

Short Note

Observations of gut contents of leptocephali in the North Equatorial Current and Tomini Bay, Indonesia

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Abstract—Visible objects in the gut contents of 13 leptocephali of 11 species and 8 families of eels were observed using photographs of daytime-caught larvae in two different types of marine habitats: the open ocean (North Equatorial Current) and a semi-enclosed deep-water bay (Tomini Bay of Sulawesi Island, Indonesia). Zooplankton fecal pellets of at least 3 shapes, transparent oval objects, and one apparent appendicularian were observed to have been ingested. These types of objects are consistent with the hypothesis that leptocephali consume marine snow and discarded appendicularian houses, which both typically contain fecal pellets. Appendicularians have not been previously reported to be consumed by leptocephali, but the apparent presence of one in a muraenid intestine suggests that they may occasionally be consumed along with their houses. Chlopsid leptocephali in both regions were observed to have consumed large amounts of food material, which indicated that their short intestines are able to expand more than previously known. Due to net avoidance, most leptocephali are collected at night when feeding may be reduced, so visible food materials are rarely observed in their intestines at night. These photographs show some marine snow-related objects that are consumed by leptocephali more clearly than previous reports.

Key words: leptocephali, anguilliformes, gut contents, feeding, appendicularians, North Equatorial Current, Tomini Bay

Introduction

Leptocephali are widely distributed at tropical and subtropical latitudes (Miller 2009) and are often abundant near continental shelf areas (Miller et al. 2002, Miller and McCleave 2007) or in offshore areas, such as in anguillid eel spawning areas (Tsukamoto 1992, McCleave and Kleckner 1987, Miller and McCleave 1994, Miller et al. 2006), but their feeding ecology is poorly known. In the open ocean they mostly live in the upper 100 meters at night and some species of leptocephali vertically migrate to deeper depths in the upper few hundred meters during the day (Castonguay and McCleave 1987, Otake et al. 1998, Miller 2009). Leptocephali are remarkably transparent, laterally compressed larvae with a unique physiology (Pfeiler and Govoni 1993, Bishop and Torres 1999, Bishop et al. 2000, Pfeiler 1999), but their biology and ecology is remarkably poorly known (Smith 1989, Miller 2009).

What leptocephali eat as a food source was a complete mystery for many years due to a lack of any visibly identifiable food contents in their guts/intestines (these terms will be

used interchangeably). The lack of visible organisms such as zooplankton in their guts and the thin layer of epidermis covering their bodies led to the hypothesis that leptocephali do not feed by ingesting food, but may absorb dissolved organic carbon (DOC) across the surface of their bodies (Pfeiler 1986; Hulet and Robins 1989). However, close examinations of leptocephalus gut contents from coastal waters near Japan were able to distinguish zooplankton fecal pellets and discarded appendicularian (larvacean) houses in leptocephalus intestines, thus proving that they ingest food material (Otake et al. 1993, Mochioka and Iwamizu 1996). Laboratory observations also found that late-stage leptocephali would eat squid paste in the laboratory (Mochioka et al. 1993), and artificially spawned and reared leptocephali were clearly shown to feed and grow under artificial conditions while being fed an artificially prepared paste diet (Tanaka et al. 2001). These various observations clearly showed that leptocephali of at least several families actively consume food to obtain nutrition and do not depend on absorbing DOC as was hypothesized.

The examinations of the gut contents of leptocephali (Otake et al. 1993, Mochioka and Iwamizu 1996) and stable

isotope analyses of their body contents (Otake et al. 1993, Kimura and Tsukamoto 2006, Miyazaki et al. 2011) support the hypothesis that leptocephali obtain their nutrition primarily at low levels of the food chain by feeding primarily on marine snow particles and that they possibly also target appendicularian houses as a readily available food source (Westerberg 1990, Mochioka and Iwamizu 1996). Marine snow is a consistent component of ocean environments where leptocephali live and grow, and appendicularians are widespread and typically abundant in these same environments (Alldredge 1976, Alldredge and Silver 1988, Fenaux et al. 1998). Because appendicularians are filter feeders that use a delicate gelatinous house with a filtering system (Flood 1991), they have to frequently discard their houses after their filters become clogged, but they can immediately inflate a new one and resume feeding (Flood and Deibel 1998, Sato et al. 2003). As a result of this, their discarded houses are thought to be abundant and an important food source for some marine organisms (Alldredge 1972, 1976).

Leptocephali have a wide variety of head and jaw shapes (Miller and Tsukamoto 1994, Miller 2009), with both blunt and very pointed jaws (Fig. 1), and their outward pointing teeth seem to be well-designed for feeding on particulate materials such as marine snow and discarded appendicularian houses (Westerberg 1990, Mochioka and Iwamizu 1996, Miller 2009). The mouths of at least some species of leptocephali have a vellum that can probably assist with sealing the buccal cavity of the mouth during swallowing (Miller 2009), but this has not been studied in leptocephali. Amorphous material that seems to contain very small particles is usually present in the guts of all types of leptocephali suggesting they may all have similar feeding ecologies (Miller 2009), and this material will often flow out of the end of their intestines (Fig. 2). Although this material is not consistent with being the result of feeding on zooplankton, its exact origin is unknown. Observations of the ultrastructure of the epithelial cells lining the intestines of leptocephali, have also suggested that these larvae may also be adapted for absorbing dissolved organic carbon from the water that may be ingested along with the particulate material (Otake 1996, Otake et al. 1993).

Some of the most recent information about the feeding biology of eel larvae is from a study that used DNA barcoding of the gut contents of small anguillid leptocephali in the Sargasso Sea of the western North Atlantic. This analysis detected sequences from a variety of marine organisms including various zooplankton or gelatinous zooplankton taxa (Riemann et al. 2010). Although it was suggested leptocephali may feed directly on these taxonomic groups, as discussed later it is likely that most of these DNA sequences came from organisms living within marine snow particles.

The present study uses photographs of distinctively visible objects in the guts of leptocephali collected using large

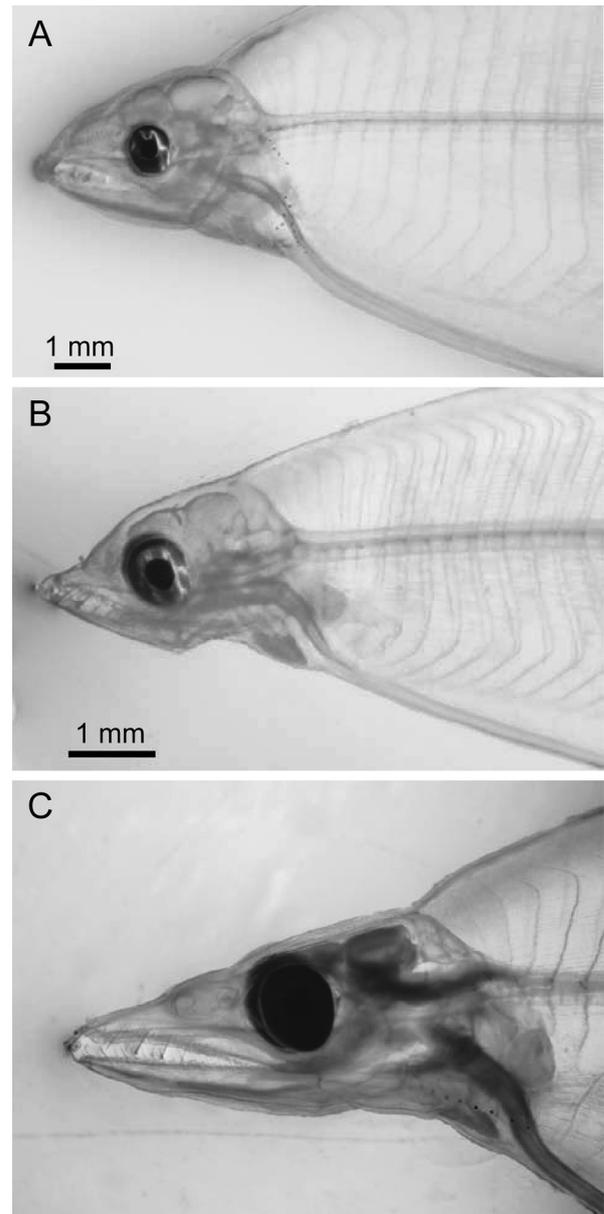


Fig. 1. The head regions of 3 species of leptocephali showing 3 different head and jaw shapes of (A) a 97 mm Uropterygiinae (Muraenidae), (B) a 33 mm *Anguilla marmorata*, and (C) a 103 mm *Gnathophis*-type (Congridae) that contained visible gut contents.

plankton nets to illustrate the presence of objects within their intestines more clearly than previous studies that occurred before the development of digital photography. The implications of the presence of these various objects and the discovery of expandable guts in the leptocephali of the family Chlopsidae are discussed in relation to the present state of knowledge about the feeding ecology and behavior of leptocephali in the ocean.

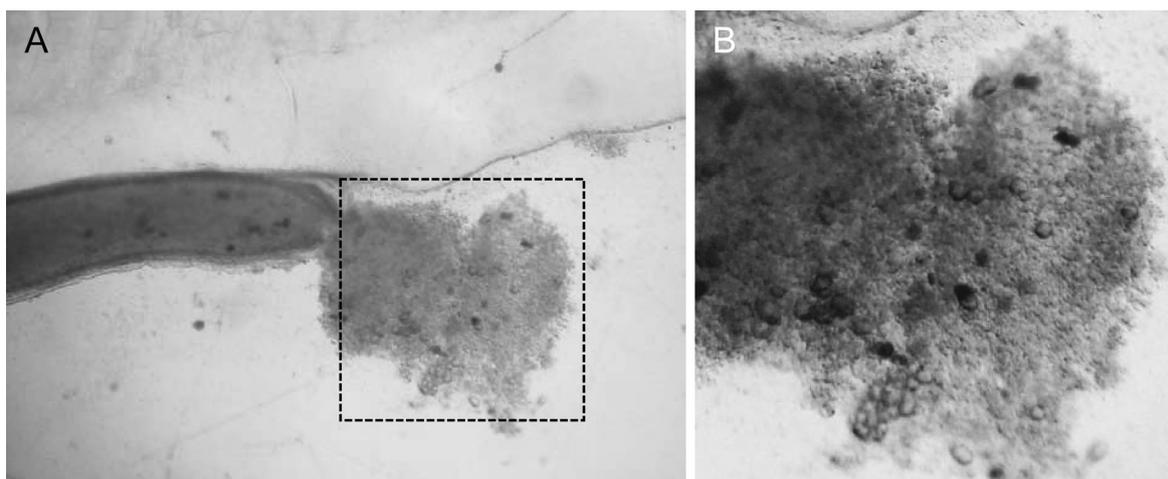


Fig. 2. Amorphous food content material containing small round objects that flowed out of the end of the gut of a 33 mm *Synphobranchinae* leptocephalus collected in Tomini Bay in Indonesia.

Materials and Methods

Leptocephali whose gut contents were observed in this study were collected during 4 research cruises of the R/V *Hakuho Maru* (JAMSTEC, and Atmosphere and Ocean Research Institute) that included 3 cruises in the North Equatorial Current (NEC) region of the western North Pacific (WNP) between April to July in 2008, 2009 and 2011 and one cruise in the central Indonesian Seas in March 2010 (Table 1). In the NEC, all but one larva were collected with a 3-m diameter mouth opening ORI-BF ring net with 0.5 mm mesh that was fished in oblique tows (0–300 m). One larva in the NEC and all larvae in Tomini Bay, of northern Sulawesi Island were collected with an 8.7 m² Isaacs-Kidd Midwater Trawl with 0.5 mm mesh fished horizontally at several different depths in the upper 150 m.

After being sorted out of the plankton samples and being placed in chilled seawater, photographs of the larvae were taken using a Nikon SMZ 1500 dissecting microscope equipped with a Nikon DMX1200F digital imaging system (Nikon, Tokyo Japan) in the NEC, or a Sony DSC-300 digital camera (Sony, Tokyo Japan) in Tomini Bay (due to a computer failure with the digital imaging system) that prevented scale bars from being used for the photographs in Tomini Bay. Specimens were then preserved in ethanol or by being frozen after they were identified to the lowest possible level according to Mochioka et al. (1982), Tabeta and Mochioka (1988) and Miller and Tsukamoto (2004) and measured to the nearest millimeter total length (TL).

The observations of the objects in the intestines of leptocephali from these sampling surveys were not quantitative (some larvae with visible gut contents may not have been photographed), and attempting to verify the identity of the objects directly was beyond the scope of this study. Verification of the identity of the apparent appendicularian in the lep-

tocephalus intestine was not possible, since this specimen was lost during the March 2011 earthquake and tsunami.

Results

All of the leptocephali that had visible objects in their intestines shown in this study were collected during the day, or during sunrise in the case of most of the specimens from Tomini Bay, at times ranging from 5:29 to 17:46 (Table 1). A larger number of leptocephali were collected at night, but visible objects in the intestines of leptocephali are rarely seen in specimens collected at night. The 11 species of leptocephali with gut contents in this study belonged to 8 families, and ranged in size from 8 to 234 mm TL (Table 1). They were collected between 12 to 18°N and 137 to 142°E in the NEC and just south of the equator between 120 to 121°E in the south-central part of the western region of Tomini Bay (see Wouthuyzen et al. 2005, 2009, for maps showing Tomini Bay).

In the NEC in 2008, 2 leptocephali were photographed that included a 33 mm *Anguilla marmorata* leptocephalus collected in the late afternoon. It was found to contain several brownish or yellowish oval-shaped zooplankton fecal pellets in the posterior portion of its intestine that appeared to be between 0.1 and 0.2 mm in length (Fig. 3). Even more distinct, were the 3 or 4 types of objects that were visible in the intestine of a 97 mm muraenid leptocephalus collected in the morning (Fig. 4). The largest was an object that appeared to be partially folded and had both purple and orange coloration (Fig. 4A, B), which may have been the main body of a appendicularian as discussed later. The other objects were elongated fecal pellets of possibly 2 shapes and also a more diffuse oval object (Fig. 4C, D). These objects were all >0.6 mm in length.

Other objects were seen in leptocephali collected in the

Table 1. List of the collection data and total length (TL) of the leptocephali or specimens in this study that contained visible objects in their intestines or were included for comparisons. The species identifications of most leptocephali in the Indo-Pacific are not yet known (Miller and Tsukamoto 2004), so specimens are listed at the lowest possible taxonomic level. The location of capture is listed as the start of the tow, and the time of capture (local time) is from the start to the end of each tow. All cruises (KH) were conducted by the R/V *Hakuho Maru*, and collections were made using either the IKMT (IK-O, S) or a large ring net (ORI-BF). The appendicularians shown in Fig. 11 are also included.

Cruise	Station	Net	Date	Location	Local time	Family	Species	TL
WNP								
KH-08-1	232	IK-O	26-Jun-2008	16–00.0 N, 137–01.2 E	16:30–17:18	Anguillidae	<i>Anguilla marmorata</i>	33
KH-08-1	360	ORI-BF	9-Jul-2008	15–00.0 N, 142–15.0 E	10:30–11:07	Muraenidae	Uropterygiinae	97
KH-09-2	91	ORI-BF	17-May-2009	18–00.3 N, 140–01.2 E	09:15–10:04	Derichthyidae	sp.	9
KH-09-2	91	ORI-BF	17-May-2009	18–00.3 N, 140–01.2 E	09:15–10:04	Nemichthyidae	<i>Nemichthys</i>	60
KH-09-2	145	ORI-BF	24-May-2009	12–50.0 N, 141–23.1 E	14:07–15:13	Derichthyidae	sp.	8
KH-11-4	58	ORI-BF	1-June-2011	12–50.8 N, 141–14.9 E	16:43–17:46	Chlopsidae	sp. 4	66
KH-05-1	27	ORI-BF	6-June-2005	13–03.3 N, 141–01.4 E	18:59–20:18	Chlopsidae	sp. 4*	65
KH-09-1	44	ORI-BF	24-Apr-2009	14–15.1 N, 142–30.0 E	05:23–06:05	Oikopleuridae	<i>Oikopleura dioica?</i>	—
Tomini Bay								
KH-09-5	4	IK-S	7-Mar-2010	00–29.7 S, 120–44.9 E	8:21–9:40	Congridae	<i>Ariosoma</i> -type	234
KH-09-5	9	IK-S	8-Mar-2010	00–29.1 S, 121–14.3 E	5:46–07:14	Ophichthidae	Ophichthinae	39
KH-09-5	9	IK-S	8-Mar-2010	00–29.1 S, 121–14.3 E	5:46–07:14	Congridae	<i>Gnathophis</i> -type	103
KH-09-5	9	IK-S	8-Mar-2010	00–29.1 S, 121–14.3 E	5:46–07:14	Chlopsidae	sp.	30
KH-09-5	9	IK-S	8-Mar-2010	00–29.1 S, 121–14.3 E	5:46–07:14	Chlopsidae	sp.	43
KH-09-5	9	IK-S	8-Mar-2010	00–29.1 S, 121–14.3 E	5:46–07:14	Chlopsidae	<i>Kaupichthys</i>	45
KH-09-5	5	IK-S	9-Mar-2010	00–44.8 S, 120–44.4 E	5:29–6:51	Synphobranchidae	Synphobranchinae	33

*This leptocephalus had no visible gut contents, but was included for comparison in Figure 7.

NEC in 2009 that included oval fecal pellets in a 60 mm *Nemichthys* (Fig. 5A) and in 8 and 9 mm Derichthyidae leptocephali (Fig. 5B–D). The *Nemichthys* larva also had a large transparent object in the same area that the fecal pellets were visible. The fecal pellets in their intestines were all <0.1 mm in length.

In the NEC in 2011, a 66 mm Chlopsidae sp. 4 (Tabeta and Mochioka 1988) leptocephalus was collected in the late afternoon in June, which had a large amount of food contents in its intestine (Fig. 6, 7A). Zooplankton fecal pellets were clearly visible inside both the anterior and posterior regions of the intestine (Fig. 6B, C), and 2 types of fecal pellets flowed out the end of the gut along with other food materials (Fig. 6B, D). The degree of fullness of the intestine of this leptocephalus was clearly much greater than a same size

larva (65 mm) of the same species caught in June of 2005 in the same region, which did not contain extensive food material and did not have an expanded intestine (Fig. 7).

The leptocephali in Tomini Bay that were photographed in March 2010 had various types of visible objects inside their intestines that included distinct fecal pellets and oval objects, and several chlopsid leptocephali were also observed to have swollen intestines that were full of gut contents. There were 3 chlopsid leptocephali (30–45 mm) collected at Station 9 in Tomini Bay that had swollen intestines containing numerous oval fecal pellets and various shapes of transparent objects (Fig. 8). A few clusters of pigment spots were visible on the upper sides of the guts of 2 of the larvae (similar to Chlopsidae sp. 6 of Tabeta and Mochioka 1988), but the rest of the dark oval objects appeared to be zooplankton

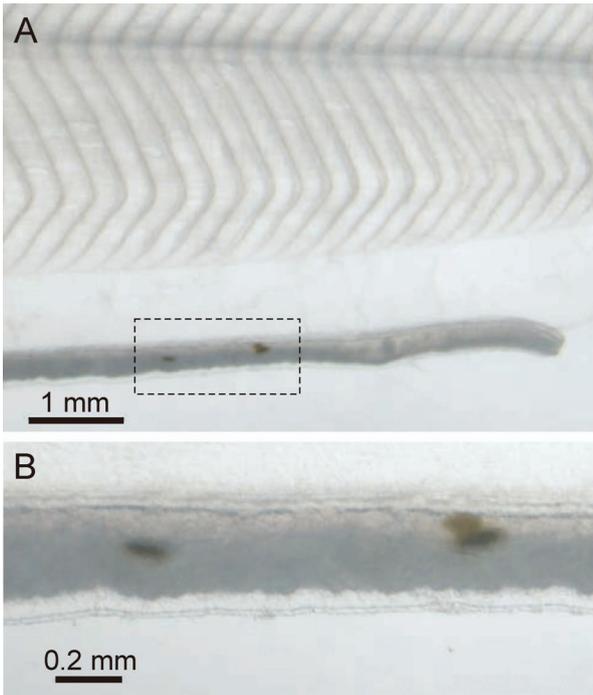


Fig. 3. Apparent zooplankton fecal pellets in the intestine of a 33 mm *Anguilla marmorata* leptocephalus (Fig. 1B) collected in the North Equatorial Current region. (A) shows the posterior part of the body near the end of the gut, and (B) is an enlargement of the area inside the rectangle in (A).

fecal pellets (Fig. 8A–C). The *Kaupichthys* leptocephalus had several oval fecal pellets and several large oval objects (Fig. 8D). The most remarkable feature of these 3 chlopsid larvae from Tomini Bay and the 66 mm chlopsid larva collected in the NEC was that their intestines were very full of food material and were much more swollen than usual compared to other chlopsid larvae that have been seen previously.

Other leptocephali collected in Tomini Bay that had visible gut contents included a 234 mm *Ariosoma*-type congrid leptocephalus (similar to *Ariosoma* type B₁ of Mochioka et al. 1982) that had dark-colored and orange-colored objects in one part of the intestine (Fig. 9A, B). It also had elongate fecal pellets with orange material near an elongated transparent oval object in another part of the intestine (Fig. 9C, D). At Station 9 in Tomini Bay where the 3 chlopsid larvae were collected, a 103 mm *Gnathophis*-type congrid had elongate fecal pellets with orange material inside its intestine, along with some lighter colored material anterior to the fecal pellets (Fig. 10A, B). An ophichthid leptocephalus also collected at that station had oval transparent objects, oval fecal pellets, and yellowish materials mixed together inside a region of curvature of the gut (Fig. 10C, D).

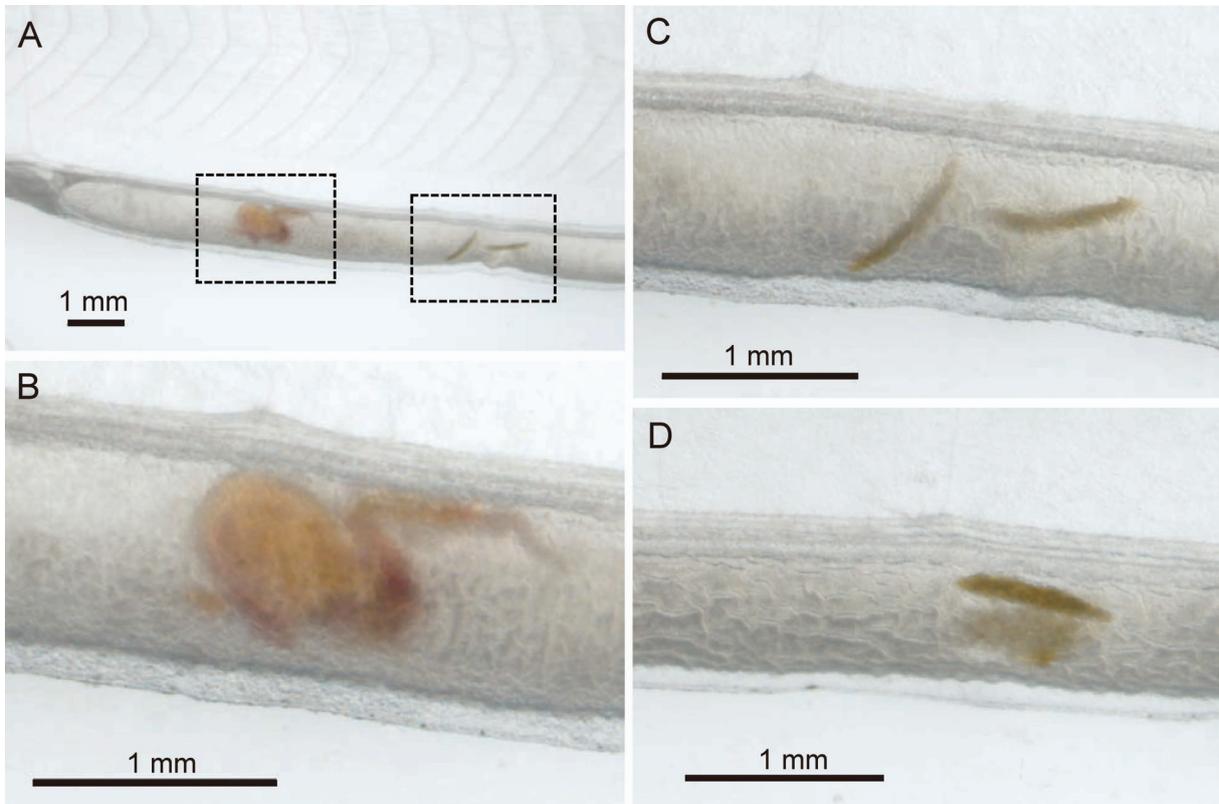


Fig. 4. Various objects in the intestine of a 97 mm Uropterygiinae leptocephalus collected in the North Equatorial Current region. (A) the anterior part of the intestine, with the rectangles showing the areas enlarged in (B) an apparent appendicularian head, left rectangle, and (C) elongate fecal pellets, right rectangle, and (D) a fecal pellet and another object.

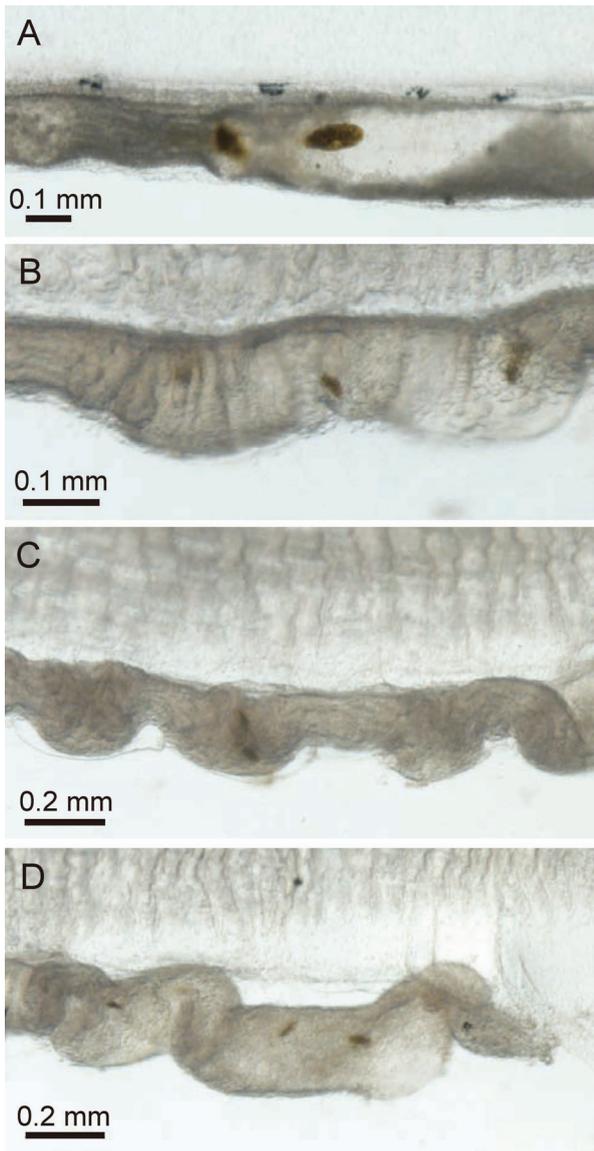


Fig. 5. Fecal pellets and transparent oval objects in the intestines of (A) a 60 mm *Nemichthys* leptocephalus with a appendicularian-shaped fecal pellet clearly visible adjacent to a transparent object, and of (B) 9 mm and (C, D) 8 mm *Derichthyidae* leptocephali with fecal pellets and other materials visible. All 3 leptocephali were collected in the North Equatorial Current region.

Discussion

The present study provided evidence that some leptocephali collected during daylight hours both far offshore in the subtropical gyre of the WNP and in a semi-enclosed deep-water tropical bay in Indonesia have fecal pellets and other objects in their guts in addition to amorphous material. Several shapes and sizes of fecal pellets were observed in the two areas along with various transparent oval objects. The number of fecal pellets seen ranged from just a few in leptocephali of the *Anguillidae*, *Congridae*, *Muraenidae*, and *Ophichthidae*, to many that were seen in one of the *chlopsid*

larvae from Tomini Bay (Fig. 8A, B). Other leptocephali collected during the day often appear to have intestines filled with amorphous material that can flow out of the gut after capture as seen in the 33 mm synphobranchid leptocephalus collected in Tomini Bay during sunrise (Fig. 2) and as shown by Miller (2009; Fig. 22C), even if they do not contain visible objects such as fecal pellets or transparent oval objects. The materials in the guts of these leptocephali can seemingly often be packed in quite densely and appear likely to be held inside the intestine by constriction of a sphincter at the end of the anus, which when relaxed, allows the gut contents to flow out (Fig. 2A, Fig. 6).

A few photographs of the intestines of other species of leptocephali have also shown gut contents including transparent oval objects and fecal pellets (Otake et al. 1993; Mochioka and Iwamizu 1996; Miller 2009). The transparent oval objects in the study of Mochioka and Iwamizu (1996) were determined to be discarded appendicularian houses. They examined the guts of 234 specimens of eight species of leptocephali (*Congridae*, *Muraenesocidae*, *Muraenidae*, *Nettastomatidae*, *Ophichthidae*) that were caught along coastal Japan, and found that 80% of the leptocephali that had food in their intestines contained appendicularian houses and 56% contained appendicularian fecal pellets; but only 17% contained other types of fecal pellets. Otake et al. (1993) examined the gut contents of *Conger myriaster*, *C. japonicus*, and *Muraenesox cinereus* collected in coastal waters and found zooplankton fecal pellets and smaller objects in the guts of more than 90% of the 613 leptocephali examined. Scanning electron microscope (SEM) observations were used to confirm that zooplankton fecal pellets and discarded appendicularian houses were present in the gut contents of the leptocephali in these studies (Otake et al. 1993; Mochioka and Iwamizu 1996). Apparent marine snow-like particulate material was also seen in the intestines of 2 *M. cinereus* leptocephali collected in light traps near a tropical island of southern Japan (Miller et al. 2010).

The observation of these types of objects in the intestines of leptocephali is consistent with the hypothesis that these unusual fish larvae feed almost exclusively on particulate material such as marine snow and discarded appendicularian houses. Most of the oval-shaped fecal pellets in the present study (Fig. 3, 5, 8, 10D) appear to be those of appendicularians as reported by Mochioka and Iwamizu (1996), and shown recently by Wilson et al. (2008) who reported on the shapes of various zooplankton fecal pellets. The more elongate fecal pellets (Fig. 4, 6, 9, 10B) appear to be from crustaceans such as euphausiids or copepods, and the reddish coloration, such as those seen in the gut contents of the 2 species of congrid leptocephali in Tomini Bay (Fig. 9D, 10B), were suggested to belong to predatory zooplankton (Wilson et al. 2008). In the present study, most of the observations of appendicularian-shaped fecal pellets were also ac-

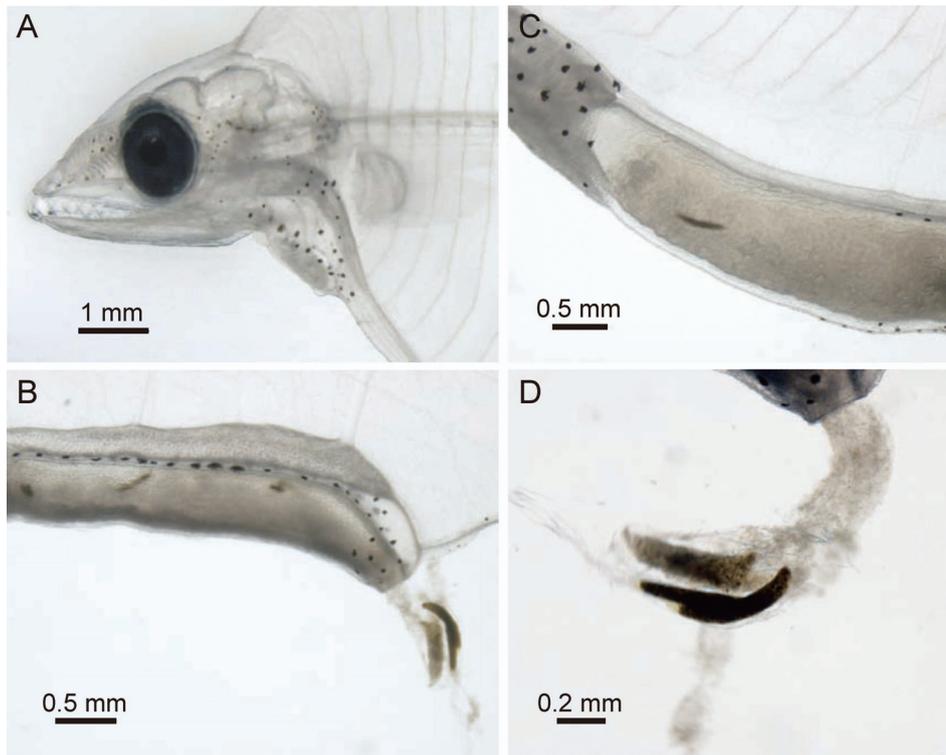


Fig. 6. The head region (A) of a *Chlopsidae* sp. 4 leptocephalus and its gut contents including zooplankton fecal pellets in the posterior (B) and anterior (C) regions of the intestine. (B) and (D) show fecal pellets and food materials contents that flowed out of the end of the intestine during examination of the leptocephalus.

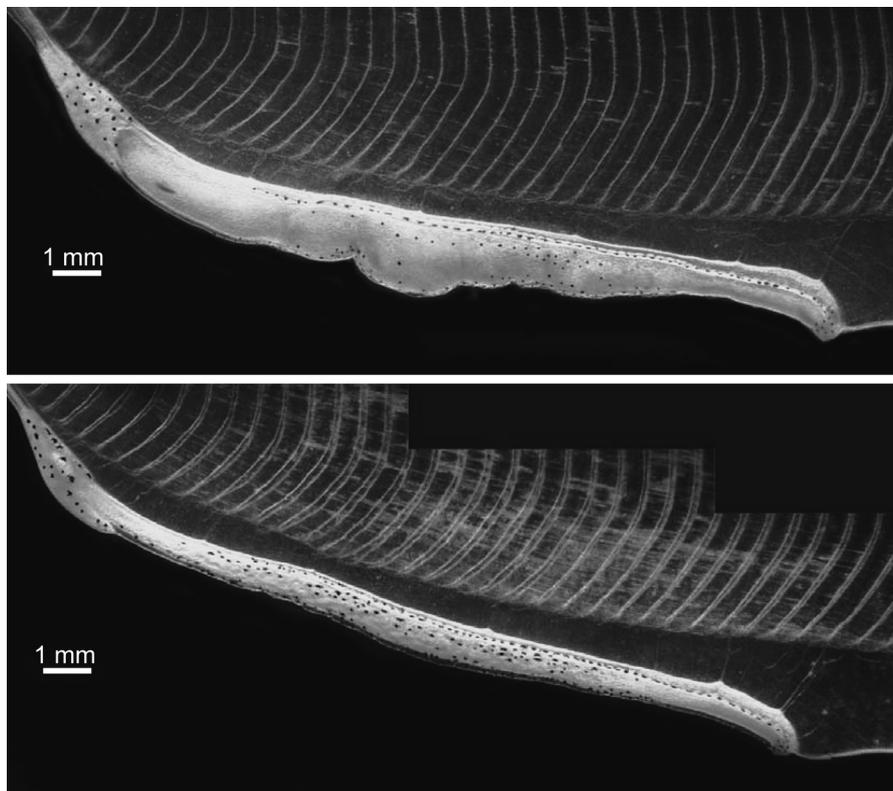


Fig. 7. The intestines of two similarly sized *Chlopsidae* sp. 4 leptocephali collected in the North Equatorial Current region that show a large amount of gut contents and expanded intestine (top, 66 mm larva collected in June 2011) also shown in Figure 6, or no apparent gut contents (bottom, 65 mm larva collected in June 2005).

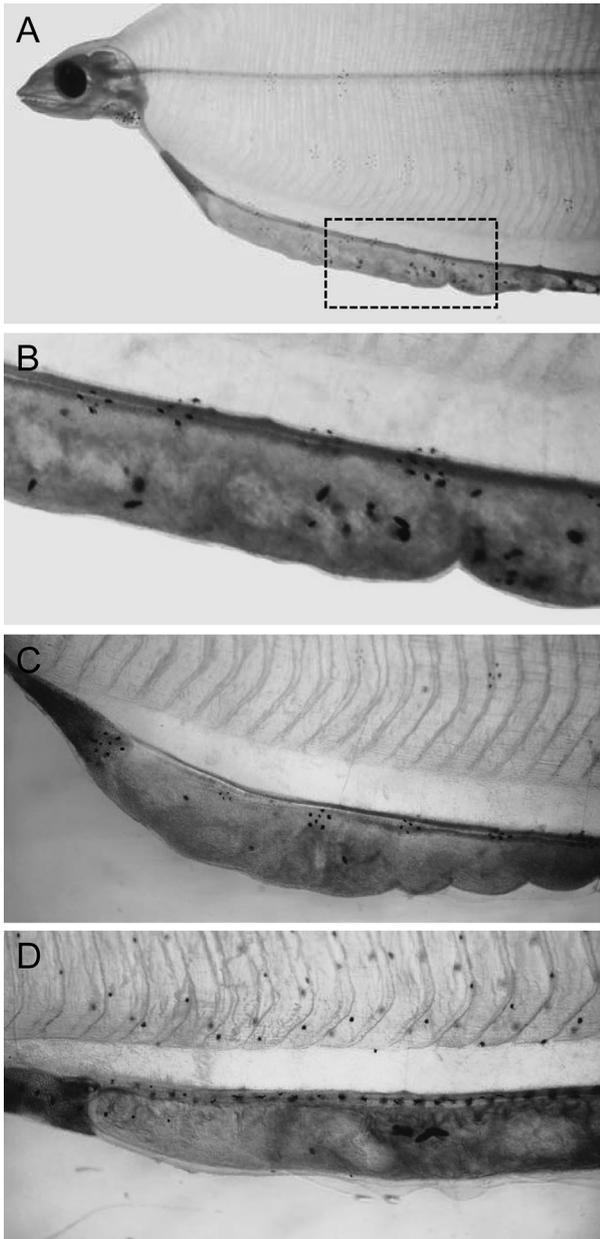


Fig. 8. Food contents inside the expanded intestines of leptocephali of the Chlopsidae that were full of food material. (A) a 30 mm TL Chlopsidae sp. that contains many fecal pellets, shown in the area in the rectangle enlarged in (B). (C) a 43 mm TL Chlopsidae sp. with a greatly expanded intestine. (D) anterior intestine region a 45 mm TL *Kaupichthys* sp. that contains fecal pellets and transparent oval objects. All 3 leptocephali were collected at the same station during sunrise in Tomini Bay, Indonesia.

accompanied by the presence of transparent oval objects that are thought to be discarded appendicularian houses (Mochizuki and Iwamizu 1996). The discarded appendicularian houses typically contain some of their own fecal pellets (Taguchi 1982, Alldredge and Sliver 1988), so the leptocephali in Figures 5, 8, 10D appear to have been feeding on discarded appendicularian houses that also contained appendicularian fecal pellets.

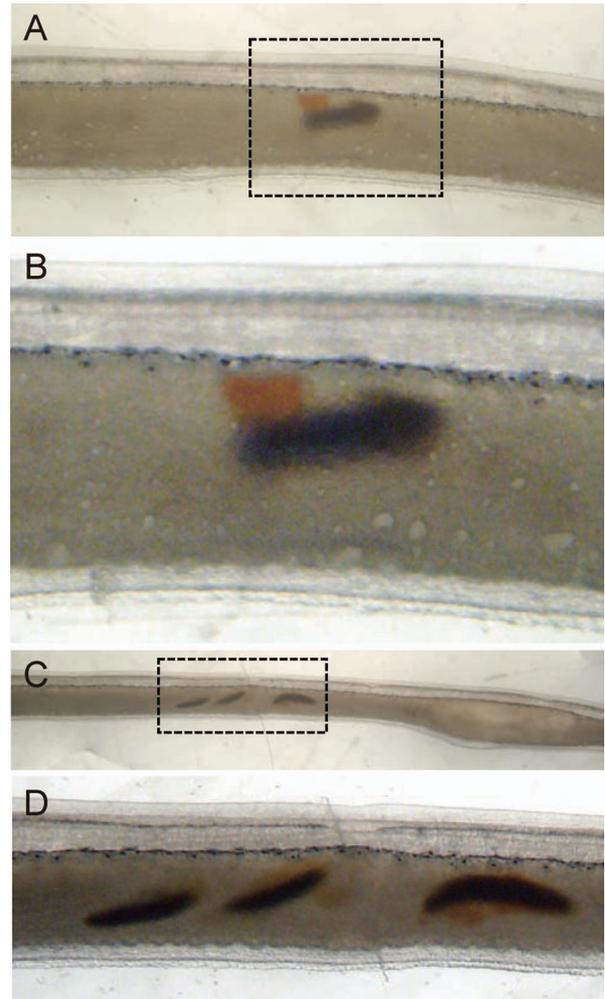


Fig. 9. Various objects in the gut of a large *Ariosoma*-type leptocephalus (234 mm) collected in Tomini Bay. (A) objects with the area in the rectangle enlarged in (B), and (C) fecal pellets in the rectangle enlarged in (D) and a large transparent oval object.

The present study also observed what appears to be the main body of an appendicularian in the intestine of a muraenid larva (Fig. 4B), which is the first report leptocephalus apparently ingesting an actual appendicularian instead of just their discarded houses. The object in the intestine looks similar in structure and color to the main body regions of a species of appendicularian that was also collected in the NEC region in April 2009 (Fig. 11). The apparent appendicularian in the leptocephalus intestine may have been eaten while still in its house. Various fishes or fish larvae feed directly on appendicularians (Purcell et al. 2004, Capitanio et al. 2005, Llopiz et al. 2010), but leptocephali are likely not adapted to digest them. Eating appendicularian houses still containing the appendicularian may be maladaptive due to the agitation that could be caused by a struggling appendicularian that could break up the house and disperse the nutrient-containing materials during ingestion of the house. Therefore, it is likely that leptocephali typically avoid houses containing appendic-

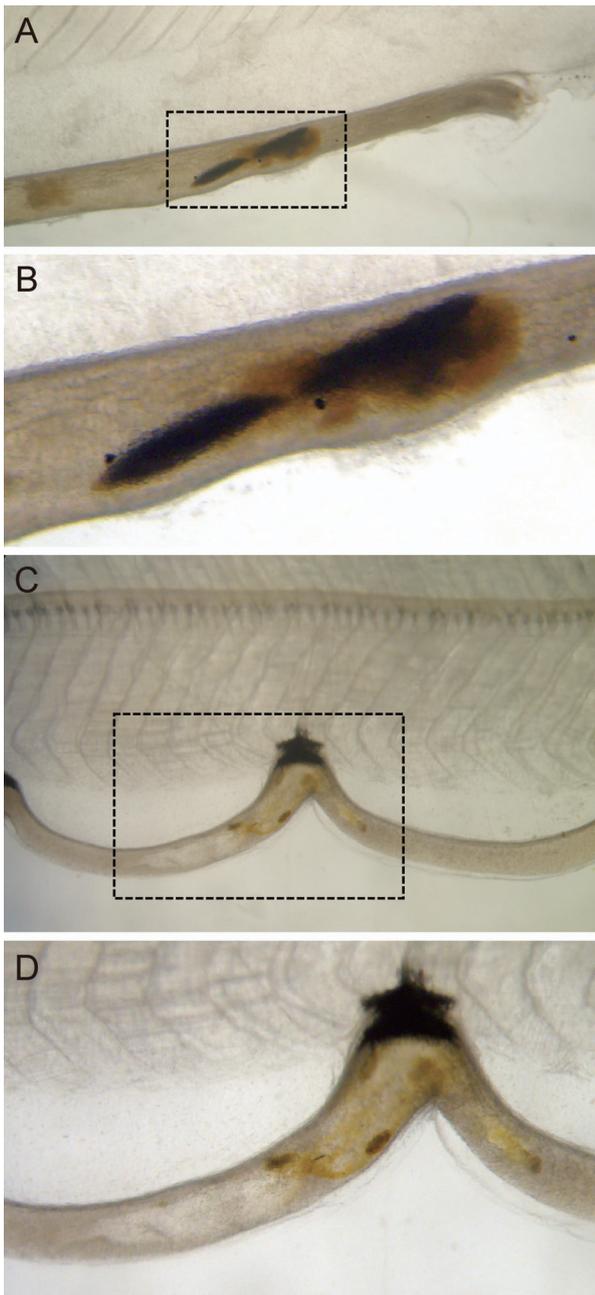


Fig. 10. Visible gut contents in (A) the posterior part of the intestine of a 103 mm *Gnathopis*-type leptocephalus with fecal pellets and orange material shown in the enlargement in (B), and (C) fecal pellets and transparent oval objects in the intestine of a 39 mm *Ophichthinae* leptocephalus with the area in the rectangle enlarged in (D).

ularians.

Another new finding of the present study is that the unusually short guts of leptocephali of the family Chlopsidae are able to expand greatly in diameter to allow the consumption of larger amounts of food material (Fig. 7, 8). The leptocephali of this family are frequently collected in tropical areas and they have been both photographed and illustrated (Smith 1969, Tabeta and Mochioka 1988, Miller and

Tsukamoto 2004), but their guts have always been narrow and tubular like other leptocephali. The two chlopsid leptocephali of the same species collected at different times of day in the NEC clearly show the contrast between expanded and non-expanded intestines depending on how much food they contain (Fig. 7). Three of the chlopsid larvae with expanded guts and 2 other species that showed the presence of apparent appendicularian houses and fecal pellets were all collected during sunrise at Station 9 in Tomini Bay (Table 1). This tow sampled primarily at two depth layers (105 m and then at 30 m), so if the larvae were caught in the 30 m layer, they may not have been inside the net very long. If this was the case and they were immediately brought on board the ship, this may have resulted in a minimal amount of loss of food material from their guts while they were in the codend of the net.

The fact that the leptocephali at this station and all the others in this study were collected during the daytime, suggests that leptocephali may feed predominantly during the day, because possible nighttime observations were not excluded from the present study. Similarly, all the leptocephali in the studies of Otake et al. (1993) and Mochioka and Iwamizu (1996) were caught during the day, so any nighttime feeding by leptocephali has not been documented yet. All leptocephali have very large eyes and therefore it is likely that they feed mostly during the day using vision to detect food particles. Some types of marine snow or appendicularian houses can have bioluminescent properties (Galt et al. 1985, Herren et al 2004), which could be used by leptocephali to see those particles and feed at night or at deep depths during the day, as hypothesized previously (Yamada et al. 2009). Although there are no studies yet about the gut contents of leptocephali at night compared to daytime, it is clear that visible food contents such as those in the present study are rare during nighttime. One problem that has likely slowed down progress on understanding the feeding ecology of leptocephali is that most leptocephali can avoid even large trawls during the day (Miller and McCleave 1994, Miller et al. 2006), so few are captured when most appear to be feeding based on existing evidence.

These types of sampling problems and the limited number of specimens of each family of leptocephali included in the present study make it difficult to determine if there were any differences in the types of food particles eaten by the leptocephali in the two different areas (the NEC and Tomini Bay). There were likely differences in the biological communities in the water column between the two areas, but similar types of food materials appeared to have been ingested in both areas, even though there were mostly different species and sizes of leptocephali that were observed with gut contents in each area.

Many questions also remain about to what extent leptocephali may specifically target appendicularian houses com-

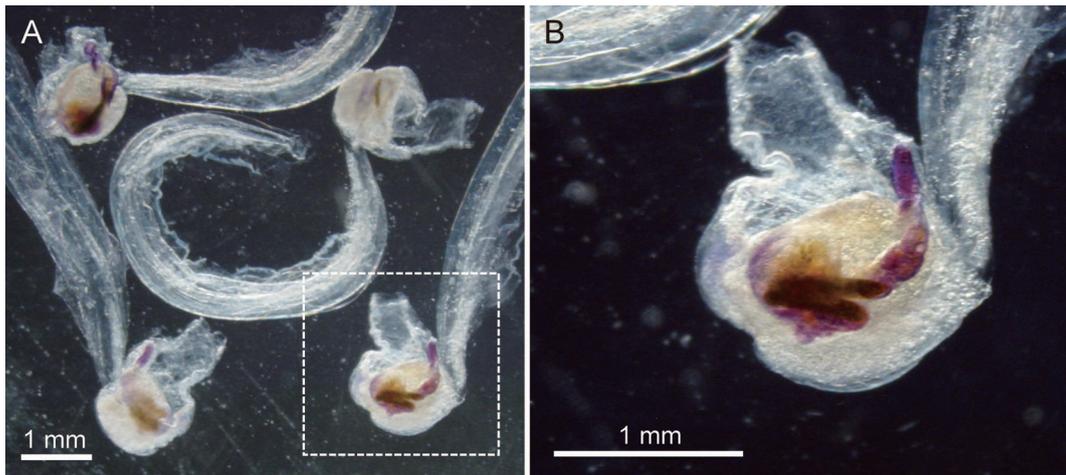


Fig. 11. Photographs of the bodies of oikopleurid appendicularians (A) that were collected in the same region of the western North Pacific as the leptocephalus that appears to contain a appendicularian in its intestine as shown in Figure 4B. (B) an enlarged view of the main body (excluding the tail) of a appendicularian in the rectangle in (A).

pared to any type of marine snow, and if they may sometimes eat other small organisms. An early study on newly hatched leptocephali found that they would eat rotifers offered to them (Tanaka et al. 1995), and ciliates have recently been reported in the intestines of leptocephali (Govoni 2010). In addition, a recent DNA barcoding study of the gut contents of small (4–14 mm) European eel, *Anguilla anguilla*, leptocephali detected the DNA sequences of a wide variety of marine organisms including crustaceans, chaetognaths, polychaetes, and cnidarians, and suggested that gelatinous zooplankton may be of fundamental dietary importance for those leptocephali (Riemann et al. 2010). The barcoding study suggested that it may be the larval stages of some of these organisms that may be the prey of leptocephali, but it did not discuss their size or how leptocephali may feed on them. Most taxa were only detected once (in a single leptocephalus) except for the Polycystinea (radiolarians), Streptophyta (plants or algae), fungi, and hydrozoans in general (hydroids, medusae and siphonophores) (Riemann et al. 2010), indicating an apparent random pattern of occurrence and detection of the rare taxa.

From a different perspective, the presence of ciliates and detection of DNA sequences of a variety of taxa among the gut contents of leptocephali are completely consistent with the existing hypothesis that leptocephali feed almost exclusively on particulate material such as marine snow and discarded appendicularian houses. They are consistent with this because invertebrates such as ciliates, various stages of copepods, and the larvae of anthozoans, mollusks, and polychaetes have been found to be associated with marine snow (Alldredge and Sliver 1988, Shanks and Walters 1997, Kjørboe 2000) and ciliates are often directly associated with appendicularian houses (Davoll and Silver 1986, Lombard et al. 2010). Therefore, these small organisms could easily be

ingested along with the particulate matter that the leptocephali were feeding on. A similar situation was proposed for an amphipod species that was suggested to have ingested organisms contained in marine snow that they would not have otherwise eaten (Lampitt et al. 1993).

There are also other factors that could contribute to the detection of the DNA of organisms that leptocephali likely do not target directly as food. For example, small pieces of organisms such as the tentacles of jellyfish, medusae, and siphonophores that may break off during agitation or interactions with other organisms, and cellular materials released when organisms are eaten by predators, could all become aggregated within marine snow particles. These tissue fragments could also be collected on the filters of appendicularian houses, or their DNA could possibly even become present in particulate material in the form of extracellular DNA that is known to exist in the ocean (DeFlaun et al. 1987, Nielsen et al. 2007). It can not be determined yet though if leptocephali may sometimes directly prey on some very small organisms individually, but so far no identifiable zooplankton or larvae have been seen in the gut contents of leptocephali, other than ciliates (Govoni 2010) and the apparent presence of a appendicularian in the gut of the muraenid larva in the present study.

If leptocephali are feeding at a very low level of the food chain by consuming particulate material as is indicated by observations of their gut contents like those shown here and in previous studies (Otake et al. 1993, Mochioka and Iwamizu 1996) and by their stable isotope signatures (Otake et al. 1993, Kimura and Tsukamoto 2006, Miyazaki et al. 2011), it indicates that leptocephali have a remarkable feeding strategy that uses a constantly produced and readily available food source. The filters of the appendicularian houses eventually clog-up, so their houses are frequently discarded

and immediately replaced (Flood and Deibel 1998, Sato et al. 2003). Therefore, they could be an abundant food source for leptocephali, because appendicularians have been shown to be widely distributed and often abundant in many areas (Alldredge 1976, Taguchi 1986, Fenaux et al. 1998). Similarly, marine snow is produced by various components of the typical biological production processes in the ocean and is universally present at often high concentrations in the upper 150–200 m of the ocean (Ichikawa 1982, Alldredge and Silver 1988, Hebel and Karl 2001, Turner 2002, Pilskaln et al. 2005). The low respiratory demand due to the body of leptocephali mostly containing inert transparent compounds and their unique physiology (Pfeiler and Govoni 1993, Bishop and Torres 1999, Bishop et al. 2000, Pfeiler 1999) appear to make feeding on particulate materials a successful feeding strategy for leptocephali. Future studies using a variety of techniques are needed to learn more about the feeding ecology of leptocephali in different marine environments around the world.

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