849\ (Discharge_{August}) + 121.05$	0.023*	0.60	8

$^*P < 0.05$; $^{**}P < 0.01$.

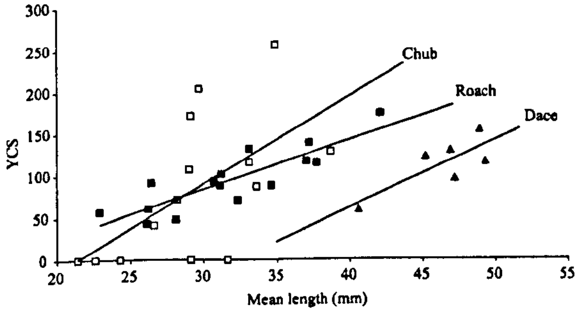

Fig. 4 Relationships between YCS and mean September 0-group fish lengths for roach (■), chub (□) and dace (▲) in the Yorkshire River Ouse.

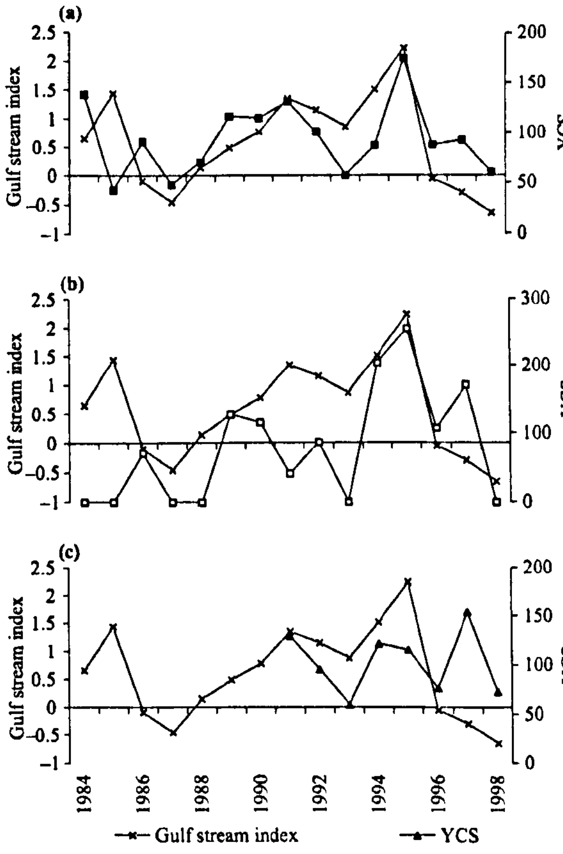

Fig. 5 Relationship between YCS of (a) roach (b) chub and (c) dace and the annual mean position of the North Wall of the Gulf Stream 1984–98 inclusive (data from Taylor & Stephens, 1980; *http://www.pml.ac.uk/gulfstream/inetdat.htm*).

YCS and the position of the North Wall of the Gulf Stream (NWGS)

Comparisons of the yearly trends in YCS of roach, chub and dace and the annual mean position of the NWGS suggested a positive relationship between the two variables (Fig. 5). Using linear regression, the best correlations for roach, chub and dace were found for the annual mean position of the NWGS, and the position of the NWGS in January and July, respectively (Table 1; equations 11–13). Note, the relationship for roach and, to a lesser extent, chub was weakened by the 1985 Gulf Stream data (no 1985 YCS data available for dace). The summer weather pattern in England is strongly influenced by the position of the NWGS (Willis *et al.*, 1995), and when the NWGS is further north than average (as in 1985) this usually coincides with warmer and drier than average years. Degree-days, discharge-days, mean 0-group fish length and YCS, however, were all indicative of a cold, wet year in 1985. Exclusion of the 1985 data point from the regressions improved the relationship of both roach and chub (Table 1; equations 14–15).

River discharge during critical life history periods

An attempt was made to identify any critical periods in the first summer of life of each of the three fish species, when they might be more susceptible to increases in river discharge. Linear regressions were performed on YCS and discharge (cumulative discharge-days above basal discharge rate) data. 'Critical periods' were difficult to discern, probably because of interannual variations in river discharge relative to the timing of fish hatching. In the case of both roach and chub, the strongest relationship between YCS and discharge was for the period from June to September inclusive (Table 1; equations 16–17, Fig. 6). YCS of dace was most significantly correlated to discharge in August (Table 1; equation 18), although there was also a weaker relationship with river discharge in April–May (Fig. 6).

Discussion

In cyprinid populations, strong year-classes are often correlated with high water temperature during the first summer of life (Mills & Mann, 1985; Cowx, 2000; Grenouillet *et al.*, 2001), and several studies have demonstrated that a major influence on summer water temperatures is the position of the North Wall of the

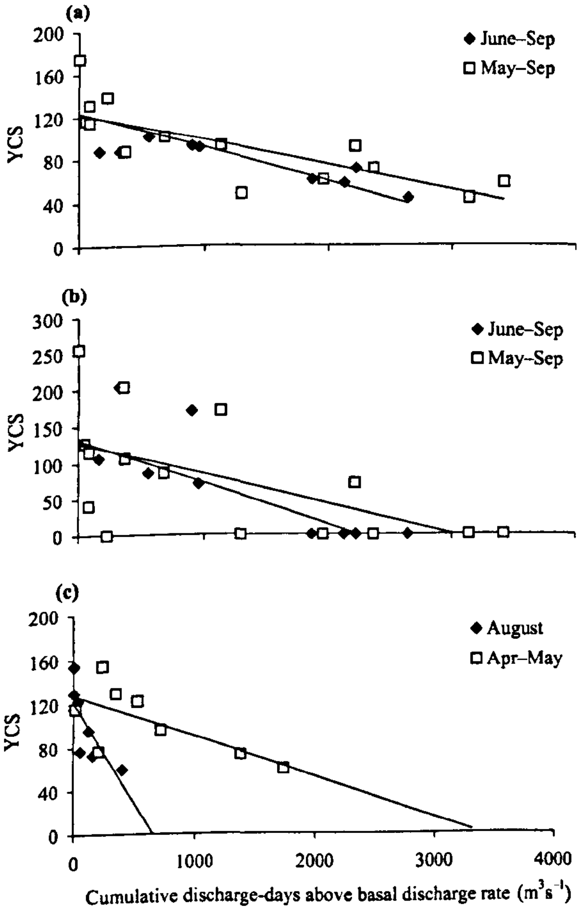

Fig. 6 Relationships between YCS of (a) roach (b) chub and (c) dace and river discharge (cumulative discharge-days above basal discharge rate) during 'critical periods' (see text for details) in the Yorkshire River Ouse. N.B. Two best correlations only shown for each species.

Gulf Stream (e.g. Taylor & Stephens, 1980). Any change in the position of the NWGS should therefore manifest itself in terms of a change in recruitment, with higher recruitment associated with a more northerly position of the NWGS (Aprahamian & Aprahamian, 2001). The present study corroborates these observations. The Gulf Stream, however, also influences river discharge (which is itself interlinked with water temperature), and stronger correlations were found between recruitment success and river discharge than for water temperature.

Newly hatched cyprinids are weak swimmers, owing to their small size (usually <10 mm) and lack of fully formed fins (Mann, 1995). Mann & Bass (1997) stated that the ability of 0-group roach and dace to hold station was positively related to fish length and water temperature, and negatively related to water velocity. The vulnerability of fish larvae to displacement by river currents means that they are usually confined to a narrow riparian zone with current velocities <2 cm s^{-1} (Mills & Mann, 1985; Mann & Mills, 1986; Lightfoot & Jones, 1996; Mann & Bass, 1997), and survival of larvae displaced by flood events can be low (e.g. some cyprinid and centrarchid fish species; Harvey, 1987). Stochastic, episodic increases in river discharge therefore can significantly influence 0-group recruitment, and may cause the density, species richness and species composition of fish communities to fluctuate yearly (Schlosser, 1985). The impact of increased river discharge on eventual YCS, however, may be determined by small differences in the timing of such events relative to vulnerable life history periods, as there is a rapid decline in susceptibility to displacement with increasing size in cyprinids (Harvey, 1987). The quicker fish grow during development therefore, the sooner the risk of displacement by river current is reduced (Mann & Bass, 1997).

A small increase in discharge in early summer may therefore be more severe in terms of 0-group fish mortality than a larger increase in late summer. In the present study, 'critical periods' (i.e. periods in the first summer of life of a species when the fish may be most susceptible to increased discharge) were difficult to discern, mainly because of interannual variations in river levels relative to the timing of fish hatching. For roach and chub, the strongest relationship between YCS and discharge was for the period from June to September inclusive, perhaps suggesting that in most years it is the flow regime over the summer as a whole, rather than discharge in short specific time periods, that is most influential in determining YCS of these species, and that the main influence of discharge on YCS is indirect (i.e. reduced growth because of suppressed water temperatures, discharge-associated increases in energy expenditure and reduced food availability) rather than direct (i.e. discharge-induced mortality).

YCS of dace was most significantly correlated with discharge in August, although there was also a weaker relationship with river discharge in April and May, when dace are in their early developmental stages and river levels are still liable to fluctuate markedly. By contrast, roach and chub hatch approximately one month later than dace in this river, when discharge is usually more stable. The generally poorer relationships for chub may partly be because of the potential for populations of this species to spawn more than once a summer (Nunn, Cowx & Harvey, 2002), which may act as an 'insurance policy' against discharge-induced 0-group mortality in early summer. In some years therefore relatively strong year-classes of chub may result, despite high mortality in early summer and smaller than average mean lengths, provided overwinter conditions are not severe. Roach and dace, on the other hand, spawn only once per summer (Mackay & Mann, 1969; Mann, 1973, 1974; Lobón-Cerviá *et al.*, 1996; Nunn *et al.*, 2002). In addition, Garner (1999) found that chub are better able to locate slow flowing patches of water than either roach or dace throughout their early development, and so may be less susceptible to increases in river discharge than roach and dace.

Although discharge and water temperature account for a great deal of the variance in YCS, there are likely to be other complicating factors of varying importance. For example, in the Yorkshire Ouse, the 1994 year-classes of all three species were stronger than those in 1996 despite conditions seemingly being more favourable in the latter (i.e. water temperature was higher and river discharge was lower in 1996 than in 1994). Large cohorts of 0-group fish may be inconsequential to eventual YCS if overwinter survival is poor, and availability (i.e. lack) of overwintering habitat may therefore severely restrict YCS of many fish species in some rivers, particularly during severe winters which experience prolonged periods of elevated flow.

Inter- and intracohort and interspecific competition may also influence YCS. Grenouillet *et al.* (2001) found that survival of roach in the first year was density-dependent, and stated that intraspecific competition within the 0-group cohort could therefore influence recruitment to older age-classes. This may be of particular importance in years of good recruitment. Cryer, Peirson & Townsend (1986) and Perrow & Irvine (1992), studying lacustrine populations of roach, demonstrated that abundant 0-group roach can sometimes show poor growth as a result of depression of their prey populations. Variations in prey (zooplankton) abundance may therefore influence the initial growth rates of fish larvae, and a switch in the diet of 0-group roach in late June from small invertebrates (Cladocera, Chironomidae) to one dominated by detritus may explain discrepancies between observed growth rates and those predicted from temperature growth models (Mann, 1997). Moreover, competition for food resources may influence 0-group overwinter mortality. Overwinter survival is positively related to fish length, although it is the condition (≈lipid content) of the fish (which is a function of length), rather than length itself, that is the key factor (Griffiths & Kirkwood, 1995; Kirjasniemi & Valtonen, 1997). It is also important therefore to consider the impacts of increased river flows on the food supply of juvenile fish, as discharge influences fish populations indirectly through its key role in controlling phytoplankton and, hence, zooplankton populations (Bass, Pinder & Leach, 1997; Marker & Collett, 1997; Reckendorfer *et al.*, 1999).

The effects of river discharge (including increases caused by anthropogenic activities) on YCS of particular fish species may therefore be either direct or indirect. For example, a poor year-class may be the result of high river flows causing high mortality during a critical period in the life history of a particular fish species, such as the larval period, or it may equally be the result of poor growth caused by a reduction in water temperature or a lack of suitable food. It was not possible in the present study, however, to separate the roles of either. Whilst it is likely that water temperature is the limiting factor with respect to fish growth, river discharge may be the factor that ultimately controls YCS, either directly or indirectly. It could be that, in effect, water temperature determines potential YCS while discharge determines realised YCS.

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Management and Ecological Note

Note on the ecology of spined loach in the lower River Trent, England

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The spined loach, *Cobitis taenia* L., is a threatened fish species, indigenous to the British mainland. The species is listed under Appendix 3 of the Bern Convention and Annex II of the EC Directive on the conservation of natural habitats and flora and fauna, the latter of which places a duty on member countries to ensure the favourable conservation status of listed species through protection of viable populations in designated Special Areas of Conservation (SACs) and throughout their range (Perrow & Jowitt 1998). The spined loach is found across almost the whole of Europe and central Asia (Wheeler 1983), but in the UK its distribution is localised and it is regarded as rare (Maitland 1972). Relatively few water bodies support populations of spined loach in the UK, with virtually all restricted to the catchments of the rivers Trent, Great Ouse, Welland, Nene and Witham (Fig. 1; Perrow & Jowitt 2000), which are believed to have been colonized at the end of the last ice age via rivers which crossed the land bridge that connected Britain to continental Europe at that time (Wheeler 1977). However, knowledge of the status of the species in the UK is patchy and this is reflected in the literature (Bohlen & Ráb 2001), where the UK was omitted from a description of the distribution of the *Cobitis* genus in Europe. The small number of studies that have been undertaken in the UK have mostly concentrated on the catchment of the River Great Ouse (e.g. Robotham 1977, 1978; Perrow & Jowitt 1998, 2000). No studies appear to have been carried out on the River Trent, although water quality improvements since the mid 1970s (Jacklin 1996) may have provided the opportunity for improvement in the status of the populations.

The study was carried out at eight sites (Fig. 1) on the lower reaches of the River Trent between Thrumpton (NGR: SK 510 315), upstream of Nottingham, and Dunham (NGR: SK 820 745), a river distance of approximately 65 km. Each site was sampled on a monthly basis, from May to October 1999 inclusive, using a double micromesh seine netting technique (Cowx, Nunn & Harvey 2001) which involved setting two nets, one inside the other, ensuring that the same area was sampled by both. Spined loach were measured, total length (nearest mm), in the field before being returned to the water.

Catches of spined loach were grouped together by month, regardless of site, thereby allowing the use of total monthly catches of spined loach for length-frequency analysis. Density of spined loach captured by seine netting (individuals m^{-2}) was estimated monthly for each site using a two-catch depletion procedure (Seber & LeCren 1967). In some cases, however, estimates of density could not be made because the number of fish in catch two was either equal to or greater than the number of fish in catch one, thereby violating one of the assumptions of the Seber & LeCren model. When this was the case, a minimum estimate was made by dividing the total number of spined loach in catches one and two by the estimated sampling area (50 m^2).

Spined loach were generally found at sites where habitat diversity was high, but were themselves present in only small numbers compared with other fish species (Harvey, Cowx & Nunn 1999), always comprising $<1\%$ of catches. A total of 172 spined loach, representing three or possibly 4-yr classes, were captured from the River Trent during the study period [$>1+$ yr-classes were difficult to separate using length-frequency data because of small catches, and this may have been exacerbated by differences in growth rate between the sexes (Perrow & Jowitt 2000)]. Lengths of spined loach ranged from 18 to 94 mm total

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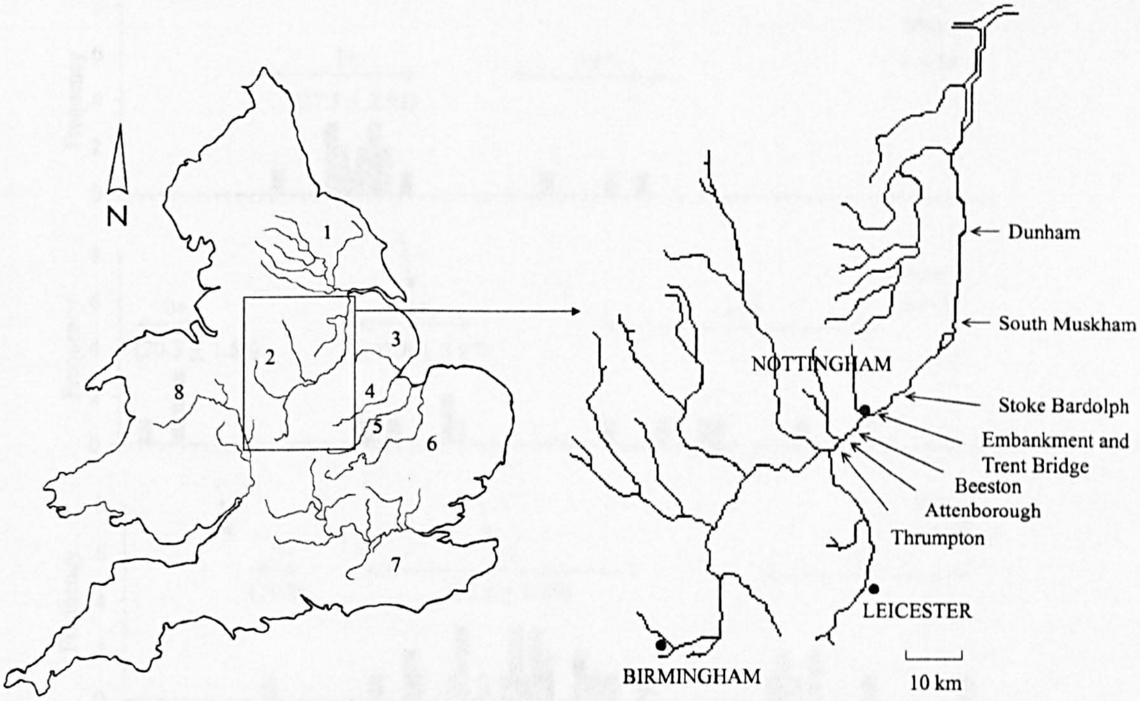

Figure 1. Location of the River Trent catchment relative to other river catchments, and River Trent site locations (numbers refer to river catchments: 1. Yorkshire Ouse, 2. Trent, 3. Witham, 4. Welland, 5. Nene, 6. Great Ouse, 7. Thames, and 8. Severn).

length (TL), with fish in the 0+, 1+ and >1+ yr-classes representing 9.3, 75.0 and 15.7% of total spined loach catches, respectively. The small number of 0+ individuals may suggest that the areas sampled are not important spawning or nursery areas, but it is more likely a reflection of the inefficiency of the seine nets at capturing such small fish (Cowx *et al.* 2001), particularly in areas of dense macrophytes where young spined loach tend to be found (Bohlen 2000a,b). Growth was demonstrated by modal progression of size classes with time through the study period using length-frequency histograms, and by increases in mean TL (mm ± SD) of each year class over time (Fig. 2). Recruitment appeared to be based on a single spawning event in June (Fig. 2), although few 0+ fish were caught and sampling may have been too infrequent to observe any subsequent spawnings. This contrasts with Bohlen (1999) and Boron & Pimpicka (2000) who observed batch spawning in the species in studies in a laboratory and a Polish reservoir, respectively. Mean lengths of all year classes increased through the study period to a maximum in the autumn, and growth was approximately linear (5–15 mm month^{-1}) through the summer before slowing in September and October (Fig. 2). The mean length of 0+ and 1+ fish at the end of the growing season (September) was 47.6 and 61.1 mm, respectively. Density estimates ranged from 0 to 1.28 individuals m^{-2} (Table 1; average when found 0.24 individuals m^{-2}), and generally exceeded what is regarded as indicative of 'good' and probably viable populations of spined loach (0.1 individuals m^{-2}; Perrow & Jowitt 2000).

Spined loach are not ubiquitous along the entire length of the lower Trent. In this study, they were captured from four of the eight sites surveyed, with 17, 27, 18 and 38% of catches coming from Thrumpton, Attenborough, Stoke Bardolph and South Muskham, respectively. No spined loach were captured from the Embankment, Trent Bridge, Beeston and Dunham. The most likely explanation for this is the different habitat at each of the sites. Spined loach inhabit areas characterised by fine substratum containing organic components (Robotham 1978; Slavík, Mattas, Jiřinec, Bartoš & Rebec 2000), and spawn in dense vegetation, which may act as a refuge for the early life stages (Bohlen 2000a,b). Fine sediments also provide a suitable food supply for spined loach (Robotham 1978) which they pump into the buccal cavity where small (0.2–0.75 mm) food particles are retained in mucus (Robotham 1977). Of the sites in this study,

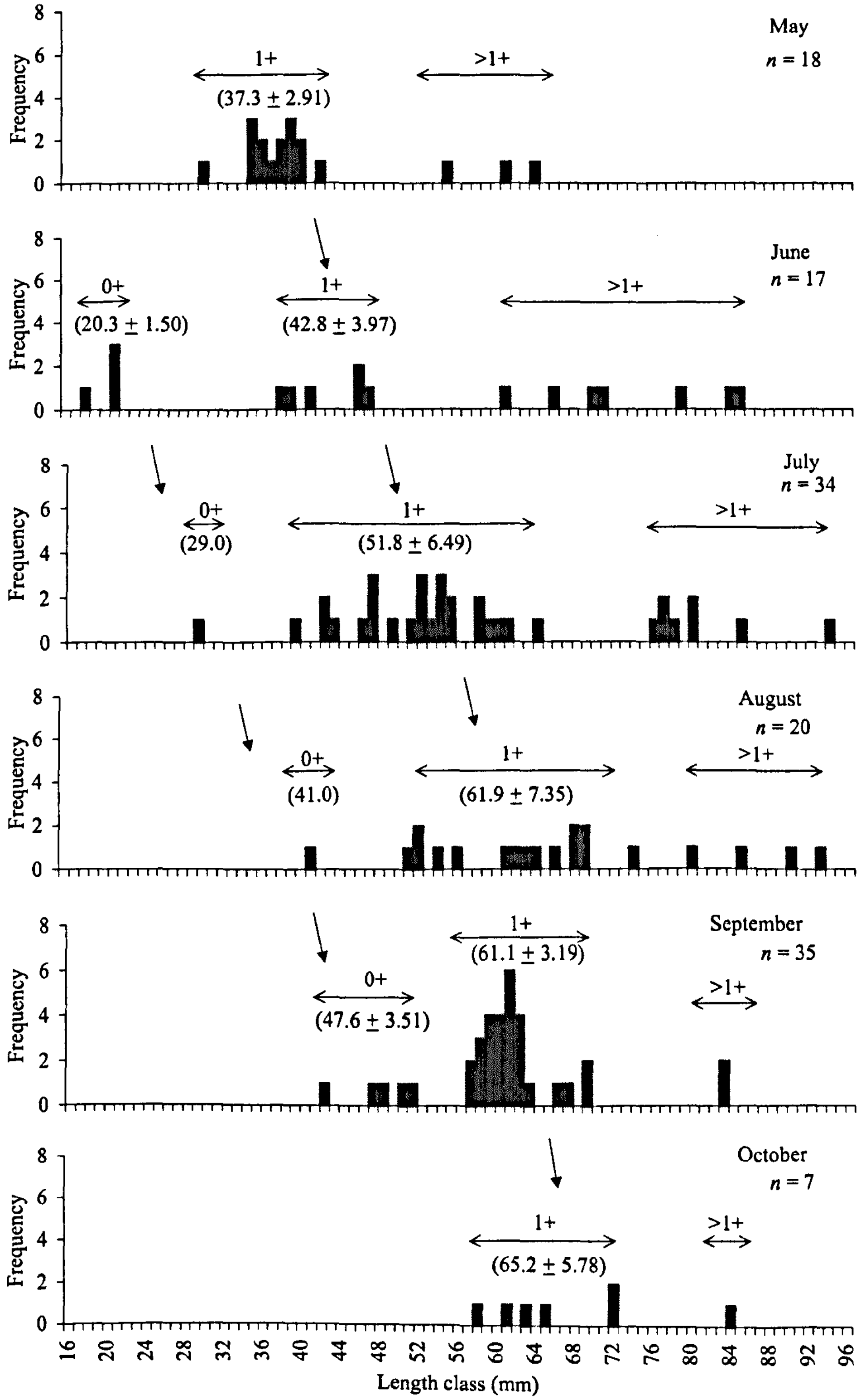

Figure 2. Length-frequency histograms for spined loach from the River Trent, all sites combined (mean length ± SD in parentheses).

Table 1. Monthly densities of spined loach from the River Trent

	Density (number m^{-2})					
Site name	May	June	July	Aug	Sept	Oct
Thrumpton	–	0.11	0.48	0.06	0.06	–
Attenborough	1.28	–	–	0.16	0.64	0.02
Beeston	–	–	–	–	–	–
Embankment	–	–	–	–	–	–
Trent Bridge	–	–	–	–	–	–
Stoke Bardolph	–	0.12*	0.18*	0.18*	0.10*	0.08
South Muskham	0.08	0.36*	0.78	0.04*	0.08*	0.06*
Dunham	–	–	–	–	–	–

*Minimum estimate – full explanation in text.

Thrumpton, Attenborough, Stoke Bardolph and South Muskham all have substrata characterised by sand and silt with large amounts of allochthonous material (in the case of Thrumpton, filamentous algae also), plus (Stoke Bardolph to a lesser extent) areas of aquatic vegetation. In contrast, the river at the Embankment and Trent Bridge has been heavily engineered for flood defence purposes and the natural substratum has been replaced with concrete revetment (which has alluvial deposits), while at Beeston the substratum consists largely of gravel and cobble. At Dunham (in the tidal reaches of the river) the substratum consists primarily of mud and silt. Significantly perhaps, none of these latter sites have aquatic vegetation.

To conclude, the River Trent appears to be important with regard to populations of spined loach and, with a catchment area of 10 500 km^2 (one of the largest in the UK), offers considerable conservation potential for the species. As such the Trent catchment, together with that of the River Great Ouse (the other principal river catchment supporting populations of spined loach in the UK), must be included in any conservation plan for the species in the UK. This is of particular importance owing to the propensity of spined loach to develop geno- or phenotypically distinct metapopulations within the *C. taenia* complex [see Bohlen 2000a,b; Bohlen & Ráb 2001; plus other papers in *Folia Zoologica* (2000) 49 (Suppl. 1) for examples in continental Europe], and the possibility that the UK contains one or more endemic races, subspecies or even species (Perrow & Jowitt 1998). Four of the sites surveyed in this study fulfilled the criteria which it is suggested constitute a good and viable population (Perrow & Jowitt 2000), namely: (i) a density of at least 0.1 individuals m^{-2}, (ii) a preponderence (> 50%) of fish 1-yr old or less, and (iii) three or four obvious age classes, with the largest fish > 85 mm in length. Therefore, it is recommended that further, more intensive and specific studies are undertaken to ascertain the wider distribution of spined loach within the Trent catchment so that appropriate conservation status can be afforded to the river for the benefit of spined loach. A prerequisite of these studies should be the development of sampling gears specifically for the efficient capture of spined loach. In addition, attempts must be made to address potential consequences of urban encroachment, change in land use (especially agricultural) practices and river engineering activities which could potentially jeopardise these populations if not carried out in a sympathetic manner.

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