Vertical distribution and feeding ecology of a copepod *Gaetanus variabilis* in the southern Japan Sea during winter

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Abstract: Vertical distribution, gut fullness and gut contents were investigated on an aetideid copepod *Gaetanus variabilis* during winter at a station in the southern Japan Sea. Most individuals of C3-C6 (adult) *G. variabilis* were distributed between 500 and 1000 m depth. While early copepodid stages resided deeper than older ones, no diel vertical migration was detected throughout the copepodid stages. Feeding activity of *G. variabilis* as judged by gut fullness scores varied with developmental stage/sex, but no diel feeding rhythm was observed. Adult males cease feeding as a reflection of degeneration of their feeding appendages. The gut content analysis showed that *G. variabilis* is a particle feeder consuming mainly upon silicoflagellates, followed by diatoms, tintinnids and fragments of metazooplankton. An estimated daily ration of *G. variabilis* population based on calculated metabolic rates was 5.03 mg C m^{-2} day^{-1}, which accounts for 4.5% of the local primary production or 54% of particulate organic carbon flux down to the 500 m depths at southern Japan Sea.

Keywords: gut content, daily ration, mesopelagic, copepods, Japan Sea

1. Introduction

While a large body of information about feeding of pelagic copepods has been accumulated on epipelagic and neritic species, little is known about those living in the deep-sea (cf. review of Mauchline, 1998). From the viewpoint of global carbon cycle, biological mineralization of organic carbon in the mid- to deep-ocean is thought to be a key process. Since a significant portion (17–60%) of planktonic respiration is hypothesized to occur in the mesopelagic layer (Biddanda and Benner, 1997; Hernández-León and Ikeda, 2005), accurate information about plankton feeding in the deep ocean is needed to evaluate the role of zooplankton in mineralization of organic carbon in the deep-sea.

The family Aetideidae is a medium to large-sized calanoid copepods inhabiting mesopelagic to bathypelagic zones of the world oceans. Aetideid copepods feed on both phytoplankton and zooplankton, and are characterized as mixed feeders or detritivores (Matthews, 1964; Arashkevich, 1969). Auel (1999) estimated that ingestion rates of aetideid copepods to be 1.6 ± 0.1 g C m^{-2} yr^{-1} in the 500–2000 m depth in the Greenland Sea, which accounts >40% of the available carbon supply in mesopelagic layers. In the Swedish fjord, Båmstedt (1981) noted that among carnivores the aetideid copepods has the highest annual mean energy requirement (43% of carnivorous energy flow). Both studies show that the aetideid copepods play a important role in material cycle and mineralization, mediating particulate matter flux in the mesopelagic zones of high latitude seas.

In the Japan Sea, the species-diversity of

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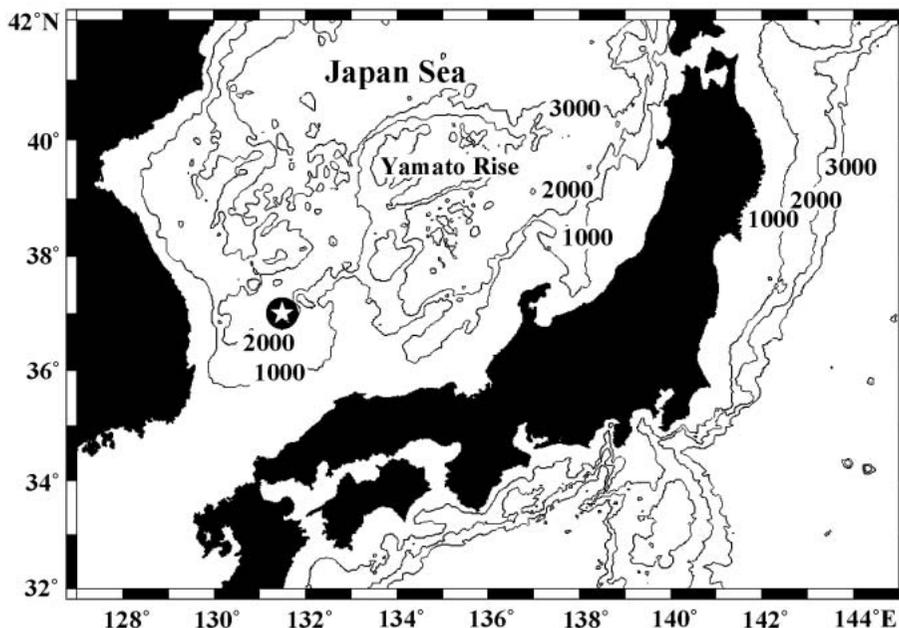
Fig. 1. Location of sampling station (circled star) in the southern Japan Sea. Depth contours (1000, 2000, and 3000 m) are superimposed.

zooplankton at depth is known to be much less than those in the adjacent regions of the North Pacific (VINOGRADOV, 1973). This is largely due to the lack of bathypelagic species in the Japan Sea, because of the connecting straits between Japan Sea and western North Pacific are shallow (<130 m) (ZENKEVITCH, 1963). In the southern Japan Sea, the number of pelagic copepod species is reported to be 62 (TAKAHASHI and HIRAKAWA, 2001) or 87 (HIRAKAWA et al., 1990). Among them, only 15 species are known to occur in the mesopelagic zone of the Japan Sea (TAKAHASHI and HIRAKAWA, 2001), where characterized by near-zero temperature. Since *Gaetanus variabilis* (=*Gaidius variabilis*) is the only suspension feeding copepod inhabiting the lower mesopelagic zone (cf. HIRAKAWA et al., 1990), it is of great interest to know the function of *G. variabilis* in the vertical material flux in the Japan Sea.

In the present study, we investigated the ecology of *G. variabilis* in the southern Japan Sea, including their vertical distribution, gut contents and gut fullness. We also calculate the daily ration of *G. variabilis* based on their metabolic rates (oxygen consumption) to assess their role in material flux in the mesopelagic zones of the Japan Sea.

2. Materials and Methods
2-1. Sample collection

In 26-27 January 1997, zooplankton samplings were made in the daytime and nighttime with oblique tows of IONESS (mesh size: 330 μm, mouth opening: 1 m^2) through 16 discrete depths between the surface and 1000 m at St. J7 (37°00′N, 131°30′E; 2130 m deep) in the southern Japan Sea (Fig. 1). IONESS (Intelligent Operation Net Environmental Sampling System: SEA Co. Ltd, Japan) is a version of MOCNESS (WIEBE et al., 1985) and capable of collection of eight samples per cast. Consecutive two IONESS casts from 16 depth strata between 1000–900, 900–800, 800–700, 700–600, 600–500, 500–400, 400–300, 300–200, 200–150, 150–100, 100–75, 75–50, 50–30, 30–20, 20–10, and 10–0 m achieved each sampling. Daytime casts were made from 11:54–14:08 (local time) and night casts from 19:22–22:07. Sunrise and sunset of 26 January 1997 was at 07:16 and 17:32, respectively. A flow meter (Rigosha, Japan) was mounted in the mouth of the net to register the
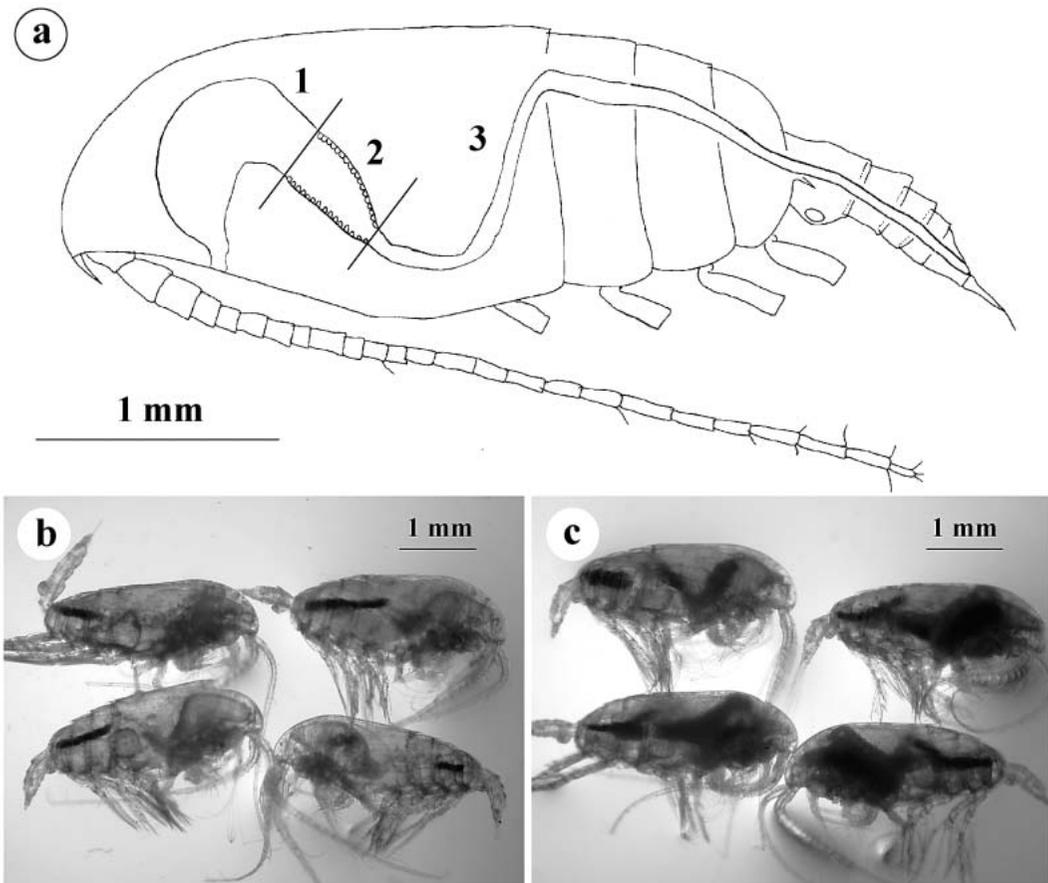
Fig. 2 *Gaetanus variabilis* C6F. (a) Diagram of digestive tract showing three principal zones (1-3). Zones 1-2 were defined as foregut and zone 3 as hindgut in this study. (b) Specimens of which only hindgut filled (gut content score: 3). (c) Specimens of which both foregut and hindgut filled (gut content score: 4). See text for details.

volume of water passing through the net. All zooplankton samples were immediately preserved in 5% borax-buffered formalin-seawater on board. Temperature and salinity data were obtained by a CTD system (SBE 911plus). Water samples were collected from 0, 20, 50, 75, 100, 125, 200, 300, and 500 m depth using water bottles, filtered through Whatman GF/F filters, and chlorophyll *a* was extracted with N, N-dimethylformamide (SUZUKI and ISHIMARU, 1990) and measured using a fluorometer (EP-777, Japan Spectroscopic Inc.). Chlorophyll *a* data were provided by Dr. H. NAGATA (Seikai National Fisheries Research Institute).

2-2. Enumeration

At the land laboratory, *Gaetanus variabilis* specimens were sorted, staged and counted from a 7/8 aliquot. Separation of females (F) from males (M) was possible from copepodid stage 4 (C4) onward (e.g. C4F or C4M). The 330 μm mesh net was considered to retain from C3 onward, as judged by diagonal size (467 μm) of the net used and the cephalosome width of each copepodid stage (mean $\pm$ 1sd, C2: 371$\pm$14; C3: 518$\pm$20; C4F: 686$\pm$57, C4M: 724$\pm$59 μm). Biomass (wet mass) of each copepodid stage was estimated from the prosome length data in YAMAGUCHI *et al.* (2005), combined with wet mass-prosome length relationships of this species (YAMAGUCHI and IKEDA, 2000).
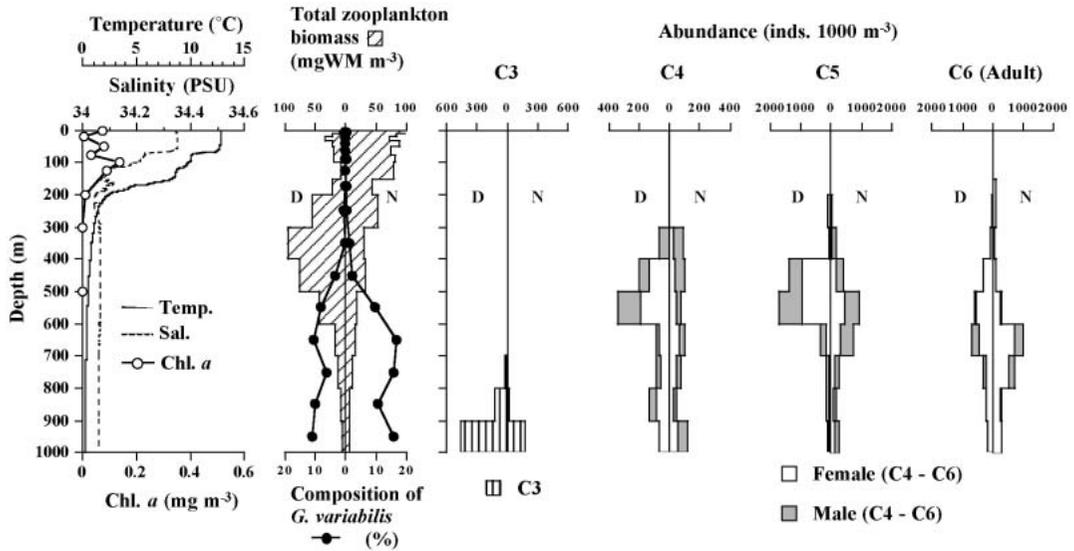
Fig. 3. Vertical distributions of temperature, salinity, and chlorophyll *a* (left), total zooplankton biomass and composition of *Gaetanus variabilis* (middle), and each copepodid stage of *G. variabilis* (middle to right). Female/male determination was done for C4 to C6. D: day, N: night.

Biomass of *G. variabilis* at each sampling stratum was computed from abundance data multiplied by individual wet mass. Percentage composition of *G. variabilis* biomass to the total zooplankton biomass was calculated from total zooplankton wet mass data provided by Dr. N. IGUCHI (Japan Sea National Fisheries Research Institute).

2-3. Gut content and gut fullness analysis

Based on the cellular structure, the gut of copepods was separated into three zones (cf. MAUCHLINE, 1998). Morphology of digestive tract of *Gaetanus variabilis* was semi-looped z-shaped (Fig. 2a), and the zones 1–2 referred as foregut and zone 3 as hindgut in this study. Under a stereomicroscope, the gut fullness of C5 and C6 (adults) was scored into 1–4 (1: gut empty, 2: only foregut filled, 3: only hindgut filled, 4: both foregut and hindgut filled; cf. Fig. 2b, c).

Nighttime samples of *Gaetanus variabilis* C6F from 600–700 m depth, where they were most numerous, were used for gut content analysis. Up to 10 individuals of which guts filled were sorted and rinsed in distilled water for overnight. Their hindguts were carefully removed from the prosome with a pair of fine

needles under a dissecting microscope and then rinsed in distilled water. The specimens were placed on a deep hole glass slide filled with distilled water and dissected using fine needles. After removing all remains of the gut wall by means of a pair of tweezers, all gut contents were picked up with a fine pipette and mounted on a small area (within the diameter of a stub) of a Millipore filter with the aid of a vacuum pump. The filter was dehydrated by alcohol series (70, 90, 99 and 100%) and deposited in a decicator overnight. The totally dried filter was trimmed and mounted on a stub, and then ionsputterred. Gut contents from all individuals were mounted together on the stub and observed under a scanning electron microscope (SEM, Joel JSM-T20).

2-4. Estimation of daily ration

Daily ration was calculated from respiration data by the method described by IKEDA and MOTODA (1978). Respiration data used in this calculation were adjusted metabolic rate (AMR; range: 3.64–4.21 μl O_2 [body N]$^{-0.85h}$h^{-1}, mean: 3.93) at 0.5℃ (close to *in situ* temperature of the present sampling site, cf. Fig. 3) reported on *Gaetanus variabilis* in the Japan Sea by IKEDA and HIRAKAWA (1998). Dry mass (D

M, μ g) of each copepodid stage of *G. variabilis* was computed from the prosome length data (YAMAGUCHI *et al.*, 2005) using an allometry equation (YAMAGUCHI and IKEDA, 2000). Assuming body N content of all *G. variabilis* copepodid stages as 9.8%DM (cf. IKEDA and HIRAKAWA, 1998), respiration rates of each copepodid stage were estimated from the mean *AMR* value. Respiration rates were then converted to carbon units assuming a respiratory quotient ($[CO_2]/[O_2]$) of 0.97 (protein metabolism, cf. GNAIGER, 1983). Carbon budget equation for copepods may be expressed as: Ingestion (I) = Growth (G) + Metabolism (M) + Egestion (E) + Excretion (U). Assuming assimilation efficiency ($[G+ M]/ I$) and gross growth efficiency (G/ I) to be 70% and 30%, respectively (cf. IKEDA and MOTODA, 1978), ingestion rates (I: μ g C individual^{-1} h^{-1}) can be calculated from M as $I= M/ (0.7-0.3)$. The rates were converted to daily basis (x 24 hours), thus estimated ingestion rates were varied from 0.22 μ g C ind^{-1} day^{-1} for C1 to 10.26 μ g C ind^{-1} day^{-1} for C6F. Since C6M of *G. variabilis* cease feeding (cf. YAMAGUCHI *et al.*, 2005), ingestion rates were not estimated for C6M. Daily ration of individuals in a given depth stratum were summed (μ g C m^{-3} day^{-1}) and integrated over 0–1000 m depth range (mg C m^{-2} day^{-1}).

3. Results
3-1. Vertical distribution and abundance

The surface temperature and salinity were 12.5°C and 34.35PSU, respectively, and both decreased rapidly with increasing depth until 200 m (Fig. 3). Below 200 m, both temperature and salinity were stable at <1.0°C and 34.05PSU, respectively, indicating the characters of "Japan Sea Proper Water" (cf. SUDO, 1987). Chlorophyll *a* showed a maximum (0.14 mg m^{-3}) at 100 m, then decreased rapidly with depth and was almost nil at 200 m.

Total zooplankton biomass peaked at 300–400 m during day, while at 0–10 m during night (Fig. 3). This day-night shift of total zooplankton biomass was attributed by two large diel vertical migrators: a hyperiid amphipod *Themisto japonica* (cf. IKEDA *et al.*, 1992) and a euphausiid *Euphausia pacifica* (cf. IGUCHI *et al.*, 1993). Biomass of *Gaetanus*

variabilis varied between 0 and 3.5 mg WM m^{-3} with depth, and their contribution to the total zooplankton biomass was greater below 500 m depths (6.3–16.7%). In terms of standing stock, biomass of *G. variabilis* was 0.93–1.02 g WM m^{-2} that accounts 2.89-2.92% of total zooplankton biomass integrated over 1000 m (31.8 –35.3 g WM m^{-2}).

Gaetanus variabilis was distributed below 150 m both day and night, and no diel changes in the vertical distribution pattern was seen across all copepodid stages (Fig. 3). C1–C3 distributed mainly below 800 m throughout the day. The depth where the 50% population resided ($D_{50\%}$, cf. Pennak, 1943) was 930 m (daytime) or 942 m (nighttime) for C3. On the other hand, C4 was concentrated at 500–600 m throughout the day ($D_{50\%}$ of C4F and C4M was 588-650 m and 537–588 m, respectively). C5 was abundant at 400–600 m extending their vertical distribution to shallower depth than C4 did ($D_{50\%}$ of C5F and C5M was 522–597 m and 537–590 m, respectively). Adult female (C6F) and male (C6M) occurred the shallowest depths (150–200 m), although their populations centered at slightly deeper depth than that of C5 ($D_{50\%}$ of C6F and C6M was 608-681 m and 664–684 m, respectively). Total abundance of C3–C6 stage *G. variabilis* integrated over the 0–1000 m water column was 675–815 individuals m^{-2}. Sex ratios (female:male) were nearly equal for C4 (1.2–1.6:1) and C5 (0.8–1.4:1), but skewed to female for C6 (3.9–5.4:1) (Fig. 3).

3-2. Gut content and daily ration

Gut fullness scores of C5 and C6 *Gaetanus variabilis* varied little between day and night but between stages (Fig. 4). All C6M exhibited empty guts throughout the day. Subsequent observations on feeding appendages of C6M revealed that their maxillae had reduced setae, suggesting that they are unable to feed. For C5F, C5M and C6F, no significant changes in gut fullness scores with depth were observed (Fig. 4). It is noted that the data 200–400 m depths are not accurate because of smaller sample size (n=1–11, cf. Fig. 3).

Observed diet components of *Gaetanus variabilis* were centric diatoms (*Thalassiosira eccentrica* and others), tintiniids (*Parafavella*
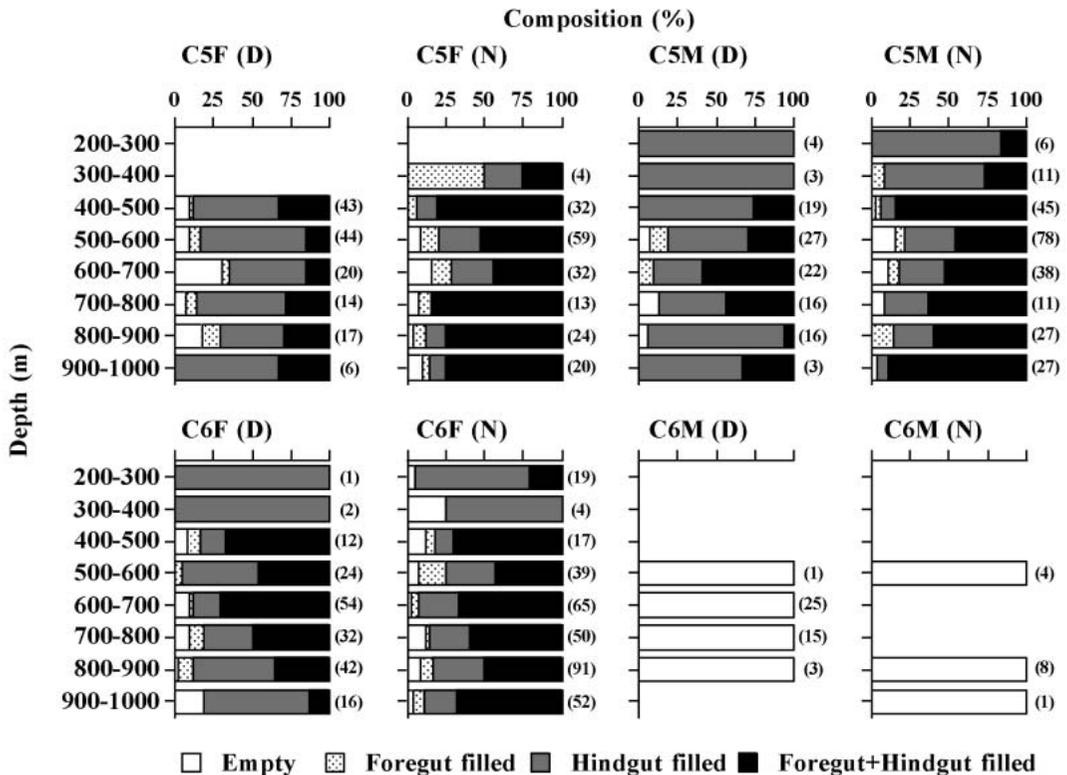
Composition (%)

Fig. 4. Vertical distribution of percentage composition of gut content score (1: empty, 2: foregut filled, 3: hindgut filled, and 4: both foregut and hindgut filled) of C5–C6 stages of *Gaetanus variabilis*. Numbers of examined specimens were shown in the parentheses. F: female, M: male; (D): day, (N): night.

sp.), silicoflagellates (*Distephanus speculum*) and fragments of metazooplankton (hook of chaetognaths) (Fig. 5). Silicoflagellates were most numerous (more than 100 cells per stub), followed by centric diatoms (>50), tintiniids (>10) and the fragments of metazoans (<10). It is noted that most of the centric diatom and tintiniid cells were observed being damaged, but silicoflagellate cells were intact.

Vertical profiles of the estimated daily ration of the total of C3-C6 of *Gaetanus variabilis* populations showed a maximum at 500–700 m depth 14.4 μg C m^{-3} day^{-1}, Fig. 6), with an integrated value over the 0–1000 m water column of 5.03 mg C m^{-2} day^{-1}.

4. Discussion
4.1. Vertical distribution

In the Oyashio region, western subarctic Pacific, a reversed (nocturnal descent) diel vertical migration pattern of a modest degree has

been reported for *Gaetanus* (=*Gaidius*) *variabilis* (YAMAGUCHI and IKEDA, 2000). However, no such the DVM was observed for the same *G. variabilis* at the station in the southern Japan Sea in this study (Fig. 3). In the northern Norwegian fjord, the vertical behavior of aetideid copepods (*Chiridus armatus*) is reported to be variable, depending on the seasonal change in day/night lengths, and the DVM ceased during the periods of summer midnight sun (no dark period) and winter darkness (no light daytime) (FALKENHAUG *et al.*, 1997). From this view, YAMAGUCHI and IKEDA's earlier study (YAMAGUCHI and IKEDA, 2000) was the compilation of data from all seasons of the year. In contrast, the present results are from January only which corresponds to the annual minimum of day length at this latitude. This difference may be attributed to this dissimilar conclusion for the DVM behavior of *G. variabilis* between these two studies.
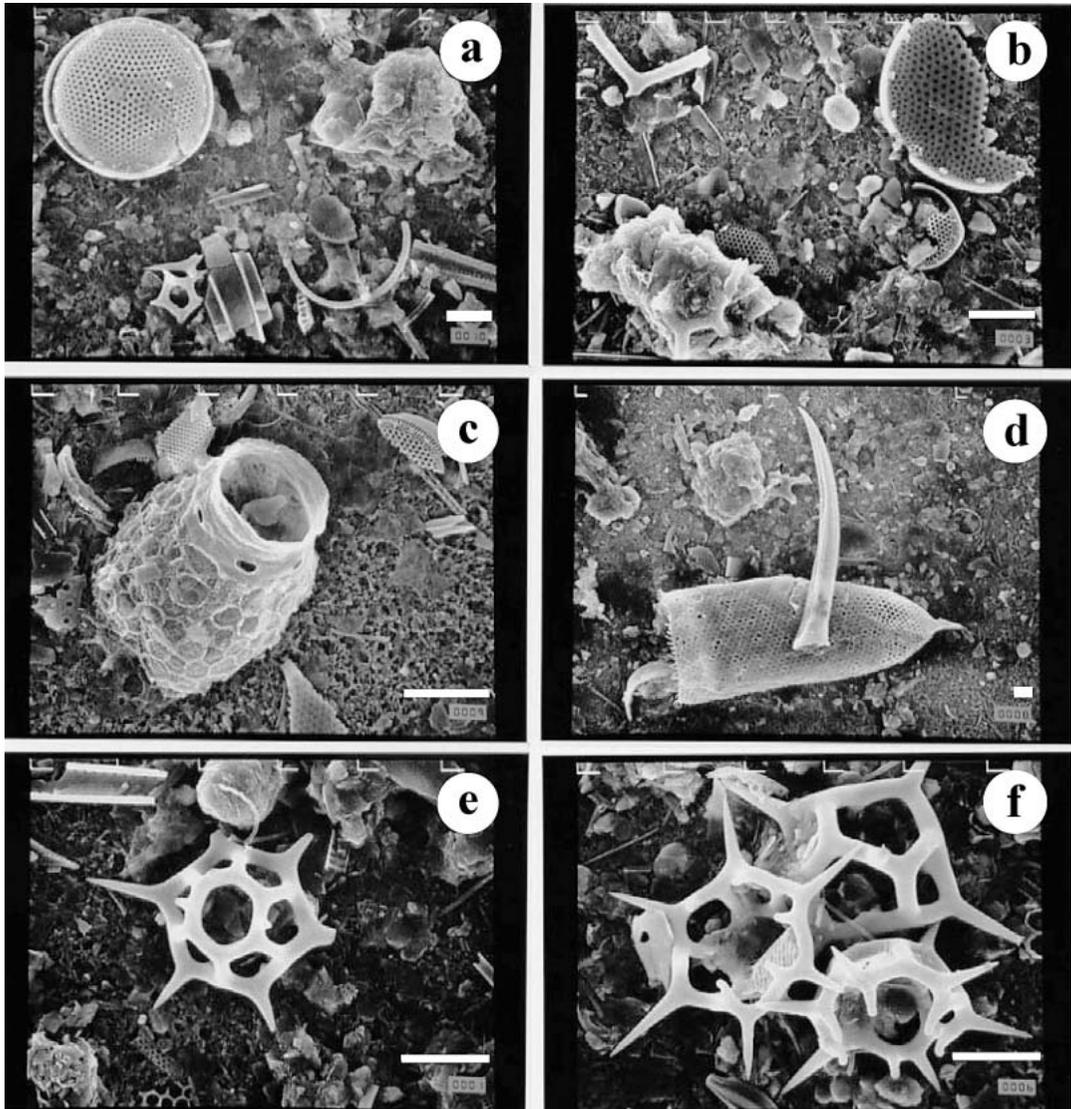
Fig. 5. SEM micrographs of gut contents of *Gaetanus variabilis* C6F. The diatom *Thalassiosira eccentrica* (a, b), tintinnids (*Parafavella* spp.) (c, d), fragment (hook) of chaetognaths (d), and the silicoflagellate *Distephanus speculum* (e, f) are seen. Scale bars indicate 10 μm.

Differential depth distribution patterns across copepodid stages of *Gaetanus variabilis* observed in this study (Fig. 3) suggest possible ontogenetic vertical migration (OVM) of this species characterized by developmental ascent. The OVM pattern and its magnitude of *G. variabilis* estimated in the present study (420 m: 942 m [$D_{50\%}$ of C3] −522 m[$D_{50\%}$ of C5F]) are consistent to those reported at Site H (41°30′N, 145°47′E) in the Oyashio region (337 m,

YAMAGUCHI and IKEDA 2000) and St. KNOT (44°00′N, 155°00′E) in the western subarctic Pacific (543 m, YAMAGUCHI *et al.*, 2004). The OVM characterized by developmental ascent is a widespread phenomenon in deep-sea copepods (WEIKERT and KOPPELMANN, 1993; RICHTER, 1994; FALKENHAUG *et al.*, 1997) and ostracods (KAERIYAMA and IKEDA, 2002). The OVM pattern is interpreted as a life history trait or strategy to reduce predation risk. They spend
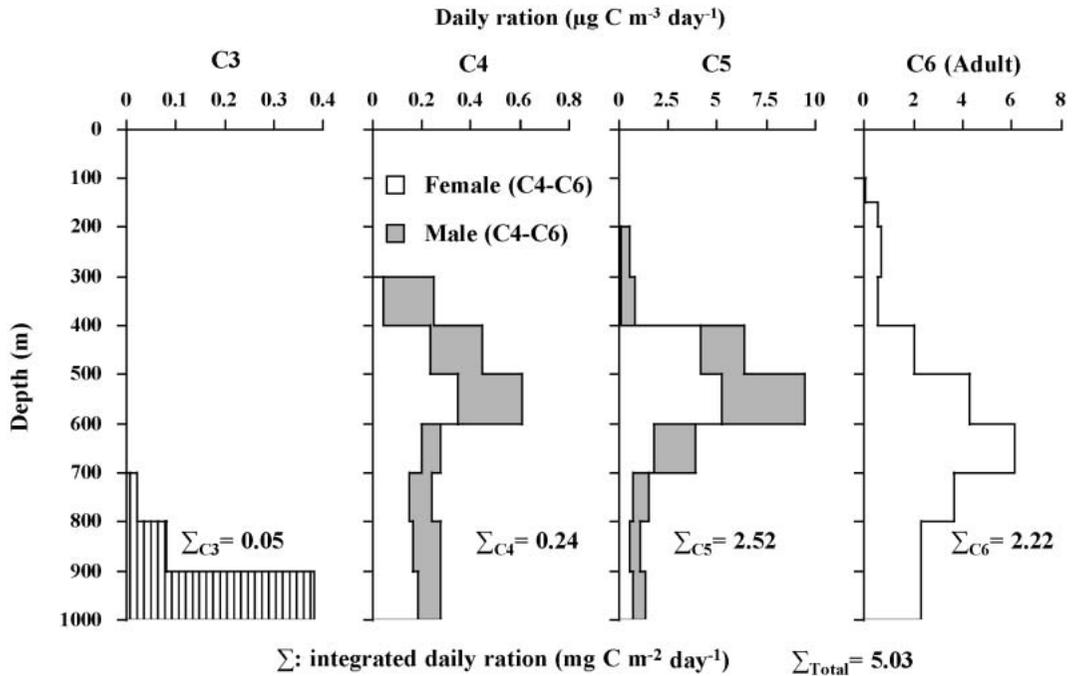
Fig. 6. Vertical distribution of daily ration of each copepodid stage of *Gaetanus variabilis*, and its total integrated over the 0-1000 m water column. Note that daily ration is based on mean abundance of day/night.

the juvenile stages in lower-predation environments (deep layer) and ascend to higher-food environments with development (YAMAGUCHI *et al.*, 2004). Since the lifetime fecundity of deep-sea zooplankton is low in general (cf. MAUCHLINE, 1991), reducing mortality at the juvenile stage is of prime importance for the maintenance of their populations.

4.2. Feeding activity

Observed degeneration of feeding appendages of C6M *Gaetanus variabilis* in this study is a common phenomenon known in aetideid copepods (MATTHEWS, 1964; MACLELLAN and SHIH, 1974). Degeneration of feeding appendages results in cease feeding (Fig. 4), then body mass of C6M becomes less than that of C5M because of its utilization for metabolism and production of spermatophores at C6M. The decrease in the body mass (i.e. negative growth) from C5M to C6M of *G. variabilis* has already been reported by YAMAGUCHI and IKEDA (2000). Longevity of C6M of aetideids is known to be shorter than that of C6F (MATTHEWS, 1964), which is reflected in the skewed sex ratios to

females in C6 (Fig. 3).

Diel feeding rhythms characterized by a marked peak at night is a common phenomenon for epipelagic copepods (ATKINSON *et al.*, 1996; SAITO and TAGUCHI, 1996; BESIKTEPE, 2001). Day and night differences in gut fullness of *Gaetanus variabilis* were less marked (Fig. 4). The depth where *G. variabilis* distributed throughout the day (400–800 m, Fig. 3) corresponds to the light intensity of 10^{-3} to 10^{-7} μW cm^{-2} in clearest oceanic water, or the thresholds for daytime predation by fish (10^{-6} μW cm^{-2}) and for phototaxis of copepods (10^{-4} μW cm^{-2}) (MACKIE, 1985). Since feeding copepods are more vulnerable to visual predation than non-feeding copepods, TSUDA *et al.* (1998) hypothesized that the copepods′ nocturnal feeding without DVM is advantageous in reducing visual predation by fish. From this view, absence of diel feeding rhythm of *G. variabilis* of this study may be related to the dim light conditions in their habitat depth throughout the day where visual predation risk is considered to be low.

Recently, SCHØYEN and KAARTVEDT (2004)

have revealed spatial and temporal variations of various scales of feeding activities of an another aetideid copepod *Chiridius armatus* by measuring fecal pellet production rates. According to their results, fecal pellet production by adult female *C. armatus* increased at nighttime during the day, in spring season of the year and for those living in shallower depths. Assuming that gut fullness is comparable to fecal pellet production, presence of clear diel feeding rhythm and the effect of depth distribution seen in *C. armatus* may be interpreted by their shallower habitats (<200 m depth) than those of *G. variabilis* (500–1000 m) in this study.

4-3. Gut contents

From the morphology of mouthpart appendages, aetideid copepods are classified to mixed feeders on both animals and plants (ARASHKEVICH, 1969). In the laboratory experiment, OLSEN *et al.* (2000) observed that the aetideid copepod *Chiridius armatus* foraged heavily on dead, non-moving prey, suggesting the use of chemoreceptors in the search for food. Microscopic observation (SEM or TEM) on gut contents of aetideid copepods revealed that "pigmented cells", diatoms, dinoflagellates, coccoliths, cysts and eggs, silicoflagellates, radiolarians and fragments of copepods (HARDING, 1974), or bacteria, olive-green materials, olive-green body/minipellets, siliceous fragments, amorphous materials, and crustacean cuticles (GOWING and WISHNER, 1986; 1992) are major components. HOPKINS and TORRES (1989) examined the gut contents of aetideid copepods (*Gaetanus tenuispinus* and *Euchirella rostromagna*) in the Southern Ocean, and found diatoms, silicoflagellates, dinoflagellates, tintinnids and radiolarians in it. Relative contribution of phytoplankton, protozoans and metazoans in the total diet components of aetideids is reported to be 52, 31 and 18%, respectively (HOPKINS and TORRES, 1989). Gut contents of *Gaetanus variabilis* in this study (Fig. 5) are consistent to that of HOPKINS and TORRES (1989) in that the most numerous components were silicoflagellates, followed by centric diatoms, tintiniids, and the fragments of metazoans.

LAMPITT *et al.* (1993) observed that *Gaetanus pileatus* ingested marine snow aggregates. Since the marine snow aggregates consist of cyanobacteria and picoplankton, each of which are too small to ingest by these classes of crustaceans, such the feeding mediated by marine snow could be a significant short cut in the food chain pathways (cf. GOWING and WISHNER, 1992). In the present study, non- or little damaged silicoflagellate cells were observed frequently in the gut contents of *Gaetanus variabilis* (Fig. 5). According to TAKAHASHI (1987), the sinking of silicoflagellates is in the form of large aggregates which sink faster than discrete cells, and silicoflagellates generally sink faster than marine snow mediated diatom assemblages. This faster sinking of silicoflagellates is a possible cause for its dominance in the gut content of mesopelagic *G. variabilis*.

4-4. Implications for carbon flux

In our calculation of carbon ingestion by *Gaetanus variabilis* from respiration rates, we assumed assimilation efficiency as 70% (cf. IKEDA and MOTODA, 1978). The assimilation efficiency may be underestimated, since ALVAREZ and MATTHEWS (1975) determined assimilation efficiency of aetideid copepod *Chiridius armatus* to be 90% on *Artemia* and 95% on mixed zooplankton in laboratory experiments. These high assimilation efficiency values are on animal food which contains high organic matter (=low ash). CONOVER (1966) reported a negative relationship between assimilation efficiency and ash contents for copepods fed various types of food. Since we found no evidence of carnivorous feeding in *G. variabilis* from gut content analysis in this study (Fig. 5), the assimilation efficiency of *G. variabilis* cannot be so high as observed for *C. armatus* by ALVAREZ and MATTHEWS (1975).

Primary production (NAGATA, 1998) and CZCS chlorophyll concentrations (KIM *et al.*, 2000) in the Japan Sea have been reported to peak in spring, and the former reaches as high as ca. 1000 mg C m^{-2} day^{-1} (calculated from Table 1 of NAGATA, 1998). Primary production has been estimated in the waters around Yamato Rise, central Japan Sea, in winter is 112 mg C m^{-2} day^{-1} (calculated from Table 1 of

NAGATA, 1998). If we apply the flux-primary production relationship established by SUESS (1980) ; $C_{flux} = C_{prod} / (0.0238\,z + 0.212)$, where C_{prod} is primary production (112 mg C m^{-2} day^{-1}) and C_{flux} is carbon flux (mg C m^{-2} day^{-1}) at a given depth (z, m), POC fluxes down to the 500 m depth was estimated to be 9.25 mg C m^{-2} day^{-1}. Compared with the winter primary production data or fluxes at 500 m depth presently available, calculated POC ingestion by *Gaetanus variabilis* (5.03 mg C m^{-2} day^{-1}, Fig. 6) accounts to 4.5% of primary production or 54.4% of POC fluxes at 500 m depth. In the 500–1000 m water column of the southern Japan Sea, the biomass of *G. variabilis* is a small fraction (6–17%) of the total zooplankton (Fig. 3). Nevertheless, this species is only component of suspension feeding copepods (HIRAKAWA *et al.*, 1990; TAKAHASHI and HIRAKAWA, 2001), and provides a significant impact on POC flux in this zone (>500 m) (Fig. 6).

In Greenland Sea, the POC consumption by euchaetid and aetideid copepods in the mesopelagic zones has been calculated as 4–28% of the local primary production (AUEL, 1999). AUEL (1999) has noted that aetideid copepods alone consume more than 40% of carbon supply to the mesopelagic zone. In Swedish fjords, the population of an aetideid copepod *Chiridius armatus* has been evaluated to have the greatest annual mean energy requirement (43% of carnivorous energy flow) among other carnivorous zooplankton (BÅMSTEDT, 1981). Thus, the feeding of the aetideid copepods is estimated to influence the carbon flux in the high latitude seas.

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