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Perspective

The Ecology of Oceanic Dispersal and Survival of Anguillid Leptocephali

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Abstract: Recruitment declines of anguillid eels are difficult to understand because both anthropogenic impacts on juveniles and adults and oceanic changes affecting larval survival or dispersal may be contributing. Anguillid larvae may passively disperse widely from offshore spawning areas but late-stage larvae or glass eels apparently must swim directionally to reach recruitment habitats. Their long larval durations vary among tropical (~3–4 months) and temperate species (5 months to >1 year). The bodies of anguillid leptocephali are filled with transparent gelatinous material, possibly reducing predation rates and providing an energy reserve for swimming and metamorphosis. Leptocephali feed on marine snow making their first-feeding success linked to primary producers contributing to marine snow production. Alternations between ubiquitous cyanobacteria dominating in low-nutrient conditions and eukaryotic phytoplankton such as diatoms that are important for marine snow production dominating in high-nutrient conditions may influence early-larval survival at first-feeding due to many eggs simultaneously hatching within sympatric spawning areas. Fewer spawning eels resulting from population reductions and variations in early-larval survival may offer some explanations for lower and fluctuating recruitment in recent decades.

Introduction

Anguillid eels are unique catadromous fishes because their leptocephalus larvae become widely distributed within tropical waters and subtropical gyres after spawning occurs offshore (McCleave and Kleckner 1987; Tsukamoto et al. 2002; Aoyama et al. 2009). Their transparent leptocephali must in many cases move across vast distances of the oligotrophic ocean to reach their recruitment areas, and low survival of their poorly understood larval stage has been hypothesized to influence recruitment levels (Knights 2003; Bonhommeau et al. 2008a,b; Miller et al. 2016). The leptocephali of the American eel, *Anguilla rostrata*, and the European eel, *A. anguilla* become widely distributed after the adults spawn in the southern Sargasso Sea of the western North Atlantic (Schmidt 1922; McCleave 2003; Miller et al. 2015a). Their larvae then move to each side of the North Atlantic subtropical gyre where they either recruit to North America (*A. rostrata*) or Europe and North Africa (*A. anguilla*) (Tesch 2003). The leptocephali of the Japanese eel, *A. japonica*, are also widely distributed to the west of their spawning area (Shinoda et al. 2011), which is located

along the West Mariana Ridge (Tsukamoto et al. 2011; Aoyama et al. 2014) in the western North Pacific, by the North Equatorial Current and the Kuroshio Current (Fig. 1). These northern hemisphere anguillid eels are temperate species, but the North Pacific population of the giant mottled eel, *A. marmorata*, a tropical species, also spawns offshore in the North Equatorial Current in an overlapping area with *A. japonica* and its leptocephali disperse even more widely (Kuroki et al. 2009; Han et al. 2012a; Leander et al. 2013). The newly discovered species the Luzon eel, *A. luzonensis*, may also spawn in the same area (Kuroki et al. 2012).

The leptocephali of some other anguillid species must also be widely distributed, but fewer of their leptocephali have been collected. There is evidence that some species in the western South Pacific make long migrations (Kuroki et al. 2008; Jellyman and Tsukamoto 2010), but also that some tropical anguillids in the central Indonesian Seas spawn after much shorter migrations (Aoyama et al. 2003). Anguillids in the western South Pacific, such as the two subspecies of *A. australis* from Australia and New Zealand, the New Zealand longfin eel, *A. dieffenbachii*, and the Australian longfin eel, *A. reinhartii*, migrate far offshore to spawn in the South Equatorial Current according to collections of their larvae (Kuroki et al. 2008; Aoyama 2009) or data from satellite pop-up tagging studies of migrating silver eels (Jellyman and Tsukamoto 2010). There is also evidence about the location of a separate tropical eel spawning area in the western South Pacific from tagging studies (Schabetsberger et al. 2015), and larval collections have indicated there is an anguillid spawning area in the eastern Indian Ocean (Jespersen 1942; Aoyama et al. 2007). The spawning areas that are known or inferred are located in westward flowing currents that transport the larvae towards boundary currents, or are closer to landmasses or islands (Fig. 1). However, the spawning area locations of some species or populations of anguillid eels (e.g. *A. bicolor pacifica*, *A. interioris*, *A. obsura*, *A. bengalensis bengalensis*) in the Indo-Pacific remain unclear due to a lack of information, so their larval dispersal patterns are unknown.

Although questions remain about the spawning ecology and larval dispersal of anguillid eels, information has begun to emerge about various aspects of the early life histories of some of the 19 species or subspecies. For example, the spawning areas of the Atlantic eels discovered by Schmidt (1922) were further studied by surveys starting in 1979 as overviewed recently (Miller et al. 2015a). In the western North Pacific, after the spawning area was discovered in 1991 (Tsukamoto 1992)

sampling surveys for eggs, pre-feeding stage preleptocephali and adults have confirmed that *A. japonica* spawns in a narrow area along the southern tip of the West Mariana Ridge in the few days before new moon periods (Tsukamoto et al. 2011; Aoyama et al. 2014). The ages at metamorphosis and estimates of total age have shown that the larval durations of anguillid eels can vary widely in relation to how far the larvae must travel to reach recruitment areas (Kuroki et al. 2014). Species that recruit over wide latitudinal ranges show clines in glass eel body sizes and ages (Wang and Tzeng 2000; Shiao et al. 2002). Early life history differences such as smaller maximum larval size and faster growth in tropical species with short migrations compared to temperate species with longer migrations may be reflecting the evolutionary history of anguillid eels (Kuroki et al. 2014), with anguillids first evolving as tropical species and their ancestors being mesopelagic eels (Tsukamoto et al. 2002; Inoue et al. 2010).

Accumulating and evaluating these types of information is important because in recent decades recruitment declines of some anguillid species have caused concern among scientists, fisheries managers and conservationists (Dekker and Casseleman 2014; Jacoby et al. 2015). The general lack of understanding of what caused the population declines resulted in 4 anguillid eel species being listed as threatened by the IUCN (Jacoby et al. 2015). Recruitment declines of the 3 Northern Hemisphere anguillids began at similar times several decades ago, which suggested that similar factors may have affected all the species (Knights 2003, Miller et al. 2016). The cumulative effects of habitat loss from extensive dam constructions had an obvious effect and a wide range of other anthropogenic impacts including pollution and parasite introductions also occurred (Haro et al. 2000; Feunteun 2002; Casselman 2003; Miller et al. 2016). The widespread construction of dams (Lehner et al. 2011; Liermann et al. 2012) and other types of modifications to aquatic ecosystems have undoubtedly reduced the species ranges and the amount and quality of remaining habitats for anguillid eels (Miller and Casselman 2013; Itakura et al. 2014; Chen et al. 2014). These factors as well as fishing pressure could be significant in many specific areas, but because they are relatively constant from year to year, they would not be expected to cause interannual fluctuations in recruitment, because the Northern Hemisphere anguillid species each form a single panmictic population (Dannewitz et al. 2005, Han et al. 2010) whose larvae recruit randomly to all locations regardless of the anthropogenic impacts on the eels that lived in each particular area previously.

This suggests that part of the problem may be in the ocean with either the success of migrating adult spawners being affected or larval survival being reduced (Knights 2003; Friedland et al. 2007; Miller et al. 2009).

Statistical correlations with the North Atlantic Oscillation (NAO) or other oceanographic parameters in the Sargasso Sea and time-series data of glass eel catches in Europe suggested the possibility that changes in oceanic conditions may be affecting recruitment success (Knights 2003; Friedland et al. 2007; Kettle et al. 2008; Arribas et al. 2012). Correlations were also found between recruitment data and sea surface temperatures as a proxy for productivity in all 3 of the Northern Hemisphere anguillid eels (Bonhommeau et al. 2008a,b; Arribas et al. 2012). Other eel catch abundance data were also correlated with fluctuations of the NAO for *A. anguilla* (Kettle et al. 2008; Durif et al. 2011). This suggested that although anthropogenic continental factors could have contributed to the overall population declines, short-term interannual fluctuations in recruitment might be related to changes in ocean-atmospheric conditions, although continental climatic factors might also influence the number of spawning eels in some years (Kettle et al. 2011).

One way that oceanic influences on recruitment might be mediated is through influences on the levels of larval survival each year (Knights 2003; Miller et al. 2016). This type of concept has remained an important consideration in fisheries science (Anderson 1988; Meyers 2002; Houde 2008) since proposed by Hjort (1914) and continues to be discussed (Robert et al. 2014; Pepin 2016). Understanding how this might occur in eels is complicated by the unique morphology (Fig. 2) and biology of leptocephali. These larvae have transparent bodies with their maximum sizes being larger than other fish larvae (Smith 1989; Pfeiler 1999; Miller 2009). Most important for understanding the ecology of leptocephali in relation to their larval survival is that they appear to feed on the type of particulate organic material (POM) called marine snow. This has been indicated by observations of their gut contents (Otake et al. 1993; Mochioka and Iwamizu 1996; Miller et al. 2011a) and their trophic position (Miller et al. 2013a) even if small leptocephali may also feed on individual organisms as has been observed in the laboratory (Tanaka et al. 1995) or hypothesized from DNA barcoding of gut contents (Riemann et al. 2010). Feeding on marine snow that is linked to primary production in the euphotic zone makes it likely that the availability of food for leptocephali is influenced by fluctuations in primary productivity (Knights 2003; Bonhommeau et

al. 2008a,b; Miller et al. 2016). If the availability of marine snow is frequently limited where eel spawning has occurred, density-dependent mortality of first-feeding larvae could influence recruitment levels when primary production is low in a particular year (Miller et al. 2016).

This paper briefly examines what is known about the ecology of leptocephali, their patterns of larval dispersal, and the factors that may affect their larval survival. The known and estimated locations of anguillid spawning areas, the locations where anguillid leptocephali have been collected, and larval transport modeling studies are overviewed. Knowledge about the biology and behavior of leptocephali is examined to help address the question of how larval survival may contribute to the recruitment success of anguillid eels. Aspects of factors related to some of these subjects have been reviewed previously (Pfeiler 1999; Tesch 2003; McCleave 2003; Aoyama 2009; Miller 2009; Kettle et al. 2011; Shinoda et al. 2011; Kuroki et al. 2014; Feunteun et al. 2015; Miller et al. 2009, 2015a,b, 2016; Pepin 2016), so only selected or recent literature is emphasized here. With increased worldwide concern over the welfare of anguillid eels (Jacoby et al. 2015) our aim is to facilitate a better understanding of their larval dispersal and ecology.

Biology and ecology of anguillid leptocephali

All anguillid and other leptocephali have laterally compressed bodies (Fig. 2) that are mostly comprised of a mucinous pouch, containing transparent glucosaminoglycan (GAG) energy-storage compounds and lipids, which is overlain by a thin layer of muscle tissue (Smith 1989; Pfeiler 1999; Pfeiler et al. 2002; Diebel et al. 2012; Miller 2009). Body organs are reduced in size making most of the body transparent with low respiration rates and giving leptocephali a different physiology and growth strategy compared to other fish larvae (Pfeiler and Govoni 1993; Bishop and Torres 1999, 2001; Bishop et al. 2000). Although anguillid larvae have no body pigmentation, other elopomorph leptocephali have a variety of melanophores (Miller 2009) or even expandable chromatophores in one family (Miller et al. 2010). The predominantly gelatinous body of leptocephali also appears to provide buoyancy that may reduce energy expenditure during swimming (Tsukamoto et al. 2009).

Anguillid leptocephali grow to sizes of about 50 mm in tropical species and about 60-90 mm in temperate species, with those of *A. anguilla* being by far the largest, at about 70-90 mm (Kuroki et al. 2014; Miller et al. 2015a). In comparison, some marine eel leptocephali grow to sizes >250 mm

(Miller et al. 2013b). The growth rates of anguillid and the few other species of leptocephali studied using their otoliths have been about 0.3–0.6 mm d⁻¹ (Miller 2009; Kuroki et al. 2014), although faster rates were suggested for some marine eel leptocephali (Bishop et al. 2000). Tropical anguillid leptocephali of the Borneo eel, *A. borneensis*, and the Indonesian longfin eel, *A. celebesensis*, have shorter distances to reach their recruitment areas and have slightly faster larval growth rates than temperate anguillid larvae (Kuroki et al. 2014). Anguillid larval durations appear to range from about 3–4 months in some tropical species to more than a year in the European eel (Bonhommeau et al. 2010; Kuroki et al. 2014; Miller et al. 2015a). After their larval feeding and growth stage they seem to begin metamorphosis into glass eels as they approach continental shelves (Tesch 2003; Otake et al. 2006; Miller 2009) and then enter coastal waters as fully transformed glass eels, which is in contrast to conger eels that enter coastal waters as leptocephali after spawning occurs offshore (Wuenschel and Able 2008; Miller et al. 2011b).

The morphology and isotopic compositions of leptocephali are consistent with marine snow being their primary food source (Miller 2009; Miller et al. 2013a; Feunteun et al. 2015). The eyes of anguillid (Fig. 2) and other leptocephali are large compared to the size of the head, and they have rod-dominated retinas, making them adapted to vision in low light (Taylor et al. 2011). They have thin and often forward pointing teeth (Miller 2009). These characteristics are consistent with visual feeding on marine snow particles, with the teeth grasping large particles for ingestion. Observations of gut contents of leptocephali found amorphous materials that could be marine snow aggregates, zooplankton fecal pellets (frequently associated with marine snow), and discarded appendicularian houses (Otake et al. 1993; Mochioka and Iwamizu 1996; Miller et al. 2011a). These materials are consistent with the composition of marine snow, which aggregates from a wide range of materials and is colonized by various microorganisms (see Feunteun et al. 2015). In addition, a DNA barcoding study on small European eel larvae found that sequences were present from a wide range of organisms (Riemann et al. 2010), which appears to be consistent with what would be expected to be found in marine snow that contains many types of organismal and other materials (Aldredge and Silver 1988; Holloway and Cowen 1997; Shanks and Walters 1997; Kiørboe 2000). Stable isotope studies indicate that leptocephali probably do not consume all types of POM or do not assimilate everything they consume (such as fecal pellets), and their isotopic

signatures and trophic position are not consistent with feeding on other food sources such as zooplankton (Miller et al. 2013a; Feunteun et al. 2015; Lienhart et al. 2016).

Other ecological aspects of leptocephali are only partly understood. Anguillid and other leptocephali in the open ocean are vertically distributed in the upper 100 m at night and in the upper 250 m during the day (Castonguay and McCleave 1987; Miller 2015). These are the same depths where marine snow particles are most abundant (Alldredge and Silver 1988, Hebel and Karl 2001). They appear to be at least generally competent swimmers according to swimming trials of conger eel leptocephali (Wuenschel and Able 2008), video observations of marine eel leptocephali in the ocean (Miller et al. 2010, 2013c), and observations of artificially spawned and reared *A. japonica* leptocephali (Yamada et al. 2008). They seem to be well-adapted to avoid large midwater trawls during the day using their swimming abilities (Miller et al. 2013b), but how they may use their swimming abilities will be discussed later.

Anguillid and other types of leptocephali may not only rely on their swimming ability to avoid being eaten by predators because they also have shape-change behaviors that result in their bodies resembling gelatinous zooplankton (Miller et al. 2013c). Most predatory fishes in tropical regions do not typically feed on gelatinous zooplankton such as jellyfish, salps and siphonophores, so leptocephali that curl-up into rounded shapes may avoid being eaten if the predator mistakes them for an un-desirable type of food item (Miller et al. 2013c). Occurrence rates of leptocephali in predatory fish gut content studies are quite low (Miller et al. 2015b). However, the shape-change behavior may not work well with indiscriminate predators such as lancetfishes (Alepesauridae) that sometimes eat leptocephali, or other fishes that include gelatinous zooplankton in their diets, such as ocean sunfish and some tuna (Matsui et al. 1970; Miller et al. 2015b). Because leptocephali grow to large sizes during their long larval stage, transparency and their behavioral adaptations may be important to reduce predation rates as they are dispersed over wide areas by ocean currents.

Distribution and dispersal of anguillid larvae

The larval dispersal patterns of anguillid eels have interested scientists because collections of leptocephali were in the past the only way to determine where they spawn. The first anguillid spawning area was discovered by Schmidt (1922) from Denmark who followed the trail of where

smaller-and-smaller larvae were collected until he found the Sargasso Sea spawning area of *A. anguilla*, and *A. rostrata* as overviewed previously (McCleave 2003; Miller et al. 2015a). Danish scientists then searched for anguillid spawning areas in the Indo-Pacific during their expedition around the world from 1928–1930 (Schmidt 1935; Jespersen 1942). They found a spawning area off West Sumatra (Fig. 1A) by collecting many small leptocephali, but only larger specimens were caught in other areas (Jespersen 1942). Japanese scientists then discovered the spawning area of *A. japonica* in 1991 (Tsukamoto 1992) after smaller and smaller larvae were collected farther offshore (Shinoda et al. 2011). These surveys expanded out across the Indo-Pacific (Aoyama et al. 2003, 2007; Kuroki et al. 2006) with evidence of offshore spawning by eels in the western South Pacific being found (Kuroki et al. 2008; Aoyama 2009) and local spawning by eels in the Indonesian seas being discovered (Aoyama et al. 2003). These collections and genetic or morphological information about anguillid population structures (Minegishi et al. 2008; Watanabe et al. 2008, 2011), and silver eel tagging studies (Schabetsberger et al. 2015; Jellyman and Tsukamoto 2010) led to ideas about the locations of Indo-Pacific anguillid spawning areas (Fig. 1A), but there is still a lack of information about many species.

Collections of leptocephali resumed after Schmidt's studies in the Sargasso Sea spawning area (Schoth and Tesch 1982; Kleckner and McCleave 1988; Munk et al. 2010; Hanel et al. 2011) and continued in the western North Pacific (Tsukamoto et al. 2011; Aoyama et al. 2014) to clarify where spawning occurs in relation to hydrographic features, or to examine how larger leptocephali disperse from their spawning area (McCleave and Kleckner 1987). Collections were also made closer to the recruitment areas of both *A. anguilla* and *A. japonica* (see Shinoda et al. 2011; Miller et al. 2015a). Leptocephalus catch data in both the western North Atlantic (Miller et al. 2015a) and the western North Pacific (Shinoda et al. 2011) up to the year 2007 were then assembled and analyzed, which provided the most comprehensive views of the larval dispersal patterns of the 3 species of Northern Hemisphere anguillid eels.

All the catch data of Atlantic eel leptocephali was assembled into a large database that was analyzed in the context of the history of the sampling surveys (Miller et al. 2015a). The dispersal patterns of both species (N=9,634 for *A. rostrata* and N=22,612 for *A. anguilla*; mostly 1905–2007) in the Sargasso Sea and the North Atlantic basin were illustrated (Miller et al. 2015a), which

showed very contrasting distributions (Fig. 3). *Anguilla rostrata* leptocephali (Fig. 3A) usually remain on the western side of the basin, but those of *A. anguilla* disperse widely across the whole basin (Fig. 3B). Figure 4 shows how the larvae may disperse outward from their overlapping spawning areas as inferred from plots of several different size classes (Miller et al. 2015a). The leptocephali of *A. rostrata* originate from a more southwestern area compared to *A. anguilla*, and after initially spreading out in all directions, they then mostly disperse to the west and north (Fig. 4A-D). The leptocephali of *A. anguilla* originate from a narrow latitudinal band and then disperse initially to the east and west before spreading in all directions except southward (Fig. 4E-H). Interestingly, no larvae > 60 mm for *A. rostrata* and *A. anguilla* were collected within the Sargasso Sea (Fig. D,H). *Anguilla rostrata* leptocephali disperse westward and enter the Florida Current (southern part of the Gulf Stream) (Kleckner and McCleave 1982), but then must cross the current to reach North America as discussed below. *Anguilla anguilla* larvae can drift westward into the Gulf Stream that transports them eastward, or some may also enter the frontal countercurrents within the Sargasso Sea that transport them northeastward (Miller et al. 2015a). Those larvae and some from the Gulf Stream could then enter the Azores Current, or some could enter the North Atlantic Current that would take them towards the northern parts of Europe (Fig. 4E)

Fewer leptocephali of *A. japonica* have been collected (N=2547; 1956–2007) than for the Atlantic eels in the data plotted by Shinoda et al. (2011) as seen in Figure 5, but additional preleptocephali were collected after 2007 in similar areas near the West Marina Ridge (Tsukamoto et al. 2011; Aoyama et al. 2014). The regional current patterns indicate that *A. japonica* larvae are transported westward by the North Equatorial Current (NEC) until they reach the area where the current bifurcates into northward and southward flows along the eastern side of the Philippines (Shinoda et al. 2011). The larvae must then enter the northward branch so they can be transported to their East Asian recruitment areas. The latitude of spawning can shift to the north or south along the ridge, apparently according to the latitude of a salinity front, and some larvae get dispersed to the north by eddies and are retained offshore at large sizes (Kimura et al. 2001; Shinoda et al. 2011; Aoyama et al. 2014). Some leptocephali get transported south of Taiwan and are taken northward along the west coast of Taiwan where they recruit (Han et al. 2012b). Others must get transported directly into the Kuroshio Current. By the time the larvae enter the Kuroshio Current in the East

China Sea they were found to be transforming into the early glass eel stage in November and December (Otake et al. 2006).

The only other anguillid species to be frequently collected as small larvae in one of its spawning areas is the giant mottled eel, *A. marmorata*. This species has multiple populations across its range that extends from the western Indian Ocean to across the western South Pacific and as far north as southern Japan (Minegishi et al. 2008; Watanabe et al. 2008). Its North Pacific population spawns offshore in the North Equatorial Current in an overlapping area with *A. japonica*, but spawning likely extends further west (Kuroki et al. 2009). Its larvae are dispersed westward by the North Equatorial Current, but unlike *A. japonica*, their larvae can disperse either northward in the bifurcation zone, or southward into the Mindanao Current that transports them into the northern Indonesian Seas where this species is common (Fig. 5B). No small *A. marmorata* leptocephali have been collected in the Indonesian Seas (Aoyama et al. 2003), which along with the findings of population structure studies (Minegishi et al. 2008), indicates that the larvae of the North Pacific population disperse widely to regions along the western and southern margins of the western North Pacific after spawning in the North Equatorial Current (Kuroki et al. 2009; Han et al. 2012a; Leander et al. 2013).

Leptocephali of *A. luzonensis* have been collected offshore at sizes of ≥ 29 mm, which suggests that this species also spawns in the North Equatorial Current (Kuroki et al. 2012). If true, this species has a unique larval dispersal and recruitment pattern compared to both *A. japonica* and *A. marmorata* because it appears to have a very narrow species range centered on the northern Philippines according the lack of its detection in other areas in studies using genetic identification of specimens (e.g. Kuroki et al. 2014).

The sampling surveys conducted in the northern Indonesian Seas region have indicated that anguillid leptocephali are usually present but not at high abundances. This was the case in the Danish survey (Jespersen 1942) and during recent surveys (Aoyama et al. 2003; Kuroki et al. 2006; Wouthuyzen et al. 2009) (Fig. 6). Anguillid leptocephali were rare in the Sulu Sea compared to the Celebes Sea, and few or none were collected in the South China Sea, Java Sea or Banda Sea. None of the surveys had sampling stations distributed with appropriate geographic coverage to be able to understand the larval dispersal patterns of each species, but they showed that anguillid leptocephali

are widely distributed in the deep water areas of the region. *Anguilla bicolor bicolor* leptocephali were abundant off West Sumatra in September-November 1929 however (Jespersen 1942), and were present in June 2003 (Aoyama et al. 2007), indicating spawning occurs in that area. It is unclear though how widely the larvae from that spawning area may be dispersed by the South Equatorial Current or by equatorial jets (Fig. 1B).

A similar situation exists in the western South Pacific where 7 anguillid species are present, because none of the spawning areas of those species have been clearly identified and their patterns of larval dispersal can only be inferred from the patterns of ocean currents (Fig. 1). Some information has provided clues about where spawning occurs and how the larvae would be dispersed. Small leptocephali (20–34 mm) were collected of *A. australis* and *A. reinhartii* south of the Solomon Islands, a few small *A. marmorata* leptocephali (19, 25 mm) have been collected to the east and 24 unidentified small anguillid larvae (~10 mm) were caught just northeast of Fiji (Kuroki et al. 2008). The sizes of these larvae indicate that there are spawning areas in the region northeast of New Caledonia and north of Fiji. Information from silver eel tagging studies also point to a spawning area of *A. marmorata* and *A. megastoma* in the region (Schabetsberger et al. 2015), and that *A. dieffenbachii* from New Zealand may spawn east of New Caledonia (Jellyman and Tsukamoto 2010). The westward flow of the South Equatorial Current would take leptocephali to regions along the margin of the western South Pacific and then the East Australian Current would take them southward along Australia where some recruit as glass eels (Shiao et al. 2002). The eastward flow of the Tasman front would then take other leptocephali towards New Zealand (regional ocean currents are reviewed by Ganachaud et al. 2014) (Fig. 1B).

Modelling studies estimating larval dispersal

Because anguillid leptocephali disperse over large-scale geographic areas it is usually impossible to conduct sampling surveys throughout their whole distribution areas during any one particular time period. Therefore, an alternative way to examine their dispersal patterns has been to use particle transport modelling. The first studies on this were conducted on *A. rostrata* (Power and McCleave 1983) and *A. japonica* (Kimura et al. 1999). These showed *A. rostrata* larvae spread out into the western part of the gyre and then into the Gulf Stream (Power and McCleave 1983), and direct

westward transport by the North Equatorial Current and into the Kuroshio was seen for *A. japonica* (Kimura et al. 1999). Several modelling studies were then done on *A. anguilla* that evaluated the transport times and routes using particles (simulated leptocephali) that either had no diurnal behavior and stayed at fixed depths (Kettle and Haines 2006; Blanke et al. 2012; Baltazar-Soares et al. 2014; Pacariz et al. 2014) or had various types of simulated diurnal behavior of changing depths between night and day (Bonhommeau et al. 2009a,b; Zenimoto et al. 2011; Meli et al. 2013) similar to their natural behaviors (Castonguay and McCleave 1987). Recent studies also included horizontal swimming behavior (Meli et al. 2013; Rypina et al. 2014; Chang et al. 2015). The various studies found that the larvae disperse widely, the behavior given to the larvae can affect their transport times and a wide range of transport times can occur. The results of modelling studies were also compared to information about larval durations that are obtained from otolith research approaches (Bonhommeau et al. 2010; Zenimoto et al. 2011). Rypina et al. (2014) showed that very few *A. rostrata* larvae would cross the Florida Current/Gulf Stream and then reach the 200 m isobath of the continental shelf without the particles using directional swimming. Chang et al. (2015) also found much greater recruitment success when horizontal swimming was used, and Meli et al. (2013) found that the best-performing scenarios were those that assumed a swimming speed of 1.0 BL s^{-1} .

Similarly, very few *A. japonica* larvae were seen to exit the Kuroshio system in East Asia under any of the simulated passive drift conditions (Kim et al. 2007; Zenimoto et al. 2009). Those modeling studies indicated that El Niño conditions and the latitude of spawning can affect the transport patterns of the leptocephali as a result of the North Equatorial Current bifurcating into north and south flows (Kim et al. 2007; Zenimoto et al. 2009). Spawning at southerly latitudes relative to the bifurcation latitude or El Niño increased the proportion of larvae entrained into the southward Mindanao Current that flows into the Celebes Sea, which is an area outside of the species range. Evidence that some leptocephali get entrained into the southward flow was found when an *A. japonica* leptocephalus was collected in the Celebes Sea (Fig. 5A; Miller et al. 2009). The movements of simulated larval particles was also investigated in the region around southern Taiwan (Han et al. 2012).

The most recent study on *A. japonica* found that the Philippines–Taiwan Oscillation (PTO), which is an oscillation of the thermocline depth between the areas east of the Philippines or Taiwan that affects the North Equatorial Current latitude and its bifurcation, had an important effect on larval recruitment (Chang et al. 2015). During positive PTO years, the thermocline rises to the east of the Philippines and deepens to the east of Taiwan. This increases the number of larvae entering the Kuroshio, compared to when the thermocline heights have the opposite pattern (deep in the south and shallow in the north) and the latitude of the North Equatorial Current shifts southward.

Modelling studies have also been used to estimate the areas where anguillid eels may spawn by following larval particles backward upstream of their recruitment areas. Jellyman and Bowen (2009) found estimated spawning areas that were generally consistent with the larval catch data (Kuroki et al. 2008) or tagging data (Jellyman and Tsukamoto 2010), but including a component of larval swimming (10 or 15 cm s⁻¹) was required to achieve those results. A larval transport modelling study was also conducted to evaluate the possible spawning locations of 4 species of anguillid eels in the western Indian Ocean region (Pous et al. 2010). The analyses indicated that it was possible that all species could share a common spawning area east of Madagascar, but that it was also possible each species may spawn in different locations within the same general area.

Possible swimming by late-stage leptocephali

Leptocephali seem to be competent swimmers (Yamada et al. 2008; Wuenschel and Able 2008; Miller et al. 2010, 2013c) and may even be excellent swimmers as seen in artificially reared leptocephali (Video S1), but whether or not they use swimming to actively migrate is unknown. Although not much is known about the spawning areas and larval dispersal patterns of some anguillid species, whether or not leptocephali must actively swim during the final stages of their larval periods to reach their recruitment areas can be considered for several species using existing knowledge about their larval distributions and the patterns of ocean currents in relation to recruitment areas. A striking feature of the maps of where different sizes of Atlantic eel leptocephali were collected is that no leptocephali > 60 mm have been caught within the Sargasso Sea (Fig. 4; Miller et al. 2015a). The larvae of both species eventually can disperse throughout the entire western part of the subtropical gyre as they grow up to that size (Fig. 4C,G), but none of the

largest sizes of leptocephali were caught there even though they were collected in areas closer to their recruitment areas (Fig. 4D,H). It is difficult to hypothesize that the large larvae would differentially die inside the Sargasso Sea and not outside of it, or that they can only be captured outside the Sargasso Sea, so it is possible that they are not typically present there. Some water recirculates within the Sargasso Sea gyre (McWilliams 1983; Marchese 1999), which along with the actions of eddies would be expected to retain at least a few large larvae. Therefore, the absence of large leptocephali in collections made in the Sargasso Sea may be evidence that the large larvae eventually swim out of the gyre.

The possibility of leptocephali swimming towards their recruitment areas has been considered (Tesch 2003; Righton et al. 2012; Miller et al. 2015a) or critically evaluated (McCleave et al. 1998) for *A. anguilla* or discussed in relation to if marine eel leptocephali may swim to reach recruitment areas (Wuenschel and Able 2008; Miller 2009). Modelling studies show that directional swimming may be important for successful recruitment (Rypina et al. 2014; Chang et al. 2015), and coral reef larvae that were historically thought to passively drift towards their recruitment areas are now known to use oriented swimming (Leis, 2002, 2006). There is no way to clearly evaluate if large *A. anguilla* leptocephali swim to reach Europe or North Africa due to the complexities of otolith aging (deposition may stop at low temperatures) and transport modelling studies (Bonhommeau et al. 2010; Zenimoto et al. 2011). But in the case of *A. rostrata* it is difficult to propose a mechanism that could transport all of their larvae across the Florida Current and Gulf Stream each year if the leptocephali did not use some sort of oriented swimming as pointed out previously (Miller et al. 2015a). If only passive processes were involved, the distribution of *A. rostrata* and *A. anguilla* leptocephali in relation to the north side of the Gulf Stream would be expected to be the same, but more *A. rostrata* leptocephali have been collected on the north side (Fig. 4D,H; Miller et al. 2015a), even though both species can be collected in the Florida Current and Gulf Stream (Kleckner and McCleave 1982; Miller et al. 2015a).

Some *A. rostrata* leptocephali could be moved out of the Gulf Stream by rings cast off to the north by meanders in the current flow or other types of protrusions, but these events are infrequent or randomly distributed in time and space and can also transport water in the opposite direction into the Sargasso Sea (Richardson 1980). Some meander-induced lateral motions may exist within

deeper layers of the Gulf Stream (Rajamony et al. 2001), or intrusions from rings can occur (Zang et al. 2015). However, there is no indication that they could be able to transport all the larvae across the strong current each year before they would be transported too far east along with all the *A. anguilla* leptocephali, as was indicated by modeling (Rypina et al. 2014). The American conger eel, *Conger oceanicus*, also spawns in the Sargasso Sea so their leptocephali must also cross the Florida Current/Gulf Stream for recruitment (see Miller et al. 2011b).

There are similar cases of where anguillid and conger leptocephali would apparently need to swim to reach their recruitment areas, such as those of species that spawn offshore in the Pacific that must cross boundary currents. The larvae of *A. japonica* and the common Japanese conger eel, *Conger myriaster*, that recruit to the northern areas must get out of the Kuroshio Current in an analogous situation as those of *A. rostrata* and *C. oceanicus* crossing the Florida Current/Gulf Stream (Miller et al. 2011b). Early-stage *A. japonica* glass eels were collected within the southern Kuroshio in the East China Sea (Otake et al. 2006), so this species may sometimes start metamorphosis before entering the current, even though conger larvae recruit to estuaries as leptocephali (Wuenschel and Able 2008). Regardless of developmental stage, the leptocephali or glass eels of *A. japonica*, *C. myriaster*, and *A. marmorata* would apparently need to swim west to get out of the Kuroshio (Fig. 5A,B). Similarly, the leptocephali or glass eels of *A. australis* *australis* and *A. reinhardtii* would likely need to swim west to get out of the southward flowing East Australian Current along the Australian coast (Fig. 1B). Some of that water turns eastward and flows along the Tasman Front while presumably transporting larvae of *A. australis schmidtii* and *A. dieffenbachii* to New Zealand. Active larval swimming would seemingly be beneficial to ensure most larvae reach New Zealand rather than continuing to the east (Fig. 1B).

Potential influences on larval survival

There presently is little or no data available about the levels of mortality from starvation or predation experienced by leptocephali in the ocean and only general mortality values have been used for modelling purposes (Bonhommeau et al. 2009b; Meli et al. 2013; Pacariz et al. 2014). The unusual biology and behavior of this type of larvae probably make it inappropriate to make assumptions about mortality based on knowledge of juvenile or adult eels or from other types of

fish larvae that have different food sources, shorter larval durations, and smaller maximum sizes. What does appear likely is that transparent leptocephali are probably usually difficult to see, they may benefit from mimicry of undesirable prey species (gelatinous zooplankton), and are active swimmers that can likely avoid most predators if detected in advance (Miller 2009; Miller et al. 2015b). These factors could affect predation rates on leptocephali, which are rare in most predator stomachs in food habits studies, but leptocephali would also digest more rapidly than many prey types, making it difficult to know how frequently they are eaten (Miller et al. 2015b).

The amount of mortality resulting from starvation is also difficult to assess, but the unique characteristic of leptocephali storing GAG compounds inside their body for use during metamorphosis into the juvenile stage (Pfeiler 1999) suggests that unlike typical fish larvae with large muscle masses, starvation may usually only be a factor at the first-feeding stage. For example, marine snow is ubiquitous in the oceans (Alldredge and Sliver 1988) and larger leptocephali would have a large GAG reserve to draw upon even if they are in areas with low concentrations of food. In fact, medium-size aquaculture-reared *A. japonica* leptocephali can survive for more than a month while continuously swimming against the steady current in a circular-shaped planktonkreisel while not being fed as seen in Video S1. This indicates they are able to use their energy reserves to swim and survive in the absence of food. Therefore, larval mortality due to starvation may typically only occur in early leptocephali that have not accumulated energy reserves from successful feeding.

Density-dependent larval mortality due to a lack of food has remained an important concept in fisheries science (Anderson 1988; Meyers 2002; Houde 2008; Robert et al. 2014) since larval mortality was proposed by Hjort (1914) as being a major determinant of year-class strength in fisheries species. It has remained difficult though to make clear correlations between spawner abundance, larval mortality and recruitment success (Pepin 2016). This is even more difficult to evaluate for eels because there is little or no data available about the abundance or survival of any of their marine life history stages (Hanel et al. 2014). Miller et al. (2016) proposed the hypothesis that density-dependent larval survival could occur in anguillid eels because all 3 northern hemisphere eel species have high female fecundity and there are about 4–7 anguillid and mesopelagic eels species spawning sympatrically in both the Sargasso Sea and western North

Pacific. Therefore the millions of larvae from just one or several anguillid eels and from other types of eels could potentially compete for marine snow particles at the same times and depth strata after hatching.

There is a lack of published data about marine snow abundance in anguillid spawning areas, but it is possible that changes in the biological communities associated with marine snow production might have occurred during the mid-1970s time period when anguillid eels began to decline (Miller et al. 2016). At least partially synchronous regime shifts in marine pelagic zooplankton assemblages appeared to occur both within and between the north Atlantic and Pacific basins in the mid-1970's and late 1980's that appear linked to temperature increases (Beaugrand et al. 2015). Shifts in the North Atlantic Oscillation (NAO) and Pacific Decadal Oscillation (PDO) also occurred (see Miller et al. 2016) during this period that corresponds to an apparent end to several decades of a lack of global temperature increases (Trenberth and Fasullo 2013).

These regime shifts may also have included a “photosynthetic population domain shift” that was proposed to have occurred in the North Pacific by Karl et al. (2001). The globally widespread and abundant photosynthetic cyanobacterium *Prochlorococcus* (Partensky et al. 1999; Flombaum et al. 2013) appeared to increase in abundance in the North Pacific gyre after 1976 causing a shift to a prevalence of cyanobacteria and a reduction of diatoms or other phytoplankton (Karl et al. 2001). When nutrient levels are high, diatoms or other eukaryotic phytoplankton appear to thrive and blooms occur, but *Prochlorococcus* is abundant when nutrients are low, with there being an apparent inverse relationship between abundances of the two types of primary producers (Partensky et al. 1999; Karl et al. 2001; Rousseaux and Gregg 2012; Casey et al. 2013). A clear inverse relationship between the abundance of *Prochlorococcus* and eukaryotic phytoplankton was seen in the northern Sargasso Sea that appeared to be influenced by the NAO phase (Casey et al. 2013; Miller et al. 2016). Phytoplankton such as large diatoms are important for producing particulate material and marine snow (Alldredge and Silver 1988; Durand et al. 2001; Buessler 1998) so during low-nutrient conditions with fewer diatoms or other eukaryotic phytoplankton, less marine snow may be produced. Satellite-derived evidence of warming and decreases in north Atlantic and Pacific gyre chlorophyll levels during 1998–2013 suggests various climate-related factors such as

warming, seasonal vertical mixing and precipitation/evaporation can influence phytoplankton productivity (Signorini et al. 2015) and presumably marine snow production.

During low eukaryotic phytoplankton production conditions, density-dependent larval mortality could occur if many eel larvae hatch in the same areas (Miller et al. 2016). Statistical correlations between recruitment indices of the European eel (Knights 2003; Friedland et al. 2007; Kettle et al. 2008; Arribas et al. 2012) or eel catches (Kettle et al. 2008; Durif et al. 2011) and the NAO index may provide indirect evidence of this. Correlations between glass eel recruitment and sea surface temperature as an indicator of productivity have also been made (Bonhommeau et al. 2008a,b; Arribas et al. 2012). If these correlations represent actual cause-and-effect relationships, they may indicate that low-nutrient and low-productivity conditions reduce marine snow production and increase the mortality of newly hatched larvae. This scenario could explain interannual fluctuations in recruitment and may have contributed to when sudden decreases in recruitment began. But factors such as habitat reductions and other anthropogenic impacts on eels in continental habitats also occurred that likely contributed to eel population reductions (Haro et al. 2000; Feunteun 2002; Kettle et al. 2011; Miller et al. 2016).

Discussion

As overviewed in previous sections, a wide range of information has been gathered about the spawning areas and larval dispersal patterns of anguillid eels, which can form the basis of future research efforts. The spawning areas and larval dispersal patterns of catadromous anguillid eels began to be studied about a century ago (Schmidt 1922) and understanding of the larval biology and life histories of these unusual fishes has progressed (see Aoyama 2009; Miller 2009; Tsukamoto et al. 2011; Kuroki et al. 2014). Anguillid and leptocephali of other elopomorphs are highly transparent, feed on marine snow, and seem to be good swimmers (Miller 2009), but the behavior and ecology of leptocephali are only beginning to be studied (Wuenschel and Able 2008; Yamada et al. 2008; Miller et al. 2010, 2013c). At least a few leptocephali of most anguillid species have been collected and those larvae and recruitment-stage glass eels have been studied using their otolith microstructure to compare the larval durations and other early life history characteristics among species (overviewed by Kuroki et al. 2014). The larvae of the species that make long

migrations to spawn offshore have a remarkable dispersal stage when they are transported over thousands of kilometers by ocean currents towards their recruitment areas and modeling studies have illustrated how this may occur (e.g. Zenimoto et al. 2009; Bonhommeau et al. 2010; Rypina et al. 2014). It has also been realized that some tropical anguillids can spawn locally over deep-water basins (Aoyama et al. 2003) and that tropical eels have shorter larval durations, faster growth, and a smaller maximum larval size than temperate species (Kuroki et al. 2014). So the dispersal of anguillid eel larvae can range from the retention of *A. celebesensis* leptocephali within the small Tomini Bay of Sulawesi Island for about 3 months (Aoyama et al. 2003; Wouthuyzen et al. 2009; Kuroki et al. 2014), to the dispersal of European eel leptocephali all across the North Atlantic basin over more than a year (Tesch 2003; Wang and Tzeng 2000; Miller et al. 2015a). Larval catches or silver eel tagging studies indicate that in addition to *A. rostrata*, *A. japonica*, *A. marmorata*, *A. australis*, *A. reinhardtii*, and *A. dieffenbachii* also make long migrations to offshore spawning areas (Kuroki et al. 2008; Aoyama 2009; Jellyman and Tsukamoto 2010), and therefore their larvae have a long dispersal stage.

However, because the spawning areas and larval distributions of most species are still poorly understood, there are a number of interesting questions that remain. The exact spawning area of too few species are known yet to be able to generalize with certainty about how the spawning location and larval dispersal patterns interact to determine where the eels need to spawn to achieve successful recruitment. This is generally understandable for the known spawning areas in the north Atlantic and Pacific (Kuroki et al. 2009; Shinoda et al. 2011; Miller et al. 2015a), but it is not as clear yet for the WSP and Indian Ocean where there are many species that recruit to different or overlapping areas. How the larvae of a particular species are able to recruit to specific growth-stage areas but not others they may pass by needs more clarification.

The clear separations in larval distributions and recruitment areas among species that spawn sympatrically may indicate that there are genetically programmed developmental patterns and larval behaviors that facilitate successful recruitment to distant areas. Timing of metamorphosis is likely an important aspect of this (Wang and Tzeng 2000; Leander et al. 2013), however it seemingly cannot explain the entire differences in transport and recruitment patterns without a component of active behavior by the leptocephali or glass eels. In each of the known cases of individual current

systems transporting multiple species of anguillid larvae that have different final destinations (Gulf Stream, NEC/Kuroshio, EAC), the early initiation of metamorphosis can prepare the larvae that recruit to the closest locations for entering coastal waters as glass eels, but some kind of active behavior is required to ensure that they exit the currents and reach the coastal waters. Therefore it appears likely that each species initiates active swimming behavior to detrain from the oceanic currents and then they swim towards the continental shelf as metamorphosing larvae or early glass eels (Miller 2009; Miller et al. 2015a). The species that recruit to more distant areas remain within the current flow and do not metamorphose or change their behaviors until later.

What is more intriguing to consider though is if these active behaviors could also be triggered while further offshore when leptocephali reach the size of metamorphosis but have been retained offshore. The lack of large > 60 mm leptocephali of both species of Atlantic eels in the Sargasso Sea is suggestive that this could occur (Miller et al. 2015a). This type of strategy seems to make sense, because otherwise large anguillid leptocephali could frequently be retained offshore by eddies and may never re-enter the appropriate current systems to take them to recruitment habitats. It makes less sense though, for pre-metamorphosis size leptocephali to use directional swimming because this would probably slow down their growth due to the extra energy expenditure and less time spent feeding.

The large energy reserves, low respiration rates (Bishop and Torres 1999; Bishop et al. 2000) and apparently good swimming abilities (Wuenschel and Able 2008) would seemingly enable large anguillid leptocephali or glass eels to use directional swimming to reach their recruitment areas if they are genetically programmed to do so. The anguilliform swimming mode is highly efficient according to studies on migration-stage silver eels (van Ginneken et al. 2005), so swimming by leptocephali may also be very efficient. Although consideration that late-stage leptocephali of anguillid and other eels may use directional swimming to reach recruitment areas like other kinds of fish larvae (Leis 2002, 2006) is at an early stage of evaluation, if they can use directional swimming it would likely have a profound effect on recruitment success as indicated by modeling studies (Rypina et al. 2014; Chang et al. 2015).

Other factors affecting the survival of leptocephali during their dispersal stage are also poorly understood. Their transparency, swimming ability, and shape-change/mimicry behavior may allow

the larvae to reach large sizes without greatly increasing predation rates (Miller et al. 2013c, 2015b). Their bodies being filled with energy storage compounds likely make them resistant to starvation once they have grown larger. After the larvae are dispersed over wide areas of the open ocean and are present at lower densities, there may be enough marine snow available as food. These factors seem to suggest that after the early larval stage, leptocephali may typically have low mortality rates. But there is presently no empirical data to support this hypothesis, and anguillid leptocephali have been found in rare cases to be eaten by fishes such as tuna and ocean sunfish as they are approaching their recruitment areas (Matsui et al. 1970; Miller et al. 2015b).

Influences on the mortality of the first-feeding larval stage may include a different set of factors though. The newly-hatched larvae are very small (~4–5 mm) making them vulnerable to a wider range of small fish or zooplankton predators, and they would only have a small amount of energy reserves. The eggs and pre-feeding preleptocephalus larvae of *A. japonica* were found to accumulate within a narrow depth strata at about 160 m (Tsukamoto et al. 2011; Aoyama et al. 2014), so if many larvae simultaneously hatch out at the same depths it is possible that food could become a limiting factor (Miller et al. 2016). The correlations between temperature/productivity fluctuations or changes in ocean-atmosphere parameters and indices of eel abundances that have been observed (*e.g.* Knights, 2003; Friedland et al., 2007; Bonhommeau et al., 2008a,b) suggest there may be a link between recruitment and larval survival that is mediated by oceanic primary production. The various factors discussed previously suggest that the critical period of larval survival of anguillid eels is likely at the first-feeding stage, but research is needed to evaluate whether or not this is true. Based on the factors considered here, there presently is little evidence that larval survival of the later stages of leptocephali are important drivers of anguillid recruitment success. One possible exception is that the Japanese eel that must entrain into the correct current flow in the NEC bifurcation zone (Kimura et al. 2001; Zenimoto et al. 2009; Chang et al. 2015).

The various factors that might influence the survival of anguillid larvae during their early life history and dispersal stages discussed in this paper can be summarized in a diagram (Figure 7). Mortality of larvae is most likely to occur under low-productivity conditions or when many larvae hatch out in the same place and time (Miller et al. 2016), but low food availability later during the larval period is likely to only cause slower growth, which might prolong the larval stage if

swimming is triggered at a certain size range. Predation is likely reduced by the extreme transparency of leptocephali and their shape-change mimicry of gelatinous zooplankton (Miller et al. 2013c, 2015b), but slower growth or longer larval periods would extend the time that they might experience predation and could affect the timing of recruitment.

Future research on the factors related to the survival and behavior of anguillid leptocephali and the locations of their spawning areas in relation to recruitment areas will contribute to a better understanding of whether or not the larval stage of eels can greatly influence recruitment success. At this stage of understanding, it is clear that the leptocephalus stage is remarkably unique physiologically (Bishop and Torres 1999; Bishop et al. 2000) and ecologically (Miller 2009) and is likely an important part of the long-term success and evolution of anguillid eels, which have radiated out to regions of the world where there are warm current systems to transport their larvae to their recruitment areas (Tsukamoto et al. 2002; Inoue et al. 2011; Kuroki et al. 2014). As more information is accumulated about their spawning areas and the distribution and behavior of their leptocephali, the new understanding of the long larval dispersal stage of anguillid eels can contribute to the management and conservation of these interesting catadromous fishes.

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Figure Captions

Figure 1. A map of the Indo-Pacific region showing (A) known (circles with solid lines) and estimated (circles with dotted lines) anguillid eel spawning areas. Known spawning areas are based on egg or larval catches, and estimated spawning areas are based on various types of information including limited larval catches, evidence about population structure, pop-up tagging studies on silver eels, or species ranges in relation to ocean current patterns, and question marks show areas with little or no supporting information. (B) Shows the general patterns of ocean surface currents in relation to the spawning area locations. The Kuroshio Current (KC), North Equatorial Current (NEC), North Equatorial Countercurrent (NECC), Mindanao Current (MC), South Equatorial Current (SEC), South Equatorial Countercurrent (SECC), East Australian Current (EAC), Tasman Front (TF), equatorial jets (EJ), Agulhas Current (AC) and Agulhas Return Current (ARC) are shown with arrows. Currents in other areas are not shown.

Figure 2. Photographs of (A) 56.4 mm and (B) 41.9 mm (anterior and posterior body regions) Japanese eel, *Anguilla japonica*, leptocephali showing their general morphology. Some tropical anguillid leptocephali have a deeper body (Kuroki et al. 2014), but all species have the same general characteristics in comparison to leptocephali of other elopomorph families. GAG: Glucosaminoglycans.

Figure 3. Maps of the locations where all sizes of (A) American eel, *Anguilla rostrata*, and (B) European eel, *Anguilla anguilla*, leptocephali were collected mostly from 1905–2007. Sizes of circles reflect abundance at each station. Red color shows metamorphosing larvae (not shown in print version). Modified from Miller et al. (2015a).

Figure 4. Plots of the regions (shaded ovals or shapes) where different size ranges of the two species of Atlantic eel leptocephali were collected mostly from 1905–2007. The major currents of the Gulf Stream (GS), Azores Current (AC), North Atlantic Current (NAC), and frontal countercurrents (FCC) are labeled in (E). Modified from Miller et al. (2015a).

Figure 5. Maps of the locations (plotted in 1-degree square) where (A) Japanese eel, *Anguilla japonica* (from Shinoda et al. 2011), and (B) giant mottled eel, *Anguilla marmorata*, (from Kuroki et al. 2009) leptocephali (>10 mm, open circles), leptocephali ≤ 10 mm (black diamonds), preleptocephali (black stars), metamorphosing leptocephali (black triangles), and glass eels (black squares) were collected from 1961–2007. Shading shows the deep-water areas where the leptocephali of each species presumably disperse into before metamorphosis (based on recruitment areas and water depths). Coastlines where each species recruits are shown with thick lines, the Celebes Sea (CS) and Sulawesi Island (SI) are labeled, and the major current systems of the North Equatorial Current (NEC), North Equatorial Countercurrent (NECC), Mindanao Eddy (ME), and Halmahera Eddy (HE) are shown with arrows.

Figure 6. Map of where anguillid leptocephali were collected in the Philippines, Indonesia and Malaysia region in 1929 during the Danish around the world expedition (filled circles: leptocephalus catches, open circles: no catches; modified from Jespersen 1942), during 5 recent surveys from 2000–2003 (filled triangles: leptocephalus catches, open triangles: no catches; from Aoyama et al. 2003, 2007, Kuroki et al. 2006) that were mostly *Anguilla marmorata*, *A. borneensis*, *A. celebesensis*, *A. bicolor pacifica*, *A. bicolor bicolor* and a few *A. interioris*, and where mostly *A. marmorata* and a few *A. bicolor pacifica*. Where leptocephali were collected in the western North Pacific from 1995 to 2007 are shown with x symbols (no-catch stations not shown; modified from Kuroki et al. 2014).

Figure 7. A conceptual diagram representing possible factors associated with mortality, growth and recruitment of anguillid leptocephali and glass eels. Widespread insufficient food at the first-feeding larval stage might reduce recruitment levels, but low food levels may only reduce growth or delay the timing of recruitment. Swimming towards recruitment habitats and reduced predation due to transparency and shape-change mimicry of gelatinous zooplankton (Miller et al. 2013c) are depicted for late the later stages of larvae before they metamorphose into glass eels.

Supplementary Video Caption

Video S1. Video imagery of Japanese eel, *Anguilla japonica*, leptocephali or metamorphosing/transitional stage larvae (becoming glass eels) swimming in a continuous flow in a planktonkreisel tank. The larvae were filmed at Nihon University during an eel exhibition and were seen to be always swimming continuously each time they were observed during daylight hours for a period of more than a month. The larvae were initially hatched and reared at the IRAGO Institute in Japan, and they were filmed by Ritsuno Yama.

Draft

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261x369mm (300 x 300 DPI)

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248x321mm (300 x 300 DPI)

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206x267mm (300 x 300 DPI)

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239x328mm (300 x 300 DPI)

108x66mm (300 x 300 DPI)