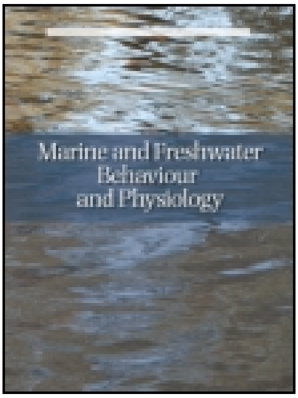

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Evidence of mimicry of gelatinous zooplankton by anguilliform leptocephali for predator avoidance

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Leptocephali are the transparent larvae of eels and their relatives, whose laterally compressed bodies contain gelatinous material. Although abundant throughout the world's oceans, leptocephali are rarely observed in their natural environment. Video recordings of leptocephali in surface waters at night at Osprey Reef in the Coral Sea revealed that 6 of 21 larvae filmed displayed a distinct shape-change behavior of curling up into fully or partially coiled shapes. Their transparency and gelatinous consistency results in the coiled leptocephali resembling the typical body shapes and consistency of gelatinous zooplankton such as jellyfish, ctenophores, siphonophores, and salps. Due to either stinging defenses or low food value, many fishes avoid consuming gelatinous zooplankton, so the curling behavior in response to threatening situations may result in mimicry of these organisms. This could provide leptocephali with higher survival rates compared with flight from pelagic predators that are close enough to detect them.

Keywords: eel; anguilliform; leptocephalus larvae; mimicry; gelatinous zooplankton; predator avoidance

Introduction

Leptocephali are the transparent larvae of anguilliform eels and their close relatives that grow to large sizes in the surface layer of the ocean (Böhlke 1989; Miller and Tsukamoto 2004; Miller 2009). They are widely distributed at tropical and subtropical latitudes and appear to be well adapted for predator avoidance due to their transparency and ability to swim both forwards and backwards (Miller 2009). Their transparency is a result of their laterally compressed bodies being almost exclusively filled with soft jelly-like material comprised mostly of water and energy-storing glycosaminoglycan compounds, which are later converted into tissues when they metamorphose into young eels (Pfeiler 1999; Bishop et al. 2000). There are only a few reports of observations of leptocephali in the ocean (Miller et al. 2009, 2010) or of leptocephali being eaten by pelagic predators (Miller 2009; Pagès and Madin 2010), so very little is known about their natural behaviors.

Leptocephali and other fishes and invertebrates migrate vertically to greater depths during the day to avoid predators (Castonguay and McCleave 1987; Lampert 1989), but other free-swimming marine animals use diverse mechanisms to reduce their visibility

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at shallow depths during the day. These include both morphological and behavioral adaptations (Ruxton et al. 2004) such as transparency (Johnsen 2001), camouflage coloration (Hanlon et al. 2009), or counter-illumination (Johnsen 2003; Jones and Nishiguchi 2004). Gelatinous zooplankton are a major group of marine organisms with many species that are highly transparent (Johnsen and Widder 1998). A smaller number of marine animals have evolved ways to mimic other organisms that predators avoid because they are dangerous, unpalatable or of low food value (Robison 1999; Norman et al. 2001; Randall 2005; Johnson et al. 2009). This is referred to as Batesian Mimicry when the mimic (harmless and palatable) species impersonates a dangerous or unpalatable model (Ruxton et al. 2004; Cheney 2010).

Mimicry in the ocean has been reported for invertebrate and vertebrate species that live in both coastal and pelagic marine environments. Many marine fish species use mimicry, including species that impersonate cleaner fish and eel species with black and white stripes so that they resemble poisonous sea snakes (Moland et al. 2005; Randall 2005). Some fish larvae, including one species of leptocephalus, have remarkable ornamental palps or long streamers, and it has been proposed that these mimic gelatinous zooplankton such as siphonophores with their long tentacles and stinging cells (Moser 1981; Moser and Charter 1996; Johnson et al. 2009). Behavioral mechanisms are also used by some species. Examples include changes in body shape or coloration such as octopus species that appear to mimic sea snakes, flatfish, or lionfish (Norman et al. 2001; Hanlon et al. 2010).

In deeper ocean regions where visibility is poor, some elongated mesopelagic fishes and invertebrates appear to mimic gelatinous zooplankton by curling up or bending their bodies when startled (Robison 1999). This change results in a round silhouette like that of an organism such as a jellyfish. Such changes in body shape may be a behavioral adaptation to deter some predators because relatively few fish species prey on gelatinous zooplankton (Purcell and Arai 2001; Arai 2005). The prevalence of this type of shape-change behavior in several fish species, annelids, and chaetognaths (Robison 1999) suggests that it provides an adaptive advantage for reducing predation.

This study reports that leptocephali have shape-change behaviors similar to those observed in other marine animals. Underwater video observations of leptocephali at Osprey Reef in the Coral Sea show that when threatened, some leptocephali perform a dynamic behavior by curling up their bodies with the head in the center. This behavior results in them resembling unpalatable gelatinous zooplankton. Because many fishes in tropical and subtropical oceanic waters, where leptocephali are abundant, probably avoid eating gelatinous zooplankton, we hypothesize that this behavior acts as a form of Batesian Mimicry that reduces the chance of predation.

Methods and materials

Observations of leptocephali were obtained during video recordings of pelagic marine organisms made by two divers at Osprey Reef (13°51′N, 146°33′E), which is an isolated coral atoll in the Coral Sea about 125 km offshore from the Great Barrier Reef of northeastern Australia (Figure 1). The divers (J. Finn and M. Norman) were suspended on ropes from the boat at depths of about 2–15 m, over water ~450 m deep. The objective was to take close-up video records of small fishes and invertebrates over deep water adjacent to the inlet channel of Osprey Reef during the crepuscular period just after sunset. The organisms were filmed as they drifted past the divers in the currents near the inlet channel or as the divers approached them directly. Video sequences of

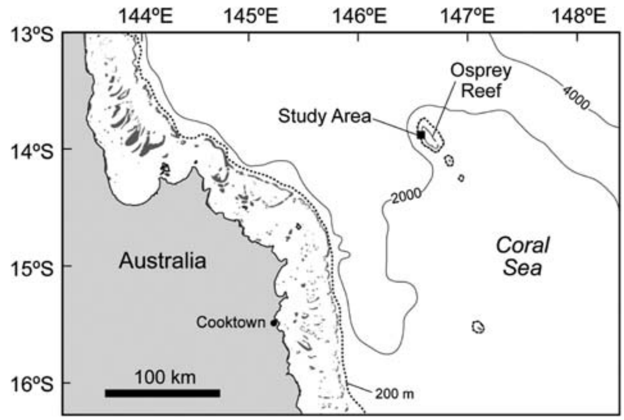

Figure 1. The location of Osprey Reef in the Coral Sea and the position of the study site on the northwest side of the atoll. This oceanic atoll is offshore of the Great Barrier Reef that extends along northeast Australia (map modified from imagery from the Great Barrier Reef Marine Park Authority of the Australian Government).

Table 1. List of the times of observations and types of behavior that was recorded for the leptocephali of each family that were filmed at Osprey Reef.

Larva no.	Date	Time	Family	Behavior	Duration (s)
L1	21 September 1999	20:12	Muraenidae	Swim	8
L2	22 September 1999	19:06	Congridae?	Swim	21
L3	22 September 1999	19:14	Muraenidae	Coil	82
L4	17 September 2000	19:34	Chlopsidae	Coil	100
L5	21 September 2000	20:20	Muraenidae	Swim	8
L6	21 September 2000	20:21	Muraenidae	Swim	159
L7	6 August 2001	19:02	Muraenidae	Coil	31
L8	6 August 2001	19:05	Muraenidae	Swim	5
L9	6 August 2001	19:21	Muraenidae?	Swim	6
L10	6 August 2001	19:29	Muraenidae?	Swim	6
L11	6 August 2001	19:29	Muraen./Congridae	Swim	1
L12	6 August 2001	19:29	Nettastomatidae	Swim	8
L13	7 August 2001	19:16	Ophichthidae	Swim	13
L14	7 August 2001	19:27	Muraenidae	Swim	36
L15	7 August 2001	19:30	Congridae	Coil	47
L16	13 August 2001	19:40	Muraenidae	Swim	64
L17	14 August 2001	18:50	Congridae	Coil	58
L18	14 August 2001	18:52	Muraenidae	Coil	56
L19	14 August 2001	19:14	Muraenidae	Swim	4
L20	8 October 2001	20:33	Muraenidae	Swim	8
L21	9 October 2001	20:30	Muraenidae	Swim	53

swimming fish larvae, crustaceans, gelatinous zooplankton, and leptocephali were recorded during these dives. The video recordings of leptocephali were made on 10 different nights between August and October of 1999, 2000, and 2001 (Table 1). The observations were made with Sony DSR-PD100 DVCAM and DCR-VX1000 MiniDV digital video cameras in underwater housings and Alpha 7000 lighting systems (dual 150 watt halogen lights).

Frame captures of the leptocephali and gelatinous zooplankton were made from recordings at the same site. Leptocephali were identified to Family or Genus level based on their head and body shapes, gut structures, and degree of tail roundness (Böhlke 1989; Miller and Tsukamoto 2004). Almost all the leptocephali could be distinguished at the family level (Table 1), or in some cases, to the genus level; but, the species identities of most leptocephali in the Indo-Pacific are not known (Miller and Tsukamoto 2004).

Results

Leptocephali were observed in underwater video recordings made at Osprey Reef during five different time periods (21–22 September 1999, 17–21 September 2000, 6–7 and 13–14 August 2001, and 8–9 October 2001) over three years (Table 1). A total of 21 leptocephali were recorded, with the largest numbers being seen in early- and mid-August of 2001 ($n = 6$ and $n = 4$, respectively). Only two or three individuals were observed during the other time periods in different months or years. All the leptocephali were observed during the 1.5-h period after sunset (19:02–20:33). The 21 leptocephali that were filmed appeared to be roughly 40–60 mm long, except for two (larva numbers L17 and L3), which appeared to be >100 mm long (Table 1). Nine of the leptocephali were swimming rapidly and were seen for a period of less than 10 s. Analyses of the underwater video recordings showed that the larvae could be grouped into at least 10

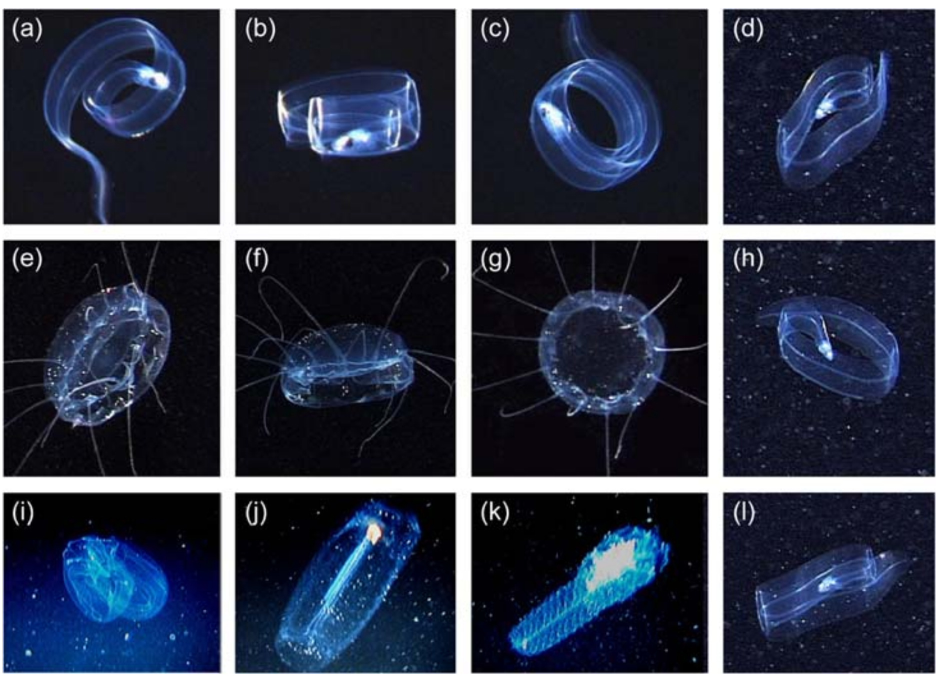

Figure 2. Images of (a–c) a *Conger* leptocephalus (L15) that changed its shape from partially to fully coiled, (d,h,l) a muraenid leptocephalus (L18) that formed a more flattened coil, (e–g) a jellyfish, apparently order Narcomedusae, (i) a lobate ctenophore, *Bolinopsis*, order Lobata, (j) a salp, *Salpa*, order Salpida, and (k) a siphonophore, *Forskalia*, order Siphonophora, that were all seen at Osprey Reef.

species from the families Chlopsidae, Congridae, Muraenidae, Ophichthidae, and Nettastomatidae.

Of the 21 leptocephali that were recorded, six stopped swimming when they detected the diver and his lights and showed various forms of behavioral shape change by curling their bodies into full or partial coils (Table 1). At least five different species of three families (Chlopsidae, Congridae, and Muraenidae) showed these behaviors. The shapes formed by the leptocephali ranged from fully formed rounded coils to flattened coils, or partial coils with much of the body extending outward, but the head was always inside the coil (Figures 2 and 3). Another common feature was that either the head or tail regions continued to move when the larvae were curling. Several of the larvae switched out of the coiled shape, swam for a short distance, and then reformed a coil before eventually swimming away from the diver.

Four of the leptocephali formed fully rounded or more flattened coils. The most distinct coil shape was made by the *Conger* leptocephalus (family Congridae) (L15; Table 1). It formed a tightly coiled round shape (Figure 2, panels a, b, and c) that it maintained for 30 s before swimming away (Video 1 – link at end of text). The chlopsid leptocephalus (L4) showed a completely coiled shape, but it also formed a partial coil with its tail region extending outward (Figure 3(a)). After forming these shapes, it vigorously swam away (Video 1). The most common types of leptocephali observed were muraenid leptocephali and two showed distinct curling behavior. Both muraenid larvae L7 (not shown) and L18 (Figure 2, panels d, h, and l) formed flat coils that were oval-shaped. They also made loose coils between periods of forming the flattened coils (Video 2 – link at end of text).

There were two leptocephali that showed shape-change behaviors, but did not form completely coiled shapes. A more elongate congrid leptocephalus of the genus *Ariosoma* (family Congridae) (L17) never formed a full coil with its whole body

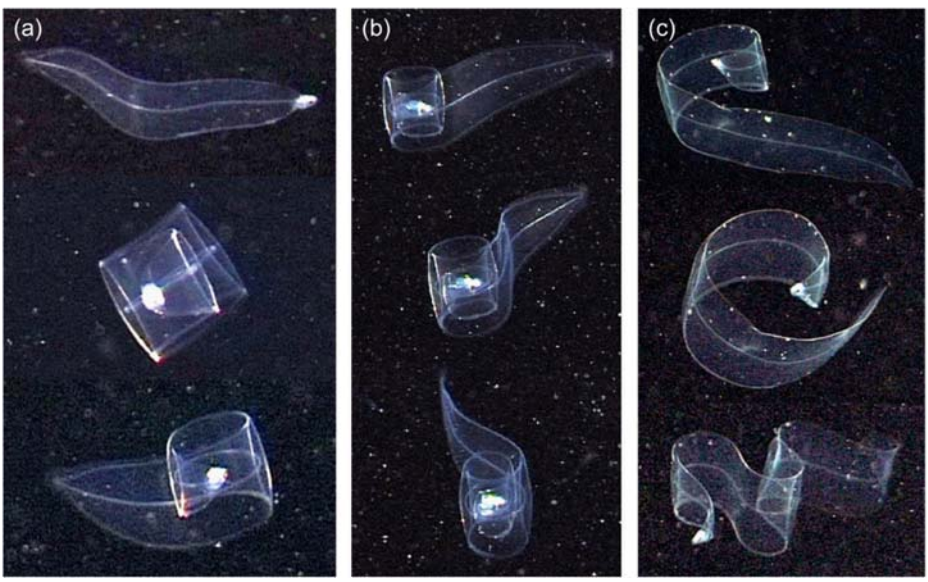

Figure 3. Images of (a) a chlopsid leptocephalus (L4) that was observed both curling up and swimming, (b) a congrid leptocephalus of the genus *Ariosoma* (L17) that formed only a partial coil with its tail extending outward, and (c) a large deep-bodied muraenid leptocephalus that curled only partially, but also showed slow swimming using a very sinuous body shape.

(Figure 3(b)). Instead, it formed a very tight coil with its anterior region, while the posterior region extended outward (Video 3 – link at end of text). The other large leptocephalus was an unusual deep-bodied muraenid (L3) that curled up to a lesser degree (Figure 3(c)). It formed a partial coil, or a large open circle. This leptocephalus also showed a different swimming technique, using deep body curves with anguilliform swimming (Video 3).

Discussion

Shape-change behavior was observed in at least five different species of congrid, muraenid, and chlopsid leptocephali during four different time periods at Osprey Reef in the Coral Sea. The shapes they formed included the fully symmetrical round coils made by the *Conger* and chlopsid leptocephali, a more flattened and elongated coil made by two muraenids, a partial coil with about half the body extending out from the coiled part in the *Ariosoma* larva, and a partial or very loose full coil made by the large deep-bodied muraenid. In all cases, the leptocephali held these shapes for some period of time even as they moved past the diver in the current. All the leptocephali also continued to move their head or tail regions, which suggest that this is not a form of resting behavior. Two previous observations indicate that this behavior is not limited to the species observed at Osprey Reef. Several taxa of leptocephali were observed performing shape-change behaviors in response to an encounter with a submersible vehicle diving along the slope of the Galapagos Islands (J.E. McCosker, personal communication) and an undamaged ocean-caught chlopsid leptocephalus was observed making a fully coiled shape during observation in a shipboard aquarium (Miller 2009).

These observations and the frequency of occurrence of curling behavior among the leptocephali that encountered divers at Osprey Reef suggest that this shape-change behavior could be an evolved response to threats by potential predators that approach sufficiently close to render successful swimming escape by the larvae unlikely. The detection of the divers and their lights by the larvae at Osprey Reef appeared to trigger the behavior, because the leptocephali were not curled when they were first seen. If a leptocephalus larva observes a predator or unfamiliar object at a sufficient distance, swimming away would be the best defense, as was seen for 71% of the larvae filmed at Osprey Reef. However, it is possible that when a predator is very close, many leptocephali may curl up into the various shapes seen in this study.

In natural lighting conditions, the shapes formed by the coiled leptocephali, in combination with their transparent and gelatinous consistency, would likely make them appear similar to the visual profiles of various gelatinous zooplankton. Several species of jellyfish, ctenophores, siphonophores, and salps were observed in one small area at Osprey Reef. These have body shapes similar to the coiled shapes made by the leptocephali (Figure 2). The visual profiles of the *Conger* leptocephalus seen from different angles included an oval that is similar to the side view of a jellyfish, or a circle that is similar to a ventral view. The more flattened coils of the muraenid leptocephali made silhouettes similar to those of salps and siphonophores, and the rounded shapes were similar to those of ctenophores or other gelatinous zooplankton.

Gelatinous zooplankton are widely distributed in the ocean surface layer (Grice and Hart 1962; Harbison et al. 1978) in the tropical and subtropical regions where leptocephali are abundant. They may be even more abundant than estimates made using plankton nets due to the breakdown of the soft tissues of some species inside plankton nets (Remsen et al. 2004; Robison 2004). While most fishes present where leptocephali are distributed probably do not feed on gelatinous zooplankton, a few species such as butterfishes (Stromateidae), lumpfishes (Cyclopteridae), spiny dogfish (*Squalus acanthias*, Squalidae), chum salmon (*Oncorynchus keta*, Salmonidae), and some slickheads (Alepocephalidae) consistently include gelatinous zooplankton in their diets (Purcell and Arai 2001; Arai 2005). These predators typically have a longer digestive tract or larger stomach than other fishes and are more frequently found in temperate regions where gelatinous zooplankton are most abundant, or at depths where there are few other types of prey (Purcell and Arai 2001; Arai 2005). This suggests that in the habitats typically used by leptocephali, gelatinous zooplankton may be common, but there may be few predators that specialize in eating them. We can, therefore, postulate that the shape-change behavior of leptocephali has been established, through natural selection, as a standard response to make leptocephali resemble unpalatable gelatinous zooplankton that most fish avoid eating.

Curling behavior by leptocephali could reduce predation by the majority of fishes that do not typically feed on gelatinous zooplankton because the predators more frequently encounter the slower swimming models (gelatinous zooplankton) than the mobile mimics (harmless and palatable leptocephali). Most predators develop search images of their prey as well as images of the organisms they learn to avoid (Ruxton et al. 2004) and may quickly learn to avoid the models before they encounter many mimics. If the shape-change behavior of leptocephali makes them resemble gelatinous zooplankton and this causes most predators to avoid eating them, then this appears to be an example of Batesian Mimicry in which the mimic species impersonates a dangerous or unpalatable model (Ruxton et al. 2004; Cheney 2010).

Because leptocephali are so transparent, shape-change behavior may reduce predation on them under a variety of conditions. It may be especially effective when leptocephali encounter predators under low-light conditions at greater depths. Some larger leptocephali show vertical migration behavior to depths of 100–250 m during the day (Castonguay and McCleave 1987), and the lower light levels at these depths might make it difficult to distinguish a coiled leptocephalus from spherical or elongated gelatinous zooplankton. Curling behavior may still be important even in very low light, because many mesopelagic fishes see very well in dim light (Warrant and Locket 2004). Even in well-lit conditions, their transparency would result in coiled leptocephali appearing similar to the consistency and shapes of transparent zooplankton (Johnsen and Widder 1998). This behavioral response could also be effective for leptocephali that do not migrate vertically during the day, because even extreme transparency can fail to provide concealment during conditions of bright light near the surface or certain angles of sunlight (Johnsen 2003).

There is one historical observation that leptocephali curling occurs under natural conditions. Grassi (1896) reported that, based on their stomach contents, ocean sunfish (*Mola mola*) were eating many European eel, *Anguilla anguilla*, leptocephali in the Straits of Messina. This is significant because the ocean sunfish is the world's largest bony fish and is one of the few large pelagic fishes that feeds on jellyfish (Pope et al. 2010). Leptocephali are competent swimmers (Wuenschel and Able 2008), so it seems unlikely that large ocean sunfish, even if they are powerful sustained swimmers (Watanabe and Sato 2008), could capture many highly mobile leptocephali unless the larvae that encountered the sunfish had stopped and curled up, allowing the sunfish to eat them.

Robison (1999) observed shape-change behavior by other species hundreds of times when using underwater vehicles in Monterey Bay and other areas. Elongate pelagic organisms such as four fish species, annelids, and chaetognaths showed a similar curling shape change in response to the potential threat of the vehicles at depths between 100 and 1000 m (Robison 1999). The curling behavior was common during the day, but only at depths where light levels were low. One species of eelpout, *Melanostigma pammela* (Zoarcidae), curled up 38% of the 509 times they were observed during multiple dives, and they typically maintained their coiled shapes for several minutes with no apparent movements. Robison (1999) proposed that in the low-light conditions at those greater depths, the curling behavior made the animals appear to be gelatinous zooplankton. The prevalence of that behavior in the underwater vehicle observations together with those of the present study suggest that mimicking of round-shaped gelatinous zooplankton by elongate species may be a successful antipredator strategy in low-light conditions.

This study suggests that leptocephali frequently perform shape-change behaviors, but further behavioral observations and experiments will be needed to confirm the hypothesis that this behavior functions as a form of Batesian Mimicry of gelatinous zooplankton.

Videos

The following three videos were available at the links below at time of publication. If at some future time the links are no longer active, the primary source videos are available from the Australian Museum research data storage system. Contact the Australian Museum: http://australianmuseum.net.au/Fishes

Video 1: Recordings at Osprey Reef of the curling behavior of a *Conger* leptocephalus (L15) that formed a tightly coiled round shape before swimming away, but then started to curl up again briefly; and the curling behavior of a chlopsid leptocephalus (L4) that showed a completely coiled shape and then also formed a partial coil part of the time with its tail region extending out from the coil.

http://www.youtube.com/watch?v=ok8MW4pdPXI

Video 2: Recordings at Osprey Reef of the curling behavior of two muraenid leptocephali (L7 and L18) that formed much flatter oval-shaped coils and also sometimes made less tightly coiled shapes. The L18 larva attempted to hold the tightly coiled shape even while being moved past the diver by water currents.

http://www.youtube.com/watch?v=UzHMghNIbIs

Video 3: Recordings at Osprey Reef of the curling behavior of a larger-sized more elongated congrid leptocephalus of the genus Ariosoma (L17) that never formed a fully coiled shape with its whole body, but formed a very tight coil using the anterior part of its body and maintained the posterior part of its body extending out from the coil; and the curling behavior of a large muraenid leptocephalus (L3) that had an unusually deep body and curled up to a lesser degree by forming a partial coil with the anterior part of its body or a large open circle using its whole body.

http://www.youtube.com/watch?v=1WsHQZ3O2Wg

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