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Planktonic ciliates as a food source for the scyphozoan *Aurelia aurita* (s.l.): Feeding activity and assimilation of the polyp stage

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ABSTRACT

To clarify the value of planktonic ciliates as a prey source for the moon jellyfish (*Aurelia aurita*), feeding rates of the polyp stage on *Favella ehrenbergii*, *Strombidium* sp., and *Myrionecta rubra* were quantified in laboratory experiments. The feeding responses on ciliates were compared with those on phytoplankton with similar equivalent spherical diameters (ESDs) by observation of the feeding behavior. The assimilation of ciliates ingested by *A. aurita* was examined by providing the ciliate *Strombidinopsis jeokjo*, labeled with nitrogen stable isotope (^{15}N), to the polyps. *A. aurita* polyps fed on all species of ciliates. Feeding rates of *A. aurita* polyps as a function of ciliate concentration were fitted to a rectangular hyperbolic equation, and the maximum feeding rate was ca. 32 cells ind^{-1} h^{-1} (0.33 μg C ind^{-1} h^{-1}) for all ciliate species. The maximum feeding rate on *M. rubra* was significantly lower than those on the other ciliate genera, which is probably caused by the smaller cell size and distinctive motility of this species. Feeding incidences, defined by the movement of polyp tentacles, rarely occurred on nanophytoplankton with ESDs of ca. 20 μm, and the feeding incidence on microphytoplankton with ESDs of ca. 30 μm was significantly lower than that on a ciliate with a similar ESD, implying that phytoplankton is not an essential prey for mature *A. aurita* polyps. After polyps fed on ^{15}N-labeled ciliates, the average nitrogen stable isotope ratio of polyps in the experimental treatments was significantly higher than that in the control, indicating that the polyps were able to assimilate nutrients from the captured ciliates. These results indicate that planktonic ciliates, a main component of microzooplankton and a frequently encountered energy source, likely serve as available food items for *A. aurita* polyps.
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1. Introduction

The scyphomedusan jellyfish *Aurelia aurita* (Linnaeus) is widespread in temperate coastal waters around the world, and dense aggregations of this species often occur during spring and summer (Hernroth and Gröndahl, 1985; Ishii et al., 1995; Lucas, 1996; Lucas and Williams, 1994; Möller, 1980; Omori et al., 1995; Schneider, 1989). Although few long-term records of jellyfish abundance exist, it appears that jellyfish and ctenophore populations have increased in recent decades, probably because of climate effects and anthropogenic changes (Purcell, 2005; Purcell et al., 2007). For example, jellyfish biomass (primarily medusa of *Chrysaora melanaster*) in the Bering Sea and Gulf of Alaska dramatically increased from 1990 to 1997, possibly associated with a climate shift to increasing solar radiation and sea surface water temperature (Purcell, 2005). Also, the *A. aurita* population has apparently increased since the 1980s in the Seto Inland Sea of Japan, partly due to increasing winter minimum sea temperature, a decline of the planktivorous fish catch, and an increase of polyp-attachment areas from waterfront construction projects (Uye et al., 2003; Uye and Ueta, 2004).

Because most jellyfish compete with planktivorous finfish by consuming the same food resources (e.g., copepods) and are potential predators of fish eggs and larvae (Möller, 1980, 1984; Olesen, 1995; Purcell, 1997; Schneider and Behrends, 1994), an increase in jellyfish biomass may diminish the fish standing stock and commercial harvest. In addition, blooms of large scyphomedusae have hampered commercial fishing activities by clogging and bursting trawl nets (Shimomura, 1959; Uye and Ueta, 2004) and have caused problems to coastal power plants by blocking intakes for cooling water (Rajagopal et al., 1989). Such negative effects of jellyfish blooms make it imperative to understand the mechanisms underlying the increase in their biomass and the occurrence of blooms.

Although *Aurelia* spp. are the most studied jellyfish group in the world, the mechanisms underlying their population increase are still unknown. They mainly have a two-stage life cycle consisting of a planktonic stage (medusa) and a benthic stage (polyp). As they mature, *A. aurita* medusae enlarge to ca. 30 cm in diameter (Schneider and Behrends, 1994; Toyokawa et al., 2000) and often form dense blooms; but they cannot increase themselves during this stage, and numerical population size is decided by the previous larval stages. The tiny polyps attach to floating substances or coastal structures where

Abbreviation: ESD, equivalent spherical diameter.
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they asexually bud more polyps; specialized polyps release numerous planktonic ephyrae (small medusae) through strobilation. Hence, the population size of *A. aurita* probably reflects the success of the benthic polyp stage in interspecific competition for space with other sessile organisms and in asexual reproduction (Ishii and Katsukoshi, 2010; Ishii and Watanabe, 2003). Increases in the number of polyps and release of ephyrae are strongly influenced by environmental factors such as temperature (Liu et al., 2009; Ma and Purcell, 2005; Purcell, 2007; Purcell et al., 1999), light (Liu et al., 2009; Purcell, 2007) and abundance of suitable food (Båmstedt et al., 2001; Ishii and Watanabe, 2003; Purcell et al., 1999) during the polyp stage.

Based on stomach contents, the main food source of scyphomedusae, such as *A. aurita*, appears to be mesozooplankton (Arai, 1997). In particular, *A. aurita* can feed on food particles in a range of sizes in contrast to planktivorous fish, which use vision to select large food organisms (Eiane et al., 1999). Therefore, small copepods, such as *Oithona* spp., which often dominate total zooplankton biomass in eutrophic embayments, are considered to be an important food source for *A. aurita* in eutrophic embayments (Ishii, 2001). Microzooplankton, mainly consisting of protozooplankton, are also numerically important components of seawater zooplankton communities worldwide (e.g., Pierce and Turner, 1992). However, there is little information on the availability of microzooplankton as a food source for scyphozoan jellyfish, and the quantitative data are limited on the medusa and ephyra stages (Båmstedt, 1990; Fukuda and Naganuma, 2001; Olesen et al., 1996; Stoecker et al., 1987; Sullivan et al., 1994). Because polyps and ephyrae are considerably smaller than medusae, it is logical to expect that the former stages can more efficiently feed on microzooplankton. Polyps are sessile and ephyrae have a limited swimming ability, so a high density of microzooplankton would be needed to increase the chance for these stages to encounter this prey. In Tokyo Bay, Ishii (2001) reported that the great abundance of polyps inferred from the great abundance of medusae is likely supported by a high density of microzooplankton. To my knowledge, however, there are no quantitative data supporting the role of microzooplankton as prey for *A. aurita* polyps.

In the present study, laboratory experiments were conducted to elucidate whether *A. aurita* polyps feed on planktonic ciliates, which are the main components of microzooplankton. The polyp stage of *A. aurita* actively fed on ciliates, and the relationships between ciliate concentrations and feeding rates of the polyps were then quantified. This is the first report on feeding activities of *A. aurita* polyps on planktonic ciliates.

2. Materials and methods

2.1. Polyps of A. aurita and ciliates

Spawning *A. aurita* medusae were captured in Mikawa Bay and Hiroshima Bay and brought to the laboratory, where the released planulae metamorphosed into polyps. The polyps were maintained at 20–25 °C and 300 μmol photon m^{-2} s^{-1} with a 12 h:12 h light–dark photocycle and provided with nauplii of *Artemia* spp. as a food source. Among the stock culture, polyps with similar body size (mean ± standard deviation of calyx diameter, 1.2 ± 0.3 mm, $n = 91$; mean ± standard deviation of tentacle number, 16 ± 1, $n = 69$) were used for the following experiments.

Planktonic ciliate strains of *Favella ehrenbergii* (two strains), *Strombidium* sp., *Strombidinopsis jeokjo*, and *Myrionecta rubra* were isolated from natural coastal seawater in Japan, and a clone strain for each species was established. Stock cultures of ciliates were maintained in 250-ml polycarbonate flasks containing 150 ml of autoclaved filtered seawater enriched with EDTA and a trace metal solution (ciliate culture medium; Stoecker et al., 1988) at 20 °C. As food sources, the dinoflagellate *Heterocapsa triquetra* (10^4 cells ml^{-1}) was provided for *F. ehrenbergii*, two nanoflagellates (a dinophyceae-*Gyrodinium* sp. [10^4 cells ml^{-1}] and the cryptophyceae*Teleaulax amphioxeia* [10^5 cells ml^{-1}]) for *Strombidium* sp., and *T. amphioxeia* (10^5 cells ml^{-1}) for *S. jeokjo* and *M. rubra*. Strains of these flagellates and the other clone strains of dinoflagellates were maintained in modified SWM3 medium (Itoh and Imai, 1987) or F/4 medium (Guillard and Ryther, 1962) at 20 °C, except for *T. amphioxeia*, which was kept at 15–18 °C.

To obtain the weight-specific carbon and nitrogen value of each polyp, six polyps in the stock cultures were individually immersed into distilled water for a few seconds to remove salts. Then, all polyps were placed together onto a fragment of glass-fiber filter (Watman GF/C, ca. 5 mm × 5 mm) in a tin cup that had been dried and weighed. Four sets of these treatments were prepared. After drying the polyps and cups at 60 °C overnight, the dry weight of each polyp was measured and the samples were stored in a desiccator. Then, each tin cup was compacted around the polyps, and the sample was analyzed using a CHN analyzer (Flash EA1112, Thermo Fisher Scientific) to measure carbon and nitrogen contents of the polyps.

2.2. Feeding experiments of polyps on a diet of ciliates

For the following experiments (Exp A, B, D, E), individual polyps in the stock culture were transported into a well of six-well plates, containing ca. 5 ml of filtered seawater; for Exp. C, each polyp was placed in a small plastic vessel containing ca. 10 ml of filtered seawater. Then the plates and vessels were stored at 20 °C for about 1 week to allow the polyps to attach to the bottom. Twelve to 15 wells or vessels in which a polyp was attached to the bottom were used for experimental treatments, and polyps were removed from three wells or vessels as control treatments. This procedure was done to eliminate the effects of bacteria film on the ciliates in the experimental treatment by providing the same conditions in the control treatments.

The following experiments on a diet of *F. ehrenbergii* (Exp A, B, C), *Strombidium* sp. (Exp D), or *M. rubra* (Exp E) were carried out (Table 1). Three to five density levels of each ciliate species were prepared by diluting the stock cultures of the ciliates with filtered seawater. Then, 7 ml of each suspension (20 ml for Exp C) was poured into three or four wells per plate containing polyps for experimental treatments and three wells per plate for control treatments. During each experiment, all the treatments were incubated with gentle agitation using a rocking mixer at 20 °C and under light conditions of ca. 300 μmol photons m^{-2} s^{-1}. Polyps were acclimated for 2 to 3.5 h to each concentration of ciliates. Samples were collected at the start and then 3 or 4 h later. After sufficient mixing with a pipette, while avoiding bubble formation, 1.5 ml (5 ml for Exp C) of the suspensions was collected and poured into a well of a 24-well plate containing acid Lugol's iodine solution for preservation (final concentration 5%). The fixed ciliates in each well were then counted using an inverted microscope.

2.3. Feeding response of polyps on phytoplankton

The ciliate cultures used in the feeding experiments included phytoplankton as prey for ciliates. To examine whether polyps respond to phytoplankton as a food source, the dinoflagellates *H. triquetra*, *Prorocentrum minimum*, *Akashiwo sanguinea*, *Gyrodinium instriatum*, and *Cochlodinium convolutum* (equivalent spherical diameter [ESD]: 12.1–39.0 μm, Table 2) were provided at concentrations of 2.5×10^2 to 21.7×10^3 cells ml^{-1} (equivalent to 9.0×10^2 to 11.4×10^3 ng C ml^{-1}) to a polyp attached on a well of a six-well plate. For comparison, two species of ciliates *Strombidium* sp. and *M. rubra* were also provided at concentrations of 0.7×10^2 to 11.8×10^2 cells ml^{-1} (equivalent to 2.3×10^2 to 10.9×10^2 ng C ml^{-1}). Then, the feeding behavior of each polyp was recorded at room temperature (ca. 20 °C) using a stereomicroscope (SZX9, Olympus) and a digital camera with movie function (Camedia SP 350, Olympus) or a digital video camera recorder

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