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Feeding habits of mesopelagic copepods in Sagami Bay: Insights from integrative analysis

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ABSTRACT

We investigated the feeding habits of mesopelagic copepods in Sagami Bay during a spring bloom, focusing on omnivorous copepods of the families Aetideidae, Metridinidae, Scolecitrichidae, and Spinocalanidae by integrative application of stable-isotope (SI) analysis, microscopic observation of gut contents, elemental analysis of gut contents and sinking particles with an electron probe micro analyzer (EPMA), and morphological analysis of mouthparts. The SI ratios (δ^{13}C and δ^{15}N) of most mesopelagic species that initially were assumed to feed mainly on marine snow (sinking particles) were allocated within the SI plots that were assumed for the consumers of particulate organic matter from the epipelagic zone. Microscopy showed different compositions of gut contents among the copepods, most of which ingested marine snow containing incompletely degraded phytoplankton and cyanobacteria. According to the EPMA analysis, percentages of terrigenous mineral particles in marine snow were significantly higher than those in most of the copepod guts, suggesting selective ingestion of sinking particles by these copepods. Morphological analysis showed that mouthparts of most of the copepods were not suitable for fine-particle feeding. These mesopelagic copepods were distributed mostly below 50 m, where Chl-*a* was essentially depleted. These observations suggest feeding specialization among mesopelagic omnivorous copepods, as well as their selective ingestion of fresher particles and/or parts among diverse fractions of marine snow.

1. Introduction

Copepods are among the major components of pelagic food webs, and mesopelagic copepods, among others, are essential to our understanding of pelagic ecosystems in at least two aspects: species diversity and biogeochemical processes.

In terms of species diversity, it is widely accepted that the number of oceanic pelagic species can be very high at any given locality (Angel, 1993). The mechanisms sustaining the co-existence of such a large number of species are central to zooplankton ecology. Several studies have addressed this issue with reference to copepod communities, e.g., feeding behavior of copepods in relation to niche separation (Mullin, 1966), spatio-temporal patterns of copepod dominance and diversity (McGowan and Walker, 1985), and vertical habitat partitioning among oceanic copepods (Ambler and Miller, 1987). However, the mechanisms generating and maintaining this diversity are still not fully understood, particularly in the mesopelagic zone, where the highest species diversity of pelagic copepods has been observed in many localities (e.g., Roe, 1972; Yamaguchi et al., 2002; Kuriyama and Nishida, 2006). Several recent studies have demonstrated feeding specialization and/or resource partitioning among species coexisting in the mesopelagic zone (e.g., Schnetzer and Steinberg, 2002; Kuriyama and Nishida, 2006; Wishner et al., 2008; Laakmann et al., 2009; Matsuura et al., 2010).

Additionally, the role of mesopelagic zooplankton in the vertical carbon flux is among the major issues in biogeochemistry. The consumption of sinking flux by zooplankton may contribute to degradation and remineralization processes in the meso- and bathypelagic zone (e.g., Koppelmann et al., 2004; Steinberg et al., 2008; Robinson et al., 2010). It has been estimated that 4 to 86% of the losses of sinking carbon flux can be attributed to zooplankton (Koppelmann et al., 2004, and reference therein). Copepods may play a significant role in the vertical carbon flux because of their large contribution to the zooplankton community in terms of both abundance and biomass. Consumption of sinking flux by copepods was calculated at 38% of total POC flux in the northwestern Pacific (Sasaki et al., 1988) and 32% in the western Pacific (Yamaguchi et al., 2002). These estimates were based on the assumption that omnivore/detritivore or suspension feeders utilize only sinking particles ('marine snow') non-selectively. However, recent studies have suggested differences in the food compositions of some deep-sea omnivorous/detritivorous copepods (e.g., Wishner et al., 2008; Laakmann et al., 2009). To estimate accurately the role of copepods in the degradation of sinking particles (or particulate

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organic material), further information on the feeding habits of deep-sea copepods is required (Buesseler et al., 2008).

Earlier workers classified the feeding modes of mesopelagic copepods into carnivory, omnivory, and detritivory based on light-microscopic observations of mouthpart morphologies (Arashkevich, 1969) and gut contents (Wickstead, 1962; Harding, 1974; Hopkins, 1985, 1987; Hopkins and Torres, 1989). The importance of marine snow as a potential food source has also been proposed (Lampitt et al., 1993), but little is yet known of the relative importance of the various types of marine snow that have been observed to date (Alldredge and Silver, 1988). Gowing and Wishner (1986, 1992) suggested generalized feeding by deep-sea copepods (but see Wishner et al., 2008). However, specialized feeding modes of deep-sea copepods have also been suggested for some groups/species, mainly on the basis of morphological analysis (e.g., Cahoon, 1982; Steinberg, 1995; Nishida and Ohtsuka, 1996; Nishida and Ohtsuka, 1997; Matsuura and Nishida, 2000; Nishida et al., 2002; Wishner et al., 2008).

The bottlenecks in studies of the feeding ecology of deep-sea copepods lie in the difficulty of performing laboratory experiments and the requirement of fresh live copepods and various types of food materials to simulate food conditions in the deep-sea, so that the primary research tool to date has been the microscopic analysis of gut contents. A major challenge in gut content analysis of deep-sea copepods has been the characterization and quantification of the items in the guts, particularly of the "amorphous materials" that often dominate the contents (e.g., Harding, 1974; Gowing and Wishner, 1986, 1992). In addition to conventional light and scanning-electron microscopy, several alternative methods have been applied to augment/enhance our knowledge, e.g., elemental analysis using energy-dispersive X-ray spectrometers (EDS) (Uchima, 1988, for *Acartia omorii* and *Oithona davisae*; Kosobokova et al., 2002, for *Spinocalanus antarcticus*), semi-quantitative analysis by transmission electron microscopy (e.g., Gowing and Wishner, 1998; Wishner et al., 2008), and epi-fluorescence microscopy for characterizing microbes (e.g., Nishida et al., 1991; Lampitt et al., 1993; Wilson and Steinberg, 2010). All of these analyses have inherent weaknesses in that the gut contents represent the feeding history only over limited time scales, i.e., within hours before the time of sample collection, and only include materials "outside" the body with no information on their assimilation by copepods. Carbon and nitrogen stable isotope analysis (Koppelmann et al., 2009; Laakmann et al., 2009) and fatty-acid composition (Morris, 1971; Laakmann et al., 2009) have been applied to investigate deep-sea food webs and the trophic positions of deep-sea copepods. However, these biochemical analyses have limited ability to characterize in detail the food items themselves. Therefore, a multidisciplinary approach is needed to investigate the feeding habits of mesopelagic copepods.

The purpose of this study was to examine the feeding habits of mesopelagic copepods, focusing on their selective utilization of food resources in central Sagami Bay during a spring bloom. To achieve this, an integrative application of carbon and nitrogen stable isotope analyses of copepod body tissues and environmental particles, microscopic gut contents analysis, morphological analysis of feeding appendages, and elemental analysis of gut contents and environmental particles was used. Additionally, vertical distributions of the targeted species were examined during day and night to compare feeding layer depths.

2. Materials and methods

2.1. Sampling

Plankton and water samples were collected from a fixed station (Stn P, 35°00′N; 139°20′E, Depth: 1450 m, Fig. 1) in Sagami Bay during a cruise of the R/V "Tansei Maru" during 21–27 April 2009. Plankton samples were collected using MTD horizontal closing nets (Motoda, 1971; 56-cm mouth diameter, 0.33-mm mesh aperture). The MTD nets were towed horizontally at 15 depths (0, 50, 95, 100, 150, 195, 200, 295, 300, 395, 400, 500, 600, 800, and 1000 m) during both day and night (Table 1). Positions of the attachment of the MTD nets to the wire were preset based on the desired sampling depth and the wire angle, which was

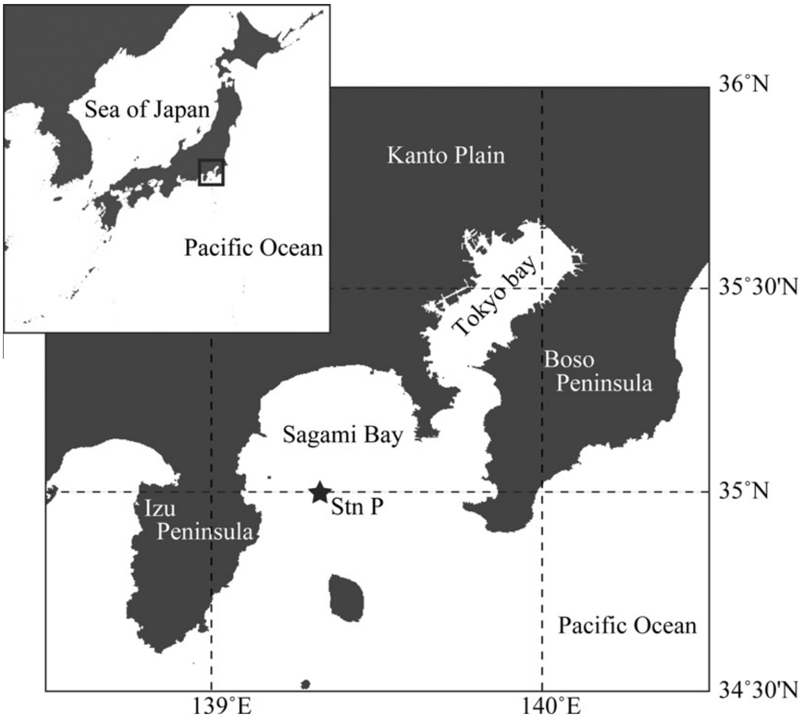

Fig. 1. Sampling station (Stn P, 1450 m water depth) in the central part of Sagami Bay, Japan.