Piscivory of the Japanese giant box jellyfish *Morbakka virulenta*

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Abstract: In this study, we investigated the trophic interactions between the Japanese giant box jellyfish, *Morbakka virulenta*, and fish in the central part of the Seto Inland Sea, western Japan, in autumn and winter. Occurring in the surface waters at nighttime, these cubomedusae, regardless of their size (1.5 to 22.5 cm in bell height), were found to be piscivorous, feeding mainly on the Japanese anchovy, as shown by their stomach contents analysis. This finding was supported by a stable isotopic analysis and by an unchanged cnidome, irrespective of the bell height of medusae. Their nocturnal occurrence near the surface often took place around the slack tide, during which the medusae were foraging with tentacles fully extended. Other associations between the medusae and fish were also observed at this time: presumed commensalism with juvenile Japanese horse mackerel, and predation by black scraper.

Key words: *Morbakka virulenta*, piscivory, Seto Inland Sea, symbiosis

Introduction

Recently, much attention is being paid to the biology of cubozoans, partly due to their enigmatic phylogenetic position within the Cnidaria (Collins et al. 2006, Benthage et al. 2010) and partly because of their unique features, such as strong toxins (Bloom et al. 1998, Nagai 2003), elaborate elegance and brainless eyes (Skogh et al. 2006, Garm et al. 2011), and the formation of creeping/swimming polyps (Toshino et al. 2013). However, the studies on cubozoans remain fewer than those on scyphozoans, probably because of their relatively restricted distribution, being confined to the tropical and subtropical regions (Toshino et al. 2013).

The Japanese giant box jellyfish *Morbakka virulenta*

(Kishinouye, 1910) (formerly *Tamoya haplonema* Müller, 1859 *sensu* Uchida (1929)) (Fig. 1), belongs to the newly established family Carukiidae of the order Carybdeida (Benthage et al. 2010), and occurs near the surface along the coasts of western Japan in autumn and winter (Kishinouye 1910, Uchida 1970, Yamada et al. 2010, Toshino et al. 2013, Okada et al. 2014). It is unique among cubomedusae species in that the fully mature adults occur from autumn to winter (Toshino et al. 2013). Its life cycle, partly clarified by Toshino et al. (2013), is characterized by: (1) the formation of blastocyst, (2) attachment of the basal disc of the polyp to the inside egg membrane, and (3) release of the swimming polyps after budding. According to Toshino et al. (2013), these unique features are most likely related to its habitat, in which suitable hard bottoms for settlement are not readily available. However, the behavior, feeding, and biological associations of *M. virulenta* have not yet

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Fig. 1. Swimming individual of *Morbakka virulenta* (about 20 cm in bell height) observed at floating pier on Ikunoshima Island, the Seto Inland Sea, on December 12, 2014.

been investigated. Although the medusae generally play a wide variety of roles as predators, prey, and hosts in the pelagic realm (Arai 1988, 2005, Purcell & Arai 2001, Ohtsuka et al. 2009), the interactions between the cubozoans and other animals are hardly ever reported.

The present study surveyed the nocturnal feeding of *M. virulenta* in the Seto Inland Sea and provides information on the commensal and/or predatory fish. The symbioses between the cubomedusae and fish are also reviewed.

Materials and Methods

Observations of nocturnal behavior under the street light

The observations of the nocturnal behavior of *Morbakka virulenta* were conducted at Ondo Port (34°11'36"N, 132°32'07"E) (depth at spring tide: 3.2–16.0 m) located in the western part of the Seto Inland Sea, western Japan on December 19, 2011, and from September 2012 to February 2013 (Fig. 2). Since our preliminary observations from 2009 to 2011 revealed that the occurrence of *M. virulenta* near the surface was restricted to the nighttime from autumn to winter, the present surveys were carried out only during the nighttime. The number of swimming individuals near the surface was counted within 5 minutes once per hour over an area (ca. 200 m²) illuminated under a street light from before sunset to after dawn on November 20–21 (neap tide), December 1–2 (half tide), and December 11–12 (middle tide) in 2012 in order to record their abundance in the near-surface waters. The observation area was calculated from an aerial photomap. The illuminance of sea surface under the street light was measured using an illuminometer (LX-1108, Mothertool Co. Ltd.) at each sampling. The surface water temperature and salinity were simultaneously recorded using a direct reading conductivity-temperature-depth profiler (ACTD-RS, JFE Advantech Co. Ltd.), respectively.

Stomach content analysis

The collections of *Morbakka virulenta* medusae with full stomachs were made mainly at Ondo Port in Hiro-

Fig. 2. Sampling sites for *Morbakka virulenta* in the Seto Inland Sea, Japan.

Fig. 3. Estimation of total length of prey *Engraulis japonicus* found in stomachs of *Morbakka virulenta*. A. Allometric relationships between eye orbit diameter and total fish length; B. Relationships between body height and total length of the fish.

shima prefecture at night from November 28 to December 10, 2011, and from September 29 to November 20, 2012 (n=25). Specimens were supplementarily collected at night from Uno Port (34°29'28"N, 133°57'10"E) (n=1, November 7, 2012) in Okayama prefecture, Onomichi Port (34°24'08"N, 133°11'29"E) (n=2, November 6, 2012), sea embankment of Takehara (34°19'33"N, 132°55'25"E) (n=2,

November 21, 2012), and at a floating pier on Ikunoshima Island (34°17'09"N, 132°55'32"E) (n=5, November 21, 2011; August 28, September 29, and October 20, 2014) in Hiroshima prefecture, located in the central part of the Seto Inland Sea (Fig. 2). Each individual was carefully captured using a scoop-net (diameter 50 cm, mesh size 2 mm). Each captured cubomedusa was put into a plastic bottle and then fixed in 4% neutralized formalin-seawater solution. The careful dissection of their gastric pouches revealed the prey items.

In the present study, the Japanese anchovy *Engraulis japonicus* Temminck & Schlegel, 1846, found in the stomachs of *M. virulenta* were nearly fully digested. However, even in such cases, the length of the orbit and height of *E. japonicus* could be measured. The total length of the consumed fish was estimated based on the relationships between their orbit and total lengths (Fig. 3A) and between their body height and total length (Fig. 3B) in the intact specimens of *E. japonicus* collected from off Takehara using a seine (n=18) on July 19, 2012 and from Ondo Port on November 13, 2012 using a scoop-net (n=33).

Stable isotopic analysis

The trophic interactions between *Morbakka virulenta* (n=3, bell height 12.0, 15.1, 20.0 cm), *Engraulis japonicus* (n=3, total length 4.6, 4.8, 5.2 cm) and a mixture of approximately 30 planktonic copepods (composed of *Tortanus gracilis* (Brady, 1883), *Centropages furcatus* (Dana, 1849), *Paracalanus parvus* s.l., *Calanus* sp., and *Pontellopsis* sp.) were estimated by means of a bulk stable isotopic analysis. All organisms were collected at night from Uno Port on November 7–8, 2013 (Fig. 2). The isotopic analysis used the marginal part of the umbrella for *M. virulenta* and parts of the body muscles for *E. japonicus*, and whole bodies of copepods. Their tissues and bodies were dried at 60°C in an oven (DOV-450P, AS ONE Co.) and ground using a mortar and pestle. The dried samples were placed in microtubes and treated with 1 mL methanol using an ultrasonic cleaner. After centrifuging the samples (5 min, 12000 rpm) (MiniSpin, Eppendorf Japan AG), the supernatant was discarded. These steps were performed on the samples in the order of dichloromethane/methanol (7 : 1, v/v) (1 mL), distilled water (1 mL), and 1N HCl (1 mL). Subsequently, the samples were washed with distilled water and dried again for the stable isotopic analysis. For the isotope ratio mass spectroscopy (IRMS) analysis, a small aliquot (0.01 to 0.07 mg) of each pre-treated dry sample was introduced into a tin capsule, which had been pre-cleaned with dichloromethane/methanol (1 : 1, v/v) and wrapped tightly.

At the Japan Agency for Marine-Earth Science and Technology (JAMSTEC), the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were measured using an elemental analyzer (Thermo Finnigan Flash EA1112) coupled to an isotope-ratio mass spectrometer (Thermo Finnigan Delta Plus XP) via a continuous flow interface (Thermo Finnigan ConFlo III) with modi-

fications to improve sensitivity (e.g., Ohkouchi et al. 2005, Ogawa et al. 2010). The carbon and nitrogen isotopic compositions are expressed as the standard delta (δ) notation relative to the Vienna Pee Dee Belemnite (VPDB) standard and to atmospheric nitrogen (Air), respectively, using the following equation:

$$\delta X = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1000$$

where X is either ^{13}C or ^{15}N and R is the ratio of the heavy to light isotopes (i.e., $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$). The analytical precision, determined by the replicate analyses of a standard (L-tyrosine; referred to as "BG-T" in Tayasu et al. 2011), was within 0.25‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Observations of symbiotic and predatory fish

The associations of the juvenile Japanese jack mackerel *Trachurus japonicus* (Temminck & Schlegel, 1844) and Japanese butterfish *Psenopsis anomala* (Temminck & Schlegel, 1844) with the cubomedusae were observed at Ondo Port at night (2330) on October 16 and at dawn (0630) on October 31, 2012, and at the floating pier on Ikunoshima Island at night (1940) on November 20, 2014 (Fig. 2). The associated juvenile fishes were captured with a scoop net after visual observations. The associations were recorded with a digital video camera (HDR-CX550V, Sony Inc.) and digital camera (STYLUS TG-3 Tough, Olympus Corporation). In addition, the predatory behavior of the black scraper *Thamnaconus modestus* (Günther, 1877) was also observed at Ondo Port soon after dawn (0645) on October 31, 2012. These associations were also recorded using the same digital video camera.

Cnidome in tentacles

The terminal parts of the tentacles (excluding the basal 5 cm of tentacles) of 23 individuals (0.7–21.0 cm in bell height) collected at Ondo Port, Takehara, and Ikunoshima Island from November 2012 to August, 2014 (Fig. 2) were dissected from the bodies, and nematocysts were extracted as described by Bloom et al. (1998). After extraction, the nematocysts were fixed in 5% formalin seawater, and the cnidomes were examined microscopically. Approximately 1000 nematocysts were counted and identified following Östman's (2000) classification of nematocysts.

Results

Nocturnal occurrence in near-surface waters under the street light

The first and last occurrences of *Morbakka virulenta* at Ondo Port were recorded on September 26 and on December 17, 2012, respectively (Fig. 4). No occurrence was recorded in mid-September 2012 or in January or February 2013. The maximum number of individuals (n=24) was recorded on December 11, 2012. *Morbakka virulenta* occurred at water temperatures ranging widely from 13.9°C

Fig. 4. Relationships between occurrence of *Morbakka virulenta* and surface water temperature at Ondo Port, the Seto Inland Sea, Japan. Numbers indicate maximum numbers of individuals occurring on each day.

(December 17, 2012) to 25.1°C (September 26, 2012) (Fig. 4). The swimming individuals of *M. virulenta* appeared near the surface just before or soon after sunset throughout the nighttime and then totally disappeared from the surface layer before dawn. The illuminance of the sea surface under the street light was constant throughout the investigation (21.0–25.5 lx). The occurrence of individuals fluctuated considerably during the night. The box jellyfish occurred around the slack water, irrespective of the tides, from November to December (Fig. 5). The individuals appearing near the surface at the slack tide were swimming slowly with their tentacles flaccidly extended.

Stomach content analysis

The stomach contents of *Morbakka virulenta* were composed predominantly of fish (Fig. 6). The main diet was Japanese anchovy, *Engraulis japonicus* (76.0%) with total lengths ranging from 2.1 to 11.4 cm. Other prey fishes were Japanese cutlassfish *Trichiurus lepturus* Linnaeus, 1758 (15.5 and 17.0 cm in total length), Japanese halfbeak *Hyporhamphus sajori* (Temminck & Schlegel, 1846) (18.0 cm), Japanese scaled sardine *Sardinella zunasi* (Bleeker, 1854) (7.5 cm), Japanese jack mackerel *Trachurus japonicus* (11.0 cm), vertical striped cardinalfish *Apogon lineatus* Temminck & Schlegel, 1842 (4.8 cm), and flat-head silverside *Hypoatherina valenciennei* (Bleeker, 1853) (3.7 cm). In addition, the pelagic shrimp *Acetes japonicus* Kishinouye, 1905 (2.5 cm in total length), and beka squid *Loliolus (Nipponololigo) beka* Sasaki, 1929 (4.8–6.0 cm in mantle length) were found in the stomachs of *M. virulenta*. In rare cases, *M. virulenta* medusae preyed on fish, such as *T. lepturus* and *H. sajori*, which were longer than their own bell height.

Stable isotopic analysis

The stable isotope ratios of nitrogen and carbon were plotted for *Morbakka virulenta*, *Engraulis japonicus*, and copepods (Fig. 7). The averaged $\delta^{15}\text{N}$ values of *M. vir-*

Fig. 5. Temporal changes in nocturnal occurrence of swimming individuals of *Morbakka virulenta* with different tides at Ondo Port, The Seto Inland Sea, Japan. A: neap tide (November 20–21, 2012); B: half tide (December 1–2, 2012); C: middle tide (November 11–12, 2012).

ulenta, *E. japonicus*, and copepods were 18.8% (range: 17.8–19.1%), 17.4 (17.3–17.7%), and 14.8%, respectively. The averaged $\delta^{13}\text{C}$ values of *M. virulenta*, *E. japonicus*, and copepods were -13.9% (-14.1 to -13.7%), -15.2% (-14.9 to -15.7%), and -17.0% , respectively.

Observations of symbiotic and predatory fish

A juvenile of *Trachurus japonicus* was observed swimming near the postero-lateral side of the bell (or the basal side of a tentacle) of *Morbakka virulenta* at Ondo Port soon after dawn (0630) on October 31, 2012 (Fig. 8A). The

Fig. 6. Relationships between bell height of *Morbakka virulenta* and total length of prey items. Total lengths of *Engraulis japonicus* found in stomachs of *M. virulenta* were either directly measured or estimated based on measurable orbit or height. Inserted circle graph showing the occurrence of frequency of each prey item of *M. virulenta*.

Fig. 7. A dual isotope plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for *Morbakka virulenta*, *Engraulis japonicus*, and planktonic copepods. Error bars represent standard deviation of mean values.

relative position of this companion remained unchanged during the entire 5 minutes observation. A juveniles of *Psenopsis anomala* was observed swimming around the exumbrella and tentacles of *M. virulenta* at the floating pier on Ikunoshima Island at night (1940) on November 20, 2014 (Fig. 8B).

The predation by *Thamnaconus modestus* on *M. virulenta* was recorded at Ondo Port soon after dawn (0645) on October 31, 2012 (Fig. 8C). The predator skillfully devoured the upper part of the exumbrella of the cubomedusa to avoid the venomous tentacles. Finally, a perforation in the subumbrella caused the cubomedusa to start sinking and lose its buoyancy (approximately 10 minutes after our observation started).

Cnidome in tentacles

The cnidome of *Morbakka virulenta* was composed of

three types of nematocysts: rod-shaped, microbasic *p*-mastigophores; large, oval, holotrichous isorhizas; oval, microbasic *p*-euryteles. However, the *p*-mastigophores were the dominant type (over 83.3%) of nematocysts, whereas the euryteles and isorhizas comprised 0.5–11.0% and 0.4–5.7% of the total nematocysts, respectively (Fig. 9).

Discussion

Feeding habits

In this study, *Morbakka virulenta* appeared near the surface after sunset, swimming and feeding on prey animals such as small schooling fish. The peak of the near-surface appearances of *M. virulenta* was often found around the slack water. The swimming individuals of *M. virulenta* usually extended their tentacles to the greatest possible length (sometimes exceeding 2 m), suggesting that they were feeding actively. This behavior was similar to that described for *Carybdea marsupialis* (Linnaeus, 1758) (Larson 1976). In *Chironex fleckeri* Southcott, 1956, the medusae extend tentacles and swim at or near the sea surface when capturing food items (Barnes 1966). Moreover, *Chironex* sp. feeds on fish while actively swimming during the nighttime (Iwanaga & Kanamoto 2007). We also observed small prey fish such as *Engraulis japonicus* being entangled by their tentacles.

The stomach content analysis of *M. virulenta* revealed that it mainly fed on *E. japonicus* (Fig. 6). The natural prey items of some cubomedusae have been reported previously. The feeding habits of *M. virulenta*, *C. marsupialis*, and *Tamoya haplonema* were reported to be piscivorous (Berger 1900, Larson 1976, Nogueira & Haddad 2008, present study). On the other hand, *Carybdea rastonii* Haacke, 1886 and *Chiropsalmus quadrumanus* (Müller, 1859) mainly feed on crustaceans (Matsumoto 1995, Nogueira & Haddad 2008). In *C. fleckeri*, Carrette et al. (2002) addressed the relationships between the composition of nematocysts and its prey items. The small medusae (bell height: 20–60 mm), in which the isorhizas of entangling and adhesive functionality were the most dominant nematocysts, fed mainly on prawns. In contrast, the large individuals (bell height: >100 mm), in which the mastigophore nematocysts containing lethal venom were predominant, preyed chiefly upon fishes. Furthermore, *Carukia barnesi* Southcott, 1967, showed the same pattern of change in prey items accompanying growth of jellyfish (Underwood & Seymour 2007). In contrast, mastigophores were dominant (>80%), irrespective of their bell height (0.7–21.0 cm) in *M. virulenta*. In the present study, we revealed that *M. virulenta* of this size-class fed mostly on the Japanese anchovy. Therefore, *M. virulenta* (bell height: 0.7–22.5 cm) seem to exhibit no developmental changes in its feeding habits, unlike *C. fleckeri* and *C. barnesi*.

The piscivory of *M. virulenta* was indirectly supported by the present stable isotopic analysis (Fig. 7). The $\delta^{13}\text{C}$

Fig. 8. *In-situ* photos of symbioses between cubomedusae and fish. A. Association of *Trachurus japonicus* with *Morbakka virulenta* at Ondo Port (34°11'36"N, 132°32'07"E), Hiroshima prefecture on October 31, 2012; B: Association of *Psenopsis anomala* with *Morbakka virulenta* at floating pier on Ikunoshima Island (34°17'09"N, 132°55'32"E), Hiroshima prefecture on November 20, 2014; C. Predation by *Thamnaconus modestus* on *M. virulenta* at Ondo Port (34°11'36"N, 132°32'07"E), Hiroshima prefecture on October 31, 2012; D. Predation by *Chironex yamaguchii* on *Herklotsichthys quadrimaculatus* at Ginowan Port (26°16'38"N, 127°43'48"E), Okinawa prefecture on July 15, 2012; E. Predation by *Carybdea brevipedalia* on *Engraulis japonicus* at Numata Port (39°00'25"N, 141°38'44"E), Iwate prefecture on September 12, 2010. Fish indicated by red arrows.

Fig. 9. Relationships between cnidome of tentacles of 23 individuals of *Morbakka virulenta* and bell height. Numbers above column indicate numbers of nematocysts examined.

and $\delta^{15}\text{N}$ values of *M. virulenta* were higher than those of *E. japonicus*. In general, a predator was enriched in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ relative to its prey by approximately 0.5–1‰ and 3‰, respectively (Michener & Schell 1994). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *E. japonicus* vary depending on the developmental stage, collecting season, and migrating populations (Lindsay et al. 1998, Miyachi et al. 2013). A time-lag occurs until the stable isotopic ratios of a prey is reflected in that of its predators (D'Ambra et al. 2014). The $\delta^{15}\text{N}$ value of *M. virulenta* did not increase by 3‰ compared to *E. japonicus*; this might reflect the $\delta^{15}\text{N}$ value of *E. japonicus* at different times, developmental stages and populations.

Symbioses between cubomedusae and fish

The symbioses between cubomedusae and fish are summarized in Table 1 based on the present and previous studies. These can be classified simply into three categories: prey, predator, and commensal. Some large-sized cubome-

Table 1. Symbioses between cubomedusae and fish. Relationships with host: PY (prey); PD (predator); CO (commensal).

Cubomedusa	Fish	Relationships	Reference
<i>Carukia barnesi</i>	Fish	PY	Purcell & Arai (2001)
<i>Carybdea marsupialis</i>	Fish (<i>Jenkinsia</i>)	PY	Larson (1976)
	Fish	PY	Berger (1900)
	Fish	PY	Martin (2004)
<i>Carybdea brevipedalia</i>	<i>Engraulis japonicus</i>	PY	Toshino (pers. obs.)
	Fish	PY	Uchida (1929)
<i>Carybdea rastonii</i>	Larval fish	PY	Matsumoto (1995)
<i>Chironex fleckeri</i>	Fish	PY	Purcell & Arai (2001)
<i>Chironex yamaguchii</i>	<i>Gnathanodon speciosus</i>	CO	Toshino (pers. obs.)
	<i>Herklotsichthys quadrimaculatus</i>	PY	Toshino (pers. obs.)
<i>Chiropsalmus quadrigatus</i>	Fish	PY	Larson (1976)
<i>Chiropsalmus quadrumanus</i>	Fish	PY	Nogueira & Haddad (2008)
	<i>Peprilus alepidotus</i> ,	CO	Beebe (1928)
	<i>Chloroscombrus chrysurus</i>	CO	Beebe (1928)
<i>Tamoya haplonema</i>	Young fish	PY	Nogueira & Haddad (2008)
	<i>Chloroscombrus chrysurus</i>	CO	Beebe (1928)
	<i>Peprilus</i> cf. <i>crenulatus</i>	CO	Lawley & Faria (2018)
<i>Morbakka fenneri</i>	Fish	PY	Gershwin (2008)
<i>Keesingia gigas</i>	Fish (Monacanthidae)	CO	Gershwin (2014)
<i>Morbakka virulenta</i>	<i>Trachurus japonicus</i>	CO	present study
	<i>Psenopsis anomala</i>	CO	present study
	<i>Trachurus japonicus</i>	PY	present study
	<i>Engraulis japonicus</i>	PY	present study
	<i>Apogon lineatus</i>	PY	present study
	<i>Hypoatherina valenciennesi</i>	PY	present study
	<i>Thamnaconus modestus</i>	PD	present study

dusae, such as *Morbakka*, *Tamoya*, and *Chironex* (Fig. 8D), are piscivorous (Carrette et al. 2002, Nogueira & Haddad 2008, present study). In *Chironex fleckeri*, the diets change ontogenetically from prawns to fish (Carrette et al. 2002). On the other hand, the Japanese anchovy was the main prey item for the small- to large-sized *Morbakka virulenta* ranging from 1.5 to 22.5 cm in bell height (present study). The large size and powerful venom of the above three cubomedusan genera also suggest that their primary prey preference is fish (cf. Nogueira & Haddad 2008). However, *Carybdea brevipedalia* Kishinouye, 1891, the maximum bell height of which is ca. 3 cm (Ueno 2003), were also observed to feed on *Engraulis japonicus* under lights at Numata Port, Iwate Prefecture, northern Japan during the nighttime (Fig. 8E) (Toshino personal observation).

Many fish are known to be associated with jellyfish mainly for the reasons of antipredation and/or feeding (Mansueti 1963, Arai 1988, 2005, Ates 1988, Bonaldo et al. 2004, Ohtsuka et al. 2009, 2010). Some medusivorous fish, such as filefish, seem to consume not only scyphomedusae, but also cubomedusae, as food (Arai 1988, 2005, Ates 1988, Purcell & Arai 2001, Bonaldo et al. 2004, Masuda 2009b, Miyajima et al. 2011, Kondo et al. 2016). Our observation of the feeding behavior by *Thamnaconus modestus*

on *M. virulenta* clearly confirmed that cubomedusae were eaten by the fish. In contrast to scyphomedusae, the commensal associations of juvenile fish with cubomedusae are extremely rare, having been recorded only five times before this study (Table 1). The juveniles of *Trachurus japonicus* and *Psenopsis anomala* have been reported to associate not only with many scyphomedusae, but also with *M. virulenta* (Yasuda 2003, Masuda 2009a, b, c, Ohtsuka et al. 2009, 2010, Kondo et al. 2016, present study). Both species of juvenile fishes were less than one year. *Trachurus japonicus* and *P. anomala* are known to utilize scyphomedusae as refugia from visual predators, as food collectors, or as food sources (Shojima 1961, 1962, Masuda 2009a, b, c, Ohtsuka et al. 2009, 2010, Kondo et al. 2016), but the interactions between *M. virulenta* and *T. japonicus* seems to be restricted to refugia. Because *M. virulenta* is a piscivore, the host cubomedusa does not play a role as food collector for *T. japonicus*. In addition, there are no reports of the juveniles of *T. japonicus* using jellyfish as food. On the other hand, the *P. anomala* juveniles have been reported to be medusivorous (Shojima 1961, Kondo et al. 2016). Therefore, the symbiotic relationships between *M. virulenta* and *P. anomala* seem to be centered on antipredation and/or feeding.

The present study has shed light on the interactions between cubomedusae and fishes. These relationships seem to be highly dynamic, changing with the growth of both, the host jellyfish and the associated fish. More attention should be paid to the interactions between cubozoans and fish to understand the marine food webs more deeply.

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