A Novel Association between Larval and Juvenile *Erythrocles schlegelii* (Teleostei: Emmelichthyidae) and Pelagic Tunicates

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We describe the first documented associations between an emmelichthyid and a pelagic tunicate. An in situ observation of larval and juvenile Japanese Rubyfish, *Erythrocles schlegelii* (Emmelichthyidae) was made during blackwater scuba dives in the epipelagic waters off the coast of the Philippines. The fish were in close association with the pelagic salp *Pegea confoderesa* (Thaliacea; Salpidae), either drifting alongside a colony of salps or residing inside individual salp cavities. Our results describe and illustrate this behavior, highlighting a previously undocumented family of fishes that associates with pelagic gelatinous invertebrates. This finding also demonstrates the importance of community science to further our understanding of the early life history of marine fishes.

OVER the last century, several studies have documented intimate interactions between juvenile fishes and pelagic gelatinous zooplankton, informally referred to as gelata (sensu Haddock, 2004), including cnidarians, ctenophores, pyrosomes, and salps (e.g., Mansueti, 1963; Haedrich, 1967; Horn, 1970; Janssen and Harbison, 1981; Jenkins, 1983; Arai, 1988; Harbison, 1993; Purcell and Arai, 2001; Ohtsuka et al., 2009). It is thought that fishes, particularly at early stages of life, benefit from an association with gelatinous marine organisms, as the gelata offer a complex, three-dimensional structure for refuge in a pelagic environment that is usually devoid of physical complexity (Mansueti, 1963; Lynam and Brierley, 2007; Griffin et al., 2019). In addition, gelata may also provide fishes with feeding opportunities in an environment where food resources are naturally scarce. Juvenile fishes may feed on the zooplankton captured by the flow of water through the gelata, those captured by jellyfish tentacles, the parasites of their host, or even feed on the gelata itself (Mansueti, 1963; Janssen and Harbison, 1981; Harbison, 1993; Riascos et al., 2012; Griffin et al., 2019). Currently, 20 families of fishes have been reported to associate with gelata, i.e., Amariopidae, Arionmatidae, Balistidae, Bathylagidae, Bramidae, Bythitidae, Carangidae, Caristiidae, Centrolophidae, Ephyppidae, Gadidae, Girellidae, Icosteidae, Myctophidae, Nomeidae, Sparidae, Stromateidae, Syngnathidae, Tetragonuridae, and Zaproridae (Mansueti, 1963; Janssen and Harbison, 1981; Auster et al., 1992; Harbison, 1993; Kingsford, 1993; Purcell and Arai, 2001; Drazen and Robison, 2004; Lynam and Brierley, 2007; Nonaka et al., 2021; Pastana et al., 2022).

Fish typicaly associate with scyphozoans (i.e., true jellyfishes), although associations may also be formed with other cnidarians, such as hydrozoans and cubozoa (Mansueti, 1963; Maul, 1964; Jenkins, 1983; Harbison, 1993; Purcell and Arai, 2001; Lawley and Júnior, 2018). Outside cnidarians, fishes also associate with tunicophores (Matthews and Shoemaker, 1952; Mansueti, 1963; Purcell and Arai, 2001). However, relatively few fishes associate with tunicates, such as salps and pyrosomes (Janssen and Harbison, 1981; Harbison, 1993).

The Emmelichthyidae, or rovers, is a small family of planktivorous fishes with 18 valid species classified in three genera: *Emmelichthys* (seven species), *Erythrocles* (six species), and *Plagiogonion* (five species; Heemstra and Randall, 1977; Johnson, 1980; Fricke et al., 2021). These fishes occur circumglobally in moderately deep coastal waters and are recognized morphologically by having highly protractile premaxillae, both jaws toothless or with few minute conical teeth, scaled and distally expanded maxillae, well-developed supramaxillae, and a large rostral cartilage (Heemstra and Randall, 1977; Johnson, 1980: fig. 18). Little is known about the biology and life history of rovers. According to Heemstra and Randall (1977), adults live in the epi- to mesopelagic zone and are usually found near the ocean floor at depths ranging from 100–400 m. Additionally, species such as *Plagiogonion rubiginosum* associate with drifting algae at or close to the ocean surface (Kingsford, 1992, 1993; Castro et al., 2002). Few accounts on the larval or juvenile stages of rovers have been published, and these are limited to brief descriptions of their morphology or color pattern (e.g., Nakahara, 1962; Heemstra and Randall, 1977; Neira et al., 2008). Herein, we describe the first documented association between larval and juvenile emmelichthiids and pelagic tunicates, providing not only significant information about the life history of rovers, but also about the unusual behavior of fishes associating with pelagic marine invertebrates.

**MATERIALS AND METHODS**

**Observations from dives.**—All night epipelagic (blackwater) drift dives were conducted by M. Bartick in the Philippines. Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX Photo documentation was made using a Nikon D500 or D850 camera with a 60 mm lens, a Sea & Sea MDX
Peninsula. Salps and fish were encountered and photographed (Fig. 1B) at an approximate depth of 15 m. Average depth of dive location was 200 m. Average depth of divers during scuba dive was 18 m. Average water temperature was 25°C. March 16, 2020, circa 21:00 local time (GMT+8). Anilao, Balayan Bay, Calampan Peninsula. Average depth of dive location was 152 m. Average depth of divers during scuba dive was 22 m. Average water temperature was 26.6°C. Salp and fish were encountered and photographed (Fig. 1C) at an approximate depth of 18 m. November 13, 2021, circa 20:00 local time (GMT+8). One mile off the coast of Negros Oriental, Zamboanguita province, Philippines. Average depth of dive location was 235 m. Average depth of divers during scuba dive was 13 m. Average water temperature was 27.7°C. Salps and fish were encountered and photographed (Fig. 1A) at an approximate depth of 20 m. Divers drifted approximately 215 m from entry point to location of photograph.

**Identification of organisms.**—Using the photographs and locality information, we compared the fish images to the color patterns, dorsal-fin morphology, and dorsal- and anal-fin ray counts listed in the studies of Nakahara (1962), Heemstra and Randall (1977), and Johnson (1984). Counts were made by hand and aided by the count tool in available in Adobe Photoshop. Once we identified the photographed fish species, we examined museum specimens to confirm their identity. A list of comparative materials used in this study can be found in the Material Examined section, with symbolic codes for institutional resources following Sabaj (2020). Identifications of the tunicates were made using Gershwin et al. (2014).

**RESULTS**

Photographed specimens were identified as two ontogenetic stages of *Erythrocles schlegelii* near or within *Pegea confoederata* (Thaliacea; Salpidae). Fish body shape and pigmentation is
depicted in Figure 1. Meristic and morphometric information taken from the photographs are as follows: body elongate-oval, moderately compressed. Greatest body depth slightly anterior to dorsal-fin origin. Dorsal-fin XI, 11, origin approximately at first third of body. Base of first dorsal-fin spine inserted slightly posterior to vertical through origin of the pelvic fin, base of last unbranched dorsal-fin ray slightly anterior to vertical through origin of the anal fin. Dorsal fin notched almost to base in front of soft-rayed portion. Anal fin III, 9, inserted slightly posterior to vertical through second dorsal fin. Caudal fin forked, lobes of similar size. Principal caudal-fin rays 17 (I,8,7,1).

Live coloration of the specimens in Figure 1A and B with conspicuously divided pigmented anterior half and transparent/hyaline posterior half. Background coloration of anterior half of the body dark brown. Pigment starting from the vertical through the anterior orbital rim and extending onto the vertical through the seventh to eighth dorsal-fin spine, body transparent posterior to that point. Pigmentation lacking on the upper and lower jaws. Eyes yellow to light green. Opercular and subopercular regions orange to light brown. Dorsal fin darkly pigmented from first to seventh or eighth spine, hyaline posteriorly. Pectoral fin hyaline. Pelvic-fin rays and interradial membrane with dark pigment along proximal three-quarters of their length, hyaline distally. Anal and caudal fins hyaline. Photographed specimens were not collected.

Live coloration of the specimen in Figure 1C with a conspicuous barred pattern. Ground coloration gray, slightly darker dorsally. Eyes golden yellow to greenish. Body marked by six vertical bars of similar width extending through the entire depth of the fish’s body. Bars mostly dark brown, with yellow to gold margins. First bar located on the head, between vertical through anterior margin of the orbital rim and the preopercular region; second bar at the predorsal region, extending ventrally onto the posterior margin of the opercle, reaching the base of the pectoral fin; third bar at the dorsal-fin base, from the third or fourth to seventh or eighth dorsal-fin spines, spreading vertically to the ventral midline of the body; fourth bar starting at the base of the second dorsal fin, from the tenth or eleventh spine to the third or fourth soft ray, ventrally reaching first anal-fin spine to second soft ray; fifth bar located between vertical through eighth soft ray and anterior portion of caudal peduncle, extending ventrally to base of last four anal-fin rays; sixth bar roundish, lighter in color, resembling a dark blotch starting at the posterior portion of the caudal peduncle and extending onto the hypural plate. First to eighth dorsal-fin spines yellow, posterior dorsal-fin spines and rays pigmented basally, hyaline distally. Pectoral fin hyaline. Pelvic fin mostly pigmented, except from hyaline distal tips of fin rays. Three anal-fin spines and first two soft rays yellow, pigment restricted to basal portion of the soft rays and spines. Caudal fin grayish proximally, hyaline distally.

**DISCUSSION**

According to Heemstra and Randall (1977) and Johnson (1980), there are three valid genera in the Emmelichthyidae: *Emmelichthys*, *Erythrocles*, and *Plagiogeneion*. The three genera differ from each other based on the degree of separation between first and second dorsal fins and length of the first dorsal-fin base (Heemstra and Randall, 1977; Johnson, 1980). Species of *Erythrocles* are the only rovers where the first (spinous) and second (soft) dorsal fins are divided to the base (vs. dorsal fin not conspicuously notched in *Plagiogeneion*; anterior and posterior dorsal fins conspicuously separated with isolated spines in *Emmelichthys*). Additionally, the length of the spinous portion of the dorsal fin is less than the head length in *Erythrocles* (vs. spinous portion greater than head length in *Emmelichthys*). We were able to identify the specimens in our images as *E. schlegelii* based on the fin shape and pigment pattern as described and illustrated by Nakahara (1962: figs. 5, 7). Larvae of this species have a conspicuous color pattern, wherein pigmentation along the flank is divided into a pigmented anterior half and non-pigmented posterior half. Larger juveniles of *E. schlegelii* have six distinctive dark bars along the head and body. Based on the descriptions of Nakahara (1962), we estimate a total length of about 10 mm for the larval specimens in Figure 1A and B and about 25 mm for the juvenile specimen in Figure 1C.

This is the first documented report of an emmelichthyid associating with a species of salp. Previous data on larval and juvenile emmelichthyids indicate that these fishes are more abundant around drifting algae than in open water (Kingsford, 1992, 1993; Castro et al., 2002), but no previous studies have described rovers associating with pelagic gelatinous organisms. Only a few fishes are known to associate with salps or pyrosomes, those being representatives of the families Amarsipidae, Carangidae, Nomeidae, Sparidae, and Tetragonuridae (Janssen andHarbison, 1981; Harbison, 1993; Pastana et al., 2022). Our observations suggest that, like members of the previously mentioned families, early stages of the Japanese Rubyfish associate with salps for shelter. During our observations in 2018, 2020, and 2021, individual fish appeared to remain motionless inside a salp or around the salp colony, drifting along with the ocean current. The Japanese Rubyfish were seen entering the salp headfirst through the atrial siphon and orienting with their heads pointing toward the salp’s mouth. Many individuals could be observed among the same salp chain, and on some occasions, individual fish would shelter in a salp on its own (Fig. 1B). Potential predators, such as squids or other fishes, were spotted near the salp chain during dives. When camera lights shined on the fish and salps for extended periods, or when multiple divers surrounded the colony, the Japanese Rubyfish often abandoned their individual salp, either moving to another individual along the chain or remaining near the colony until the disturbance subsided (Fig. 1A, B). On a few occasions of illumination or disturbance, the fish completely abandoned their salps, swimming toward deeper waters. Current hypotheses assessing the association of fishes with pelagic gelatinous invertebrates indicate that young fishes find shelter and protection within the gelata (Mansueti, 1963; Griffin et al., 2019). According to these hypotheses, pelagic ctenophores, jellyfishes, pyrosomes, or salps provide a complex three-dimensional structure that offers larval or juvenile fishes refuge in a pelagic environment known for its remarkable uniformity. Our observations support this hypothesis and indicate that *E. schlegelii* use both solitary salps and salp colonies as shelter during early life history stages (Fig. 1).

In addition to shelter and protection, pelagic gelatinous organisms also provide young fishes with feeding opportunities. Juvenile fishes may feed on the parasites of gelata,
steal their prey, or feed directly on the pelagic invertebrates
in which they are sheltering. According to Heemstra and
Randall (1977), the adult morphology of emmelichthyids indicates
that they feed heavily on zooplankton. Moreover, observations by previous researchers and our own in this
study highlight the presence of a few minute teeth in the oral
jaws, or the complete absence thereof, coupled with bristle-
like teeth in the pharyngeal structures of some emmelich-
thyid species (Heemstra and Randall, 1977; Johnson, 1980).
This suggest that emmelichthyids predominately feed on
planktivorous organisms. While adults may be active
plankton pickers, it is possible that early stage emmelich-
thyids could be feeding on food resources captured by or
passing through the salps.

Information on the biology and life history of emmelich-
thyids is scarce, and data on the behavior of early stage E.
schlegeli has been virtually unknown prior to this study. The
captured images and videos of this behavior by blackwater
divers were critical to this study, and we stress the importance
of fostering community science collaborations like those in
this study. The recent study by Nonaka et al. (2021) similarly
highlights the importance of community science, as the
images and videos captured by divers provided critical data on
the morphology of the larvae of marine fishes, and their
interactions with other planktonic organisms. We hope others
interested in increasing our understanding of the early life
history of marine fishes view this study as an example of how
scientifically informative these collaborations can be.

MATERIAL EXAMINED

Emmelichthys nitidus: USNM 306086 (3 ethanol; 70.1–71.8
mm standard length [SL]).

Emmelichthys struhsakeri: USNM 388679 (5 ethanol, 1 cleared
and double-stained; 78–94 mm SL); USNM 424606 (1 ethanol; 117.1 mm SL).

Erythrocles acarina: USNM 306080 (1 ethanol; 111.2 mm SL).

Erythrocles monodi: USNM 405223 (1 ethanol; 76.7 mm SL).

Erythrocles schlegeli: USNM 266501 (1 ethanol; 16.6 mm SL);
USNM 403355 (1 ethanol; 240 mm SL).

Plagiogeneion fiolenti: USNM 307758 (paratype, 2 ethanol;
154.4–162.7 mm SL).

DATA ACCESSIBILITY

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com/groups/Blackwaterphotogroup/), an online forum that
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