Ecology of Anguilliform Leptocephali: Remarkable Transparent Fish Larvae of the Ocean Surface Layer

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Abstract
This review examines the present state of knowledge about the ecology of anguilliform leptocephali, which are the unique but poorly understood larvae of eels. All eels spawn in the ocean and their leptocephali live in the ocean surface layer. Their presence worldwide and basic biology have not been extensively studied due to their strong ability to avoid standard plankton nets and their fragile transparent bodies. Leptocephali have laterally compressed bodies and contain a high proportion of transparent energy storage compounds. They have diverse morphological features, but appear to feed only on particulate material, such as marine snow or discarded larvacean houses. Some information on their chemical composition, respiration, growth rates, depth distributions, swimming ability, metamorphosis, and recruitment patterns has been reported, which highlights the interesting and unique aspects of leptocephalus larvae. Regional zoogeography and reproductive ecology of adults and ocean currents affect the spatial and temporal distribution patterns of leptocephali, which have long larval durations, but most life histories and larval recruitment behaviors remain undocumented. Their transparency, feeding strategy, and large size seem to be a unique and successful larval strategy, but the abundance and ecological significance of leptocephali in the ocean appear to have been underestimated.

1. Introduction

The ecology of larval fish has been studied for many years because of their importance in understanding the population dynamics of commercially important fish species around the world. Their interesting morphology and ecology also has been studied to learn about the wide variety of behavioral and morphological adaptations used by fish larvae, which are often quite different in appearance than their juveniles and adults (Moser 1981; Leis and McCormick 2002; Leis 2006; Masuda 2009). However, one major group of fish larvae that has received less attention for various reasons are leptocephali, which are the larvae of marine and freshwater eels and their close relatives that live in the ocean (Castle 1984; Smith 1989a; Mochioka 2003; Lecomte-Finiger 2004). There has been increasing concern recently though, that changes in the ocean due...
to alterations in the ocean–atmosphere system may be affecting the survival of anguillid leptocephali (see Miller et al. 2009a), so there is a need to gain a greater understanding of the ecology of leptocephali.

Leptocephali are poorly known largely because they grow much larger than typical fish larvae, and they are rarely collected by the standard-sized plankton nets used by fisheries scientists and biological oceanographers. As will be reviewed below, they have large eyes, mechanoreceptors, and can actively swim both forwards and backwards, so this in combination with their large size appears to make leptocephali well adapted to avoid small plankton nets (≤1 m diameter) or any sized trawl during the day (Castonguay and McCleave 1987a; Miller and McCleave 1994; Miller and Tsukamoto 2004; Miller et al. 2006a). Another problem that has slowed the progress in research on leptocephali is that these larvae typically show no resemblance to the juvenile or adult forms of each species, so it is extraordinarily difficult to match larval forms to adult species using morphological characteristics.

Leptocephali differ so much from their adult forms that for about a century they were thought to be a unique type of marine fish (Smith 1989a). Eventually it was realized that leptocephali are actually the larval forms of the fishes of the superorder Elopomorpha, which includes species with both eel-like and typical fish-like bodies. The true eels of the Anguilliformes all have elongate body forms and swim using typical anguilliform locomotion (Gray 1933) that enables them to swim in both directions (D’Août and Aerts 1999). This order includes about 15 families, with all but one family being almost entirely marine species throughout their life histories (Böhlke 1989a). The eels of the Anguillidae are the catadromous eels that live in freshwater and estuarine habitats as juveniles and adults, but spawn in the ocean and have leptocephalus larvae (Tesch 2003; Aoyama 2009). The gulper and swallowing eels of the historical order Saccopharyngiformes are also eel-like in body form, and genetically appear to be contained within the Anguilliformes (Inoue et al. 2004). The bonefishes and spiny eels of the Albuliformes (including the historical Notacanthiformes), and the tarpons and ladyfishes of the Elopiformes have more typical fish-like bodies and do not resemble eels even though they all share the common larval form of leptocephalus larvae. All of these elopomorph orders are distributed worldwide from tropical to temperate waters and in the deep sea for some species (Nelson 2006), although anguillids are absent in the South Atlantic and eastern Pacific oceans (Aoyama 2009).

Despite their global distribution and the existence of more than 800 species of eels (Nelson 2006), little is known about the life histories of most species or the ecology of their leptocephali (Böhlke 1989a,b; Smith 1989a; Miller and Tsukamoto 2004). Adults are difficult to study due to the nocturnal and often fossorial behavior of most eels, or the deep depths at which many species live in the ocean. Leptocephali are difficult to collect unless large trawls are fished at night (Miller and Tsukamoto 2004, 2006), but even if they are collected, leptocephali rarely survive being captured due to their fragile body form.

Leptocephali are unusual due to their highly laterally compressed bodies, which are almost totally transparent (Fig. 1). They are transparent as a result of their bodies mostly containing transparent energy storage material consisting primarily of glycosaminoglycan (GAG) compounds (Pfeiler 1999; Pfeiler et al. 2002), which also provide structural support for the body until they are converted into new body tissues when the leptocephali metamorphose into juvenile eels at the end of their larval phase. These larvae are very fragile though, because their body is covered with a thin layer of tissue that is only a few cell layers thick (Hulet 1978; Suzuki and Otake 2000; Nakamura et al. 2002) and is easily damaged.

Leptocephali exhibit a wide variety of body shapes that range from very long and thin to deep, with rounded or pointed tails (Fig. 2). Head shapes also vary greatly (Fig. 3; but see below). Maximum sizes of leptocephali can range from about 50 mm to greater than 300 mm (total length) (Castle 1984; Smith 1989a; Böhlke 1989b), but they remain transparent and very fragile regardless of their size or body shape until they metamorphose into juvenile eels.

Research on leptocephali primarily began after expeditions started searching for the spawning place of the Atlantic eels by collecting their leptocephali in the early part of the last century (Schmidt 1922; Boëtius and Harding 1985; McCleave 2003). During these early surveys for anguillid leptocephali, which expanded into the Indo–Pacific (Jespersen 1942), various other taxa were also collected, and some of these marine eel leptocephali were later studied (e.g.
Research on leptocephalus morphology and their species identifications achieved greater advances as a result of collections made in more recent years in the western South Pacific (Castle 1963, 1964, 1965a,b,c), the Gulf of Guinea of western Africa (Blache 1977), and to an even greater extent in the western North Atlantic (Smith 1969, 1974), where most leptocephali were eventually identified to the species level (Smith 1979; Böhlke 1989b). Other more recent studies compared regional catches of leptocephali to the known distributions of adults (Richardson and Cowen 2004a,b; Ross et al. 2007). In most parts of the world however, such as in the Indo–Pacific, the species identifications are still not known for the majority of leptocephali (Mochioka et al. 1982, 1991; Tabeta and Mochioka 1988a; Miller et al. 2002a, 2006a; Miller and Tsukamoto 2004, 2006).

Fig. 1. Photographs of leptocephali of the Japanese eel, _Anguilla japonica_, that were artificially spawned and reared in the laboratory at the IRAGO Institute in Japan. The larvae are approximately 30–50 mm long, and about 200 days old. Photographs are courtesy of Yoshiaki Yamada.
There has been research on the distributions, life history characteristics, and assemblage structure of leptocephali in a variety of regions of the world using various levels of identification. In the western North Atlantic, the distributions of anguillid leptocephali were studied in more detail to help define the spawning areas of the two species, the European eel, *Anguilla anguilla*, and the American eel, *Anguilla rostrata*, which have overlapping spawning areas in the southern Sargasso Sea (Schoth and Tesch 1982; Kleckner *et al.* 1983; McCleave *et al.* 1987; Kleckner and McCleave 1988; Tesch and Wegner 1990). These surveys for anguillid leptocephali also collected many marine eel species whose life histories were examined (McCleave and Miller 1994; Miller and McCleave 1994; Miller 1995, 2002a; Wippelhauser *et al.* 1996). Studies on the assemblages of leptocephali in these areas were conducted as well (Miller and McCleave 1994, 2007; Miller 1995). Leptocephali also have been collected in the Gulf of Mexico (Smith 1989a; Crabtree *et al.* 1992), over or along the edge of the continental shelf of the southeastern US east coast (Fahay and Obenchain 1978; Ross *et al.* 2007), and around Barbados in the eastern Caribbean Sea region (Richardson and Cowen 2004a). In the northeastern North Atlantic, research has mostly focused on leptocephali of anguillids (Tesch 1980; Bast and Strehlow 1990; McCleave *et al.* 1998) and a few other taxa of leptocephali (e.g. Strehlow *et al.* 1998; Correia *et al.* 2002a,b, 2003). A few taxa have been reported from the east coast of South America in recent years (De Castro and Bonecker 2005; Figueroa and Ehrlich 2006).
Various surveys for leptocephali in the Indo–Pacific region have been conducted recently to learn about the spawning areas of tropical and temperate anguillid species in the western Pacific and Indonesian Seas, which have resulted in many areas being sampled (e.g. Fig. 4). These studies have centered on the anguillid eels that spawn offshore (Tsukamoto 1992, 2006; Aoyama et al. 1999, 2007; Ishikawa et al. 2001; Miller et al. 2002b; Tsukamoto et al. 2003; Kuroki et al. 2009a) or those that spawn in the Indonesian Seas (Aoyama et al. 2003; Wouthuyzen...
In 1991, the spawning area of the Japanese eel, *Anguilla japonica*, was discovered (Tsukamoto 1992), and subsequent surveys collected recently hatched preleptocephali near the West Mariana Ridge, which includes several shallow seamounts (Tsukamoto 2006, 2009). It was also found that a population of the giant mottled eel, *Anguilla marmorata*, spawns in the same general area as *A. japonica* (Miller et al. 2002b; Kuroki et al. 2009a), and spawning areas of other anguillids were detected in several other regions (Aoyama et al. 1999, 2003; Kuroki et al. 2008a). As a result of the surveys for anguillid leptocephali in the western Pacific region, the species composition, assemblage structure, and life history characteristics have been examined for marine eel leptocephali (Minagawa et al. 2004; Wouthuyzen et al. 2005; Miller et al. 2006a, b), and other research resulted from fisheries related collections (Takahashi et al. 2008).

In conjunction with some of these surveys for leptocephali in both the Pacific and Atlantic oceans, data on the depth distributions of leptocephali were gathered (Schoth and Tesch 1984; Castonguay and McCleave 1987a; Kajihara et al. 1988; Otake et al. 1998). These studies indicated that leptocephali live in the surface layer of the ocean at depths mostly in the upper 100 m at night, and likely deeper during the day to depths typically less than 250–300 m for some species that make diurnal vertical migrations.

Some leptocephali from recent surveys also have been used to study the age and growth and species identifications with otolith and gene-sequencing techniques. Gene-sequence analysis has become the standard technique for identifying anguillid leptocephali in the Indo–Pacific where counts of their numbers of myomeres (muscle segments that correspond to the number of vertebrae in adults) often overlap among the different species (Aoyama et al. 1999, 2003, 2007; Kuroki et al. 2006a, 2008a). Genetic sequences have also been used recently to match leptocephali to their adult species (Ma et al. 2007, 2008a), which is a technique that will facilitate matching of adult and larval forms in the Indo–Pacific where little progress has been made in identifying leptocephali. New data on the likely ages of Indo–Pacific leptocephali have been gained from studies on their otolith microstructure, with anguillid (Ishikawa et al. 2001; Tsukamoto et al. 2003; Kuroki et al. 2005, 2006a, b, 2007, 2008a), congrid (Lee and Byun 1996; Kimura et al. 2004) and other families of marine eel leptocephali having been studied (Ma et al. 2005; Lee et al. 2008). These studies have found that the growth rates of different species of...
leptocephali may vary based on differing life history characteristics (Ma et al. 2005; Kuroki et al. 2006a). Otolith increments also have been examined in a few species of leptocephali in the North Atlantic such as in anguillids (Castonguay 1987), conger eels (Correia et al. 2002a,b, 2003), and a few other species (Bishop et al. 2000). Other studies have examined otolith deposition rates of leptocephali held in captivity as they metamorphose into juveniles (Chen and Tzeng 1996; Powles et al. 2006). Variations in otolith increment widths and Sr:Ca ratio data obtained from glass eel otoliths has provided information on the timing of metamorphosis in various species (Otake 2003; Aoyama 2009).

Some studies have also examined the biology and physiology of leptocephali collected in the wild to learn about their ecology. These studies have included examinations of gut contents, which were found to contain particulate matter such as marine snow, fecal pellets, or discarded larvacean (appendicularian) houses (Otake et al. 1990, 1993; Mochioka and Iwamizu 1996). The types of material observed in the guts indicate that leptocephali feed on marine snow-like material, but not zooplankton or phytoplankton. Other types of studies on leptocephali have included enzyme assays to examine levels of respiration (Pfeiler and Govoni 1993), oxygen consumption experiments (Bishop and Torres 1999), or analyses of the chemical composition of their bodies (Donnelly et al. 1995; Pfeiler et al. 1998; Bishop et al. 2000). Physiological measurements and age estimates made on four species of leptocephali from the eastern Gulf of Mexico were used to model the energetics of these species (Bishop and Torres 2001). However, some of the most extensive research on the physiology and chemical composition of leptocephali has been done on bonefish larvae (Albuliformes), since they can often be easily collected in coastal waters and quickly moved to the laboratory (e.g. Pfeiler 1986, 1996, 1997, 2001; Padrón et al. 1996). Few studies on most taxa of leptocephali have been done though, due to the difficulty in collecting healthy specimens in nets at sea and keeping them alive on board research vessels.

The development of artificial culture techniques for anguillid species such as Anguilla japonica (Tanaka et al. 2001, 2003; Tanaka 2003), provides new potential for conducting basic research on the biology and behavior of leptocephali in the laboratory though. The ultimate goal is to provide a consistent supply of artificially spawned and reared glass eels for aquaculture, but the recent success in rearing leptocephali through metamorphosis into the yellow eel stage (Tanaka et al. 2003) has enabled all stages of eels to be available for laboratory research. This has resulted in comparative studies on phototaxis (Yamada et al. 2009) and buoyancy (Tsukamoto et al. 2009) of different stages leptocephali and glass eels reared in the laboratory. Such studies represent a new research frontier that can help improve our understanding of leptocephali until techniques can be developed to study wild-caught leptocephali.

Another recent development that is assisting research on leptocephali was the rapid development of digital imaging technology. The availability of digital cameras and digital imaging systems for microscopes have enabled freshly caught leptocephali to be photographed during sampling surveys (Miller and Tsukamoto 2004). Few photographs of leptocephali were published during the era of film cameras, so these new photographs have helped to document the morphology of leptocephali in several recent studies (Kuroki et al. 2005, 2008a; Kimura et al. 2006; Tsukamoto 2006) or books and reviews (Miller and Tsukamoto 2004, 2006). This review of the present state of knowledge about the ecology of anguilliform leptocephali will also use many digital photographs of freshly caught leptocephali to illustrate various aspects of how the morphology of leptocephali may be related to their ecology.

The objective of this review is to provide a broad overview of the ecology of leptocephali that ranges from where leptocephali are found in the ocean, to what can be deduced about their biology and ecology from their morphology and from studies conducted on them using various analytical techniques. This begins with an overview of what is known about the basic morphology, biology, and behavior of leptocephali, which is followed by a section on the zoogeography of leptocephali that describes where the various types of eels live, and where their larvae are likely to be distributed. Then, aspects of the ecology of leptocephali are evaluated to provide an overall picture of the present state of knowledge about leptocephali and on the possible ecological significance of these cosmopolitan, surface dwelling larvae.
2. Biology of leptocephali

2-1. Developmental stages

Leptocephali have several different morphologically distinguishable stages that seem to be consistent among all anguilliform taxa. Eels have large eggs compared to many other fishes, which can range from about 1–4 mm in diameter, and have a large perivitelline space (Castle 1984; Smith 1989a; Umezawa et al. 1991; Horie et al. 2002). The Anguilliformes is one of the few orders of fishes that have the characteristic of yolk extension (Virta and Cooper 2009), which can be seen in the posterior extension of the yolk in the newly hatched larva in Fig. 5. Some eel larvae appear to be born in a morphologically very undeveloped state with almost no development of the features of the head, as has been observed in species hatched in the laboratory, such as *A. japonica* (Fig. 5; Okamura et al. 2002), *Muraenesox cinereus* (Umezawa et al. 1991), and *Conger myriaster* (Horie et al. 2002). Other species though, such as ophichthids may hatch at a more developed state with the eyes and some early teeth already formed (Leiby 1979a, 1989). Evidence of more advanced development before hatching was seen in what appears to be a muraenid larva collected while still within the egg case, which had fully developed eyes and early jaws (Fig. 6). Larvae of *A. japonica* (Fig. 7A) and Serrivomeridae (Fig. 7C) collected in the ocean, suggest these taxa, at least, hatch in a very undeveloped state and then develop the morphological features of the head during the preleptocephalus stage (Fig. 8).

![Fig. 5. Drawings of recently hatched *Anguilla japonica* larvae hatched in the laboratory from 1–7 days after hatching, showing the location of various types of mechanosensory cells. Scale bars are 1 mm. Reprinted with permission of John Wiley & Sons, Inc. from Okamura A, Oka HP, Yamada Y, Utoh T, Mikawa N, Horie N, Tanaka S. Development of lateral line organs in leptocephali of the freshwater eel *Anguilla japonica* (Teleostei, Anguilliformes). *Journal of Morphology*, 2002; 254: 81–91. © 2002, Wiley-Liss, Inc., A Wiley Company.]
Fig. 6. Photograph of what appears to be a larva of the Muraenidae that was collected in the western North Pacific near the West Mariana Ridge while it was still inside of an egg case before hatching.

Fig. 7. Photographs of preleptocephali of *Anguilla japonica* (A), Ophichthidae (B), and Serrivomeridae (C), showing the undeveloped morphology of recently hatched wild-caught anguilliform larvae. Scale bars are 1 mm.
The preleptocephalus stage is defined as the period just after hatching when the larva is still absorbing its oil globule and not actively feeding on external food. These larvae have poorly developed eyes, few or no teeth, and an oil globule. The size of preleptocephali of various taxa may range from about 3–7 mm, but no comparative analysis has been published. An oil globule is clearly present in anguillid preleptocephali (Fig. 8; Tsukamoto 2006; Kuroki et al. 2009a) and in ophichthid and serrivomerid preleptocephali (Fig. 7). The oil globule of the ophichthid species shown in Fig. 7B and of another species collected along coastal Japan (Kimura et al. 2006) shows a golden color. At least some species are born with no teeth, or just rudimentary teeth that may be easily damaged in the net (Fig. 8). Teeth appear and grow during early posthatching development. The eggs and preleptocephali of most species of marine eels have not been described, so much research remains to be done on the early development of each family of eels.

The leptocephalus stage begins after the oil globule is absorbed and the eyes and teeth are formed. Larvae at this early stage have relatively few, but very long, forward pointing teeth (Fig. 9), and this stage has been referred to by Leiby (1979b, 1989) as the engyodontic stage. Body shapes of these small leptocephali are generally similar (Fig. 10), even though they may ultimately develop more long and thin or deeper bodies. As leptocephali grow larger, the long teeth are replaced by shorter ones, more teeth are formed, and the teeth point less forward (Figs. 3, 11). These larvae have been referred to as the euryodontic stage (Leiby 1979b, 1989). This transition appears to occur at around 20 mm in ophichthids (Leiby 1989) and other leptocephali (Castle 1984), and can also be seen in the development series of Derichthys serpentinus of Castle (1970) (Fig. 11).

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**Fig. 8.** Photographs of the head regions of preleptocephali of the Japanese eel, *Anguilla japonica*, at various stages of development ranging from having unpigmented eyes and no teeth (A), to fully formed eyes and jaws with teeth (D), but all larvae still having an oil globule. Scale bar in (C) is 1 mm. Reprinted by permission of Macmillan Publishers Ltd: *Nature*. 2006; **439**: 929. Tsukamoto K. Spawning of eels near a seamount.
Leptocephali keep growing until they reach a species specific maximum size. This maximum size varies from about 50–100 mm in many species and up to 300 mm or more in some taxa such as *Ariosoma* and *Nemichthys*. The full size leptocephali then metamorphose into the glass eel or elver stage (Fig. 12). During the process of metamorphosis the laterally compressed body of the leptocephalus changes to be more rounded. Towards the end of the transformation into the glass eel and elver stages their bodies become pigmented. See Section 2-7 for a more detailed discussion of metamorphosis in eels.

### 2-2. Morphological features

Although body shapes (Figs. 2, 13) and head shapes (Figs. 3, 14–17) can vary widely among taxa, leptocephali all have similar basic morphological features. Drawings and photographs of the diverse body shapes of leptocephali and guides to identify them have been published (e.g. Blache 1977; Smith 1979; Fahay 1983; Tabeta and Mochioka 1988a; Böhlke 1989b; Miller and Tsukamoto 2004). All leptocephali are strongly laterally compressed and transparent, with a small tubular gut along the ventral margin. Dorsal, anal, and pectoral fins are present starting in the euryodontic leptocephalus stage, but the pectoral fin does not have rays until metamorphosis (Smith 1989a). Body shapes can vary from very long and thin as in some congrids, nemichthyids, and some nettastomatids, to deep bodied such as in chlopsids, some congrids,
nettastomatids, eurypharyngids, and cyematids (Fig. 2). Other leptocephali (Nettenchelys, Nettastomatidae) have fairly deep bodies, but a long and thin tail (Fig. 13). The head shapes of leptocephali also vary widely, mostly due to the structure of the jaws in various taxa (Figs. 14, 15). Their heads range from being very sharp and elongate in Cyema atrum (Fig. 15A), to having pointed snouts in some congrids and ophichthids, or being rounded in many species of muraenids (Fig. 14F). The most unusual head shape is that of the leptocephali of the gulper eels, Eurypharynx pelecanoides, which have an oblique gape, a long lower jaw, and very long thin teeth extending forward from the top of the upper jaw (Figs. 10C, 15B). This jaw structure is similar to that of the juvenile and adult gulper eels, which got their species name from their pelican-like mouth (Böhlke 1989a). Even more remarkable perhaps is that some species of synaphobranchids of the subfamily Illyophinae have strange “rostral filament” projections from the tip of the snout (Smith 1974), which can be quite long (Fig. 16). These projections can have patches of pigment or even secondary branches (Castle 1984) or palp-like extensions (Fig. 16C). Many nettastomatid leptocephali have forward pointing teeth or small rostral cartilages on the tip of the snout (Smith and Castle 1982), but they do not extend as far as in synaphobranchids.

Even though head features and shapes can vary widely in leptocephali, they all have the same basic components of other fish larvae (Fig. 17). The shapes of their large eyes can vary considerably though, ranging from telescopic eyes (tubular with a spherical lens on top) in
Synaphobranchidae (Figs. 14C, 15E, 16, 17B), to perfectly round in others such as Anguilla and Thalassenchelys (Figs. 15C, D). Other species have more oval eyes (Fig. 15). Leptocephali have large brains and a heart that is visible through the body wall (Fig. 17), but they lack well developed gills until they approach metamorphosis. The operculum is open so water can be ejected from the buccal cavity during feeding. There is very little ossification of the head or body other than the teeth until metamorphosis. Leiby (1979a, 1989) described the osteology of ophichthid leptocephali.

The gut and internal organs of leptocephali are generally quite small and inconspicuous. Their tubular gut can be completely straight with no visible swellings or there can be distinct swellings and curvatures along the gut (Figs. 2, 13, 18). The swellings appear to be liver tissue, but other organs also contribute in some cases. Anteriorly, the esophagus extends from the oral cavity, over the heart (Figs. 17A, B), and along the anteroventral margin of the body until it reaches the rudimentary stomach, which is located at the beginning of the intestine (Fig. 18). The lack of a distinguishable stomach is typical of most fish larvae (Govoni et al. 1986). A visible swelling at this location often includes the liver and gallbladder (Fig. 18). The liver lobes...
Fig. 12. A developmental growth series of *Anguilla japonica* larvae reared in the laboratory from a newly hatched larva (preleptocephalus, 3.6 mm in total length, 0 days old) to the maximum size at the end of the leptocephalus stage (59.0 mm, 260 days old), and the glass eel stage (58.5 mm, 268 days old). The body size of leptocephali diminished slightly during the process of metamorphosis. Specimens older than 260 days are the same individual. Reprinted with kind permission from Springer Science + Business Media: *Marine Biology*. Positive buoyancy in eel leptocephali: an adaptation for life in the ocean surface layer. 156, 2009, 835–846. Tsukamoto K, Yamada Y, Okamura A, Tanaka H, Miller MJ, Kaneko T, Horie N, Utoh T, Mikawa N, Tanaka S. Figure 2. © 2009, Springer-Verlag. (Original photographs provided by Hideki Tanaka of the National Research Institute of Aquaculture).
can be split among several different gut swellings, and the kidney is a linear structure located on top of the gut at various locations depending on the species (Fig. 17C).

All congrid leptocephali lack any major gut swellings, but in one group the straight tubular gut extends outside of the body and trails freely behind the body. This is referred to as an exterillium gut (see Ariosoma type leptocephalus in Fig. 2, with most of the exterillium gut broken off), and they can be longer than 150 mm in some species of large bathymyrid leptocephali (Arioso, Parabathymyrus) that have this type of gut (Mochioka et al. 1982; Tabeta and Mochioka 1988a; Smith 1989a). These extensions appear to simply lengthen the gut to increase absorptive surface area as they do in other fish larvae (Moser 1981), but they have not been studied in leptocephali.

Fig. 13. Photographs of 5 species of leptocephali that have different body shapes and gut morphology.
The body of leptocephali is transparent mainly because it is comprised mostly of transparent material contained in a mucinous pouch (Pfeiler 1999) and their circulatory system contains colorless blood. Extending through the center of the body are the spinal chord (Yoshida et al. 1995), notochord, and dorsal aorta (Fig. 17). Other components of the circulatory system extend along the gut, and there are several vertical blood vessels including the renal arteries that extend vertically up to the dorsal aorta (Hulet 1978). The blood is transparent because leptocephali lack red blood cells (Hulet and Robins 1989).

The integument of leptocephali is thin and fragile. The mucinous pouch is overlain by a thin layer of muscle tissue that is organized into individual muscle segments, called myomeres. The myomeres are overlain by a thin layer of epidermal cells, which are only a few cells thick.
The skin of *A. japonica* leptocephali generally consists of only one layer of club cells that include secretory vacuoles or a few epidermal cells, which overlay the dermis (Suzuki and Otake 2000). The same was observed in late-stage *Conger myriaster* leptocephali, which during metamorphosis also developed more layers of club cells, a layer of epidermal cells underneath, and some mucus cells (Fig. 19; Nakamura *et al.* 2002). Because the skin of leptocephali is so thin and they do not develop substantial gills until after metamorphosis begins, it has generally been assumed that they mostly respire through gas exchange across their integument (Pfeiler 1999).

2-3. Sensory organs

Leptocephali have several different sensory systems that they likely use for feeding or predator avoidance. Visual and olfactory systems are obvious from their external morphology or the size of different parts of the brain (Pfeiler 1989), and these two senses are thought to be the dominant senses of leptocephali (Smith 1989a). All leptocephali have large eyes even though their position can vary from being in about the middle of the head, to being raised on the top of the head such as in *Cyema atrum* (Fig. 15A). The consistently large eyes emphasize their likely
Thalassenchelys leptocephali can have a remarkably large eye that fills the space between the upper jaw and the top of the head (Fig. 15C). Relative eye size is not so large though in Thallasenchelys leptocephali that reach very large body sizes of about 300 mm (Castle and Raju 1975). The apparently large size of the optic lobe of the brain of leptocephali, also supports the inference that vision is an important sense for eel larvae, because the leptocephali of Anguilla japonica (Tomoda and Uematsu 1996) and Ariosa balearicum (Hulet 1978) have been reported to have large optic lobes. For A. japonica, the relative size
of the optic lobe decreases in the juvenile stage, when eels are no longer visual feeders (Tomoda and Uematsu 1996). A 50-mm long Anguilla leptocephalus was found to have only one type of rod-like retinal photoreceptor (Pankhurst 1984), which is similar to the observations of only rods in the retina of A. balearicum leptocephali (Hulet 1978). These observations suggest that leptocephalus eyes are adapted to low light conditions, as is true of some adult eels (Hess et al. 1998). This is in contrast with many other types of fish larvae, which have been found to have pure cone retinas (Evans and Fernald 1990).

Two categories of eyes are present in leptocephali: normal and telescopic eyes. The latter are found only in the Synaphobranchidae (Figs. 14C, 15E, 16, 17B) and some notacanthids (Smith 1974, 1979). In the two subfamilies of synaphobranchids, a large spherical lens is positioned on top of a tube containing the retina (Fig. 15E). This eye structure is thought to be related to the slightly deeper depths and lower light where these larvae live (Smith 1989a). Other deep-sea fishes have similar eyes (Warrant and Locket 2004). Perhaps the eyes look upward so they can see the silhouettes of food particles against the downwelling light. The eyes of these eel larvae change into more normal shaped eyes during metamorphosis (Smith 1974), which is the opposite sequence to many deep-sea fishes that develop telescopic eyes as juveniles, after a larval stage in the surface layer with normal eyes (Evans and Fernald 1990).
Olfaction is also probably available to leptocephali. All leptocephali have a pair of olfactory rosettes just in front of the eyes (Figs. 14, 15, 17, 20), but they do not appear to be developed until the late engyodont stage (Figs. 9, 11). These structures vary in size among species and sizes of leptocephali, with *Thalassenchelys* being an example of having a small nasal organ (Fig. 15D) and *Gorgasia* having a large one (Fig. 17A). It is usually positioned just in front of the eye, but in synaphobranchids with a very long snout, it is positioned near the end of the snout (Fig. 17B). The nasal organs of most species appear to get larger with age and can be greatly enlarged in metamorphosing leptocephali (see Section 2-7). Some species develop nostrils that extend outside of the body during metamorphosis, which likely remain in the juveniles and adults. It appears that the nasal organs of many species may have two openings, one anterior and

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**Fig. 19.** Sections showing the changes in the thickness of the skin of *Conger myriaster* larvae at the stages of premetamorphic leptocephalus (A), metamorphosing leptocephalus (B), and postmetamorphosis (C) using immunohistochemical staining. Arrows show club cells (mostly red color); mucous cells (mc); epidermal cells (ec); dermis (dm); muscle (m). Scale bars are 10 µm. Reprinted with permission of Wiley-Blackwell from Nakamura et al. Development of epidermal and mucosal galectin containing cells in metamorphosing leptocephali of Japanese conger. *Journal of Fish Biology*, 2002; 61: 822–833. © 2002, The Fisheries Society of the British Isles.
one posterior, based on scanning electron microscope (SEM) observations (Appelbaum and Riehl 1993). This would allow water to flow over the olfactory rosette tissue as the leptocephalus swims through the water. However, Nemichthys scolopaceus leptocephali have only one opening to the nasal organ (Appelbaum and Riehl 1993).

Leptocephali also appear to have a rudimentary lateral line system to provide mechanoreception. Okamura et al. (2002) used SEM to examine the development of mechanoreceptor cells in newly hatched larvae of A. japonica that were obtained from artificially matured and spawned eels. Those larvae had three types of these sensory cells distributed on various parts of their body at different developmental stages (Fig. 5). These types were classified as Type I with hair

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**Fig. 20.** Photographs of the head regions showing the nasal organ in both panels and sensory pores in the lower jaw of a metamorphosing muraenid leptocephalus in (B). The three largest visible sensory pores are shown with black arrows, and the velum (see Section 2-4) is shown with a red arrow.
cells bearing a single kinocilium, lacking stereocilia, and distributed mainly on the head; Type II (Fig. 21), which is an ordinary superficial neuromast of the lateral line system, common in other teleost larvae (Fuiman et al. 2004), distributed on the head and trunk; and Type III that is an unusual neuromast with radially oriented hair cells, located on each side of the head starting from the day of hatching (Okamura et al. 2002). Type I was found on the head (Fig. 5), which appeared at 0–4 days posthatching, and were suggested to be canal neuromasts that later become enclosed in a canal, since they correspond to the position and number of pores in the supra- and infraorbital canals on the head of adult eels. Type II neuromasts distributed along the side of the body, appeared starting on day 1 (Fig. 5) and were thought to later become lateral line canal neuromasts or accessory superficial neuromasts. Some Type II neuromasts also later appeared on the head after 10 days and may later become accessory superficial neuromasts on the heads of the eels. Type III neuromasts were seen on the side of the heads of the day 0–7 larvae (Fig. 5), but their presence in later stages is uncertain.

The general implications of this study on larval A. japonica is that at least this particular species of leptocephalus is adapted to detect mechanosensory stimuli, such as those created by potential predators, as is thought to be the case in other types of fish larvae (Fuiman and Magurran...
The potential importance of this mechanosensory system for leptocephali in general is supported by observations of neuromasts located on the head of several other species of anguilliform leptocephali that have also been observed using SEM (Appelbaum and Riehl 1993). Although these mechanoreceptors observed in leptocephali of *A. japonica* and other species using SEM are not apparent while examining freshly caught leptocephali, large sensory pores that presumably contain mechanoreceptors appear along the lower jaw of some species during metamorphosis (Figs. 11, 20B).

Future studies are needed on the sensory biology of leptocephali, but the basic observations that have been made so far indicate that leptocephali have mostly similar sensory systems of other marine fishes that enable them to detect mechanical, olfactory, and visual cues. However, since anguillid glass eels, and yellow eels have been found to have a geomagnetic sense (Nishi *et al.* 2004; Nishi and Kawamura 2005), the function of which is most likely to guide migrating adult eels back to their spawning area (see Tsukamoto 2009) using a geomagnetic map sense as hypothesized for other marine animals (Lohmann *et al.* 2008). If true, this would require that leptocephali also have the ability to imprint on the geomagnetic cues that characterize the area where they were born. Therefore it is possible that at least some leptocephali, such as anguillids, also have a geomagnetic sense.

**2-4. Feeding ecology**

What leptocephali use as a food source was a mystery for many years, and even now their feeding ecology is poorly known. It has been difficult to understand what leptocephali feed on because no identifiable objects such as small zooplankton have been seen in their guts after being captured in nets and examined onboard research vessels. There is often an unidentifiable material inside the intestine, which can flow out the end of the gut while a leptocephalus is being observed after capture (Fig. 22C). However, the lack of visually identifiable organisms in their guts and the thin layer of epidermis covering their body led to the hypothesis that leptocephali absorbed dissolved organic carbon (DOC) across the surface of their bodies (Pfeiler 1986; Hulet and Robbins 1989). Hulet (1978) incorrectly thought that the gut was occluded and non-functional based on sections made of *Ariosoma balearicum* leptocephali, and the observation of tiny microvilli-like extensions of the epidermis of some leptocephali was seen as support for the direct absorption of DOC hypothesis (Hulet 1978; Hulet and Robbins 1989). There were no successful attempts to test this hypothesis, likely due to the difficulty of obtaining healthy leptocephali and the constraints of carrying out labeled isotope experiments that can exclude the uptake of the tracers by bacteria attached to the leptocephali.

Eventually the gut contents of leptocephali of various families that were collected in coastal regions of Japan were carefully examined, or they were directly observed to feed in the laboratory. Leptocephali of *Muraenesox cinereus* were observed to eat squid paste (Mochioka *et al.* 1993), and the red paste could clearly be seen in their guts after it was ingested (Fig. 23). They ignored zooplankton in the tank and were not attracted to fish paste. Their feeding on squid paste stopped at metamorphosis when the gut started to move forward (Mochioka *et al.* 1993). Otake *et al.* (1993) examined the gut contents of *Conger myriaster, C. japonicus*, and *M. cinereus* and found zooplankton fecal pellets or smaller particles in the guts of most of the more than 600 leptocephali examined. They also found that the nitrogen isotope ratio of the bodies of leptocephali (gut excluded) was very low, supporting the evidence found in their gut contents that they were feeding on particulate material and gaining their nutrition at the bacterial level of the food chain (Otake *et al.* 1993). Otake *et al.* (1990) also suggested ciliates may have been present in the guts of *Anguilla japonica* leptocephali, but this was not confirmed, and they may simply have been attached to ingested particulate matter. Govoni (in press) also reported ciliates in the guts of ophichthid leptocephali, so these organisms may also contribute to the diet of leptocephali in some areas.

Mochioka and Iwamizu (1996) examined the guts of eight species of leptocephali (Congridae, Muraenesocidae, Muraenidae, Nettastomatidae, Ophichthidae) that were also caught along coastal Japan. The particles in their guts were identified as either larvacean houses, larvacean
fecal pellets, or zooplankton fecal pellets. More detailed SEM observations confirmed that objects such as zooplankton fecal pellets and parts of discarded larvacean houses were present in the guts of some leptocephali (Fig. 24). Mochioka and Iwamizu (1996) detected structures that appeared to be the mesh screens (Figs. 24B, C) used as filters within the larvacean houses (Flood and Deibel 1998). Oval objects that are likely zooplankton fecal pellets are also occasionally seen inside the guts of leptocephali collected in offshore areas far from the higher productivity coastal waters where previous studies were conducted (Fig. 22). These types of observations disproved the hypothesis that leptocephali do not feed and only get their nutrition by absorbing DOC.

The eventual success in getting artificially spawned _A. japonica_ leptocephali to grow under laboratory conditions (Tanaka _et al._ 2001) has provided further evidence that leptocephali actively ingest food. Initially, some early stage leptocephali were observed to eat rotifers, but this food source would not keep them alive very long (Tanaka _et al._ 1995). It was later found that seemingly the only material that would stimulate the larvae to eat and grow was shark egg yolk paste (Tanaka _et al._ 2001, 2003). Differentiation of the alimentary canal was complete by 7 days after hatching in _A. japonica_ preleptocephali, indicating that they had developed the ability to absorb food by this young age (Ozaki _et al._ 2006a). Other studies examined the digestive enzymes of early stage _A. japonica_ larvae and established the presence of trypsin in first feeding larvae (Kurokawa _et al._ 1995; Kurokawa and Pedersen 2003; Pedersen _et al._ 2003) and in other species (Kruse _et al._ 1996), but these studies did not reveal much about the likely natural food of leptocephali.
Although leptocephali will eat a prepared paste if it contains shark egg yolk, this material is not a natural food. The yolk likely contains some chemical compound that stimulates a feeding response, which is positively reinforced by the nutrition provided by the food, resulting in successful feeding and growth. Other than the obvious possibility that the compound is related to what they naturally eat as larvae, another possibility is that it is related to an important food item they eat later in life, and they have an innate and irresistible attraction to that chemical regardless of their life history stage, due to its significance in feeding during the juvenile stage. Fish or other types of eggs are one possibility for this, because it is well known among fishermen that horseshoe crabs laden with eggs are the best bait for the American eel. Despite much effort though, it is presently unclear what special ingredient in shark egg yolk triggers a feeding response in larvae that seem to feed on particulate material such as marine snow or discarded larvacean houses in the ocean.

It has been suggested that leptocephali may target larvacean houses as a food source in the ocean (Westerberg 1990; Mochioka and Iwamizu 1996), but it is presently unclear whether leptocephali are feeding specialists or if any type of available particulate matter, such as marine snow, is sufficient as a food source. Larvacean houses were found in 80% of the guts of leptocephali that contained food in the study of Mochioka and Iwamizu (1996), suggesting that they were an important part of the diet of leptocephali in that region of coastal Japan. The forward pointing teeth appear to be well-designed to grasp larvacean houses (Westerberg 1990; Mochioka and Iwamizu 1996) and to help squeeze the house material and any associated bacterial or other particles, such as fecal pellets, into the oral cavity. These forward pointing teeth also would enable excess material to be ejected away from the mouth to avoid fouling the teeth.

There are other morphological features that may be important for feeding by leptocephali. Many leptocephali have a velum that hangs down from the edges of the roof of the mouth (Hulet 1978; Hulet and Robins 1989), which would provide a lining or a seal for the oral chamber when the mouth is closed (Figs. 20B, 25). This thin tissue may enable water containing a wide size range of particles to be forced into the esophagus. Another factor is that observations of the fine structure of leptocephalus guts have suggested that they are adapted for intestinal water
absorption, so DOC in the water surrounding the particulate matter is also likely absorbed, providing additional nutrition (Otake et al. 1995; Otake 1996; Ozaki et al. 2006a).

2-5. Physiology and energetics

The fragility of leptocephali and the difficulty in capturing them has limited the amount of physiological research done on them, but due to their transparent bodies and unusual diet, they appear to have a unique physiology compared to most fish larvae. Perhaps what makes them so

Fig. 24. Various photographs of a larvacean (appendicularian) house removed from the intestine of Conger myriaster leptocephalus, with an arrow indicating one of a pair of oval mesh screens (A), the minute rectangular mesh structure of a larvacean house feeding filter (B) and the fine-mesh sheet of the filter from the intestine of a Muraenichthys gymnotus leptocephalus (C), a cross section of the esophagus of a C. myriaster leptocephalus including an opaque particle (D), the inner structure of a fecal pellet and opaque particle from the intestine of a Muraenichthys gymnotus leptocephalus (E, F), and fecal pellets from the intestine of a M. cinereus leptocephalus (G, H). Reprinted with kind permission from Prof. Noritaka Mochioka and Springer Science + Business Media: Marine Biology, Diet of anguillid larvae: leptocephali feed selectively on larvacean houses and fecal pellets. 125, 1996, 447–452. Mochioka and Iwamizu. Figure 2. © 1996, Springer-Verlag.
unique is the transparent GAG material filling their bodies, which unlike the muscle tissue that comprises a high proportion of the body of typical fish larvae, is not metabolically active material. As a result of this, their respiration rates are low compared to their body mass (Pfeiler and Govoni 1993; Bishop and Torres 1999), and become proportionally even lower as they increase in size by building a larger relative content of GAG material and water (Bishop et al. 2000).

In one study, the respiration rates of several species of leptocephali were determined using electron transport system (ETS) assays on fresh and frozen leptocephali, which included two conroids, two ophichthids and a species of bonefish (Pfeiler and Govoni 1993). ETS activity is assumed to represent the maximum potential oxygen consumption rate (see Pfeiler and Govoni 1993). This study clearly showed a decrease in wet-weight-specific ETS activity with increase in body length in premetamorphic leptocephali (Pfeiler and Govoni 1993), which was consistent with a previous ETS activity study that included leptocephali (Schalk 1988). Bonefish leptocephali were also tested in respirometers, which showed that respiration rates increased during metamorphosis as GAG and other materials were converted into respiring tissues (Pfeiler and Govoni 1993).

Other estimates of leptocephalus respiration were obtained by testing anguilliform leptocephali in respirometry chambers or using enzyme assays (Bishop and Torres 1999). This study showed the same pattern of a decrease in wet-weight-specific respiration with increasing body mass and water content using the respirometry chambers (Fig. 26) and in enzyme assays of citrate synthase and lactate dehydrogenase activities (Bishop and Torres 1999). These measurements in combination with estimates of excretion during the respirometry, and growth estimates from otolith analyses (Bishop et al. 2000) were then used to model the energetics of these species of leptocephali (Bishop and Torres 2001). Those analyses indicated that leptocephali devote most of their energy not to growth as is the case with most fish larvae, but to metabolism. It was estimated that 60–92% of their total ingested energy was used for metabolism, which combined with their very low mass-specific respiration rates, made them physiologically very different from other fish larvae.

In addition to respiration data for leptocephali, there are also basic data on their chemical composition and RNA/DNA content. Pfeiler (1999) reviewed the literature on the chemical composition, biology, and physiology of leptocephali, and some more recent studies have been published. The gelatinous extracellular matrix of GAG comprises most of the bodies of leptocephali, but this matrix contains a high percentage of water that ranges from about 90–95% of the total body content (Pfeiler and Govoni 1993; Donnelly et al. 1995; Pfeiler 1999; Bishop et al. 2000; Wuenschel and Able 2008). The general chemical composition of leptocephali has
been examined in a few species such as the congrids, *Ariosoma balearicum* (Donnelly et al. 1995) and *Paraconger caudilimbatus*, a muraenid (*Gymnothorax saxicola*), an ophichthid (*Ophichthus gomesii*) (Bishop et al. 2000), as well as in non-anguilliform bonefish leptocephali (Pfeiler 1988, 1991, 1993; Pfeiler et al. 1998, 2002). These studies have found that different species of leptocephali are comprised of roughly similar proportions of protein, lipids, carbohydrates, and nucleic acids. The GAG carbohydrate compounds are long-chain mucopolysaccharides that may comprise 10% or more of the dry mass. They provide both structural support for the muscle tissue needed for swimming and act as an energy storage material in preparation for metamorphosis (Pfeiler 1999; Pfeiler et al. 2002).

Pfeiler et al. (2002) recently reported that hyaluronan is the principal GAG in the body matrix of seven species of anguilliform and in ladyfish *Elops saurus* (Elopiformes) leptocephali, but it was a minor GAG component in the bonefish *Albula* sp. (Albuliformes). Previous reports that chondroitin and chondroitin sulfate were the primary eel GAG compounds (Pfeiler 1993) may have been incorrect due to technical difficulties in accurately identifying them (Pfeiler et al. 2002). Trace amounts of unsaturated disaccharides of chondroitin sulfate were also present in the more recent study of eel leptocephali (Pfeiler et al. 2002). In addition to its presumed role in maintaining the structural integrity and hydration of the gelatinous body of the leptocephalus, hyaluronan was postulated to function as a storage polysaccharide in those species in which it is the predominant GAG. In bonefish leptocephali, keratan sulfate appears to be the dominant form of GAG, with hyaluronan and chondroitin sulfate being minor components (Pfeiler et al. 1988, 1993).

Most biochemical and physiological research on leptocephali has been done on bonefishes (genus *Albula*) as they approach recruitment age and begin to metamorphose (Pfeiler 1986, 1997, 2001; Padrón et al. 1996; Pfeiler et al. 1998). How precisely these findings apply to anguilliform leptocephali is unclear. Studies on some species of anguilliform leptocephali in the western North Atlantic have found that they have high blood osmolalities compared to most...
marine fishes, but have values below that of seawater (Hulet et al. 1972; Hulet and Robins 1989). These values ranging from roughly 500–1000 mOsm kg\(^{-1}\) H\(_2\)O suggest that some premetamorphic leptocephali are closer to being isotonic with seawater than any other fishes (Hulet et al. 1972; Hulet and Robbins 1989). Mean blood osmolalities of premetamorphic *A. balearicum* samples, for example, were 792–910 mOsm kg\(^{-1}\) H\(_2\)O, compared to a value of about 1058 kg\(^{-1}\) H\(_2\)O for seawater (Hulet and Robbins 1989). Blood osmolalities of *Rhynchoconger flavus* may tend to decrease from about 804 to 611 mOsm kg\(^{-1}\) H\(_2\)O as leptocephali increase in size from 50 to 100 mm, but the relationship between size and osmolality was not clear, and was obtained from specimens collected during different cruises (Hulet and Robbins 1989). Other anguilliform leptocephali showed osmolalities in a similar range, with the lowest value recorded from a nettastomatid (483), and the highest from a congrid (1057) (Hulet and Robbins 1989). Tsukamoto et al. (2009) reported a mean value of 450 mOsm kg\(^{-1}\) H\(_2\)O for the extracellular matrix of *A. japonica* leptocephali that were reared in the laboratory, and suggested that this low osmolality is likely an important factor in their buoyancy.

Leptocephali have no swim bladder, but they appear to have high buoyancy compared to many other marine organisms that live in the surface layer of the open ocean (Tsukamoto et al. 2009). Eels do not develop a swim bladder until after metamorphosis near the end of the glass stage, based on observations of an anguillid (Zwerger et al. 2002), so their lipid content, high water content, and almost complete lack of ossified structures may contribute to their buoyancy (Pfeiler 1999). A comparative study of the specific gravity of 25 taxa of 7 phyla of zooplankton and 6 taxa of leptocephali found that leptocephali were among the species with the lowest specific gravities and highest buoyancies (Tsukamoto et al. 2009). Most ocean-collected leptocephali had lower specific gravities (1.028–1.032) than a variety of crustaceans and pelagic mollusks (~1.040–1.450 for 13 taxa), but had values similar to the gelatinous zooplankton, including jellyfish, salps, ctenophores, and chaetognaths (~1.020–1.034 for 8 taxa).

Buoyancy of leptocephali during their ontogeny was also examined by Tsukamoto et al. (2009) using artificially spawned and reared eggs and larvae of *A. japonica*. Preleptocephali had very low specific gravities, probably due to their oil globule, but once the globule was absorbed and the larvae were ready to initiate feeding, their specific gravities increased (Fig. 27). As the leptocephali grew and accumulated higher proportions of extracellular matrix material, their specific gravities decreased steadily. During metamorphosis however, their specific gravities rapidly increased again, and the glass eel stage showed the highest values and were negatively buoyant (Fig. 27). This apparent ontogenetic change in the buoyancy of *A. japonica* was hypothesized to have some adaptive value for this species (Tsukamoto et al. 2009), because the eggs and preleptocephali would tend to float towards shallow depths where food is more abundant, but as they grow they need to be free to migrate vertically on a diel cycle. As they grow near their maximum size, however, high buoyancy would tend to assist their migration back to their recruitment areas.

Chloride cells scattered over the surface of the body (Fig. 28A; Sasai et al. 1998; Kaneko et al. 2003, 2008) probably help maintain buoyancy by sustaining osmolalities lower than seawater (Tsukamoto et al. 2009). Apparent chloride cells have also been observed in *Ariosoma balearicum* and *Anguilla rostrata* leptocephali (Leonard and Summers 1976; Hulet 1978) and in bonefish larvae (Pfeiler and Lindley 1989). In freshly caught undamaged leptocephali, small objects can be seen scattered over the integument that may be chloride cells (Fig. 28B), but this needs to be confirmed. Other fish larvae have osmoregulation abilities (Varsamos et al. 2005) and typically use a swim bladder to obtain buoyancy, or sometimes have other structures such as expanded fins or fin folds to help reduce sinking (Moser 1981).

### 2-6. Growth of leptocephali

Growth rates of leptocephali have been estimated primarily from change in body size among samples collected at different times and from analysis of otolith microstructure. Smith (1989a) was able to observe changes in size of the leptocephali of some species in different seasons in the Gulf of Mexico, and apparent growth of cohorts of some species can be seen in the catch data of Blache (1977). But examples of this type of data being available are

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The other method that has been used recently is the examination of increments in the sagittal otoliths of leptocephali, which are likely to be deposited daily as they are in other fish larvae under normal circumstances (Campana and Neilson 1985). Several studies have validated that daily rings are deposited in the otoliths of anguillid glass eels that have recruited to coastal areas in both temperate (Tsukamoto 1989; Martin 1995; Cieri and McCleave 2001) and tropical species (Arai et al. 2000; Sugeha et al. 2001a). Daily deposition was indicated in a study of artificially spawned and reared _A. japonica_ early stage leptocephali (Umezawa et al. 1989; Shinoda et al. 2004). Although there have been no validation studies on larger premetamorphic stage leptocephali, all species of anguillid leptocephali that have been examined from tropical or subtropical latitudes have otolith increments that can be clearly seen in SEM imagery of otolith cross sections (Fig. 29). Clear increments have also been observed in other taxa of anguilliform leptocephali such as _Dysomma_ and _Saurenchelys_ (Ma et al. 2005), and in _Conger_ leptocephali (Lee and Byun 1996; Correia et al. 2002a, 2003, 2004) at least during the time periods that the larvae were living in warm-water regions. These studies suggest that leptocephali that are feeding and growing normally deposit daily otolith increments.

Fig. 27. Ontogenetic changes in specific gravity of _Anguilla japonica_ during its early life history. The specific gravity values of 6 batches of eggs (about 1 mm in diameter) that hatched 46 hours after fertilization at 22°C (green circles). The specific gravity values of preleptocephali are means of 10 specimens of 6 batches (light blue triangles). Symbols of the other stages are leptocephalus (blue diamonds), metamorphosing leptocephalus (purple triangles) and glass eels (red circles), that represent individuals from at least 3 larval batches. The two horizontal broken lines indicate the specific gravity of seawater at 26°C (upper: 1.023) and 22°C (lower: 1.024), which roughly correspond to the water temperatures at depths of 100 and 200 m in the North Equatorial Current (15°N, 140°E), respectively. Reprinted with kind permission from Springer Science + Business Media: _Marine Biology_, Positive buoyancy in eel leptocephali: an adaptation for life in the ocean surface layer. 156, 2009, 835–846. Tsukamoto K, Yamada Y, Okamura A, Tanaka H, Miller MJ, Kaneko T, Horie N, Utoh T, Mikawa N, Tanaka S. Figure 2. © 2009, Springer-Verlag.
Additional evidence of daily increment deposition throughout the leptocephalus stage has been obtained from back-calculated hatching date analyses in some species that indicate lunar spawning patterns. Studies on A. japonica leptocephali used the back-calculated hatching dates estimated from their otolith increments to formulate the hypothesis that the silver eels spawn only during new moon periods within their spawning season (Ishikawa et al. 2001; Tsukamoto et al. 2003). This hypothesis has been subsequently validated by collections of recently hatched preleptocephali just after new moon periods in the spawning area during several different years (Tsukamoto 2006, 2009). A similar pattern was observed in the back-calculated hatching dates of a wide size range of Kaupichthys leptocephali (Chlopsidae) collected around Sulawesi Island in the central Indonesian Seas (Fig. 30; Lee et al. 2008). However, estimated hatching dates of
this genus corresponded to full moon periods. This difference is likely related to the contrasting environments (subtropical open ocean versus coastal tropical seas) in which these two types of eels spawn (Lee et al. 2008). The common lunar spawning patterns supports the hypothesis that otolith rings are deposited daily in leptocephali, because if rings were not deposited daily, the patterns of lunar spawning could not be detected in otoliths.

The clear increments in otoliths of several species of eel leptocephali (Fig. 29) have been used to estimate their larval growth rates. These studies have found that anguillid leptocephali appear to grow at mean rates from about 0.23 mm/d for Atlantic eels that experience lower water temperatures during their early growth, to much faster growth rates of up to 0.61 mm/d in the

Fig. 29. Scanning electron microscope micrographs of cross sections of the otoliths of leptocephali of Anguilla celebesensis (37.5 mm) (A), Anguilla borneensis (42.0 mm) (B), and Saurenchelys stylura (42.0 mm), which show the likely daily otolith growth increments. HC: hatching check, FFC: first feeding check (C). (A, B) adapted with permission from Marine Ecology Progress Series, 309, Kuroki M, Aoyama J, Miller MJ, Wouthuyzen S, Arai T, Tsukamoto K. Contrasting patterns of growth and migration of tropical anguillid leptocephali in the western Pacific and Indonesian Seas. 233–246, 2006, Figures 5c, d. © 2006, Inter-Research; (C) reprinted with permission of Wiley-Blackwell from Ma T, Miller MJ, Shinoda A, Minagawa G, Aoyama J, Tsukamoto K. Age and growth of Saurenchelys (Nettastomatidae) and Dysomma (Synaphobranchidae) leptocephali in the East China Sea. Journal of Fish Biology, 2005; 67: 1619–1630. © 2005, The Fisheries Society of the British Isles.
tropical species *A. celebesensis* (Table 1). Castonguay (1987) examined the age and growth of the leptocephali of two Atlantic anguillids in the Sargasso Sea, and there have been studies on the leptocephali of the other species of northern temperate anguillid species, *A. japonica* (Tsukamoto et al. 1992, 2003; Ishikawa et al. 2001) and *A. australis* (Kuroki et al. 2008a). There have also been studies on the age and growth of tropical species of anguillid leptocephali in the central Indo–Pacific (Kuroki et al. 2005, 2006a,b, 2007), and off west Sumatra (Kuroki et al. 2007). Some species for which only a few specimens have been examined for growth rates, such as *K. myriaster* (Kuroki et al. 2006a), *S. styx* (Kuroki et al. 2006a), or *A. marmorata* (Kuroki et al. 2006a), have almost the same growth rates as *K. hyoproroides* (Table 1).

Mean growth rate values obtained from Indo–Pacific anguillid leptocephali have been between 0.35 and 0.61 mm/day (Table 1), but it appears that individual growth rates slow down as the larvae reach full size and begin to metamorphose. For example, *A. marmorata* and *A. bicolor pacifica* leptocephali reached a maximum size of about 50 mm and then appeared to stop increasing in total length even though their ages continued to increase (Fig. 31). A similar reduction in growth was seen in *K. hyoproroides* leptocephali in the Indonesian Seas as they reached early metamorphosis (Fig. 30; Lee et al. 2008). It is possible that they may stop increasing in total length if they reach their maximum size while still offshore away from the appropriate cues to trigger metamorphosis.

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**Table 1.** Mean growth rates (GR), sizes (total length: TL), and ages of leptocephali from the Indo–Pacific that have been studied using SEM observations of their sagittal otoliths. Mean growth rates are a mixture of values estimated from regressions of age and TL, or means of individual growth rates. Some large leptocephali that had reached their maximum sizes with slower growth rates were excluded. Maximum growth rates of individual leptocephali in each study (Max. Ind-GR) are also shown. WNP = western North Pacific. N = number of leptocephali examined for otolith microstructure.

<table>
<thead>
<tr>
<th>Species by Region</th>
<th>Area collected</th>
<th>N</th>
<th>TL range (mm)</th>
<th>Age (d)</th>
<th>GR (mm/d)</th>
<th>Max. Ind-GR</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Anguilla japonica</em></td>
<td>WNP</td>
<td>17</td>
<td>10.0–37.0</td>
<td>12–73</td>
<td>0.46</td>
<td>0.68</td>
<td>Ishikawa et al. (2001)</td>
</tr>
<tr>
<td><em>Anguilla bicolor pacifica</em></td>
<td>WNP/Indonesian Seas</td>
<td>43</td>
<td>24.0–54.1</td>
<td>40–128</td>
<td>0.42</td>
<td>0.62</td>
<td>Kuroki et al. (2006a)</td>
</tr>
<tr>
<td><em>Anguilla marmorata</em></td>
<td>WNP/Indonesian Seas</td>
<td>42</td>
<td>8.0–50.7</td>
<td>22–137</td>
<td>0.48</td>
<td>0.65</td>
<td>Kuroki et al. (2006a)</td>
</tr>
<tr>
<td><em>Anguilla borneensis</em></td>
<td>WSP</td>
<td>12</td>
<td>19.0–50.9</td>
<td>25–155</td>
<td>0.47</td>
<td>0.64</td>
<td>Kuroki et al. (2008a)</td>
</tr>
<tr>
<td><em>Anguilla celebesensis</em></td>
<td>Indonesian Seas</td>
<td>5</td>
<td>8.5–49.0</td>
<td>20–106</td>
<td>0.55</td>
<td>0.57</td>
<td>Kuroki et al. (2006a)</td>
</tr>
<tr>
<td><em>Anguilla bicolor bicolor</em></td>
<td>E. Indian Ocean</td>
<td>40</td>
<td>12.3–47.8</td>
<td>17–110</td>
<td>0.61</td>
<td>0.74</td>
<td>Kuroki et al. (2006a)</td>
</tr>
<tr>
<td><em>Anguilla australis</em></td>
<td>WSP</td>
<td>15</td>
<td>20.5–48.3</td>
<td>32–150</td>
<td>0.45</td>
<td>0.62</td>
<td>Kuroki et al. (2008a)</td>
</tr>
<tr>
<td><em>Anguilla reinhardtii</em></td>
<td>WSP</td>
<td>10</td>
<td>20.0–34.0</td>
<td>28–62</td>
<td>0.60</td>
<td>0.68</td>
<td>Kuroki et al. (2008a)</td>
</tr>
<tr>
<td><em>Conger myriaster</em></td>
<td>Eastern Japan</td>
<td>68</td>
<td>78.9–107.7</td>
<td>111–239</td>
<td>0.54–0.68</td>
<td>0.82</td>
<td>Kimura et al. (2004)</td>
</tr>
<tr>
<td><em>Dysoxomasp.</em></td>
<td>E. China Sea</td>
<td>22</td>
<td>8.4–33.5</td>
<td>17–66</td>
<td>0.44</td>
<td>0.53</td>
<td>Ma et al. (2005)</td>
</tr>
<tr>
<td><em>Saurenchelys styx</em></td>
<td>E. China Sea</td>
<td>21</td>
<td>10.0–48.6</td>
<td>16–75</td>
<td>0.68</td>
<td>0.83</td>
<td>Ma et al. (2005)</td>
</tr>
<tr>
<td><em>Kaupichthys hyoproroides</em></td>
<td>Indonesian Seas</td>
<td>24</td>
<td>24.7–60.8</td>
<td>39–161</td>
<td>0.46–0.65</td>
<td>0.67</td>
<td>Lee et al. (2008)</td>
</tr>
</tbody>
</table>

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Fig. 30. The relationship between total length and age of the *Kaupichthys* leptocephali collected around Sulawesi Island in September 2002 that was estimated from their otolith increments. The leptocephali that may have begun the process of metamorphosis based on their otolith increment widths are shown with black circles. The Von Bertalanffy’s growth curve that was fitted to the data is shown. Reprinted with kind permission from Springer Science + Business Media: *Marine Biology, Distribution and early life history of Kaupichthys leptocephali* (family Chlopsidae) in the central Indonesian Seas, 153, 2008, 285–295. Lee TW, Miller MJ, Hwang HB, Wouthuysen S, Tsukamoto K. Figure 8. © 2008, Springer-Verlag.
These studies also indicate that there are some differences in growth patterns between temperate and tropical anguillid leptocephali, which may be related to their different scales of migration. One obvious difference is that the maximum size of tropical leptocephali (50–55 mm; Jespersen 1942; Kuroki et al. 2009b) is less than that of temperate species (typically about 70 mm) that can reach about 85 mm in A. anguilla, which has the longest larval migration (Tesch 1980; Boëtius and Harding 1985; Kleckner and McCleave 1985; Bast and Strehlow 1990). Kuroki et al. (2006a) compared the growth rates of four different tropical anguillid leptocephali (Fig. 31) that recruit to habitats in the central Indonesian Seas. The leptocephali of the two species with short migrations from local spawning areas, A. borneensis and A. celebesensis (Aoyama et al. 2003), were found to have slightly higher growth rates than A. marmorata that migrates from an offshore spawning area in an overlapping region with A. japonica (Kuroki et al. 2009a), and A. bicolor pacifica which is thought to spawn outside of the Indonesian Seas (Kuroki et al. 2006a). These different growth rates were hypothesized to be related to the distance of the larval migration of each species, with temperate species having the slowest growth rates. The influence of temperature is difficult to exclude in most comparisons, but in one case where similar sized leptocephali of a tropical (A. reinhardtii) and a temperate (A. australis) species were collected at the same stations to the south of the Solomon Islands in the western South Pacific, the tropical species had a higher growth rate even though both species likely had experienced the same water temperatures (Kuroki et al. 2008a). Shiao et al. (2002) also suggested that A. reinhardtii had faster larval growth rates than A. australis based on examinations of the otolith microstructure of glass eels of the two species.

Marine eel leptocephalus otolith studies have found even greater variability in growth rates among different species or regions (Table 1). A study of the age and growth of two species collected during the KT-00-16 survey in the East China Sea (Fig. 31; Miller et al. 2002a) found different growth rates between species (Fig. 32). The otolith increments in these two species indicated that Saurenchely stylura had a mean growth rate of 0.68 mm/d compared to 0.44 mm/d in Dysomma sp. (Ma et al. 2005). The maximum size of S. stylura (~150 mm) is likely considerably larger than that of Dysomma sp. (~80 mm), which is one possible explanation for its apparent faster growth rate even though they were collected at mostly the same stations (Fig. 32). Kimura et al. (2004) found that Conger myriaster leptocephali before metamorphosis had mean growth that ranged from 0.54–0.68 at three different sites of eastern Japan.

Analyses of the otolith microstructure of the four species of leptocephali studied in the eastern Gulf of Mexico (muraenid, Gymnothorax saxicola, and ophichthid Ophichthus gomesii,

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**Fig. 31.** Plots of the ages and total lengths of tropical species of anguillid leptocephali from the western Pacific and central Indonesian Seas based on their otolith increments, showing Anguilla marmorata (triangles), Anguilla bicolor pacifica (circles), Anguilla celebesensis (crosses) and Anguilla borneensis (diamonds), with metamorphosing leptocephali (M) and glass eels (G) of some species indicated by letters within the symbols. Reprinted with permission from Marine Ecology Progress Series, 309, Kuroki M, Aoyama J, Miller MJ, Wouthuyzen S, Arai T, Tsukamoto K. Contrasting patterns of growth and migration of tropical anguillid leptocephali in the western Pacific and Indonesian Seas. 233–246, 2006, Figure 6. © 2006, Inter-Research.
two congrids *Ariosoma balearicum, Paraconger caudilimbatus* found highly variable apparent growth rates among individuals within each species, with very fast mean growth rates of greater than 1 mm/d in all of the species (Bishop *et al.* 2000). The estimated growth rates of *P. caudilimbatus* leptocephali were lower and less variable than the other species though, and their growth rates slowed down with increased size as has been observed in Indo–Pacific species. Growth rates of the other species in that study were much more variable, and if the ages were accurate, would indicate very rapid growth rates (>2–3 mm/d). These leptocephali were not collected during the same sampling survey as in the study by Ma *et al.* (2005), but were collected during several surveys (Bishop *et al.* 2000) with potentially differing water temperature conditions.

There are no published studies on the otolith microstructure of muraenids and ophichthids from the Indo–Pacific that can help evaluate the aging results of Bishop *et al.* (2000), but observations of large *Ariosoma major* leptocephali from the western North Pacific indicate that at least some *Ariosoma* otolith increments may be difficult to accurately discern and count (A. Shinoda pers. comm.). Basic examinations of the age data for *A. balearicum and O. gomesii* (Bishop *et al.* 2000) for example, indicate that in the otoliths of some individuals of these two species (particularly in the 24–44 and 20–25 increment number ranges, respectively), they had the same number of otolith increments, but their body lengths varied by as much as about 75–80 mm or more. It is unclear if such wide variation in size of individuals of apparently the same age could be due to differences in temperatures they experienced, feeding success, or some other factors. Therefore, it is difficult to determine if such apparently high growth rates in some of the specimens of each these species of leptocephali from the Gulf of Mexico are...
accurate or not, since they are significantly higher than those estimated by the otolith increments of leptocephali of other species.

2-7. Metamorphosis

One of the remarkable features of anguilliform leptocephali is their drastic morphological transformation during metamorphosis into the glass eel or elver stage. Such a major change in body shape and structure is required because of the very different habitats and food materials used by eels compared to their larvae. The laterally compressed and transparent bodies of leptocephali are adapted for a pelagic life in the surface layer of the ocean where they feed on particulate matter and must avoid predators. Once they transform into young eels they enter a wide range of benthic marine habitats, move into estuaries or freshwater in the case of Anguilla, or live in the mesopelagic zone, where the fragile leptocephalus body form and feeding strategy would not be appropriate.

Several external morphological changes occur in leptocephali at the beginning of metamorphosis such as a thickening of the head, enlargement of the olfactory organ, and a loss of the teeth (Figs. 20B, 33, 34). In many nettastomatid leptocephali the olfactory rosette becomes very enlarged and elongate during metamorphosis (Smith and Castle 1982). In some metamorphosing muraenid leptocephali, the gills become larger and are visible (Fig. 34), whereas no gills are typically seen in premetamorphic leptocephali (Figs. 14, 15). The other major changes that occur during metamorphosis are that the gut and the origins of the dorsal and anal fins move forward, as can be seen in Ariosoma gilberti from the eastern Pacific (Fig. 35) and in Conger oceanicus from the Atlantic coast of New Jersey (Fig. 36). Because the gut is moving forward with tissue being reabsorbed, the larvae do not feed during metamorphosis (Otake 2003). The relative position of the gut as it moves forward typically has been used as an indicator of the metamorphic stage of leptocephali (e.g. Lee and Byun 1996; Otake et al. 1997; Bell et al. 2003; Kimura et al. 2004). The sensory pores on the head and the nostrils of some species begin to form during the metamorphosing leptocephalus stage (Figs. 11, 20B, 33). In species with markedly different head shapes such as the mesopelagic Nemichthys that have long curved jaws, the jaws appear to rapidly extend forward even when the larvae are still in the leptocephalus stage (Fig. 33B). This also occurs in serrivomerid leptocephali (Beebe and Crane 1936; Miller and Tsukamoto 2004). A major enlargement of the olfactory organ is apparent in the metamorphosing synaphobranchid in Fig. 33A. Red blood cells begin to form in at least some late stage metamorphosing leptocephali such as Derichthys serpentinus (Fig. 37B), or during the glass eel stage in Conger myriaster collected in coastal waters of southern Japan that metamorphosed while held in an aquarium (Fig. 37A). Toward the end of metamorphosis when the young eels are about to start feeding again, there is increased ossification of the skull and vertebral column, and this increased development of the skeleton generally coincides with depletion of the gelatinous support matrix (Pfeiler 1999).

What exactly causes metamorphosis to begin in leptocephali is not known (Otake 2003), but it is generally thought to occur after a certain size required for metamorphosis is reached and environmental cues trigger the process. A basic age or size may be important for mesopelagic eel larvae, since they may be able to metamorphose anywhere in deep water and successfully begin their juvenile phase. But in the case of eel larvae recruiting to shallow marine habitats or coastal areas, metamorphosis before nearing a suitable juvenile habitat could result in starvation and death, or being eaten by predators, since young eels are likely poorly adapted to live in the open ocean. This suggests that there are environmental cues such as chemical compounds, bottom depth, or salinity, which may act as triggers to initiate metamorphosis when leptocephali approach continental shelves or islands. In the absence of such cues, most leptocephali may delay metamorphosis, as has been indicated in other types of fish larvae such as Acanthuridae and Labridae (Victor 1986; McCormick 1999).

A careful examination of the geographic distribution of most species of metamorphosing leptocephali has not been done. European eel leptocephali have been found to metamorphose into glass eels in waters deeper than 1000 m as they approach Europe (Antunes and Tesch 1997),
so the trigger for their metamorphosis is unclear. Collections of metamorphosing American eel leptocephali are limited, with a few being collected far offshore and some over or near the edge of the continental shelf (Kleckner and McCleave 1985). Similarly, some metamorphosing leptocephali of *A. japonica* have been collected offshore along the western margin of the Philippine Sea (Arai *et al.* 1997; Tsukamoto 2006). By the time they enter the Kuroshio Current south of

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**Fig. 33.** Photographs of the head regions of metamorphosing leptocephali of an 88.0 mm *Dysomma* (Ilyophinae, Synaphobranchidae) (A), a 243 mm *Nemichthys* (Nemichthyidae) (B), and a 74.3 mm Chlopsidae (C). Nostrils can be seen in (A) and (C), and the jaws have begun to extend in the nemichthyid leptocephalus before completing metamorphosis (B).
Japan, some have almost completed their metamorphosis into glass eels (Otake et al. 2006), so metamorphosis in anguillids may be triggered well before they arrive at the continental shelves. Miller et al. (2006b) pointed out that the biggest catches of metamorphosing Ariosa scheelei leptocephali in a survey around Sulawesi Island were made at stations that had a shallow layer of lower salinity water near the surface, and questioned if this could be a possible cue for triggering metamorphosis. Chen et al. (2008) suggested that the lower salinity of coastal waters could be important to trigger metamorphosis in tarpon larvae.

Regardless of the trigger, thyroid hormones appear to be important in the process of metamorphosis (Otake 2003). An abrupt increase in thyroid hormones was observed in C. myriaster leptocephali during the onset of metamorphosis (Yamano et al. 1991). Similarly, thyroid hormones were not detected in artificially reared A. japonica leptocephali until metamorphosis (Yamano et al. 2007). Experiments using a thyroid hormone inhibitor with tarpon leptocephali showed that metamorphosis would not proceed when thyroid hormones were blocked (Shiao and Hwang 2006), indicating they are a key component of metamorphosis in leptocephali. Conversely, cortisol levels were high in premetamorphic C. myriaster leptocephali, but then decreased to low levels throughout metamorphosis, suggesting that cortisol may be involved in maintaining the premetamorphic state (Yamano et al. 1991). This suggests that the initiation of metamorphosis requires a decrease in cortisol production as thyroid hormones increase. Low temperature may also be able to delay metamorphosis based on findings with tarpon larvae (Chen et al. 2008).

Fig. 34. Photograph of the head of a 59.3 mm metamorphosing Uropterygiinae leptocephalus of the family Muraenidae, showing a large nasal organ, developing gills, and a large sagittal otolith.
Although the factors that initiate metamorphosis are difficult to determine, studies on otolith microstructure of some species of leptocephali and glass eels have revealed information about the possible age at metamorphosis and duration of metamorphosis. Otolith microstructure of metamorphosing Anguilla japonica (Arai et al. 1997), A. marmorata (Kuroki et al. 2005) and C. myriaster leptocephali (Otake et al. 1997), and glass eels of A. japonica (Otake et al. 1994; Chen and Tzeng 1996; Arai et al. 1997) and the Atlantic eels (e.g. Wang and Tzeng 2000) have been examined using SEM observations of increments and Sr:Ca ratio measurements. These studies suggested that there was a rapid increase in otolith increment widths during metamorphosis that was accompanied by a decrease in Sr:Ca ratios (Fig. 38). Using these otolith characteristics, the timing of metamorphosis of the leptocephalus stage has been estimated in glass eels collected in coastal waters for both temperate and tropical anguillid glass eels (Marui et al. 2001; Otake 2003). Mean ages at metamorphosis for various anguillid species have been reported to range from less than a 100 days in A. celebesensis (Arai et al. 2001) to almost 250 days in A. dieffenbachii (Marui et al. 2001). The other tropical and temperate species of glass eels that have been examined generally have larval durations within this range (see Aoyama 2009 for a recent review), but the European eel may have a longer larval duration than any other species (see Kuroki et al. 2008b). The same pattern of increment widths during metamorphosis has been observed in the Atlantic species of Conger, whose ages at metamorphosis have been estimated using this method (Correia et al. 2003, 2004) and in a species of muraenid (Ling et al. 2005).

The number of increments in the zone of increased increment widths has also been used to estimate the duration of metamorphosis using glass eel otoliths. This duration is likely dependent on temperature based on metamorphosing tarpon larvae (Chen et al. 2008) and comparisons of tropical and temperate anguillid larvae (Otake 2003). The apparent durations of metamorphosis in anguillid larvae have ranged from 9 days in a tropical species to more than 60–70 days in

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**Fig. 35.** Drawings of various developmental stages of Ariosa gilberti from the eastern Pacific ranging from a leptocephalus before metamorphosis to an elver after metamorphosis. Triangles show the anterior positions of the dorsal and anal fins, which move much farther forward along with the gut (just in front of anal fin) during metamorphosis. The scale bars show 5 mm, but not all drawings are proportional in size. Modified from Raju SN. Congrid Eels of the Eastern Pacific and Key to Their Leptocephali. NOAA Technical Report NMFS 22, U.S. Department of Commerce. 1985; 1–19.
 temperate species (see Marui et al. 2001; Otake 2003; Aoyama 2009). The hypothesis that changes in the otolith can be used to determine the timing of metamorphosis has been supported by several studies that examined different stages of larvae before and after metamorphosis. Kuroki et al. (2005) showed that the increase in increment width started during metamorphosis in the leptocephalus stage of A. marmorata, along with a decrease in Sr:Ca ratios. By comparing premetamorphic leptocephali to a metamorphosing specimen and oceanic glass eels (see Fig. 39), it was found that there was an increase in increment width in the metamorphosing leptocephalus, and an increase followed by a decrease in the oceanic glass eels. Lee and Byun (1996) found the same pattern of increment width increase in metamorphosing C. myriaster leptocephali, but not in premetamorphic individuals. In glass eels of A. marmorata and other anguillid species, the increment widths decrease even further by the time they recruit to coastal areas and are collected (Marui et al. 2001; Kuroki et al. 2005). An increase in increment width during metamorphosis was also found in tarpon leptocephali held in the laboratory (Shiao and Hwang 2006; Chen et al. 2008). Powles et al. (2006) showed that otoliths of ophichthid leptocephali, Myrophis punctatus, continued to deposit increments during metamorphosis, but they did not analyze increment widths. No increase in increment widths were observed in anguillid glass eels that recruited to Iceland however, which may have been due to the cold temperatures and slow metamorphosis experienced by those individuals during their leptocephalus stage.

Fig. 36. Drawings of three stages of Conger oceanicus larvae that recruited to estuarine habitats in New Jersey of the US east coast. Modified with permission of the American Society of Ichthyologists and Herpetologists from Bell GW, Witting DA, Able KW. Aspects of metamorphosis and habitat use in the conger eel, Conger oceanicus. Copeia 2003; 2003: 544–552.
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(Kuroki et al. 2008b). In general though, it appears that the increase in increment widths in larval eel otoliths is a useful marker for the timing of onset of metamorphosis that can be used to compare the larval durations among different eel species, as illustrated by Marui et al. (2001).

2-8. Swimming behavior

The swimming ability of leptocephali has been poorly documented, but they appear to be very capable swimmers. The ability to swim is important for migrations to recruitment areas, speed of vertical migrations, and for being able to avoid predators. General observations of healthy leptocephali held in aquaria suggest they are good swimmers (Miller and Tsukamoto 2004) and are able to burst swim for at least short periods. A recent nighttime video observation of an ophichthid leptocephalus swimming over deep-water off the island of Hawaii (video available at: http://www.australianmuseum.net.au/movie/Ophichthid-leptocephalus-Kona-Hawaii/) also showed a very active swimming style that included rapid changes of swimming direction (MJ Miller and MJ D’Avella unpublished manuscript). Because of their use of anguilliform swimming movements (Gray 1933; D’Août and Aerts 1999), they also are able to swim both forwards and backwards. Artificially spawned and reared Anguilla japonica leptocephali of 30–60 mm lengths were negatively phototaxic, swimming at speeds of 3.6 ± 2.7 cm s⁻¹ horizontally and 2.8 ± 1.1 cm s⁻¹ upwards away from a sudden light stimulus (Yamada et al. 2009). Their ability for long term sustained swimming, such as during the long migration of A. anguilla leptocephali recruiting to Europe, is unknown though, and has been a matter of considerable speculation (McCleave 1993; McCleave et al. 1998).

Wuenschel and Able (2008) measured critical swimming speed ($U_{crit}$) of recently recruited Conger leptocephali and glass eels and anguillid glass eels in a laboratory swim channel.
Fig. 38. A diagrammatical representation of the change in otolith increment width and Sr:Ca ratio in the otoliths of anguillid larvae from hatching to metamorphosis, and to the transition to the glass eel stage. Reprinted with permission from Marine Ecology Progress Series, 213, Marui M, Arai T, Miller MJ, Jellyman DJ, Tsukamoto K. Comparison of early life history between New Zealand temperate eels and Pacific tropical eels revealed by otolith microstructure and microchemistry. 273–284, 2001, Figure 7. © 2001, Inter-Research.

Fig. 39. Scanning electron microscope images of the otoliths of Anguilla marmorata leptocephali at the premetamorphic stage (top), metamorphosing leptocephalus stage (middle), and the oceanic glass eel stage (bottom). White circle shows the metamorphosis check. Adapted from Kuroki et al. (2005).
Critical swimming speed is a useful index of swimming ability obtained by swimming fish at increasing speed intervals until they reach exhaustion (Fisher 2005; Fisher et al. 2005). *Conger oceanicus* larvae were collected during April–June at water temperatures of 14.0–24.5°C, and were separated into premetamorphic and metamorphosing leptocephali (ER–M1) and glass eels (M2–M3) as illustrated in Fig. 36 and described by Bell et al. (2003). $U_{crit}$ of *C. oceanicus* ranged from 12.0–26.8 cm s$^{-1}$ for ER–M1 stage metamorphosing leptocephali and 4.1–25.0 cm s$^{-1}$ for M2–M3 stage glass eels (Fig. 40C). *Anguilla rostrata* glass eels that recruited to the same area from January to June at temperatures of 4.0–21.0°C were considerably smaller (48.7–68.1 mm) than the *Conger* leptocephali (80.2–117.8 mm) and glass eels (68.3–90.0 mm). *Anguilla rostrata* glass eels were separated into stage 1 and stage 2 glass eels based on their degree of pigmentation, and they had $U_{crit}$ values that were 6.5–21.1 cm s$^{-1}$ and 8.2–14.1 cm s$^{-1}$, respectively (Fig. 40B). Later stages (M2–M3) of *C. oceanicus* showed greater variability in $U_{crit}$ than earlier stages (ER–M1) or *A. rostrata* glass eels (Fig. 40). The strongest swimmers of either species appeared to be the late stage metamorphosing *C. oceanicus* leptocephali and a few of their glass eels. Although these were shorter than the earlier stage leptocephali, their greater percent dry weights suggested they had greater muscle mass (Fig. 40A). These individuals with $U_{crit}$ values greater than about 20 cm s$^{-1}$ all had longer bodies than the *A. rostrata* glass eels, which may account for part of their stronger swimming ability.

Fig. 40. Plots of the percent dry weights of *Anguilla rostrata* glass eels (light blue circles, early-stage; blue circles, late-stage) and *Conger oceanicus* late-stage or metamorphosing leptocephali (yellow squares, ER1–M1 stages as shown in Fig. 36) or glass eels (black squares, M2–M3 stages) (A), and their critical swimming speeds ($U_{crit}$) (B and C) that were measured in larvae that had recruited to coastal New Jersey of the US east coast. Modified with kind permission from Prof. Kenneth W. Able and Dr. Mark Wuenchel, and from Springer Science + Business Media: Marine Biology, Swimming ability of eels (*Anguilla rostrata*, *Conger oceanicus*) at estuarine ingress: contrasting patterns of cross-shelf transport? 154, 2008, 775–786, Wuenchel MJ, Able KW, Figures 2, 4b, 5b. © 2008, Springer-Verlag.
Temperature was significantly related to $U_{\text{crit}}$ values for both the stage 1 *A. rostrata* glass eels and the *C. oceanicus* ER–M1 stage leptocephali. Most of the *Anguilla* glass eels were tested at temperatures of 4–16°C and most of the *Conger* at 16–24°C, so the faster critical speeds of the metamorphosing *Conger* leptocephali and early glass eels is difficult to interpret. Temperature affects both the physiology of fish larvae and the characteristics of the water they must swim through (Fuiman and Batty 1997; von Herbing 2002). The $U_{\text{crit}}$ values of various families of primarily tropical coral reef area fishes range higher, from about 20–60 cm s$^{-1}$ at 20–30°C (Fisher 2005; Fisher et al. 2005).

Observations of live leptocephali and the findings of Wuenschel and Able (2008) suggest leptocephali are capable swimmers, but further swimming stamina experiments are needed to evaluate their long term swimming ability. The anguilliform swimming mode in adult silver eels has been found to be extremely efficient (van den Thillart et al. 2009). This efficiency has been demonstrated by silver eels that can swim for 6 months or more without feeding, and seemingly still have enough fat reserves for reproduction (van den Thillart et al. 2009). This suggests that leptocephali with a similar anguilliform swimming mode may be well-adapted for long-term slow swimming.

3. Zoogeography of leptocephali

3-1. Taxonomic groups of eels

Leptocephali are distributed worldwide from tropical to lower-temperate latitudes because a variety of taxa of eels live at these latitudes. The best known eels are of the family Anguillidae, which live in freshwater and estuarine habitats in most regions of the world, but their leptocephali are only found in areas of the ocean close to their specific spawning areas (Miller 2003; Aoyama 2009). Three anguilliform families (Congridae, Muraenidae, Ophichthidae) are particularly rich in species and are distributed worldwide, except at high latitudes. These families include species whose juveniles and adults range from shallow, nearshore marine habitats, out over the continental shelf and slope, and down to depths of 1000 m or more in a few species (Böhlke 1989a). Other less diverse families that also live in shallow marine habitats worldwide include the Chlopsidae, Moringuidae, and Muraenidae. Although many marine eels likely live in shallow tropical areas, typically only a few species of muraenid eels (Gilbert et al. 2005), the colonial garden eels (Thresher 1984; Smith 1989b), or ophichthids with color patterns mimicking sea snakes (Randall 2005) are commonly observed by divers during the day. Other eels of the Nettastomatidae and some Synaphobranchidae may live primarily over the outer continental shelf or on the upper slope. Synaphobranchids are among the most common fish on the abyssal plain at depths of 1000–3000 m (Haedrich and Merrett 1988; King et al. 2006). Eels of the Derichthyidae, Eurypharyngidae, Nemichthyidae, and Serrivomeridae live entirely mesopelagic lives in the upper few thousand meters of the world’s oceans (Böhlke 1989a). Some species such as the cyematids may live even deeper. Therefore, eels of at least a few taxa are found in almost all marine habitats worldwide, except perhaps pelagically over the continental shelf and in very cold waters in the polar regions.

3-2. Spawning areas of eels

Where eels spawn in the ocean in relation to currents is a critical determinant of how their larvae become distributed. But due to the difficulty in observing spawning eels, their spawning areas are mostly known only from catches of small leptocephali. Their spawning locations range widely from shallow water to offshore regions of the ocean due to the various life histories of each family or species of eels.

All anguillid species spawn over deep water (Tsukamoto et al. 2002; Miller 2003; Tesch 2003; Aoyama 2009), but the distance offshore that they migrate can vary from less than about 100 km in the case of the tropical species *A. celebesensis* (Aoyama et al. 2003), to many thousands of kilometers for temperate anguillid species in the northern and southern hemisphere.
subtropical gyres (Fig. 41). Although all temperate anguillids have long migrations, tropical eels have a wider range of migration distances and types of spawning areas. Their known spawning areas range from local spawning (*A. celebesensis* and *A. borneensis* in the Indonesian Seas; Fig. 42), to offshore spawning by the northern population of *A. marmorata* in the North Equatorial Current region in an area that overlaps with the temperate species *A. japonica* (Kuroki *et al.* 2009a) (Fig. 42). This population of *A. marmorata* is both genetically (Minegishi *et al.* 2008) and morphologically (Watanabe *et al.* 2008) distinct from other populations of that species that spawn in different areas. A similar case of both tropical and temperate anguillids spawning offshore in about the same area appears to exist for the tropical *A. reinhartii* and the temperate *A. australis*. Both spawn somewhere in the South Equatorial Current of the western South Pacific (Kuroki *et al.* 2008a).

Fig. 41. The spawning areas of the northern temperate species of anguillid eels in the subtropical gyres of the western North Atlantic showing the Florida Current (FC), Gulf Stream, and North Atlantic Drift (A), and in the western North Pacific showing the North Equatorial Current (NEC), Mindanao Current (MC) and Kuroshio Current (B). The region where spawning likely occurs by the southern temperate anguillid species in the western South Pacific is also shown along with the South Equatorial Current and the East Australian Current (C). Adapted with permission of the American Fisheries Society from *Challenges for Diadromous Fishes in a Dynamic Global Environment*. Haro A, Avery T, Beal K, Cooper J, Cunjak R, Dadswell M, Klauda R, Moffitt C, Rulifson R, Smith K (eds). Review of ocean-atmospheric factors in the Atlantic and Pacific oceans influencing spawning and recruitment of anguillid eels. Miller MJ, Kimura S, Friedland KD, Knights B, Kim H, Jellyman JD, Tsukamoto K. Am. Fish. Soc. Symp. 69. Bethesda, Maryland. 2009a; pp. 231–249, Figure 2.
In contrast to anguillids, most species of marine eels may typically spawn within or near their adult habitats (Miller 2002b). Mesopelagic eel species may just spawn where they live in offshore areas of the open ocean, because they are often widely distributed (Castonguay and McCleave 1987b; Karmovskaya 1990; Miller and McCleave 1994; Smith and Miller 1996; Wippelhauser et al. 1996; Miller et al. 2006a). How they choose where to spawn is not known though, and how their spawning locations affect the distribution of leptocephali has not been studied. Similarly, some muraenids likely spawn wherever they live in shallow water habitats (Moyer and Zaiser 1982; Ferraris 1985), as do garden eels (subfamily Heterocongrinae), which live colonially in burrows in shallow areas (Thresher 1984). Therefore, the many islands or atolls in the Indo–Pacific, which have coral reef and other types of habitats (Fig. 4B) used by congrid, chlopsid, muraenid, and ophichthid eels, are source areas for their leptocephali to spread throughout the western Pacific and Indonesian Seas region. Some species may also spawn over the continental shelf or migrate towards the edge of the shelf (Cohen and Dean 1970; Ross and Rohde 2003). There is evidence of many marine eel species living and spawning in warm tropical areas, such as the Indonesian Seas (Wouthuyzen et al. 2005), where the biodiversity
of fishes is generally the highest in the world (Randall 1998; Allen and Adrim 2003; Carpenter and Springer 2005). Fewer species of eels appear to live and spawn in colder water areas, such as the eastern North Pacific though, based on the limited number of leptocephali reported there (Raju 1985; Matarese et al. 1989).

Most surveys for leptocephali have been in offshore waters due to the oceanic spawning of anguillid eels, and these collections have shown that very few marine eels migrate very far offshore to spawn. Congrids such as Conger oceanicus (McCleave and Miller 1994) and some Ariosoma balearicum (Miller 2002a) appear to migrate offshore to spawn, but most other marine eels that live in continental shelf habitats do not appear to migrate much past the edge of the shelf. Collections of leptocephali over or near shelf areas or around islands also have shown that most shallow water marine eels do not migrate very far offshore to spawn. The exact spawning areas of marine eels are generally not known, but the smallest leptocephali of most shallow water eels are typically collected over or near the edge of the continental shelf (Castle and Roberston 1974; Miller et al. 2002a; Kimura et al. 2006) or in close proximity to shallow water habitats (Castle 1968; Miller 1995, 2002b; Miller et al. 2002a, 2006a; Miller and McCleave 2007), suggesting nearby spawning areas.

A survey in the late fall along the outer shelf of the East China Sea (Fig. 32) found evidence of spawning by many species of eels (Miller et al. 2002a). The two most abundant species of leptocephali were Gnathophis nystromi nystromi (Congridae) and Dysomma anguillare (Synaphobranchidae), which based on their distributions of small leptocephali were spawning at the outer edge of the shelf (Fig. 43). The exact stations at which the smallest leptocephali of the two species were caught differed slightly though, suggesting that D. anguillare was spawning a little farther out over the slope than G. nystromi nystromi. All sizes of leptocephali of the Muraenidae, Ophichthidae, and Saurenchelys (Nettastomatidae) were also abundant over the outer shelf (Fig. 44), indicating that spawning occurred near the edge of the shelf. Small leptocephali of G. nystromi nystromi and a few other species were also collected along the outer edge of the continental shelf of northeast Japan (Kimura et al. 2006), which is similar to observations from other studies on various species of Gnathophis around the world (Castle 1968; Castle and Roberston 1974).

### 3-3. Distribution and abundance of leptocephali

The abundance of leptocephali in any particular area is likely directly related to the proximity of that area to the spawning locations of the species and the regional patterns of ocean currents that disperse the larvae. The leptocephali of eels that live over the continental shelf have been found to be very abundant near their spawning areas such as along the edge of the shelf in the East China Sea due to large catches of small leptocephali (Figs. 43, 44; Miller et al. 2002a). Similarly, leptocephali of congrid, chlopsid, muraenid, and ophichthid eels were very abundant in the Northwest Providence Channel of the Northern Bahamas at the southwest edge of the Sargasso Sea in the western North Atlantic (Fig. 45; Miller and McCleave 2007). However, there are often strong currents adjacent to these high density concentrations of leptocephali, such as the Kuroshio Current in the East China Sea and the Florida Current (southern part of the Gulf Stream) adjacent to the northern Bahamas, which likely transport many leptocephali further offshore.

Some species of leptocephali can be quite abundant offshore in the open ocean, as a result of local spawning or offshore transport by frontal jets (Miller and McCleave 1994). Leptocephali of the mesopelagic eels that are abundant in some offshore areas during their spawning seasons include Derichthyidae (Castonguay and McCleave 1987b), Nemichthyidae (Karmovskaya 1990; Wippelhauser et al. 1996) and Serriroemeridae (Miller and McCleave 1994; Miller et al. 2006a). Anguillid leptocephali also are sometimes abundant in regions near their offshore spawning areas (Kleckner and McCleave 1988; Tsukamoto 1992) and then they become widely distributed in their larval development and migration areas (Kleckner and McCleave 1985; McCleave and Kleckner 1987; Kettle and Haines 2006; Kuroki et al. 2009a,b). In more enclosed areas such as the Indonesian Seas, leptocephali of all types of eels mix together with
various geographic patterns of abundances (Wouthuyzen et al. 2005; Miller et al. 2006b) (Figs. 42B, 46).

Studies on leptocephali that have included long transects with numerous stations have shown that although leptocephali are present throughout the sampling regions, the patterns of relative abundance of the different taxa are related to the geography of the adult habitats, apparent differences in larval dispersal behaviors, and the oceanographic structure of the
regions. In a survey for leptocephali that included a transect across the southwest Sargasso Sea and stations within and near the northern Bahamas (Miller and McCleave 2007), clearly different patterns of distribution and regional size of leptocephali were observed for some species (Fig. 45). Various species such as chlopsids, some congrid, a moringuid, muraenids, and ophichthids were most abundant and their smallest leptocephali were collected in the Northwest Providence Channel and to a lesser extent to the north in the Florida Current. These species were either absent at the offshore stations (e.g. the garden eel, Heteroconger halis, and most ophichthid leptocephali such as Myrophis platyrhynchus) or were less abundant and larger offshore (e.g. chlopsid, moringuid, and A. balearicum leptocephali) (Fig. 45). Anguillid (McCleave and Kleckner 1987), derichthyid (Castonguay and McCleave 1987b), and nemichthyid (Wippelhauser

Fig. 45. Plots of the total length of 5 species of leptocephali at each station of a sampling survey in late September and early October of 1984 in the southwest Sargasso Sea, showing two general patterns of larval distributions: 1) widespread distributions at all stations (Moringua edwardsi–Moringuidae, Ariosoma balearicum–Congridae, Chlorhirus suensonii–Chlopsidae); 2) restricted distribution at Station 12 in the Northwest Providence and Stations 1 and 2 in the Florida Current (Myrophis platyrhynchus–Ophichthidae, Heteroconger halis–Congridae–garden eel). The stations shown in the upper left panel correspond to the stations along the x-axis of the plots. The red square (upper left panel) shows the study site in Fig. 60. Modified with permission from Marine Ecology Progress Series, 344, Miller MJ, McCleave JD. Species assemblages of leptocephali in the southwestern Sargasso Sea. 197–212, 2007, Figures 1, 3, 5, 7. © 2007, Inter-Research.
et al. 1996) leptocephali were also abundant offshore in this transect across the southwest Sargasso Sea (Miller and McCleave 2007).

A long north–south transect across the subtropical gyre in the western South Pacific showed a similar, but somewhat different distribution pattern of leptocephali (Miller et al. 2006a). In
this transect, serrivomerid leptocephali were very abundant at a wide range of sizes in the warmer water regions in the north from latitudes 5–17°S, but were less abundant and generally larger in the colder water of the southern part of the gyre (Fig. 47). Leptocephali of anguillids and shallow water eels were also rare in the colder water, but they were abundant in a more limited region in the central part of the transect at the latitude of the southern branch of the South Equatorial Current near the southern edge of the warm water (12–16°S, Fig. 47). The anguillid abundance there may have been due to spawning areas at that latitude, and the abundance of shallow water marine eel families of leptocephali may have been due to the presence of adults on the larger island groups, such as Fiji, and Tonga, Samoa. The westward flow of the South Equatorial Current likely transported some of the leptocephali offshore where they were cap-

Fig. 47. Catch rates of 9 families of leptocephali at each station along 175°E transects north and south of the Fiji Islands (A–C), and temperature and salinity sections down to 500 m made from the CTD profiles at each sampling station in the western South Pacific (bottom panels), in August 1995 during the KH-95-2 sampling survey. The black lines below the station labels of the catch rate plots indicate which stations were sampled at night. The Fiji islands are located from 16°–18°S, to the east of Stn. 73–76. These transects can be seen in the bottom right side of Fig. 4A. Catch rates are calculated based on the number of leptocephali collected per amount of water filtered by the net. Reprinted from Deep-Sea Research I, 53, Miller MJ, Aoyama J, Mochioka N, Otake T, Castle PHJ, Minagawa G, Inagaki T, Tsukamoto K. Geographic variation in the assemblages of leptocephali in the western South Pacific, 776–794, 2006, with permission from Elsevier. © 2006, Elsevier Ltd.
tured at some stations of the transect, but they were rare to the north where there are few islands, and to the south in the colder water that was likely flowing to the east (Miller et al. 2006a). Serrivomerid, muraenid and other leptocephali were abundant and present at a wide range of sizes at each station just to the north of Fiji (Fig. 48). Similar geographic differences in abundances of some species of leptocephali were observed in transects that crossed temperature fronts in the Sargasso Sea (Miller and McCleave 1994).

The detailed distributions of leptocephali in the world’s oceans is beyond the scope of this review, since there are many less extensive reports on leptocephali. These reports indicate that at least some leptocephali can be collected anywhere that appropriate sampling effort is applied at tropical and subtropical latitudes. The taxonomic composition of leptocephali in each area may vary widely however, depending on the geography of adult habitats or the time of year, as discussed in the next section. The geographic variation of presence of species of leptocephali is

Fig. 48. Plots of the total length of the individual leptocephali of several taxa collected at each station along 175°E transects north and south of the Fiji Islands (same stations as Fig. 47). Reprinted from Deep-Sea Research I, 53, Miller MJ, Aoyama J, Mochioka N, Otake T, Castle PHJ, Minagawa G, Inagaki T, Tsukamoto K. Geographic variation in the assemblages of leptocephali in the western South Pacific, 776–794, 2006, with permission from Elsevier. © 2006, Elsevier Ltd.
illustrated by a plot of species diversity presented by Minagawa and Miller (2005) that shows a high species diversity in the Indonesian Seas, as was indicated by Wouthuyzen et al. (2005) and Minagawa et al. (2004), but also high diversity near the Solomon Islands in the western South Pacific (Fig. 4A), as found by Miller et al. (2006a). The lowest diversities were observed in far offshore areas where the leptocephali of shallow water eels are only present in low abundances. However, another factor is that the leptocephali of some species such as ophichthids and garden eels seem to be rarely transported offshore into these areas compared to other species, except in areas with very strong currents (Miller 1995; Miller and McCleave 1994, 2007; Miller et al. 2006a).

3-4. Seasonal occurrence of leptocephali

Another factor that clearly affects the distribution, abundance and taxonomic composition of leptocephali in some regions is the seasonality of spawning. Most of what is known about seasonality of spawning has been gathered about anguillid eels. Spawning seasons of temperate anguillids have been roughly estimated from the timing of the downstream migrations of silver eels into the ocean (Jellyman 2003; Tesch 2003) and the catches of their small leptocephali (McCleave 2008). Temperate anguillids typically migrate in the late summer or fall and their leptocephali are abundant in their offshore spawning areas and larval migration routes in the next spring and summer (e.g. McCleave and Kleckner 1987; Kleckner and McCleave 1988; Tsukamoto 1992; Tsukamoto et al. 2003). The timing of spawning of tropical anguillids is much less understood, however, even though seasonal differences have been observed in the presence or size of leptocephali in the central Indonesian Seas (Wouthuyzen et al. 2009) and off west Sumatra in the eastern Indian Ocean (Jespersen 1942; Aoyama et al. 2007).

Even less is known about the seasonality of spawning of most marine eels though, since reproductive behaviors of most species can not be monitored. Therefore, catches of leptocephali are presently the best way to learn about the general seasonal patterns of spawning by marine eels. In tropical areas, such as the Indonesian Seas, published and unpublished data from various surveys have shown that a wide variety of species of leptocephali appear to be present throughout the year (Miller et al. 2002c, 2004; Wouthuyzen et al. 2005; Miller et al. unpubl. data). Although leptocephali are present all year, the seasonality of spawning of most species of eels is not known, so it can not be assumed that most species of marine eels spawn all year. Chlopsid eels have been suggested to have spawned over five consecutive months in the central Indonesian Seas based on analyses of otoliths from leptocephali collected in September (Fig. 30; Lee et al. 2008), but more research is needed to evaluate the spawning seasons of eels in tropical regions.

At higher subtropical and in temperate areas, such as near Japan, there is some evidence that various taxa of eels have seasonal patterns of spawning based on catches of leptocephali. Seasonal variation in taxonomic composition, relative abundance, size, and geographic distribution of leptocephali collected in late spring (May–Jun) and late autumn (Oct–Dec) were compared in the East China Sea and in Suruga Bay of eastern Japan (Fig. 49; Minagawa et al. 2007). There were indications that some taxa of eels were spawning all year in the more southern region of the East China Sea, although species such as Dysomma anguillare were absent there in the late spring (Fig. 49B). Further north in Suruga Bay, it appeared that there was a much stronger pattern of seasonality of spawning, with far fewer leptocephali being present in the late spring (Figs. 49C, D). This suggested that at the temperate latitudes, such as at Suruga Bay (34°N), most marine eels may stop spawning during the winter months when water temperatures are colder. Studies on a few species of marine eels in East Asia, such as Ariosoma meeki (Ishii et al. 2003), Conger myriaster (Okamura et al. 2000; Utoh et al. 2005), and Muraenesox cinereus (Takai 1959, 1979), have found seasonal patterns of reproductive maturation, suggesting that these eels have spawning seasons in fall.

There is also some information available about the seasonality of spawning of marine eels in other regions of the world based on catches of leptocephali. In the Gulf of Mexico, at a similar latitude as the East China Sea, catches of leptocephali suggest seasonal spawning of the congrids
Rhynchoconger flavus and Xenomystax congroides, but other congeners such as Uroconger syringinus, appeared to spawn all year (Smith 1989a). Occurrences of small Gnathophis leptocephali in coastal waters of New Zealand, eastern Australia, and South Africa suggested seasonal spawning, but spawning off western Australia may occur year round (Castle 1968; Castle and Roberson 1974). Castle (1969) showed that leptocephali of various families were collected at all times of year along a north–south transect that was repeatedly sampled in the eastern Indian Ocean off western Australia and south of Java Island of Indonesia. Catches were greatest from May to August with higher species richness occurring in the north closer to Java and greater abundances occurring further south near Australia due to large catches of Ariosoma and Gnathophis leptocephali.

In the tropical region of the Gulf of Guinea off western Africa, Blache (1977) reported that in extensive sampling over a 10-year period, many species, including several congeners, showed evidence of seasonal spawning at latitudes of about 5°N to 18°S. Based on a lack of catches of
leptocephali, there was an apparent absence of spawning activity from July to October (Blache 1977), which corresponds directly to the period of wind-driven upwelling of cold water in the region (Okumura and Xie 2004). This suggests that although this region is close to the equator, the colder water temperatures during the upwelling season may cause eels to stop their spawning activity, as has been suggested at higher latitudes.

Seasonal patterns in the catches of leptocephali of mesopelagic eels in the Sargasso Sea have indicated that at least some of these species only spawn during part of the year. For example, although derichthyid leptocephali were abundant in the summer and fall across the southwest Sargasso Sea (Castonguay and McCleave 1987b), they were absent in the same general region in the winter and spring (Miller and McCleave 1994). The opposite pattern was observed for Serrivomer leptocephali, which were abundant in the winter and spring (Miller and McCleave 1994), but almost completely absent in the summer and fall (Miller and McCleave 2007). Other species are present in both seasons, so more research is needed to gain a better understanding of the many factors that can affect the zoogeography and temporal occurrence of leptocephali.

4. Ecology of leptocephali

4-1. Depth distribution and vertical migration

There have only been a few published reports on the depth distribution of leptocephali, primarily due to the difficulty of using large enough nets that can sample discrete layers of the ocean. All of the studies that have been done, however, have indicated that leptocephali are most abundant in the upper 100 m at night, but their exact depth distributions during the day have remained difficult to determine because of likely net avoidance. Studies on leptocephali in the western North Pacific (Kajihara et al. 1988) and on A. japonica (Otake et al. 1998) have indicated a shallow depth distribution of leptocephali in the upper 100 m at night. Small A. japonica leptocephali were most abundant between 60 and 90 m at night during two surveys in the western North Pacific (Otake et al. 1998). Schoth and Tesch (1984) examined the depth distribution of small anguillid leptocephali in the Sargasso Sea and found evidence of vertical migration from about 30–70 m during night to 70–280 m during the day.

The most extensive study on the depth distribution of leptocephali was conducted by Castonguay and McCleave (1987a) during several surveys for leptocephali in the Sargasso Sea, in the late winter/spring spawning season and in the summer/fall when anguillid leptocephali are larger in size. Data from this study indicated that the smaller recently spawned leptocephali of A. rostrata and A. anguilla were present at a range of depths between 50 and 350 m during both day and night (Fig. 50). As the leptocephali grew they were present only in the upper 100 m at night and showed increasing evidence of vertical migration to greater depths during the day (Fig. 50; Castonguay and McCleave, 1987a). At one site, where >40 mm anguillid leptocephali were collected in the southwest Sargasso Sea in August (Fig. 50, bottom right panel), most leptocephali during nighttime were collected within the thermocline at 50–70 m in temperatures of about 24–25°C (see McCleave and Kleckner 1987), but none were collected in the mixed layer of 27°C water in the upper 30 m, or below the thermocline at 100–125 m depths (Castonguay and McCleave 1987a).

A similar pattern of depth distribution in the upper 100 m at night was reported by Castonguay and McCleave (1987a) for various species of marine eel leptocephali, but there were indications of differences in distributions among taxa within each season. Leptocephali of the mesopelagic eel, Derichthys serpentinus, showed evidence of vertical migrations similar to Anguilla, with most being collected from 30–70 m at night in the summer and fall (Fig. 51). A variety of other species of leptocephali were also collected including those of mesopelagic and shallow water eels (Fig. 52). Some species such as Avocettina infans and Serrivomer brevidentatus (mesopelagic) were most abundant in the upper 50 m depth at night, but various other species were more abundant at 50–100 m (Fig. 52). In contrast, Ariosoma balearicum was distributed evenly between those two depth ranges at night (Castonguay and McCleave, 1987a). The catch data also showed that in contrast to other species, such as Anguilla and D. serpentinus, Nemichthys
scolopaceus leptocephali < 80 mm did not seem to migrate vertically and could be caught in the shallow layers during the day, but at least some of the larger sizes did migrate vertically. Little or no evidence was found that some species such as A. balearicum, A. infans, or C. oceanicus were migrating vertically.

These observations that leptocephali are generally found in the upper 100 m at night and within the upper 300 m during day has been confirmed by catches of leptocephali in many deployments of the much larger multiple-net MOCNESS-10 trawl system (10 m² mouth opening, Wiebe et al. 1985) in studies on mesopelagic fishes (e.g. Backus and Craddock 1982) or salps (e.g. Madin et al. 2006) during a wide variety of cruises in the western North Atlantic. Most leptocephali were collected in nets that fished at least part of the time in the upper 100 m at night, and few were ever collected deeper than 300 m in the many nets that fished in deep layers during both day and night (Miller unpubl. data).
One region where a few leptocephali were collected in slightly deeper layers than usual was in the Florida Current, which flows along the South Atlantic Bight of the US east coast. Two MOCNESS-10 surveys of mesopelagic fishes were conducted that consisted of four transects of stations across the Florida Current (Kleckner and McCleave 1982; Miller 1995, 2002a). These collections resulted in many hours of fishing effort at night and 1,231 congrid larvae being collected, but only one leptocephalus was caught in a net that fished exclusively below 200 m. During the day, there was even more fishing effort at depths from 300–900 m, and 18 out of 114 total congrid leptocephali were collected in nets that fished deeper than 300 m. All but one of these were A. balearicum leptocephali (8 were undergoing metamorphosis), which suggests that their deep distributions may have been caused by recruitment-related behavior, since larvae of one population are thought to cross this region of the Florida Current to reach their recruitment areas (Miller 2002a). Most leptocephali, however, were caught in nets that fished between the surface and various greater depths.

A few more recent deployments of the MOCNESS-10 were well-designed to examine the fine-scale depth distribution of leptocephali between 0–100 m at night and confirmed the observations of Castonguay and McCleave (1987a) that different species of leptocephali show con-
Contrasting depth distributions (Miller unpubl. data). For example, near Bermuda in the northern Sargasso Sea in November, *Serrivomer* leptocephali were most abundant at 40–70 m where *Anguilla* were distributed, but *A. balearicum* were most abundant at 20–40 m (Fig. 54). Similarly, in the same region in April, *A. balearicum* were mostly at 0–20 m, but *N. scolopaceus* were divided between the upper two depth layers (Fig. 54). More interesting though, is that there was a clear seasonal difference in the depth distributions of leptocephali that appeared to be related to the different temperature structures between seasons. During both seasons, the leptocephali were almost exclusively collected above the thermocline at night (Fig. 54), suggesting that leptocephali were avoiding the colder water below the thermocline.

Other sources of information have suggested that leptocephali sometimes may be distributed deeper than they typically are in offshore areas, similar to in the Florida Current. Tesch (1980) reported evidence of deeper distributions of late-stage leptocephali of *A. anguilla*
(mostly 60–85 mm) as they were approaching Europe for recruitment, which were possibly as deep as about 300–650 m during the day. They were most abundant at 50–100 m at night. These collections were made in horizontal tows of an IKMT though, so some contamination from shallower depths could not be ruled out. Ross et al. (2007) also indicated that some marine eel leptocephali collected along the southeast US coast just inshore of the Florida Current were at greater depths (about 300–800 m) than typically observed, but at least part of their data were collected with open nets that may have unavoidably collected some leptocephali in shallower layers than the targeted fishing depth. However, since a few leptocephali were collected at greater depths by several nets of the MOCNESS-10 in the Florida Current (Fig. 53), which should not have any contamination from other depths, it is possible that when leptocephali are approaching the continental shelves where they have the potential to recruit, they migrate vertically to greater depths, perhaps searching for the bottom.

At the other extreme, it is clear that leptocephali in the open ocean at least, can also sometimes be found in the neuston layer at or near the surface at night, within about the upper 1 m of the ocean. Ariosoma scheelei leptocephali were collected at the surface at 11 of the 25 stations around Sulawesi Island in May (1.5 m ring net towed next to the ship), but no metamorphosing individuals were caught at the surface (Miller et al. 2006b). Leptocephali were also frequently collected in the same way at the surface to the northwest in the Sulu Sea in both February and November (Miller et al. 2004; Miller and Tsukamoto unpubl. data). These taxa included

Fig. 53. Plots of catch rates of congrid leptocephali collected by the MOCNESS-10 opening and closing trawl in 4 transects of stations across the Florida Current that are plotted as the number of leptocephali (ind.) caught per minute each net fished, at night (A) and during daytime (B), during August 1978 and February 1979 surveys for mesopelagic fishes. Data are plotted as catch rates and the minimum depth fished by each net (nets fished at various depth ranges deeper than each minimum depth). Note the very different y-axis scales for catch rates during night and day. See Kleckner and McCleave (1982), and Miller (1995) for maps of the stations sampled during these surveys.
A. scheelei, but also ophichthids, muraenids and at least five other species in low numbers. Similar catches of Ariosoma or other species such as Gnathophis have been made at the surface or in the upper 10 m in the western North Pacific (Tabeta and Mochioka 1988b; Mochioka et al. 1991; Miller and Tsukamoto unpubl. data). Extreme examples of this neustonic distribution were 98 A. scheelei leptocephali (71–140 mm) collected in the Philippine Sea in July (18°00’N, 131°00’E) and 148 Gnathophis leptocephali (60–104 mm) in the western South Pacific in early September (27°27’S, 163°63’E), both in 20 min net deployments (Miller and Tsukamoto unpubl. data). To catch that many leptocephali in a short deployment of a small net, implies that many Gnathophis and Ariosoma leptocephali were at the surface in those particular areas.

Ross et al. (2007) reported that 20% of the 1,277 leptocephali they collected with various sampling gear were caught in neuston nets fished at the surface along the edge of the Florida Current off the southeast US east coast. Those leptocephali included muraenids (Gymnothorax spp.), ophichthids, A. balearicum, and a few other congrids including Heteroconger luteolus (a garden eel). These were mostly collected at night, but some were also collected during the day (Ross et al. 2007).

These surface collections of leptocephali in both the Atlantic and Pacific oceans indicate that some species of leptocephali are present in the neuston layer in some circumstances during both night and day. Their presence at the surface during the day was also confirmed when seabirds were reported to be catching Ariosoma and nemichthyid leptocephali in one area in the South Atlantic (Figueroa 1997), which suggested the presence of high-density aggregations of leptocephali. Possible reasons for greater numbers of leptocephali at the surface could involve feeding, predator avoidance, or temperature regulation in relation to growth. However, Kimura et al. (1994) hypothesized that Japanese eel leptocephali move up to shallower depths to take advantage of the northward flow resulting from Ekman surface drift as they approach the bifurcation zone of the North Equatorial Current (Fig. 41B), which would facilitate their entrainment into the northward flowing current branch.

4-2. Survival and predation

There is presently very little information available about the survival of leptocephali or the amount of predation they experience. No studies have been done on their survival rates, but a general estimate of the mortality of leptocephali of the European eel has been made recently using numerical modeling (Bonhommeau et al. 2009a). Reduced food availability due to changes in productivity has been hypothesized to have a negative effect on the larval survival of the North Atlantic anguillid eels (Castonguay et al. 1994; Knights 2003; Friedland et al. 2007;
Bonhommeau et al. 2008a,b; Miller et al. 2009a). One possible factor affecting survival may be the availability of appropriately sized particles for feeding by the early stage larvae, since they may be especially vulnerable to mortality after they deplete their yolk reserves. These factors have been suggested to be potentially responsible for the declining populations of northern temperate anguillid eels, because correlations have been found between recruitment and various factors such as the North Atlantic Oscillation index (Knights 2003; Friedland et al. 2007; Kettle et al. 2008), temperature as a proxy for productivity (Bonhommeau et al. 2008a,b), or the likely latitude of frontal features (Kimura et al. 2001; Kimura and Tsukamoto 2006; Friedland et al. 2007) as is discussed in Section 5-5.

Another factor that would be important in determining the survival of leptocephali in the ocean is their immune system. They appear to have components of an immune system based on research on A. japonica leptocephali, which detected the presence of lectin in the club cells that line their bodies (Suzuki and Otake 2000). This may provide some defense against pathogens that come in contact with their skin, but some specimens also showed free leukocyte-like cells in the connective tissue of their guts. Other cells potentially related to the immune system were observed, but since most organs including those related to immune cell production are poorly developed in leptocephali, the extent of their defenses against pathogens is unclear (Suzuki and Otake 2000).

It is also unclear how much predation occurs on leptocephali by other marine organisms. Their high degree of transparency likely reduces the ability of predators to see them. But the fragile and gelatinous nature of leptocephali, with few or no ossified hard parts, probably makes them difficult to detect or identify in stomach content studies of pelagic fishes. There is some evidence though that predators can sometimes see them and catch them. Seabirds were observed feeding their young large leptocephali off the coast of Brazil (Figueroa 1997), and “eels and eel larvae” were reported as being among the gut contents of dolphin fish (Coryphaena hippurus) collected east of Taiwan during winter (Wu et al. 2006); but the latter case appears to be unusual compared to other studies of the food habits of dolphin fish. Some types of sea snakes are known to target small moray eels as prey (Reed et al. 2002; Ineich et al. 2007; Brischoux et al. 2009), and marine mammals such as dolphins sometimes feed on eels when they are abundant (Amir et al. 2005), but there is apparently no predator that is known to feed regularly on leptocephali.

Transparency is an important strategy of a wide variety of organisms in the open ocean to reduce predation, by making it difficult for predators to distinguish the outline of the organism (Johnsen 2001). Leptocephali appear to have evolved a strategy of being almost totally transparent. Although it is not evident in persevered or even recently deceased leptocephali in which the thin layer of muscle tissue on each side of the body is no longer transparent, live leptocephali appear almost completely transparent (Figs. 1, 55). Selection pressure for transparency is one possible reason that leptocephali do not form red blood cells until late in the metamorphic process, since red colored blood might be very visible during the daytime. The body surface of leptocephali also appears to be very reflective (Fig. 55), which could provide crypsis in some light conditions as reflective coloration does for many pelagic fishes (Johnsen 2003).

Another feature that may have evolved to reduce the ability of predators to see and capture leptocephali is their wide variety of pigmentation patterns. Some leptocephali have melanophores on their heads, guts, side of their bodies (Figs. 13, 14, 56), internally, or even on the iris (Fig. 57E). The size and arrangement of these spots can range from large dendritic melanophores or large patches of small melanophores, to tiny melanophores scattered all over the body (see Blache 1977; Smith 1979; Böhlke 1989b; Miller and Tsukamoto 2004). One common pattern is a single row of melanophores or small rows of pigment on the myosepta between the myomeres that extend along the midline of the body. Others patterns are melanophores spaced out along the entire length of the gut (e.g. congribs, Fig. 56), or pigment on top of the liver swellings (e.g. ophichthids, Fig. 18B). A remarkable new video observation of a swimming ophichthid leptocephalus at night off Hawaii (MJ Miller and MJ D’Avella unpublished manuscript) indicated that the pigment spots along its gut were enlarged dorsally and were paired structures (http://www.australianmuseum.net.au/movie/Ophichthid-leptocephalus-Kona-Hawaii/). This marked difference in shape and size compared to those of other ophichthid leptocephali after
being collected and preserved (Leiby 1989), suggests that the size and shape of some of these internal pigment patches containing melanophores and possibly other types of chromatophores, may be changeable and controlled by the nervous/endocrine systems in some ophichthids as they frequently are in the skin of other fishes (Fujii 2000; Grether et al. 2004).

The various spots or pigment patches in leptocephali are likely designed to break up the visual outline of the body, or the less transparent features such as the head, gut, and liver swellings while the leptocephali are moving, by a process referred to as flicker fusion (Moser 1981). Many dark spots moving quickly within the body outline of a leptocephalus may disrupt the ability of the predator’s visual system to distinguish the outline of the leptocephalus. Similarly, black spots on various regions of the gut would likely break up the linear image of the tubular gut containing food, thus making it less visible within the rapid body undulations during their anguilliform swimming motions.

A few taxa of leptocephali also have various kinds of yellow (xanthic) pigmentation, but the function of this type of pigment is unclear. Yellow pigmentation is found on the anterior part of the esophagus and liver swellings of Neenchelys (Ophichthidae) and Saurenchelys (Nettastomatidae) (Figs. 57A, C), and internally around the eyes of some muraenids (Figs. 57B, F). At least one species of muraenid also has small yellow xanthophores scattered all over the side and top of its head, mixed with melanophores (Fig. 57E). Yellow pigment also commonly

![Frame-capture photographs of a chlopsid leptocephalus filmed after being captured and placed in an aquarium on board a research vessel, showing it curling up in what is hypothesized to be behavioral mimicry of gelatinous zooplankton, which are typically avoided by predators.](image-url)
occurs on the dorsal surface of the eye in some congrids and ophichthids (Fig. 57D). This yellow pigment is mixed with black spots and may be more common than can be judged from photographs.

The function of this yellow pigment in leptocephali may be related to the wavelengths of light that it absorbs. For example Warrant and Locket (2004) pointed out that the yellow lenses

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**Fig. 56.** Photographs of various types of pigment spots (melanophores) on the guts or side of the body of leptocephali of congrids (A, F), chlopsids (B, C), a synaphobranchid (Synaphobranchinae) (D), and *Leptocephalus holti* (Cyematidae) (E).
of the eyes of some deep-sea fishes selectively absorb light in the blue part of the spectrum, thus cutting out most of the light that could have reached the retina. Removing most of the blue background light enhances the slightly greener counter-illumination, which could highlight the outline of prey organisms. The yellow pigmentation in leptocephali may also selectively absorb blue light, which could serve to contribute towards camouflaging the larvae by making some body features less visible. Yellow pigment has also been suggested to provide some protection
against damage to fish larvae by ultraviolet (UV) and visible light (Moser 1981). It may function this way around their eyes, or on their liver tissue. In the case of the species with yellow pigment patches above their eye (Fig. 57D), it may absorb light shining down from above.

These types of questions and the issue of the survival rates of leptocephali are presently just a matter of speculation due to a lack of information. Observations of live leptocephali make it clear that their ability to swim both forwards and backwards is likely an important factor in avoiding predators. Having the choice to immediately evade an approaching predator in two possible directions makes it difficult for the predator to know which direction the leptocephalus will go when attacked. In addition, it is possible that leptocephali can use a form of behavioral mimicry to confuse some predators as they rapidly approach them. A leptocephalus of *Chilorhinus suensoni* (Chlopsidae) observed in an aquarium on board a research vessel in the Sargasso Sea exhibited a curling up behavior to form a tight ball (Fig. 55). Many fish species are known to mimic other organisms that most fishes avoid eating (Randall 2005), so it is possible that leptocephali curl up so that they will appear to be a jellyfish, salp, siphonopore, or ctenophore (Fig. 55). These transparent gelatinous invertebrates are typically found at the same depths as leptocephali but are unpalatable. A species of congrid leptocephalus has also been observed performing this same behavior (pers. observ.), so more information is needed to determine if this curling behavior may be a common predator avoidance strategy of leptocephali.

Leptocephali are also occasionally vulnerable to ectoparasites, including those that appear to be some type of parasitic hydroid (Fig. 58). This type of parasite is rare on leptocephali in the Indo–Pacific, but it also has been observed on a few leptocephali collected in the western North Atlantic (pers. observ.). How many leptocephali may die from this parasitism and thus not be collected is unknown. It is also possible that some larger invertebrates have the ability to prey on small leptocephali considering that a small nemichthyid leptocephalus was recently documented to have been eaten by a chaetognath (Fig. 59; Johnson et al. 2006). Whether or not the leptocephalus was captured and ingested while within the net is not known, but it shows that chaetognaths may be predators of small leptocephali. Future research is needed to evaluate predation pressure on leptocephali and to determine what other factors, such as poor feeding conditions, can affect their survival.

### 4.3. Recruitment behavior

All different types of leptocephali live in the surface layer of the ocean ranging from the outer edge of the continental shelf to far out in the open ocean, but each species must return to its own particular juvenile growth habitat. For anguillid eels, recruitment (defined here as entering their juvenile habitats) occurs after metamorphosis into glass eels, which then enter freshwater and estuarine habitats. Various studies have examined the recruitment patterns of anguillid glass eels in both temperate and tropical regions (e.g. Sugeha et al. 2001b; Sullivan et al. 2006, 2009). Less studied are the larvae of mesopelagic eels, which presumably metamorphose at a certain size and move into deeper water to start their juvenile stage, based on studies of the life histories of these eels (e.g. Beebe and Crane 1936; Böhlke 1989a). In contrast, leptocephali of families of shallow water and continental slope eels must move away from the deep ocean and recruit to the appropriate depths for each species. Species that live as juveniles and adults in very shallow water coastal areas over the shelf, such as around tropical coral reefs, in sandy areas, or on banks, must enter these habitats from deeper water.

Although the leptocephali that recruit to those habitats have never been studied in particular to determine the factors affecting their recruitment patterns, some useful data have been obtained in general studies on fish larvae that recruit to coastal areas in tropical habitats. These larval recruitment studies were conducted using either channel nets anchored to the bottom, but fishing just below the surface, or crest nets attached to the bottom in small channels in the outer reef crests. Both types of nets have collected substantial numbers of recruiting leptocephali in some areas.

One of these areas that was sampled using channel nets was part of research designed to study the recruitment patterns of grouper larvae moving onto the large shallow area referred to
as the Great Bahama Bank (GBB) of the northern Bahamas (Shenker et al. 1993). The GBB is a distinctively shaped bank located at the southwest corner of the Sargasso Sea, which drops off very rapidly to depths >1000 m on all sides (Figs. 45, 60B, C). Shenker et al. (1993) used channel nets primarily fished in the upper 1 m that were deployed at 4 locations near Lee Stocking Island on the west side of Exuma Sound of the GBB (Fig. 60A) to sample fish larvae flowing onto the banks during flood tides. During two years of sampling from December to February, 8,067 leptocephali were collected, which was far more that any other family of fish larvae (Thorrold et al. 1994a). Almost all (95.7%) of those leptocephali were collected at night, and the catches showed clear periodicity (Fig. 60D) correlated to the number of hours of no moonlight with strong flood tide and wind (Thorrold et al. 1994b). These catches had a periodicity of 28 days (Thorrold et al. 1994b) and the catches at all 4 locations showed the same temporal patterns (Thorrold et al. 1994a), with location 2 providing the most leptocephali and location 4 providing the fewest (Shenker et al. 1993).

In the same kind of sampling in summer, leptocephali of the Ophichthidae (N = 2605) were most abundant, but moringuids (N = 807), congridcs (N = 400), chlopsids (N = 343) and muraenids (N = 157) were also collected (Thorrold et al. 1994c). During the summer though, labrid and clupeid larvae were more abundant than all leptocephali combined. The catches in the summer also showed a clear periodicity with a 14-day semilunar cycle that was clearly seen in the catches of ophichthids (Fig. 60E; Thorrold et al. 1994c).

Other studies on the recruitment of fish larvae have used crest nets, which sampled tidal flows over the outer edge of barrier reefs in tropical coral reef areas in western Australia (McIlwain 2003), French Polynesia (Dufour et al. 1996), and the Caribbean Sea (Nolan and Danilowicz 2008). In western Australia, 1,430 leptocephali were collected in two Oct/Nov to March sampling seasons, with four families of other larval fishes having higher abundances. The objectives were to examine the magnitude of larval supply between years and its periodicity, and to compare the synchrony in larval supply at scales of 500 m and 5 km. In the area sampled in both years, 1.7 times as many leptocephali were collected in the first year. Leptocephali showed a significant correlation in arrival data over 5 km, but at a 1-day lag. Interestingly, of all the taxa of fish larvae collected, leptocephali showed the strongest lunar cycle of catches, with a periodicity of 27 days (McIlwain 2003). In French Polynesia, leptocephali were the fifth most abundant taxon of large fish larvae collected in crest nets at 5 sites on different sides of Moorea.
Fig. 59. Photographs of a 25 mm chaetognath (Sagitta hexaptera) that had ingested an approximately 17 mm Nemichthys sclopetaricus leptocephalus. The leptocephalus is folded and both its head and tail point towards the anterior end of the chaetognath. Reprinted from Johnson et al. (2006).
Island, with 2,399 being collected (Dufour et al. 1996). Various patterns of lunar cycles of catches were observed at these sites also. A more recent study compared the catches of both channel nets and crest nets at Turneffe Atoll off Belize to evaluate which type of net is better for collecting recruiting fish larvae (Nolan and Danilowicz 2008). Crest nets were found to consistently collect more larvae than the channel nets fished at the surface in mangrove channels, and this was clearly true for leptocephali, with 81% being caught in the crest nets. This study also seemed to be generally consistent with previous studies, with higher catches being related to the lunar cycle and the strength and direction of winds, but leptocephali were not analyzed separately or distinguished into different taxa.
These various studies that have documented leptocephali recruiting into tropical habitats, raise some interesting questions. The cyclical patterns of recruitment suggest the possibility that leptocephali are abundant in the waters just offshore of the banks where they have been collected, and that they may wait for the appropriate environmental conditions to move onshore. It is also possible that passive oceanographic processes combined with net avoidance during moonlight could explain these recruitment processes if stronger tides simply transport more leptocephali onshore. However, it is possible that leptocephali are adapted to time their inshore movements during periods with the strongest tidal transport and the lowest risk of predation. If this is the case, then it is also possible that leptocephali from offshore areas may accumulate just offshore near the shelf break and then remain nearby using active swimming behavior until it is the appropriate time to move inshore.

The observations of leptocephali recruiting into shallow water indicate that many species enter these habitats as leptocephali, and not as glass eels as in anguillids. A similar pattern occurs with Conger oceanicus, which is spawned offshore in the Sargasso Sea, but recruits back to temperate latitudes as leptocephali (Able and Fahay 1998; Bell et al. 2003). These Conger leptocephali have been captured while entering estuarine habitats in New Jersey (Fig. 36; stage ER – M1) from April–June (Wuenschel and Able 2008). Leptocephali of the common ophichthid Myrophis punctatus also enter this estuarine system (Able and Fahay 1998), and probably along the entire coastline to the south and into the Gulf of Mexico, since for example, they are also captured in tidal currents flowing into estuarine habitats in North Carolina (Pfeiler and Govoni 1993). In East Asia, Conger myriaster also are commonly collected in shallow coastal areas as they begin to metamorphose (e.g. Otake et al. 1994; Lee and Byun 1996). Future research using appropriate sampling gear in carefully selected locations will likely find that leptocephali of many species of common coastal marine eels can be collected as they enter their growth habitats in areas ranging from tropical to southern temperate latitudes worldwide.

5. General discussion and future perspectives

5-1. Biology of leptocephali

Much remains to be learned about the biology of leptocephali, because in some respects, what has been learned about their morphology and behavior creates more questions than it answers. Their highly compressed transparent bodies seem to act as energy storage reservoirs that also provide structural support (Pfeiler 1999; Pfeiler et al. 2002), buoyancy (Tsukamoto et al. 2009) and a strong swimming ability (Wuenschel and Able 2008) until metamorphosis. They live in the surface layer (Figs. 50–54) where there is the highest degree of biological activity and food availability and at least some of them show vertical migrations like many other marine organisms (Lampert 1989). Due to a minimum amount of respiring tissue, their metabolic demands are low (Pfeiler and Govoni 1993; Bishop and Torres 1999), thus enabling them to feed on readily available bacteria or protozoa attached to particulate matter that contain little energy (Otake et al. 1993; Mochioka and Iwamizu 1996); yet they apparently grow quite fast (Table 1) and reach large sizes.

The hypothesis that leptocephali feed exclusively on particulate matter or its associated DOC, is supported by two general factors. The first is that no zooplankton have ever been seen in their guts, but their guts typically contain a detritus-like material. Second, stable isotope studies indicated the trophic level of leptocephali is at the lowest levels of the food chain (Otake et al. 1993; Kimura and Tsukamoto 2006). This type of feeding strategy is logical, however, because marine snow and discarded larvacean houses are typically very abundant in the surface layer of the ocean, and by feeding on this material, they will not directly compete for food with most other fish larvae. Zooplankton fecal pellets (Turner 2002), discarded larvacean houses (Alldredge 1976), and marine snow (Alldredge and Silver 1988) are common components of the water column in the upper few hundred meters of the ocean. These particulate materials form aggregates containing bacteria, phytoplankton, and protozoa, as well as the mucus-like larvacean houses that collectively form marine snow (Alldredge and Silver 1988), which is a food source
of various types of zooplankton (Alldredge 1976). Some fish larvae also feed directly on discarded larvacean houses, because they are often abundant and they are immediately replaced by a new house when their filters clog (Alldredge 1972, 1976; Sato et al. 2003). Other fish feed directly on the larvaceans themselves (Capitanio et al. 2005; Llopir and Cowen 2009), but by feeding only on discarded larvacean houses or marine snow, leptocephali do not directly impact the organisms producing their food source.

Particulate organic material that includes marine snow and discarded larvacean houses is typically most abundant in the upper 100 m of the water column in regions such as the North Pacific subtropical gyre and along its western margins (Ichikawa and Nishizawa 1975; Ichikawa 1982; Hebel and Karl 2001; Pilskaln et al. 2005). Because marine snow is most abundant in the surface layer where leptocephali live, it is a logical food source for them. Some larvacean houses (Galt et al. 1985) and some types of marine snow (Herren et al. 2004) have bioluminescent properties that could make it possible to be seen and eaten at night by leptocephali which appear to be adapted for night vision. It remains to be determined, however, under what types of light conditions and depths leptocephali feed on particulate material.

Another major question is whether there are any differences in feeding strategies or the materials that different species eat. The greatly different lengths and orientations of the teeth of small leptocephali compared to the larger ones suggest that there may be a specific range of size of particles that they primarily target. Based on the relative teeth size, these particles may be large compared to the mouth of the small engyodontic stage leptocephali with large teeth (Figs. 9, 11), and smaller relative to the head of larger euryodontic stage leptocephali with small teeth (Figs. 11, 14, 15). The morphological diversity of head and jaw structures suggest the possibility that various species may use different tactics to locate food or may target different food sources. For example, are the wide range of jaw shapes among taxa of leptocephali related to feeding on different types of particulate matter? Or are they simply related to the developmental constraints during metamorphosis with the larvacean needing to have similar jaw structures to the adults, as may be the case in the gulper eels (Eurypharynx pelecanoides, Figs. 9, 10, 15)? The leptocephali of Thallassenchelys that reach very large sizes, but whose adults are unknown (apparently related to Colocongridae, Lopez et al. 2007), have two larger front teeth that differ from other species (Fig. 15C), so it is possible that these teeth are related to feeding on a special type of food source consumed by the larger leptocephali that can reach >300 mm.

The most extreme examples of morphological specializations likely related to feeding are the upward pointing telescopic eyes of the Synaphobranchidae (Fig. 15E), and the rostral filaments possessed by some species of the synaphobranchid subfamily Ilyophinae (Fig. 16). Telescopic eyes are commonly seen in deep-sea fishes and are thought to be used in feeding for looking upward to see the silhouettes of prey above in very low light conditions (Warrant and Locket 2004). More difficult to understand, though, are the apparently cartilaginous extensions from the tip of the rostrum of some species. They can be quite long or even have branching structures or palp-like extensions. They have never been studied in particular, so their structure and function is unknown. One idea is that the long filament could be used to locate food in very low light conditions by waving it back and forth to feel for larvacean houses or other large pieces of particulate matter. Using them to stimulate bioluminescent organisms to produce light that they could use for visualizing food items is another speculative idea. The palp-like structures seen in Fig. 16C look very similar to the bioluminescent barbels of many types of deep-sea fishes, but presently the function of these interesting structures cannot be determined without detailed morphological analyses, or chance observations of their behavior in the ocean.

Other more achievable research problems still remain regarding the biology of leptocephali, however, such as their comparative anatomy, physiology, depth distribution and feeding behavior. For example why do leptocephali almost exclusively reside in the upper 100 m at night and why do some species vertically migrate during the day and others apparently do not? If leptocephali are visual feeders as appears to be likely, feeding in daytime is perhaps most likely, unless they can target food particles with bioluminescent properties, as mentioned previously. An alternative hypothesis is that they reside in the upper layers at night to be in the warmest water to facilitate faster growth, but some vertically migrate to deeper, lower light regions presumably
to avoid predation during the day. Many marine fishes have UV vision (Johnson and Widder 2001) as do some larval fishes (Britt et al. 2001; Browman et al. 2006), but it is unclear if this has any relationship to the ecology of leptocephali. There appears to be enough light for UV vision down to 200 m (Losey et al. 1999), which could facilitate feeding at deeper depths during the day, or alternatively the UV vision of predators could somehow make leptocephali more visible at shallow depths during the day. More data are needed on the daytime depth distributions of leptocephali, because existing data are clearly biased by net avoidance.

Other basic issues that need to be examined are the ecology of metamorphosis and recruitment. The triggers of metamorphosis are presently unknown for leptocephali and the recruitment dynamics of marine eels have never been examined. Can all leptocephali delay metamorphosis if they reach their maximum size but are drifting far offshore and how many actually wait nearby their recruitment areas before swimming onshore when they reach a certain size? By applying otolith aging techniques to a wider range of species and recruiting leptocephali in addition to those collected offshore, the mysteries of what happens when these fragile, transparent larvae change into threatening, voracious predators may be revealed.

5-2. Leptocephalus growth

Progress has been made towards understanding the growth rates of leptocephali, which grow up to much larger sizes than most fish larvae, but relatively few anguilliform species have been studied. Analyses of otolith microstructure of leptocephali and glass eels have typically observed well-defined increments, with the exception of the outer opaque zone that apparently occurs when leptocephali move through cold waters and experience slow growth (Lee and Byun 1996; Antunes and Tesch 1997). Species collected in the mostly warm Indo–Pacific region have growth rates <1 mm/d and linear relationships between age and body length, with growth slowing down as maximum size is reached (Table 1; Figs. 30–32). These relationships and the finding of apparent lunar cycles of spawning based on backcalculated hatching dates (Ishikawa et al. 2001; Tsukamoto et al. 2003; Lee et al. 2008), suggest that increments are deposited daily in these species (Powles et al. 2006).

There are differences in growth rates among species, however, which may be related to their maximum size and their distances of migration, as proposed by Kuroki et al. (2006a) for anguillid leptocephali. Larval growth rates and timing of metamorphosis may be key factors in the early life histories of anguillid eels for defining their recruitment areas (Chen and Tzeng 1996; Wang and Tzeng 2000; Shiao et al. 2002; Kuroki et al. 2006a, 2008a). There also may be different growth strategies of marine eel leptocephali, related to their maximum body sizes or dispersal strategies as discussed below. This hypothesis is supported by the observation that the growth rate of the leptocephali of a synaphobranchid species with a smaller maximum size was lower than the growth rate of a nettastomatid species with a larger maximum size, which were collected during the same survey in the East China Sea (Fig. 32).

These types of inter-taxon differences could be a contributing factor to the findings of the age and growth study on leptocephali from the Gulf of Mexico, which found similar results to those of Indo–Pacific species for one species, but found much higher variability and some very high apparent growth rates for the three other species that were studied (Bishop et al. 2000). The cause of this variability is unknown because otolith microstructure of these taxa has not been examined in the Indo–Pacific. It is possible that the conditions for leptocephalus growth are better (or sometimes worse) in the eastern Gulf of Mexico, or that the species studied frequently have particularly high growth rates compared to other species that have been studied in the Indo–Pacific. However, it can not be assumed that visible otolith increments are deposited daily in all leptocephali or in all larval stages of eels, since so little is known about the biology and behavior of most species.

Deposition of daily increments is thought to be related to physiological cycles that cause increment formation, which in the case of fish larvae, could be linked to a cessation of feeding at night or vertical migration into lower temperatures in deeper water. However, there is evidence that otolith increments might stop being deposited in some anguillid glass eels, based on the
mismatch of many of their back-calculated hatching dates and the known spawning season of temperate species such as Anguilla rostrata, as indicated by collections of small leptocephali in their spawning area (McCleave 2008). This period when increments are not deposited likely occurs during the glass eel stage because studies on metamorphosing anguilliform and elopiform leptocephali have found that otolith deposition continues during metamorphosis (Chen and Tzeng 1996; Powles et al. 2006) and wider increments are formed (Figs. 38, 39). In addition, experiments have shown that glass eels held at temperatures of 12°C or lower stop depositing otolith increments (Umezawa and Tsukamoto 1991; Fukuda et al. 2009).

Since glass eels typically do not feed until they begin their upstream migration, if they hide in the substrate and wait for the appropriate water temperature or other cues to start their upstream migration (see Linton et al. 2007), a hypothesis can be proposed that there may be a reduction or cessation of otolith deposition as a result of their lack of feeding or activity. This could occur during such a period of inactivity, because otolith deposition requires the secretion of otolith matrix proteins, and the entry of calcium into the endolymph that is then crystallized onto the otolith surface, with increments being formed by alternation between mineral-rich and organic-matrix-rich layers (Campana 1999; Morales-Nin 2000; Takagi et al. 2005). These processes may be partially under hormonal control (Morales-Nin 2000), and a lack of feeding, or stress to the fish, has been shown to disrupt normal increment formation in some fishes (see references in Fukuda et al. 2009). So the lack of feeding or activity in glass eels that may hide in the substrate to conserve energy until they migrate upstream, this period of lack of deposition may correspond to what has been referred to as the “freshwater check” (Fig. 38) as mentioned previously (Kuroki et al. 2008b; Fukuda et al. 2009). If this check is actually formed when glass eels stop migrating and wait in the substrate for a variable period of time, the freshwater check would represent an accurate age at first recruitment if daily increments were formed prior to its formation. But due to the potential missing time not recorded by visible increments within the zone of the check, the back-calculated hatching dates of glass eels estimated from the otolith rings would not be accurate, as was indicated by McCleave (2008).

In contrast to inactive anguillid glass eels, species of leptocephali that have a daily cycle of feeding and growth or vertical migration between different temperatures (Figs. 50, 51; Castonguay and McCleave 1987a) will likely deposit daily increments in their otoliths. This may occur in many species of leptocephali, but in some metamorphosing Conger leptocephali (Lee and Byun 1996; Correia et al. 2002a, 2003) or in the otoliths of some late stage A. anguilla leptocephali or glass eels (Antunes and Tesch 1997), there is a diffuse zone in the outer regions of their otoliths where increments are irregular or are not clearly visible using standard etching techniques. This zone may correspond to a region of slow but continuous otolith growth before and after metamorphosis, possibly due to the fish experiencing low water temperatures (Antunes and Tesch 1997). Both A. anguilla and the temperate species of Conger would likely experience a period of cold water temperature during the last stages of their migration to coastal areas that may cause a much slower growth rate in the leptocephali or reduced metabolism in the glass eels that disrupts the formation of clearly visible daily increments. With a technique of otolith etching at a different angle though, Lee and Byun (1996) were able to discern faint increments, even though efforts using various other etching techniques could not (Correia et al. 2006).

A better understanding of otolith daily increments will help to resolve the question of whether or not A. anguilla leptocephali can actually cross the North Atlantic and recruit at ages of one year or less as suggested by increment counts (Lecomte-Finiger 1992, 1994), or if it takes considerably longer as discussed by McCleave et al. (1998). Modeling studies of larval transport of A. anguilla leptocephali suggest it would take about 2 years or less to cross the Atlantic basin using currents (Kettle and Haines 2006; Bonhommeau et al. 2009a,b). However, the possibility of these leptocephali using directional swimming behavior to speed up the migration cannot be excluded, since leptocephali are capable swimmers (Wuenschel and Able 2008). These types of questions highlight the need for more knowledge about the factors regulating growth and otolith deposition in leptocephali and glass eels. Further otolith studies are needed on a wide range of anguillid and marine eel leptocephali to document their growth rates and larval durations.
5-3. Zoogeography and diversity of leptocephali

Because leptocephali have a long larval duration, their patterns of distribution and abundance can be complex and determined by a variety of factors. Three key factors are likely to determine the spatial and temporal abundance of anguilliform leptocephali in each particular area of the world’s tropical and subtropical ocean regions. The first is the biodiversity of eels in the region and the distribution of available habitat for anguillid eels and for shallow water or continental slope marine eel species. For example, the biodiversity of leptocephali is very high in the central Indonesian Seas (Wouthuyzen et al. 2005), and to a lesser degree near the GBB of the northern Bahamas (Fig. 45; Miller and McCleave 2007), but is much lower in offshore areas of subtropical gyres (Fig. 4; Miller and McCleave 1994; Miller et al. 2006a).

A second factor that determines abundance is where the various species spawn in relation to ocean surface currents. Many species appear to spawn along outer continental shelves, such as in the East China Sea (Miller et al. 2002a; Minagawa et al. 2005; Minagawa and Miller 2005) and the southwest Sargasso Sea (Miller 1995; Miller and McCleave 2007), where densities and species richness of leptocephali are likely much higher than offshore where fewer species spawn. In some areas, strong currents pass by the edge of continental shelves where eels spawn, such as the western boundary currents of subtropical gyres (the Florida Current/Gulf Stream, the Kuroshio Current, and the East Australian Current). These currents and their recirculations likely have a major effect on the distributions of leptocephali in the western regions of these gyres. More precise information on spawning areas for each type of marine eel is needed, since there appears to be a range of distances of spawning migrations, as is discussed below.

The third factor in leptocephalus abundance is the seasonality of spawning of different species of eels. Temperate anguillid eels clearly have seasonal cycles of migration and offshore spawning that result in their leptocephali being abundant in the spawning areas and larval migration routes at certain times of year. Less is known about the spawning seasons of tropical anguillids that appear to spawn at various times of the year (Arai et al. 2001; Kuroki et al. 2006a), but may have seasonal cycles of downstream migration and spawning linked to tropical monsoon cycles (Wouthuyzen et al. 2009). Similarly little is known about seasonal patterns of spawning of most marine eels, but some information is available in a few areas of the world where collections have been made at multiple times of year, such as off South Africa (Castle 1968), the Sargasso Sea (Miller and McCleave 1994, 2007), Gulf of Mexico (Smith 1989a), Gulf of Guinea (Blache 1977), or at least during two times of the year near Japan (Miller et al. 2002a; Kimura et al. 2006; Minagawa et al. 2007) and in the Indonesian Seas (Miller et al. 2002b,c, 2004; Wouthuyzen et al. 2005). These studies have found that some taxa of marine eels show clear seasonal patterns of spawning, but others do not. In offshore areas the presence of leptocephali of at least some mesopelagic eels such as derichthyids and serrivomerids is seasonal (Castonguay and McCleave 1987b; Miller and McCleave 1994, 2007; Miller et al. 2006a; Miller and Tsukamoto unpubl. data). Much more research is needed to determine the spawning seasons of each type of marine eel and for tropical anguillids in order to gain a better understanding of the seasonal cycles of distribution and abundance of leptocephali in each region of the world.

In the Indo–Pacific and in other regions outside of the western North Atlantic, a major obstacle to progress in understanding the seasonal presence and geographic distribution patterns of leptocephali is the inability to identify most leptocephali to the species level. This is due to an almost complete absence of morphological features or non-overlapping meristic characters possessed by both the larval and adult forms of each species. This is especially true for highly diverse families, such as Muraenidae, which appear to have many leptocephali within the genus Gymnothorax that are very similar morphologically (Castle 1965a; Smith 1989b). In addition, the larvae of some muraenid eels have never been distinguished, possibly a result of different patterns of habitat use or larval behavior, as suggested by an extraordinarily large greenish metamorphosing leptocephalus, which was photographed recently as it was apparently recruiting to a shallow water coral reef area in southern Indonesia (Fig. 61; Miller et al. 2009b).

Due to the greater number of species of marine eels in the Indo–Pacific, the problem of leptocephalus identification represents a major challenge that will be greatly facilitated using
genetic techniques for matching larvae with adults of the same species (Miller and Tsukamoto 2006). DNA sequences have already been used to identify some congrid leptocephali (Ma et al. 2007, 2008a) or to report cryptic genetic lineages within widely distributed species, such as *Uroconger lepturus* (Ma et al. 2008b) or bonefishes (Colborn et al. 2001). As adult genetic sequences become available, greater use of genetic identification techniques can be made, like those being used to identify anguillid leptocephali (e.g. Aoyama et al. 1999, 2003, 2007) and proposed for fish larvae in general (Richardson et al. 2007; Teletchea 2009). For example, DNA barcoding techniques have recently been applied to many fish species in Australia (Ward et al. 2005). Real-time polymerase chain reaction (PCR) techniques can also be used to identify eggs and small leptocephali onboard research vessels to enable targeted sampling strategies during cruises (Watanabe et al. 2004; Minegishi et al. 2009). Genetic sequence analyses also have been used to suggest the possible phylogenetic relationship of the large leptocephali of *Thalassenchelys* (Fig. 62A) for which there are no known adults (Lopez et al. 2007); and similar studies can reveal new understanding about other unknown leptocephali such as the Type I of Smith (1979) (Fig. 62B). Using genetic sequencing techniques in conjunction with morphological descriptions of leptocephali, a better understanding of the biodiversity, zoogeography, and life histories of anguilliform eels will be possible in the Indo-Pacific and other regions of the world.

5-4. The leptocephalus larval strategy

A leptocephalus larva is the seemingly the only shared character of the ancient and diverse fishes of the Elopomorpha (Inoue et al. 2004), which may have existed for about 220–260 million years (Inoue et al. 2005), and the leptocephalus larval strategy may be a key component of...
the long-term success of these fishes. Leptocephali have several specific adaptations to live in the ocean surface layer. By being adapted to feed on particulate matter that can come from a variety of sources, eel larvae are potentially less vulnerable to changes in populations of individual marine species, such as zooplankton. This feeding strategy of using a low energy-content food source is possible because most of their bodies have only a small amount of respiring tissue, and contain a high proportion of metabolically inert GAG energy storage materials. Thus, they are able to grow greatly in length while accumulating materials that will later be converted into tissue during metamorphosis, yet their metabolic demand does not increase substantially as they grow larger (Pfeiler and Govoni 1993; Bishop and Torres 1999, 2001).

The unusual physiology and structure of leptocephali combines a high degree of transparency and a very mobile body form. Transparency is a common strategy in the ocean, with a wide range of invertebrate taxa having transparent species (Johnsen 2001), and leptocephali seem to be a wonderful example of how natural selection can produce an extremely transparent form even at large sizes. The obvious advantage of being transparent is to reduce the visibility of organisms to predators that use vision to locate their prey (Fuiman and Magurran 1994; Johnsen 2001, 2003). Leptocephali also have a variety of pigmentation patterns that likely serve to break up the outline of the body or body features, to make it difficult for visual predators to see them clearly. They may also use behavior to avoid predation by curling up and mimicking unpalatable gelatinous zooplankton (Fig. 55). Predator avoidance is clearly a key component of the leptocephalus larval strategy.

Their transparency and mobility makes it possible for leptocephali to grow to larger sizes than typical fish larvae, which are less transparent and would be more vulnerable to predation. Their large size at metamorphosis means that even after the shrinkage in length as the GAG material is converted into muscle and other tissues, the glass eels that recruit to their respective habitats are still relatively large compared to most other recruitment-stage fishes. This would

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**Fig. 62.** Photographs of a 65.0 mm *Thalassenchelys* leptocephalus collected in the western North Pacific (A), and a 63.3 mm Type I (Smith 1979) leptocephalus from the western South Pacific (B), whose adult forms are unknown.
likely reduce the range of predators as the young eels enter their juvenile growth habitats, as has been indicated for other types of fish larvae (Miller et al. 1988).

Another aspect of the leptocephalus larval strategy is that it appears to be adapted for using the relatively predator-free open ocean for feeding and growth. The threat of predation is likely much lower offshore because productivity is lower and there is typically less food to support large predator populations. So by feeding on a ubiquitous food source such as particulate material, eels are able to use the open ocean for an extended period of larval development to reach large sizes before recruitment.

There are variations in the geographic patterns of how leptocephali use the open ocean, though, because the distributions of various taxa are quite different. Temperate and some tropical anguillid larvae have a strategy of using westward flowing currents to transport them back to their recruitment areas while they feed and grow to their maximum larval size (Tsukamoto et al. 2002; Kuroki et al. 2008a, 2009a,b). The alternative strategy of local spawning and larval retention near their adult growth habitats would probably not be successful in temperate regions, due to the accumulations of large numbers of leptocephali along the continental margins where there are many predators and colder temperatures. A different strategy used by some marine eels appears to be based on using the recirculation patterns of the western regions of subtropical gyres, as in a population of Ariosoma balearicum that lives adjacent to the Sargasso Sea (Miller 2002a) and Ariosoma major that lives along the margin of the western North Pacific (Miller et al. unpl. manuscript). A short migration offshore to spawn on the eastern side of the western boundary current of each subtropical gyre, appears to result in the larvae of these Ariosoma species using the entire western regions of each gyre as larval development areas (Miller 2002a), and not just the low latitude parts of the gyres like in anguillids. A similar strategy, but at a smaller scale, is used by tropical anguillids that migrate short distances offshore to spawn over deep water in regions where their leptocephali will remain near the species range and can recruit back to that same general area. Species such as A. borneensis and A. celebesensis in the central Indonesian Seas are examples of this (Aoyama et al. 2003; Kuroki et al. 2006a). The other apparent strategy is to spawn over or near the edge of the shelf so that at least a portion of the larvae will remain near their adult habitats. Most muraenids, ophichthids, and garden eels appear to use this spawning and larval distribution strategy.

There may be variations in the larval dispersal patterns resulting from this local spawning pattern, however, that could be due to different behavioral tactics used by some leptocephali. The distinctly lower offshore abundances of garden eel leptocephali and of most ophichthid species suggest these taxa of leptocephali may use swimming behavior or some other mechanism to stay near the continental shelf or around islands where they were born. There is increasing evidence that larval swimming behavior and self-recruitment are important for many coral reef fishes (see Leis 2002, 2006; Leis and McCormick 2002; Leis and Carson-Ewart 2003), so it is likely important for some marine eels as well. Olfactory cues or the sound of coral reefs have been investigated as possible cues for fish larvae to find recruitment habitats when they reach settlement stage (Atema et al. 2002; Leis and Lockett 2005). The strong swimming ability of leptocephali in conjunction with their large size could enable them to swim back to the shelf even if they were transported offshore during their early larval stage. Future studies on the fine-scale distribution of leptocephali in relation to the shelf break and ocean currents and on the swimming ability of different species will help to reveal which species appear to use larval retention strategies and which are more adapted for dispersal.

5-5. Oceanic changes and leptocephalus recruitment

The leptocephalus strategy appears to be well adapted to life in the ocean surface layer, but there are increasing indications that the population dynamics of some eel species may be linked to changes in the ocean that affect their larvae. Declines of northern temperate anguillids have been hypothesized to be related at least in part to changes in the ocean (Castonguay et al. 1994; Knights 2003). Studies testing for correlations between recruitment and various physical and biological parameters in the ocean suggest that the leptocephalus stage may be vulnerable to
changes in the ocean resulting from fluctuations of the ocean–atmosphere system (see Miller et al. 2009a for a recent review). Changes in spawning location or alteration of currents could affect recruitment by preventing successful larval migration back to their recruitment areas (Kimura et al. 2001; Kim and Tsukamoto, 2006; Friedland et al. 2007; Kim et al. 2007; Tsukamoto 2009; Zenimoto et al. 2009), but these larval transport factors are not directly related to the biology of leptocephali. Changes in productivity in the surface layer, however, could affect larval survival by reducing feeding success of leptocephali (Knights 2003; Friedland et al., 2007; Bonhommeau et al. 2008a,b). In particular, several recent studies have found correlations between recruitment and productivity-related factors. Correlations have been found between the North Atlantic Oscillation index and recruitment of Anguilla to the Netherlands (Knights 2003; Friedland et al. 2007) or other parts of Europe (Kettle et al. 2008). The North Atlantic Oscillation may be related to a variety of changes in the North Atlantic, so an effect on productivity or community structure that could impact the feeding success of leptocephali may be the mechanism behind these correlations. Other studies have found direct correlations between sea surface temperature or productivity fluctuations and recruitment in both of the northern hemisphere subtropical gyres (Bonhommeau et al. 2008a,b). Increasing ocean temperatures tend to reduce productivity, so sea surface temperature increases in the global ocean (e.g. Levitus et al. 2000) have the potential to reduce productivity, which could affect the feeding success of leptocephali. Not enough is known about the feeding ecology of leptocephali to know at which stage these effects could occur. It may be during the critical first feeding period after yolk absorption when the young larvae may be most vulnerable to starvation. These factors highlight the need for a better understanding of leptocephalus ecology in the ocean, not only to help conserve the economically important anguillids and conger eels, but also marine eels whose role in marine ecosystems is still unknown.

5-6. Ecological significance of leptocephali in the surface layer

Knowledge about leptocephali is perhaps a unique story in the history of marine biology, since there have been extensive surveys for fishes, fish larvae and zooplankton in most regions of the world’s oceans, but the sampling gear in the vast majority of cases has been unable to collect many leptocephali. The primary problem is that leptocephali are able to avoid the standard plankton nets that are adequate to collect representative samples of most fish larvae and zooplankton, such as the 1-m plankton net, twin bongo nets, or the 1-m MOCNESS (see Wiebe and Benefield 2003 for a review of plankton net technology). The visual system of leptocephali during the day or their mechanosensory system at night in combination with the potential for bioluminescent organisms to make nets visible at night (Ross et al. 2007), probably give leptocephali the chance to avoid plankton nets in most circumstances, in the same ways that fish larvae in general are adapted to avoid predators (Fuiman and Magurran 1994). Leptocephali, however, have the added advantage of being able to evade the net by either swimming forwards or backwards, or being able to quickly change swimming directions due to their flexible body. Their larger size is also likely a major factor in their net avoidance abilities. In addition, many of the larger nets deployed to catch pelagic marine fishes had mesh sizes that were too large, or the fishing effort was too deep. These factors seemingly have resulted in underestimates of the abundance of leptocephali in tropical and subtropical regions.

This underestimation would not be particularly important if leptocephali were zooplanktivores, like most other fish larvae. However, the existence of large numbers of fish larvae that feed on particulate matter and reach large sizes, may have greater implications for understanding the carbon cycle of the ocean than simply an underestimation of grazing on zooplankton by fish larvae. There have been extensive efforts to understand the dynamic fluxes of particulate material (technically referred to as particulate organic carbon: POC) in the surface layer of the ocean, since this is a critical factor in understanding the carbon cycle in the ocean (e.g. Hebel and Karl 2001; Pilskaln et al. 2005; Honjo et al. 2008; Lee et al. 2009). Many studies have used sediment traps to determine how much POC sinks out of the surface layer where
primary production occurs and POC is produced by various biological processes (Buesseler et al. 2007; Honjo et al. 2008). One recurring theme in studies trying to model the dynamics of POC is that the estimated amount of POC produced but not consumed by animals in the surface layer typically is much greater than what is actually collected in sediment traps. Siegel et al. (2008) summarized the general results of experiments to assess the production of sinking particles and their vertical flux during major biogeochemical research programs by stating: “These experiments nearly always resulted in a poor correspondence between determinations of primary production rates measured in the euphotic zone and the sinking flux at depth. This raises the question why are the observations between primary production and export flux often poorly related?”

Various hypotheses have been proposed to account for this mismatch, such as material escaping from the traps due to hydrodynamic factors and POC being broken up by the swimming activities of zooplankton before reaching the traps or even inside the traps (Buesseler et al. 2007; Honjo et al. 2008). However, none of these studies considered the fact that there are hundreds of species leptocephali found everywhere in the tropical and subtropical oceans, that reach large sizes and appear to be feeding on POC year-round. A recent modeling study narrowed down the likely requirement to make models of particle flux match the observed data. Stemmann et al. (2004) stated that to stop the high flux of large particles to deeper layers as appears to be happening, “… requires the mesozooplankton to feed preferentially on large settling particles using remote detection, totally ingesting the particles.” Although they pointed out that this does not match the capabilities of the zooplankton that were considered to be the grazers of particulate matter, this description corresponds well with the likely feeding behavior of leptocephali.

It seems possible that due to the indications that leptocephali are widely distributed and often quite abundant in many regions, that they may have at least some level of impact on the cycling of POC in the ocean surface layer that needs to be considered in models of the ocean carbon cycle. The high abundances of leptocephali along continental shelves (Miller et al. 2002a; Miller and McCleave 2007), in anguillid or mesopelagic eel spawning areas (Castonguay and McCleave 1987b; Kleckner and McCleave 1988; Tsukamoto 1992; Miller and McCleave 1994; Wippelhauser et al. 1996; Miller et al. 2006a), in areas such as convergence zones associated with fronts (Miller and McCleave 1994), of species such as Ariosoma in some regions (Miller 2002b; Miller et al. 2006b; Miller and McCleave 2007), and the relative abundance of leptocephali among the fish larvae recruiting to shallow tropical habitats (e.g. Shenker et al. 1993; McIlwain 2003), argue for the likelihood that leptocephali may be important components of many marine ecosystems worldwide. This is especially true if their abundances are underestimated by the large trawls presently used to collect them due to some degree of net avoidance. Further data on the abundance of anguilliform leptocephali will be obtained in ongoing research on samples from the northwest Coral Sea made with a 70 m² mouth opening midwater trawl (see Dennis et al. 2001), which indicate that large numbers of leptocephali were present in that region within the upper 200 m during both day and night (MJ Miller and JM Leis unpubl. data).

The various types of information that are presently available about leptocephali, suggest that more knowledge about all aspects of these transparent larvae is needed to obtain a better understanding of their role in the dynamics of the ocean. Leptocephali clearly transport carbon and other elements from the ocean surface layer to many different ecosystems, which seemingly has not been discussed previously in the literature, except perhaps for anguillids, which enter freshwater. For example, the larvae of the Cyematidae, Eurypharyngidae, Derichthyidae, Nemichthyidae, and Serrivomeridae recruit to the mesopelagic layer and deeper waters. Larvae of the Synaphobranchidae recruit to deep benthic habitats where their juveniles and adults are important components of the deep-sea fauna. Nettastomatid and a variety of species of larvae of other families recruit to continental slope habitats. Carbon is also transported in the form of metamorphosing leptocephali or glass eels to the shallow water regions of continental shelves or around islands worldwide. Presently, these components of the global ocean carbon cycle and the role of leptocephali and their recruiting larvae in marine communities in general are completely
unquantified, and seemingly unrecognized for the most part. However, Honjo et al. (2008) pointed out the need to gain a better understanding of the biological influences on carbon transport from organisms, such as vertically migrating zooplankton, so research efforts are also needed to evaluate the ecological importance of eels and leptocephali in the many marine ecosystems in which they live worldwide.

5-7. Future research perspectives

This review points out some of the many questions that remain to be answered about these remarkable fish larvae. Leptocephali are present in the surface layer of the ocean all over the world, except at very high latitudes, but they have been rarely seen or caught compared to other fish larvae or zooplankton, so they represent a new research frontier in helping to increase understanding of marine ecosystems and regional biodiversity (Miller and Tsukamoto 2006). Adult eels whose larvae can be collected using large trawls fished at night are themselves even harder to study due to their cryptic behaviors, so studies on leptocephali can provide useful information about the biodiversity of eels and the potential variations in their life histories.

Studies on the biology and behavior of leptocephali are quite limited, but may be able to increase using recently developed techniques to spawn and rear leptocephali in the laboratory (Tanaka et al. 2001, 2003). This could lead to more experimental studies related to their ecology (Tsukamoto et al. 2009; Yamada et al. 2009) and physiology (Ozaki et al. 2000, 2006b). Leptocephali can be collected and held in aquaria as they recruit to coastal areas, but they typically metamorphose rapidly, thus providing a limited period of time for research compared to artificially reared leptocephali.

Much of the biochemical and physiological research on leptocephali has been done on bonefishes (Pfeiler 1999), so more studies on a wider range of anguilliform species are needed. These will build on previous research (Hulet and Robins 1989; Donnelly et al. 1995; Pfeiler and Govoni 1993; Bishop and Torres 1999, 2001; Bishop et al. 2000), which has found that leptocephali are remarkably different physiologically than other fish larvae. These types of studies along with a greater understanding of the distributional ecology of leptocephali in relation to hydrographic features and ocean currents will be essential for knowing how eels and their larvae fit into the ecology of the oceans. With changing ocean-atmosphere conditions causing a warming of the worlds oceans (Levitus et al. 2000), there is a need to understand all components of marine ecosystems, especially those, such as leptocephali, that appear to be abundant, but whose ecological role in the ocean is poorly understood. Future research will likely reveal many details about the mysterious biology of leptocephali that have remained hidden in the ocean, where these remarkable glass-like larvae have always been swimming just outside of our view.

Acknowledgements

The efforts of many people made this review possible, and I especially thank Prof. Katsumi Tsukamoto for providing the chance to examine and photograph freshly caught leptocephali in the western Pacific, Indian Ocean, and Indonesian Seas, and for many years of productive research collaboration on leptocephali. I also thank Prof. James D. McCleave for starting my interest in leptocephali and for collaboration on leptocephali from his Sargasso Sea collections, Jim Craddock and Karsten Hartel for providing access to the WHOI leptocephali collections, and Larry Madin for providing the chance to collect leptocephali with the MOCNESS-10 and to film the live chlopsid leptocephalus. Tae Won Lee, Mari Kuroki, and Tao Ma conducted much of the otolith research overviewed here, and the pioneering leptocephalus research of Tsuguo Otake and Noritaka Mochioka are also acknowledged. Jun Aoyama, Satoshi Ishikawa, Shun Watanabe, Takaomi Arai, Akira Shinoda, Yobuo Kimura, Gen Minagawa, Yuki Minegishi, Tatsuki Yoshinaga, Yuzuru Suzuki, Atsushi Fukui, Machiko Oya and many others also have assisted with research efforts on leptocephali over the years and have sorted through many plankton samples to provide the chance to study these remarkable transparent larvae. Sam Wouthuyzen, Hagi Yulia Sugeha, and Ono Kurnaen Sumadhihara of LIPI, Indonesia helped make the collaborative sampling surveys in the Indonesian Seas a success. The captains and crew of the research vessels Hakuho Maru, Tansei Maru, and Baruna Jaya VII also helped our sampling efforts during many cruises. The scientists at the IRAGO Institute have conducted a new generation of ecologically related research on artificially cultured leptocephali, and I especially thank Yoshiaki Yamada for providing photographs showing the transparency of
leptocephali. Jerry Powel kindly provided the photographs of the large greenish leptocephalus, and Matthew D’Avella provided the interesting video of the ophichthid leptocephalus. I also thank David G. Smith and the late Peter Castle who were some of the pioneers of leptocephalus identification, and their lasting contributions to this field will continue to be useful as research on leptocephali progresses around the world in the future. David G. Smith and an anonymous reviewer provided suggestions that significantly improved the paper.

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*Aqua-BioScience Monographs* VOL. 2 NO. 4 2009


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