Note

Larvae of the threadsail filefish *Stephanolepis cirrhifer* feed on eggs and planulae of the jellyfish *Aurelia* sp. under laboratory conditions

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Abstract: Although population dynamics of the egg and planula stages of jellyfish are key factors that predict the abundance of polyps and subsequent jellyfish blooms, information about predation on these stages of jellyfish is lacking. We examined whether threadsail filefish *Stephanolepis cirrhifer*, an efficient predator of *Aurelia* sp. medusae in the wild, could feed on eggs or planulae of *Aurelia* under laboratory conditions. *S. cirrhifer* larvae at 17 days post hatching (dph) with 4.9±0.8 mm standard length fed on significantly more eggs or planulae (maximum value: 151 inds. per 15 min.) than other growth stages of *S. cirrhifer* larvae (0–18 inds. per 15 min.). Considering prey-size selectivity in fish larvae, the mouth size of *S. cirrhifer* at 17 dph matches well with consuming jellyfish eggs or planulae as prey. These results suggest that *S. cirrhifer* larvae, during their free-swimming stage or possibly at the beginning of their jellyfish-commensal stage, can be potential predators of eggs or planulae of jellyfish.

Key words: filefish, jellyfish, planula, predator, prey-size selectivity

Cnidarian jellyfish generally have both a sessile stage, i.e., polyp, and a planktonic stage, i.e., egg, planula and medusa, during their life history. Although population dynamics of jellyfish have been considered difficult to predict because of their complex life history (Conley & Uye 2015), Schneider & Behrends (1994) reported that the abundance of medusae of the jellyfish *Aurelia aurita* (L.) was affected by the population size and survival of planulae, polyps, and ephyrae. The abundance of planulae in particular determines that of polyps, which asexually produce ephyrae, and thus may have a strong influence on jellyfish blooms (Lucas 2001). There have been a substantial number of publications on the predators of polyps and medusae. For instance, nudibranchs actively feed on jellyfish polyps (Hernroth & Gröndahl 1985, Hoover et al. 2012), birds (Suazo 2008), marine turtles (Holland et al. 1990), and at least 124 fish species (Arai 1988, Pauly et al. 2009) have also been reported to feed on medusae. However, to our knowledge, there is a lack of information on predators of the planktonic larval stages of jellyfish, such as eggs or planulae.

The threadsail filefish *Stephanolepis cirrhifer* (Temminck & Schlegel) is a coastal fish inhabiting Western Pacific waters from off Hokkaido to the East China Sea (Ivankov & Samylov 1979, Randall & Lim 2000) and a major predator of medusae (Masuda et al. 2008). It spawns adhesive demersal eggs in summer (Fujita 1988) and after a free-swimming pelagic stage, either individuals or schools of larvae and juveniles (6–30 mm standard length [SL]) often associate with various medusae, such as the giant jellyfish *Nemopilema nomurai* (Kishinouye) or another rhizostome jellyfish *Rhopilema asamura* Uchida (Masuda 2006). Juveniles reaching 20–30 mm SL tend to settle near coastal rocky reefs or seaweed bed habitats and are generally solitary (Masuda et al. 2010). The jellyfish *Aurelia* spp. are distributed worldwide in coastal areas from 70°N to 40°S latitude (Yasuda 2003), and they spawn in the summer (Conley & Uye 2015). Spawned eggs are held in the brood pouches on the oral arms of medusae (Yasuda 2003). Planulae hatched from eggs are released from medusae and spend approximately 1 h to one week as planktonic organisms before settlement and metamorphosis into polyps in coastal areas (Gröndahl 1989, Lucas 2001, Vagelli 2007). Therefore, *S. cirrhifer* are likely to encounter either planktonic or sessile stages of this jellyfish or other coastal species during their life cycle. During summer, although larval, juvenile, or adult *S. cirrhifer* may encounter planulae of the jellyfish, these may be too small as prey for either juvenile or adult *S. cirrhifer*. The egg or planula of *Aurelia* sp. has a round shape of approximately 120–230 µm in diameter or an oval shape of approximately 200–300 µm in length, respectively; there are, however, eggs and planulae twice as large as the normal ones known from the Sea of Japan (reviewed by Yasuda 2003). Our goal was to reveal a potential mechanism...
for top-down control from fish to the early stages of jellyfish. To this end, we examined whether *S. cirrhifer* larvae can feed on eggs or planulae of the jellyfish *Aurelia* sp. under laboratory conditions.

*Stephanolepis cirrhifer* of 2, 7, 12, 17, and 22 days post hatching (dph) were selected for the study (Fig. 1). Fertilized eggs of *S. cirrhifer* were purchased from a private hatchery (Nisshin Marine Tech, Aichi, Japan) and transferred to the Maizuru Fisheries Research Station of Kyoto University (MFRS; 35°29′N, 135°22′E) located on Wakasa Bay, Sea of Japan. The eggs of *S. cirrhifer* were immediately placed into two 500 L circular tanks (104 cm×64 cm, diameter×depth) with a continuous supply of filtered seawater. *Stephanolepis cirrhifer* eggs hatched on 3 July 2011. We reared the fish outdoors without direct sunlight, and they were fed SS-type rotifers *Brachionus rotundiformis* Tschugunoff of approximately 90–150 µm in length (Tanaka et al. 2005) for 2–10 dph, S-type rotifers *B. rotundiformis* of approximately 90–170 µm for 10–12 dph and L-type rotifers *B. plicatilis* Müller of approximately 110–240 µm and *Artemia* spp. nauplii of approximately 540–850 µm (Harada & Yamamoto 2000) from 13 dph onward. The SL of ten fish from each experimental age group was measured using a stereomicroscope, and yielded the following results: 2 dph: 2.4±0.1 mm; 7 dph: 2.7±0.2 mm; 12 dph: 3.8±0.5 mm; 17 dph: 4.9±0.8 mm; 22 dph: 8.7±1.4 mm (mean±SD). The notochord length was treated as SL in larvae until flexion of the spinal cord was complete.

Mature females of *Aurelia* medusae (umbrella diameter: 19.4±3.6 cm, mean±SD) were collected from a floating dock at the MFRS and within 5 min were transferred via a bucket to a 500 L circular tank with a continuous supply of filtered seawater. These medusae were used for the study within 24 h of collection.

One mature female medusa was placed in a 10 L transparent circular tank (experimental tank: 30 cm×15 cm, diameter×depth) filled with filtered seawater, left for 15 min, and subsequently removed. In this way, eggs (or planulae) were released from the medusa with mucus. The presence of both eggs and planulae was confirmed based on images of the gut contents of *S. cirrhifer* (see below, Fig. 2). However, in some cases, they were difficult to discriminate; therefore, for the purposes of the present study, we used the expression “eggs (or planulae)” to represent either/both forms. The experimental seawater was stirred a few times using a glass rod just after removal of the medusa. Subsequently, 5 mL of seawater was sampled from the experimental tank using a 10 mL pipette to estimate the density of eggs (or planulae). Ten *S. cirrhifer* larvae from each age group were placed in the experimental tanks and left for 15 min. One experimental tank and one medusa were used for each age group of *S. cirrhifer* larvae. The experiment was conducted at 0900–1200 at ambient water temperature (24.9±1.0°C, mean±SD). *Stephanolepis cirrhifer* larvae were then euthanized using an overdose of 2-phenoxyethanol, and the number of jellyfish eggs (or planulae) in the sampled seawater and gut contents was immediately counted using a stereomicroscope. Each *S. cir-
larva was placed on a glass slide and its gut contents were egested from the anus by gently squeezing the body using a cover glass. During the course of the study, accidental mortality of *S. cirrhifer* larvae due to handling stress was evident in one, three, one, and one individuals at 7, 12, 17, and 22 dph, respectively; these fish were omitted from the analysis. For statistical analysis, owing to the heteroscedasticity of the data, the Kruskal–Wallis test was applied, followed by the Steel–Dwass test as a post-hoc test, to compare the number of eggs (or planulae) in the gut contents of *S. cirrhifer* larvae among the age groups, using the JMP version 5.0.1 J software (SAS Institute; www.sas.com). The statistical significance level was set at $\alpha = 0.05$.

Jellyfish eggs (or planulae) were observed in low numbers at every stage of larvae tested, with the exception of the 17 dph age group (4.9±0.8 mm SL, Fig. 3). Larvae at 17 dph fed on 151 eggs (or planulae) per 15 min (maximum value) and the number of jellyfish eggs (or planulae) in their gut contents was significantly higher in comparison to other age groups ($p < 0.05$). Fish at this age frequently pecked on the mucus left by the medusa. The diameter of the jellyfish eggs (or planulae) collected from the *S. cirrhifer* gut contents was approximately 150–200 µm, although this could not have been measured accurately because most were deformed owing to the experimental procedure for egestion. Jellyfish eggs (or planulae) were not found in any of the seawater samples, indicating that they were either present at low densities or were not evenly distributed throughout the experimental tank.

To our knowledge, this is the first report of any significant predation on jellyfish eggs or planulae by fish, albeit under laboratory conditions. Only *S. cirrhifer* larvae at 17 dph fed on a substantial number of jellyfish eggs (or planulae), although the present study could not provide data on the absolute feeding efficiency. In natural waters, *Aurelia* sp. hold their eggs in the brood pouches and release only planulae, and so *S. cirrhifer* larvae would have few chances to feed on these eggs unless they directly attacked the brood pouches.

The body length and/or mouth size are major determinants of prey-size selectivity in fish larvae (Hunter 1981). *Stephanolepis cirrhifer* larvae used in the present study were fed SS- or S-type rotifers up to 12 dph (3.8±0.5 mm SL). In the present study, only the normal size of eggs or planulae of approximately 150–200 µm long were observed. Therefore, considering the prey size of *S. cirrhifer* larvae up to 12 dph in the present study, jellyfish eggs (or planulae) may have been too large to be suitable prey, although whether *S. cirrhifer* at this stage can feed on larger prey than S-type rotifers is still unknown.

In contrast, *S. cirrhifer* larvae at 17 dph would have fed mainly on L-type rotifers in the present study and then shifted to *Artemia* spp. nauplii even as they continued to grow. The size of eggs (or planulae) of *Aurelia* sp. in the present study was within the typical size range of L-type rotifers. Therefore, it is likely that the average size of the eggs (or planulae) of *Aurelia* sp. may have matched well with the mouth size of *S. cirrhifer* larvae specifically at 17 dph (4.9±0.8 mm SL). However, the same did not apply for *S. cirrhifer* larvae at 22 dph (8.7±1.4 mm SL). Nevertheless, no eggs or planulae were observed in the sampled seawater; therefore, we cannot exclude the possibility that the density of eggs (or planulae) in the experimental tanks had not been
equal among the respective age groups. In addition, because of the lack of replications in the experimental tank, we cannot exclude the possible difference between the condition of eggs (or planulae) and/or handling stress.

*Stephanolepis cirrhifer* exhibits ontogenetic change in its predator–prey interactions with *Aurelia* sp. (Miyajima-Taga et al. 2016). Although early larvae of *S. cirrhifer* are preyed upon by medusae, the development of avoidance ability to escape predation, and tolerance to nematocyst strings in *S. cirrhifer* larvae arise from 3 mm SL, the size of the free-swimming pelagic stage, and are complete at 6 mm SL, the size at which they start to associate with jellyfish. They then become capable of feeding on medusae at 22 mm SL. Therefore, *S. cirrhifer* larvae are likely to feed on eggs or planulae of jellyfish at the free-swimming pelagic stage or possibly at the beginning of the jellyfish-commensal stage. Mucus of *Aurelia* sp. usually includes nematocysts, although in the present study some nematocysts in the mucus might have been discharged by the stirring before larvae were introduced. Considering that the *S. cirrhifer* larvae might have fed on the eggs (or planulae) in mucus, their nematocyst tolerance might have affected the feeding behavior.

In this commensal relationship, *N. nomurai* is a frequent host of *S. cirrhifer* juveniles. This jellyfish species has slightly smaller eggs and planulae than *Aurelia* sp.; Kawahara et al. (2006) reported that the size of eggs was 60–80 µm in diameter and planulae were 170 µm in length and 130 µm in width, whereas Toyokawa et al. (2010) suggested that the mature oocytes would be 73–108 µm and approximately 180 µm maximum. Also, they spawn fertilized eggs rather than planulae. Thus, *S. cirrhifer* larvae may feed on eggs (or planulae) of *N. nomurai* at a smaller size than that demonstrated in the present study. The next stage of the study will be to detect fish larvae feeding on jellyfish eggs or planulae in natural waters, and thus to evaluate the potential mechanism of top-down control by larval fish on jellyfish abundance.

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