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An assessment of the European eel population on the Azores Archipelago

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By

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Abstract

The European eel (Anguilla anguilla (L.)) is well documented throughout most of its extensive continental range, nonetheless, the existence of individuals at the Azores Archipelago, the extreme west of the species´ continental range, were acknowledged but not studied. Geographically isolated and with the shortest migration to their putative spawning ground, individuals of the Azores would be expected to have the greatest chances of spawning success and may provide an important contribution of adults to a heavily declined and threatened population. Until now, it was surmised that freshwaters of the Azores did not constitute natural habitats for the species and freshwater individuals did not reach the ´silver´ migratory phase, therefore, exempting this autonomous region of Portugal from European Eel Management Plans established to conserve the species.

Sampling on four Azorean islands has verified that eels were distributed throughout the majority of the river systems sampled and in one brackish lake. Larger individuals were found higher in catchments and natural barriers forcing a limiting effect on upstream distribution. The lack of estuaries and reduced availability of sheltered habitat in mainstem rivers acted to restrict the highest eel abundance to the most upstream point of sampling and to smaller watercourses. The single brackish lake sampled showed the highest abundance of eels on the archipelago, likely a result of its productive and sheltered habitat and because it presented the only suitable inland habitat for eels on that island. Multiple silver eels were caught in freshwaters from October-December, with males seemingly completing downstream migration earlier than females.

The verification of freshwater residence and silvering on this strategically located archipelago, at least 1300km closer to the putative spawning ground than the rest of mainland Europe, should be followed by an extension of Portugals' existing Eel Management Plans to specifically incorporate the Azores archipelago.

1. Introduction

The European eel (*Anguilla anguilla* (L.)) occupies an extensive continental range, being distributed throughout approximately 90,000 km² in Europe and parts of North Africa (Moriarty and Dekker 1997). Described as a facultatively catadromous species, *A. anguilla* typically spends the growth portion of its life in fresh waters but embarks on a oceanic spawning migration, with all individuals theoretically spawning at a single site somewhere within the Northwest Atlantic Ocean (Schmidt 1912, 1925; Tesch 1977). Evolving from a tropical marine ancestor (Aoyama et al. 2001), this catadromy gives *A. anguilla* a means to utilize freshwater resources relatively free from competition, whilst still retaining their marine larval form. Although never verified, spawning has long been theorized to take place in the southern portion of the Sargasso Sea (Schmidt 1912), a sea that is encapsulated within an ocean gyre, bordered by four ocean currents and encompasses the Bermuda Islands in its west. Upon hatching, the eels´ larval form (leptocephali) are transported via ocean currents to Europe´s continental shelf, where on arrival they metamorphose into glass eels, become increasingly pigmented during several juvenile stages until classified as fully pigmented elvers and subsequently pervade continental habitats to grow (Tesch 1977; Aoyama 2009). At this period of growth, during which they are known as yellow eels, the population generally consists of freshwater residents, saltwater residents and inter-habitat migrants (Tzeng *et al.* 2000; Arai *et al.* 2006), with some individuals never entering freshwater at all, thus the facultative nature of their catadromy. This growth stage typically lasts between 2-20 years (Tesch 2003; Arai *et al.* 2006), after which they undergo a second (silvering) metamorphosis to become silver eels, physiologically and morphologically preparing them for an oceanic spawning migration (Fig.1; Tesch 2003; Durif *et al.* 2005). It is suggested that environmental stimuli initiate the onset of silvering and subsequent migration so that all mature adults arrive simultaneously at the spawning grounds (Bruijs and Durif, 2009).

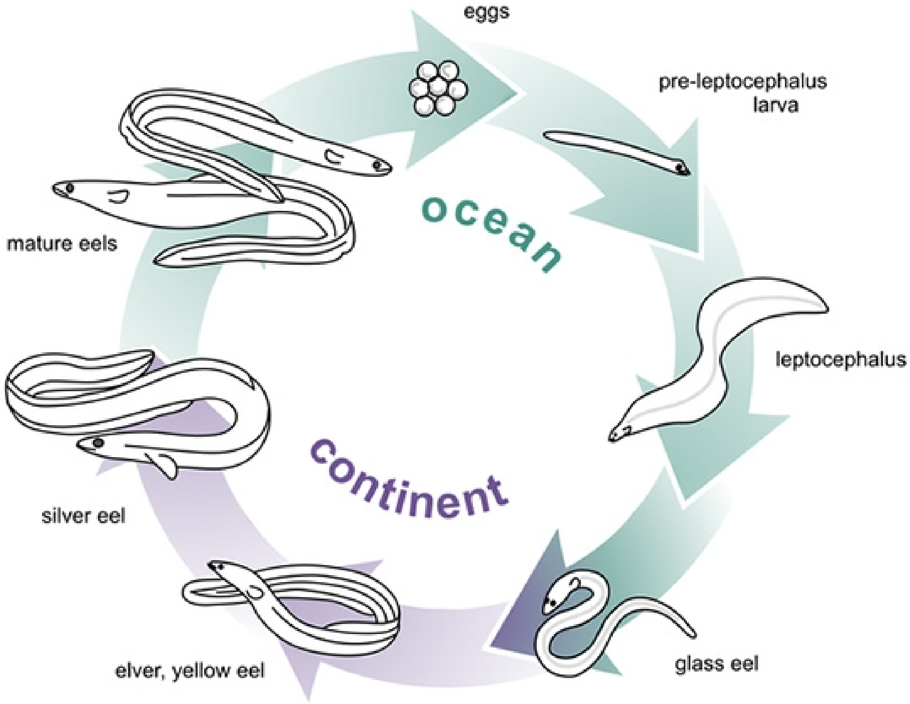


Fig. 1. Lifecycle of the eel. Adapted from Henkel *et al.* (2012)

Currently listed as a critically endangered species (Jacoby and Gollock 2014) and protected under various regulations (CITES 2007; EC Regulation 1100/2007), a better understanding of complicated and episodic life history of *A. anguilla* is needed to support evidence-based conservation efforts and protect the species throughout its various continental and oceanic life stages. In an attempt to better understand the species´ spawning migration and verify the putative spawning site in the South Sargasso Sea (Schmidt 1925), eels have been tracked west from mainland Europe. However, tracking (using pop-off satellite tags) in the North Atlantic Ocean, only succeeded as far as the Azores Archipelago, an autonomous region of Portugal, approximately halfway to the putative spawning ground, with a large proportion of tracked eels succumbing to predation (Righton *et al.* 2016).

From mainland Europe, this oceanic migration is long (5000-10,000 km) and evidently perilous. However, individuals at the Azores, the extreme west of the species´ continental range, have the shortest migration to the putative spawning ground and would therefore, be expected to have the greatest chances of spawning success. Nonetheless, despite being more than 1300 km west of mainland Europe, little is known about the eels inhabiting the Azores Archipelago. Although a small number of studies have acknowledged the existence of the eels on the archipelago (Schmidt 1912; Albuquerque 1954; Cabral *et al.* 1990; Arruda 1992; Azevedo 1995; Santos *et al.* 1997) and despite being known as the islands' only endemic freshwater fish species (Morton and Britton 2003), there are no records of distribution, abundance, habitat use or size structure. Up until now, Portuguese Eel Management Plans have excluded the Azores, because although their presence is recognised, it was surmised that its freshwater individuals did not reach the ′silver′ migratory phase (Cabral *et al.* 1990). Notwithstanding, because it is comparatively close to the Sargasso Sea and is likely to be geographically isolated from the transferable diseases currently effecting the continental population, this little-studied sub-population may provide an important contribution of adults with a greater chance of spawning success to the heavily declined and threatened population.

1.1 Aims and Objectives

Comprehensive studies, of *A. anguilla′s* yellow eel population dynamics and timing of silver eel migration, have been undertaken throughout much of the species range. Study results for this widespread species, have provided insights into sub-populations at localities and contributed to overarching hypotheses about the entire, theoretically panmictic, population. Whilst data exists for much of *A. anguilla′s* range, a lack of research means data have been absent for the sub-population at the Azores Archipelago. This sub-population provides an important subject for study, with its proximity to the putative spawning grounds and geographical isolation from the transferable diseases that affect the continental population.

This research aims to ascertain the presence and abundance of yellow eels on four Azorean islands, the existence of freshwater individuals reaching the ′silver′ migratory phase and affirm a need for inclusion of the Azores in Portuguese Eel Management Plans. Findings will also support evidence-based conservation efforts by contributing to the understanding of the yellow eel growth-phase and timing of silver eel migration throughout *A. anguilla′s* diverse range. It is proposed that the distribution, population structure and the timing of silver eel migration of this Azorean sub-population will compliment pre-existing observations at comparative study locations.

The aim of this study was to investigate the sub-population of European eels in freshwater and brackish habitats in the Azores Archipelago. The specific objectives were to:

- Assess the geographical distribution of eels across the archipelago, focusing on Terceira, Santa Maria, Flores and São Miguel islands
- Examine spatial (intra- and inter-watercourse) variations in the abundance and size of eels on São Miguel, the largest island
- Verify the existence of silver (migratory) eels in the archipelago
- Assess temporal variations in silver eel abundance and size in the Ribeira Quente, the largest river on São Miguel

2. Literature Review

2.1 Population structure of anguillid eels

The family Anguillidae totals 16 distinct species, with three of its tropical species comprising two sub-species each (Aoyama 2009). This family of eels, despite completing reproduction in oceanic waters, inhabit continental waters during their growth phase and otolith microchemistry studies have shown that these eels exhibit a form of facultative catadromy, with some individuals never entering fresh water at all (Tzeng *et al.* 2000; Tsukamoto and Arai 2001; Daverat 2006; Daverat and Tomás 2006).

Despite extensive ranges that can span thousands of kilometres and encompass diverse growth habitats, the majority of studies suggest anguillid eels have panmictic population structures. Thus, for each species, all migrants return to spawn at a single oceanic site, with ocean currents subsequently dispersing the larvae throughout the continental growth phase range (Schmidt 1925; Tesch 1977; Aoyama 2009). Most genetic studies support the panmictic theory for *A. anguilla*, *A. japonica (the Japanese eel*) and *A. rostrata (the American* eel) (Sang *et al.* 1994; Dannewitz *et al.* 2005; Mank and Avise 2003). By contrast, an analysis using highly polymorphic microsatellite DNA markers did find significant genetic differences between *A. anguilla* from geographically separate sub-populations spanning Iceland to the Baltic Sea (Wirth and Bernatchez 2001). These observations were inferred to have been caused by restricted gene flow and seemed to contradict the panmixia theory (Aoyama 2009). However, when similar analyses of eels from different cohorts revealed substantial temporal variations in markers, it was suggested that the conflicting observations originated from spatial genetic patterns (Dannewitz *et al.* 2005; Pujolar *et al.* 2006) and that panmixia was therefore the most likely population structure. Whilst shorter migration distances for tropical anguillids provide a greater chance of restricted gene flow, that temperate anguillid eels migrate thousands of kilometres in strong oceanic currents to spawn, gives feasibility to the panmixia theory (Aoyama 2009).

2.2 Evolution and phylogeny of the genus *Anguilla*

As with all members of the superorder Elopomorpha, anguillid eels possess a larval marine form, the leptocephalus (Inoue *et al.* 2004). Acceptance of the panmixia theory has facilitated the unraveling of the evolutionary history and phylogenetic relationships of the genus through this larval form. It has been suggested that the genus *Anguilla* diverged from a tropical marine ancestor, with adaptations allowing freshwater tolerance and a means to utilize habitats free from competition with other ancestral eels (Aoyama et al. 2001). Catadromous migration evolved as subsequent generations continued this advantageous utilization of freshwater resources whilst still retaining their marine larval form. Temporal and/or spatial separation eventually permitted the divergence of the anguillid eels into many species (Aoyama 2009). The speciation, which resulted in the 16 extant anguillid species, can be explained as variations of the migration loop concept (Ishikawa *et al.* 2004). For anguillid species continuing to inhabit the tropics, speciation via this concept would most likely commence with the creation of a new spawning site. This would be initiated concurrently with or followed by the separation of continental growth habitats (Ishikawa *et al.* 2004; Aoyama 2009; Aoyama et al. 2001). It has been suggested that tropical eel leptocephali may occasionally be transported further and to much higher latitudes than intended (Tsukamoto *et al.* 2002). If these higher-latitude eels subsequently migrated back to their original spawning ground, a new and much larger migration loop could form, perhaps eventually resulting in the spatial or temporal separation of the loops. Whilst this may explain the speciation of the present-day tropical anguillid species it may, within the *Anguilla* evolutionary time-frame, also have resulted in the creation of the temperate eel groups from tropical species (Tsukamoto *et al.* 2002). The evolution of a common ancestor to distinct present-day temperate Atlantic eel species (*A. anguilla* and *A. rostrata*) would likely have initiated with the expansion of the ancestor´s freshwater range. This habitat expansion, followed by the spatial or temporal separation of spawning sites via continental drift and oceanic currents, could have culminated in reproductive isolation (Aoyama 2009). To successfully recruit to both sides of the Atlantic, despite continuing to spawn at a similar site and time, the two genetically distinct populations had to evolve, with differing leptocephali metamorphosis timing being key (Tsukamoto *et al.* 2002). This genetically inherent difference allowed for the leptocephali of both species to metamorphose on arrival at their corresponding sides of the Atlantic ocean (Tsukamoto *et al.* 2002; Aoyama 2009). Within all extant anguillid eel species, there exist vast variations in the timing of leptocephalus metamorphosis (248-459 days for *A. anguilla* and 248-365 days for *A. rostrata*), supporting the idea of speciation via such mechanisms (Kuroki 2007).

Succeeding the complete sequencing of mitochondrial DNA (mDNA) for all species of the family Anguillidae (Minegishi *et al.* 2005), an estimation of phylogenetic relationships and evolutionary history was shaped (Aoyama *et al.* 2009). Sequencing perceived a tropical species, *A. mossambica* (Minegishi *et al.* 2005) or *A. borneensis* (Aoyama et al. 2001), as the most basal species of the genus *Anguilla*, suggesting temperate eels and their corresponding long-distance migrations did evolve from tropical species with much shorter migrations (Tsukamoto *et al.* 2002). The genomic analysis by Aoyama *et al.* (2001) grouped the Atlantic eels (*A. anguilla* and *A. rostrata*) in a clade with the East African eel (*A. borneensis*). It was this sister relationship, combined with the existing continental isolation between the two groups, that resulted in the Tethys Corridor Hypothesis, according to which anguillid eels were transported westward, from a region believed to now be Indonesia, by paleo-circumglobal currents to the Western Ocean (present-day Atlantic Ocean) through the prehistoric Tethys Sea, a channel that once connected the Eastern and Western Oceans (Aoyama et al. 2001). Given that an estimated 40-70 million years of anguillid eel evolution has occurred (Aoyama et al. 2001), the divergence of the Atlantic eel group as a result of known geologic and oceanic changes seems likely. Continuing continental drift and changing oceanic currents would have subsequently resulted in the creation of two distinct Atlantic anguillid species as previously mentioned.

2.3 Spawning grounds of temperate eels

Three species within the family Anguillidae inhabit the Northern Hemisphere, all of which migrate great distances between their continental growth habitats and corresponding spawning grounds. These species are *A. anguilla* and *A. rostrata* in the Atlantic Ocean, and the *A. japonica* in the Pacific Ocean.

The spawning locations of these anguillid eels had long perplexed fisheries biologists and, although it was theorized that distant oceanic spawning grounds may exist, the first evidence was only discovered in the last century by the Danish biologist Johannes Schmidt (1922). After completing expansive North Atlantic surveys spanning two decades, Schmidt caught leptocephali of both Atlantic species (*A. anguilla* and *A. rostrata*), with decreasingly smaller and therefore younger individuals centered within the South Sargasso Sea (Schmidt 1922, 1925). He identified this region as containing an overlapping spawning ground for both species and future leptocephali sampling expeditions reinforced his findings. Small leptocephali of both species were caught within an overlapping portion of the South Sargasso and the breeding grounds of *A. rostrata* were revealed to be slightly east of those of *A. anguilla* (Schoth and Tesch 1982). A spawning season during late winter and spring was speculated for both species, using the timing of when the smallest larvae were caught (Schmidt 1922; Schoth and Tesch 1982; McCleave *et al.* 1987). Even more recent expeditions demonstrated that both spawning grounds were situated between approximately 50°W and 75°W (Kleckner and McCleave 1988). The proximity of spawning grounds and comparable timing of both Atlantic eel species, can be further reinforced by a genetic study in Iceland, whereupon RAD (Restriction site Associated DNA) sequencing identified 10.7% of the 159 eels tested were of admixed ancestory, a result of hybridisation between *A. anguilla* and *A. rostrata* (Pujolar *et al.* 2014). Schoth and Tesch (1982) had previously hypothesised that the boundaries of the spawning area were a high-temperature front to the north and a combined high temperature and salinity front to the south. Kleckner and McCleave´s 1987 expedition investigated this theory and proved the warm, saline, surface water of the South Sargasso Sea´s northern front to be the northern larval boundary (Kleckner and McCleave 1988). The exact locations of the Atlantic eel spawning sites remain unknown, despite attempts using modern pop-off satellite tracking technology attached to migrating adults (Aarestrup *et al.* 2009).

Following Schmidt´s initial discovery in the Atlantic Ocean, attempts were made to identify where spawning occurred in the Pacific Ocean for *A. japonica* (Jespersen 1942). Planktonic surveys identified a spawning region situated approximately 140°E in the North Equatorial Current, bordered to the north by a salinity front (Tsukamoto 1992; Kimura and Tsukamoto 2006). Further historical data analysis, in regards to the spawning of *A. japonica*, revealed correlations with subsurface seamounts of the Philippine Plate and specific lunar conditions. Theories suggested eels spawned within the proximity of these seamounts during a new moon lunar phase. The theories were validated during multiple expeditions, with captures of many newly hatched preleptocephali in the proximity of the West Mariana Ridge seamounts during a new moon (Ishikawa et al. 2001; Tsukamoto 2006). The comparable life histories and long-distance migrations of the three Northern Hemisphere anguillid eels suggest that the Atlantic eels may spawn under homogenous environmental conditions and locations, as discovered for *A. japonica*.

2.4 Growth and oceanic dispersal of leptocephali

Evidently, from both current and theorized historical dispersal, the association of oceanic currents and the location of eel spawning grounds are pivotal to the eventual distribution of their leptocephali. All of the Anguillidae spawn within areas of deep water (Tsukamoto *et al.* 2002; Aoyama 2009), however, how far from land spawning occurs can vary between species, from around 100 km in some tropical species to many 1000 km in temperate eels (Aoyama *et al.* 2003; Aoyama 2009). Although the locations of anguillid spawning grounds have largely been inferred from catches of leptocephali, catching the larvae has continually proven difficult (Schmidt 1922, Miller 2009). Apart from the remoteness of the spawning grounds, leptocephali typically grow larger than other fish larvae, are nocturnal, avoid plankton nets and are fragile, so standard plankton-netting techniques and equipment are mostly ineffective (Miller 2009). In addition, the larvae of all species do not resemble their adult form, which renders identification via morphological characteristics difficult and means the life histories of these larvae are poorly understood (Miller and Tsukamoto 2004).

Female *A. anguilla* produce approximately 2 million eggs per 1 kg of weight and each egg averages around 1 mm in diameter, is pelagic, not sticky and floats to the water surface following artifically spawning via hormonal stimulation in laboratory conditions (Pederson, 2003; Palstra *et al.* 2005). Larvae undergo several transitions through morphologically distinct stages, namely preleptocephalus, engyodontic leptocephalus and euryodontic leptocephalus, followed by metamorphosis into juvenile glass eels (Leiby 1989). *A. japonica* hatches in a relatively undeveloped condition without fully formed head features, as shown in field (Tsukamoto *et al.* 2002) and laboratory studies (Okamura *et al.* 2002a). The larvae develop such features as they enter the preleptocephalus stage; the stage defined by recent hatching and feeding endogenously (on an oil globule reserve) rather than exogenously (Tsukamoto 2006; Miller 2009). Once the oil globule reserve is completely utilized and both eyes and a few long forward teeth have developed, the larvae are classified as an engyodontic leptocephali (Leiby 1989; Miller 2009). Continued development into the larger euryodontic leptocephalus is accompanied by the replacement of the few large teeth with many shorter teeth and the development of anal, dorsal and pectoral fins (Leiby 1989).

Both leptocephali stages are typified by transparent and laterally compressed bodies, large eyes, outward-pointing teeth and an ability to swim both forward and backward, using the same anguilliform locomotion as in juvenile and adult eels (Miller and McCleave 1994; Miller and Tsukamoto 2004; Miller 2009). This body transparency arises from transparent metabolically inert glycosaminoglycan (GAG) that forms the majority of the body mass, acting as energy storage and structural support (Pfeiler *et al.* 2002; Miller 2009). With GAG, rather than metabolic tissues, making up the majority of their bodies' mass, leptocephali have low metabolic demands, which do not increase greatly with increasing development and size (Pfeiler and Govoni 1993). These low energy demands facilitate life within the ocean surface layer (Miller 2009), allowing leptocephali to feed on abundant particulate marine snow, larvacean houses and faecal matter rather than energetic, energy-rich zooplankton (Otake *et al.* 1993). A transparent form not only benefits leptocephali in terms of energy costs, but likely reduces the chances of predation within this surface layer. Planktonic trawling studies have shown that leptocephali exhibit daily vertical migrations, most likely another predator-avoidance adaptation, with *A. anguilla* leptocephali inhabiting the region between 30-70 m during the night and 70-280 m during the day (Schoth and Tesch 1984). Further studies in the Sargasso Sea have revealed evidence of increasingly deep vertical migrations for larvae of *A. anguilla* and *A. rostrata* as they grow larger and more developed (Castonguay and McCleave 1987). There are many advantages for development within this surface layer of the open ocean and the numerous biological and behavioral adaptations of leptocephali support a life perfectly suited to such an environment (Miller 2009). A feeding strategy concentrating on particulate matter minimises competition with other fish larvae (Miller 2009) and utilizes a readily available food source in the otherwise low-productivity waters of the open ocean (Pfeiler and Govoni 1993). Such low-productivity waters attract equivalently low populations of predators and by residing there for a considerable portion of their early developmental stage, they can arrive for recruitment in coastal waters substantially larger and further developed than other fish larvae, again aiding in predator avoidance (Miller *et al.* 1988). For temperate anguillid species, spawning close to their growth habitats would subject them to greater predator populations and a colder environment, sub-optimal conditions for development (Miller and Tsukamoto 2004; Miller 2009). For *A. japonica*, laboratory investigations demonstrated larvae possess a variety of sensory mechanoreceptor cells, including a primitive lateral line sensory arrangement (Okamura *et al.* 2002a). Predation of leptocephali is poorly documented, perhaps in part because of their fragility and rapid digestion (Miller 2009), but their developmental location, transparent form, sensory receptors and anguillid-motion swimming abilities should reduce predation risk (Miller *et al.* 1988; Figueroa 1997). As mentioned previously, leptocephali use the typical anguillid swimming motion, allowing both forward and backward travel. This is energy efficient, as seen in the long-distance migration ability of silver eels (van den Thillart *et al.* 2009) and allows relatively fast bursts of speed for *A. japonica* leptocephali in laboratory experiments (Yamada *et al.* 2009). As well as aiding predator avoidance, efficient swimming may contribute to the successful dispersal of larvae in their recruitment regions. As Schmidt (1922) discovered, anguillid eels spawn in the open ocean, with the larvae subsequently transported to growth habitats via ocean currents. The length of time eels remain as a leptocephali within the ocean currents is crucial in determining their species' range and recruitment to the correct growth habitats (Miller and Tsukamoto 2004; Kuroki 2007). Leptocephali and glass eel otolith microstructure studies, focusing on daily otolith incremental depositions and Sr:Ca (Strontium:Calcium) ratios, have helped shed light on the age at which leptocephali metamorphose into glass eels (Tsukamoto 1989; Wang and Tzeng 2000; Otake 2003; Aoyama 2009). Daily otolith increment widths were shown to increase and otolith Sr:Ca ratios rapidly decrease during the metamorphosis of leptocephali into glass eels (Arai *et al.* 1997), providing a marker for leptocephalus age at metamorphosis and allowing larval growth rate, growth duration and maximal size to be estimated (Wang and Tzeng 2000; Kuroki 2007). Within the various species of Anguillidae, these studies showed variation in growth rates between the temperate Atlantic eels and tropical species, with mean rates of 0.23 and 0.61 mm/d, respectively (Castonguay 1987; Kuroki *et al.* 2006a; Miller 2009). The relation of larval migration distance to different growth rates was hypothesised by Kuroki *et al.* (2006), although the influence of water temperature on growth rate cannot be omitted (Miller 2009). Contesting water temperature effects, similarly sized larvae of a tropical eel (*A. reinhardtii*) and a temperate eel (*A. australis*) were collected together in the South Pacific and the tropical *A. reinhardtii* was shown to have a higher growth rate, despite both having been exposed to analogous water temperatures throughout their growth (Kuroki 2007). This seemed to suggest, at least for those two species, that water temperature was not the main determinant of growth rate and instead growth rate was more likely correlated with a longer migration distance required for the successful recruitment of *A. australis*. It has been suggested that faster growth rates for species with smaller migration distances allow their leptocephali to arrive in recruitment areas at an optimal size, ready for metamorphosis into glass eels. Larval migration distance also seems to correlate with maximal leptocephalus size, with tropical larvae reaching 50-55 mm (Aoyama 2009; Kuroki *et al.* 2009), whilst temperate larvae can grow up to 70-85 mm (Kleckner and McCleave 1985; Aoyama 2009). In the Anguillidae, the largest leptocephali and longest larval migration are both found in *A. anguilla* (Tesch 1980; Kleckner and McCleave 1985). Large intra-species variations in larval duration also exist for eels recruiting to the same areas (Kuroki 2007) and different latitudes (Wang and Tzeng 2000). Studies on the recruitment of *A. japonica* glass eels revealed that their leptocephali periods could differ by almost 90 days (Shinoda 2004), despite simultaneous timing and location of recruitment. Overall, despite large intra-species variations, it is suggested that species with longer migrations have slower growth rates and arrive at their recruitment areas at a much larger maximal size. As mentioned previously, the spawning of *A. anguilla* and *A. rostrata* overlap in an area of the South Sargasso Sea (Schoth and Tesch 1982), with larvae of both species then transported by westward-flowing currents (Kuroki *et al.* 2009). With a larval period of 248-459 days, *A. anguilla* delays recruitment until reaching its expansive European range, whilst the shorter larval period of 248-365 days in *A. rostrata* (Kuroki 2007) allows early successful recruitment at the American continent. It has been suggested by Pujolar *et al.* (2014) that the existence of hybrids in Iceland, resulting from *A. anguilla* and *A. rostrata* ancestory, may be in part due to Icelands location midway between continental Europe and the putative spawnings grounds. Their existence, at such a mid-point location, could infer an intermediate larval timing resulting from their mixed ancestory.

For the successful recruitment of Atlantic anguillid eels (*A. anguilla* and *A. rostrata*) to their continental growth habitats, larvae have to be transported by the North Atlantic subtropical gyre across great distances (Schmidt 1922). Spawning of the two species occurs within an overlapping region, with *A. anguilla* distributed further east and *A. rostrata* further west (Kleckner and McCleave 1988), and following spawning in spring (McCleave *et al.* 1987; Tesch 2003), their larvae become widely distributed (Schmidt 1922) within the North Atlantic basin. An amalgamation of almost a hundred years of gathered data, which included 22612 *A. anguilla* leptocephali and 9634 *A. rostrata* leptocephali (Miller *et al.* 2015), was analysed to follow the leptocephali dispersal of both species after spawning. It was demonstrated that *A. rostrata* first dispersed outwardly in all directions from the southwestern portion of the North Atlantic basin, followed by a more directional dispersal towards the north and west (Miller *et al.* 2015). Continuing in this direction, *A. rostrata* larvae enter a portion of the Gulf Stream named the Florida Current (Kleckner and McCleave 1988), before finally crossing this current to reach the continental shelf of the American continent for recruitment. It is unlikely that natural mechanisms transport these larvae across this current since the only theorized mechanisms are random and infrequent (Rypina *et al.* 2014; Miller and Tsukamoto 2016). Particle transport modeling studies demonstrated that to cross the Florida Current, leptocephali would most likely have to adopt directional swimming (Rypina *et al.* 2014). The American conger (*Conger oceanicus*), another member of the Anguilliformes with leptocephalus larvae, also spawns in the Sargasso and their larvae also cross the Florida Current. This further supports the idea of adopting directional swimming to cross this current, since random and infrequent oceanic transportation mechanisms cannot account for both species' yearly recruitment (Miller *et al.* 2011; Miller and Tsukamoto 2016).

The dispersal of *A. anguilla* contrasts with that of *A. rostrata*. Larvae of *A. anguilla* emerge slightly east of *A. rostrata* and begin by dispersing both east and west, followed by even wider dispersal in all directions, except the south (Miller *et al.* 2015). Compared to *A. rostrata*´s northwesterly concentrated dispersal, *A. anguilla* disperses extensively throughout almost the entire basin (Miller *et al.* 2015). The eventual distribution of *A. anguilla* throughout its European continental range may occur via multiple routes, with their widely dispersed larvae fragmented throughout different ocean currents. Ensuing the initial pattern of dispersal, *A. anguilla* may continue west into an easterly flowing portion of the Gulf Stream or northeast via counter-currents in the Sargasso Sea (Miller *et al.* 2015). These counter-current larvae and perhaps a portion of the Gulf Stream larvae are then introduced into the Azores Current which transports them east or alternatively they enter the North Atlantic Current which transports them to Northern Europe (Miller *et al.* 2015). As discussed, *A. anguilla* has a large variation in the duration of the larval period and whilst the species does not have to navigate the crossing of the Florida Current like *A. rostrata*, particle transport modeling was used to predict the transport times of larvae, accounting for a number of variable behaviours such as diel migrations and horizontal swimming (Bonhommeau et al. 2009; Rypina *et al.* 2014; Miller and Tsukamoto 2016). Although it is theorized that *A. anguilla* larvae adopt horizontal swimming throughout migration (Righton *et al.* 2012), the considerable duration and complexity of the migration makes it impossible, using current otolith techniques or dispersal models, to ascertain how much of a part swimming plays in their eventual dispersal throughout continental Europe (Bonhommeau et al. 2009; Miller *et al.* 2015; Miller and Tsukamoto 2016). Variations in oceanic dispersal are also likely to occur as a result of fluctuating oceanic conditions, most notably the North Atlantic Oscillation, which has previously shown to be correlated to *A. anguilla* recruitment within Europe (Friedland *et al.* 2007; Kettle *et al.* 2008).

It has been shown that *A. anguilla* and *A. rostrata* both spawn over quite a large expanse within the South Sargasso Sea and individual, precise spawning locations are not the determining factor in their eventual continental distribution; instead, innate behaviours such as horizontal swimming perhaps play a much larger part than has currently been proven. In contrast, *A. japonica* was shown via catches of leptocephali < 10 mm in body length (Tsukamoto 2006) to have a much smaller and more precise spawning location situated within a bifurcating current, with southerly and northerly flows. To successfully recruit to continental habitats, leptocephali must be transported by the northern current and so the precise positioning of their spawning ground is vital (Miller 2009).

2.5 Metamorphosis and continental recruitment

After a considerable dispersal time, leptocephali are transported to continental waters where they metamorphose into elongate glass eels and move into coastal shelf waters to inhabit fresh, brackish or marine waters in their yellow 'growth' phase (Tesch 2003). This metamorphosis involves shifting from a fragile oceanic form to a more appropriate form for continental water life, with feeding strategies better adapted to growth-phase habitats (Miller 2009).

Whilst the majority of metamorphosing leptocephali have been caught within continental shelf waters (Kleckneer and McCleave 1985), some have also been caught before arrival at the continental shelf for *A. rostrata* (Kleckneer and McCleave 1985), *A. japonica* (Otake *et al.* 2006) and *A. anguilla* (Antunes and Tesch 1997). Metamorphosis within continental shelf waters would seem to be the best strategy, as glass eels would be poorly adapted for open ocean life, due to vulnerabilities to predators, starvation and environmental fluctuations (Miller 2009). Without the appropriate cues and in colder water temperatures, a delay in metamorphosis has been observed for other leptocephalus-bearing Elopomorphs (McCormick 1999; Chen *et al.* 2008), likely a strategy to inhibit metamorphosis until optimal conditions for juvenile survival have been reached. As previously mentioned, increases in daily otolith increments and Sr:Ca ratios are observed during leptocephali metamorphosis and, in addition to providing an insight into the duration and growth rate of the leptocephalus stage, it allows an estimation of metamorphosis duration (Wang and Tzeng 2000; Otake 2003). The duration of metamorphosis is greatly dependent on temperature, with variations between 9-70 days for tropical and temperate anguillid eel species (Otake 2003; Aoyama 2009; Miller 2009).

The onset of metamorphosis is likely stimulated by environmental cues associated with the continental shelf, such as water depth, decreased salinity and chemical compounds (Miller 2009), with some studies showing an increase in thyroid hormones play a part (Otake 2003). Metamorphosis begins with an increase of the olfactory organ size, loss of teeth and thickening of the head, combined with the forward-shifting position of dorsal fins, anal fins and gut (Miller 2009). Throughout metamorphosis, leptocephali decrease in size and become increasingly pigmented, due to increased skeletal development, a reduction of transparent GAG tissue (Pfeiler 1999; Miller 2009) and the development of pigmentation cells (Tsukamoto 1990). This progressive pigmentation is used to classify several juvenile stages, as glass eels develop into fully pigmented elvers and then eventually the yellow growth phase (Elie *et al.* 1982).

During metamorphosis, glass eels of *A. anguilla* migrate into coastal waters throughout the year, with location-specific migration peaks correlated most strongly with latitude, but also dependent on an array of oceanic mechanisms (Harrison *et al.* 2014). Glass eel coastal migration in France begins in September with a peak in winter (Laffaille et al. 2000), whilst in British waters migration peaks occur later during February-May (Defra 2010). Two migration peaks were discovered at Europe's most southerly estuary in Spain, occurring late autumn and spring, with the lowest migration occurring during summer (Arribas *et al.* 2012). In Norway and towards the northern boundaries of their range, migration has been seen to peak in January-March (Durif *et al.* 2011). Annual changes in glass eel recruitment to estuaries has been shown to be caused, in part, by the North Atlantic Oscillation index and water temperatures within the Sargasso Sea, whilst short-term recruitment fluctuations are likely caused by localised environmental conditions such as turbidity, temperature, rainfall and wind (Arribas *et al.* 2012; Harrison *et al.* 2014). River flow itself has proven to be an important cue for inland migration of glass eels, transporting natural odorants and acting as an olfactory attractant (Tesch 2003). The majority of glass eel migration activity occurs during the hours of darkness and especially directly following the onset of night. Whilst low-light conditions are preferred (Jellyman 1979; Tesch 2003), it has been demonstrated that a proportion of glass eels will migrate upstream during the day (Adam *et al.* 2008). The anguillid body shape may provide an energy-efficient method of swimming, yet it has its limitations regarding speed and is somewhat insufficient against current exceeding 30 cm/s (Adam *et al.* 2008). Therefore, to migrate upstream in estuaries efficiently, glass eels have been shown to utilise tidal currents in what is called Selective Tidal Stream Transport (STST) (McCleave and Kleckner 1982). This endogenous mechanism involves glass eel remaining on the substrate during tidal ebbs and moving into the water column during tidal floods (Harrison *et al.* 2014), passively transporting them upstream in estuaries and possibly reducing their energy expenditure up to 90% (Weihs 1978). Glass eels must adopt active swimming as they are transported further upstream (Deedler 1958), where the influences of tidal streams diminish. A switch in behaviour has been observed at the freshwater-saltwater interface, with glass eels changing from the passive STST mechanism to active counter-current swimming

(Tesch 2003). Water temperature has proven to be a determining component of this behavioural switch, with a threshold of 10-15 °C for *A. anguilla* (Gascuel 1986).

As discussed, anguillid eels are facultatively catadromous and whilst it seems that many glass eels adopt upstream counter-current swimming, some remain and grow in estuaries and marine waters (Tesch 2003). This choice seems to be, at least in part, related to body condition and the endocrine system (Edeline *et al.* 2005, 2006), with lower-condition individuals settling in estuaries rather than completing an upstream migration (Edeline *et al.* 2006). This may be due to the direct impact a lower body condition has on the eel's endocrine system, bringing about increased production of cortisol, decreased production of thyroid hormones and stimulating gill and intestinal adaptations for saltwater residency (Wilson *et al.* 2004; Edeline *et al.* 2005). Higher-condition individuals may also be able to sustain estuarine migration via continued endogenous feeding, whilst lower-condition individuals may have to settle within estuaries to feed (Bureau Du Colombier *et al.* 2008). In summary, larval metamorphosis is thought to initiate upon arrival at the continental shelf (Tesch 1980, 2003) and finish after a completed estuarine migration (Lecomte-finiger 1983).

2.6 Growth phase - Sex differentiation

Following this estuarine migration, the juvenile growth phase begins and whilst some elvers settle in estuarine or marine habitats, others continue migrating upstream. This continued upstream migration has been linked to rising water temperatures during spring, with the main *A. anguilla* elver migrations (runs) occurring between 10-17 °C (Deedler 1984). It has also been demonstrated that colder summer temperatures may inhibit elver runs and therefore increase the number of elvers remaining in estuarine waters (Hvidsten 1985). Whilst temperature has been shown to initiate elver runs, other seasonal environment factors are suggested to influence the length of time it continues (Moriarty 1986). The duration of this elver migration season is directly associated with the yearly distances an elver can travel upstream, shown as averaging 47 days in the River Thames (Naismith and Knights 1988), a distance which is of course influenced by various other factors such as river structure, flow and anthropogenic barriers. Following the cessation of upstream migration and once body length of > 30 cm have been reached (Tesch 2003), juvenile eels settle within growth habitats as sexually undifferentiated ‘yellow eels’ (Tesch 2003; Davey & Jellyman 2005). The name for this growth stage appropriately comes from the yellow/green hue to their skin (Tesch 2003) and unlike the larval portion of their lives, is less well documented.

Yellow eels inhabit a wide variety of habitats, entering with only an ambiguous primordial gonad and it is during this period that eels become sexually differentiated (Colombo and Grandi 1996). The onset of sexual differentiation seems to be a result of size rather than age and for *A. anguilla* it begins when eels reach a length of 200 mm and usually concludes at a length of 350 mm (Colombo *et al.* 1984), with females often differentiating at a smaller size (>190 mm) than males (>270 mm) (Amin 1997). It has been suggested that sex determination could be initiated during the first juvenile year, with elver growth rates shown to influence sex (Holmgren *et al.* 1997). Following differentiation, males and females adopt very different developmental strategies. Males follow the quickest route to maturation, by initially growing faster and maturing at the smallest size for a successful spawning migration, therefore increasing their chances of pre-reproductive survival (Tesch 2003; Davey and Jellyman 2005). The female strategy is the inverse, with much slower initial growth but a much greater final size and age. Females trade premature mortality for sufficient energy stores required for egg maturation and the exponential increase in fecundity that comes with increased size (Davey and Jellyman 2005). There are arguments suggesting females adopt a similar strategy to males, maturing at the smallest size for successful spawning (Vøllestad 1992), and it is possible that the maturation of females is a result of both sides of this argument, dependent on local habitat and conditions (Oliveira 1999). This compromise suggests females would adopt a size-maximising strategy when subjected to favourable conditions and a time-maximising strategy when conditions were unfavourable (Oliveira 1999; Jellyman 2001). Whilst both sexes show growth variation, females exhibit the largest variation in growth rates, size and age at spawning migration (Davey and Jellyman 2005). Wild populations often have skewed sex ratios that differ between localities and, due to the random continental dispersal of eel leptocephali, this is most likely a result of environmentally influenced phenotypic expression, rather than genotypic expression (Roncarati *et al.* 1997; Tesch 2003). For a developing eel to maximise fitness, it must adopt the life strategy best suited to its surrounding environmental conditions and so differentiation into a particular sex will most likely be a result of conditions experienced at an early stage. Eels with fast initial growth, resulting from higher temperatures, productive habitats and higher intrinsic growth rates, are likely to adopt the time-maximising strategy and develop as males (Helfman *et al.* 1987), whereas slower-growing eels of lower fitness can counterbalance an initial reduced fitness by reaching a much greater size at spawning and so will likely develop as females (Helfman *et al.* 1987). This initial faster growth in *A. anguilla* males seems to occur up until a critical size of 260 mm and 60 g as demonstrated by Holmgren and Mosegaard (1996), after which it is succeeded by a faster growth rate in females. Density is another well-documented condition thought to affect sex differentiation. It has been shown that males are prevalent where eel densities are high, mainly dominating the lower reaches of rivers, whereas females are more prevalent in the lower densities associated with a rivers higher reaches (Aprahamian 1988; McCarthy *et al.* 1998; Tesch 2003). Studies on wild populations have supported this distribution of sexes in catchments low in density (Krueger and Oliveira 1999) and lacking in females (McCleave and

Jellyman 2004) and studies on cultured eels have shown that overstocking frequently results in the proliferation of males (Holmgren 1996; Tesch 2003). The exact mechanisms by which density could control sex differentiation are unclear but it is reasonable to suggest an underlying factor would be intraspecific competition for food. Increased competition may directly influence individuals to adopt a time-maximising male strategy to outcompete conspecifics and enhance their ability to survive. Alternatively, competitive interactions may indirectly raise testosterone levels resulting in faster growth (Davey and Jellyman 2005). These adaptations may be a reaction to immediate survival threats or in preparation for future competitive bottlenecks (Davey and Jellyman 2005). As mentioned, the sexes show a common dispersal, with males prevalent in the lower reaches of catchments and females in the higher reaches (Tesch, 2003). This may be a result of density but it is also likely that the longer-lived females will radiate further throughout a catchment than the time-saving males. Other environmentally influenced sex ratio patterns have been suggested, for example as a result of latitude (Helfman *et al.* 1987), but these have been contested and patterns are likely a response to localised environmental factors such as temperature and productivity (Oliveira *et al.* 2001). In combination with natural environmental factors, anthropogenic activities have been shown to affect sex ratios. Barriers, such as weirs and hydroelectric dams, can form an obstacle that is impassable for most or all upstream migrating elvers (Tesch 2003) and this may result in higher downstream densities and lower upstream densities, bolstering skewed sex ratios even further. Cannibalism has proven to be prevalent amongst cultured eels (Tesch 2003) and is likely to occur at high densities in the wild. Large cannibalistic female eels perhaps regulate yellow eel abundance (McCleave and Jellyman 2004; Davey and Jellyman 2005) and so fisheries targeting large individuals may limit this natural regulation, therefore increasing density and male prevalence.

2.7 Growth phase - habitat use and activity

The growth stage of *A. anguilla* normally lasts between 2-15 years for males and 4-20 years for females, averaging at 6.0 and 8.7 years in males and females, respectively (Tesch 2003; Arai *et al.* 2006). Within this time frame, eels inhabit a wide range of benthic habitats, with habitat selection during this stage having high behavioural plasticity (Tesch 2003). Whilst initial recruitment from marine to fresh or estuarine waters may occur during the juvenile stage, so-called facultative catadromy can extend throughout the yellow eel growth stage. Analyses of otolith Sr:Ca ratios in post-elver *A. anguilla* individuals have shown that the majority of eels do remain as either fresh or marine water residents throughout their growth periods, yet some do function as intermediates, living in estuaries and moving between marine and fresh waters throughout their growth (Tzeng *et al.* 2000; Arai *et al.* 2006). The utilisation of an estuarine habitat is advantageous to eels (Arai *et al.* 2006), with high food availability, low turbulence, plentiful shelter, reduced predation and low osmoregulatory costs (Blaber *et al.* 1985). These advantages will likely encourage eels to live in estuarine environments and as such, estuarine individuals are prevalent within anguillid species, including *A. anguilla* (Tzeng *et al.* 2000; Arai *et al.* 2006). Recruitment to fresh waters has been demonstrated to be, at least in part, density-dependent (Ibbotson *et al.* 2002) and so declines in the worldwide *A. anguilla* population may have less of an effect on these important estuarine sub-populations (Walker *et al.* 2014). In some localities, the size of the estuarine environment is limited by high altitude coastal land patterns (Arai *et al.* 2006) and so individuals may be forced to grow in just marine or fresh waters. Habitat choice has been shown to vary with eel size, even when spread over every type of micro-habitat available (Laffaille *et al.* 2003).

Anguillid eels have been shown to be photophobic, exhibiting mainly nocturnal behaviour that peaks from the crepuscular period until midnight (Parker and McCleave 1997; Hedger *et al.* 2010). Some individuals may be diurnally active, especially during light-reducing conditions such as high turbidity and cloud cover (Tesch 2003; van Ginneken *et al.* 2005). A study by Barry *et al.* (2016b) revealed activity may even be linked to certain morphotypes, with narrow-headed morphotypes showing greater crepuscular activity, in comparison to broad-headed individuals that showed greater nocturnal activity.

Periods of activity in yellow eels have also been related to the lunar cycle and peak during minimal lunar luminosity (Lamothe *et al.* 2000), again most likely due to low-light preferences. Studies on the effects of tidal flow on *A. anguilla* activity have given conflicting results, with McCleave and Arnold (1999) demonstrating that individuals use ebb and flood tides to move in and out of estuaries, whilst Walker *et al.* (2014) found no link between tide and activity. Water temperature does influence behaviour, with higher levels of activity under higher temperatures (Tesch 2003), however, light still seems to be the primary behavioural influencing factor. This low-light preference is likely a result of predator avoidance and the fact that foraging is achieved via olfactory rather than ocular cues (Riley *et al.* 2011).

Feunteun *et al.* (2003) classified the movement of yellow eels into three behavioural groups, namely founders, pioneers and home-range dwellers. Founders were shown to colonise the first suitable habitat that was encountered, whilst pioneers migrate to the upper boundaries within a catchment and the home range dwellers would remain within a given area for the majority of their growth (Feunteun *et al.* 2003). Studies on anguillid eels have demonstrated that they do have large home ranges, varying between 0.01 km² (Helfman *et al.* 1983) and 3.25 km² (Parker 1995), and Beguer-Pon *et al.* (2014) demonstrated via acoustic tracking that individuals of *A. rostrata* travelled distances of up to 418 km. The homing abilities of eels have also been tested (Tesch 1967; Deedler and Tesch 1970; Rossi *et al.* 1987). Tesch (1967) translocated 1538 marked *A. anguilla* 180 km from their point of capture and a small proportion eventually returned to their original capture sites. Tesch (1967) suggested eels may adopt this homing behaviour as a way to minimise the costs associated with adapting to an unfamiliar habitat. Seasonality of home ranges has been observed in *A. rostrata*, with individuals showing migrations from estuaries in summer to river refuges in winter (Thibault *et al.* 2007) and site fidelity has also been reported (Beguer-Pon et al. 2014).

2.8 Growth phase - foraging ecology

The foraging ecology of *A. anguilla* yellow eels shows great plasticity and encompasses a diverse diet (Sinha and Jones 1967; Tesch 2003). Diet is dependent upon the daily rhythm of an individual eel's behaviour and the annual abundance of prey. Typically, a greater foraging effort occurs during darkness and mostly in summer (Tesch 2003). Temporal studies on eel stomach fullness revealed that most were empty during the first hours of darkness but filled overnight, suggesting foraging behaviour was not as successful or did not occur during the first hours of darkness (Cairns 1942). Stomach fullness has also been reported to peak during spring (March-May), coinciding with the developmental period of many invertebrate larvae, before decreasing to minimal fullness in November (De Nie 1987).

Prey acquisition, during the yellow eel stage, is based primarily on olfactory cues rather than sight and studies on the oculomotor nerve of yellow eels have shown that eye use in yellow eels is most likely minimal (Tesch 2003). Whilst yellow eels generally have small eyes with a reduced ability, it has been shown that under the correct environmental conditions where light is reduced, eyes may be larger and better developed to aid in orientation (Grassi and Calandruccio 1897b; Tesch 2003). In comparison, to a relatively underused and underdeveloped sense of sight, eels have an extremely well developed olfactory system and during the yellow eel stage is the most extreme example of an olfactory animal found among fishes (Tesc, 2003). The olfactory surface area of eels is several times greater than many other freshwater fish species and the location of food has shown to be primarily related to osmotaxis (Tesch 1970).

Eel prey is directly related to eel size, as eels have relatively small jaws and so mainly ingest items that are suited to their body size (Tesch 2003). The diet of *A. anguilla* mostly consist of a vast array of benthic invertebrates, including molluscs, crustaceans and insect larvae (Sinha and Jones 1967). Some individuals have been shown scavenging on dead organisms (Coad 2005), whereas others are primarily piscivorous (Sinha and Jones 1967). Studies within Northern Ireland showed that the percentage of eels that ate fish increased markedly with eels size (Moriarty 1973). It has been noted that some individuals may even forage terrestrially, feeding on invertebrates out of the water (Coad 2005). An ability to forage terrestrially results from the eel's capacity to use both branchial and cutaneous modes of respiratory gas exchange (Tesch 2003).

Studies have highlighted phenotypic plasticity in regards to head width and diet, with wider headed individuals feeding primarily on fish and narrow-headed individuals on invertebrates (Proman and Reynolds 2000; Ide *et al.* 2011). The panmictic population structure of *A. anguilla* suggests the two head width morphotypes are a result of selective pressure during growth, rather than genetic variation (Ide *et al.* 2011) and this division of specialisation within a localised population would likely help reduce intraspecific competition. The vastly variable habitat use of the species, highlights their equally vast diets and the phenotypic plasticity shown for head width displays an ability to readily adapt to variable diets and/or habitats.

2.9 Growth phase - growth rate and lipid stores

The extent of *A. anguilla´*s growth stage is sex-dependent, varies considerably throughout its range and is reliant primarily upon water temperature and productivity (Tesch, 2003; Degani 2016). This is especially pronounced on a latitudinal scale, where eel growth is faster in warmer southern waters than colder northern waters and optimum growing temperatures seem to be around 25 - 26 °C (Boetius 1967). Examples of growth rates recorded in Europe include 14-46 mm/year in Ireland (Moriarty 1983), 48 mm/year in Germany (Berg 1985) and 53 mm/year in France (Panfili *et al.* 1994). In contrast, the mean lengths of mature silver eels appear larger in northern latitudes than southern or central latitudes (Tesch 2003), although mean lengths may differ between years. For silver males, mean lengths throughout their range, appear to be between 350 - 460 mm, with extremes of 290 and 540 mm (Tesch 2003), whilst female mean length are between 500 - 610 mm, with extremes of 380 and 1000 - 1500 mm (Gandolfi-Hornyold 1930; Tesch 2003).

Feeding has shown to cease during the final silver migratory stage of anguillid eels (Tesch 2003) and so to complete a successful spawning migration, eels must obtain sufficient lipid energy stores during their yellow growth stage (Larsson *et al.* 1990; Durif *et al.* 2005; Belpaire *et al.* 2009). The minimum lipid thresholds needed for a successful spawning migration were estimated using flume studies on silver eels and results varied between 13.5% (Palstra *et al*, 2007) and 28% (Larsson *et al.* 1990). Whilst lipid stores prove crucial to reproductive success, there seems to be no critical size or age for silvering and spawning migration to occur (Arai *et al.* 2006).

2.10 Silver phase - onset and duration of silvering

Pre-puberty silvering in eels describes a second partial metamorphosis during which yellow growth-stage eels undergo several marked changes in their morphology and physiology

(Bruijs and Durif 2009), preparing them for the transition between fresh and salt water (Durif *et al.* 2005). The morphological transformations include increased ocular size, segmentation of the lateral line, increased pectoral fin size, increased thickness of integument and a more pronounced counter-shading that is darkened dorsally and silver ventrally (Pankhurst 1982; Tesch 2003; Durif *et al.* 2005). Physiological transformations include gut regression, changes in the visual pigment ratios, alteration in swim bladder structure, alterations in the composition of skeletal muscle and the development of gonads (Durif *et al.* 2005; Balm *et al.* 2007).

Between the yellow and silver eels of *A. anguilla* there is a considerable overlap in size and age, demonstrating that eels do not initiate silvering at a fixed size or age (Arai *et al.* 2006) and the underlying mechanisms behind the onset of silvering or its various stages are not completely understood (Balm *et al.* 2007). Durif *et al.* (2005) used principal component analysis (PCA) to categorize the stages of silvering by means of several silvering parameters: body length, Fulton´s condition factor, Pankhurst´s (1982) ocular index, Durif *et al.* (2005) fin index, gonadotropin and growth hormone levels, gonadal mass, digestive tract mass and liver mass. This PCA analysis enabled silver eels to be categorized as either undifferentiated resident, male silver migrant or one of four female silvering stages (resident, pre-migrant, upstream migrant, downstream migrant) (Durif *et al.* 2005).

Whilst there has been steady progress within the artificial maturation of eels via hormonal treatment (Fontaine 1964; Boetius 1980), the environmental cues behind the onset of silvering and eel gametogenesis are relatively understudied (Burgerhout *et al.* 2019). In many well-documented cases, the reproductive development of teleost fish is linked to photoperiod and temperature, with photoperiod assumed to be the principal determinant (Pankhurst and Porter 2003) and it seems the same can likely be said for an eels silvering process. The triggering of smoltification in salmonids by photoperiod and temperature (Hoar 1988) can be directly compared to the anguillid silvering process because both teleost families undergo morphological and physiological adaptations for the move from fresh to marine waters (Durif and Elie 2008). These environmental cues synchronize the onset of puberty, ensuring that maturing individuals adapt for a simultaneous spawning migration. The onset of eel silvering seems to be initiated by a peak in growth hormone and begins in spring (Durif *et al.* 2009), however, studies suggest that the silvering process may be influenced over a much longer period with even December temperatures having an effect (Sandlund *et al.* 2017). Environmental conditions and food availability influence the important accumulation of muscular fat required for spawning success (Belpair *et al.* 2009; Sandlund *et al.* 2017) and the duration of the silvering process itself. Favourable conditions decrease the duration of the silvering process and lower August temperatures have shown to initiate an earlier migration

(Durif and Elie 2008). Of course, the vast range of latitudes in which *A. anguilla* exists means that the species is subjected to large variations in temperature throughout its range. Eels have demonstrated they migrate earlier in the colder northern waters of places such as Norway (Vøllestad *et al.* 1986). Northerly located eels have to migrate further than many of their southern counterparts and so an earlier northern migration, would likely compensate for the greater migration time required and synchronize the arrival of all eels at the spawning grounds (Durif and Elie 2008). These northern migrants, as well as experiencing colder temperatures throughout their growth, have shorter annual growth periods and so for silvering and sufficient accumulation of fat to occur, the silvering process must be initiated well before the short summer season (Sandlund *et al.* 2017). Therefore with a much shorter annual growth period, temperature variations may likely play a more integral part in the silvering process in northern sub-populations than their southern counterparts (Sandlund *et al.* 2017). The completion of silvering does not coincide with full maturation and instead, gonads are regressed when eels migrate to the ocean, only becoming fully developed when nearing their oceanic spawning ground (van Ginneken *et al.* 2005).

2.11 Silver phase - downstream migration

Once silvering has concluded, eels embark on a seaward spawning migration, generally in groups at specific times and under specific environmental cues (Tesch 2003). The biological process of silvering is timed to coincide with specific environmental conditions, namely conditions that result in increased discharge and low light (Okamura *et al.* 2002b; Bruijs and Durif 2009). Such conditions are prevalent in autumn to spring. As previously mentioned, the onset of silvering differs with latitude, as does the timing of migration, with silver eels migrating sooner at higher latitudes (Vøllestad *et al.* 1986), most likely correlated with the longer migration distances required. In Norway for example, migration may begin during July and peak in September/October (Vøllestad *et al.* 1986), whereas in France, migration possibly begins in September but does not peak until November (Durif and Elie 2008). Studies in Holland (Bruijs *et al* 2003) and Sweden (Westin 2003) reported migration peaks during autumn and also during spring. Migration is generally considered to be a continuous process, with eels moving downstream over a short period (Durif *et al.* 2003) and Bruijs *et al.* (2003) showed that on the River Meuse, 50% of silver eels migrated during just 20 days of the year. In contrast, migration may be discontinuous, with a stepwise migration occurring over a prolonged period (Durif *et al.* 2003; Stein *et al.* 2016). Distance from the sea has shown to affect the migration mechanism and Durif *et al.* (2003) suggested that multiple migratory seasons may be required for eels to fully migrate the length of very large rivers, with silver eels taking residency and regressing to their yellow growth phase between seasons. A telemetry study by Stein *et al.* (2016) showed that migration probability was related to the distance from the sea, with eels in a rivers upper reach less likely to complete migration than eels in the lower reach. In Denmark, Aarestrup *et al.* (2008) showed a portion of eels migrated downstream relatively fast but then were suspended for a period of residency in coastal marine waters before continuing with oceanic migration. The rate at which eels migrate downstream generally increases with proximity to the sea (Aarestrup *et al.* 2010) and although the effects of river discharge on the timing of migration are well documented, river discharge seems to have no observed effect on migration rate (Aarestrup *et al.* 2008; Béguer-Pon *et al.* 2018). As mentioned, silver eels may revert to their yellow continental stage on particularly long river migrations and this is also the case for eels whose escape is temporarily or permanently blocked (Durif *et al.* 2005). Eels may silver and de-silver periodically with the seasons in such cases and eels prevented from migrating may reach abnormally old ages as shown by a trapped individual that reached 55 years of age in Denmark (Walter 1910; Tesch 2003). This apparent migration flexibility could account for the considerable variations seen in the duration of migration and the speed at which it occurs (Aarestrup *et al.* 2008; Stein *et al.* 2016; Béguer-Pon *et al.* 2018).

Eels in their silver stage continue to exhibit distinct nocturnal behaviour and so downstream migration occurs predominantly during darkness, although darkened conditions relating to turbidity and cloud cover may initiate migration (Durif *et al.* 2003; Bruijs and Durif 2009). Migration usually ceases during the hours of daylight and high artificial light levels during the night may even form a barrier to migration (Vøllestad *et al.* 1994; Durif *et al.* 2003). As well as daylight, moonlight seems to have a marked effect on silver eel migration, working as an inhibiting factor during the full moon but stimulating migration during the darker lunar phases (Tesch 2003; Bruijs and Durif 2009). Whilst it is generally accepted that the light of the full moon inhibits migration, results differ between studies that have tried to determine which lunar phase provides the greatest stimulus. Some studies suggest that the greatest activity occurs during the third quarter lunar phase (Poole *et al.* 1990; Tesch 2003), others during the first quarter lunar phase (Haraldstad *et al.* 1985), whereas Durif and Elie (2008) concluded it was greatest during both the third quarter lunar phase and the dark of the new moon. The exact mechanisms behind the effects the moon has on migration have also been debated, with Boetius (1967) suggesting lunar phase rather than light provides the stimulating effect, whereas the majority of studies show moonlight as having the effect (Deedler 1954; Haraldstad *et al.* 1985; Vøllestad *et al.* 1986). It is now generally accepted that moonlight throughout an eels life triggers an endogenous circadian rhythm and even when moonlight is obstructed on a cloudy night, eel behaviour will cycle with the lunar phase, with peaks during times when moonlight should be low (Bruijs and Durif 2009). The movement of eels during these darker conditions is most likely associated with predator avoidance behaviour (Sandlund *et al.* 2017).

Atmospheric pressure has also be correlated with downstream silver migrations, where eels have been shown to move during the passage of atmospheric depressions (Hvidsten 1985). These atmospheric depressions bring with them microseismic oscillations and the stimulatory effects have been noted when occurring independently of other stimulating factors (Deedler 1954; Bruijs and Durif 2009).

Together with light levels, river discharge has been regarded as one of the most important environmental stimuli affecting silver eel migrations and in many cases, high river discharge has been correlated with increased silver eel migration (Lowe 1952; Tesch 1977, 2003). The utilisation of high flows would, in theory, make energetic sense, as eel swimming speeds would increase with river flow without an increase in energy expenditure. The rate of eel migration likely increases with increased discharge, however the effects that increased discharge has as an actual migration trigger remains uncertain (Bruijs and Durif 2009), with some studies showing little correlation. A limited correlation between flow and silver eel catch was observed over a study period of 12 years in the River Loire (Durif and Elie 2008). The fact that many habitats have no perceptible current, at least discounts discharge as the fundamental stimuli (Bruijs and Durif 2009). An aspect of discharge that may affect silver eel behaviour, other than increased flow and water level, is the associated turbidity it brings (Durif *et al.* 2003). Turbidity may occur regardless of discharge, caused by wind or precipitation. Turbidity due to high winds has been correlated with eel migration on the River Shannon (Cullen and McCarthy 2003) and turbidity due to rainfall on the Lough Derg (McGrath *et al.* 1979).

Whilst the annual timing of silver eel migration ensures individuals reach the spawning ground at the same time as their conspecifics, discrete downstream migrations influenced by environmental stimuli, result in migration occurring during darkness and in large numbers, most likely an adaption for predator avoidance (Sandlund *et al.* 2017).

2.12 Silver phase - oceanic migration

Escaping silver eels have been intercepted by fisheries in rivers and estuaries for hundreds of years and so the behaviour surrounding their seaward spawning migration is well studied (Tesch 2003). However, during the marine phase of their migration, they become very hard to study and even the recent developments in telemetry- based research have only just started to reveal the complex behaviours associated with estuarine navigation and their oceanic migration.

Silver eels of *A. anguilla* migrating out of the lower reaches of rivers have been shown using selective tidal stream transport (STST), utilising the ebbing tide for faster seaward transport in the North Sea (Tesch 1972, 2003; McCleave and Arnold 1999), however other studies show no such association (Davidsen *et al.* 2011). The utilisation of STST would benefit silver eels, reducing energy expenditure (Weihs 1978) and orientating migrating eels seawards (McCleave and Arnold 1999). In a study using anosmic and control silver eels of *A. rostrata*, control eels showed a much faster estuarine migration and greater use of STST than their anosmic conspecifics (Barbin *et al.* 1998). This suggests olfaction plays an integral part during the estuarine phase of the silver migration, using organic and inorganic chemical scents carried by tidal flows, to navigate out of estuaries (Barbin *et al.* 1998).

Whilst Aarestrup *et al.* (2008) found silver eels were suspended for a period of residency in coastal waters, fast seaward transport would likely be beneficial to silver eels, reducing potential mortality in predator rich coastal waters. Miniaturised pop-off archival satellite tags (PSAT) have shown eels commence diel vertical migrations (DVMs) during their oceanic spawning migration, with eels swimming at greater depths during the day (100 - 400 m) than at night (500 - 800 m) (Aarestrup *et al.* 2009; Righton *et al.* 2016). The upper depth of DVMs is influenced by the lunar cycle as shown for *A. japonica* with increased upper depths associated with increased lunar luminosity (Chow *et al.* 2015). It is speculated that by avoiding higher light levels, DVMs aid in predator avoidance (Aarestrup *et al.* 2009; Béguer-Pon *et al.* 2018). Other theories suggest the low pressures encountered during vertical migrations may initiate gonadal development (Jellyman and Tsukamoto 2002) or that such swimming has greater efficiency and is less energetically demanding (Watanabe *et al.* 2016). The silvering metamorphosis prepares eels for such deep migrations, with greatly increased numbers of photosensitive rod cells, creating vision better suited to the deep oceanic conditions (Pankhurst 1982; Tesch 2003). During the first coastal phase of their oceanic migration, eels initially follow the continental shelf, swimming against prevailing currents (Aarestrup *et al.* 2009; Béguer-Pon *et al.* 2015a) and probably using coastal salinity and temperature fronts as navigation (Béguer-Pon *et al.* 2015a). During the second deep oceanic phase of migration, eels leave the continental shelf, swimming in open oceanic waters in a relatively straight line with daily horizontal speeds varying from 2 - 51 km/day (Aarestrup *et al.* 2009; Righton *et al.* 2016; Béguer-Pon *et al.* 2018). This variation in speeds suggests that some eels may reach the spawning grounds during peak spawning, believed to occur in April, whereas others may arrive the following year (Righton *et al.* 2016). Predation of eels by other fish species and marine mammals (Aarestrup *et al.* 2009; Righton *et al.* 2016) during oceanic migration has been documented. It is not yet known exactly how eels navigate this deep oceanic phase, but a lack of horizontal thermohaline gradients suggests navigation occurs via inherited compass direction or a geomagnetic map (Durif *et al.* 2013; Béguer-Pon *et al.*, 2018). For *A. anguilla*, individuals have been tracked from continental Europe in a westerly direction as far as the Azores Archipelago (Righton *et al.* 2016), however migratory behaviour during the further 2000 km of migration to the proposed spawning site of the Sargasso Sea, is yet unknown.

2.13 Threats and a declining population

A. anguilla is heavily exploited throughout almost the entirety of its endemic range, in almost all of Europe, some North and West African countries. Eel catches resulted in 1.5% of total inland water landings in 2010, reduced from 7.5% in 1950 (FAO 2014) and high demand makes the catch worth approximately 5 - 30% of the total landings (FAO 2014; Dekker and Beaulaton 2016). The exploitation of *A. anguilla* has been documented as far back as the year 1085 (Anonymous 1086) and presently the eel is targeted at multiples stages in its complex life stages. Fisheries of *A. anguilla* target the recruiting glass eels, yellow growth stage eels and seaward migrating silver eels (ICES WGEEL 2012). This targeting exploitation, together with various other anthropogenic, biotic and environmental pressures has reduced *A. anguilla* stocks drastically (Jacoby and Gollock 2014). Over the last 45 years, this has resulted in estimated declines of 90-95% in glass eel recruitment and greater than 50% in yellow and silver eel numbers (ICES WGEEL 2012). Large knowledge gaps exist regarding *A. anguilla*, including the relationships between its multiple life stages, so assessing the status of the population has been difficult (Dekker *et al.* 2007). The population is believed to be below safe biological limits and is therefore listed as critically endangered (Jacoby and Gollock 2014). In 2007, in addition to its critically endangered listing, *A. anguilla* was included in the CITES Appendix II to ensure its trade would be controlled to a sustainable level (CITES, 2007). During the same year, Eel Regulations (EC Regulation 1100/2007) were implemented in the EU Member States to reduce anthropogenic mortalities to increase silver eel escapement to estimated natural levels of 40% and promote stock recovery (Jacoby and Gollock 2014). Reductions of silver fisheries during 2009 was perhaps a factor promoting 1.5 - 10% increases seen in glass eel recruitment from 2010 - 2012, however, such variations may be a result of natural recruitment fluctuations and the adult stock will likely continue to suffer from the vast declines observed since the 1980s (ICES WGEEL, 2012; (Jacoby and Gollock 2014)).

In addition to overexploitation, some of the most prevalent anthropogenic threats to eels include pollution, habitat degradation/loss and the manipulation of waterways (Dekker 2003; ICES WGEEL, 2012). During the continental growth phase, eels are subjected to a plethora of lipophilic pollutants, that originate primarily from domestic, industrial, and agricultural practices (Jacoby and Gollock 2014)). Eels fast during their transatlantic spawning migration (Boetius, 1980) and so in preparation, eels replace water and proteins with increased quantities of lipid energy reserves (Degani *et al.* 1986), reserves that are metabolised on route to the spawning grounds (Robinet and Feunteun 2002). Some pollutants, such as the insecticide fenitrothion (Sancho *et al.* 1998), may directly decrease an eel's ability to store lipids and therefore decrease the chance of successful spawning migration. Other pollutants, such as PCBs (polychlorobiphenyls) and PAHs (polycyclic aromatic hydrocarbons; Hontela *et al.* 1995; Robinet and Feunteun 2002) accumulate in eel fatty tissues and during migration, the metabolisation of lipids release these persistent xenobiotics back into circulation, especially into developing gonadal tissues (Robinet and Feunteun 2002). The accumulation of such pollutants in the gonads can reduce spawning success by preventing sexual maturation and damaging gametes (Geeraerts and Belpaire 2010).

A growing concern to eel success is the manipulation of the natural waterways that provide habitat for resident yellow eels and migration pathways for recruiting juvenile and escaping silver eels (Jacoby and Gollock 2014). Water management and Hydropower schemes have shown high mortality rates as a result of screen impingement and turbine entrainment (MacNamara and McCarthy 2014). The elongate anguillid form makes eels especially vulnerable during turbine passage and studies have shown mortalities of up to 100% occur during the turbine passage of silver eels (Dumont 2006). Dams, weirs and other barriers have significantly decreased longitudinal connectivity (Egg *et al.* 2017), preventing upstream and downstream migration altogether in some cases (Jacoby and Gollock 2014). Van der Meer (2012) reported a total of 24,350 hydropower plants in Europe and despite implemented technical standards, including ‘eel-friendly' pumps, many hydropower plants still present an impassable migration barrier (Egg *et al.* 2017). As well as technical modifications (Winter *et al.* 2006), operational modifications may allow the passage of silver eels during critical migration windows (Bolland *et al.* 2019). Whilst immediate impacts resulting from anthropogenic activities can be witnessed, such as the case of eel entrainment in hydropower plants, impacts may also be occurring on a more gradual scale. Such is the case with changing oceanic conditions concerning global warming (Bonhommeau *et al.* 2008). The survival of early-stage eel leptocephali is strongly correlated with the availability of oceanic food resources, and changes in ocean climate over the last 40 years have been attributed to changes in food availability (Miller *et al.* 2009) and possibly the decline of eel populations (Bonhommeau *et al.* 2008). Indirect anthropogenic effects associated with the decline of the *A. anguilla* population include disease transmission, usually facilitated by an intermediate parasite and transmitted via non-native introductions, from wild to cultured eels or vice versa (Barker and Cone 2000; Peeler *et al.* 2011). The parasitic swimbladder nematode *Anguillicoloides crassus* is of particular concern, endemic to East Asia but transmitted from its native host, *A. japonica*, to both *A. anguilla* and *A. rostrata* (Kirk 2003). The parasite greatly impairs swimbladder function and in extreme cases, swim bladders may haemorrhage, fill with fluid and result in death, as seen in mass eel mortalities in Lake Balaton, Hungary (Molnár *et al.* 1991). Although the effects of *A. crassus* have been witnessed during the continental eel stage, it is suggested that swim bladder loading of the parasite, may also affect the silver eel spawning migration through reducing migration speeds and inhibiting diel vertical migrations (Sjöberg *et al.* 2009).

3. Materials and methods

3.1 Study area

The Azores archipelago comprises nine islands of varying sizes, that are divided into Western, Central and Eastern sub-groups. Four of these nine islands (São Miguel, Flores, Santa Maria and Terceira), representing at least one island from each of the three sub-groups, were sampled in the current study during multiple expeditions (Fig. 2). Within this section, Materials and Methods, these four islands have been ordered from least to greatest amount of fishing effort per island.

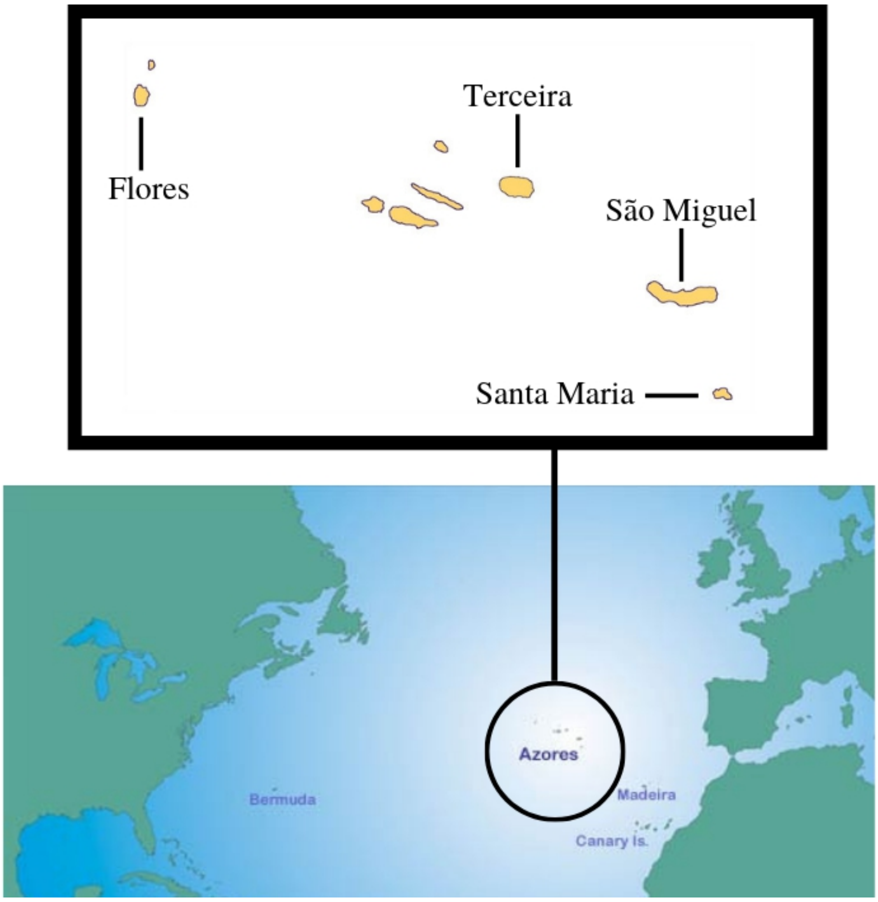


Fig. 2. Location of the Azores Archipelago and the four sampled islands. Adapted from Geekyexplorer (2008).

In regards to bathymetry, the Azores mid-Atlantic location sets it aside from continental Europe as it lacks Europe´s continental shelf. Instead, the archipelago’s coastal waters reach depths of over 1000 metres just a few kilometres from its shores.

3.1.1 Climate

The climate of the Azores can be described as subtropical oceanic. Summer temperatures average between 24 - 26°C during the day and 17 - 18°C at night whilst winter temperatures average 17 - 18°C and 11 - 12°C for day and night respectively (Climatestotravel 2019). Precipitation increases from < 1000 mm/year to > 1400 mm/year from East to West within the islands of the archipelago, with the highest annual precipitation found in the most westerly group of islands (Flores and Corvo islands). The majority of this precipitation occurs from September - March, and levels normally peak from November - January (Hydrometeorological Network of Azores, 2019). Throughout the rest of the year, precipitation occurs on average 5 - 7 days per month throughout the islands. Island comparisons of precipitation for 2018 can be seen in Fig. 3.

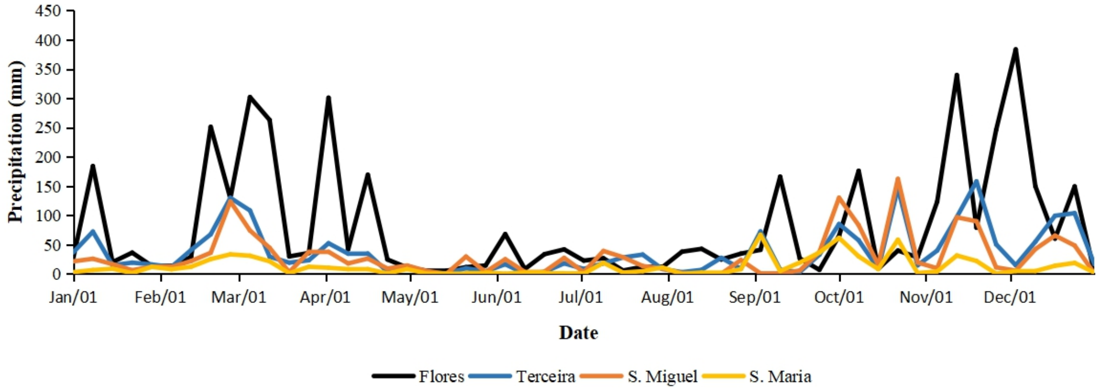


Fig. 3. Cumulative weekly rainfall during 2018 on each of the four islands sampled. Created with data downloaded from the Hydrometeorological Network of Azores (2019).

3.1.2 River and lake systems of the Azores

The Azorean islands are relatively small in global terms, the largest being São Miguel and smallest Corvo with areas of 759 km² and 17 km², respectively. The maximum altitude varies from 398 - 2351 m between islands and all islands, bar Graciosa, have a maximum altitude above 500 m (Visitazores 2019). Therefore, in terms of altitude and surface area, the islands have relatively steep profiles and small river basins. Rivers on the island are typified as "flashy", whereupon a short lag time exists between precipitation and peak discharge and an equally short lag time between peak discharge and the return to base flow conditions. This flashy nature can be demonstrated with a flow duration curve for the studies most intensively sampled river, Ribeira Quente, where Q95 is 24% of the Qmean (Fig. 4).

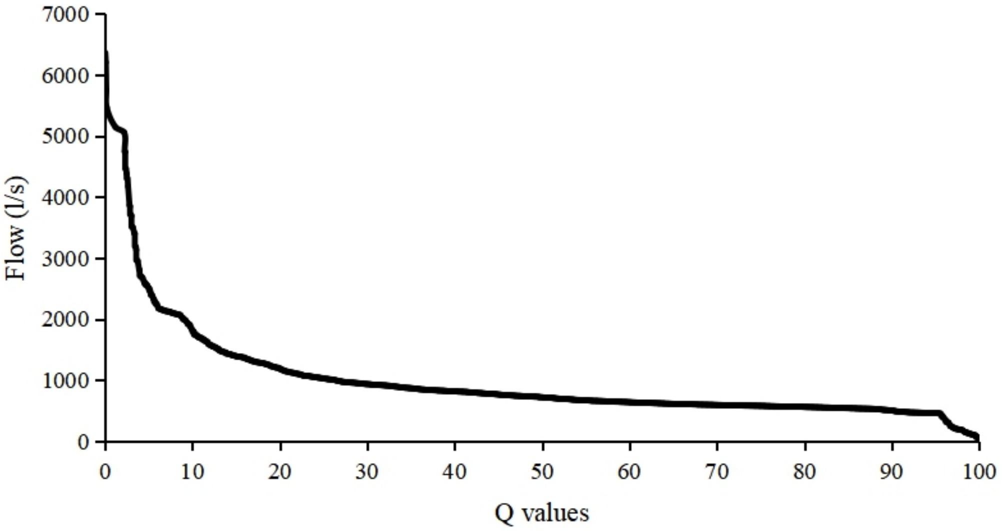


Fig. 4. Flow duration curve for Ribeira Quente on São Miguel, during the last five years (2014 - 2018). Flow is measured at a gauging weir situated approximately one third of the way down the river system (Lat: 37.766; Long: -25.290). Created with data downloaded from the Hydrometeorological Network of Azores (2019).

These short flashy rivers have typically gouged out deep and reasonably straight channels, often intercepted by multiple cascades depending on the underlying geology and these cascades are most prevalent near the rivers source and coastal discharge. Vertical rather than lateral erosion dominates Azorean river systems, with river channels rarely exceeding 3 m in width. Large quantities of igneous pumice and vegetation are transported downstream from the upper reaches of rivers and the buoyant nature of this material means it is readily transported to the ocean. Although surface runoff is rapid, the underlying bedrock of the islands is dominated by permeable, igneous geology allowing some water to percolate within. The sub-tropical oceanic climate of the Azores means precipitation does occur all year round and in the winter this precipitation is persistent, whilst in the summer months, it is sporadic, with rivers reduced to little or no flow.

The Azores archipelago has turmoil volcanic origins, currently evident in the archipelagos volcanic crater-marked surface. The majority of larger craters, mostly at high altitude, are filled with water, forming isolated unconnected lakes. Whilst a few lakes do have outflows of some type, water levels within them are primarily maintained via subterranean percolation through the porous volcanic bedrock.

3.2 Data collection

All data for this MSc thesis have been obtained during multiple scoping trips of random sampling during 2017 - 2018 and a longer consistent autumnal sampling period during 2018.

Sampling was conducted using primarily three different types of passive fishing equipment: fyke nets, apollo traps, and concertina baited traps. Equipment type and quantity were of limited availability on the Azores and its selection was based upon ease of transportation and deployment within the field, with the specific equipment used at each sampling location being dependent upon habitat and in the case of freshwater lakes, site accessibility. Minimum captured eel size was determined by the analogous 8 - 10 mm mesh of all trap types and no traps restricted the capture of eels at the maximum size for the species.

Within River systems and the single brackish lake sampled, an optimal sampling strategy was employed, whereupon equipment use ensured sites were sampled optimally, in an attempt to catch the majority, if not all eels of the minimum size. For this optimal fishing strategy, fyke nets were often used in combination with either/both apollo and concertina baited traps. Fyke nets were deployed in all areas where a calculated positioning could intercept travelling eels and successfully guide them into the trap portion of the net. Apollo and concertina baited traps were deployed in all deeper portions of a site where fyke nets could not be deployed in a calculated fashion. This optimal fishing strategy was used at all river systems and the single brackish lake sampled as they were entirely accessible. In comparison, the sampling of freshwater lakes was restricted by minimal site accessibility, to only small proportions of each water body.

3.2.1 Passive fishing gear

The fyke net (Fig. 5) is a fish trap most often used in the shallow waters of tidal zones or rivers.

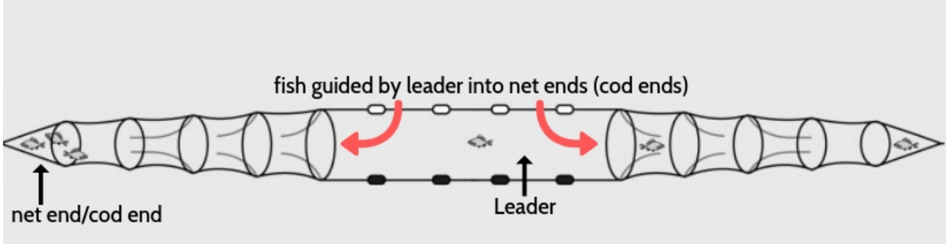


Fig. 5. A double-ended fyke net with connecting leading. Adapted from Duluthfishnet (2019).

All fyke nets used were of a double-ended type, consisting of two cone-shaped netting bags (net-end) connected via a length of netting (leader) and although total fyke size differed, all mesh netting was 8 - 10 mm. Fyke nets purposefully guided eels, via the leader, into the net-ends and placement/fyke-size ensured maximum efficiency at each site. Nets are fixed on the substrate with rope and weights and the leader guides fish towards one of two trapping bag ends (cod ends). Nets were set in various ways in accordance with river flow, structure and expected eel movement, with multiple nets often fixed together in ‘chains’ to sample a larger area. Within relatively fast-flowing rivers, nets were ideally set at a 45° angle to the river bank within its faster flowing deeper edge, whereas in slower moving water fyke nets were also set mid-river (parallel to the bank) and also perpendicular to the river bank at a 90° angle. In cascade pools, fyke nets were ideally set parallel and against the upstream cascade wall, where subsurface overhangs were common, but never directly underneath the cascading water. In an attempt to catch all migrating silver eels, in Ribeira Grande (Flores Island) and Ribeira Quente (São Miguel Island), two fyke nets from opposing river banks were set in the lower reach, both at a 45° angle with downstream cod ends attached together mid-river to effectively create a complete net barrier to all eels migrating towards the ocean. During sampling, it was learned and later implemented, that fyke nets should ideally be attached to an immovable object via strong cordage at only one cod end, to survive being swept away or ripped apart during commonly occurring high flows. To ensure comprehensive sampling in brackish and freshwater bodies, fyke nets were deployed next to outfalls, along the margins and within deeper mid-water areas.

Concertina baited traps (Fig. 6) are collapsible fish traps comprising of a metal spring frame covered by 8 - 10 mm mesh netting and with two conical net entrances.

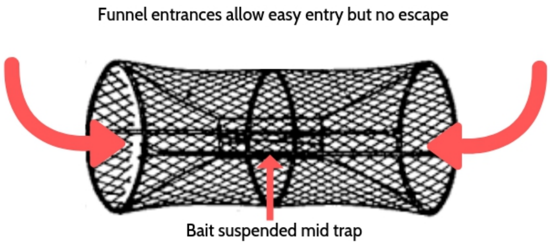


Fig. 6. Double concertina baited trap. Adapted from Westmarine (2009).

Suspended bait (approximately 40 g of fish of the family *Clupeidae*) purposefully attracted (guided) eels into one of two entrance-only openings preventing escape once inside the trap. Traps were weighted and set on the substrate within deeper cascade pools/river sections where fyke placement was difficult and could not be set optimally. Concertina traps were always attached firmly to the river bank with cordage to prevent trap loss during high flows.

An apollo trap is a rigid fish trap (Fig. 7), attracting fish via bait through a series of entrances that allow entry but prevent escape.

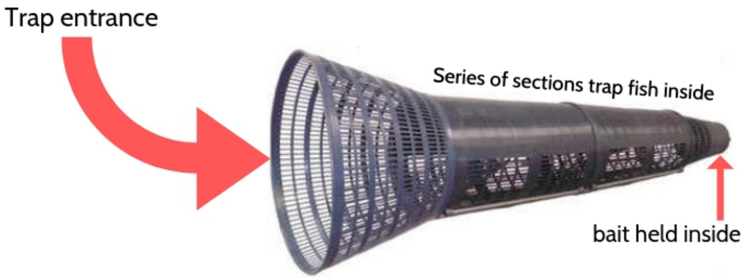


Fig. 7. Apollo trap design. Adapted from Architecturalstudio (2009)

Weighted using steel rods and set on the river substrate, the plastic Apollo traps used in the Azores were approximately 1.5 metres in length, had a mesh size of 8 - 10 mm and were baited with approximately 40 g of fish from the Clupeidae family. This bait purposefully attracted (guided) eels into the entrance-only opening and preventing escape once inside the trap.The use of Apollo traps was limited to deep cascade pools during scoping trips on São Miguel and Flores Islands.

3.2.2 Active fishing gear

A fine-mesh (0.5 mm) pond net (Fig. 8) was actively used in a sweeping motion to catch eels in aqueous and riparian vegetation during daylight and in combination with a battery-powered torch to find and catch active eels during night.

Fig. 8. Fine-mesh pond net (NHBS 2019).

3.3 Sampling structure

Passive fishing gear was deployed in water bodies during daylight and set to passively fish during the darkness of night when eels are typically most active, with the number of fishing units (net-ends) per site varying between 1 - 14 net-ends/24 hrs/site. Gear fished for approximately 24 hours and was emptied daily. Total body length (mm), total body weight and silvering morphometric data of ocular diameter (mm) (Pankhurst 1982) and pectoral fin length (mm) (Durif *et al.* 2005) were collected for all eels where possible. Notes were also taken on the visual inspection of eels focusing on the silvering characteristics of lateral line segmentation and counter-shading (Pankhurst 1982).

3.3.1 Geographical distribution of eels across the Azores Archipelago

To assess spatial variations in abundance and size structure of eels and the existence of migratory silver-stage individuals in the Azores Archipelago, several scoping trips of random sampling were performed at four (Terceira, Santa Maria, Flores and São Miguel) of the nine Azorean islands for periods of between one and ten days during 2017 - 2018. An intensive period of autumnal sampling was also performed at São Miguel Island for 44 nights in 2018.

All sampling on Terceira island was performed by Dr Adam Piper (ZSL) and Dr Matt Gollock (ZSL) using 11 double-ended fyke nets per night over four consecutive nights, giving a total 44 net-ends/24 hrs over the entire sampling period.

Santa Maria Island was sampled during two separate scoping trips, firstly by Dr Adam Piper and Dr Ros Wright (Environment Agency) on 21/6/2018 and secondly by Dr Ros Wright, George Cowan (UoH), and Sara Rodríguez Ramallo (UoH) on 27 - 29/5/2019. Fyke nets and concertina baited traps were deployed at Santa Maria Island over a combined four nights totaling 22 net-ends/24 hrs.

Flores Island was sampled during two separate scoping trips, firstly by Andy Don (Environment Agency) and Randolph Velterop (Natural England) over four nights (9 - 16/12/2017) and secondly by Andy Don, Randolph Velterop, George Cowan and Sara Rodríguez Ramallo for 10 consecutive nights (8 - 17/10/2018). Fyke nets, concertina baited traps, and apollo traps were used during both scoping trips totaling 39 net-ends/24 hrs and 182 net-ends/24 hrs, respectively. Multiple storms and daily precipitation affected gear deployment during the second Flores Island scoping trip, with regular high flows reducing the possible fishing effort.

São Miguel Island was sampled by Dr Ros Wright during an initial scoping trip of 4 nights, between 9 - 16/12/2017, totaled an effort of 41 net-ends/24 hrs. A second intensive sampling period of 44 nights, between 28/9/2018 and 6/12/2018, was conducted by George Cowan, Sara Rodríguez Ramallo, Dr Ros Wright, Dr Adam Piper, Andy Don and Randolph Velterop, totaling 1014 net-ends/24 hrs. Fyke nets, concertina baited traps, pond nets and apollo traps were used throughout both trips.

3.3.2 Intra-island spatial variations in eels of São Miguel Island

Of the nine islands, São Miguel Island was chosen for a study of intra-island variations in size structure and abundance. Selection was based on São Miguel Island´s large size, apparent habitat diversity and a great number of river/lake systems, with sampling focused on eleven river systems and two lake systems. River systems were sampled with fyke nets, concertina baited traps, pond nets and apollo traps, totaling 686 net-ends/24 hrs of fishing effort. Lake systems were sampled using fyke nets totaling 328 net-ends/24 hrs of effort. Chains of double-ended fykes were deployed in the two lakes Lagoa das Sete Cidades and Lagoa das Furnas for 5 and 21 nights respectively. Additionally, a single fyke net-end completely covered escapement from the single outflow of Lagoa das Furnas for 39 consecutive nights and was emptied every 1 - 2 days.

During July 2018 and before sampling, São Miguel Island suffered a drought. This greatly affected the coastal portion of two north coast rivers, Ribeira do Guilherme and Site 11, exhausting them of any water and completely isolating pools. Many of these smaller pools subsequently dried, resulting in the death of many eels. and several live eels were relocated to larger pools with favourable conditions. Length data was collected from all eels. No passive sampling techniques were used at Site 11.

3.3.3 Inter-watercourse spatial variations in eels of two river systems (Ribiera Quente and Povoação)

Sampling in two of São Miguel´s largest river systems, Ribiera Quente and Povoação, used fyke nets, concertina baited traps, pond nets and apollo traps, totaled 445 net-ends/24 hrs and 103 net-ends/24 hrs, respectively. The river systems contrasted in structure and provided a comparison of spatial variations in abundance and size structure between two river systems.

3.3.4 Intra-watercourse spatial variations in eels of a mainstem river (Ribiera Quente)

As São Miguel´s longest river, Ribeira Quente was chosen for spatial variations in abundance and size structure along its three reaches (upper, middle and lower). Fyke nets and concertina baited traps were used totaling 445 net-ends/24 hrs.

3.3.5 Intra-watercourse spatial variations in eels of a mainstem river compared to its tributary (Povoação)

In comparison to other river systems of São Miguel, the lower reach of the Povoação river system possessed a much greater number of tributary rivers that fed into its mainstem rivers. Therefore, this river system was chosen to explore spatial variation in abundance and size structure of a tributary river in comparison to a mainstem river. Fyke nets and concertina baited traps were used totaling 103 net-ends/24 hrs.

3.3.6 Temporal variations in silver eel abundance in the Ribeira Quente, the largest river on São Miguel Island

The river Ribeira Quente was used as an index river to assess temporal variations in silver eel abundance and possible environmental factors that may influence their abundance, enabling the first estimation in timing of silver eel migration in the Azores. Efforts were made to sample nightly on each consecutive night over a full lunar cycle from 29/11/2018 - 3/12/2018. However, several high flows on Ribeira Quente during this period proved detrimental to fishing gear and inhibited deployment, resulting in periods of no sampling during 22 - 28/10/2018, 17 - 19/11/2018 and 22 - 26/11/2018. Fyke nets and concertina baited traps were used for sampling, totaling 445 net-ends/24 hrs.

3.4 River gradient profiles

Data for river gradients and location of barriers were created for this study. For Ribeira Quente and Povoação, the systems were mapped as accurately as possible using a Garmin GPS, whilst other systems were mapped using information from Google (2019).

3.5 Division of sites within systems

Some systems were sampled at only a single location, whilst others were sampled at various locations. Multiple sampling locations within a system were grouped into specific sites: if they were separated from other sampling locations by an upstream barrier (> 2 m) likely impassable to yellow eels, were located on the same river type (e.g. mainstem or tributary), or were of proximity with one another and ≥ 1 km from other sites. For intra-island spatial analyses, watercourses were divided into two groups, sites located on mainstem rivers or sites located on all other river types. For intra-watercourse spatial variations, the Ribeira Quente was divided into three reaches and the Povoação river system was divided into sites at mianstem rivers and sites at a tributary.

3.6 Detailed topography of islands and their sites

3.6.1 Terceira Island

Belonging to the Azores Central Group, Terceira is the third-largest island of the archipelago with a total surface area of 403 km² and a maximum altitude of 1021 metres. Contrasting to all other islands in the study, only a single system was sampled on the eastern coast of Terceira Island (Fig. 9). Whilst one other potential river systems were investigated, they were deemed shallow spate systems and therefore unsuitable for eel habitation. The single system sampled was Lago da Parque do Paul, a brackish lake (≈ 2.5 km²) with connectivity to the sea via culverts. Both riparian and aquatic plants provided partial coverage and the main body of the lake had a clay bottom whilst tributary channels were bottomed by deep anoxic silt.

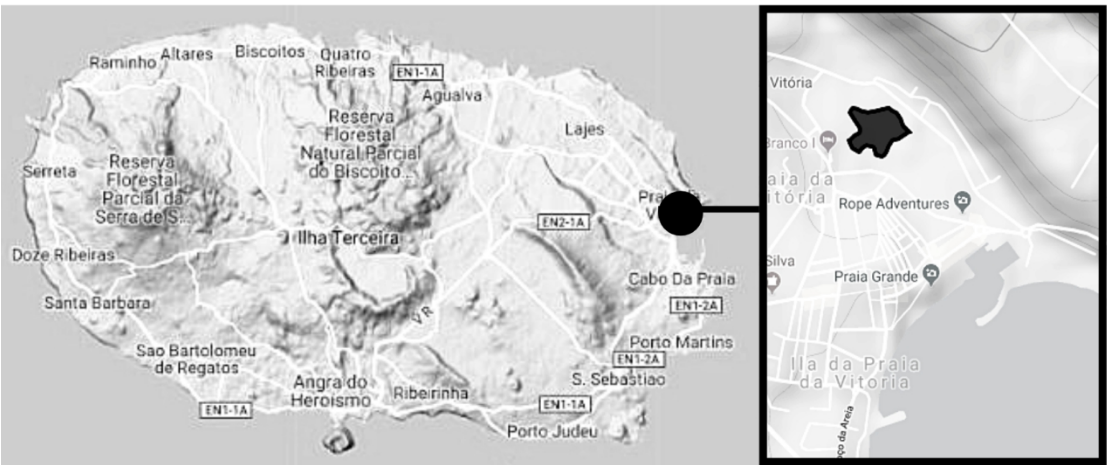


Fig. 9. Topographical map of Terceira Island. The location of Lago da Parque do Paul sampling site, at Latitude (Lat): 38.735° and Longitude (Long): -27.061, is identified by a black circular marker and the water body is shown in greater detail by the black polygon. Adapted maps downloaded from Google (2019).

3.6.2 Santa Maria Island

Belonging to the Azores Eastern Group, Santa Maria Island is the archipelagos seventh-largest Island, possessing a total surface area of 97 km² and a maximum altitude of 587 metres. Six river systems believed suitable to eel habitation were investigated during two scoping trips. Ribeira do Lemos, a narrow and shallow river situated on the northwestern shore, showed no presence of eels and so no sampling occurred. A single eel was observed during daylight in a single nameless easterly located cascade pool (≈20 m²) but ocean-only access halted further sampling. Eels were observed during daylight in all four of the remaining systems investigated and reasonable accessibility permitted sampling to occur. The locations of these systems are shown in Fig.10.

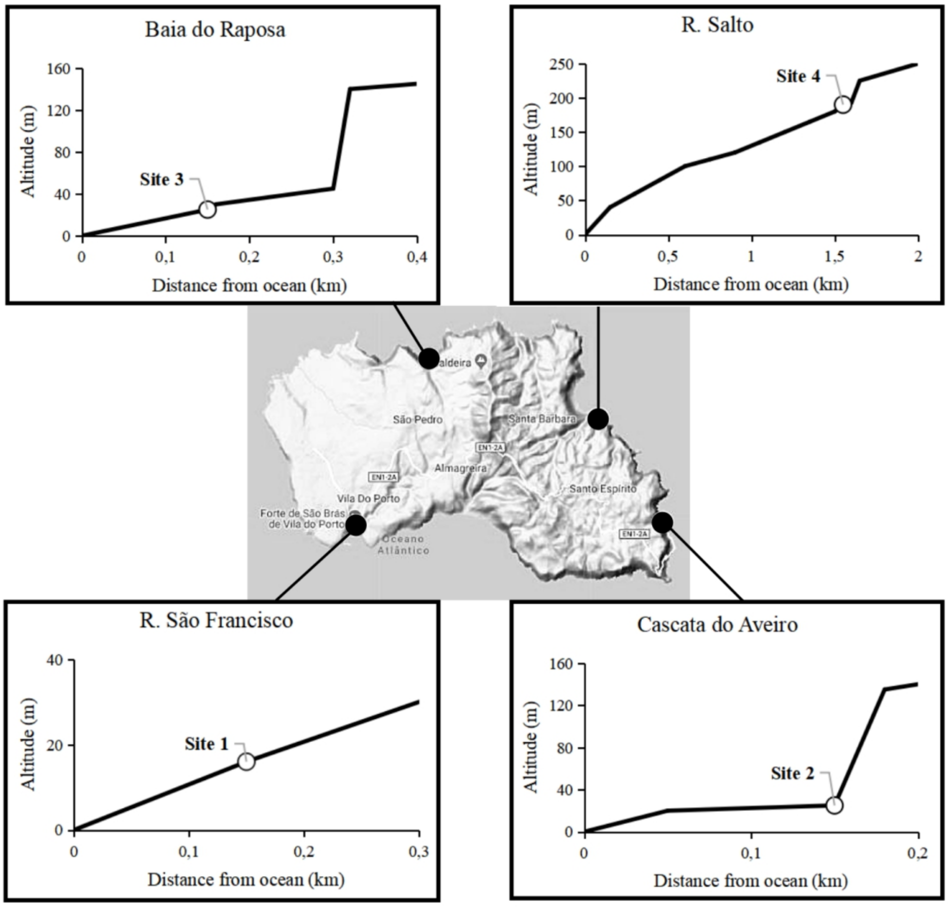


Fig. 10. Topographical map of Santa Maria Island. River systems studied are indicated by black circular markers, combined with charts plotting their gradient and sampling site locations. Adapted maps downloaded from Google (2019).

The stream, Ribeira de São Francisco bordering the southerly town of Vila do Porto consisted of numerous small pools and a channel approximately 1 metre in width. Sampling occurred in its lowest pools (Site 1 [Lat: 36.947; Long: -25.145]) , which are exposed to saltwater during ocean storm surges and had a high proportion of coverage by both aquatic and riparian vegetation.

Cascata do Aveiro (Site 2 [Lat: 36.948; Long: -25.021]), a large cascade pool (≈ 400 m²) situated on the east coast has seasonal ocean connectivity, a silty bed, no plant coverage and large undercut sections below the upstream wall. The cascade upstream of Site 2 was 100 metres in height and likely proves impassable to juvenile eels migrating upstream.

Site 3 (Lat: 37.003; Long: -25.116), a cascade pool (≈ 30 m²) located in Baia do Raposa on the north coast and backed by an upstream cascade of 6 metres had ocean connectivity and whilst sampling could occur, larger upstream cascade pools proved inaccessible.

The easterly located Ribeira do Salto (Site 4 [Lat: 36.977; Long: -25.061]) comprised a river, intersected by a 40 m cascade (Cascata Cai-Água) and associated cascade pool ≈ 1.6 km from its coastal discharge. The river was approximately 2 metres in width, with a gradual gradient, a multitude of large pools, a layer of dense decaying organic matter on its bed and a high proportion of coverage by terrestrial, riparian and aquatic vegetation. The pool below Cascata Cai-Água covered an area of ≈ 400 m^2, had coverage by only aquatic vegetation and a layer of dense decaying organic matter at its bottom.

3.6.3 Flores Island

Belonging to the Azores Western Group, Flores is the most westerly island within the entire archipelago, the sixth-largest Island with a surface area totaling 143 km^2 and a maximum altitude of 915 metres. During two scoping trips, sampling focused on the western and southeastern reaches of Flores, in three river systems (Ribeira Grande, Ribeira Funda, and Poço do Bacalhau), two freshwater lakes (Lagoa Rasa and Poço da Ribeira do Ferreiro) and the Fazenda artificial reservoir. These particular locations were chosen due to a historical presence of eels and the relative proximity of the many systems together, however, dense vegetation and limited infrastructure restricted access to river systems. The locations and gradients of the sampled rivers on Flores Island are shown in Fig.11.

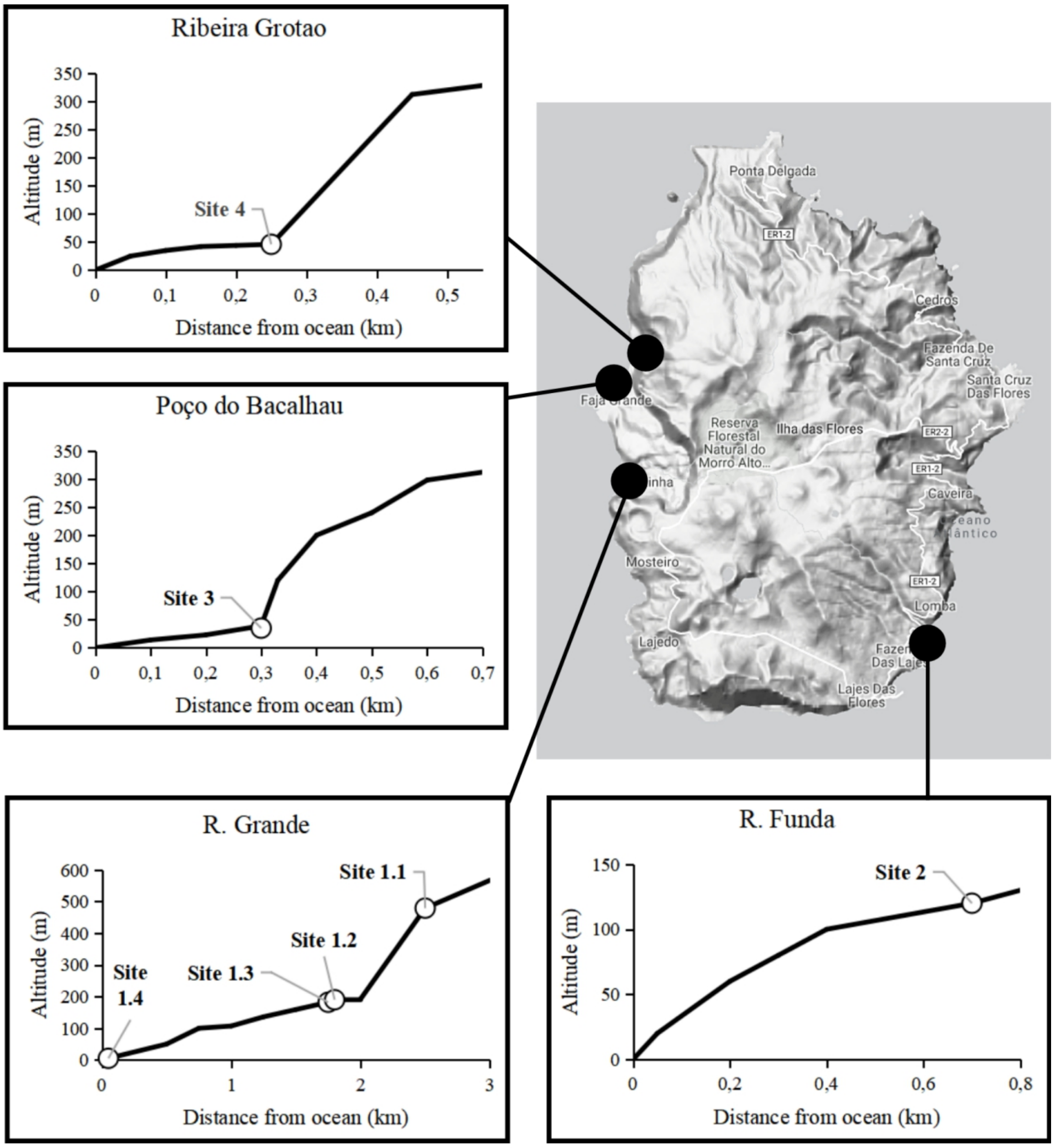
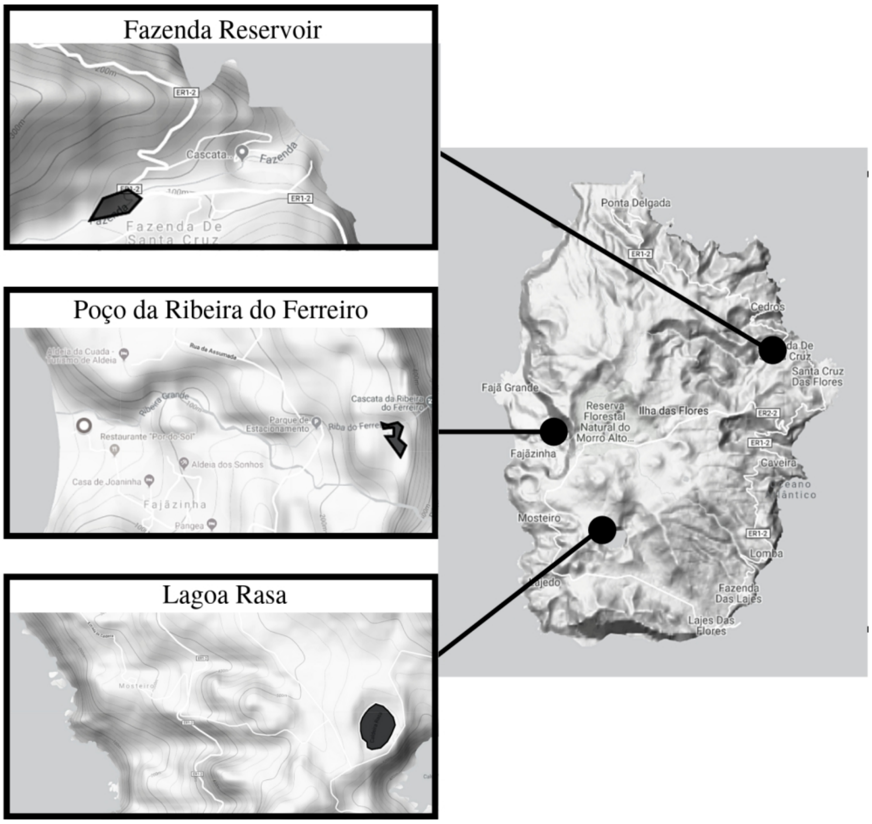


Fig. 11. Topographical map of Flores Island. River systems studied are indicated by black circular markers, combined with charts plotting their gradient and sampling site locations. Adapted maps downloaded from Google (2019).

Ribeira Grande was surrounded by dense terrestrial vegetation, comprised a steep rocky central channel (≈ 3 - 4 metres wide), intersected by a 300m high cascade 3km from its coastal discharge. Riverside access to this central channel was only possible at its coastal discharge (Site 1.4 [Lat: 39.438; Long: -31.1259]) and approximately 2km upstream (Site 1.3 [Lat: 39.435; Long: -31.244]). Many tributaries fed into Ribeira Grande but the majority were unreachable due to dense vegetation. One accessible feeder channel, Fajazinha mill tributary (Site 1.2 [Lat: 39.434; Long: -31.245]) fed into Ribeira Grande from slightly flooded pasture through a series of flooded ditches. The flow was partly controlled by Fajazinha Mill, a corn-grinding mill in regular use and habitat was typified by masses of riparian and aquatic plants, with a bed covered in a dense layer of decaying plant matter (≈ 20 cm deep). Additionally, another feeder tributary was sampled (Site 1.1), at a height parallel with the top of the 300 m high cascade that intersected Ribeira Grande´s mainstem river.

Ribeira Funda (Site 2 [Lat: 39.401; Long: -31.166]) comprised a single central channel with no substantial tributaries along the 1.5 km of its accessible length. Lined with dense terrestrial and riparian vegetation, the steep rocky central channel (≈ 3 - 4 metres wide) included multiple derelict water mill structures and cascade pools. Local reports suggested Ribeira Funda historically supported high densities and large individuals of eels.

Poço do Bacalhau (Site 3 [Lat: 39.458; Long: -31.255]) and Ribeira Grotao (Site 4 [Lat: 39.466; Long: -31.257]) differ from the other previously mentioned sites sampled on Flores Island as they both comprise a large pool backed by a cascade of approximately 300 m in height, less than 1 km from their coastal discharges. These upstream cascades likely form an impassable barrier to glass eels migrating upstream and therefore no sampling occurred above these cascades. Both had a relatively low flow with seasonal ocean connectivity, some terrestrial vegetation coverage, and a fine silt bottom. The locations and surface shape of the sampled freshwater bodies on Flores Island are shown in Fig. 12.



Fazenda Reservoir

Poço da Ribeira do Ferreiro

Lagoa Rasa

Fig. 12. Topographical map of Flores Island. The location of Freshwater bodies studied are indicated by black circular markers and their surface area is shown in greater detail by a black polygon. Adapted maps downloaded from Google (2019).

Lagoa Rasa (Site 5 [Lat: 39.409; Long: -31.225]), a lake situated 2.7 km inland from the southwesterly coast, at an altitude of > 500 m, was highly isolated, with only minimal terrestrial vegetation around its borders and with no obvious connectivity to any river system. Rather than a surface outflow, Lagoa Rasa´s water levels are maintained via evaporation and subterranean percolation through volcanic bedrock.

The lake Poço da Ribeira do Ferreiro (Site 6 [Lat: 39.437; Long: -31.239]) is located at an altitude of 263 m, situated 1.8 km inland from the islands western coastline and is situated within the drainage basin of the river Ribeira Grande (Site 1). It is dense in terrestrial, riparian and aquatic vegetation. Multiple cascades drain into Site 5 and water exits via the 1 metre wide Ribeira do Ferreiro, connecting the lake to the central river of Ribeira Grande.

Fazenda water impoundment reservoir (Site 7 [Lat: 39.462; Long: -31.160]), a hydroelectricity facility, intercepts the river Ribeira d´Além da Fazenda and is situated 1.8 km from the eastern coast at an altitude of 139 m. The reservoir, surrounded by terrestrial and some riparian vegetation, had been drained and de-silted, with much of its substrate removed by mechanical machinery less than one month before sampling. The majority of discharge is delivered by pipe to the main turbine and this pipe is fitted with 15 mm screening, preventing entrainment of most large eels.

3.6.4 São Miguel Island

Eleven river systems and two lakes were studied on São Miguel Island, the largest island of the archipelago with an area of 759 km². Eight of these river systems were sampled at multiple sites throughout their course using passive sampling techniques for a period ≥ 24 hours, two river systems were sampled similarly but at only a single site and one river system was sampled at a single site using only active hand-netting for a period < 24 hours.

3.6.4.1 Ribeira Quente river system

The Ribeira Quente system was studied the most intensively out of all systems on São Miguel Island and the Azores Archipelago (Fig. 13).

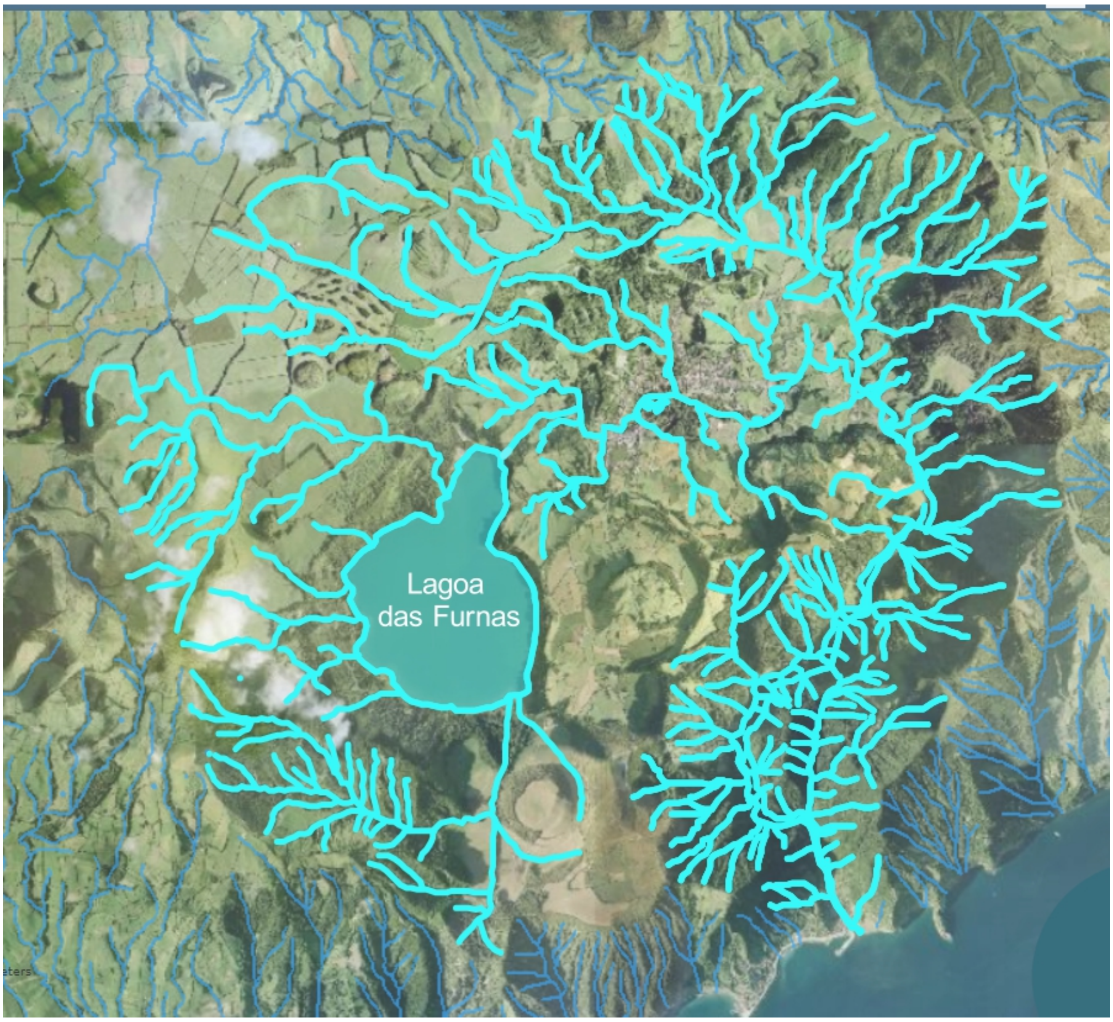


Fig. 13. Map of the Ribeira Quente system with system channels highlighted in blue. Adapted from maps downloaded from Regional Directorate for the Environment of Azores (2020).

As the only significant coastal discharge within a drainage basin relatively large by Azorean standards and at more than 6 km long, its central river Ribeira Quente is the archipelagos longest mainstem river and is partitioned into upper, middle and lower reaches by two hydroelectric dams. These two dams (Fig. 14), managed by Electricidade dos Açores (EDA), restrict yellow eel movement upstream and are located 1530 m and 4550 m from the ocean.

Fig. 14. Two hydroelectric dams intersecting Ribeira Quente at 1530 m (left) and 4550 m (right) from the ocean.

The river temperature was highly variable throughout its course due to the geothermal nature of the area and temperature differences of almost 50°C were recorded in the mainstem river flow between two locations (19.4°C and 69.3°C) during the same day. Six Sites (Fig. 15) were sampled along its length at approximately 1 km intervals, with two locations per each of the three reaches and thus grouping Sites 1.1 (Lat: 37.770; Long: -25.304) and 1.2 (Lat: 37.769; Long: -25.294) in the upper reach, Sites 1.3 (Lat: 37.756; Long: -25.299) - 1.4 (Lat: 37.752; Long: -25.305)in the middle reach and Sites 1.5 (Lat: 37.744; Long: -25.306) - 1.6 (Lat: 37.740; Long: -25.301) in the lower reach.

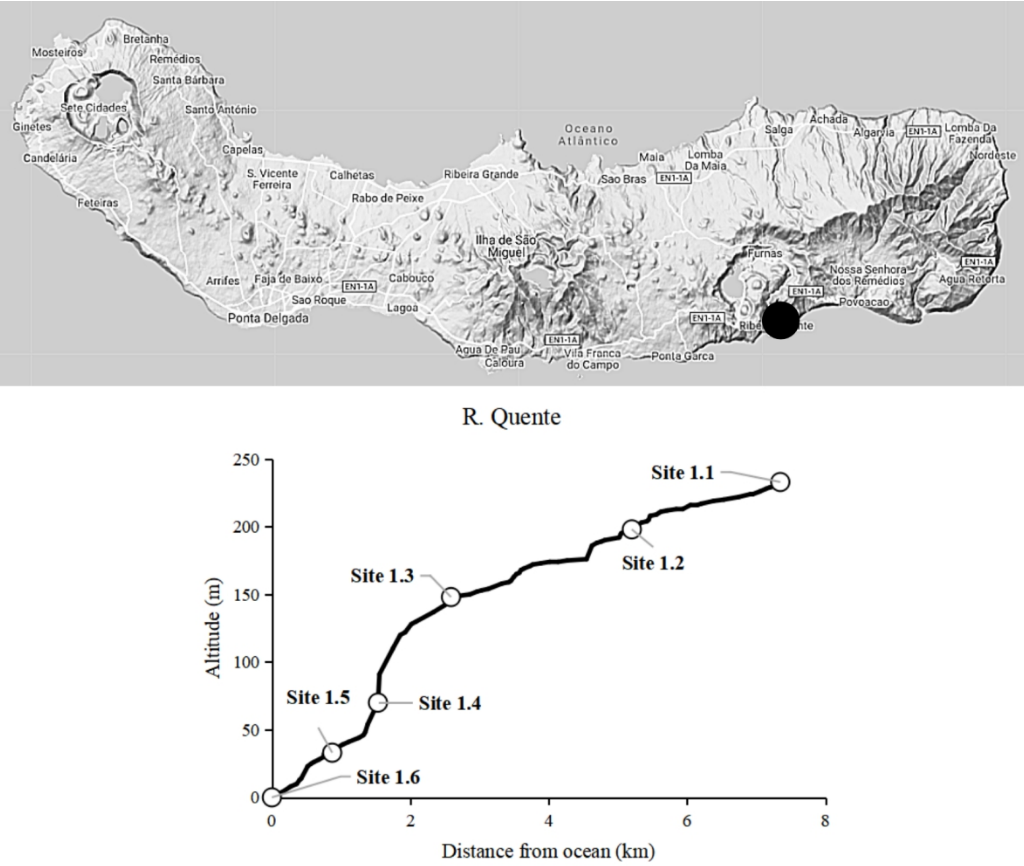


Fig. 15. Topographical map of São Miguel, detailing the location of Ribeira Quente and combined with charts plotting its gradient and sampling site locations. Adapted maps downloaded from Google (2019).

The lower and middle reaches were characterised by a steep gradient, regularly scoured rocky river bed, large accumulations of volcanic pumice, few small tributaries, sparse riparian vegetation and a high proportion of terrestrial tree shading. These two reaches were greatly affected by hydroelectric activities, regularly reducing water to a minimal level of almost no flow and then releasing weekly to bi-weekly scouring flows in an attempt to prevent the accumulation of volcanic pumice around inflows. The aforementioned scouring flows, partly prevented the growth of riparian and aquatic plants, reduced the aggregation of organic material on the river bed and greatly increased river traction. There was an observation of a dead European silver eel and of multiple dead carp (*Cyprinus carpio*) followed one such scouring flow on 11 August 2018.

The upper reach showed great contrast, flowing down a gradual gradient within a wide valley, larger tributaries and many terrestrial, riparian and aquatic plants throughout. Within the upper reach, a varying portion of water was diverted into plantations of semi-aquatic Yam plants (genus *Dioscorea*) but water level had greater stability than the middle to lower reach and the river bed had a much greater aggregation of organic material. In the upper reach, three similarly sized tributaries converged to from the mainstem of Ribeira Quente, two of which were of a temperature < 20°C and one >30°C but sampling was concentrated below these tributaries on the Ribeira Quentes mainstem.

3.6.4.2 Povoação river system

The Povoação river system is the larger of two significant coastal discharges within a southerly draining basin and one of the five largest rivers on São Miguel Island (Fig. 16).

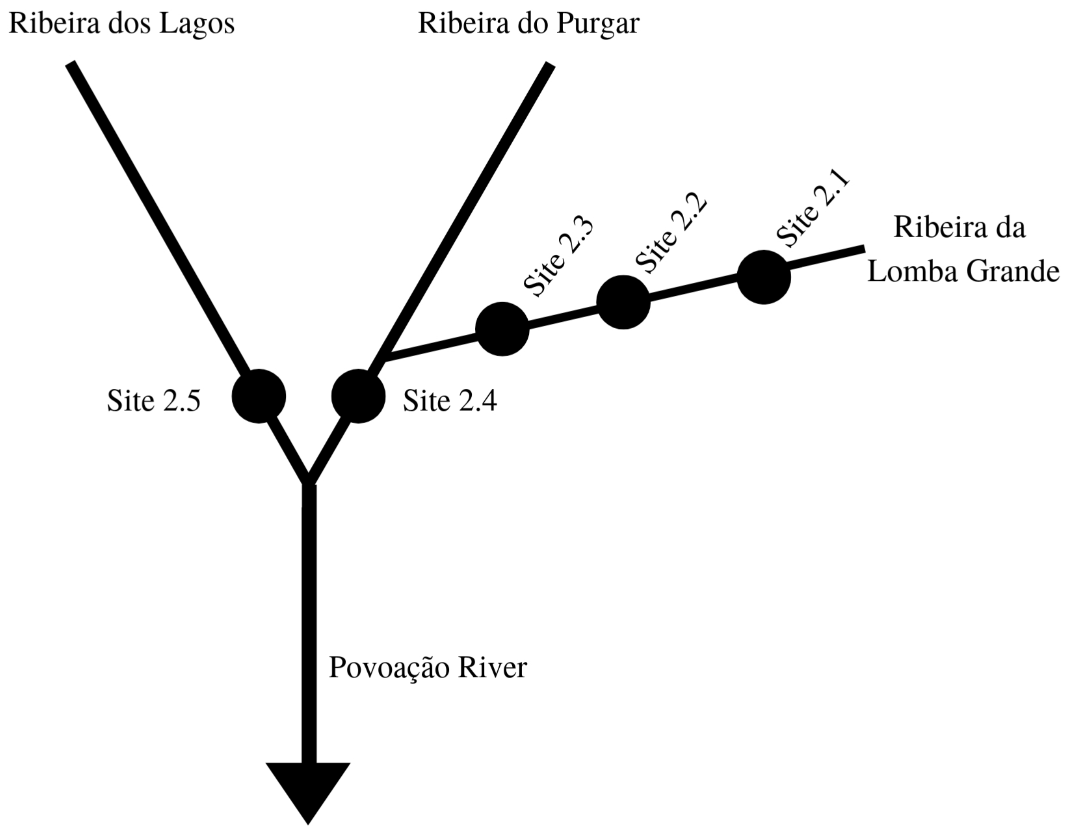


Fig. 16. Mainstem rivers (Ribeira do Purgar, Ribeira dos Lagos and Povoação), the Ribeira da Lomba Grande Tributary and the location of their confluences in the Povoação system, with flow direction indicated by arrow direction.

Sites 2.5 (Lat: 37.752; Long: -25.242) and 2.4 (Lat: 37.752; Long: -25.241), whilst located on different mainstems, are both approximately parallel to one another (in distance from the ocean and altitude) and have been plotted at the same position in the gradient plot of the Povoação system (Fig. 17)

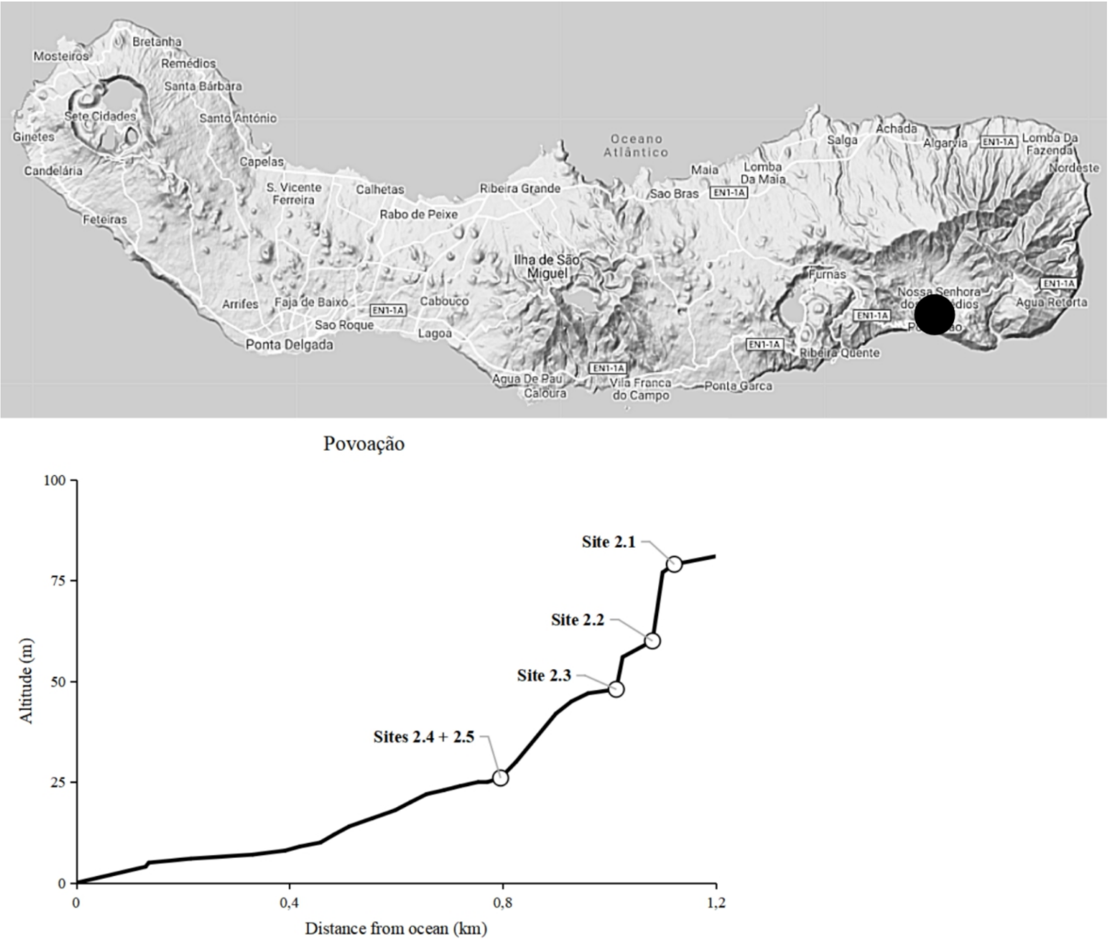


Fig. 17. Topographical map of São Miguel, detailing the location of Povoação river system and combined with charts plotting its gradient and sampling site locations to the furthest point of sampling on the tributary, Ribeira da Lomba Grande. Adapted maps downloaded from Google (2019).

From estuary to 0.7 km upstream, the Povoação River is ≈ 10 m wide, has a gravel substrate, a slight gradient, limited riparian vegetation and a multitude of weirs 0.2 - 1.5 m in height. Upstream of this lowest 0.7 km, the river divides into two proportionate mainstems ≈ 5 m wide, each with a succession of weirs for a further 0.4 km upstream before both entering parallel canyons. The left mainstem Ribeira do Purgar (Site 2.4) and the right Ribeira dos Lagos (Site 2.5) both had a steep gradient, rocky substrate, limited riparian vegetation and a high proportion of terrestrial vegetation shade. Limited access halted sampling of these two mainstems any further than 1.2 km upstream of the coast and no connectivity was believed to exist between these tributaries other than their confluence, 0.7 km from the coast.

A large tributary (≈ 2 m wide) connected with Ribeira do Purgar 0.85 km from the system´s coastal discharge and eels were regularly observed laying exposed during daylight hours. This tributary, Ribeira da Lomba Grande, was of a steep gradient, completely shaded by terrestrial vegetation and characterised by a series of two cascades with associated downstream cascade pools. The lower cascade was 8 m in height, forming a likely barrier to upstream yellow eel but not glass eel/elver movement. This lower cascade pool had an area ≈ 18 m², a maximal depth of 1.5 m, undercut sections below the upstream wall and a fine silt substrate. This lower cascade pool and the downstream portion of Ribeira da Lomba Grande formed Site 2.3 (Lat: 37.751; Long: -25.240).

The upstream cascade was 20 m in height, forming a likely barrier to upstream movement of all larger eel stages. It´s associated downstream cascade pool (Site 2.2 [Lat: 37.751; Long: -25.238]) had an area of ≈ 100 m², a maximal depth of 2 m, undercut sections below the upstream wall and a fine silt substrate. The remains of rats and larger mammals were observed in this uppermost cascade pool during every visit, both during and after the sampling period, possibly occurring from the butchering of animals at an upstream farmstead. Site 2.1 was a portion of the river directly upstream of the uppermost cascade.

3.6.4.3 Ribeira de Pelane

The location, gradient, and sites sampled in Ribeira de Pelane are illustrated in Fig. 18.

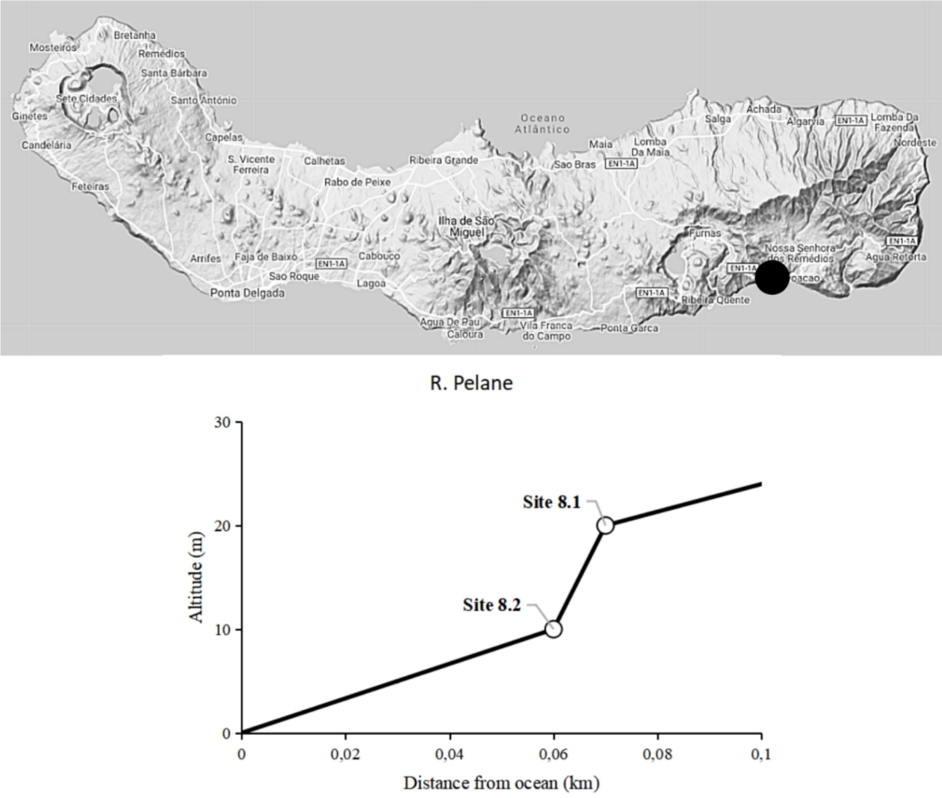


Fig.18. Topographical map of São Miguel, detailing the location of Ribeira Pelane and combined with charts plotting its gradient and sampling site locations. Adapted maps downloaded from Google (2019).

Ribeira de Pelane, situated within the same drainage basin as the Povoação River System discharges from the islands southern shore and is typified by a steep gradient, rocky and organic substrate, some riparian vegetation and shading by terrestrial vegetation. Upstream it flows through farming pastures and downstream through a gully (Site 8.1 [Lat: 37.448; Long: -25.251]) between two villages before a final cascade ≈ 10 m in height onto the shore. Site 8.2 (Lat: 37.747; Long: -25.250) was located downstream of this final cascade ≈ 50 m from the ocean.

3.6.4.4 Ribeira do Faial da Terra River

The gradient and sampling site locations of Ribeira do Faial da Terra are demonstrated in Fig. 19.

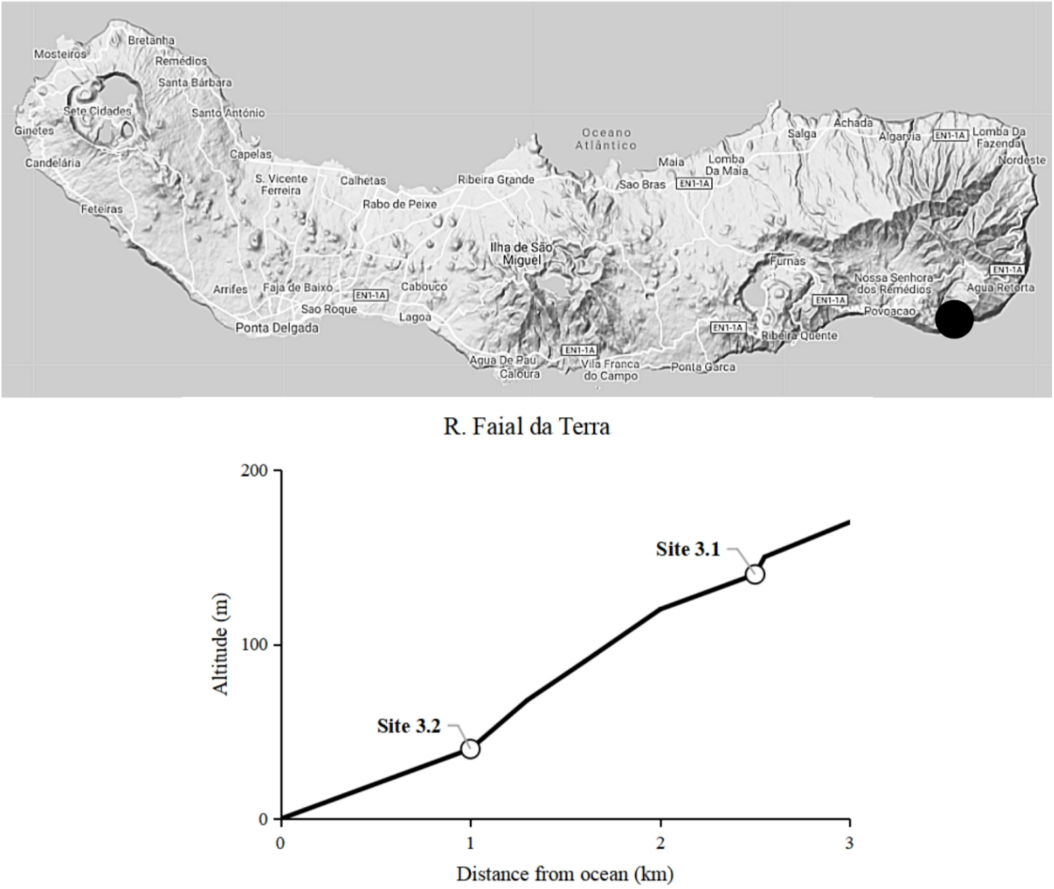


Fig. 19. Topographical map of São Miguel, detailing the location of Ribeira do Faial da Terra and combined with charts plotting its gradient and sampling site locations. Adapted maps downloaded from Google (2019).

Ribeira do Faial da Terra, one of the five largest rivers on São Miguel Island discharges from the islands southeastern shore. The lower reach of the river (Site 3.2 [Lat: 37.746; Long: -25.200]) flows through the town of Faial da Terra and is typified by multiple weirs (0.2 - 4 m high), a gravel substrate, some riparian vegetation and a lack of shading. The river upstream has a much greater proportion of riparian vegetation, scattered weirs of no considerable height, a steeper gradient and the majority of the river is shaded by terrestrial vegetation. As well as in the lower reach, sampling also occurred in a large cascade pool (Site 3.1 [Lat: 37.761; Long: -25.197]) at an approximate altitude of 140 m and a distance of 2 km from the ocean. This cascade pool had an area ≈ 70 m², a maximal depth of 2 m, a silty substrate and was backed by an upstream cascade ≈ 8 m in height that formed a likely barrier to upstream yellow eel but not glass eel/elver movement.

3.6.4.5 Ribeira Grande

The location, gradient, and single site sampled in Ribeira Grande is illustrated in Fig. 20.

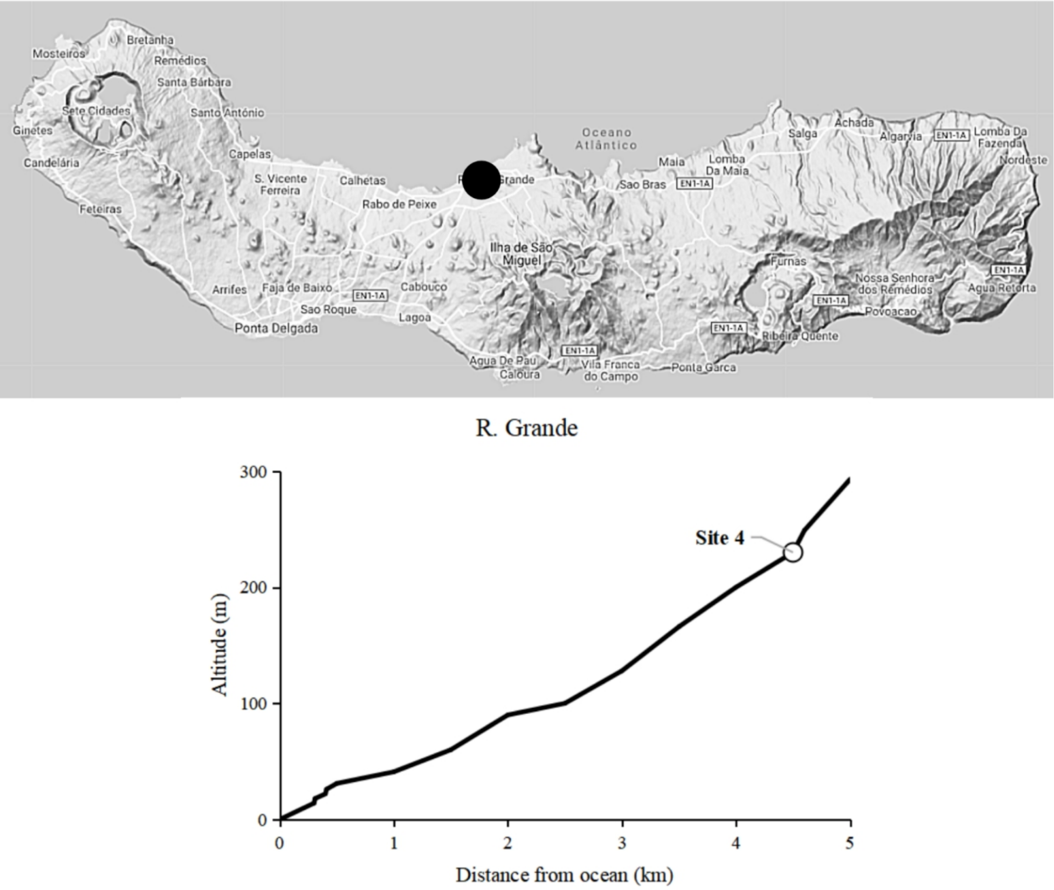


Fig. 20. Topographical map of São Miguel, detailing the location of Ribeira grande and combined with charts plotting its gradient and sampling site locations. Adapted maps downloaded from Google (2019).

Ribeira Grande, one of the five largest rivers on São Miguel Island, discharges from the island´s northern shore. Its lower reach flows between crop fields, cattle pasture and the town of Ribeira Grande. This lower reach was investigated as a site for potential sampling but access proved difficult and surface runoff from farmland produced flows too great for the sampling techniques used during this study. A cascade on the river, 40 m in height and named

Salto do Cabrito, was located at an altitude of 230 m and a distance of 4.5 km from Ribeira Grande´s coastal discharge. Downstream of this cascade was its associated cascade pool (Site 4.1 [Lat: 37.796; Long: -25.495]) that had an area ≈ 70 m², a maximal depth of 2.5 m, undercut sections below the upstream wall, partial shading by terrestrial vegetation and a fine silt substrate. This cascade formed a likely barrier to upstream yellow eel and perhaps even glass eel/elver movement. A portion of the flow upstream of this cascade was diverted for hydroelectric use, yet flow over the cascade remained constant.

3.6.4.6 Ribeira da Praia and Ribeira das Três Voltas

The locations, gradients, and sites sampled in both Ribeira da Praia and Ribeira das Três Voltas are illustrated in Fig. 21.

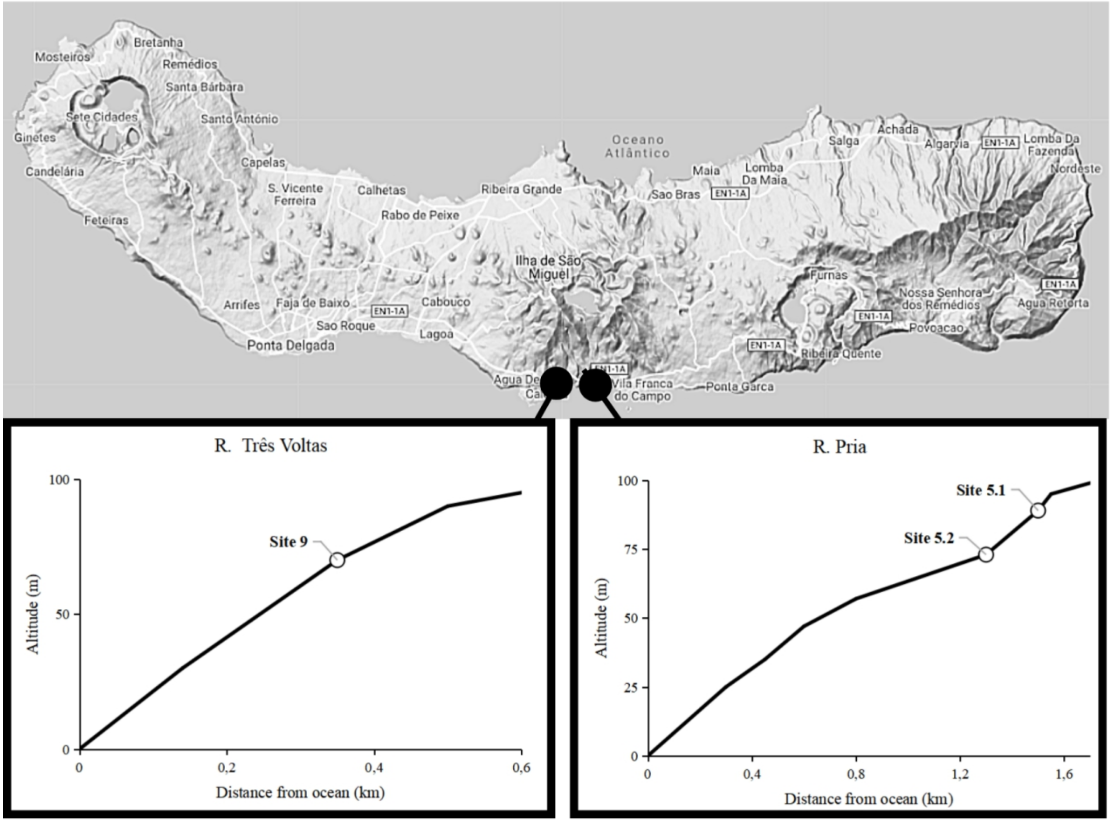


Fig. 21. Topographical map of São Miguel, detailing the locations of Ribeira das Três Voltas and Ribeira da Praia. Combined with charts plotting its gradient and sampling site locations. Adapted maps downloaded from Google (2019).

Ribeira das Três Voltas discharges from the islands southern shore and is typified by a steep gradient, gravel substrate, some riparian vegetation and partial shading by terrestrial vegetation. Site 9 was sampled between 350 - 500 m from its coastal discharge at an altitude of 70 - 90 m.

Ribeira da Praia also discharges from the island´s southern shore. However, the majority of this water no longer flows in the original river, is instead intercepted by hydroelectric intakes ≈ 2.2 km from its coastal discharge, diverted via piping to generate electricity and rejoins the original river channel at an outflow 0.5 km from the coast. Flows periodically occur within the entire length of the river channel, due to workings of the hydroelectric plant or high precipitation but this has resulted in the semi-isolation of two sequential cascade pools, Site 5.1 (Lat: 37.721; Long: -25.466) and Site 5.2 (Lat: 37.721; Long: -25.467), both ≈ 60 m², 2 m deep and backed by a cascade 3 m in height. These cascade pools both had a high proportion of terrestrial vegetation shading, undercut sections and a gravel substrate with large quantities of decaying vegetative matter. During multiple visits, the river sections directly upstream and downstream of these two cascades were without any flow.

3.6.4.7 Ribeira Coelhas and Ribeira Cachoco

The locations, gradients, and sites sampled in both Ribeira Coelhas and Ribeira Cachoco are illustrated in Fig. 22.

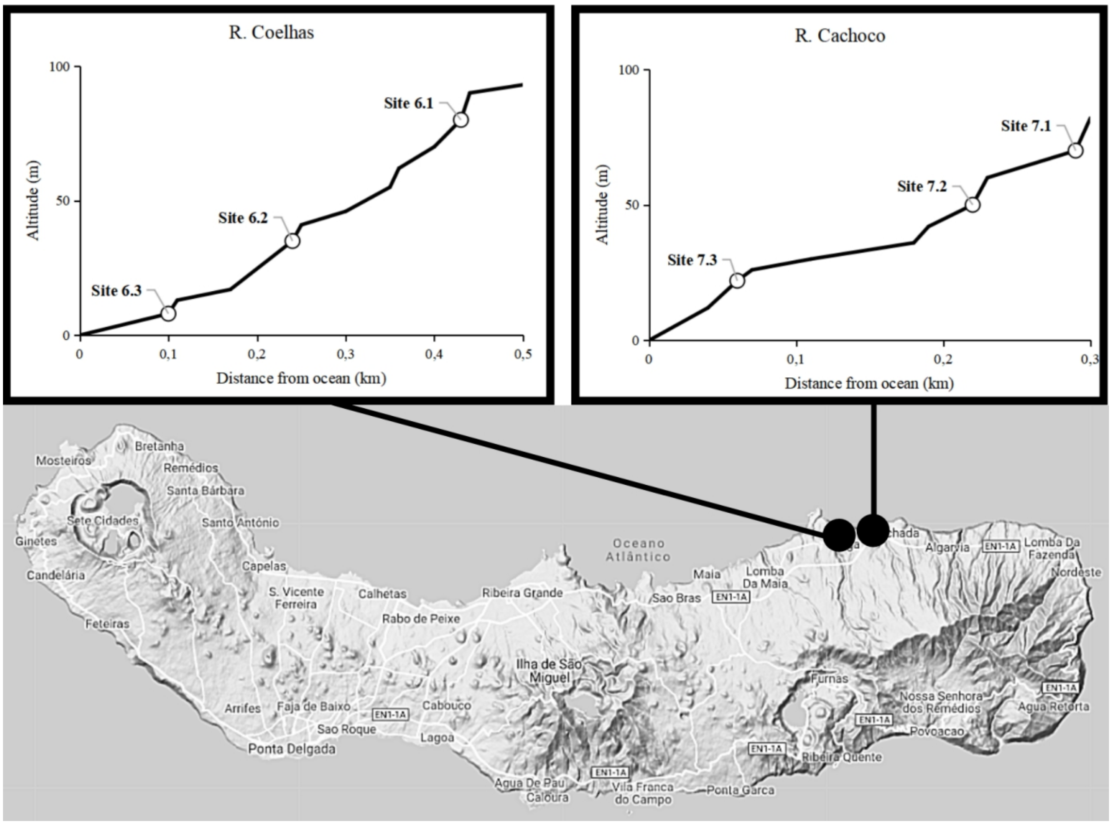


Fig. 22. Topographical map of São Miguel, detailing the locations of Ribeira Coelhas and Ribeira Cachoco. Combined with charts plotting its gradient and sampling site locations. Adapted maps downloaded from Google (2019).

Ribeira Coelhas (Sites 6.1[Lat: 37.852; Long: -25.294], 6.2 [Lat: 37.854; Long: -25.296], 6.3[Lat: 37.854; Long: -25.296]) and Ribeira Cachoco (Sites 7.1 [Lat: 37.853; Long: -25.289], 7.2 [Lat: 37.853; Long: -25.289], 7.3 [Lat: 37.854; Long: -25.289]), flow relatively parallel and have northern coastal discharges situated at a distance of ≈ 0.5 km from one another. An analogous river topography most likely results from shared geology, with both rivers comprising a similar series of cascades and associated cascade pools within 0.5 km of their coastal discharges. The downstream portion of both rivers have a rocky substrate, lack riparian vegetation and have large boulders providing cover within their cascade pools. All cascades are > 3 m in height formed a likely barrier to upstream yellow eel movement and for both rivers, the cascade of the uppermost cascade pool sampled was ≥ 10 m in height, possibly acting as a barrier to glass eel/elver movement. The most noticeable difference between the two was a lack of any terrestrial vegetative shading in Ribeira Cachoco compared to a partial shading in Ribeira Coelhas.

3.6.4.8 Ribeira Funda

The location, gradient, and study site of Ribeira Funda are illustrated in Fig. 23.

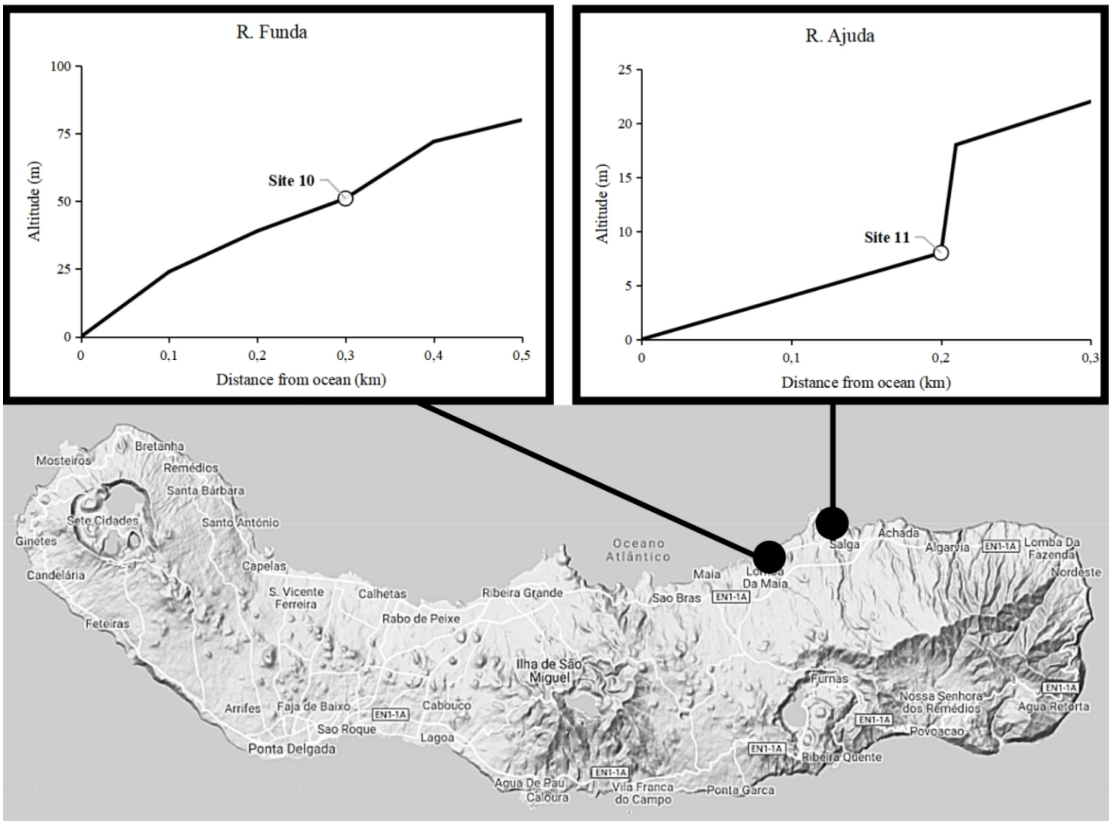


Fig. 23. Topographical map of São Miguel, detailing the locations of Ribeira Funda and Ribeira Ajuda. Combined with charts plotting its gradient and sampling site locations. Adapted maps downloaded from Google (2019).

Ribeira Funda discharges on the north coast and the sampled portion (Site 10 [Lat: 37.839; Long: -25.362]) of its lower reach is typified by a series of small cascades ≤ 3 m and associated cascade pools with a rocky substrate and large boulders providing sub-aqueous cover. Vegetation increases with distance from the ocean and the upstream cascade pools had both riparian vegetation and terrestrial vegetative shading, whilst the downstream pools did not. Over 0.3 km from the ocean, access to the river became difficult.

3.6.4.9 Ribeira Ajuda

No exact name could be located for this particular river and so has been named after the area in which it is situated and the nearest village, Ajuda. The location, gradient and study site of Ribeira Ajuda are illustrated in the previous figure (Fig 23). Ribeira Ajuda discharges on the islands north coast. The study site, Site 11 (Lat: 37.856; Long: -25.4307)was a large coastal cascade pool ≈ 60 m^2, 2 m deep, 0.2 km from the ocean and backed by a cascade ≈ 10 m in height. This upstream cascade formed a likely barrier to upstream yellow eel movement and perhaps also to glass eel/elver movement. A coniferous forest was located upstream of the cascade whilst the cascade pool had a fine silt bottom and several large boulders forming subaqueous cover. Flow from the river passed over a sand and gravel beach to connect with the ocean and saltwater likely fills the cascade during high ocean levels and storm conditions. This ocean-connecting channel disappears beneath the sand when the flow is insufficient.

3.6.4.10 Lagoa das Furnas and Lagoa das Sete Cidades

The sampled lakes are situated at opposite ends of the island and both sit within volcanic calderas (Fig. 24).

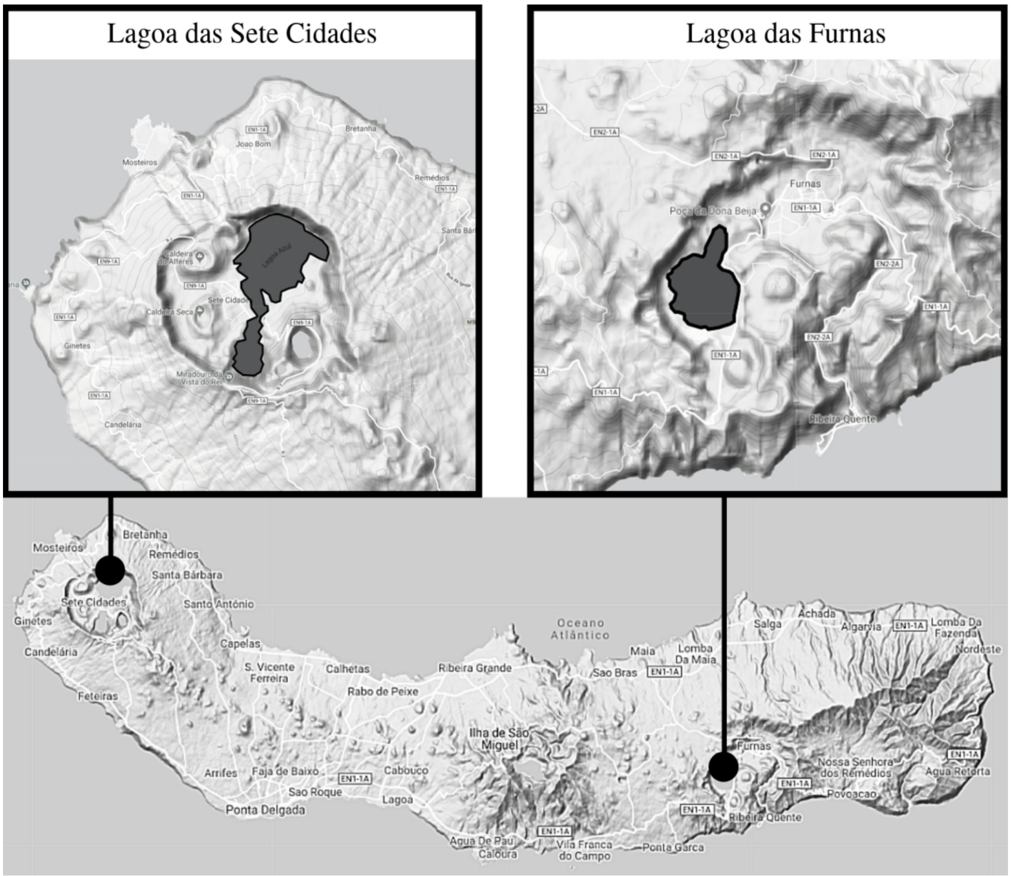


Fig. 24. Topographical map of São Miguel. The locations of Lagoa das Sete Cidades (and Lagoa das Furnas are indicated by black circular markers and their surface area is shown in greater detail by a black polygon. Adapted maps downloaded from Google (2019).

Lagoa das Furnas (Site 12 [Lat: 37.765; Long: -25.328]) has a surface area of 1.93 km², a maximum depth of 15 m and is situated at an altitude of 281 m on the southeastern portion of São Miguel Island, ≈ 2.5 km from its southern coast. This shallow lake is located within a volcanic crater of an active volcano. Geothermic calderas partially heat the northwestern shore of the lake and water flows in via a stream in the same area. Directly opposite, on the southwestern shore of the lake, the lakes only outflow has been artificially modified and water outflow is controlled. This lake is surrounded by forestry and fertilized pasture, resulting in highly eutrophic conditions and frequent algal blooms (Santos *et al.* 2005).

Lagoa das Sete Cidades (Site 13 [Lat: 37.876; Long: -25.789]) has a surface area of 4.35 km², a maximum depth of 33 m (Scarth *et al.* 2001)and is situated at an altitude of 259 m on the western tip of São Miguel Island, ≈ 2.2 km from its western coast (Fig. 24). Located in the large crater of a dormant volcano, this lake consists of two separate lakes joined via a channel and is the largest body of water within the Azores region. Several small non-permanent streams flow into the lake and the only outflow, situated on lakes western shore, has been artificially modified. This outflow is controlled and only opened a few times a year if water levels reach critical heights. The water level is instead maintained via evaporation and water percolating through the porous volcanic bedrock to the ocean. Information, from the Directorate for the Environment of the Azores, confirmed that the outflow was closed throughout the entire study due to lower than average water levels within the lake. The surrounding land use is forestry and fertilized pasture, resulting in a highly eutrophic lake.

3.7 Data Analysis

3.7.1 Assessing eel silvering state and sex

Silver eels were identified by visual assessment in the field (lateral line segmentation, enhanced counter-shading, proportionately large eyes and darkened pectoral fins) and later by analysis of silvering morphometric data (ocular, pectoral fin, length, and weight). Fine-scale ocular and pectoral data were gathered using electronic calipers, accurate to 0.01 mm for use in silvering calculations only, so that silvering stage and sex could be accurately classified. Using the method of Durif *et al.* (2005), three morphological indices were calculated in conjunction with one another, facilitating eels to be categorized as either undifferentiated resident, male silver migrant or one of four female silvering stages (resident, pre-migrant, upstream migrant, downstream migrant). The three indices used to calculate silver stages are as follows:

Pankhurst´s (1982) Occular Index (IE): $\mathbf{I_E = ([(A + B)2/4 * \pi]/L) * 100}$

(Where **A** is horizontal eye diameter, **B** is vertical eye diameter and **L** is total body length).

Durif *et al.* (2005) Fin Index (I_F): $\mathbf{I_F = 100\ L_{PF}\ L_T^{-1}}$

(Where $\mathbf{L_{PF}}$ is pectoral fin length and is $\mathbf{L_T}$ is total body length).

Fulton´s condition factor (K): $\mathbf{K = 100\ (\ M / L^3\ )}$

(Where **M** is total body mass and **L** is total body length).

Extreme differences in counter-shading and ocular size between yellow eel (growth-phase) and silver eel (migration phase) can be observed with two eels caught in Ribeira Quente during the study (Fig. 25)

Fig. 25. Two contrasting eels caught at Ribeira Quente, yellow resident (top) and silver migrant (bottom).

3.7.2 Assessing yellow eel sex

It has been demonstrated that sex differentiation of A. anguilla concludes when body lengths of > 350 mm are attained (Colombo et al. 1984) and comparisons of silver eel throughout their range has shown silver male mean lengths vary between 350 - 460 mm, with extremes of 290 and 540 mm (Tesch 2003). With yellow eels being precursor to the silver eel stage, these aforementioned silver male mean lengths can be used to catagorize yellow eels as either undetermined sex or yellow female.

With reference to these observations and for the greatest accuracy within this study, only the extreme mean silver length (540 mm) was used when determining the sex of yellow eels. Therefore yellow eels ≤ 540 mm were of an undetermined sex and yellow eels > 540 mm were determined to be female.

3.7.3 Analysis of abundance (CPUE)

Spatial variations in eel abundance, catch-per-unit-effort (CPUE), were calculated from all eels caught, both yellow and silver (Naismith and Knights 1993) in river systems and brackish lakes, whereas temporal variations in silver eel abundance (section 3.6.7) were calculated for only silver eels caught in the Ribeira Quente. CPUE calculations did not include freshwater lakes (i.e. all lakes of Flores and São Miguel Islands) and rivers (i.e.Ribeira Grotao on Flores Island) where no eels were caught.

To calculate daily CPUE, each concertina trap, apollo trap, and each fyke cod-end was calculated as a single unit of fishing effort when deployed overnight for an approximate 24-hr period. Therefore, a double-ended fyke deployed over a single night would equal 2 net-ends/24 hrs and a single baited concertina or apollo trap deployed over a single night would equal 1 net-end/24hrs effort. Only catches from passive sampling techniques were used for calculations, where CPUE could be standardized as eels/net-end/24 hrs. A single standardised CPUE for varied fishing equipment was deemed suitable for calculations, due to the fact that the sampling structure at each site was uniformly optimised for the highest catch per 24 hrs/site, as described previously in section **3.2 Data collection**. The suitability of this standardised CPUE was reinforced by an analogous mesh (8 - 10 mm), a trap entrance size that restricted no maximum size of eel and also on the grounds that all trap types purposefully guided eels, via bait or leader, into the trap.

Active techniques, eels caught by hand or hand-net, were omitted from all CPUE calculations. CPUE (eels/net-ends/24 hrs) was calculated for each site, on all islands, over each 24-hr period.

3.7.4 Geographical distribution of eels across the Azores Archipelago

Eels caught during all scoping trips (2017 - 2019) were included for inter-island analyses. Pooled data from all islands, was used to calculate the total number of eels (combined yellow and silver eels) and the complete weight and length ranges (minimum-maximum) for the Azores. For each island; the minimum, maximum, mean, median and standard deviation of eel weight, eel length and CPUE (pooled from daily CPUE data at each site) were calculated and then tabulated. Median weights, lengths and CPUE´s were compared between islands using non-parametric Kruskal-Wallis H-tests, followed by Dunn's procedure with a Bonferroni correction for multiple comparisons. The distributions of weight and length were compared between islands using 2-sample Kolmogorov-Smirnov tests and the total length distributions at each island were visualized in length-frequency histograms.

3.7.5 Intra-island spatial variations in eels of São Miguel Island

Only eels caught on São Miguel Island during 2018 were included for analyses. The complete island weight and length ranges (minimum-maximum), resulted from combined yellow and silver eels, from all sites on São Miguel. The minimum, maximum, median and standard deviation of eel weight and length were calculated for each site of every river system, then tabulated with the number of yellow eels, number of silver eels and the river type in which they were caught.

For further analyses, sites were categorized into two groups, of mainstem river sites and all other river type sites (cascade pool and tributary river sites). Median weights, lengths and

CPUE´s were compared between the groups using non-parametric Mann-Whitney U tests and the distributions of weight and length were compared using 2-sample Kolmogorov-Smirnov tests. Weight, length and CPUE distributions were visualized as boxplots.

3.7.6 Inter-watercourse spatial variations in eels of two river systems (Ribiera Quente and Povoação)

Only eels caught during 2018 in Ribiera Quente and Povoação river systems (São Miguel Island) were used in inter-watercourse spatial analyses. All data from all sites were pooled for each system. Maximum, median, mean and standard deviation were calculated for CPUE, weight and length at each system.

Median weights, lengths and CPUE´s were compared between systems using non-parametric Mann-Whitney U tests and the distributions of weight and length were compared between systems using 2-sample Kolmogorov-Smirnov tests. The weight distributions at each system were visualized as boxplots and length distributions as both boxplots and length-frequency histograms.

3.7.7 Intra-watercourse spatial variations in eels (Ribiera Quente and Povoação)

Only eels caught during 2018 were used for the two intra-watercourse spatial analyses of Ribeira Quente (a comparison of three reaches of a mainstem river) and Povoação (a comparison between a mainstem river and a tributary Ribeira da Lomba Grande).

Ribeira Quente was divided, by the presence of two intersecting hydroelectric dams, into upper (Sites 1.1 and 1.2), middle (Sites 1.3 and 1.4) and lower (Sites 1.5 and 1.6) reaches, whereas Povoação was grouped as sites at a mainstem river (Sites 2.4 - 2.5) or sites at a tributary river (Sites 2.1, 2.2 and 2,3). The maximum, median, mean and standard deviation were calculated for CPUE, weight and length for each of Ribeira Quentes three reaches and for both river type groups at Povoação.

For the intra-watercourse analyse of Ribeira Quente, median weights, lengths and CPUE´s were compared between reaches, using a non-parametric Kruskal-Wallis H-test, followed by Dunn's procedure with a Bonferroni correction for multiple comparisons. For the intra-watercourse analyse of Povoação, median weights, lengths and CPUE´s were compared between groups, using a non-parametric Mann-Whitney U test.

The distributions of weight and length, for each of the two intra-watercourse analyses, were compared using 2-sample Kolmogorov-Smirnov tests. The weight distributions between sites/groups were visualized as boxplots and length distributions as both boxplots and length-frequency histograms.

3.7.8 Temporal variations in silver eel abundance in Ribeira Quente, the largest river on São Miguel Island

Count of silver eels (male and female), silver eel CPUE and silver eel length were analysed to determine temporal variations in silver eel abundance and size in Ribeira Quente. To identify peaks in silver eel count, male and female silver eel daily counts were plotted against capture date in a bar chart. A scatterplot of combined male and female silver eel lengths were plotted against the capture date and Spearmann´s correlation coefficient was used to determine potential correlations between capture date and silver eel length.

The maximum, mean and standard deviation in silver eel CPUE were calculated. To investigate the effects of lunar activity on silver eel abundance, dates were categorized under the four lunar phases (first-quarter, full, third-quarter, new), using percentage of the moon illuminated and peak lunar phase data, downloaded from the US Naval Observatory Astronomical Applications Department (Navo 2019). Each lunar phase was categorized as a seven day period, where the middle (fourth day) is the phase peak (Adrian 2001). Silver eel CPUE and lunar luminosity were plotted in a chart against the date, with lunar phases detailed above. Mean silver eel CPUE, for each of the four lunar phases, were compared using a one-way ANOVA, followed by Scheffe posthoc test (Rooker and Dennis 1991).

To investigate the effects of high river discharge on silver eel abundance in Ribeira Quente, the number of events that exceeded the Q10 flow percentile (1081.15 l/s) in 2018, i.e. the flow (l/s) which was equalled or exceeded for 10% of 2018. River discharge data were downloaded from the Regional Directorate for the Environment of the Azores (2019). Silver eel catches that correlated with high flow events (during daylight/night/between sunset and midnight) were identified, considering the full 24 hours before net/eel retrieval. Silver eel CPUE at midday on the date of eel retrieval, the hourly mean flow and Q10 were plotted against the date in a scatterplot to identify silver eel catches that correlated with Q10 flows. Silver eel CPUE and the count of silver eels, following flows ≥ Q10 and flows < Q10, were compared using non-parametric Mann-Whitney U tests.

4. Results

4.1 Geographical distribution of eels across the Azores Archipelago

A. anguilla were caught on all four of the Azorean islands sampled, in all but one river system. By contrast, despite extensive effort, eels were only caught in a single (brackish) lake, with none caught from four other (freshwater) lakes and a single artificial reservoir. In total, data were collected from 711 eels during the 73 nights of sampling, with lengths ranging from 42-971 mm and weights from 20-2095 g (Table 1).

Table 1. Overview of all eels caught on each of the four study islands during 2017-2018, including the numbers, abundance (CPUE), and length and weight ranges.

Island	No. eels	CPUE (eels/net-end/24 hrs)					Length (mm)					Weight (g)				
		Min.	Max.	Mean	S.D.	Median	Min.	Max.	Mean	S.D.	Median	Min.	Max.	Mean	S.D.	Median
Terceira	261	3.75	9.13	5.92	2.41	5.41	194	864	482	82.6	474	20	2025	442	283.4	400
S. Maria	57	1.00	6.00	2.28	2.12	1.38	180	828	512	124.0	480	150	1445	353	270.0	260
Flores	58	0	4.00	0.33	0.71	0.07	294	751	520	93.2	536	85	1008	367	171.2	370
S. Miguel	335	0	6.00	0.43	0.69	0.25	42	971	472	184.8	486	35	2095	410	331.6	320

Terceira had the highest maximum, median and mean abundance of eels for any island, with respective CPUEs of 9.13, 5.41 and 5.92 (± 2.41) eels/net-end/24 hours (Table 1). Terceira´s CPUE values reflect two large and two moderately large catches, resulting exclusively from Lagoa da Parque do Paul, the single sampled site. Terceira far exceeded the CPUE of the remaining three islands, the lowest of which was Flores. Flores had a maximum CPUE of 4.00 eels/net-end/24 hrs, a median CPUE of 0.07 and a mean CPUE of 0.33 (± 0.71) (Table 1), resulting from many small and zero catches. São Miguel had a maximum CPUE of 6 eels/net-end/24 hrs, a median of 0.25 eels/net-end/24 hrs and a mean of 0.43 (± 0.69), resulting from a majority of small catches. Santa Maria had a maximum CPUE of 6 eels/net-end/24 hrs, a median of 1.38 eels/net-end/24 hrs and a mean of 2.28 (± 2.12) (Table 1), resulted from one large and many medium catches. There was a significant difference in median CPUE of inter-island comparisons, excluding comparisons between Flores and São Miguel and between Santa Maria and Terceira (Kruskal-Wallis H-test, followed by Dunn´s test with Bonferroni correction, $P > 0.05$).

Yellow stage eels were caught on all islands and silver stage eels were caught on all but Santa Maria Island. With 1050 net-ends/24 hours, over 75% of the sampling effort was concentrated on São Miguel, resulting in 335 eels, the highest total number for any island. São Miguel also displayed the greatest variation in size, with minimum to maximum weights of 35-2095 g and lengths of 42-971 mm (Table 1). Between the four islands, median lengths varied by only 62 mm (474-536 mm) and median weights by 140 g (260-400 g).

Length was not significantly different between islands (Kruskal-Wallis H-test, *P* > 0.05), whereas weight was significantly different between Terceira (Mdn = 400 g) and São Miguel (Mdn = 320 g) (Kruskal-Wallis H-test, followed by Dunn´s test with Bonferroni correction, *P* < 0.05).

Terceira and Santa Maria were the only islands that did not have significantly different length distributions (2-sample Kolmogorov-Smirnov test, *P* > 0.05) (Fig. 26), whilst Flores and São Miguel were the only islands that did not have significantly different weight distributions (2-sample Kolmogorov-Smirnov test, *P* > 0.05).

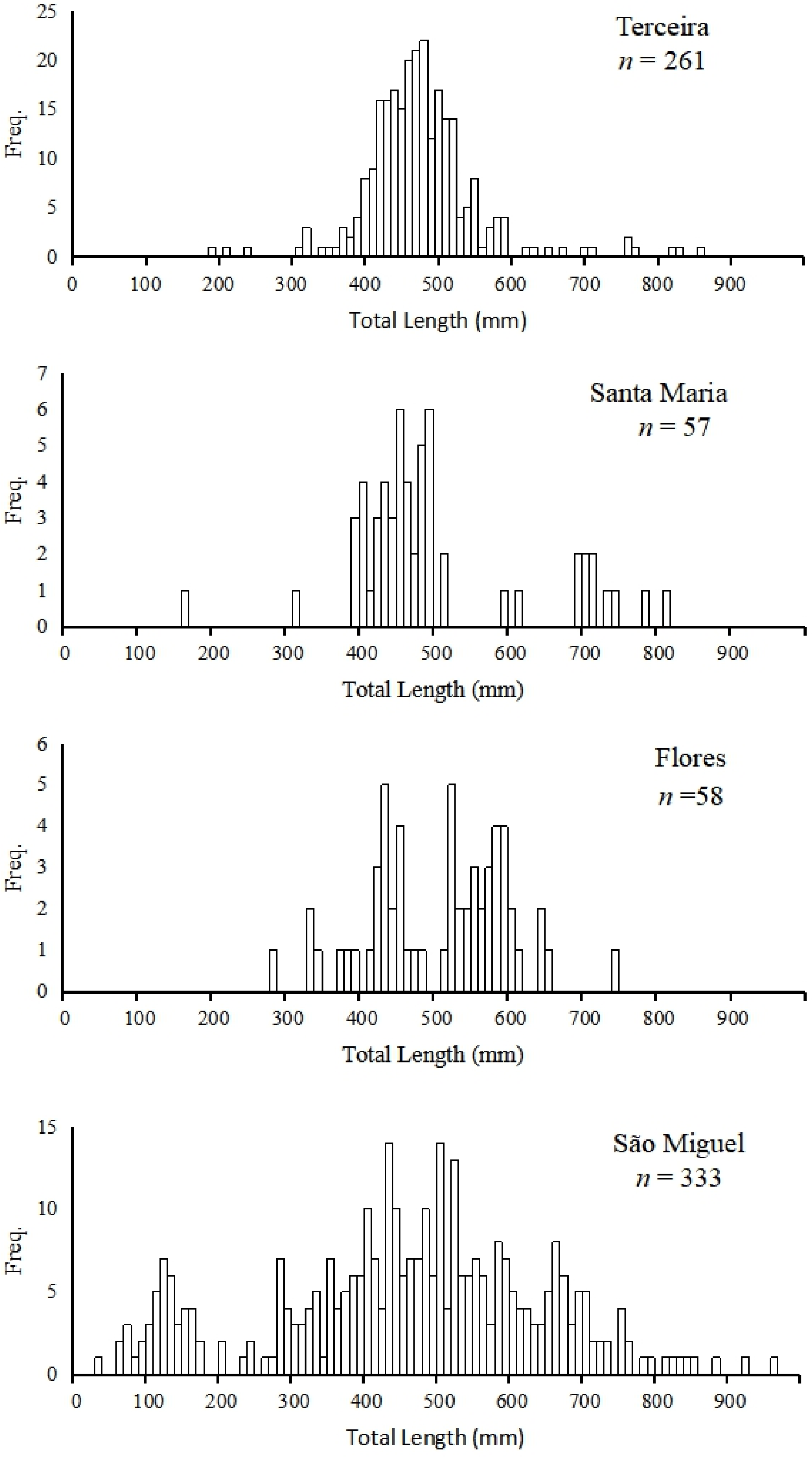


Fig. 26. Length distributions of all eels, both yellow and silver, captured from each of the four islands (09/12/2017-03/12/2018).

4.2 Intra-island spatial variations in eels of São Miguel Island

For accurate spatial analysis, only data from the 2018 continuous sampling period have been included for São Miguel Island intra-island comparisons. Eels were caught within all river systems on São Miguel and 65% of eels were caught within two river systems, Ribeira Quente and Povoação, with respective catches of 122 and 86 eels. Ribeira Ajuda followed with data collected from 51 eels (15%), including 43 mortalities from drought conditions. The remaining 61 eels (20%) were caught within the other eight river systems (Table 2).

Table 2. Catch of eels for all São Miguel Island river systems sampled during 2018.

River/ system	Site	River Type: River (R) Stream (S) Mainstem (M) Tributary (T) Cascade Pool (P)	Yellow eels	Silver eels	Total Length (mm)					Total Weight (g)				
					Min.	Max.	Median	Mean	S.D.	Min.	Max.	Median	Mean	S.D.
R. Quente	1,1	M/R	5	1	622	729	694	685	35	495	760	613	614	89
	1,2	M/R	31	4	394	971	630	635	115	105	1935	420	516	361
	1,3	M/R	2	0	545	651	598	598	53	265	570	418	418	153
	1,4	M/R	30	3	302	683	483	498	90	55	675	183	244	169
	1,5	M/R	17	6	340	702	515	530	93	50	635	230	301	175
	1,6	M/R	18	6	260	846	429	448	131	25	1420	145	203	246
Povoacao	2,1	T	0	0	-	-	-	-	-	-	-	-	-	-
	2,2	P/T	35	10	132	935	542	572	141	80	2095	330	501	422
	2,3	P/T	27	1	390	870	543	566	126	150	1450	438	471	270
	2,4	M/R	8	0	308	680	375	419	116	45	550	163	204	150
	2,5	M/R	5	1	325	500	385	399	70	60	300	170	162	81
Faial de Terra	3,1	P/R	7	2	362	584	408	428	62	250	600	300	350	122
	3,2	M/R	14	2	319	661	469	486	102	75	565	355	327	150
R. Grande	4	P/R	2	3	495	740	570	577	87	860	1200	955	995	113
R. Praia	5,1	P	1	0	768	768	768	768	-	1040	1040	1040	1040	-
	5,2	P	0	0	-	-	-	-	-	-	-	-	-	-
R. Coelhas	6,1	P/S	0	0	-	-	-	-	-	-	-	-	-	-
	6,2	P/S	0	0	-	-	-	-	-	-	-	-	-	-
	6,3	P/S	1	2	457	689	568	571	95	175	695	370	413	214
R. Cachaco	7,1	P/S	2	0	501	633	567	567	66	275	575	425	425	150
	7,2	P/S	4	0	446	676	493	527	88	170	635	238	320	184
	7,3	P/S	3	0	559	605	589	584	19	370	385	375	377	6
R. Pelane	8.1	S	8	0	295	486	371	375	61	196	501	348	353	111
	8.2	P/S	0	1	894	894	894	894	-	1850	1850	1850	1850	-
R. Tres Voltas	9	S	1	0	317	317	317	317	-	414	414	414	414	-
R. Funda	10	P/S	6	2	213	565	414	404	115	187	770	482	479	167
R. Ajuda	11	P	51	0	73	305	145	160	61	-	-	-	-	-

On São Miguel, 285 yellow eels and 37 silver eels were caught, with lengths ranging from 73-971 mm (mean = 487 mm, S.D. = 185 mm) and weights of 25-2095 g (mean = 393 g, S.D. = 327 g) (Table 2). Eels were caught in all but four sites (Sites 1.1, 5.2, 6.1, 6.2). Despite similar gradient profiles and proximity to one another (< 1 km), eels inhabited all three of the sequential cascade pools in Ribeira Cachaco (Sites 7.1-7.3), but only the most downstream pool in Ribeira Coelhas (Site 6.3).

Excluding sites that resulted in zero eel catches, the mainstem of rivers generally resulted in a low CPUE, with < 10% of CPUEs ≥ 0.5 eels/net-end/24 hrs, whereas all other river types typically had higher catches, with > 61% of CPUEs ≥ 0.5 eels/net-end/24 hrs (Fig.27). Indeed, the median CPUE of sites at the mainstem of rivers was significantly lower than the CPUEs of all other river type sites (Mann-Whitney *U*-test, $P < 0.05$).

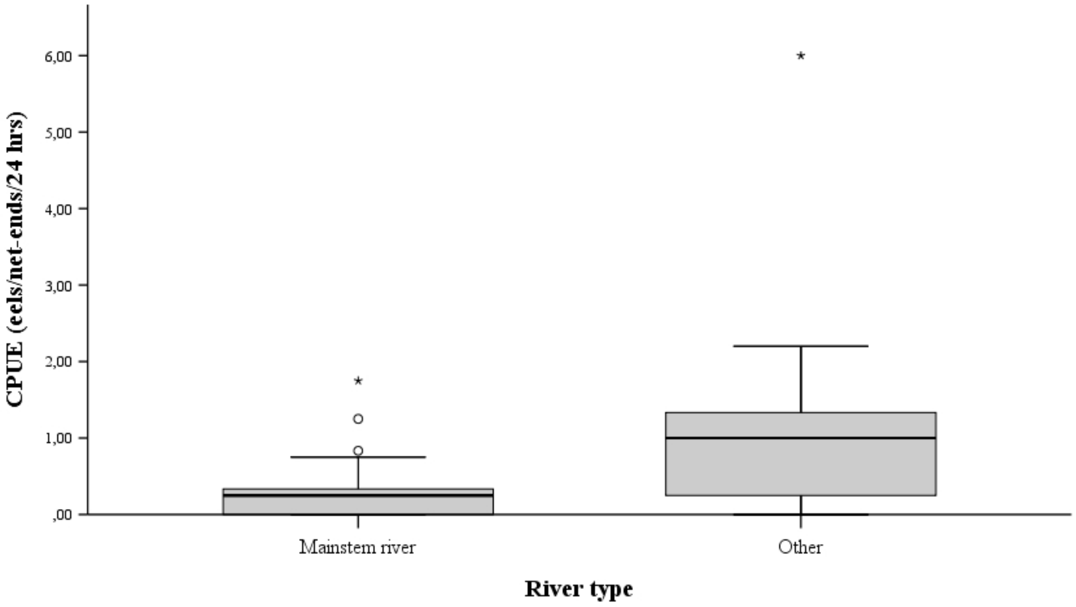


Fig. 27. Boxplots of abundance (CPUE) of eels at mainstem river sites and all other river type sites on São Miguel Island. IQR (interquartile range): Interval into which the central 50% of data fall. Median is indicated by the black bar in the box, circles indicate mild outliers and asterisks indicate extreme outliers. A catch of four eels in two fyke nets (Site 1.4) accounts for the extreme outlier of sites at mainstem river and a catch of six eels in a single concertina baited trap (Site 2.2) accounts for the extreme outlier of all other river types.

A total of 152 eels, with lengths of 260 - 971 mm (mean = 526 mm, S.D. = 129 mm) and weights of 25 - 1935 g (mean = 331 g, S.D. = 272 g), was caught at mainstem river sites (Fig. 28). A total of 119 eels were caught at all other river type sites with lengths of 132 - 935 mm (mean = 534 mm, S.D. = 142 mm) and weights of 80 - 2095 g (mean= 494 g, S.D. = 358 g).

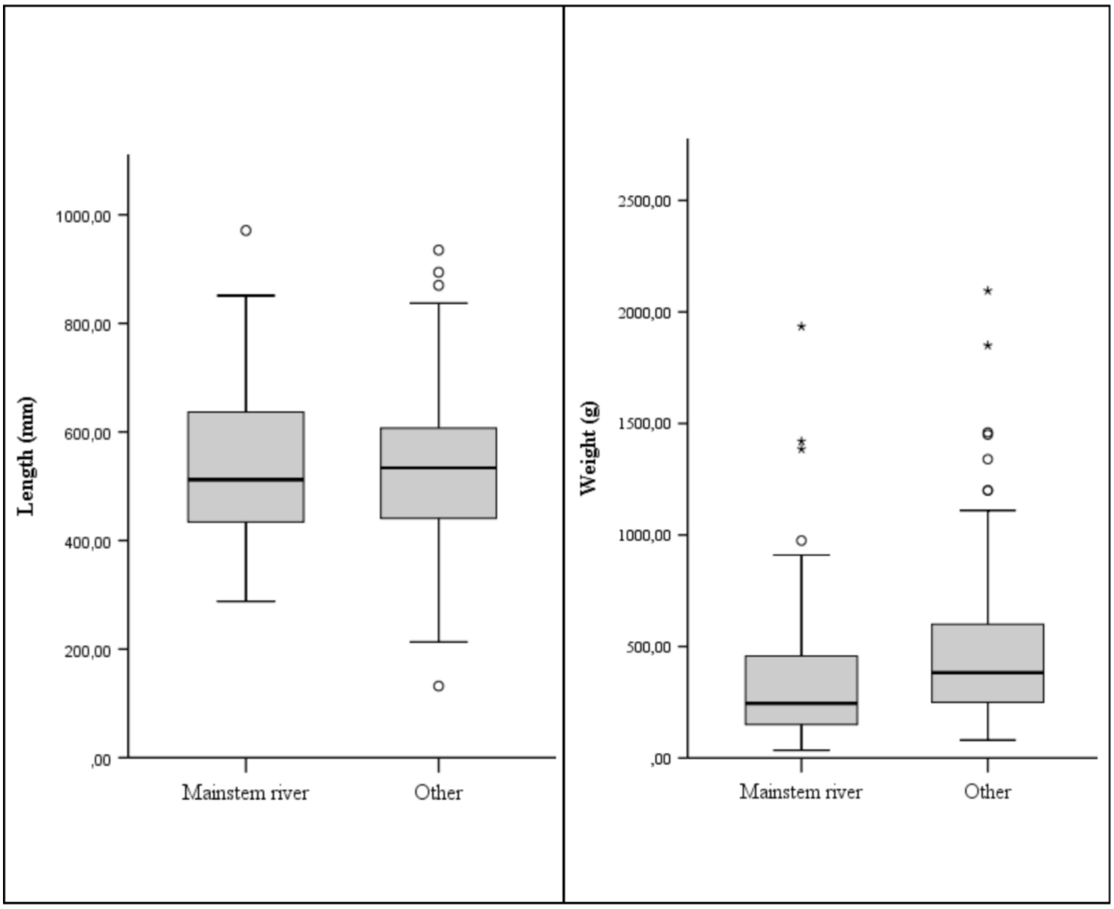


Fig. 28. Boxplots of eel length and weight at mainstem rivers and all other river types. IQR: Interval into which the central 50% of data fall. Median is indicated by the black bar in the box, circles indicate mild outliers and asterisks indicate extreme outliers. Four large silver females and a single yellow female account for all extreme outliers.

Length was not significantly different between sites at mainstem rivers (Mdn = 512 mm) and sites at all other river types (Mdn = 534 mm) (Mann-Whitney *U*-test, $P > 0.05$), whereas weight was significantly lower for sites at mainstem rivers (Mdn = 245 g) than for sites at all other river types (Mdn =383 g) (Mann-Whitney *U*-test, $P < 0.05$).

Sites at mainstem rivers and other river types did not have significantly different length distributions (2-sample Kolmogorov-Smirnov test, $P > 0.05$), however, weight distributions were significantly different (2-sample Kolmogorov-Smirnov test, $P < 0.05$).

4.3 Inter-watercourse spatial variations in eels of two river systems (Ribiera Quente and Povoação)

Ribeira Quente had a mean CPUE of 0.26 (± 0.31) eels/net-end/24 hrs resulting from a majority of small catches, whereas the Povoação system had a mean CPUE of 0.95 (± 1.27) eels/net-end/24 hrs, resulting from one large and several medium and small catches. CPUE was significantly higher at the Povoação system than at Ribeira Quente (Mann-Whitney *U*-test, $P < 0.05$).

A total of 123 eels was caught at Ribeira Quente with lengths of 260 - 971 mm (mean = 545 mm, S.D. = 127 mm) and weights of 25 - 1935 g (mean = 356 g, S.D. = 291 g) (Fig. 29). A total of 87 eels were caught at the Povoação system with lengths of 132 - 935 mm (mean = 549 mm, S.D. = 144 mm) and weights of 60 - 2095 g (mean = 441 g, S.D. = 364 g) (Fig. 29).

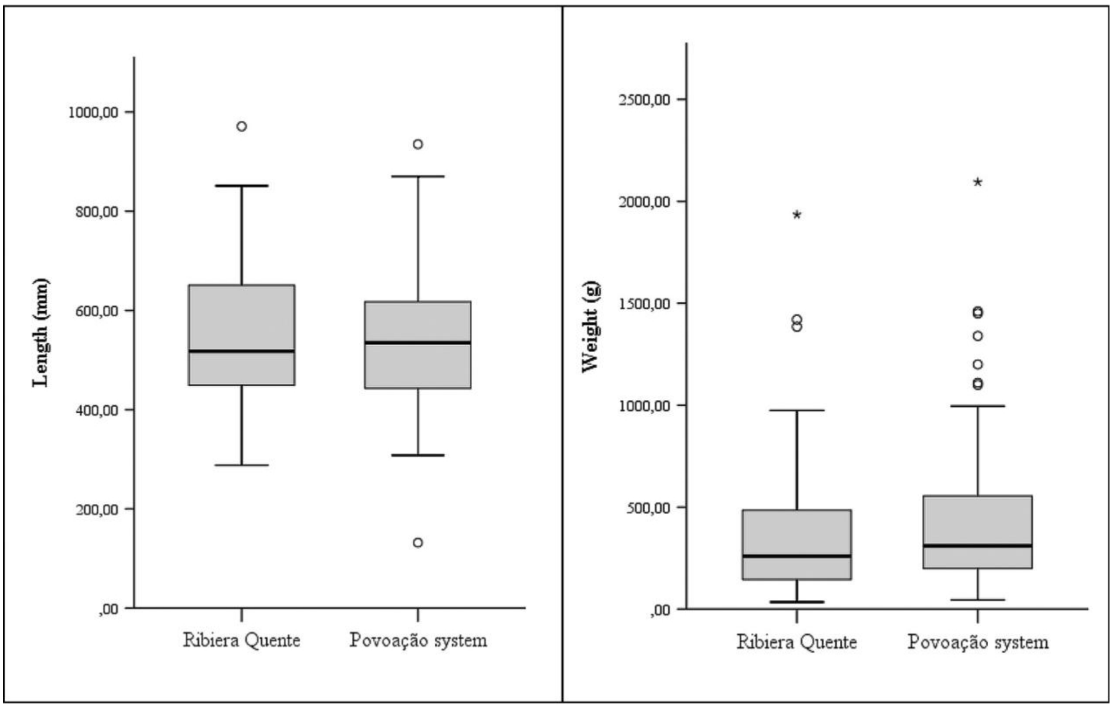
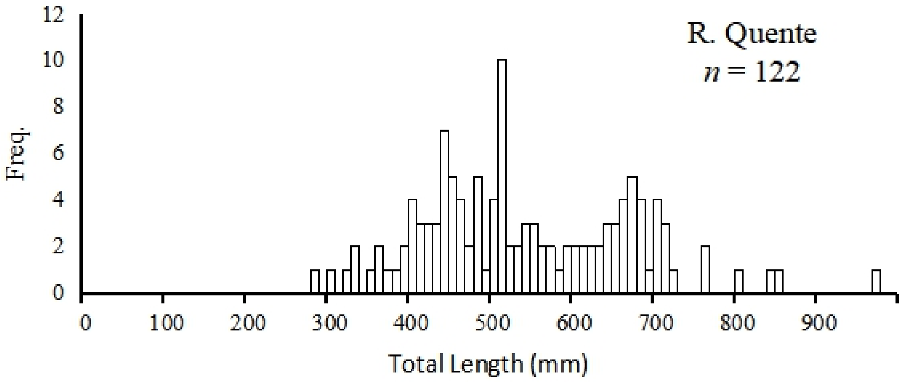


Fig. 29. Boxplots of eel length and eel weight at Ribeira Quente and the Povoação system. IQR: Interval into which the central 50% of data fall. Median is indicated by the black bar in the box, circles indicate mild outliers and asterisks indicate extreme outliers. The two heaviest eels (>1.9 kg) caught on the Azores, both silver females, account for the two extreme outliers in weight.

Length was not significantly different in Ribeira Quente (Mdn = 518 mm) and the Povoação system (Mdn = 535 mm) (Mann-Whitney *U*-test, $P > 0.05$), whereas weight was significantly different for Ribeira Quente (Mdn = 260 g) and the Povoação system (Mdn =310 g) (Mann-Whitney *U*-test, $P < 0.05$). Eel length and weight distributions were not significantly different in Ribeira Quente and Povoação (2-sample Kolmogorov-Smirnov test, $P > 0.05$). Length distributions of eels for each of these two systems can be seen in length-frequency histograms (Fig. 30).



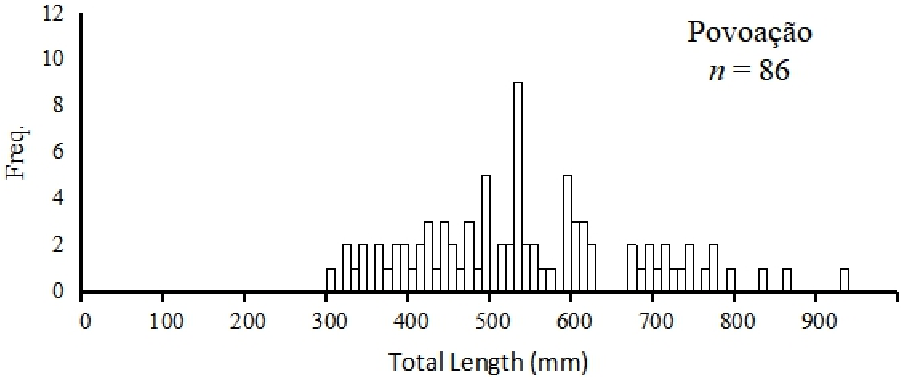


Fig. 30. Length distributions of eels captured from Ribeira Quente and Povoação (all sites combined). All eels, both yellow and silver, are included.

4.4 Intra-watercourse spatial variations in eels of a mainstem river (Ribiera Quente)

In Ribeira Quente, eels were caught in all three reaches, with 42, 35 and 46 eels for the upper, middle and lower reaches, respectively. CPUE remained fairly uniform throughout Ribeira Quente´s three reaches (Mdn = 0.25 - 0.29 eels/net-end/24 hrs, S.D. = 0.24 - 0.34 eels/net-end/24 hrs) and were not significantly different (Kruskal-Wallis H-test, $P > 0.05$). Size varied only slightly from the lower to the middle reach, with median length increasing by 3% (469 - 484 mm) and median weight decreasing by 6 % (200 - 188 g) (Fig. 31). From the middle to the upper reach, increases in size were more pronounced, with median length increasing by 32% (484 - 639 mm) and median weight increasing by 140 % (188 - 450 g) (Fig. 31). The greatest standard deviation in length resulted from the lower reach (S.D. = 115 mm), whereas for weight, it was the upper reach (S.D. = 337 g).

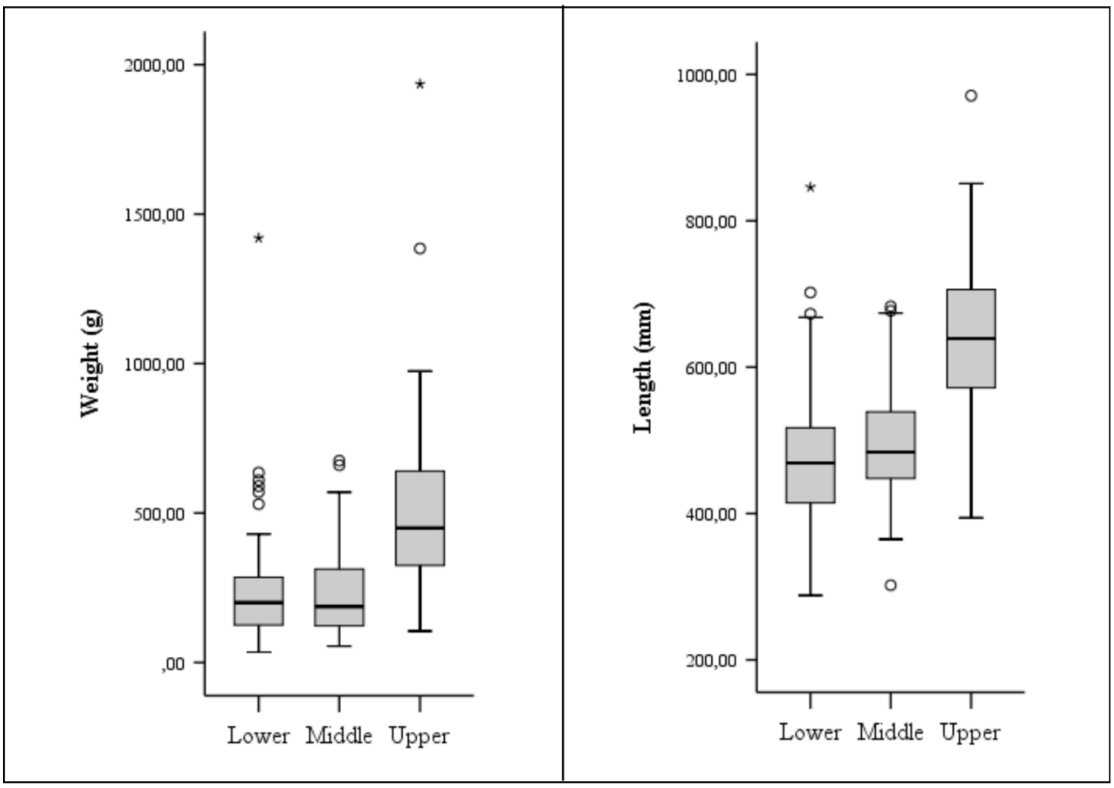


Fig. 31. Boxplots of eel length and weight at the three reaches of Ribeira Quente. IQR: Interval into which the central 50% of data fall. Median is indicated by the black bar in the box, circles indicate mild outliers and asterisks indicate extreme outliers. Extreme outliers are discussed in the text.

An extreme outlier was identified in the lower reach, a silver stage female with a total body length of 846 mm and weighing 1420 g (Fig. 32). An extreme outlier was also identified in the upper reach, another silver stage female and the longest individual caught on the Azorean islands surveyed as part of this research, with a total body length of 971 mm and a weight of 1935 g.

There was no significant difference between the median length and weight of the lower and middle reaches (Kruskal-Wallis H-test, followed by Dunn´s test with Bonferroni correction, $P > 0.05$), whereas the median weight and length of the upper reach were significantly higher than both the lower and middle reaches (Kruskal-Wallis H-test, followed by Dunn´s test with Bonferroni correction, $P < 0.05$).

There were no significant differences in the length and weight distributions in the middle and upper reaches (2-sample Kolmogorov-Smirnov test, $P > 0.05$), whereas the weight and length of the upper reach had a significantly different distribution, in comparison to both other reaches (2-sample Kolmogorov-Smirnov test, $P < 0.05$). These differences were due to a lack of smaller individuals in the upper reach and a lack of larger individuals in both the lower and middle reaches. This uneven distribution of length is illustrated in length-frequency histograms (Fig. 32).

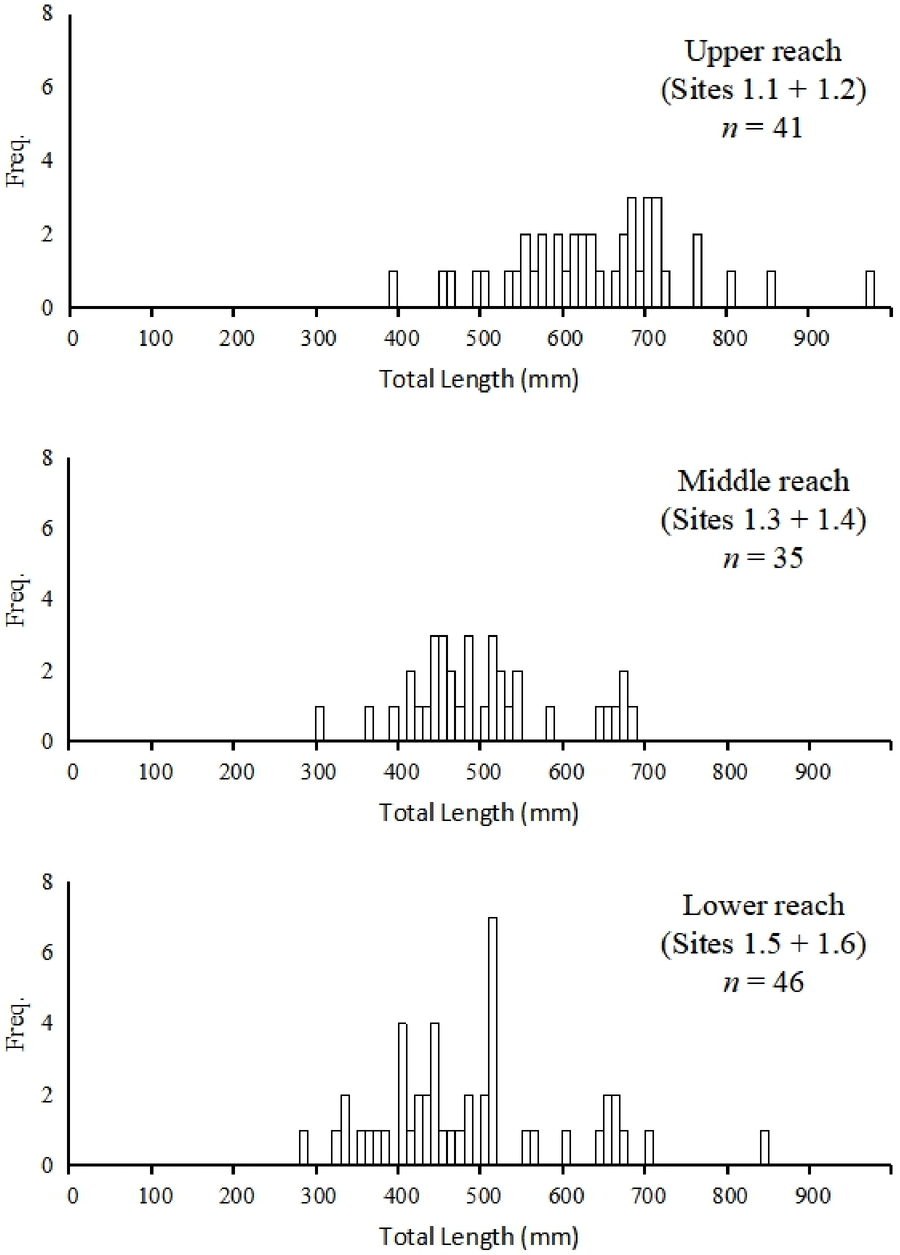


Fig. 32. Length-frequency histograms for Ribeira Quente´s three reaches. All eels, both yellow and silver, are included.

4.5 Intra-watercourse spatial variations in eels of a mainstem river compared to its tributary (Povoação)

Over 80% of the Povoação river system eels were caught at Sites 2.2 (45 eels) and 2.3 (28 eels) on the tributary of Ribeira da Lomba Grande. Zero eels were caught at Site 2.1, also on the Ribeira da Lomba Grande tributary and directly upstream of a cascade ≈20 m in height.

Sites 2.4 and 2.5, at the mainstem rivers of the Povoação system (Ribeira do Purgar and Ribeira dos Lagos) resulted in catches of eight and six eels, respectively. The fishing effort at mainstem rivers (60 net-ends/24 hrs) was approximately equivalent to fishing effort at the tributary (54 net-ends/24 hrs). Excluding Site 2.1, where there were zero eel catches, the maximum and mean CPUE of Ribeira da Lomba Grande tributary were 6 and 1.59 (± 1.51) eels/net-end/24 hours, respectively. Catches of eels at the mainstem rivers resulted in a maximum and mean CPUE of 0.5 and 0.25 (± 0.17) eels/net-end/24 hours, respectively. The CPUE values for the tributary were a result of São Miguel Island´s largest catch of 22 eels/ 24 hrs and many medium-sized catches of eels. The CPUE values for the mainstem rivers were a result of many small catches of eels. The CPUE at Ribeira da Lomba Grande tributary (Mdn = 1.17 eels/net-end/24 hrs) was significantly higher than the CPUE at the mainstem rivers of the Povoação river system (Mdn = 0.25 eels/net-end/24 hrs) (Mann-Whitney *U*-test, $P < 0.05$).

Eel lengths at the tributary (mean = 576 mm, S.D. = 136 mm) were generally much larger than at the mainstem rivers (mean = 410 mm, S.D. = 103 mm) and eel weight was also much larger at the tributary (mean = 490 g, S.D. = 374 g) than at the mainstem rivers (mean = 186 g, S.D. = 131 g) (Fig. 33). Median weight and length at the tributary were significantly higher than at the mainstem rivers (Mann-Whitney *U*-test, $P < 0.05$).

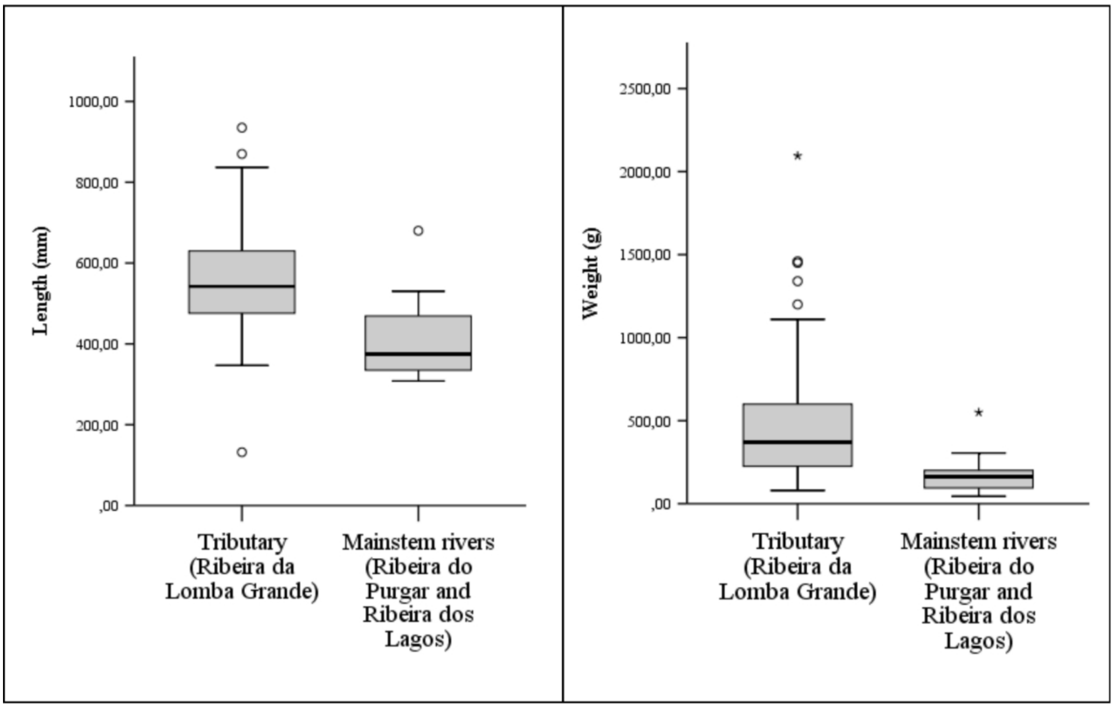


Fig. 33. Boxplots of eel length and weight at a tributary and mainstem rivers on the Povoação river system. IQR: Interval into which the central 50% of data fall. Median is indicated by the black bar in the box, circles indicate mild outliers and asterisks indicate extreme outliers. Extreme outliers are discussed in the text.

Two extreme outliers exist in the boxplot for weight (Fig. 34). The tributary outlier is the island's heaviest eel (2095 g), whereas the outlier at the mainstem river (550 g), is only an extreme in relation to the rest of its mainstem river grouping, all ≤ 305 g. The weight and length distributions of Ribeira da Lomba Grande tributary were significantly different, in comparison to both mainstem rivers (2-sample Kolmogorov-Smirnov test, $P < 0.05$). These differences were due to a lack of large and medium-sized individuals at the mainstem river sites and few small individuals at the tributary sites, as seen in length-frequency histograms (Fig. 34).

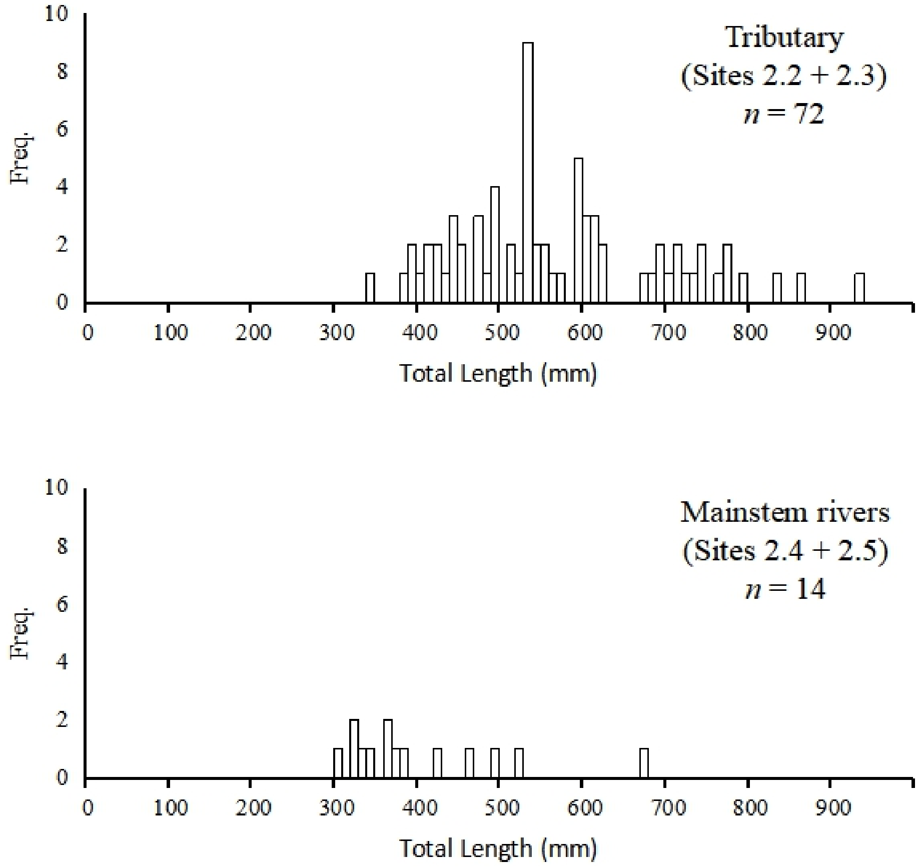


Fig. 34. Length-frequency histograms for a tributary and mainstem rivers on the Povoação river system. All eels, both yellow and silver, are included.

4.6 Temporal variations in silver eel abundance in the Ribeira Quente, the largest river on São Miguel Island

A total of 22 silver eels was caught in Ribeira Quente during the sampling period. A peak in male silver eel catch was observed from 29 October until 5 November, when seven were caught; the eighth and final male silver eel was caught on the night of 12 November (Fig. 35). Fourteen female silver eels were caught in the sampling period (21 October - 3 December), but there was no clear peak in abundance (Fig. 35). Three silver eels, the highest number during a single 24 hr period, were caught on 29 October.

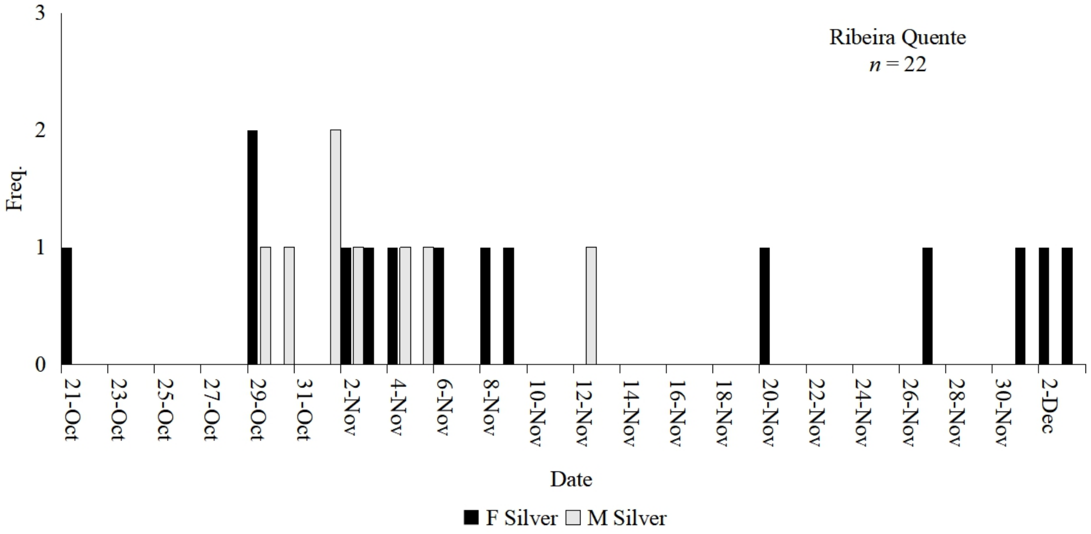


Fig. 35. Count of male and female silver eels caught in Ribeira Quente.

A statistically significant, moderate positive correlation between date and silver eel length was observed, with the length of silver eels increasing from 21 October - 3 December (Spearmann´s rank correlation: rs = 0.483, $p < 0.05$), which corresponded with a general increase in female length and a decrease in male abundance during the period (Fig. 36).

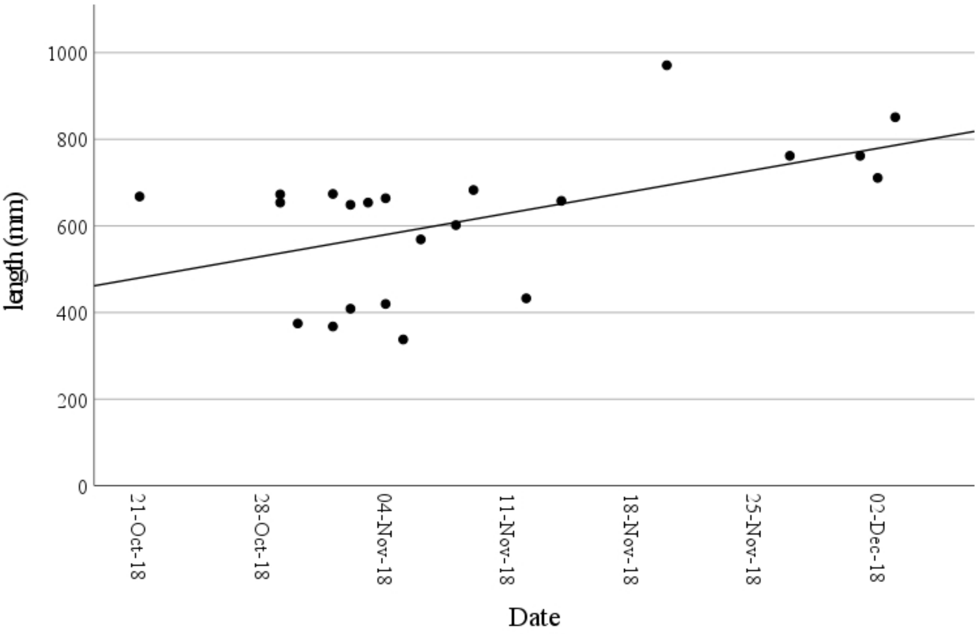


Fig. 36. Length of silver eels against the date in Ribeira Quente.

The CPUE for silver eels was low throughout the study period, with a maximum and mean of 0.2 and 0.05 (± 0.05) eels/net-end/24 hrs, respectively.

The number of silver eels caught and the numbers of nights sampled during each lunation period were; two eels at the first lunar quarter (six nights sampled), one eel at the full lunar quarter (three nights sampled), fourteen eels at the third lunar quarter (thirteen nights sampled) and five eels at the new lunar quarter (eight nights sampled). CPUE remained similar throughout the first (mean = 0.034 (± 0.054) eels/net-end/24 hours), full (mean = 0.042 (± 0.072) eels/net-end/24 hours), third (mean = 0.061(± 0.056) eels/net-end/24 hours) and new (mean = 0.042 (± 0.041) eels/net-end/24 hours) lunar quarters (Fig. 37).

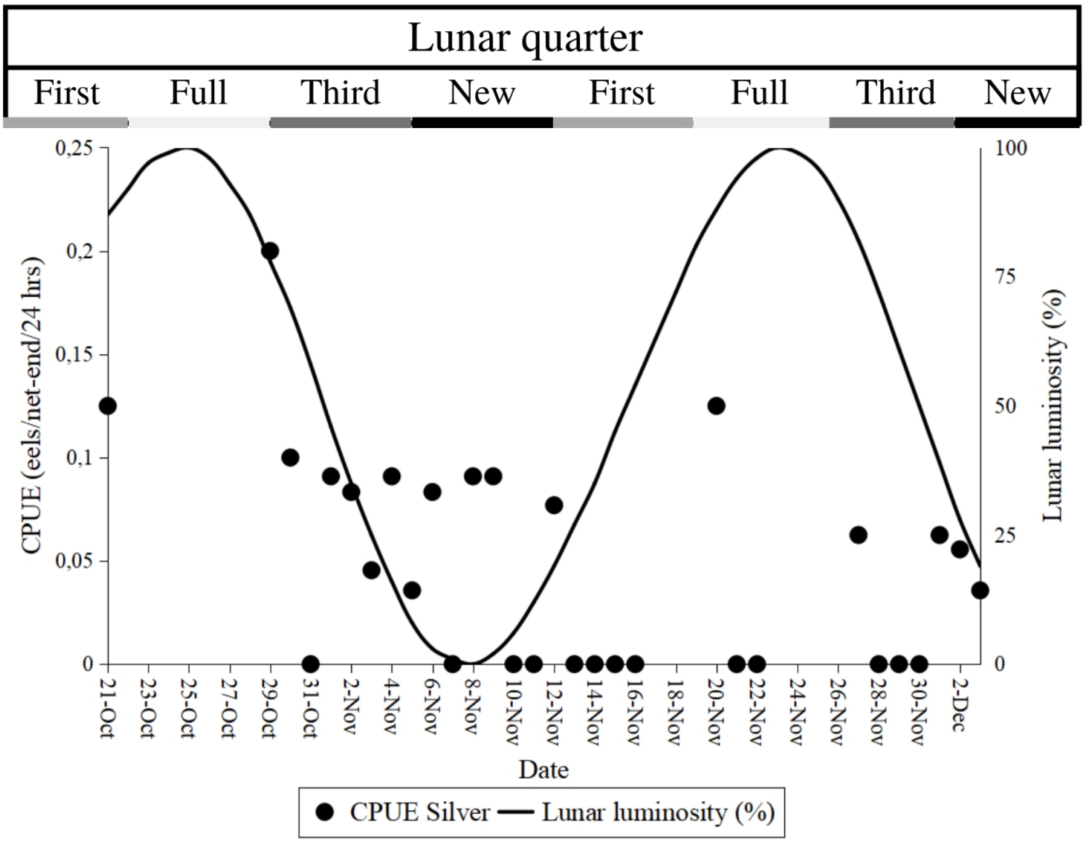


Fig. 37. CPUE of silver eels in Ribeira Quente, against the percentage of the moon illuminated (lunar luminosity) and the four quarter lunar phases. Dates refer to catch retrieval rather than gear deployment.

There were no significant differences in the mean CPUE of silver eels caught on each of the lunar phases, or the mean number of silver eel caught on each of the lunar phases (one-way analysis of variance (ANOVA): Scheffé's post hoc comparison, $P > 0.05$).

The majority of silver eel catches occurred when the river flow was at summer levels and only on four dates (21 October, 4 - 5 November, 3 December) did silver eel catches coincide with high flows > 90 percentile (Q10 = 1081.15 l/s) for the mean daily flow of 2018 (Fig. 38).

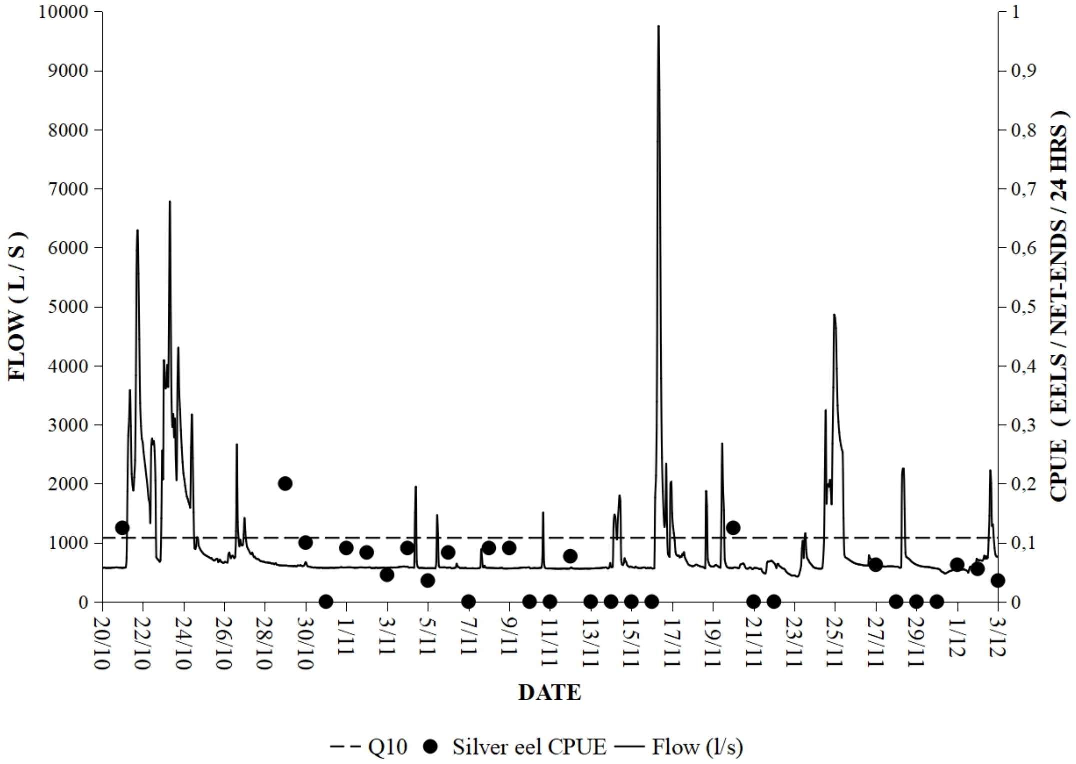


Fig. 38. Hourly mean flow of Ribeira Quente during the sampling period, showing the 90 percentile flow (Q10) of 2018 and silver eel CPUE. Silver eel CPUE values have been plotted at midday (12:00) on the date of eel retrieval.

There was no linear relationship between silver eel catch and river flow as assessed visually (Fig. 39).

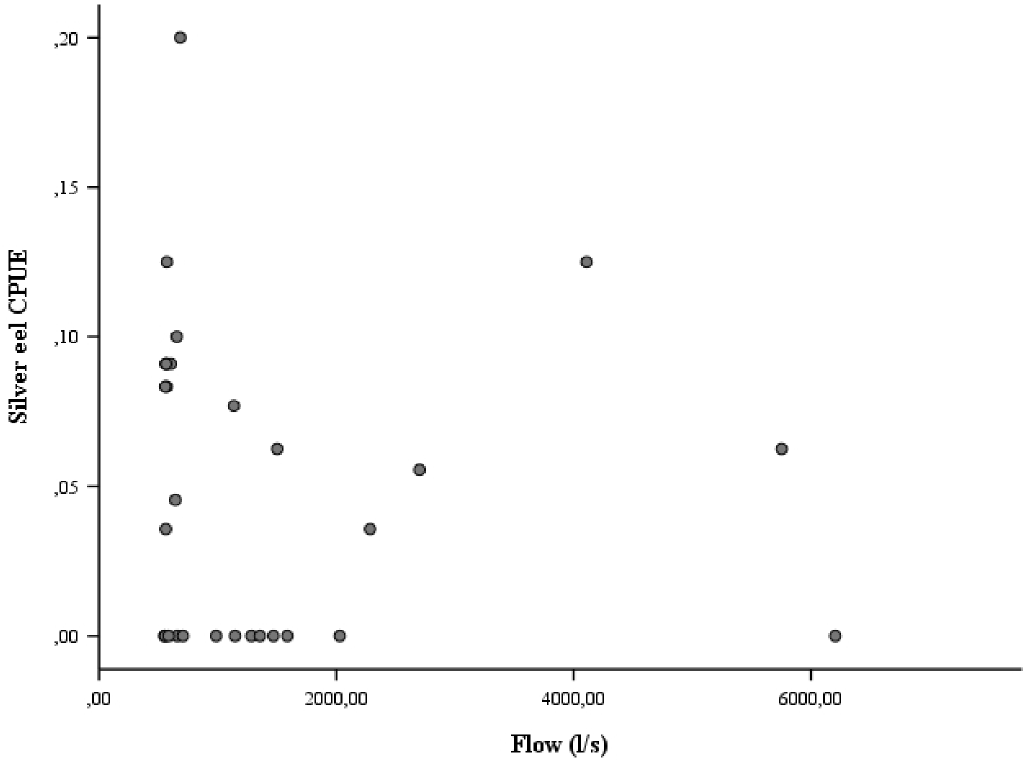


Fig. 39. CPUE of silver eels, against daily mean river flow in Ribeira Quente. Dates refer to catch retrieval rather than gear deployment.

On only two of these dates (21 October and 3 December) were eels captured following a 24-hour net deployment when high flow occurred at night. The silver eel captured on 3 December was the only individual caught coinciding with a high flow that occurred between sunset and midnight. There were no significant differences in CPUE of silver eels or total individuals of silver eels caught on river flows > 90 percentile (1081.15 l/s) and river flows < 90 percentile (Mann-Whitney *U*-test, *P* > 0.05).

5. Discussion

A. anguilla is recognized as the Azores Archipelago´s only endemic freshwater fish species (Morton and Britton 2003), but its distribution and demography has not been studied and due to a lack of research, it is unknown, for example, whether freshwater individuals reach the silver migratory phase. The current study has proven that each of the four study islands (Terceira, Santa Maria, Flores and São Miguel) support yellow eels and on Islands where autumn sampling was conducted (Terceira, Flores and São Miguel), silver eels were caught in fresh and brackish waters. Numerous yellow eels were caught on Santa Maria Island in May, but no sampling was conducted during the autumn season, when silvering metamorphosis occurs and the majority of silver eels are captured.

5.1 Eel distribution in river systems

Sampling suggested that eels inhabited all but one of the twenty river systems investigated, with the latter likely a result of insufficient sampling effort (one night). As mentioned, the Azores islands are relatively small, with total areas of 17 - 759 km² and all maximum altitudes, bar Graciosa Island, are above 500 m. This results in relatively steep river profiles and small river basins, with short flashy rivers eroding deep and reasonably straight channels, often intercepted by multiple cascades near the rivers' sources, and coastal discharge. Mainstem rivers were typically intersected by a large cascade (5 - 300 m in height) within their upper reach and whilst eels were caught downstream of these cascades, no sampling was performed upstream, therefore limiting the knowledge of eel distribution upstream of these mainstem river cascades. Streams were typified by multiple cascades along their length and sampling, both downstream and upstream of these cascades gave mixed results, as shown for Ribeira Cachaco and Ribeira Coelhas (two parallel rivers on São Miguel Island). Despite similar habitat and gradient profiles and each with three sequential pools backed by cascades approximately 3 m, 3 m and 10 m in height, eels were shown to inhabit all three of the sequential cascade pools in Ribeira Cachaco, but only the most downstream in Ribeira Coelhas. This variable distribution suggests that whilst upstream eel movement may not have been completely restricted by cascades, it may have been influenced by variations in individual behaviour, perhaps in response to different connectivity at each of the most downstream pools. Variability in eel movement behaviour has been widely reported, and Feunteun *et al.* (2003) identified four distinct movement behaviours that were driven by density and variations in habitat preference according to age or size. In that study, eels were identified as either "pioneers" that migrate to a system's upper boundaries, "founders" that settle in the first available habitat, "home range dwellers" that establish themselves in an area for an extended period of time, or "nomads" that move upstream as they search for suitable habitat (Feunteun *et al.* 2003). In the case of Ribeira Cachaco and Ribeira Coelhas, their most downstream pools each differed in ocean connectivity. Ribeira Cachaco´s most downstream pool was approximately 20 m above sea level, with downstream flow passing between/under a substrate of large rocks at a steep gradient before connecting with the ocean. Whereas Ribeira Coelhas´s most downstream pool was < 10 m above sea level, had an uninterrupted downstream flow at a gradual gradient, was directly connected with the ocean and experienced tidal inflows. It is possible that Ribeira Coelhas´s most downstream pool may have provided an attractive habitat in which most eels chose to remain, because of the increased productivity synonymous with brackish conditions (Helfman *et al.* 1984) and direct connectivity to a marine habitat for foraging. It seems likely that in the most downstream pool of Ribeira Cachaco, where there was no ocean connectivity or brackish conditions, it would be advantageous for eels to move upstream in search of a more suitable habitat. It is also possible that eels were present in all of the cascade pools sampled for both rivers, but in low numbers.

In a tributary river (Ribeira da Lomba Grande) of the Povoação river system, many eels were caught in a pool between a downstream cascade ≈ 8 m in height and an upstream cascade ≈ 20 m in height, whereas no eels were caught upstream of the latter. From the current study it can be surmised that, although vertical cascades ≤ 10 m do not completely obstruct the upstream distribution of eels in Azorean rivers, they may have a limiting effect. Studies have shown that eels of all sizes can climb vertical surfaces via surface irregularities and vegetation (Tesch 1977; Deelder 1984; Knights and White 1998), with vegetation being prevalent on vertical cascade surfaces in the Azores. Whilst no eels were caught above the upstream cascade at Ribeira da Lomba Grande, a prevalence of vegetation on vertical cascade surfaces in the Azores should, in theory, permit the upstream passage of at least small eels. At the Moses-Saunders Dam in Canada, American eels were shown to ascend a series of trough sections that scaled the dam in a zig-zag fashion, climbing a total of 29 m high in altitude and 156 m in distance (Whitfield and Kolenosky 1978). Although a critical cascade height for eel passage in the Azores is unknown, a similar pattern of climbing as in the previous example would theoretically permit eels to ascend cascades much higher than the 10 m demonstrated by this study. A lack of eel presence upstream of Ribeira da Lomba Grande´s ≈ 20 m cascade may be explained by favourable conditions below the cascade, rather than the cascade forming a impassable barrier.

There are few hydroelectric facilities on the Azores, and although two hydroelectric dams exist on the river Ribeira Quente, elver traps monitored by EDA (Electricidade dos Açores) revealed the unassisted passage of elvers over the largest dam (≈ 20 m in height) and sampling demonstrated eels were distributed throughout the entire river system. Although these barriers did not form an impassable barrier to the upstream migration of elvers/glass eels at Ribeira Quente, the river system of Ribeira da Praia was completely altered by hydroelectric facilities, with almost all water diverted from the original river channel via pipes. Two semi-isolated, sequential cascade pools were located on this de-watered reach, with minimal to no flow entering them, and just a single large eel (1.04 kg) was caught in the upstream pool, despite sampling in both. Likely, the eel was essentially trapped in the pool and the lack of connectivity also made it unlikely that new recruits would be able to enter the cascade pools or the river upstream. This was the only case where anthropogenic activity was considered to completely alter the upstream limit of eel distribution on the Azores.

5.2 Eel distribution in lakes

Despite extensive sampling effort at six lakes, eels were only caught in the single brackish lake sampled (Lago da Parque do Paul), on Terceira Island. As in mainland Europe, the distribution of eels in the Azores will be negatively influenced by barriers obstructing connectivity (Feunteun *et al.* 1998; van der Meer 2012), distance from the ocean (Naismith and Knights, 1993) and increasing altitude (Foldvik *et al.* 2019). The Azores islands are typically small in land coverage (maximum width of ≈ 15 km) and the majority of lakes of the Azores are located at the central, highest portion of the islands, in isolated extinct/dormant volcanic craters, with high walls and no connectivity. This high altitude, isolated form is likely unsuitable for eel habitation and was studied at two locations, Lagoa Rasa (> 500 m altitude on Flores Island) and Lagoa das Sete Cidades (259 m altitude on São Miguel Island). Two study locations impacted by anthropogenic barriers, Lagoa das Furnas (281 m altitude on São Miguel Island) and Fazenda water impoundment reservoir (139 m altitude on Flores Island), had their single outflows altered and regulated by anthropogenic structures, reducing and possibly obstructing eel passage altogether. The lake Poço da Ribeira do Ferreiro (263 m altitude on Flores Island), whilst having no eel catch, did have limited connectivity to a mainstem river (Ribeira Grande) but only via a single small tributary river that was intersected by multiple weirs and cascades. As shown, the five lakes with zero eel catch had limited connectivity, yet where eels were caught at Lago da Parque do Paul (≤ 20 m altitude), there was direct connectivity to the ocean. It can be suggested that poor connectivity limits eel distribution in lakes of the Azores and increased altitude/distance from the ocean are associated with the prevalence of poorly connected natural crater lakes, rather than being primary influential factors. The limiting capacity of barriers on the distribution of eels and other fish species is well documented (Verreault *et al.* 2004; Lasne *et al.* 2008; Acou *et al.* 2009). To overcome some barriers, eels can climb wet, vertical walls or travel overland (Knights and White 1998; Tesch 2003), however, since many Azorean lakes have no connecting overland flow, natural colonization in these lakes is unlikely. Independent of geography and connectivity, the utilization of only one standardized sampling technique may also have influenced eel catch at lakes. Fyke netting was adopted as the primary sampling technique throughout all islands and the accurate representation of the eel population using this one technique, at discrete locations, is not practical in even small lakes (Jurajda *et al.* 2009). Therefore, it can be argued that many lakes may support eel populations but the catch was limited by effort, identification of the correct sampling location within each lake, the implementation of just a single standardized method of sampling and perhaps a reduced catch probability due to low numbers of eels.

5.3 Eel abundance and size structure

The abundance of eels differed between islands, probably because all islands differed greatly in habitat type and availability, although some of the differences may be attributed to the exploratory nature of sampling and the targeted sampling of favourable eel habitats as identified throughout the progression of the study. Although eels were distributed throughout most river systems, their abundance in systems was generally low. By far the greatest abundance of eels was found in the brackish lake, Lago da Parque do Paul, sampled on Terceira Island. For comparison, a total of 261 eels was caught at this single site on Terceira in 44 net-ends/24 hrs, whereas throughout 11 river systems and two lakes on São Miguel, 335 eels were caught in 1055 net-ends/24 hrs. Similar to an estuarine habitat, the utilisation of a sheltered brackish habitat (with low flow and direct ocean connectivity) would be advantageous to eels (Helfman *et al.* 1987; Arai *et al.* 2006), with high food availability, low turbulence, plentiful shelter, reduced marine predators and low osmoregulatory costs (Blaber *et al.* 1985), likely encouraging eels to live in Lago da Parque do Paul. No substantial river systems exist on Terceira and the one stream that does flow throughout the year was shallow and unlikely to support many eels. Since even the lake itself was not fed by substantial rivers/streams, eels recruiting to Terceira would be unable to diffuse far inland and thus in combination with the advantages of lake residence, the high eel abundance may also have resulted from a lack of alternative habitats. Arai *et al.* (2006) demonstrated that eels in Ireland were mostly limited to marine or freshwater environments, because Ireland´s high altitude, coastal land patterns generally lacked estuarine habitats. At Terceira Island, a lack of both estuarine and freshwater habitats likely forces eels to reside in either the lake or marine waters. Analyses of otolith Sr:Ca ratios in post-elver *A. anguilla* demonstrated that eels display a high behavioural plasticity (Tesch 2003), with some eels functioning as intermediates, living in estuaries and moving between marine and fresh waters throughout their growth (Tzeng *et al.* 2000; Harrod *et al.* 2005; Arai *et al.* 2006). Therefore, it is quite possible that many eels at Terceira Island function as intermediates, utilizing the lake for shelter but using both the lake and marine waters for foraging. Higher density, coastal populations are also usually associated with the prevalence of males (Davey and Jellyman 2005), which throughout their range attain mean lengths of 350 - 460 mm and extremes of 290 and 540 mm (Tesch 2003). Within Lago da Parque do Paul, mean eel length was 482 mm and > 60 % (161 eels) were > 460 mm in length. Sex differentiation has been shown to conclude when body lengths of > 350 mm have been attained (Colombo *et al.* 1984), so with only 7 eels (2.7%) at a body length < 350 mm and > 60 % eels > 460 mm caught in the lake during the study, it can be suggested that a higher proportion of the eels sampled at this coastal lake may be female. This contrasts with other studies, whereby estuaries and the lower reaches of rivers show a higher proportion of males (Helfman *et al.* 1987; Tesch 2003; Davey and Jellyman, 2005). On São Miguel Island, a peak in silver male catch was observed in the Ribeira Quente (29 October until 5 November) and the final male silver eel was caught on the night of 12 November, whereas female silver eels were caught throughout the entire study period, ending on 3 December. Consistent with other studies, where male silver eels are demonstrated to leave earlier than females (Deelder 1970; Haraldstad and Vøllestad 1985), a lack of smaller eels at the time of sampling (9-16 December) on Terciera Island, may be in part due to silver males having already departed. This is of course speculation, based on the findings of other studies and male size at Terceira Island may fall outwith the expected male mean lengths.

As mentioned, eel abundance was demonstrated to be relatively low in river systems and a distinct difference in eel abundance was shown between mainstem rivers and all other river types (e.g tributary rivers and streams). At the mainstem rivers, seasonal fluctuations in flow were pronounced and although low-flow summer conditions enabled the growth of aquatic and riparian vegetation, common high flows (> Q10) from autumn to spring removed the majority of vegetation and induced high levels of river traction. Therefore, during a large proportion of the year, the available habitat in mainstem rivers was low because aquatic/riparian vegetation lacked and substrate was constantly shifting. This may explain why the highest abundances of eels at large river systems in autumn/winter were found where available habitat was more permanent (in tributary rivers and beneath the large undercut cascades that commonly intercepted the upper reach of mainstem rivers), a widely reported observation for eel *Anguillid* species (Burnet 1952; Hegediš *et al.* 1996; Domingos *et al.* 2006). A more permanent and likely more productive habitat, may also explain why there was a significant difference in weight, but not length, between mainstem rivers and other river types.

This contrast in abundance was most defined at Ribeira da Lomba Grande, a tributary of São Miguel Island´s Povoação river system. At this tributary 73 eels were caught with a maximum CPUE of 6 eels/net-end/24 hrs, whereas a similar effort at two mainstem river sites of the same river system, produced a total of only 14 eels and a maximum CPUE of just 0.5

eels/net-end/24 hrs. Within this river system, by direct daily observation, fluctuations in flow appeared less pronounced at the tributary than at its mainstem rivers and the tributary's deep pools with undercut walls provided a greater proportion of permanent sheltered habitat. This pattern of eel abundance may differ during more favourable river conditions in summer, as demonstrated in other studies where eels exhibited seasonal movements between productive feeding areas (Feunteun *et al.* 2003; Rosten *et al.* 2013) and also seasonal movement between suitable habitats to survive winter freezes (Tomie *et al.* 2015). Whilst favourable habitat is likely the primary influence of abundance, this particular tributary had several further attributes that may have further influenced eel abundance, most notably two cascades of 8 m and 20 m. The 20 m upstream cascade was shown to be a likely barrier to further upstream migration and as demonstrated in other studies, a barrier may cause eels to congregate downstream rather than dissipate further upstream (Feunteun et al. 1998; Domingos *et al.* 2006). This pool, where 45 eels were caught, was between two cascades and it is possible that eels would be deterred from moving back downstream over the 8 m cascade where the flow was constricted, a behaviour demonstrated in flume (Newbold *et al.* 2015) and fine-scale telemetry studies (Piper *et al.* 2015). The high abundance of eels confined between these cascades may have acted as an attractant to other eels, with conspecific odours shown to stimulate positive chemotaxis in other studies (Briand *et al.* 2002). In addition, throughout this study, multiple rat carcasses and the entrails of large mammals were also observed within the tributary´s waters at every visit, and as known opportunistic scavengers (Tesch 2003), the odour of animal carcasses may have attracted further foraging eels. It is suspected that a farm butchers its animals upstream before depositing them in the tributary, where rats were probably feeding on carcasses and were drowned during high flows. This high availability of food may partially explain why there was a notable difference in eel weight for the Povoação river system (where 84% of eels were caught at Ribeira da Lomba Grande tributary), compared to the other large river system studied (Ribeira Quente) and why seven of São Miguel Island´s 15 eels > 1 kg were caught at this tributary. Eels caught at the tributary had a mean body length of 576 mm and it was demonstrated that only 15 eels (20.5%) of the 73 eels captured at the tributary were < 460 mm in body length. With a mean body length greater than the upper extreme of male size (540 mm) for their range (Tesch 2003), and with almost 80% of eels with a body length above the normal mean upper limit expected for males (460 mm), it suggests that a higher proportion of eels at the tributary were females. As mentioned previously, a higher proportion of males would generally be expected at higher densities and with the tributary demonstrating to have the highest abundance on São Miguel Island, a possibly higher proportion of female eels, similarly to Terceira Island, contrasts with the majority of other studies (Davey and Jellyman 2005).

In contrast to other areas where European eels have been studied, a typical characteristic of Azorean river structure and especially prevalent on Santa Maria and Flores Islands, was large coastal pools < 500 m from the ocean, with ocean connectivity (that fluctuates with the tide and river flow), minimal vegetation and an upstream cascade up to 300 m in height. Eel abundance in these cascade pools was relatively high when compared to most other river types.This may be a result of small eels (glass eel and elver) that recruit during conditions of greater flow or via minimal sub-surface flows (under pebble substrate) and essentially become trapped by a lack of sufficient upstream or ocean connectivity as they grow. Nearly all eels caught within these pools had multiple bite marks along the length of their bodies, irrespective of being caught together or alone in a net, and the lack of predators and the configuration of the bite marks makes it almost certain that they originate from conspecifics. With higher densities, a lack of other fish species and minimal invertebrate prey items, aggressive behaviour and cannibalism may feature more heavily in these populations (Degani and Bamidgeh 1983). It was also observed that in each of these pools, many eels were active during daylight and with, *A. anguilla* known to generally exhibit negative phototaxis, with normal activity usually confined to low light conditions (Tesch 2003; López-Olmeda 2012), it is possible that the observed diurnal activity may have been adopted as a competitive or cannabalism avoidance strategy due to the minimal food availability and high eel density. This diurnal behaviour may also be a result of a lack of other predatory species and human interaction.

According to most studies, eel abundance/density within a river system usually decreases with distance from the ocean (Naismith and Knights 1993; Chancerel 1994; Davey and Jellyman 2005), however for Ribeira Quente and Faial da Terra, abundance increased with distance from the ocean and was greatest at the most upstream point of sampling. This is similar to the findings of Laffaille *et al.* (2003) at a small catchment of northwest France and seems to suggest that, despite seemingly low densities, many eels do not settle in the first available freshwater habitat they find. Instead, the often poor and fluctuating habitat encountered at the lower reaches of mainstem rivers, perhaps stimulates adoption of the "nomad" movement behaviour, pushing eels upstream in search of more suitable habitat, especially if an estuarine environment is lacking (Feunteun *et al.* 2003). Although this density pattern in rivers did not follow the norm, mean and median eel size increased upstream, as in other studies (Domingos *et al.* 2006; Lasne and Laffaille 2008; Lasne *et al.* 2008). It was apparent that the presence of large individuals was lacking in the lower reaches of mainstem rivers, whereas the presence of smaller individuals was lacking in the upper reaches.

The observation of primarily larger individuals in the upper river reaches support this idea that individuals have adopted a "nomad" behaviour, whereupon smaller individuals in lower reaches have continously migrated further upstream in search of more suitable habitat and then upon finding it, have settled and grown. Although markedly greater than the lower river reaches, the still relatively low abundance of eels in the upper reaches may account for the prevalence of larger individuals, as similarly low abundance conditions have shown to frequently produce females, the larger of the sexes (Davey and Jellyman 2005). A lack of larger individuals and the prevalence of smaller individuals in lower river reaches, may result from fluctuating and somewhat dangerous habitat, as limited shelter may make survival difficult for larger eels during the regular high flow events of winter.

5.4 Insights into the timing of silver eel migration

Silver eels were caught at the brackish lake on Terciera Island, as well as at several river systems on Flores and São Miguel Islands, although the only river system sampled on consecutive nights for an extended period was Ribeira Quente. The completion of silvering is timed to coincide with specific environmental conditions, namely conditions that result in increased river discharge and low light (Okamura *et al.* 2002b; Bruijs and Durif 2009), with such conditions being prevalent in autumn to spring. The timing of migration differs with latitude (Vøllestad *et al.* 1986) and for the Azores islands, it was hypothesised that downstream seaward migration would likely begin in September and not peak until November, as observed at similar latitudes (Durif and Elie 2008; Bruijs and Durif 2009). In the Azores, the earliest eel that displayed late-stage silver morphological characteristics and appeared to be mid-migration was intercepted at the beginning of October (10/10/2018) on Flores Island, whereas the latest was intercepted on São Miguel Island, in early December (03/12/2018), the final day of the study and could indicate that silver eel migration was still ongoing post study.

In Ribeira Quente, female silver eels were caught throughout the sampling period, with no clear peak in the catch, whereas a peak in male silver eel catch was observed from 29 October until 5 November, with the final male silver eel caught on the night of 12 November. This would suggest that males may migrate earlier than females, a pattern that is generally observed throughout the range of *A. anguilla* (Deedler, 1970; Haraldstad and Vøllestad, 1985; Sandlund *et al.* 2017). In other studies, the timing of silver eel migration has been correlated with increased river discharge (Lowe, 1952; Tesch, 1977, 2003), although in the Azores, the flashy nature of rivers means that high flows are common throughout autumn to spring and in this study, no correlation was made. Low light conditions, with an emphasis on lunar activity, have also proven to be one of the most important environmental stimuli affecting silver eel migrations (Tesch, 2003; Bruijs and Durif, 2009). The consecutive nights of sampling at

Ribeira Quente encompassed a full lunar cycle and whilst there was no statistically significant difference in silver eel catch during each of the four lunar phases, there did appear to be a greater number of silver eels caught during the last quarter lunar phase and the new moon phase. These findings are supported by the majority of studies that find silver eels leave on the third quarter phase (Poole *et al.* 1990; Durif and Elie, 2008) and the dark of the new moon phase (Durif and Elie, 2008; Bruijs and Durif, 2009). From the temporal silver eel portion of this study, although minimal data only gives us an insight, it can be suggested that eels of the Azores follow a similar pattern of silver migration to their mainland Europe conspecifics. Interestingly, a silver male was also caught in the mouth of Ribeira Quente in April (17/04/2019), followed by two other eels displaying silver metamorphic characteristics. While it is common to see a second spring peak (February-March) in eel migration (Domingos, 2003; Westin, 2003), mid-April would appear later than usual and whilst visual inspection and morphometric data clearly indicated the eels as silver, a less pronounced silver livery, might suggest a regression back to their yellow eel form (Durif *et al.* 2005).

6. Conclusion

This study provides the first insights into the sub-population of European eels in the Azores and the first verification of the existence of silver (migratory) eels in the freshwaters of the archipelago. Although many characteristics of this sub-population seem to fit within the general knowledge of European eels, the topography of the Azores provides a somewhat unique habitat for eels. It was demonstrated, that eels on the Azores were distributed throughout the majority of the river systems sampled and in one brackish lake. Autumn and winter abundance was highest at streams and cascade pools, where the shelter was plentiful and habitat more stable, rather than in mainstem rivers where flow and habitat were unstable. Natural cascade barriers seemingly influence abundance and distribution in a similar way to anthropogenic barriers throughout the rest of Europe, however, many of these natural barriers were shown to create a suitable habitat for eel residence, rather than have a detrimental effect.

Despite a much shorter oceanic migration to the Sargasso, >1300 km less than from mainland Portugal, silver eels were present and appeared to be migrating from October to December, a similar time-frame to eels at mainland regions of the same latitude. A shorter journey would imply a greater chance at spawning success, due to decreased swimming distances and a likely decrease in possible predation events. The geographical isolation of the Azores from the rest of mainland Europe and a lack of introduced coarse fish species since 1979 (Ribeiro and Collares-Pereira 2009) also has important implications for the spawning success of the Azores eel population. The parasitic swim-bladder nematode *Anguillicoloides crassus*, transmitted via non-native introductions (Kirk 2003), was first reported in Europe in 1982 (Neumann 1985) and is now widespread and found in the majority, if not all catchments where European eel populations are present (Welby, 2019). The swim bladder loading of the parasite, whilst shown to directly reduce eel condition, may also affect the success of silver eel spawning migration through reducing migration speeds and inhibiting of diel vertical migrations (Sjöberg *et al.* 2009). The lack of eel and coarse fish introductions in the Azores, together with the archipelagos geographical isolation, suggests that this isolated population may be free from *A. crassus* infection, adding weight to the theory that eels of the Azores may have a greater chance at spawning success. Unfortunately, during this study there were multiple catches of two (seemingly undocumented) tropical fish species (*Poecilia reticulata* and *Amatitlania nigrofasciata*) showing their inhabitance in the geothermally heated river of Ribeira Quente (George Cowan, unpublished), with both species having demonstrated an ability to host *A. crassus* (Moravec and Konecny 1994; Emde *et al.* 2016). With aquarium fish likely introduced from mainland Europe, a chance of accidental *A. crassus* transmission to eels of the Azores is possible.

Considering the geographical isolation of the Azores and its proximity to the putative spawning grounds of A. anguilla, it would seem a logical step to conduct genetic studies of this sub-population. There has been some discussion over the genetic differences found between geographically separate A. anguilla sub-populations (Wirth and Bernatchez 2001), that question the validity of the species panmictic breeding theory. Therefore, genetic studies of the Azores sub-population, isolated at the western extremity of the species´ range may provide an insight into the legitimacy of the widely accepted panmictic theory. Iceland, at a similar longitude to the Azores, is approximately halfway across the Atlantic Ocean from Europe and consequently is of proximity to the species putative spawning grounds in the Sargasso Sea. Genetic studies of the Icelandic A. anguilla sub-population identified hybrid individuals resulting from A. anguilla and A. rostrata hybridisation (Pujolar *et al.* 2014) and it can be speculated that genetic studies of the Azores sub-population may identify comparable hybridisation. As proposed by Pujolar *et al.* (2014), the occurrence of hybrids in Iceland may demonstrate an intermediate larval migratory behaviour in hybrids, where the timing of larval metamorphosis is between that of the two parental species. Therefore, a genetic study of the Azores sub-population may help further understanding of larval migration timing and its mechanics for both A. anguilla and A. rostrata. Overall, a genetic study on the Azores would help assess genetic diversity among the entire A. anguilla population and aid in the understanding of the species´ status.

During this study, two large silver females with weights of 2095g and 1935g were caught and in 2008 an eel of apparent 6 kg was caught (Unknown, 2008), by chance, at the freshwater interface in the Ribeira Quente. With increased eel size comes increased fecundity (Davey and Jellyman, 2005), and females have been shown to produce approximately 2 million eggs per 1 kg of weight (Pederson, 2003; Palstra *et al.* 2005). So with 50% declines seen in silver eel numbers over the last 45 years (ICES WGEEL 2012), this study has shown that the freshwaters of the Azores not only contribute silver eels, with a possibly greater chance of spawning success, to the European eel panmictic spawning population but may also contribute a valuable proportion of highly fecund females.

Until now Portuguese eel management plans, that adhere to European Eel Regulations (EC Regulation 1100/2007), have given an exemption to the Azores because although eel presence is recognised, it was surmised that its freshwater individuals did not reach the ´silver´ migratory phase (Cabral *et al.* 1990). The findings of this study, having established that freshwater habitats of the Azores constitute natural habitats for the European eel and contribute silver eel to the species´ spawning biomass, has implications for the future management of the archipelagos´ river basins. The relatively high abundance of eel caught at Lago da Parque do Paul, Terceira Island, also suggest that such a brackish habitat is of high importance to the eels of the Azores and the management of such brackish habitats, which number few on the archipelago, should also be considered. Currently, for the first time on the Azores, the construction of a new EDA hydropower project (at the Ribeira Grande basin on Flores Island) has had to propose changes that adhere to the Portuguese eel management plans, as establishing measures for the recovery of the stock of European eel (EC Regulation 1100/2007). Such measures should at least include maintaining connectivity to areas that are established as natural eel habitats, providing eel passage over the proposed Ribeira do Ferreiro dam, ensuring safe recruitment of elvers/glass eels and escapement of silver eels and adequately screening water intakes to prevent eel entrainment at turbines. The project has also considered the future restoration of a wetland area to provide an alternative habitat for eels (Conservation of the eel population in Ribeira Grande, Flores: implications for the planned hydroelectric power plant. Unpublished manuscript). At the Ribeira Quente hydroelectric facilities (São Miguel Island), despite a lack of an eel management plan, two elver traps maintained by their head engineer (Alexandre Miguel Gomes Pereira) have facilitated the relocation of elvers upstream of both dams for the last several years (Unpublished). However, the escapement of silver eels from the Ribeira Quente is a matter of concern, as there is no safe downstream passage available and whilst the two dams do release weekly/bi-weekly scouring flows, dead/wounded carp and a dead silver eel were observed following such flows. These scouring flows are supposedly required to remove the large masses of substrate that regularly accumulate at intakes during the autumn and winter. To ensure the escapement of at least 40 % of the silver eel biomass as required by European Eel Regulations (EC Regulation 1100/2007), operational changes (e.g. periodic lower flows) are required during periods of critical silver eel migration that facilitate escapement without impacting eel condition. This study has demonstrated that silver eel migration likely peaks during October - December, especially during darker lunar conditions and it is recommended that operational changes are implemented during this period at Ribeira Quente, the proposed Ribeira do Ferreiro dam on Flores Island and at any other hydroelectric facilities on the Azores where eel presence can be verified.

To fully understand the eel sub-population of the Azores, it is recommended that a more comprehensive study on the timing of silver eel migration be completed and sampling techniques that were less biased towards eels above a certain size, such as electrofishing (Baldwin and Aprahamian 2012), be implemented where possible. However, other sampling techniques may prove difficult, as the majority of habitats high in eel abundance are inaccessible to boats, overly deep for “backpack” electrofishing gear and in general have difficult access. It is also likely that the partially geothermic river of Ribeira Quente would provide a somewhat unique future opportunity to investigate the effects of temperature on eels, especially regarding its effect on the onset of silvering and rate of growth. The Azores Archipelago has a widely distributed and, in some places, abundant sub-population of European eels. The archipelago's strategic position to the Sargasso Sea, at least 1300km closer than the rest of mainland Europe and its geographical isolation has important implications regarding its contribution of spawning adults to the eels panmictic population and have been overlooked until now.

7. References

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