Reproduction of *Aurelia aurita* s.l. (Cnidaria: Scyphozoa) polyps: Functional response and energy budget

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1. Introduction
It is important to clarify why scyphozoan medusa populations show such remarkable annual fluctuations, sometimes developing massive blooms, sometimes not. The benthic polyps play a key role to control the medusa population size, because they reproduce asexually by multiple modes and release numerous planktonic ephyrae, which develop into medusae. Hence, it is ultimately necessary to clarify which factors are responsible for the reproduction and population dynamics of benthic polyps. In this study, we constructed a bioenergetic model in the scyphozoan polyps for the first time, and used it to determine the net growth (somata and offspring) rates of the polyp stage of *Aurelia aurita* sensu lato, a cosmopolitan jellyfish species.
2. Materials and Methods
Aurelia aurita polyps used in this study were derived from the stock-cultures, which originated from medusae caught in Hakata Bay, northern Kyushu, in 2011. We examined the effects of temperature and salinity on carbon-weight-specific respiration rate, and the effects of temperature, prey type and prey density on carbon-weight-specific ingestion rate on various natural zooplankton taxa (e.g. copepods and benthos larvae) in the laboratory. A carbon budget model constructed from these experiments was applied to the natural polyp population in Fukuyama Harbor, the Inland Sea of Japan.
3. Results and Discussion
3-1. Respiration rate
The carbon-weight-specific respiration rate of *A. aurita* polyps increased exponentially with increasing temperature from 8 to 28°C. However, salinity did not affect the respiration rate, which was constant at salinities ranging from 15 to 33.
3-2. Ingestion rate
Polyps could capture and ingest various natural mesozooplankton from the Inland Sea of Japan at much higher rates than those feeding on microzooplankton (i.e. ciliates), indicating that the major food for polyps is mesozooplankton. The general functional response of polyps feeding on various prey taxa was expressed by a linear increase in ingestion rate as a function of prey density, although it was affected by the size and/or swimming ability of prey organisms. Accordingly, the clearance rate was constant irrespective of prey density, and increased linearly with temperature from 8 to 26°C.
3-3. Carbon budget model and its application to natural polyp population
Integrating above-mentioned results, we constructed a carbon budget model of *A. aurita* polyps as a function of temperature and mesozooplankton prey density. An application of this model to polyps in Fukuyama Harbor (monthly average temperature: 9.7–27.2°C, monthly average copepod biomass: 9.7–82.7 mg C m^{-3}) suggested that they consistently attain a positive growth rate, ranging from 0.0039 to 0.34 μg C μg C^{-1} d^{-1}. Our model also predicts that oligotrophic areas where mesozooplankton biomass is always less than the critical level, not meeting the minimum requirement for metabolism, i.e., 4.6–8.6 mg C m^{-3}, may not constitute polyp habitat.
4. Conclusion
As the growth rate of polyps elevates with the increase of mesozooplankton biomass, eutrophication is considered a major driving force for medusa blooms. The moon jellyfish formerly known as *A. aurita* is now a species complex, which consists of at least 10 cryptic species by genomics in addition to *A. aurita* s.s. If

the seasonal life cycle and physio-ecological characteristics of these species are similar to our *A. aurita*, being tentatively designated as *Aurelia* sp. 1, our bioenergetic model may be applicable to the polyp populations in any temperate coastal waters.

Keywords: jellyfish bloom, polyp, functional response, bioenergetics