

Short Note

Leptocephali collected in light traps near coral reef habitats of Ishigaki Island in the southern Ryukyu Island chain

Michael MILLER^{1*}, Yohei NAKAMURA^{1†}, Takuro SHIBUNO^{2††} and Katsumi TSUKAMOTO¹

¹ Atmosphere and Ocean Research Institute, The University of Tokyo, 5–1–5 Kashiwanoha, Kashiwa, Chiba, 277–8564, Japan

* E-mail: miller@aori.u-tokyo.ac.jp

² Ishigaki Tropical Station, Seikai National Fisheries Research Institute, 148–446, Fukai-Ohta, Ishigaki Okinawa 907–0451, Japan

† Present address: Graduate School of Kuroshio Science, Kochi University, 200 Monobe, Nankoku, Kochi, 783–8502, Japan

†† Present address: National Research Institute of Aquaculture, 422–1, Nakatsuhamaura, Minami-ise, Mie, 516–0193, Japan

»» Received 30 November 2009; Accepted 23 May 2010

Abstract—The habitats used by leptocephali are poorly known except for a few studies on their depth distributions or collections of recruiting leptocephali in some areas. Leptocephali have been reported to be collected by light traps in tropical coastal habitats, but their species composition or development stages have not been clarified. We report the collection of small numbers leptocephali in light traps set within and adjacent to coral reef habitats along the west coast of Ishigaki Island of the Ryukyu Island chain of Japan. Four muraenid and one ophichthid leptocephali at the early-metamorphosis stage were collected at the outer reef edge in May and June of 2007 and 2008. Two pre-metamorphosis stage *Muraenesox cinereus* leptocephali were collected between the inner and outer coral reefs in August 2006. Visible gut contents in the muraenesoscid larvae suggested they were feeding near the reefs. These collections clarify that both metamorphosing and pre-metamorphosing leptocephali can be caught in light traps, but it remains questionable if light traps effectively sample for leptocephali in near-shore habitats. Future research needs to evaluate the degree to which light traps can collect leptocephali by comparing their catches to other evidence about the presence of leptocephali in the same habitats at night.

Key words: Leptocephali, Anguilliformes, light traps, sampling methods, Ryukyu Islands, Ishigaki Island, coral reefs

Introduction

Leptocephali are the remarkably transparent and exclusively marine larvae of eels and their close relatives that grow to large sizes (Smith 1989, Miller and Tsukamoto 2004, Miller 2009). They live in the ocean surface layer after being born at a range of distances from coastal areas depending on the family or species of eel (Miller 2009). In offshore areas of the open ocean they live in the surface layer and some species vertically migrate to deeper depths in the upper few hundred meters during the day (Castonguay and McCleave 1987). However, other than observations of higher abundances at the edges of continental shelf areas (Miller et al. 2002) or near large shallow banks (Miller and McCleave 2007), their near-shore habitat use patterns or behavioral characteristics are not known (Miller 2009). This is mostly due to their strong ability to avoid small plankton nets or most nets fished during the day (Castonguay and McCleave 1987, Miller and McCleave 1994, Miller et al. 2006).

Studies on the spatial and temporal patterns of recruitment of fish larvae at some tropical locations around the world have collected leptocephali moving inshore to coral reef areas or shallow habitats using crest nets or channel nets to sample tidal currents (Dufour and Galzin 1993, Thorrold

et al. 1994a, b, Doherty and McIlwain 1996, Dufour et al. 1996, McIlwain 2003, Nolan and Danilowicz 2008), but these leptocephali have not been directly studied, except by Harnden et al. (1999). Other studies on the species composition or settlement patterns of fish larvae using light traps have also reported the collection of a few leptocephali (e.g. Hendriks et al. 2001, Wilson 2003, Sponaugle et al. 2005, Carassou et al. 2009), but like most studies using nets, these studies have only identified leptocephali to the family level, with no information about their size or developmental stages being provided.

In coastal areas of Japan and Korea, *Conger myriaster* or *Muraenesox cinereus* leptocephali have been collected in large set nets and boat-seines used by fishermen to collect clupeoid fish larvae (Mochioka et al. 1993, Otake et al. 1997, Lee and Byun 1996). Some of these leptocephali are metamorphosing and others are not, but will do so quickly if transferred to aquaria (Mochioka et al. 1993). Late-stage and metamorphosing leptocephali of *Conger oceanicus* have also been collected in estuarine habitats of the US east coast (Bell et al. 2003).

These various observations indicate that large-size and often metamorphosing leptocephali reside in or enter shallow water as they prepare to recruit to the coastal habitats where

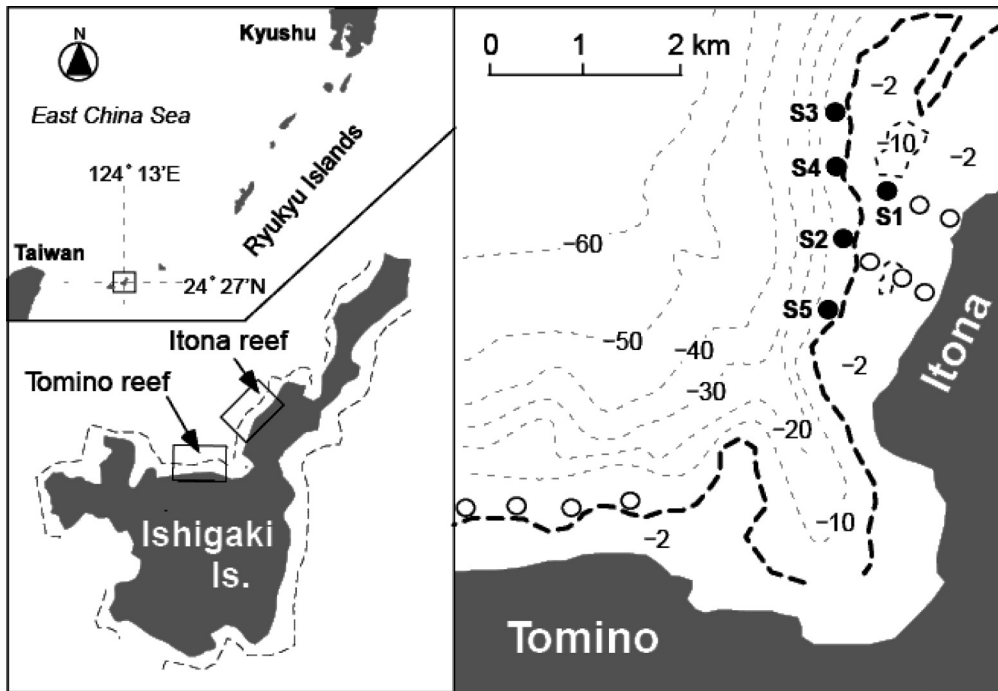


Fig. 1. Map showing the location of Ishigaki Island of the southern Ryukyu Island chain of Japan, and the two study areas (Tomino and Itona reefs) in relation to depth contours around the island. Light trap locations where leptocephali are shown (black circles), and light trap deployment locations where no leptocephali were collected are shown (white circles) in the right panel. The stations where leptocephali were collected at the Itona site are labeled (see Fig. 2). Thick dashed line (left and right panels) shows the outer edge of the reef areas.

they live as juvenile eels. However, in areas without strong tidal currents or appropriate locations for setting nets, light traps could be alternative ways to collect leptocephali if they effectively sample this type of fish larvae.

The present study describes the leptocephali collected during the light trap studies of Nakamura et al. (2009a, b) at Ishigaki Island (Fig. 1). This area has well developed fringing coral reefs (Fig. 2) due to the influence of the warm Kuroshio Current that flows northward just to the west of the Ryukyu Islands, despite the island being located at a high latitude. Ishigaki Island has a rich fauna of coral reef fishes (Lecchini et al. 2003, Shibuno et al. 2008), although the anguilliform fish community there has not been studied. One study did examine the process of metamorphosis in leptocephali of the ladyfish, *Elops hawaiiensis* (Elopidae, Elopiformes), that were collected in the lower reaches of the Nagura River of Ishigaki Island (Sato and Yasuda 1980). The present study reports on the leptocephali collected in light traps at Ishigaki Island and evaluates the question of whether light traps may collect representative samples of leptocephali residing or entering clear water tropical marine habitats such as those of the southern Ryukyu Island chain.

Materials and Methods

Research on the spatial variability and habitat associa-

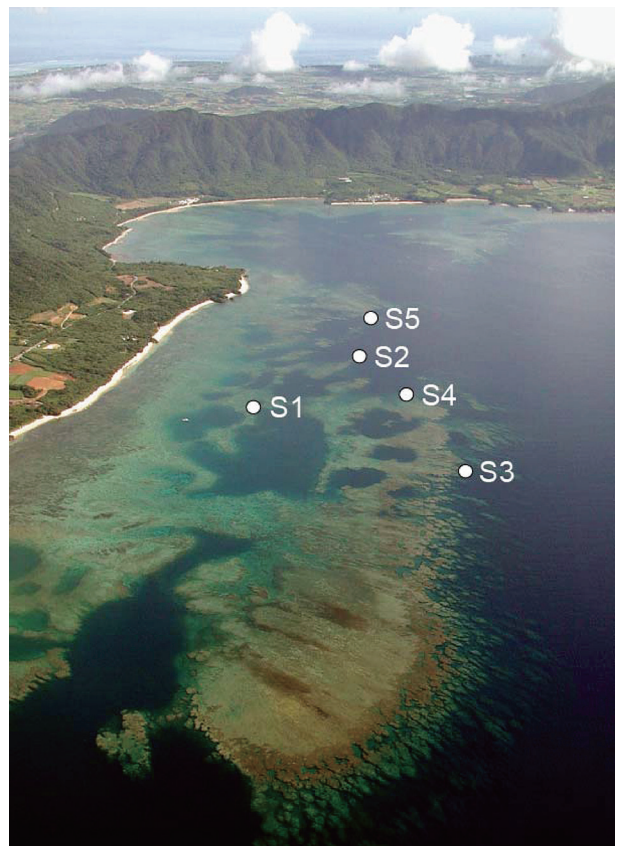


Fig. 2. Aerial photograph of the Itona reef study area looking to the south, showing the locations where leptocephali were collected in light traps.

tions of coral reef fish larvae was carried out at Ishigaki Island of the southern Ryukyu Islands Japan using light traps (Nakamura et al. 2009a, b). The southwestern end of Ishigaki Island is adjacent to the Sekisei Lagoon (the only well developed barrier reefs in Japan) that extends across to the eastern side of Iriomote Island (distance 20 km). The present study analyzes the catches of leptocephali during deployments of light traps in two areas (Tomino and Itona reefs) along the northwestern shoreline of Ishigaki Island from 2006 to 2008 (Fig. 1).

The coral reef habitats at Itona reef extend out up to about 300 m from shore and include shallow coral rubble areas closest to shore, then branching coral areas (1–3 m at low tide), and tabular corals along the outer reef margin (Fig. 2) at depths of 5–15 m at low tide (Nakamura et al. 2009a). Inshore of the coral reef habitats are seagrass beds, which extend 30–100 m from shore. The reef flat on Tomino reef (0.5–1 m at low tide, 2–3 m at high tide) is characterized by coral rubble and reef rocks. Outside of the coral habitats at these two sampling areas was a sandy sea bottom extending offshore (ca. 15–20 m deep).

Light traps were deployed at 14 different locations within each of the four different types of habitats during the study, in the two areas that were separated by 3 kilometers (Fig. 1). The type of light trap used in these studies is shown



Fig. 3. Underwater photograph of the light trap used in the present study attached to a surface buoy that is connected to a line attached to a bottom anchor, at an outer reef edge sampling site at the Itona reef site.

in detail by Nakamura et al. (2009b) and is shown in Fig. 3 while being deployed on the outer reef margin in front of tabular corals at the Itona reef site. Each rectangular shaped light trap had one 15 mm wide funnel opening on each side of the 520 mm tall, and 330 mm wide, Perspex chamber containing a 6 W fluorescent lamp (National BF-8951). The top of the traps, which were protected by a stainless steel frame on all sides, were attached to a buoy at the surface resulting in the 4 entrance openings of the traps being within the upper 1 m of the water column (Fig. 3). The collection bag (1 mm mesh) at the bottom of the traps permitted substantial water movement into and out of the traps (Nakamura et al. 2009b). The light traps were deployed at 1800 hours and retrieved the following morning at 0900 hours, at various periods of all lunar phases.

The light traps were deployed at one or both of the two sites at various times during late spring and summer during 3 different years. In 2006 they were deployed at Itona reef on 26 July, and 2, 16, 25 August using 2 light traps anchored on the 4 main habitats (tabular corals, branching corals, coral rubble and seagrass beds) and separated from one another by at least 50 m (8 light traps each night). On 22 August 2006, larvae were removed from the traps every 3 h from 19:00 to 07:00 at the seagrass bed and branching coral area using one light trap in each area. In 2007 traps were deployed weekly from 10 May to 26 September (21 times) using 3 light traps anchored on the reef slopes (tabular coral areas) at Itona reef (Fig. 1). In 2008, traps were deployed weekly from 14 April to 16 June (11 times), using 4 light traps anchored on the reef slopes at Itona and Tomino reefs (8 light traps each day), respectively. Water temperature at Ishigaki Island in April was $\sim 25^{\circ}\text{C}$ and in August was $\sim 29^{\circ}\text{C}$.

Immediately after collection, all fish larvae were preserved on ice. Leptocephali samples were sorted from the other fish larvae in the laboratory and were then either frozen or preserved in ethanol. They were later identified to the lowest possible taxonomic categories following Tabeta and Mochioka (1988) and Miller and Tsukamoto (2004), and their total lengths (TL) were measured to the nearest 0.1 mm. The total number of myomeres (TM) and other meristic and morphological features such as pigmentation were examined to separate different species. Photographs of the gut contents of the *Muraenesox cinereus* leptocephalus were taken using a Nikon SMZ-800 dissecting scope and a Sony DSC-W300 digital camera.

Results and Discussion

The deployments of light traps at various times and places within the two study sites at Ishigaki Island between April and August during three different years (N=141 total trap deployments for one night of fishing equivalents) col-

Table 1. Collection data and morphological characteristics of leptocephali collected by light traps at Ishigaki Island, showing their total length (TL, mm), total number of myomeres (TM), developmental stage (meta=metamorphosing), and the lunar period when they were collected (NM=new moon, TQ=third quarter).

Study site	Collection date	Lunar	TL	TM	Species/taxon	Stage
Itona reef-S1	22 Aug 2006	NM	81.0	151	<i>Muraenesox cinereus</i>	Non-meta
Itona reef-S1	22 Aug 2006	NM	75.5	148	<i>Muraenesox cinereus</i>	Non-meta
Itona reef-S2	18 May 2007	NM	68.3	115	Muraeninae	Meta
Itona reef-S3	5 June 2007	TQ	62.8	159	Ophichthinae	Meta
Itona reef-S4	15 June 2007	NM	53.8	118	Muraeninae	Meta
Itona reef-S5	6 May 2008	NM	37.0	113	Muraeninae	Meta
Itona reef-S4	29 May 2008	TQ	79.4	127	Muraeninae	Meta

lected a total of 7 leptocephali. All of these were collected in traps deployed at the Itona reef site, and mostly in the outer reef edge traps. These leptocephali were collected from several days after full moon to just after new moon (Table 1). Muraenid leptocephali were collected in traps deployed at sites S2, S4 and S5, an ophichthid at S3, and the 2 *Muraenesox cinereus* leptocephali were caught together at S1 (Table 1, Fig. 1, 2).

One or possibly 2 species of moray eel leptocephali (37.0–79.4 mm TL) with very similar morphological features of pigmentation and dorsal fin position were collected at 3 of the outer sites (Fig. 2) with 2 being collected on separate dates in both 2007 and 2008 (Table 1). These 4 muraenid leptocephali (family Muraenidae) were of the subfamily Muraeninae and had begun the process of metamorphosis, based on their absence of teeth and thickening of their head (Miller and Tsukamoto 2004; Miller 2009). A 62.8 mm TL metamorphosing ophichthid leptocephalus (snake eels, family Ophichthidae) was also caught at one of the outer reef trap sites in 2007. This specimen and the muraenid leptocephali were at an early stage of metamorphosis before the body starts to become rounded and pigmented (see Tawa and Mochioka 2009). The leptocephali of these two families can not yet be identified to species level in the Indo-Pacific however, due to the large number of species with overlapping morphological and meristic characters and the general lack of similarity between the larvae and adults of eels (Miller and Tsukamoto 2004, 2006).

In contrast to the other specimens collected, 2 pre-metamorphosing leptocephali identified as *Muraenesox cinereus* of the family Muraenesocidae (pike congers) were collected at one of the trap sites (S1) located inshore of the outer reef edge in 2006 (Fig. 2). This site was over the edge of branching *Acropora* corals at a depth of about 2 m (Nakamura et al. 2009a). These two leptocephali were of a similar size (75.5, 81.0 mm TL), and had extensive gut contents (Fig. 4), indicating that they had likely been feeding at the time of capture. They were collected in the trap from 22:00 to 01:00. Based on the apparently rapid evacuation rates of leptocephali after feeding (Mochioka et al. 1993), they had likely

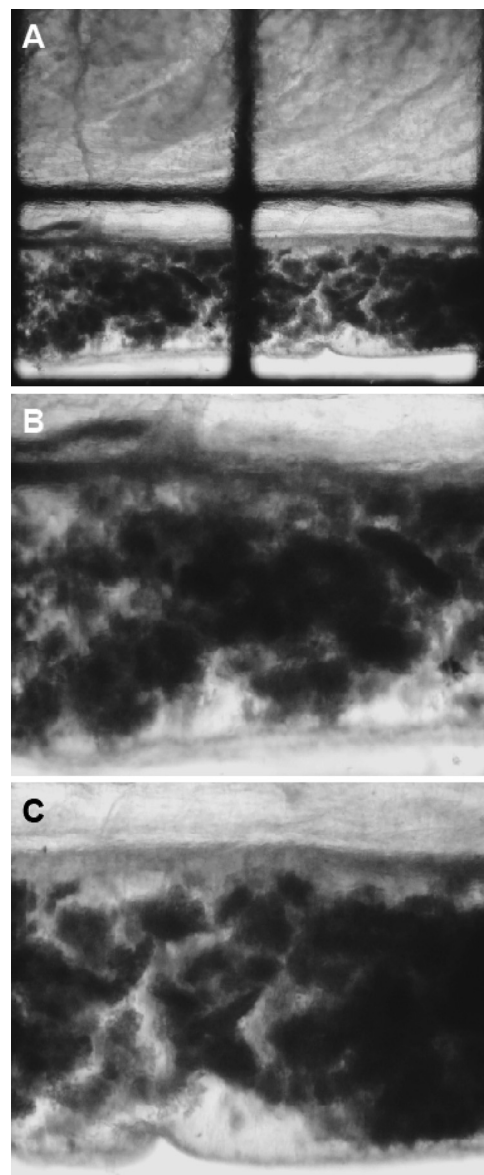


Fig. 4. Photographs of the gut contents inside the intestine of a 75.5 mm *Muraenesox cinereus* leptocephalus collected within the reef area of the Itona reef site. (A) shows the intestine region just behind the kidney and last vertical blood vessel (with a 1 mm horizontal background grid), (B) is an enlargement of the left side of the image of the intestine shown in (A), and (C) is of the right side.

been feeding shortly before entering the trap, or possibly while within the trap, if they entered it soon after it was deployed. The other leptocephali collected during this study did not have food material evident in their guts, because metamorphosing leptocephali do not feed, since their gut is in the process of moving forward (Otake 2003).

The finding of feeding *M. cinereus* leptocephali in an in-shore area of coral reef habitat is an apparently unique observation, since most catches of leptocephali using plankton nets have been made offshore or over the outer shelf and slope (Miller 1995, 2009, Miller et al. 2002, 2006, Miller and McCleave 2007). *Muraenesox* leptocephali however, are typically absent in offshore collections (e.g. Miller et al. 2002, 2006), and therefore they appear to have a very restricted habitat use pattern of living and feeding near shore or possibly over continental shelves. This collection of *Muraenesox* leptocephali while feeding near coral reefs supports the hypothesis that their leptocephali have a very restricted habitat use pattern compared to other families of leptocephali that are frequently collected offshore. Ophichthid leptocephali and those of garden eels (congrid subfamily Heterocongrinae) also appear to have retention mechanisms that limit their offshore distributions (Miller 2009), but not to the extreme degree that is suggested for *Muraenesox* larvae.

Many leptocephali can be collected presumably when they are ready to recruit and enter coral reef and other habitats, such as using set nets and crest nets as mentioned previously (Thorrold et al. 1994a, b, Dufour et al. 1996, Harnden et al. 1999, McIlwain 2003, Nolan and Danilowicz 2008). This is consistent with the collection of the metamorphosing muraenid and ophichthid leptocephali at the outer edge of the reef at Ishigaki Island. These leptocephali may have been approaching the reef as they were metamorphosing in preparation for transformation into small eels and recruitment into the benthic habitats around the island. However, since they would not be feeding during metamorphosis, it raises the question of why they had entered the light traps.

Light traps are known to be selective in what taxa of larval fish they attract and capture, although the reasons for this have generally remained unclear (Doherty 1987, Hernandez and Lindquist 1999, Leis and McCormick 2002). In the case of leptocephali, which do not feed on the zooplankton that are attracted into the trap by the light (and thus attract some types of fish larvae to feed on them), it is even less clear why some leptocephali occasionally enter light traps. It is possible that they are attracted to the region near the light where particulate matter may be more visible, since leptocephali appear to feed exclusively on particles like marine snow or discarded larvacean (appendicularian) houses (Otake et al. 1993, Mochioka and Iwamizu 1996). If many other fish larvae were attracted into a trap, there could be a visible buildup of particles such as fecal material in the traps, which might appear as possible food to a leptocephalus. Or they

may just be curious about the light or the organisms in the trap.

Regardless of the reason why they enter light traps such as in the present study, it appears likely that this is not a common occurrence in light trap studies. In the present study about 8,617 other fish larvae (excluding Clupeidae) entered these traps during the sampling in 2006 compared to only 2 leptocephali (Nakamura et al. 2009a), but total larvae in other years were not enumerated. This low percentage of leptocephali being caught compared to other taxa of fish larvae is also typical of studies such as those on the Caribbean coast of Panama where 9 congrid leptocephali (family Congridae) were collected out of 3,801 total larvae (Wilson 2003). In the Florida Keys, 24 leptocephali of muraenid and ophichthid species were among 7,892 total larvae collected in light traps (Sponaugle et al. 2005). However, many light trap studies have not reported the presence of any leptocephali in their larval fish catches (e.g. Thorrold 1992, Choat et al. 1993, Hernandez and Lindquist 1999, Simpson et al. 2004, D'Alessandro et al. 2007).

Researchers also have conducted studies to evaluate the effectiveness of light traps in relation to other sampling techniques, and some of these studies have collected leptocephali. A comparison of channel nets and light traps on the Great Bahama Bank showed that leptocephali were collected by the channel nets, but not the light traps at the same locations (Anderson et al. 2002). They also found that for fish larvae in general, light traps were more selective taxonomically, and less efficient at the high current site; but they were more efficient than channel nets at the low current site. Carassou et al. (2009) collected Anguillidae, Congridae, Muraenidae (including juveniles), and Nettastomatidae in two types of light traps at New Caledonia, with one type (Ecocean light trap) catching more than another type (Aquafish light trap). No leptocephali were collected by plankton net, underwater seine, or in an artificial reef sampling device though. In contrast, Brogan (1994) caught "anguilliform larvae" in a small plankton net over reefs, but none were collected in light traps in the Gulf of California. Hendriks et al. (2001) collected some congrid, muraenid, and tarpon leptocephali using a light source and dipnets at the surface along the Caribbean coast of Panama and also caught 8 congrid and 71 *Megalops atlanticus* (tarpon, Elopiformes) in light traps. The congrids were only caught in traps deployed 1.5 m off the bottom, but the tarpon larvae were caught both near the bottom and in traps deployed 1.5 m below the surface. In Onslow Bay, North Carolina, on the US east coast, 2 ophichthid leptocephali were collected by neuson nets at the surface, but no leptocephali were collected in two types of light traps (Hernandez and Lindquist 1999). As noted by Leis and McCormick (2002), most studies have found some clear differences in the types of taxa of fish larvae collected by light traps and other sampling methods that are likely related to

the behavioral characteristics of each type of larval fish taxon (Choat et al. 1993, Brogan 1994, Hickford and Schiel 1999, Hendriks et al. 2001, Hernandez and Shaw 2003, Carassou et al. 2009). Current speed can also have an important effect on catches of larval fishes by light traps (Anderson et al. 2002, Lindquist and Shaw 2005).

In the specific case of leptocephali, the low percentage of catches compared to other taxa in tropical light trap studies, and the likely presence of many leptocephali in the region where these studies were conducted, suggest that light traps are not very effective at sampling for leptocephali. Light trap studies in tropical habitats such as the Great Bahama Bank (Anderson et al. 2002), the coast of Panama (Wilson 2003), the Florida Keys (Sponaugle et al. 2005), and the present study at Ishigaki Island were all in areas where many leptocephali are likely present at least nearby. This seems likely based on the abundance of leptocephali found using plankton nets near the Great Bahama Bank, over outer continental shelves, and in western boundary currents passing by some of these areas that were sampled with light traps (Miller 1995, Miller et al. 2002, Miller and McCleave 2007). In addition, channel nets and crest nets have collected many leptocephali moving onshore presumably as they are metamorphosing and recruiting to shallow habitats (Dufour et al. 1996, McIlwain 2003, Thorrold et al. 1994a, b, Nolan and Danilowicz 2008). Leptocephali have also been collected over continental shelves in subtropical areas (Fahay and Obenchain 1978, Castle and Roberston 1974, Miller et al. 2002).

However, it is unclear if many leptocephali actually reside in the water column near coral reef habitats before they move inshore for recruitment (Miller 2009). For example, they may be abundant just offshore where they are collected by plankton nets, but they may not come close to shore where most light traps are deployed until they are ready to recruit and thus are not feeding and would not be attracted to light traps for feeding purposes. There is presently not enough knowledge about the behavior and habitat use patterns of leptocephali to assess this though, because they are very transparent and hard to see, and there are only a few reported observations of leptocephali in coastal waters or at deeper depths (Beebe 1934, Miller 2009, Miller et al. 2009, 2010).

The present study however, verifies that a few metamorphosing leptocephali are occasionally attracted into light traps even if they are not feeding. It also showed for the first time that actively feeding *M. cinereus* leptocephali were attracted into the traps, and that this particular species uses near shore coral reef habitats for feeding in some circumstances at least. Due to the unique feeding ecology of leptocephali that only feed on particulate material (Otake et al. 1993; Mochioka and Iwamizu 1996), perhaps they would not be expected to show a strong attraction to light traps for feed-

ing unless there is an obvious build-up of particulate material in the traps. Although this brief analysis suggests light traps are likely not effective at sampling leptocephali in areas where they would possibly be present, more information is needed about the near-shore presence or absence of leptocephali to know if this is true or not. Behavioral studies on whether or not leptocephali are attracted to light at night are also needed to fully understand the ability of light traps to collect leptocephali.

Acknowledgements

We are grateful to Y. Takada, O. Abe, K. Hashimoto, M. Kobayashi, T. Hayashibara, and A. Nishihara (Seikai National Fisheries Research Institute) for assistance with the fieldwork. We also thank R. Suzuki for providing the aerial photograph of Itona reef. This study was supported by a Research Fellowship of the Japan Society for the Promotion of Science for Young Scientists (No. 18-10371) to Y. Nakamura.

References

- Anderson, T. W., Bartels, C. T., Hixon, M. A., Bartels, E., Carr, M. H. and Shenker, J. M. 2002. Current velocity and catch efficiency in sampling settlement-stage larvae of coral-reef fishes. *Fish. Bull.* 100: 404–413.
- Beebe, W. 1934. *Half Mile Down*. Duell, Sloan and Pearce, New York
- Bell, G. W., Witting, D. A. and Able, K. W. 2003. Aspects of metamorphosis and habitat use in the conger eel, *Conger oceanicus*. *Copeia* 2003: 544–552.
- Brogan, M. W. 1994. Two methods of sampling fish larvae over reefs: a comparison from the Gulf of California. *Mar. Biol.* 118: 33–44.
- Carassou, L., Mellin, C. and Ponton, D. 2009. Assessing the diversity and abundances of larvae and juveniles of coral reef fish: a synthesis of six sampling techniques. *Biodivers. Conserv.* 18: 355–371.
- Castle, P. H. J. and Robertson, D. A. 1974. Early life history of the congrid eels *Gnathopis habenatus* and *G. incognitus* in New Zealand waters. *N. Z. J. Mar. Freshw. Res.* 8: 95–110.
- Castonguay, M. and McCleave, J. D. 1987. Vertical distributions, diel and ontogenetic vertical migrations and net avoidance of leptocephali of *Anguilla* and other common species in the Sargasso Sea. *J. Plankt. Res.* 9: 195–214.
- Choat, J. H., Doherty, P. J., Kerrigan, B. A. and Leis, L. M. 1993. A comparison of towed nets, purse seine, and light aggregation devices for sampling larvae and pelagic juveniles of coral reef fishes. *Fish. Bull.* 91: 195–209.
- D'Alessandro, E. D., Sponaugle, S. and Lee, T. 2007. Patterns and processes of larval fish supply to the coral reefs of the upper Florida Keys. *Mar. Ecol. Progr. Ser.* 331: 85–100.
- Doherty, P. J. 1987. Light-traps: selective but useful devices for quantifying the distributions and abundances of larval fishes. *Bull. Mar. Sci.* 41: 423–431.
- Doherty, P. and McIlwain, J. 1996. Monitoring larval fluxes through the surf zones of Australian coral reefs. *Mar. Freshw. Res.* 47: 383–390.

- Dufour, V. and Galzin, R. 1993. Colonization patterns of reef fish larvae to the lagoon at Moorea Island, French Polynesia. *Mar. Ecol. Progr. Ser.* 102: 143–152.
- Dufour, V., Riclet, E. and Lo-Yat, A. 1996. Colonization of reef fishes at Moorea Island, French Polynesia: temporal and spatial variation of the larval flux. *Mar. Freshw. Res.* 47: 413–422.
- Fahay, M. P. and Obenchain, C. L. 1978. Leptocephali of the ophichthid genera *Ahlia*, *Myrophis*, *Ophichthus*, *Pisodonophis*, *Callechelys*, *Letharchus*, and *Apterichtus* on the Atlantic continental shelf of the United States. *Bull. Mar. Sci.* 28: 442–486.
- Harnden, C. W., Crabtree R. E. and Shenker, J. M. 1999. Onshore transport of elopomorph leptocephali and glass eels (Pisces: Osteichthyes) in the Florida Keys. *Gulf Mex. Sci.* 17: 17–26.
- Hendriks, I. E., Wilson, D. T., Meekan, M. G. 2001. Vertical distributions of late stage larval fishes in the nearshore waters of the San Blas Archipelago, Caribbean Panama. *Coral Reefs* 20: 77–84.
- Hernandez, F. J. Jr. and Lindquist, D. G. 1999. A comparison of two light-trap designs for sampling larval and presettlement juvenile fish above a reef in Onslow Bay, North Carolina. *Bull. Mar. Sci.* 64: 173–184.
- Hernandez, F. J. Jr. and Shaw, R. F. 2003. Comparison of plankton net and light trap methodologies for sampling larval and juvenile fishes at offshore petroleum platforms and a coastal jetty off Louisiana. *Amer. Fish. Soc. Symp.* 36: 15–38.
- Hickford, M. J. H. and Schiel, D. R. 1999. Evaluation of the performance of light traps for sampling fish larvae in inshore temperate waters. *Mar. Ecol. Progr. Ser.* 186: 293–302.
- Lecchini, D., Adjeroud, M., Pratchett, M. S., Cadoret, L. and Galzin, R. 2003. Spatial structure of coral reef fish communities in the Ryukyu Islands, southern Japan *Oceanologica Acta* 26: 537–547.
- Lee, T. W. and Byun, J. S. 1996. Microstructural growth in otoliths of conger eel (*Conger myriaster*) leptocephali during the metamorphic stage. *Mar. Biol.* 125: 259–268.
- Leis, J. M. and McCormick, M. I. 2002. The biology, behaviour, and ecology of the pelagic, larval stage of coral reef fishes. In: Sale PF (ed) *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic, San Diego, pp. 171–199.
- Lindquist, D. C. and Shaw, R. F. 2005. Effects of current speed and turbidity on stationary light-trap catches of larval and juvenile fishes. *Fish. Bull.* 103: 438–444.
- McIlwain, J. L. 2003. Fine-scale temporal and spatial patterns of larval supply to a fringing reef in Western Australia. *Mar. Ecol. Progr. Ser.* 252: 207–222.
- Miller, M. J. 1995. Species assemblages of leptocephali in the Sargasso Sea and Florida Current. *Mar. Ecol. Progr. Ser.* 121: 11–26.
- Miller, M. J. 2009. Ecology of anguilliform leptocephali: remarkable transparent fish larvae of the ocean surface layer. *Aqua-BioSci. Monogr.* 2: 1–94.
- Miller, M. J. and J. D. McCleave. 1994. Species assemblages of leptocephali in the subtropical convergence zone of the Sargasso Sea. *J. Mar. Res.* 52: 743–772.
- Miller, M. J. and J. D. McCleave. 2007. Species assemblages of leptocephali in the southwestern Sargasso Sea. *Mar. Ecol. Progr. Ser.* 344: 197–212.
- Miller, M. J. and Tsukamoto, K. 2004. An introduction to leptocephali: Biology and identification. Ocean Research Institute, University of Tokyo, 96 pp.
- Miller, M. J. and Tsukamoto, K. 2006. Studies on eels and leptocephali in Southeast Asia: A new research frontier. *Coastal Mar. Sci.* 30: 283–292.
- Miller, M. J., Otake, T., Minagawa G., Inagaki, T. and Tsukamoto, K. 2002. Distribution of leptocephali in the Kuroshio Current and East China Sea. *Mar. Ecol. Progr. Ser.* 235: 279–238.
- Miller, M. J., Aoyama, J., Mochioka, N., Otake, T., Castle, P. H. J., Minagawa, G., Inagaki, T. and Tsukamoto, K. 2006. Geographic variation in the assemblages of leptocephali in the western South Pacific. *Deep-Sea Res I* 53: 776–794.
- Miller, M. J., Powel, J. and Tsukamoto, K. 2009. Observation of a large metamorphosing leptocephalus in a coral reef habitat at Sangeang Island, Indonesia. *Zool. Stud.* 48: 107.
- Miller, M. J., D'Avella, M. J. and Tsukamoto, K. 2010. Enlarged chromatophores in an actively swimming ophichthid leptocephalus observed over deep-water off Kona, Hawaii. *Zool. Stud.* 49: 324.
- Mochioka, N. and Iwamizu, M. 1996. Diet of anguillid larvae: leptocephali feed selectively on larvacean houses and fecal pellets. *Mar. Biol.* 125: 447–452.
- Mochioka, N., Iwamizu, M. and Kanda, T. 1993. Leptocephalus eel larvae will feed in aquaria. *Environ. Biol. Fish.* 36: 381–384.
- Nakamura, Y., Shibuno, T., Lecchini, D., Kawamura, T. and Watanabe, Y. 2009a. Spatial variability in habitat associations of pre- and post-settlement stages of coral reef fishes at Ishigaki Island, Japan. *Mar. Biol.* 156: 2413–2419.
- Nakamura, Y., Shibuno, T., Lecchini, D. and Watanabe, Y. 2009b. Habitat selection by emperor fish larvae. *Aquat. Biol.* 6: 61–65.
- Nolan, C. J. and Danilowicz, B. S. 2008. Advantages of using crest nets to sample presettlement larvae of reef fishes in the Caribbean Sea. *Fishery Bull.* 106: 213–221.
- Otake, T. 2003. Metamorphosis. In: Aida K, Tsukamoto K, Yamauchi K (eds) *Eel Biology*. Springer, Tokyo. pp. 61–74.
- Otake, T., Ishii, T., Ishii, T., Nakahara, M. and Nakamura, R. 1997. Changes in otolith strontium:calcium ratios in metamorphosing *Conger myriaster* leptocephali. *Mar. Biol.* 128: 565–572.
- Otake, T., Nogami, K., and Maruyama, K. 1993. Dissolved and particulate organic matter as possible food sources for eel leptocephali. *Mar. Ecol. Progr. Ser.* 92: 27–34.
- Sato, M. and Yasuda, F. 1980. Metamorphosis of the leptocephali of the ten-pounder, *Elops hawaiiensis*, from Ishigaki Island, Japan. *Japanese J. Ichthyol.* 26: 315–324.
- Shibuno, T., Nakamura, Y., Horinouchi, M., and Sano, M. 2008. Habitat use patterns of fishes across the mangrove-seagrass-coral reef seascape at Ishigaki Island, southern Japan. *Ichthyol. Res.* 55: 218–237.
- Simpson, S. D., Meekan, M. G., McCauley, R. D. and Jeffs, A. 2004. Attraction of settlement-stage coral reef fishes to reef noise. *Mar. Ecol. Progr. Ser.* 276: 263–268.
- Smith, D. G. 1989. Introduction to leptocephali. In *Fishes of the Western North Atlantic*. Böhlke, E. B. (ed.), pp. 657–668, Part 9, Volume 2, Sears Foundation for Marine Research, New Haven.
- Sponaugle, S., Lee, T., Kourafalou, V., and Pinkard, D. 2005. Florida

- Current frontal eddies and the settlement of coral reef fishes. *Limnol. Oceanogr.* 50: 1033–1048.
- Tabeta, O. and Mochioka, N., 1988. Leptocephali. *In* An atlas of the early stage fishes in Japan, Okiyama, M. (eds.), pp. 15–64, Tokai University Press, Tokyo. (in Japanese)
- Tawa, A. and Mochioka, N., 2009. Identification of aquarium-raised muraenid leptocephali, *Gymnothorax minor*. *Ichthyol. Res.* 56: 340–345.
- Thorrold, S. R. 1992. Evaluating the performance of light traps for sampling small fish and squid in open waters of the central Great Barrier Reef lagoon. *Mar. Ecol. Progr. Ser.* 89: 277–285.
- Thorrold, S. R., Shenker, J. M., Mojica, R., Maddox, E. D. and Wishinski, E. 1994a. Temporal patterns in the larval supply of summer-recruiting reef fishes to Lee Stocking Island, Bahamas. *Mar. Ecol. Progr. Ser.* 112: 75–86.
- Thorrold, S. R., Shenker, J. M., Maddox, E. D., Mojica, R. and Wishinski, E. 1994b. Larval supply of shorefishes to nursery habitats around Lee Stocking Island, Bahamas. II. Lunar and oceanographic influences. *Mar. Biol.* 118: 567–578.
- Wilson, D. T. 2003. The arrival of late-stage coral reef fish larvae in near-shore waters in relation to tides and time of night. *In*: The Big Fish Bang. *Proceed. of 26th Ann. Larval Fish Conf.* 2003. Edited by H. I. Browman and A. B. Skiftesvik. Institute of Marine Research, Bergen, Norway. pp. 345–364.