Natural predators of polyps of Aurelia aurita s.l. (Cnidaria: Scyphozoa: Semaeostomeae) and their predation rates

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Abstract: The size of medusa populations in most scyphozoan species can be affected by the size of their benthic polyp populations, which reproduce asexually to give birth to planktonic ephyrae, but also are subject to predation by natural enemies. In this study, five gastropod species (Calliostoma unicum, Pleurobranchaea japonica, Hermissenda crassicornis, Sakuraeolis enomimensis and S. sakuracea) and three crustacean species (Rhynchocinetes uritai, Latreutes anoplonyx and Hyastenus diacanthus) were found to prey on polyps of the moon jellyfish, Aurelia aurita s.l., in Japanese coastal waters. In particular, C. unicum, P. japonica, H. crassicornis, R. uritai and H. diacanthus consumed more than 300 polyps per predator per day in the laboratory. These predators are common on natural rocky or pebbled seabeds, but are very scarce on various substrates in concrete-walled fishing ports, particularly on the undersurfaces of floating piers, where A. aurita polyps are attached in abundance. Transplanting natural predators to substrates with dense polyp colonies, just prior to their seasonal strobilation, is a possible countermeasure to prevent recurrent medusa blooms.

Key words: coastal waters, jellyfish bloom, natural enemy, predation, polyp

Introduction

The moon jellyfish, Aurelia aurita (Linnaeus) s.l. (see Dawson & Martin 2001, Dawson 2003, Ki et al. 2008 for cryptic species of this genus), is the most common scyphozoan jellyfish species in the world’s temperate coastal waters. It has frequently caused problematic blooms, particularly in waters with significant anthropogenic impacts such as fish stock depletion, eutrophication and marine constructions (e.g., Graham 2001, Purcell et al. 2007, Dong et al. 2012). For example, one polyp with excess food at 26°C can increase in only three weeks to as many as 57 individuals by budding (Uye, unpubl.), and one strobilating polyp can form as many as 21 discs (Ishii & Watanabe 2003), each of which transforms into a larval medusa (or an ephyra). These numbers suggest that a single polyp present in summer–fall could potentially give birth to more than 1,000 ephyrae in winter, the season of ephyra liberation. Therefore, the asexual reproduction of polyps strongly determines the abundance of medusae in the following season.

To understand the mechanisms underlying the recent increase in frequency and extent of medusa blooms, it is essential to investigate the effects of various factors on polyp population dynamics. Temperature, salinity, light, oxygen concentration, food availability and competition for space have all been demonstrated to be important factors (Coyne 1973, Watanabe & Ishii 2001, Miyake et al. 2002, Willcox et al. 2008, Toyokawa et al. 2011, Duarte et al. 2012). Losses due to predation can also be a factor affecting polyp population dynamics (Cargo & Schultz 1967, Oakes
Nudibranchs are the best-known polyp predators, and some pycnogonids (e.g. *Callipallene brevirostris* (Johnston)), amphipods (e.g. *Caprellia equilibra* Say), anomurans (e.g. *Pagurus longicarpus* Say) and brachyurans (*Lobophyllia dubia* H. Milne Edwards and *Neopanope texana sayi*, a synonym of *Dyspanopeus sayi* (Smith)) also eat jellyfish polyps (Oakes & Haven 1971, Hutton et al. 1986). However, there have been few determinations of actual predation rates by these predators. Hernroth & Gröndahl (1985b) found that the nudibranch *Flabellina verrucosa* (Sars) (recently moved from the genus *Coryphella*) consumed ca. 400 *A. aurita* polyps per day; and Hoover et al. (2012) reported that the nudibranch *Hermissenda crassicornis* (Eschscholtz) ate up to 102 polyps of *Aurelia labiata* Chamisso & Eysenhardt, per hour. These results imply that the interaction between jellyfish polyps and their natural enemies may be much more important than generally assumed, due to the lack of information about potential predators and their predation rates.

The aim of the present study was to make an inventory of potential predators of *A. aurita* polyps in Japanese coastal waters and to determine their potential predation rates in laboratory experiments. The ecological significance and potential application of their predatory capacity in controlling the polyp populations are discussed.

### Material and methods

Planulae of *Aurelia aurita* originating from mature medusae were collected in Kure, the Inland Sea of Japan (or Seto Inland Sea), in August, 2005, and settled on rectangular (9×16 cm or 9×9 cm) or round (15 cm diameter) plastic plates placed at the bottom of plastic containers (30 cm diameter). Later, the settled polyps were fed with *Artemia* sp. (Utah, USA) nauplii at 22–25 °C for 1–3 months until the density increased to at least 1 polyp cm$^{-2}$, and then they were subjected to the experiments below.

Firstly, a preliminary experiment was conducted to identify which animals eat *A. aurita* polyps. A total of 78 species (both invertebrates and vertebrates) were collected mainly by SCUBA dives in Etajima, Kure, Suo-Oshima and Takehara, in the Inland Sea of Japan, and Matsue and Okinoshima in the Sea of Japan (Fig. 1 and Table 1). The medusa shrimp *Latreutes anoplonyx* was isolated from the oral arms of the giant jellyfish *Nemopilema nomurai* Kishinouye collected in the Sea of Japan. The animals collected were transported in ambient seawater to the laboratory in Higashi-Hiroshima in plastic containers within a cooler. Species were identified using various illustrated texts of Japanese fauna (Okada et al. 1965, Nishimura 1992, 1995, Nakano 2004). In the laboratory, they were kept individually and starved for a day before introducing a polyp-bearing plate. Small polyps on the plates were removed with a dissecting needle, leaving monitored for 1–3 days. Temperatures during experiments were kept within 4°C of the ambient temperature at which the predator was captured.

Secondly, the predation rates were measured for 8 species identified as potential predators in the above experiment (see Results). To maintain these predators, they were fed with shrimp meat and/or *A. aurita* polyps. After measurement of body length and wet weight (electric balance, Ohaus Co.), they were kept individually and starved for a day before introducing a polyp-bearing plate. Small polyps on the plates were removed with a dissecting needle, leav-
Natural predators of jellyfish polyps

Table 1. List of animals tested for feeding on *Aurelia aurita* polyps. Eight species (filled circle) ate significant numbers of whole polyps and two species (open circles) ate just parts of a few polyps.

| Species (average body length: cm) | Results | Species (average body length: cm) | Results |
|----------------------------------|---------|-----------------------------------|---------|
| Phylum MOLLUSCA                   |         | Madrella gloriosa (4.0)           |         |
| Class Polyplacophora             |         | Superfamily Trionioidea           | Tritonia festiva (6.4) |
| *Ichneumochiton comptus* (3.3)    |         | Superfamily Flabellinoidea        | Flabellina bicolor (3.5) |
| Class Gastropoda                 |         | Superfamily Fionoidea             | Cuthona sp. (1.9) |
| Superfamily Fissurelliodea       |         | Superfamily Aeolidioidea          |         |
| *Scutus sinensis* (1.8)          |         | Hermisenda crassicornis (2.0)     |         |
| Superfamily Trochoidea           |         | Pteraeolidia ianthina (3.0)       |         |
| *Chlorostoma lischkeii* (2.0)     |         | Sakuraeolis enosimensis (1.5)     |         |
| *Omphaloloxo pfeifferi carpenteri* (3.1) |     | Sakuraeolis gerberina (1.7)       |         |
| *Omphaloloxo rustic* (2.0)       |         | Sakuraeolis sakuracea (2.9)       |         |
| *Monodonta labio f. confusa* (1.8) |     | *Aeolidia* sp. (1.7)              |         |
| *Monodonta nannotoides* (1.0)     |         |                                   |         |
| *Cantharida japonica* (0.7)      |         |                                   |         |
| *Calloistoma uniculum* (1.9)     |         |                                   |         |
| Superfamily Turbinoida           |         | Phylum ARTHROPODA                 |         |
| *Turbo (Batillus) cornutus* (6.4) |         | Class Malacostraca               |         |
| *Lunella coronatus corensis* (1.3) |     | Caprella sp. (1.5)                |         |
| *Astralum haemachatum* (2.5)     |         | Rhynchocinetes uritai (2.5)       |         |
| Superfamily Cypaeoida            |         | Heptacarpus pandaloides (1.9)     |         |
| *Primovula rhodia* (1.5)         |         | Heptacarpus sp. (5.7)             |         |
| Superfamily Bucinoida            |         | Latreutes anoplonyx (3.0)          |         |
| *Japeuthia ferrea* (3.0)         |         | Palaemon pacificus (1.9)          |         |
| *Euplica scripta* (1.6)          |         | Cibarnarius sp. (0.5)             |         |
| *Mitrella bicincta* (1.0)        |         | Pagurus geminus (0.5)             |         |
| *Mokumea divisicata* (0.3)       |         | Pagurus lanuginosus (0.5)         | ●         |
| *Niotha livescens* (1.8)         |         | Pagurus sp. (0.5)                 | ●         |
| Superfamily Muricoidea           |         | *Hapalognathus dentatus* (1.6)     | ●         |
| *Thais bronii* (2.7)             |         | Acheaeus japonicus (1.0)          | ●         |
| *Thais clavigera* (2.1)          |         | Pugettia quadridens quadridens (1.5) |         |
| Superfamily Limapontioida        |         | Pugettia minor (1.5)              | ●         |
| *Ercolania boudleae* (0.5)       |         | Hyastenus diaeanthus (1.7)         | ●         |
| Superfamily Pleurobranchioidea   |         | Gaetice depressus (2.2)           | ●         |
| *Pleurobranchia japonica* (3.3)  |         | Helice tridens (2.5)              | ●         |
| Superfamily Doridoida            |         | Phylum ECHINODERMATA              |         |
| *Aldisa albatarossi* (2.6)       |         | Class Asteroida                   |         |
| *Aldisa cooperi* (2.3)           |         | *Asterias amurensis* (1.0)        | ●         |
| *Platydoris tabulata* (5.5)      |         | *Asterina pectinifera* (3.2)      | ●         |
| *Chromodoris orientalis* (4.3)   |         | *Asterina boyleri* (1.5)          | ●         |
| *Chromodoris tinctoria* (1.6)    |         | Astropecten latespinosus (-)      | ●         |
| *Hypselodoris festiva* (3.5)     |         | Coscinasters acutispina (4.6)     | ●         |
| Superfamily Onchidoidoida        |         | Henricia okishimai (2.3)          | ●         |
| *Diaphorodoris mitsu* (1.0)      |         | Class Echinoidea                  |         |
| *Goniocidella savignyi* (0.4)    |         | *Anthocidaris crasissipina* (5.0) | ●         |
| *Hopkinsia hiroi* (0.8)          |         | *Mesoplia globulus* (2.4)         | ●         |
| *Okenia distincta* (0.3)         |         | Phylum VERTEBRATA                 |         |
| Superfamily Polycoeloida         |         | Class Osteichthyes                |         |
| *Kaloplacanus ramosus* (3.8)     |         | *Favonigobius gymnauchen* (4.6)   | ●         |
| *Plocamopherus tilesii* (5.0)    |         | Mugil cephalus cephalus (9.0)     | ●         |
| *Tambja sp.* (1.0)               |         | Platycephalus sp.2 (7.0)          | ●         |
| *Gymnodoris citrina* (3.1)       |         | Plectorhinus cinctus (8.0)        | ●         |
| Unassigned Superfamily           |         | Rudarius ercodes (2.4)            | ●         |
| *Madrella ferrugina* (3.5)       |         | Takifugu poecilonotus (5.1)       | ●         |
ing only polyps of calyx diameter ≥ca. 0.5 mm. The initial density on each plate ranged from 1.2 to 7.5 polyps cm$^{-2}$, with a mean of 3.2 polyps cm$^{-2}$. The experiment ran for 1–4 days at ambient temperatures (13–26°C, within 4°C of the natural range for a given predator species). The plates were photographed at 24 h intervals, and the numbers of polyps eaten were counted to calculate the predation rate for each predator. Relationships between the predator wet weight ($W$, g) and predation rate ($P$, polyps predator$^{-1}$ day$^{-1}$) were examined using regression analyses (SPSS statistical software, Version 10.0). Best-fit equations were determined and those with the least variance were tested for significance ($p\leq0.05$).

SCUBA dives (2 people×20 dives×2 tanks (2 hours) per dive in 2006–2009) to search for cnidarian polyps and their natural predators were carried out at more than 10 localities along the coast of Eta Island in Hiroshima Bay (Fig. 1). This island is irregular in shape and is composed of three regions: Eta, Higashi-Nohmi and Nishi-Nohmi. About half of the dives were conducted at Iruka Point (Fig. 1), a natural rock- and pebble-bedded area. Dives were also performed at Korenaga Port (Fig. 1), a concrete-walled local fishing port, to monitor benthic fauna on riprap, vertical concrete walls, and on the underside of floating piers and buoys. The occurrence of $A. aurita$ polyps and their predators was recorded at these two contrasting sites.

Results

Inventory of polyp predators

Of 78 species belonging to the Mollusca (47 species), Arthropoda (17 species), Echinodermata (8 species) and Vertebrata (6 species), only 8 species ate substantial numbers of $A. aurita$ polyps (Table 1 & Fig. 2). Five were gastropod species: Calliostoma unicum (Dunker), Pleurobranchaea japonica Thiele, Hermisenda crassicornis, Sakuraeolis enosimensis (Baba) and Sakuraeolis sakuraecea Hirano. Three were crustacean species: Rhynchocinetes uritai Kubo, Latreutes anoplonyx Kemp and Hyastenus diacanthus (De Haan). It was noteworthy that they never consumed podocysts. A crab, Achaeus japonicus (De Haan), and a sea star, Henricia ohshima Hayashi, con-

Fig. 2. Photographs of predators of Aurelia aurita polyps. (A) Calliostoma unicum; (B) Pleurobranchaea japonica; (C) Hermisenda crassicornis; (D) Sakuraeolis enosimensis; (E) Sakuraeolis sakuraecea; (F) Rhynchocinetes uritai; (G) Latreutes anoplonyx; (H) Hyastenus diacanthus. Scale bars=1 cm
sumed only parts of a few polyps on just one occasion and so were not designated as polyp predators. When molluscs, excluding the five species listed above, approached polyps closely enough to touch them with their tentacles, they were usually stung and recoiled immediately. A nudibranch, *Goniodoridella savignyi* Pruvot-Fol, died ca. 6 hours after contact with polyps, perhaps as a result of nematocyst poison. Crustaceans, excluding the four species listed above, showed no specific response to polyps, and eventually walked right over them. Eight echinoderm species damaged polyps by crawling over them, but did not eat any, except for *H. ohshimai*. None of the fish species tested ate polyps.

**Predation rates**

*Calliostoma unicum*

When this trochid gastropod crawled close enough to touch a polyp, it pulled its head back instantly, perhaps due to nematocyst stings, but then proceeded to the polyp with its head up and pushed its mouth area over the polyp. The polyp and nearby attached microalgae were scraped completely with the chitinous radula, so that the surface of the plate was clean. The spatial feeding pattern shown by a representative snail of 0.82 g wet-weight is depicted in Fig. 3A: it ate 270 polyps (area: 48 cm²), 180 polyps (22 cm²), 269 polyps (51 cm²) and 116 polyps (23 cm²) daily from the first to the fourth day, each time clearing all of the polyps on the plate. It gradually crawled around the plate looking for polyps, and consuming all in its path. The feeding of this species was basically continuous throughout the day, except for occasional halts. Despite a wide range of body weights from 0.82 to 5.2 g, the mean daily predation rate among 7 specimens at temperatures of 21–25°C was relatively constant (277 polyps predator⁻¹ day⁻¹, Fig. 4A).

*Pleurobranchaea japonica*

This sea slug showed no hesitation from nematocyst stings and scraped polyps off the plate with its radula, in a fashion similar to that of *Calliostoma unicum*. The predation rate varied widely from 83 to 549 polyps predator⁻¹ day⁻¹ at 15–17°C for 5 animals weighing from 0.8 to 7.1 g, but with no significant relationship between the predation rate and animal size (Fig. 4B).

*Hermissenda crassicornis*

As with *Calliostoma unicum*, this nudibranch withdrew from the polyp’s nematocysts, but then moved toward the polyp to eat it. The predation rate increased from 43 polyps predator⁻¹ day⁻¹ by the smallest animal (0.23 g) to 535 polyps predator⁻¹ day⁻¹ by the largest one (2.3 g) at 13–17°C. A significant linear regression model for predation rate versus weight was expressed by $P=253 \cdot W+12.2$ (Fig. 4C).

*Sakuraeolis enosimensis*

Five small specimens weighing from 0.07 to 0.48 g were available. They ate fewer polyps than the other nudibranch predators, perhaps due to their smaller body size. Their predation rate varied from 8 to 45 polyps predator⁻¹ day⁻¹ at 16–18°C. A significant linear regression model was: $P=85 \cdot W+1.6$ (Fig. 4D).

*Sakuraeolis sakuracea*

Only two specimens weighing 0.39 and 1.42 g were available, and they consumed 26 and 131 polyps predator⁻¹ day⁻¹, respectively, at 15–17°C (Fig. 4E).

*Rhynchocinetes uritai*

This shrimp species removed polyps from the plate by
grasping the bases of polyp stalks with a chela of the first or second pereopod and carrying them to the mouth. The shrimp tended to eat the polyps in one area and then move to an adjacent area, although some polyps were left uneaten temporarily until all of them were consumed (Fig. 3B). Of five specimens studied, the predation rate was lowest (118 polyps predator\(^{-1}\) day\(^{-1}\)) for the smallest (0.13 g) and highest (409 polyps predator\(^{-1}\) day\(^{-1}\)) for the largest (0.96 g) at 15–19°C. A significant linear regression model was expressed by \(P=365 W + 55.2\) (Fig. 4F).

**Latreutes anoplonyx**

Two specimens of *Latreutes anoplonyx* were available (0.26 and 0.39 g), and they consumed 53 and 67 polyps predator\(^{-1}\) day\(^{-1}\), respectively, at 15–17°C (Fig. 4G). The feeding behavior was basically the same as for *Rhynchoci-
Hastenus diacanthus

This crab grabbed at the bases of polyp stalks with a pair of chelipeds, removing them one by one to eat. It walked almost randomly on the plate, eating the polyps it encountered (Fig. 3C). Its predation rate varied from 47 to 672 polyps predator⁻¹ day⁻¹ at 22–26°C. An exponential equation was a better fit than a linear function to describe the relationship between predation rates and predator body weight: \( P = 136 W^{0.82} \) (Fig. 4H).

SCUBA observations

No Aurelia aurita polyps were found on the natural rock- and pebble-bedded areas at Iruka Point (Fig. 1), where Calliostoma unicum was often found on the brown alga Ecklonia sp. attached to a rocky substrate. At Iruka Point, nudibranchs such as Sakuraeolis enosimensis and S. sakuracea were usually encountered on rock surfaces, and Pleurobranchaea japonica was found on both boulders and on pebbled sea bottoms, particularly on the underside of pebbles. The shrimp Rhynchocinetes uritai was common on rocky shores at Iruka Point, often aggregating in rock crevices. In contrast, we found numerous A. aurita polyps inside Korenaga Port, specifically on the underside of floating piers where none of the above-mentioned polyp predators were found, except for S. enosimensis.

**Discussion**

A total of 78 species available were tested but only eight of them were found to be potential predators of Aurelia aurita polyps. These eight species may possess some protective or adaptive mechanisms against nematocysts, so that they can ingest them. For example, Calliostoma is typically a herbivore, scraping up algae and detritus using its characteristic rhipidoglossate radula. However, it is equally adept at grazing on hydroids and soft corals, perhaps because of a thick buccal cuticle that may protect it from nematocysts during ingestion (Perron & Turner 1978). Sea slugs of the genus Pleurobranchaea are euryphagic predators and scavengers, eating both live and dead prey, including anthozoans, hydrozoans, with some cannibalism (Cattaneo-Vietti et al. 1993). The absence of poisoning by Pleurobranchaea janonica in response to nematocysts fired from polyps suggests that their tentacles and oral region are protected by their cuticular epithelium.

The three species of nudibranchs that ate A. aurita polyps, (Hermisenda crassicorni, Sakuraeolis enosimensis and S. sakuracea) belong to the superfamily Aeolidioidea, many species of which are known to feed on hydroids (Swennen 1961, Salvini-Plawan 1972, Avila & Kuzirian 1995, Hirano 1999). Aeolidids retain nematocysts, which they acquire from their cnidarian prey, within their cnidocyte sacs for defense against predators (Thompson & Bennett 1969, Greenwood & Mariscal 1984). Hence, these aeolid species have a number of protective mechanisms, such as cuticular gut linings, protective epithelia and mucous secretions (Greenwood 2009). However, three other aeolidstested, Pteraeolidia ianthina (Angas), Sakuraeolis germana Hirano and Aeolidina sp., did not feed on A. aurita polyps at all (Table 1).

Although many crustaceans are protected from nematocysts by their chitinous exoskeletons, only two shrimps (Rhynchocinetes uritai and Latreutes anoplonyx) and one crab (Hastenus diacanthus) preyed on A. aurita polyps. The claws on their pereopods enabled them to grasp polyps, pick them up and move them to their mouths.

The eight identified potential predators, except for the jellyfish-associated shrimp L. anoplonyx, are common in the lower-littoral to sub-littoral zones in the Inland Sea of Japan and southern Sea of Japan, especially on rocky and pebble seabeds. These provide habitats for various sessile animals, including hydrozoans and anthozoans, which may be exposed to predation by sympatric predators, as has been observed elsewhere (Dumont et al. 2011). Nevertheless, during the present study A. aurita polyps were never found on exposed natural rocks and pebbles or on macroalgae.

It has become a common observation that overhanging areas of artificial structures harbor dense A. aurita polyp colonies (Miyake et al. 2002, Matsumura et al. 2005, Di Camillo et al. 2010, Toyokawa et al. 2011, Duarte et al. 2012). Dive observations during the present study showed that the natural enemies of A. aurita polyps are common on rocky and pebbled shores outside fishing ports, but are very scarce under suspended structures in port enclosures. This may be due to limited access to those suspended structures by benthic predators (Dumont et al. 2011). Polyps located under floating platforms are almost free from predation pressure and are thus able to increase their numbers greatly.

The feeding experiments showed that the eight polyp predators studied could not consume podocysts, as was also observed with aeolid nudibranchs by Cargo & Schultz (1967) and Gröndahl (1988). In most cases, they ate the whole polyp body, leaving no basal part from which a new polyp could regenerate (Gilchrist 1937, Lesh-Laurie & Corriel 1973). The predation rates by the species in the present study were significant, as demonstrated by three gastropods (C. unicum, P. japonica and H. crassicornis) and two crustaceans (R. uritai and H. diacanthus). All of them consumed the maximum number of >300 polyps each per day. It is here proposed that this high predation capacity of natural enemies could be used to regulate A. aurita polyp populations aggregated on artificial structures. Among the five species with high polyp predation rates, C. unicum may be the best candidate for transplantation to artificial structures, because it is the most numerous in the field and it can adhere to overhanging structures. An experimental transplantation of one C. unicum (wet weight: 2.6 g) to the underside of a floating pier (length:
48 m, width: 6 m, average polyp density: 3 polyps cm⁻²) was conducted in Kuba fishing port in Hiroshima Bay in November 2011. A 3-hour monitoring by SCUBA diving revealed that it consumed ca. 40 polyps (calyx diameter: ≥ca. 0.5 mm) per hour, a much higher rate than that in the laboratory experiment. Assuming a moderate predation rate (e.g. 300 polyps predator⁻¹ day⁻¹, Fig. 4A) by C. unicum and no asexual reproduction of polyps, all the polyps on the pier (estimated to be ca. 9 million; unpublished observations) could be eliminated within a month or so if three C. unicum per m² were to be transplanted there. The best timing for killing polyps by transplanted predators would be in the autumn, just before the initiation of strobilation, which regularly starts in December in the Inland Sea of Japan (unpublished). Assessment of any negative ecological impact, if any, created by transplanted predators, is needed before this proposed biological control of A. aurita can be put into practice.

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