HOKKAIDO UNIVERSITY

Title	Structure, biomass distribution and trophodynamics of the pelagic ecosystem in the Oyashio region, western subarctic Pacific
Author(s)	Ikeda, Tsutomu; Shiga, Naonobu; Yamaguchi, Atsushi
Citation	Journal of Oceanography, 64(3), 339-354 https://doi.org/10.1007/s10872-008-0027-z
Issue Date	2008-06
Doc URL	https://hdl.handle.net/2115/59805
Rights	The final publication is available at Springer via http://dx.doi.org/10.1007/s10872-008-0027-z
Type	journal article
File Information	HUSCUP-Oyashio.pdf

Hokkaido University Collection of Scholarly and Academic Papers : HUSCAP

J. Oceanogr. 64: 339-354 (2008)

Structure, biomass distribution and trophodynamics of the pelagic ecosystem in the Oyashio region, western subarctic Pacific

Tsutomu Ikeda*, Naonobu Shiga, Atsushi Yamaguchi

Plankton Laboratory, Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-machi, Hakodate, Hokkaido, 041-0821 Japan

*Corresponding author

Tsutomu Ikeda, e-mail: tom@pop.fish.hokudai.ac.jp

Running head: Pelagic ecosystem of the Oyashio region

Keywords: Oyashio, pelagic ecosystem, community structure, biomass, production, trophic level, ecological efficiency, keystone species

Abstract

Biomass distribution and trophodynamics in the oceanic ecosystem in the Oyashio region are presented and analyzed, combining the seasonal data for plankton and micronekton collected at Site H since 1996 with data for nekton and other animals at higher trophic levels from various sources. The total biomass of biological components including bacteria, phytoplankton, microzooplankton, mesozooplankton, micronekton, fishes/squids and marine birds/mammals was 23 g C m^{-2}, among which the most dominant component was mesozooplankton (34% of the total), followed by phytoplankton (28%), bacteria (15%) and microzooplankton (protozoans)(14%). The remainder (9%) was largely composed of micronekton and fish/squid. Marine mammals/birds are only a small fraction (0.14%) of the total biomass. Large/medium grazing copepods (*Neocalaus* spp., *Eucalanus bungii* and *Metridia* spp.) accounted for 77% of the mesozooplankton biomass. Based on information about diet composition, predators were assigned broadly into mean trophic level 3-4, and carbon flow through the grazing food chain was established based on the estimated annual production/food consumption balance of each trophic level. From the food chain scheme, ecological efficiencies as high as 24% were calculated for the primary/secondary production and 21% for the secondary/tertiary production. Biomass and production of bacteria were estimated as 1/10 of the respective values for phytoplankton at Site H, but the role of the microbial food chain remains unresolved in the present analysis. As keystone species in the oceanic Oyashio region, *Neocalanus* spp. are suggested as a vital link between primary production and production of pelagic fishes, mammals and birds.

1. Introduction

The western boundary current of the subarctic circulation in the North Pacific is called the 'Oyashio' (Reid, 1973). The Oyashio originates from the Eastern Kamchatka Current, which mixes with cold, less saline Okhotsk Sea water on its way southwest along the Kuril Islands (Kono, 1997). The Oyashio flows offshore of southern Hokkaido, and reaches the east coast of northern Honshu, Japan, after which it turns east at about 40° N, parallel with the extension of the Kuroshio. The latter, warmer current originates to the east of the Philippins and flows northeast along the Ryukyu Islands and Honshu (Fig. 1). The "Oyashio region" as defined in this study refers to a broad, triangular oceanic area (ca. 3.0×10^5 km^2) between the southwestward, downstream limit of the Oyashio and its eastward, return stream, excluding coastal zones (Fig. 1).

The pelagic ecosystem in the Oyashio region is characterized by rich nutrients and the incidence of massive diatom blooms during spring (Saito et al., 2002). In the subarctic Pacific, the Oyashio region located at the western-end differs from the eastern region (typically represented by Station P) in several features: (1) macronutrients are often depleted as a result of diatom blooms (no blooms occur and nutrients are maintained at high level throughout the year at Station P; Harrison et al., 2004); (2) primary production is higher (new production; 78 vs. 35-50 g C m^{-2} y^{-1}; Wong et al., 2002); (3) mesozooplankton biomass in the epipelagic zone is much higher [annual mean; 115 (Odate, 1994) vs. 61 mg wet weight m^{-2} (calculated from Fig. 7 of Parsons and Larri, 1988)]; and (4) it possibly fosters greater planktivorous pelagic fish populations such as jack mackerel, Japanese anchovy, Japanese sardine and Pacific saury, which migrate through the area seasonally (Taniguchi, 1999). All these results

suggest that the Oyashio region is highly productive, but details about seasonal features of the structure, biomass distribution of major components, and trophodynamics in the pelagic ecosystem have been poorly synthesized.

During the period from September 1996 to October 1997, we sampled monthly in an area established in the slope water of the Oyashio region off southeastern Hokkaido (41°30' to 42°30'N and 145°00' to 146°00'E, 2000-7000 m deep, hereafter referred to as Site H, Fig. 1) off southeastern Hokkaido to evaluate the biomass and life cycles of mesozooplankton. To achieve that objective, the depth of sampling was designed to cover the entire ontogenetic migration range of the large grazing copepods previously evaluated at Station P in the eastern subarctic Pacific (Miller et al., 1984). Since October 1997, a less intensive follow-up study has been continuing, including bacteria, phytoplankton and micronekton in this region. This study is a synthesis of all published and unpublished data collected at Site H, supplemented by a 10-year (1990-1999) monitoring program (including nutrients and chlorophyll a) on the stations along the A-line (acrossing Site H) by Hokkaido National Fisheries Research Institute (Kasai et al., 2001). Literature data on animals at higher trophic levels were combined with those of lower trophic levels to broaden the perspective of the Oyashio region ecosystem.

2. Environmental conditions

2.1. Hydrography

At Site H, the annual range of the sea surface temperature was large, ranging from 2°C (March to April 1997) to 18°C (September to October 1996 and 1997)(Fig. 2). The Oyashio water, characterized by salinities from 33.0 to 33.3 and temperature below

3°C (Ohtani, 1971), occurred in the upper 150 m from February to April 1997. After April, less saline, seasonally-warmed water (possibly originating from the Okhotsk Sea; T. Kono, pers. comm.) occupied the upper 50 m of the water column. Surface temperatures above 10°C were observed from September to November 1996 and from June to October 1997, when the thermocline was well established at 20 to 50 m. Effects of warm core rings originating from the Kuroshio extension were seen in September of both 1996 and 1997, and from December 1996 to January 1997, as judged by temperature at 200 m (>4°C) and salinity in the 0 to 200 m layer (>33.5)(Fig. 2). The temperature and salinity in the 200 to 1500 m layer were stable and nearly constant at 2 to 3°C and 33.5 to 34.5, respectively, throughout the year.

With regard to the seasonal cycle of hydrographic conditions in the upper layers anomalous southward intrusions of the Oyashio have been observed in winter of some years, which is due to the barotrophic response of the ocean to the change in the wind stress characterized by the southward development of the enhanced Aleutian Low (Sekine, 1999).

The dissolved oxygen minimum layer is at 500-1000 m in the western subarctic Pacific, including the Oyashio region (cf. Favorite et al., 1976). In the minimum layer, our seasonal observation showed that the oxygen concentration at Site H declines to 0.8 ml O_2 l^{-1} or 10% saturation (Ikeda et al., 2004) .

2.2. Nutrients

Seasonal cycles characterized by highs in winter and lows in summer are an annual event of nutrient concentrations in the surface layer of the Oyashio region (Kasai et al., 2001). During our sampling from September 1996 through October 1997, the

maxima were seen in winter (25 μM nitrate, 42 μM silicate, and 1.8 μM phosphate) and minima in summer (<0.1μM nitrate, 2 μM silicate, and 0.1 μM phosphate) at A4-A7, A-line stations within Site H (Kasai et al., 2000). While the decrease from winter to summer is due to uptake by the diatom bloom (Fig. 2), it is not explicitly known whether or not nutrient depletion among other processes (zooplankton grazing, cell sinking, light limitation etc) is the main cause for the termination of the bloom in the Oyashio region as a whole (Saito et al., 2002; Saito and Tsuda, 2003). Kuma et al. (pers. comm.) considers that iron depletion possibly occurs in the surface layers, since iron concentration decreased from winter (0.6-1.0 nM) toward summer (<0.3 nM) at Site H.

3. Biological components

3.1. Bacteria

Heterotrophic bacteria were stained with DAPI and filtered onto 0.2 μm black Nucleopore filters and counted with an epifluorescence microscope. Near-monthly sampling from the surface to 3000 m depth during May through December 2002 at Site H revealed the biomass density of heterotrophic bacteria to be 2.6-4.3 g C m^{-2} with a mean of 3.7 g C m^{-2} (Table 1). At Station KNOT, Yamaguchi et al. (2004) reported bacterial biomass values of 4-8 g C m^{-2} over the 0-2000 or 5000 m water column during fall-winter, which is within 2-fold of the value for Site H. At A3 (a station more inshore than Site H, cf. Fig. 1), heterotrophic bacterial biomass integrated over the euphotic depth (30-50 m) ranged from 0.35 (winter) to 1.5 g C m^{-2} (summer) with a mean of 0.85 g C m^{-2} (Shinada et al., 2001); however, the data at A3 cannot be compared with those at Site H or Station KNOT because of a large difference in the

depth ranges integrated (30-50 m vs. 2000-5000 m) for the calculation of the biomass. Bacterial biomass per unit volume of water decreases with increasing depth, but this depth-related reduction is known to be less radical than those of phytoplankton, protozooplankton and metazooplankton (=mesozooplankton) in the western North Pacific (Yamaguchi et al., 2002).

In the western subarctic Pacific, annual production/biomass (P/B) ratios of bacteria derived from the data of bacterial biomass and production (determined by the ^{3}H-leucine incorporation method) decrease rapidly with increasing depth (5-7 in the 0-100 m layer, and 0.1-0.2 in that from 1000-4000 m), with a mean of ca. 4 for 0-2000 or 3000 m (Nagata et al., 2000). By combining the P/B ratio with the biomass mentioned above, the annual bacterial production at Site H was estimated to be 14.4 (= 3.6 × 4) g C m^{-2} (Table 1).

3.2. Phytoplankton

Incidence of a massive phytoplankton bloom is an annual event in the Oyashio region, though there are year-to-year variations in the timing and magnitude of the bloom (Kasai et al., 2001). During our zooplankton sampling program at Site H in 1996-1997, chlorophyll *a* at the surface was around 0.4 mg m^{-3} from August 1996 to the end of February 1997 and then increased rapidly to > 9 mg m^{-3} in May 1997 (Fig. 2). During this period, concentrations above 2 mg m^{-3} extended down to 50 m. The surface chlorophyll *a* concentrations had decreased to 2 mg m^{-3} by the end of June and to 0.4 mg m^{-3} toward the end of 1997. Chlorophyll *a* concentrations were <0.4 mg m^{-3} below 100 m throughout the year. Assuming a carbon/chlorophyll *a* ratio of 60 (Batchelder and Miller, 1989), the range of seasonal variations equates to 2.2-97 g C m^{-2},

with an annual mean of 6.6 g C m^{-2} (Table 1). The results of size-fractionation indicate that most chlorophyll *a* during the spring bloom is >10μm. The fraction <2μm increased with water temperature but never exceeded 20% (Kasai, 2000). Water samples were collected at Site H during 2002-2004 (2 years) and seasonal succession of phytoplankton communities (cell size: >10 μm) studied by the Utermöhl method (Hasle, 1978) was characterized by the predominance of centric diatoms during spring blooms (*Chaetoceros* in the 2003 bloom and *Thalassiosira* in the 2004 bloom), followed by dinoflagellates in summer and pennate diatoms (*Fragilariopsis*, *Neodenticula*, *Thalassionema*) in winter. Over the same period, a total of 52 species of centric diatoms, 25 pennate diatoms, 15 dinoflagellates and 3 silicoflagellates were recorded at Site H (Masuda and Shiga, unpublished; Fukui and Shiga, unpublished).

Annual total production of phytoplankton (new plus regenerated) has been estimated as 146 g C m^{-2} by combining scattered seasonal data (Kasai, 2000), and 200-300 g C m^{-2} by a global productivity model based on satellite-derived chlorophyll concentration data (Behrenfield and Falkowski, 1997). Annual new production, based on the seasonal depletion in nitrate in the top 50 m of the water column, varied from 66 to 91 g C m^{-2} (mean: 78) during 1995-2000 in the Oyashio region (Wong et al., 2002)(Table 1).

3.3. Microzooplankton

No microzooplankton data are currently available at Site H. At A3, microzooplankton biomass (flagellates, ciliates, copepod nauplii) in the euphotic zone (30-50 m) ranged from 0.58 g C m^{-2} (winter) to 1.9 g C m^{-2} (summer) with an annual mean of 1.1 g C m^{-2} (Shinada et al., 2001). At station KNOT, microzooplankton

biomass has been determined as 1-4 g C m^{-2} for the 0-2000 or 5000 m water column in fall-winter (Yamaguchi et al., 2004), and can be re-calculated as 3.2 g C m^{-2} for the 0-2000 m water column to facilitate comparison to the biomass of bacteria and that of mesozooplankton (Table 1).

Shinada et al. (2001) computed annual production of microzooplankton at A3 as 5.2 g C m^{-2} (annual P/B ratio is therefore 4.7) for the euphotic zone only, and this value should not be applied to the microzooplankton biomass in the 0-2000 m water column on the premise that the P/B ratio declines with increasing depth, as was demonstrated for bacteria above. Therefore, it was not possible to estimate the annual production and annual prey (=bacteria) consumption by microzooplankton at Site H in this study.

3.4. Mesozooplankton.

Monthly samplings were done for one year (September 1996 to October 1887) at Site H using a closing net (60 cm mouth diameter, 100 μm mesh size; Kawamura, 1989), which was towed vertically through five depth strata between 0 and 2000 m [0-bottom of thermocline (BT), BT-250, 250-500, 500-1000 and 1000-2000 m]. The analyses of mesozooplankton samples thus collected have yielded information about biomass and life cycle patterns of most abundant species, including copepods, chaetognaths, euphausiids, ostracods, hydromedusae and appendicularians (Table 2). The towing speed of the closing net was 1 m sec^{-1}, which would be fast enough to capture most meso-size and young macro-size zooplankton, but "net-avoidance" cannot be ruled out for active macrozooplankton such as euphausiids and amphipods, leading to potential underestimation of the biomass of the latter two taxa. While no alternative samples were available for euphausiids, the biomass of amphipods were collected by Bongo nets

(70 cm mouth diameter, 333 μm mesh openings) which were towed from 500 m depth to the surface every 1-2 months during 1996-1998 (Yamada et al., 2002; Yamada and Ikeda, 2006).

Biomass density of each species at a given sampling date was calculated based on a length-to-dry mass (DM) relationship or developmental stage-DM tables (see literatures cited for each species in Table 2), combined with population structure defined by size (body length) for amphipods, ostracods, chaetognaths, coelenterates and appendicularians or developmental stages for copepods in the 0-2000 m water column. The biomass thus obtained at each sampling date was then integrated over the entire sampling period (396 days) to obtain its annual mean. The biomass of each mesozooplankton species was expressed as DM originally, but was converted to carbon mass (CM) in this study, using a factor of CM/DM = 0.5 (Omori, 1969). The sum of annual mean biomass of all mesozooplankton (plus some macrozooplankton) was 8.21 g C m^{-2} (Table 2). Copepods occupied 85.5% of the total biomass, followed by chaetognaths (8.8%). The remaining taxa were all less than 2%, e.g., euphausiids (1.9%), amphipods (1.3%) and others. Among copepods, *Neocalanus cristatus* was the most dominant species in terms of biomass, followed by *Eucalanus bungii*, *N. plumchrus* , *Metridia pacifica*, *N. flemingeri* and *M. okhotensis*, and these 6 copepods altogether contributed 76.6% of the total (Table 2). These results are in good agreement with those in the 0-4000 m water column reported by Vinogradov and Arashkevich (1969) off Kurile-Kamchatka (north of the Oyashio region), although their survey was limited to the summer season only (June-August). Despite anticipated net avoidance behavior by euphausids, the present result (0.15 g C m^{-2}) is very similar to the average biomass (0.11 g C m^{-2}) of *Euphausia pacifica* in the North Pacific Ocean

reported by Lasker (1966). Recently, Taki (2006) analyzed seasonal Norpac net samples along the coastal waters off south-eastern Hokkaido (41-43°N) and estimated the annual biomass of *E. pacifica* to be 0.38 g C m^{-2} or 2.5 times the value at Site H.

Information about annual P/B ratios is currently available for *Neocalanus* spp. (Kobari et al., 2003), *Metridia pacifica* (Ikeda et al., 2002), the four amphipods (Yamada and Ikeda, 2006) and *Euphausia pacifica* (Taki, 2006). For the other species, on which no data are currently available, their annual P/B ratios were computed from the generalized equation of Banse and Mosher (1980) in which the annual P:B was expressed as a function of caloric content of matured females (M, kcal equivalent, cf. Table 2) of invertebrates. Annual P (= Annual B × Annual P/B) thus computed was used as a basis to derive annual food consumption (Annual F) by using a balanced equation proposed for zooplankton (Ikeda and Motoda, 1978). According to Ikeda and Motoda (1978), Annual F (= 3.33 × Annual P) is derived if one assumes assimilation efficiency to be 70% and gross growth efficiency to be 30%. To facilitate our understanding of the pelagic trophic structure, mesozooplankton species were separated into herbivores and carnivores, though the species classified as herbivores may better be called omnivores or particle feeders (cf. Mauchline, 1998).

3.5. Micronekton

During the period from August 2002 to August 2003, micronekton was sampled near monthly intervals with Bongo nets (70 cm mouth diameter, 0.33 mm mesh) from 1000 m depth to the surface at Site H. From these seasonal samples, biomass densities and major component species of crustaceans and fish were analyzed. To express biomass in carbon mass (CM), dry mass (DM) was assumed to be 20% of wet mass

(WM) and CM to be 50% of DM (cf. Omori, 1969).

As crustacean micronekton, five mysids (*Eucopia australis, Meterythrops microphithalma, Gnathophausia gigas, Boreomysis californica* and *Acanthomysis dimorpha*) and six decapods (*Hymenodora frontalis, Bentheogennema borealis, Gennadas propinquus, Acanthephyra quadrispinosa, Sergestes similis* and *Sergia japonica*) occurred in the seasonal samples. The abundance ranged from 13-56 individuals m^{-2} for mysids, and 7.9-11.6 individuals m^{-2} for decapods. Annual mean biomass was computed as 0.32 g C m^{-2} for mysids, and 0.52 g C m^{-2} for decapods (total: 0.84, Table 1).

A total of 11 species were identified as micronektonic fish, and *Cyclothone alba, C. atraria, Diaphus theta, Leuroglossus schmidti* and *Stenobrachius nannochir* predominated in terms of biomass. Seasonally, the abundance changed from 0.5 to 14.4 individuals m^{-2} (0-1000 m) or 0.15 to 0.90 g C m^{-2} (annual mean: 0.64, Table 1). At the three stations in the waters between Oyashio and Kuroshio (transitional zone) off Honshu, Watanabe et al. (1999) reported an average myctophid fish biomass as 18.5 ($\pm$4.7, SD) g WM m^{-2} in summer, which is equivalent to 1.9 g C m^{-2} (= 18.5 × 0.2 × 0.5) or three times higher than our annual mean value. Watanabe et al. (1999) used a large commercial net with mouth openings as large as 200 m^2 (as compared to 0.77 m^2 of our Bongo net), whereby the most critical problem of net avoidance by the fishes is thought to be minimized in their sampling. Nevertheless, incomplete coverage of all seasons makes it difficult to compare their results with those at Site H.

No information about annual P/B ratios is presently available for either fish or crustacean micronekton. By defining the representative body mass of newly mature specimens of the fish as 10 gWM, and of the crustaceans as 0.5 gWM, equivalent

calorific contents were computed as 10 and 0.5 Kcal, respectively (1 g WM = 1 Kcal, Banse and Mosher, 1980). Substituting these caloric contents into Banse and Mosher's equation, we obtain the annual P/B ratio of 1.5 for the former and 0.8 for the latter (Table 1). Following the same procedure for mesozooplankton, Annual P and Annual F thus obtained for fish micronekton were 0.96 and 3.2 g C m^{-2}, respectively, and those for crustacean micronekton were 0.67 and 2.2 g C m^{-2}, respectively (Table 1).

3.6. Fish and squid

The biomass is a total of those of Pacific sardine (*Sardinops sagax*), walleye pollock (*Theragra chalcogramma*), salmon (Salmonidae spp.), lanternfish (Myctophidae spp.), Pacific saury (*Cololabis saira*), Japanese anchovy (*Engraulis japonicus*), other fish and unspecified squid during 1980s (7.2 t WM km^{-2}) and 1990s (4.0 t WM km^{-2}) (Springer et al., 1999). A mean of the two periods (6 t WM km^{-2}) is equivalent to 0.6 g C m^{-2} (Table 1) if one assumes the same conversion factors used for mesozooplankton biomass. Ivanov (1997) investigated the composition and biomass of fish (including fish micronekton) and squid (mostly *Gonatopis borealis* and *Watasenia scintillans*) in the upper mesopelagic zone (200-500 m) of the eastern Oyashio region [Region 3 in Ivanov (1997)] during October-December 1992 and August 1992, and reported the fish biomass to be 18.3 t WM km^{-2} (or 1.8 gC m^{-2}) and squid biomass 0.9 t WM km^{-2} (or 0.09 g C m^{-2}). According to the FAO Yearbook of Fisheries Statistics, the annual landing of marine fish and invertebrates in Fishing Area 61 (Northwest Pacific) was 1.18-1.33 t WM m^{-2} (=0.11-0.13 g C m^{-2}) in 1989-1995 (FAO, 1997). Standing stock has been estimated for individual fishes; the summer biomass of Japanese sardine (*Sardinops melanostictus*) when its standing stock peaked

in 1984 was 3.2×10^6 tons WM per 48×10^3 km^2 (cf. Wada, 1991) or 6.6 g C m^{-2} by using the same conversion factors mentioned above. A recent estimate of Pacific saury migrating the Oyashio region is 3 g C m^{-2} [calculated from: 400×10^6 tons per 5.49×10^6 km^2, taking into account the duration of migration being 5 mo (August-December) in the year (http://www.myg.affrc.go.jp/)]. The severe lack of information led us to take the data in Springer et al. (1999) as a minimal estimate of annual standing stock of fish and squid in the Oyashio region.

To calculate annual P/B ratios of the group of Fishes/squids, a Pacific saury (100 g WM or 100 Kcal) was taken as a representative mature adult size, and Banse and Mosher's equation predicted a ratio of 0.8 for this size of fish. The Annual P was computed as 1.6 g C m^{-2}, and Annual F to support the production was 1.6 g C m^{-2} (Table 1).

3.7. Marine mammals

According to Springer et al. (1999), the western subarctic Pacific including the Oyashio region is inhabited by 24 cetaceans and 7 pinnipeds. The most abundant species is Dall's porpoise (*Phocoenoides dalli*), which is distributed across the entire subarctic Pacific. Based on the information about the population size (estimated as 1.2×10^6 individuals), assumed body mass of an individual (150 kg), and the total habitat area ($19{,}937\times10^3$ km^2) of the subarctic Pacific (WSA, ESA, WTZ and ETZ regions; Springer et al., 1999), the biomass was computed as 0.0090 kg WM km^{-2}, which is equivalent to 0.0016 g C m^{-2} [conversion factors: DM/WM = 0.35 (Prosser, 1962), and CM/DM = 0.5](Table 1).

The Northwestern Pacific is inhabited by 25,000 Minke whales (*Balaenoptera*

acutorostrata) weighing 5 t WM, 23,000 Brydes whales (*B. edeni*) weighing 15 t WM, 28,400 Sei whales (*B. borealis*) weighing 20 t WM, and 102,000 Sperm whales (*Physeter catodon*) weighing 25 t WM (population data: http://www.icrwhale.org/02-A-18.htm; representative body mass is arbitrary). The biomass of the four whales was summed and divided by the total habitat area ($10{,}566 \times 10^3 \mathrm{m}^2$), yielding 0.34 t WM km^{-2} or 0.060 g C m^{-2} (conversion factors; DM/WM = 0.35, CM/DM = 0.5). Since these whales migrate to the western subarctic Pacific during spring/summer only, the biomass was halved to calculate their annual mean biomass (=0.030 g C m^{-2}) in the Oyashio region (Table 1).

The pinnipeds, Steller's sea lion (*Eumetopias jubatus*) among others, may be important top predators in the subarctic region (Springer et al., 1999; Hunt et al., 2000), but their impacts in the Oyashio pelagic ecosystem are thought to be limited, since they stay near rookeries in summer and forage nearshore waters, which are not taken into account in this study.

Annual P/B ratios of Dall's porpoises and the whales were calculated from Banse and Mosher's equation, assuming representative body masses of mature specimens as 200 kg (=300×10^3 kcal) and 15,000 kg (=22.5×10^6 kcal), respectively. As a result, Annual P was calculated as 0.00032 g C m^{-2} for Dall's porpoises and 0.0015 g C m^{-2} for the whales. Annual F was calculated independently, because information is available on their daily food consumption data [7% of body mass for Dall's porpoises (Hunt et al., 2000), and 4% of body mass for minke whales (Tamura, 1998)]. The minke whale data were used for the other whales. Taking account of their feeding seasons (all seasons for the Dall's porpoises, and 180 days in the year for the whales), Annual F was estimated to be 0.041 g C m^{-2} for the Dall's porpoises and 0.22 g C m^{-2} for the whales.

3.8. Marine birds

Springer et al. (1999) and Hunt et al. (2000) summarized the abundance and biomass of marine birds in the subarctic Pacific and its marginal seas. However, the data for the Oyashio region defined in this study are considered as part of Kuroshio/Oyashio Currents Zone (KR/OY) and Western Transitional Zone (WTZ), and the data of KR/OY are inadequate. The number of marine bird species occurring in the broad areas is 35-40, with the predominance of Stormy-Petrels (*Oceanodroma* spp.) and Fulmars (*Fulmarus glacialis*)/Shearwaters (*Puffinus* spp.) in the western subarctic Pacific (Hunt et al., 2000). The biomass density estimated for the WTZ is 15.8 kg km^{-2} (=0.003 g C m^2)(Springer et al., 1999) or 3.2 kg WM km^{-2} (=0.0005 g C m^2)(Hunt et al., 2000). While the reason for the difference between the two estimates is not clear, we adopted the lower estimate of the latter paper in this study (Table 1). While no Annual P value is available, Annual F (per 96 day summer) was given as 0.026 g C m^{-2} for the WTZ (Hunt et al., 2000).

4. Discussion

4.1. Mesozooplankton as the major biological component

The total biomass density of all organisms in the pelagic ecosystem in the Oyashio region is 23 g C m^{-2} (Table 1), among which the most dominant category is mesozooplankton (34% of the total), followed by phytoplankton (28%), bacteria (15%) and microzooplankton (protozoans)(14%). The remainder (9%) is largely composed of micronekton and fish/squid. Marine mammals and birds are only a tiny fraction (0.14%) in the total biomass. The total biomass per unit area (m^{-2}) thus estimated for

1 the organisms in the Oyashio region is more than 10 times higher than that (1.8 g C m^{-2})
2 of the biomass of humans on the Japan Islands at present (128 million people on
3 377,835 km^{-2}, assuming 30 kg per person and conversion factors of DM/WM = 0.35 and
4 CM/DM = 0.5 used for marine mammals above).
5 Our 1996-1997 survey at Site H revealed that six large/medium grazing copepods
6 (*Neocalaus* spp., *Eucalanus bungii* and *Metridia* spp., cf. Table 2) were the major
7 components of mesozooplankton biomass (77%, cf. Table 2), and their biomasses
8 underwent marked seasonal and bathymetric (0-250 and 250-2000 m) variations in
9 response to seasonal phytoplankton abundance (Fig. 3). In the 0-250 m water column,
10 the biomass was maintained at a low level from September to March of the following
11 year, increased rapidly in April-July through the phytoplankton bloom (Fig. 3), then
12 decreased toward Octorber (annual mean: 1.85 g C m^{-2}). In the 250-2000 m layer,
13 high biomass of these copepods seen in early September, decreasing gradually toward
14 April of the next year, then increasing again until August-October of the same year
15 (annual mean: 4.45 g C m^{-2}). *Neocalanus* spp. are known to spawn at depth in advance
16 of the phytoplankton bloom, and their early copepodids are ready to utilize
17 phytoplankton during the bloom, a feature quite different from the spawning habit of
18 *Calanus* spp. in the North Atlantic (Miller et al., 1984; Kobari and Ikeda, 1999, 2001a,
19 b; Tsuda et al., 1999, 2004). Unlike *Neocalanus* spp., *Calanus* spp. in the North
20 Atlantic (and *Eucalanus bungii* and *Metridia* spp. in the Oyashio region) spawn in the
21 surface layer during the spring phytoplankton bloom, thus causing a delay in their
22 biomass peak until after the phytoplankton bloom (cf. Parsons et al., 1984). The
23 biomass of *Neocalanus* spp. found in the 250-2000 m layer at Site H is fated to die off
24 after completing their annual life cycle and predated by chaetognaths (Terazaki, 1991)

and other carnivores at that depth, but part of their biomass is thought to return to the food chain of the epipelagic zone through the predation by diel migrating myctophid fishes (Moku et al., 2000).

In addition to the six large/medium copepods, the euphausiids (*Euphausia pacifica* and *Thysanoessa* spp., cf. Table 2) are assigned as herbivores in this study. Among them, *E. pacifica* has been reported to depend on phytoplankton as its diet, and to spawn in response to the phytoplankton bloom in the southern Japan Sea (Iguchi et al., 1993) and off California (Brinton, 1976). During our survey in 1996-1997 at Site H, *E. pacifica* appeared to spawn a few months after the phytoplankton bloom, possibly because water temperatures at the time of the bloom were too cold to induce their spawning (2-10^{o}C as compared to the 9-16^{o}C, optimal spawning temperature for *E. pacifica*, cf. Brinton, 1976). Our estimate of the spawning season at Site H is consistent with those of Taki (2006) for the population of *E. pacifica* along coastal waters off south-eastern Hokkaido. In contrast, *Thysanoessa inspinata/longipes* larvae were abundant during the phytoplankton bloom at Site H (Okazaki and Ikeda, unpublished). Depending on environmental changes, the duration and intensity of euphausiid spawning could vary from one year to the next, as has been observed for *E. pacifica* and *T. inspinata* populations off central Oregon (Feinberg and Peterson, 2003). While the importance of euphausiids at Site H is not marked in terms of biomass (Table 2), they are known to be a major link between phytoplankton (plus some microzooplankton) and walleye pollock in the coastal Oyashio region (Yamamura, 2004) and minke whales in the Okhotsk Sea (Tamura and Fujise, 2002).

Over the period 1951-1990, mesozooplankton biomass in the Oyashio region has been reported to have fluctuated by a factor of two (Odate, 1994). Tadokoro et al.

(2005) analyzed part of Odate's sample series (1972-1999, ca. 30 years) taxonomically, and noted that the *Neocalanus* biomass was high in the mid-1970s, decreased in the late 1970s, and recovered in the late 1980s. As the cause for the long-term variation in the *Neocalanus* biomass, Todokoro et al. (2005) considered top-down control by Japanese sardine, the standing stock of which varied inversely with that of mesozooplankton. However, the amplitude of inter-annual variations in the stock size of the Japanese sardine during 1960s and 1990s is much greater (×1000) than that of the *Neocalanus* biomass. It has been shown that interannual fluctuation patterns of mesozooplankton and fish in the subarctic Pacific do not necessarily coincide with analyses at basin scales, suggesting the possible existence of match-mismatch between the two (Taniguchi, 1999; Ito et al., 2004). A recent study by Chiba et al. (2006), in which copepods were clustered into five seasonal groups, led to an alternative explanation of the long-term variation of mesozooplankton biomass in the Oyashio region during the last 50 years (1953-2001). According to them, the variation was a response to climate changes affecting the temperature of the water column from winter through summer, and specifically to the length of the productive season of each year (i.e., bottom-up control). The Aleutian Low has been considered a major climate forcing of the broad Kuroshio and Oyashio ecosystems, including primary production and sardine production (Miller et al., 2004).

4.2. Trophic structure: Production/consumption balance

Trophic structure is a basis for analyzing the dynamics of each biological component within the pelagic ecosystem. With phytoplankton as the primary producer (trophic level = 1), diet composition data for the other biological components or the

dominant species of the component such as micronekton (Hopkins and Sutton, 1998), fish micronekton (Beamish et al., 1999; Moku et al., 2000; Sassa and Kawaguchi, 2005), Pacific saury (Sugisaki and Kurita, 2004), walleye pollack (Yamamura, 2004), Japanese sardine (cf. Tadokoro et al., 2005), squids (Kawabata and Kubota, 2002; Watanabe et al., 2004), marine mammals and seabirds (Beamish et al., 1999; Springer et al., 1999; Hunt et al., 2000; Tamura and Fijise, 2002) were used to determine the most likely trophic level for each group of organisms (Table 1). The number of trophic levels thus estimated ranged from 3 to 4 for Fishes/Squids (mid-trophic level: 3.5), and from 3 to 5 for Marine Mammals/Marine Birds (mid-trophic level: 4).

Pelagic organisms, excluding large animals at higher trophic levels, are transported in and out of the Oyashio region system by the currents (Fig. 1). Assuming a current speed of 20-30 cm s^{-1} at 200-300 m depth, Kono (2000) calculated the fate of copepods in the mesopelagic zone of the Oyashio region. According his results, copepods carried out of the Oyashio region to the east will return to the Oyashio region again in about 1 year, if they are entrained into the Western Gyre (total distance: 8,000 km), or in about 2 years if they travel in the Subarctic Current System (and are then entrained into the Alaskan Gyre and then the Western Gyre, total distance: 15,000 km). Kono (2000) indicated also that the horizontal transport and dispersal of the population of copepods (and other zooplankton) by the Oyashio are variable, depending on the vertical migration behaviors at various time scales (diel and seasonal) of each species. As a first attempt at analysis of the broad food chain in the pelagic ecosystem of the Oyashio region, we assumed that the biomasses transported in and out of the Oyashio region defined in Fig. 1 are balanced on an annual basis for all the groups of organisms in Table 1.

A schematic food chain in the oceanic Oyashio region was constructed (Fig. 4). It is noted that the current human biomass density on the Japanese islands falls somewhere between those of trophic levels 2 and 3. With phytoplankton (PHYTO) and marine birds and mammals (MB/MM) as primary producers and top predators, respectively, the carbon flow through the food chain was estimated based on calculated Annual P/Annual F of the three intermediate trophic level groups [herbivorous mesozooplankton [MESOZ(H)], carnivorous mesozooplankton [MESOZ(C)] plus micronekton (MICRONEK), and fishes and squids (FISH/SQUID)]. Human exploitation (FISHERY) was taken into account as a component of top predators (Fig. 4). If one takes the lower estimate of annual total primary production (146 g C m^{-2}), our calculation indicates that the ecological efficiencies are 24% [= 35.4 × 100/146] for the secondary/primary production and 21% [= (5.7 + 0.97 + 0.67) × 100 /35.4] for the tertiary/secondary production. Since some secondary consumers (trophic level 3) are included in Fishes/Squids, the tertiary/secondary production efficiency would be underestimated to some extent. Similar calculations with higher estimates of annual primary production (200-300 g C m^{-2}, from Behrenfield and Falkowski, 1997) lead to an ecological efficiency of 12-18% [= 35.4 × 100/(200 or 300)] for the secondary/primary production. Since the ecological efficiencies are considered to be 10-20% in most marine food chains (cf. Parsons et al., 1984), the higher estimate of primary production may be more realistic in the food chain scheme (Fig. 4). The annual secondary production calculated in this study (35 g C m^{-2}) is close to that (40-50 g C m^{-2}) in the outer shelf and slope waters of the southeastern Bering Sea, which are also known as one of the highly productive regions in the world (Vidal and Smith, 1986). Annual mean B, and calculated Annual P and F of FISH/SQUID and MM/MB (Dall's porpoises,

Whales and Marine birds) of this study are subject to large uncertainties. Nevertheless, Annual F of animals at higher trophic level is matched by Annual P of their immediate prey organisms in this simplified food chain (Fig. 4); FISHERY and Annual F by MM/MB accounted to 27% (= 0.13 × 100/0.48) and 60% (= 0.29 × 100/0.48), respectively, of Annual P of FISH/SQUID.

The trophic structure scheme in Fig. 4 is based on a grazing food chain and does not include the microbial food chain. The latter is thought to be functional throughout the year at the nearshore site (A3, Fig. 1) in the Oyashio region (Shinada et al., 2001). Kobari et al. (2003) observed that the main diets of *Neocalanus* spp. changed from diatoms to ciliates during April and July in the Oyashio region, suggesting the importance of microbial food chains to support the food demands of these copepods in summer. As part of mesozooplankton community at Site H (Table 2), small copepods (*Oithona* spp., *Oncaea*/*Triconia* spp.) and ostracods may be associated closely with the microbial food chain in the epipelagic/mesopelagic zones. In a recent study, grazing of small copepods including *Oithona* spp. and *Pseudocalanus*, were found to account for 70-99% of zooplankton grazing in the Greenland Sea during summer, when large *Calanus* spp. (equivalent to *Neocalanus* spp. in the Oyashio region) descend to enter the diapause (Møller et al., 2006). In addition, appendicularians have been thought to be a component of secondary production characterized by an extremely high production potential (Annual P/B ratio as high as 176 for the population in Toyama Bay, southern Japan Sea, cf. Tomita et al., 1999). At Site H, a total of 23 appendicularian species was recorded from the samples of the 1996-1997 sampling program, with *Oikopleura longicauda* being the predominant species (Shichinohe, 2000). A sharp biomass peak of *O. longicauda* was seen in September 1997 when phytoplankton biomass was low.

The lack of a close relationship between appendicularian biomass and phytoplankton biomass was also noted in Toyama Bay, where the former peaked in June and the latter in January-March (Tomita et al., 1999). Because of the lack of appropriate data other than biomass, we are unable to calculate production/consumption values for small crustaceans and appendicularians in the Oyashio region in this study. These gaps in our knowledge need to be filled in future studies for a better understanding of pelagic food chains in the Oyashio region.

In the coastal ecosystem of the Oyashio region (<150 m deep along the southeastern coast of Hokkaido, cf. Fig. 1), Yamamura (2004) studied population dynamics of walleye pollock (*Theragra chalcogramma*) and its associated prey (largely *Euphausia pacifica*) consumption in a trophodynamic model. His simulation led him to conclude that the production of *E. pacifica* population was not sufficient to support the pollock populations in this coastal region and suggested a possible advective supply of the prey to the coastal ecosystem. In the coastal zone, walleye pollack was reported to be eaten extensively by minke whales during June and September (Tamura and Fujise, 2002). According to Yamamura's simulation data, the annual mean biomass of *E. pacifica* (10 gWW m^{-2}, or 1 g C m^{-2} using the same conversion factors as this study) exceeds that of *Neocalanus* spp. (7.7 g WW m^{-2}, or 0.8 g C m^{-2}) and therefore generates the largest component of the secondary production in the coastal zone.

4.3. Ecosystem comparison

In the previous East-West comparisons of the broad subarctic Pacific ecosystem, the West data were represented by those at Station KNOT, located in the southwest edge of the western subarctic gyre (Fig. 1). The major difference between the Oyashio

region (Site H) and KNOT is in their hydrography; the former is under the influence of the cold and less saline water from the Okhotsk Sea. The effects of the warm core rings derived from the Kuroshio extension are also recognized in subsurface layers at times at Site H (Fig. 2). Because of this, the ranges in seasonal variations in surface temperature and salinity observed at Site H (2-18^{o}C and 32.2-33.5, cf. Fig. 2) are slightly broader than those (2-15^{o}C and 32.5-33.0, respectively) observed at KNOT. In terms of primary production (new production) estimated from seasonal depletion of nitrate (Wong et al., 2002), there are only small differences between the western subarctic gyre (67 g C m^{-2} y^{-1}) and the Oyashio region (78 g C m^{-2} y^{-1}), despite the fact that the spring/summer phytoplankton bloom in the former is reportedly less pronounced (max. <2 mg chlorophyll a m^{-3}, Imai et al., 2002). Mesozooplankton assemblages are the same in the two regions, and life cycle patterns of *Neocalanus* spp. (Kobari and Ikeda 1999, 2001ab), *Metridia* spp. (Padmavati et al., 2004) and *Eucalanus bungii* (Shoden et al., 2005) have been evaluated as being synchronized in these two regions. The lack of time-series data of mesozooplankton over one year at KNOT means that any determination of the regional differences in terms of annual mean biomass is tenuous.

For ecosystem comparison we selected the Barents Sea (mean depth: 230 m, area: 1.4×10^{6} km^{2}, locating 70-80^{o}N in the North Atlantic Ocean), the ecosystem dynamics of which have been studied extensively (Sakshaug et al., 1994; Wassmann et al., 2006). In the present comparison, Annual mean B, and Annual P and F data of Sakshaug et al. (1994) were used, but revised Annual F data of Wassmann et al. (2006) were also used (Table 1). As the habitat of pelagic organisms, the northern part of the Barents Sea is under the influence of cold Arctic currents (<0^{o}C) and the southern part by the warmer

Atlantic currents (3-6^{o}C). Among the biological components in the Barents Sea, "Calanus+krill" are the major herbivorous meso/macrozooplankton, and "capelin+cod" are the major fish components. Bearing in mind the differences in the environmental conditions between the Oyashio region and the Barents Sea, the annual mean biomass density of phytoplankton, mesozooplankton, fishes, whales and marine birds are the same order of magnitude in these two ecosystems. On the other hand, bacterial biomass in the Barents Sea (0.4 g C m^{-2}) is one order of magnitude less than that (3.6) in the Oyashio region. The shallow ecosystem in the Barents Sea (230 m, as compared with 2000 m in the Oyashio region) may be considered the major reason, since among various planktonic taxa (phytoplankton, protozooplankton or mesozooplankton), the biomass of bacteria per unit volume of water declines most slowly with depth, so that the depth of integration affects the result most seriously in bacteria (Yamaguchi et al., 2004).

No appreciable differences between the Oyashio region and the Barents Sea are seen in Annual P of phytoplankton ("total" and "new") or of animal groups at equivalent trophic levels such as fishes/squids versus Capelin+cod or whales plus Dall's porpoises versus whales. However, Annual P of bacteria is higher but that of Calanus+krill is lower in the Barents Sea than the respective values in the Oyashio region. In the light of the rapid decline in bacterial P/B ratios with increasing depth (Nagata et al., 2000), higher Annual bacterial P (despite lower biomass) in the Barents Sea ecosystem than the Oyashio ecosystem may be due to much higher bacterial P/B ratios integrated over the water column of the former (depth: 230 m) than the latter (2000 m). Compared with herbivorous mesozooplankton in the Oyashio region, lower Annual P of Calanus+krill in the Barents may be interpreted as resulting from slower growth rates at lower water

temperatures (<0-6^{o}C as compared with 2-18^{o}C in the Oyashio region, cf. Fig. 2), combined with its lower biomass.

Some differences are seen between the Annual F estimates as between Sakshaug et al. (1994) and Wassmann et al. (2006) for the same animal groups, and Wassmann et al. explained that this was due to an accumulation of stomach analysis data since the study of Sakshaug et al. Comparing the data of Wassmann et al. with ours, it is evident that Calanus+krill in the Barents Sea consume only 1/10 of the food eaten by herbivorous mesozooplankton in the Oyashio region. As mentioned above, lower water temperature in the Barents Sea and lower biomass density of Calanus+and krill as representative herbivores are responsible for their lower food consumption. Such marked differences are not evident among animals at higher trophic levels ($\geq$3), and the between-ecosystem differences in the Annual F of a given group (including fisheries) hardly exceeds a factor of four. Summed Annual F by the animals at trophic levels $\geq$3 and fisheries was greater in the Oyashio region (2.0 g C m^{-2}) than in the Barents Sea (1.20, Wassmann et al. data), and the major source of differences is in Annual F estimates between the groups of Fishes/Squids in the Oyashio region and Capelin+Cod in the Barents Sea.

In the Barents Sea food chain, copepods (*Calanus finmarchicus* and *C. glacialis*), capelin (*Mallotus villosus*) and herring (*Clupea harengus*) are regarded as key species, mediating between phytoplankton and all large predators (cod, marine birds, seals and whales) including fisheries (Sakshaug et al., 1994; Wassmann et al., 2006). In the pelagic food chain in the Oyashio region, the present results suggest that the top candidates for keystone species status are the *Neocalanus* copepods, followed by euphausiids (*Euphausia pacifica*), especially in coastal waters (Yamamura, 2004).

Pelagic fishes, such as Pacific saury or Japanese sardine/anchovy, play important roles, but they are seasonal migrators to the Oyashio region and are subject to considerable year-on-year variations in stock size (Ito et al., 2004). While the scope of this study was largely limited to the oceanic ecosystem of the Oyashio region, walleye pollock and Steller sea lion (*Eumetopias jubatus*), in addition to euphausiids, are dominant components of the coastal ecosystem of this region.

Acknowledgment

We are grateful to C.B. Miller for reading an early draft of the manuscript and constructive comments. We thank R.R. Hopcroft for valuable comments to improve the manuscript. Thanks are extended to students of our Plankton Laboratory who generated most of the plankton data used in this study. This study was supported partly by Grant-in-Aid for Scientific Research (S) 16108002 “Historical transition and prediction of Northern Pacific ecosystem associated with human impact and climate change”.

References

Banse, K. and S. Mosher (1980): Adult body mass and annual population production/biomass relationships of field populations. *Ecol Monogr*., **1980**, 355-379.

Batchelder, H.P. and C.B. Miller (1989): Life history and population dynamics of *Metridia pacifica*: results from simulation modelling. *Ecol. Model*., **48**, 113-136.

Beamish, R.J., K.D. Leask, O.A. Ivanov, A.A. Balanov, A.M. Orlov and B. Sinclair (1999): The ecology, distribution, and abundance of midwater fishes of the subarctic Pacific gyres. *Prog. Oceanogr*., **43**, 399-442.

Behrenfield, M.J. and P.G. Falkowski (1997): Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol. Oceanogr*., **42**, 1-20.

Brinton, E. (1976): Population biology of *Euphausia pacifica* off southern California. *Fish. Bull. US*, **74**, 733-762.

Chiba, S., K. Tadokoro, H. Sugisaki and T. Saino (2006): Effects of decadal climate change on zooplankton over the last 50 years in the western subarctic North Pacific. *Global Change Biol*., **12**, 907-920.

FAO (1997): *FAO yearbook of fishery statistics* Vol. 80, FAO, Rome, 713pp.

Favorite, F., A.J. Dodimead and K. Nasu (1976): Oceanography of the subarctic Pacific region, 1969-1971. *Bull. int. N. Pacif.Fish. Comm*., **33**, 1-187.

Feinberg, L.R. and W.T. Petersen (2003): Variability in duration and intensity of euphausiid spawning off central Oregon, 1996-2001. *Prog. Oceanogr*., **57**, 363-379.

Harrison, P.J., F.A. Whitney, A. Tsuda, H. Saito and K. Tadokoro (2004): Nutrient and plankton dynamics in the NE abd NW gyres of the subarctic Pacific Ocean. *J.*

Oceanogr., **60**, 93-117.

Hasle, G.R. (1978): Using the inverted microscope. p. 191-201. In *Phytoplankton manual*, ed. by A. Sournia, UNESCO, Paris.

Hopkins, T.L. and T.T. Sutton (1998): Midwater fishes and shrimps as competitors and resources partitioning in low latitude oligotrophic ecosystems. *Mar. Ecol. Prog. Ser*., **164**, 37-45.

Hunt, G.L., H. Kato and S.M. McKinnel (2000): Predation by marine birds and mammals in the subarctic North Pacific Ocean. *PICES Scientific Report* **14**, 165pp.

Iguchi, N., T. Ikeda and A. Imamura (1993): Growth and life cycle of a euphausiid crustacean (*Euphausia pacifica* Hnasen) in Toyama Bay, southern Japan Sea. *Bull. Japan Sea Natl. Fish. Res. Inst*., **43**, 69-81. (in Japanese with English abstruct)..

Ikeda, T., K. Hirakawa and N. Shiga (2002): Production, metabolism and production/biomass (P/B) ratio of *Metridia pacifica* (Crustacea; Copepoda) in Toyama Bay, southern Japan Sea. *Plankton Biol. Ecol*., **49**, 58-65.

Ikeda, T. and S. Motoda (1978): Estimated zooplankton production and their ammonia excretion in the Kuroshio and adjacent seas. *Fish. Bull. US*, **76**, 357-367.

Ikeda, T., F. Sano and A. Yamaguchi (2004): Metabolism and body composition of a copepod *Neocalanus cristatus* (Crustacea) from the bathypelagic zone of the Oyashio region, western subarctic Pacific. *Mar. Biol.*, **145**, 1181-1190.

Imai, K., Y. Nojiri, N. Tsurushima and T. Saino (2002): Time series of seasonal variation of primary productivity at station KNOT (44^{o}N, 155^{o}E) in the sub-arctic western North Pacific. *Deep-Sea Res. II*, **49**, 5395-5408.

Ito, S., H. Sugisaki, A. Tsuda, O. Yamamura and K. Okuda (2004): Contributions of the VENFISH program: meso-zooplankton, Paccific saury (*Cololabis saira*) and walleye pollock (*Theragra chalcogramma*) in the northwestern Pacific. *Fish. Oceanogr*., **13**(Suppl. 1), 1-9.

Ivanov, O.A. (1997): Composition and biomass of the fishes and cephalopods of the upper mesopelagial of the Kuril and Kamchachatka waters of the Pacific Ocean. *J. Ichthyol*., **37**, 147-158.

Kaeriyama, H. and T. Ikeda (2002): Vertical distribution and population structure of the three dominant planktonic ostracods (*Discoconchoecia pseudodiscophora, Orthoconchoecia haddoni* and *Metaconchoecia skogsbergi*) in the Oyashio region, western North Pacific. *Plankton Biol. Ecol*., **49**, 66-74.

Kaneko, M. (2005): On the ecology of Oithonid copepods in the western subarctic Pacific. *MSc. Thesis, Graduate School of Fisheries Sciences, Hokkaido Univ*., 39pp. (in Japanese).

Kasai, H. (2000): Seasonal change of nutrients and primary production in the Oyashio region. *Bull. Plankton Soc. Japan*, **47**, 116-118.

Kasai, H., H. Saito, M. Kashiwai, T. Taneda, A. Kusaka, Y. Kawasaki, T. Kono, S. Taguchi and A. Tsuda (2001): Seasonal and interannual variations in nutrients and plankton in the Oyashio region: A summary of a 10-years observation along the A-line. *Bull. Hokkaido Natl. Fish. Res. Inst*., **65**, 55-134

Kawabata, A. and S. Kubota (2002): Characteristics of mantle length composition, maturity and stomach contents related to fluctuations of the migrant stock abundance of *Todarodes pacificus* around the Pacific coast of the northern Honshu, Japan. p.10-16. In: *Proceedings of the 2001 Annual Meeting of Squid*

Stock Research, Hachinohe Branch, Tohoku National Fisheries Research Institute, Hachinohe (in Japanese).

Kawamura, A. (1989): Fast sinking mouth ring for closing NORPAC net. *Bull. Jpn Soc. Sci. Fish*., **55**, 1121

Kobari, T. and T. Ikeda (1999): Vertical distribution, population structure and life cycle of *Neocalanus cristatus* (Crustacea: Copepoda) in the Oyashio region, with notes on its regional variations. *Mar. Biol*., **134**, 683-696.

Kobari, T. and T. Ikeda (2000): Life cycle of *Neocalanus* species in the Oyashio region. *Bull. Plankton Soc. Japan*, **42**, 129-135. (in Japanese with English abstract).

Kobari, T. and T. Ikeda (2001a): Life cycle of *Neocalanus flemingeri* (Crustacea: Copepoda) in the Oyashio region, western subarctic Pacific, with notes on its regional variations. *Mar. Ecol. Prog. Ser*., **209**, 243-255.

Kobari, T. and T. Ikeda (2001b): Ontogenetic vertical migration and life cycle of *Neocalanus plumchrus* (Crustacea: Copepoda) in the Oyashio region, with notes on its regional variations in body size. *J. Plankton Res*., **23**, 287-302.

Kobari, T., A. Shinada and A. Tsuda (2003): Functional roles of inerzonal migrating mesozooplankton in the western subarctic Pacific. *Prog. Oceanogr*., **57**, 279-298..

Kono, T. (1997): Modification of the Oyashio Water in the Hokkaido and Tohoku areas. *Deep-Sea Res*. I, **44**, 669-688.

Kono, T. (2000): The intermediate layer of the Oyashio as an environment for copepods. *Bull. Plankton Soc. Japan*, **47**, 102-110. (in Japanese with English abstract).

Lasker, R. (1966): Feeding, growth, respiration, and carbon utilization of a euphausiid crustacean. *J. Fish. Res. Bd. Can*., **23**, 1291-1317.

Mauchline, J. (1998): The biology of Calanoid copepods. *Adv. Mar. Biol*., **33**, 1-701.

Miller, A.J., F. Chai, S. Chiba, J.R. Moisan and D.J. Neilson (2004): Decadal-scale climate and ecosystem interactions in the North Pacific Ocean. *J. Oceanogr*., **60**, 163-188.

Miller C,B., B.W. Frost, H.P. Batchelder, M.J. Clemons and R.E. Conway (1984): Life histories of large, grazing copepods in the subarctic ocean gyre: *Neocalanus plumchrus, Neocalanus cristatus* and *Eucalanus bungii* in the Northeast Pacific. *Prog. Oceanogr*., **13**, 201-243.

Moku, M., K. Kawaguchi, H. Watanabe and A. Ohno (2000): Feeding habits of three dominant myctophid fishes, *Diaphus theta*, *Stenobrachius leucopsarus* and *S.nannochir*, in the subarctic and transitional waters of the western North Pacific. *Mar. Ecol. Prog. Ser*., **207**, 129-140.

Møller, E.F., T.G. Nielsen and K. Richardson (2006): The zooplankton community in the Greenland Sea: Composition and role in carbon turnover. *Deep-Sea Res. I*, **53**, 76-93.

Nagata, T., Fukuda, H., R. Fukuda and I. Koike (2000): Bacterioplankton distribution and production in deep Pacific waters: Large scale geographic variations and possible coupling with sinking particle fluxes. *Limnol Oceanogr*., **45**, 426-435.

Nishibe, Y. and T. Ikeda (2004): Vertical distribution, abundance and community structure of oncaeid copepods in the Oyashio region, western subarctic Pacific. *Mar. Biol*., **145**, 931-941.

Nishiuchi, K. (1999): Life histories and interannual variations in chaetognaths in the western North Pacific Ocean. *Ph. D thesis, Graduate School of Fisheries Science, Hokkaido Univ*., 116 pp. (in Japanese).

Odate, K. (1994): Zooplankton biomass and its long-term variation in the western North Pacific Ocean, Tohoku Sea area, Japan. *Bull. Tohoku Natl. Fish. Res. Inst*., **56**, 115-173 (in Japanese with English abstruct).

Ohtani, K. (1971): Studies on the change of the hydrographic conditions in the Funka Bay. II. Characteristics of the waters occupying the Funka Bay. *Bull. Fac. Fish. Hokkaido Univ*., **22**, 58-66..

Omori, M. (1969): Weight and chemical composition of some important zooplankton in the North Pacific Ocean. *Mar. Biol*., **3**, 4-10.

Padmavati, G. (2002): Abundance, vertical distribution and life cycle of *Metridia pacifica* and *M. okhotensis* (Copepoda: Calanoida) in the Oyashio region, western subarctic Pacific Ocean. *Ph. D thesis, Graduate School of Fisheries Science, Hokkaido Univ*., 83 pp.

Padmavati, G., T. Ikeda and A. Yamaguchi (2004): Life cycle, population structure and vertical distribution of *Metridia* spp. (Copepoda: Calanoida) in the Oyashio region (NW Pacific Ocean). *Mar. Ecol. Prog. Ser*., **270**, 181-198.

Parsons, T.R. and M. Lalli (1988): Comparative oceanic ecology of the plankton communities of the subarctic Atlantic and Pacific Ocean. *Mar. Biol. Annu. Rev*., **26**, 317-359.

Parsons, T.R., M. Takahashi and B. Hargrave (1984): *Biological Oceanographic Process*, 3rd Edition. Pergamon Press, Oxford, 330pp.

Prosser, C.L. (1962): Water: osmotic balance. p. 6-56. In *Comparative Animal Physiology*, ed. by C.L. Prosser and F.A. Brown Jr, W.B. Saunders Co., Philadelphia and London.

Reid, J.L. (1973): *North Pacific Ocean waters in winter*. The Johns Hopkins

Oceanographic Studies No. 5. The Johns Hopkins Press, Baltimore, MD, pp 1-9.

Saito, H. and A. Tsuda (2003): Influence of light intensity on diatom physiology and nutrient dynamics in the Oyashio region. *Prog. Oceanogr*., **57**, 251-263.

Saito, H., A. Tsuda and H. Kasai (2002): Nutrient and plankton dynamics in the Oyashio region of the western subarctic Pacific Ocean. *Deep-Sea Res. II,* **49**, 5463-5486.

Sakshaug, E., A. Bjørge, B. Gulliksen, H. Loeng and F. Mehlum (1994): Structure, biomass distribution, and energetics of the pelagic ecosystem in the Barents Sea: a synopsis. *Polar Biol*., **14**, 405-411.

Sassa, C. and K. Kawaguchi (2005): Larval feeding habits of *Diaphus theta*, *Protomyctophum thompsoni*, and *Tarletonbeania tayori* (Pices: Myctophidae) in the transition region of the western North Pacific. *Mar. Ecol. Prog. Ser*., **298**, 261-276.

Sekine, Y. (1999): On variations in the subarctic circulation in the North Pacific. *Prog. Oceanogr*., **43**, 193-203.

Shichinohe, Y. (2000): Seasonal variations in abundance and vertical distribution of appendicularians in the Oyashio region, western subarctic Pacific. *MSc. Thesis, Graduate School of Fisheries Sciences, Hokkaido Univ*., 62pp. (in Japanese).

Shinada, A., T. Ikeda, S. Ban and A. Tsuda (2001): Seasonal dynamics of planktonic food chain in the Oyashio region, western subarctic Pacific. *J. Plankton Res*., **23**, 1237-1247.

Shoden, S. (2000): Biological and ecological study on *Eucalanus bungii* (Copepoda: Calanoida) in the Oyashio region, western North Pacific Ocean. *MSc. Thesis, Graduate School of Fisheries Sciences, Hokkaido Univ*., 34 pp. (in Japanese).

Shoden, S., T. Ikeda and A. Yamaguchi (2005): Vertical distribution, population structure and lifecycle of *Eucalanus bungii* (Copepoda: Calanoida) in the Oyashio region, with notes on its regional variations. *Mar. Biol*., **146**, 497-511.

Springer, A.M., J.F. Piatt, V.P. Shuntov, G.B. Van Vliet, V.L. Vladimirov, A.E. Kuzin and A.S. Perlov (1999): Marine birds and mammals of the Pacific subarctic gyres. *Prog. Oceanogr*., **43**, 443-487.

Sugisaki, H. and Y. Kurita (2004): Daily rhythm and seasonal variation of feeding habit of Pacific saury (*Cololabis saira*). *Fish. Oceanogr*., **13**(Suppl.), 63-73.

Tadokoro, K., S. Chiba, T. Ono, T. Midorikawa and T. Saino (2005): Interannual variation in *Neocalanus* biomass in the Oyashio waters of the western North Pacific. *Fish. Oceanogr*., **14**, 210-222.

Takahashi, D. and T. Ikeda (2006): Abundance, vertical distribution and life cycle patterns of the hydromedusa *Aglantha digitale* in the Oyashio region, western subarctic Pacific. *Plankton Benthos Res*., **1**, 91-96.

Taki, K. (2006): Biomass and production of the euphausiid *Euphausia pacifica* along the coastal waters off north-eastern Japan. *Fish. Sci*., **72**, 221-232.

Tamura, T. (1998): Feeding ecology of minke whales *Balaenoptera acutorostrata* in the western subarctic Pacific and Antarctic wataers. *Ph. D thesis, Hokkaido Univ*., 125pp.

Tamura, T. and Y. Fujise (2002): Geographical and seasonal changes of the prey species of minke whale in the Northwestern Pacific. *ICES J. Mar. Sci*., **59**, 516-528.

Taniguchi, A. (1999): Differences in the structure of the lower trophic levels of pelagic ecosystems in the eastern and western subarctic Pacific. *Prog. Oceanogr.*, **43**, 289-315.

Terazaki, M. (1991): Deep sea chaetognaths. p. 117-121. In *The biology of chaetognaths*, ed. by Q. Bone, H. Kapp and A.C. Pierrot-Bults, Oxford Univ. Press, NY.

Tomita M, T. Ikeda and N. Shiga (1999): Production of *Oikopleura longicauda* (Tunicate: Appendicularia) in Toyama Bay, southern Japan Sea. *J. Plankton Res*., **21**, 2421-2430.

Tsuda, A., H. Saito and H. Kasai (1999): Life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* (Calanoida: Copepoda) in the western subarctic Pacific. *Mar. Biol*., **135**, 533-544.

Tsuda, A., H. Saito and H. Kasai (2004): Life histories of *Eucalanus bungii* and *Neocalanus cristatus* (Calanoida: Copepoda) in the western subarctic Pacific. *Fish. Oceanogr*., **13(Suppl. 1)**, 63-73.

Vidal, J. and S.L. Smith (1986): Biomass, growth, and development of populations of herbivorous zooplankton in the southeastern Bering Sea during spring. *Deep-Sea Res*., **33**, 523-556.

Vinogradov, M.E. and E.G. Arashkevich (1969): Vertical distribution of interzonal copepod filter feeders and their role in communities at different depths in the north-western Pacific. *Oceanology*, **9**, 399-409.

Wada, T. (1991): Stocks of Japanese sardine. Bull. Japan Soc. *Fish. Oceanogr*., **55**, 398-402. (in Japanese).

Wassman, P., M. Reigstad, T. Haug, B. Rudels, M.L. Carroll, H. Hop, G.W. Gabrielsen, S. Falk-Petersen, S.VG. Denisenko, E. Arashkevich, D. Slagstad and O. Pavlova (2006): Food webs and carbon flux in the Barents Sea. *Prog. Oceanogr*., **71**, 232-287..

Watanabe, H., M. Moku, K. Kawaguchi, K. Ishimaru and A. Ohno (1999): Diel vertical migration of myctophid fishes (Family Myctophidae) in the transitional waters of the western North Pacific. *Fish. Oceanogr*., **8**, 115-127

Watanabe, H., T. Kubodera, T. Ichii and S. Kawahara (2004): Feeding habits of neon flying squid *Ommastrephes bartramii* in the transitional region of the central North Pacific. *Mar. Ecol. Prog. Ser.*, **266**, 173-184

Wong, C.S., N.A.D. Waser, Y. Nojiri, W.K. Johnson, F.A. Whitney, J.S.C. Page and J. Zeng (2002): Seasonal and interannual variability in the distribution of surface nutrients and dissolved inorganic carbon in the northern North Pacific: influence of El Nino. *J. Oceanogr*., **58**, 227-243.

Yamada, Y. and T. Ikeda (2006): Production, metabolism and trophic importance of four pelagic amphipods in the Oyashio region, western subarctic Pacific. *Mar. Ecol. Prog. Ser*., **308**, 155-163.

Yamada, Y., T. Ikeda and A. Tsuda (2002): Abundance, growth and life cycle of the mesopelagic amphipod *Primno abyssalis* (Hyperiidea: Phrosinidae) in the Oyashio region, western subarctic Pacific. *Mar. Biol*., **141**, 333-341.

Yamaguchi, A. and T. Ikeda (2000a): Vertical distribution, life cycle and body allometry of two oceanic calanoid copepods (*Pleuromamma scutullata* and *Heterorhabdus tanneri*) in the Oyashio region, western North Pacific Ocean. *J. Plankton Res*., **22**, 29-46.

Yamaguchi, A. and T. Ikeda (2000b): Vertical distribution, life cycle, and developmental characteristics of the mesopelagic calanoid copepod *Gaidius variabilis* (Aetideidae) in the Oyashio region, western North Pacific Ocean. *Mar. Biol*., **137**, 99-109.

Yamaguchi, A. and T. Ikeda (2001): Abundance and population structure of three mesopelagic *Paraeuchaeta* species (Copepoda: Calanoida) in the Oyashio region, western North Pacific Ocean with notes on their carcasses and epizoic ciliates. *Plankton Biol. Ecol*., **48**, 104-113.

Yamaguchi, A., Y. Watanabe, H. Ishida, T. Harimoto, K. Furusawa, S. Suzuki, J. Ishizaka, T. IkedaT and M.M. Takahashi (2002): Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Pacific (WEST-COSMIC). *Deep-Sea Res. I*, **49**, 1007-1025.

Yamaguchi, A., Y. Watanabe, H. Ishida, T. Harimoto, K. Furusawa, S. Suzuki, J. Ishizaka, T. Ikeda and M. Takahashi (2004): Latitudinal differences in the plankton biomass and community structure down to the greater depths in the western North Pacific. *J. Oceanogr*., **60**, 773-787..

Yamamura, O. (2004): Trophodynamic model of walleye pollack (*Theragra chalcogramma*) in the Doto area, northern Japan: model description and baseline simulations. *Fish. Oceanogr*., **13**(suppl. 1), 138-154.

Table 1. Annual mean biomass (B) and annual production (Annual P) of major component organisms in the pelagic ecosystems of the Oyashio region and Barents Sea. For details on "mesozooplankton", see Table 2. Annual food consumption (Annual F) was computed for the heterotrophic components (two estimates in the Barents Sea were separated by roman and italic). See text for details.

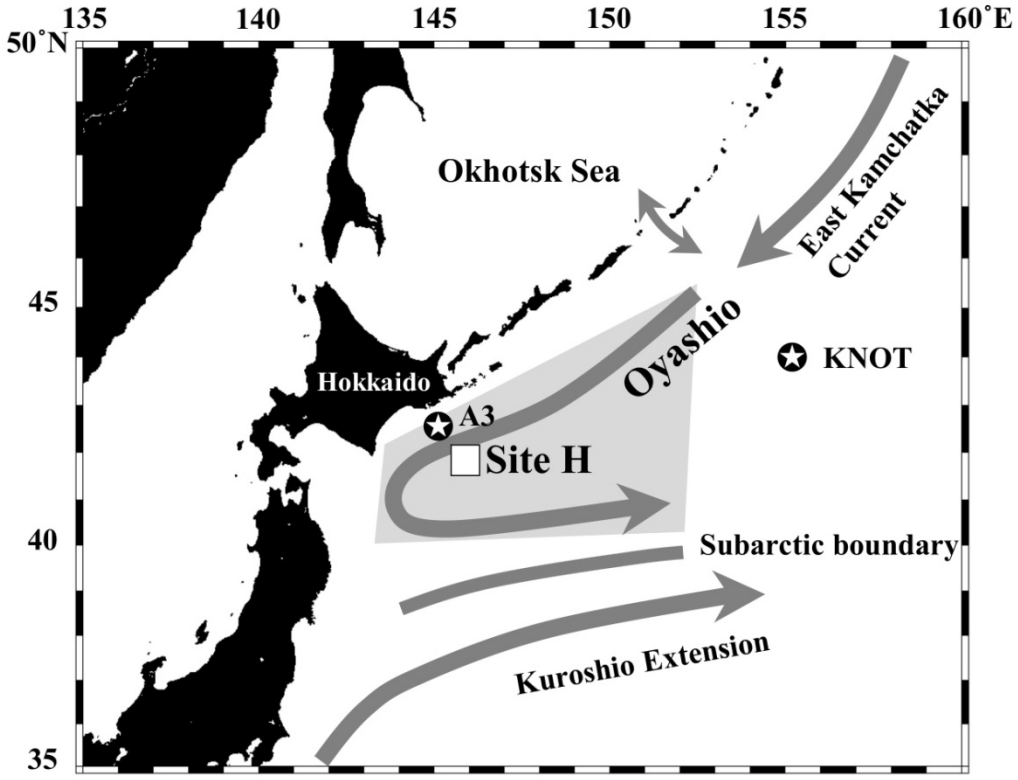
	Oyashio region (this study)					Barents Sea (Sakshaug et al., 1994; *Wassmann et al., 2006*)				
Food chain	Trophic level	Component organisms	B ($g\ C\ m^{-2}$)	Annual P ($g\ C\ m^{-2}$)	Annual F ($g\ C\ m^{-2}$)	Component organisms	B ($g\ C\ m^{-2}$)	Annual P ($g\ C\ m^{-2}$)	Annual F ($g\ C\ m^{-2}$)	*Annual F ($g\ C\ m^{-2}$)*
Microbial	2	Bacteria	3.6[1]	14.4[11]		Bacteria	0.4	80		
	3	Microzooplankton	3.2[2]							
Grazing	1	Phytoplankton	6.6[3]	Total: 146[12] New 78[13]		Phytoplankton	2.0	110 60		
	2	Mesozooplankton (herbivores)	6.6[4]	35.4[4]	118[19]	Calanus+krill	3.0	9.5		*9*
	3	Mesozooplankton (carnivores)	1.3[5]	5.7[5]	19[19]					
	3	Fish micronekton	0.64[6]	0.96[14]	3.2[19]					
	3	Crustacean micronekton	0.84[7]	0.67[15]	2.2[19]					
	3.5(3-4)	Fish/squids	0.6[8]	0.48[16]	1.6[19]	Capelin+Cod	0.72	0.3	0.35[24]	*0.9*
	4.5(4-5)	Dall's porpoises	0.0016[8]	0.00032[17]	0.041[20]	Seals	0.007	0.0003	0.06	*0.09*
	4(3-5)	Whales	0.03[9]	0.0015[18]	0.22[21]	Whales	0.042	0.0014	0.23	*0.05*
	4(3-5)	Marine birds	0.0005[10]	?	0.026[22]	Seabirds	0.001	0.0002	0.05	*0.11*
		Fishery			0.13[23]	Fishery (capelin)			0.085	*0.05*
		Summed Annual F for trophic levels 3.5-4.5			**2.02**				**0.775**	**1.20**

1) Matsunaga and Yamaguchi (unpublsihed), Appendix 1
2) Yamaguchi *et al*. (2002) at KNOT
3) Calculated from Kasai *et al*. (2001) assuming C/Chl*a* ratio = 60
4) Herbivorous copepods and euphausiids (cf. Table 2)
5) Carnivorous species (cf. Table 2)
6) Yokokura and Yamaguchi (unpublished), Appendix 3
7) Kanazawa and Ikeda (unpublished), Appendix 3
8) Springer (1999)
9) The total of Minke, Brydes, Sei and Sperm whales
10) Hunt *et al*. (2000)
11) Annual P/B = 4 is assumed from 0-4000 m data of Nagata *et al*. (2000)
12) Kasai (2000)
13) Wong *et al*., (2002)
14) Annual P/B = 1.5 from Banse and Mosher's (1980) equation 13
15) Annual P/B = 0.8 from Banse and Mosher's (1980) equatopn 4
16) Annual P/B = 0.8 from Banse and Mosher's (1980) equation 13
17) Annual P/B = 0.2 from Banse and Mosher's 1980) equation 14
18) Annual P/B = 0.05 from Banse and Mosher's (1980) equation 14
19) F = 3.33 × P (cf. Ikeda and Motoda, 1978)
20) F = B × 0.07 × 365 (Hunt *et al*., 2000)
21) F = B × 0.04 × 180 (Tamura, 1998)
22) WTZ data (92 day summer) assuming prey with 3kj g^{-1} (Hunt *et al*., 2000)
23) Annual landing from Northwest Pacific 1.3 × 0.2 × 0.5 (Area 61, FAO, 1997)
24) Cod only

Table 2. Annual mean biomass (B, separated into 0-250 and 250-2000 m depth strata), annual production:biomass (Annual P/B) ratios, caloric content of females reached maturity (M) and annual production (Annual P) of various zooplankton species at Site H in the Oyashio region, western subarctic Pacific Ocean. Bold figures denote key herbivores and italic ones key carnivores in this region. Contribution of biomass of each species to the total is noted as %.

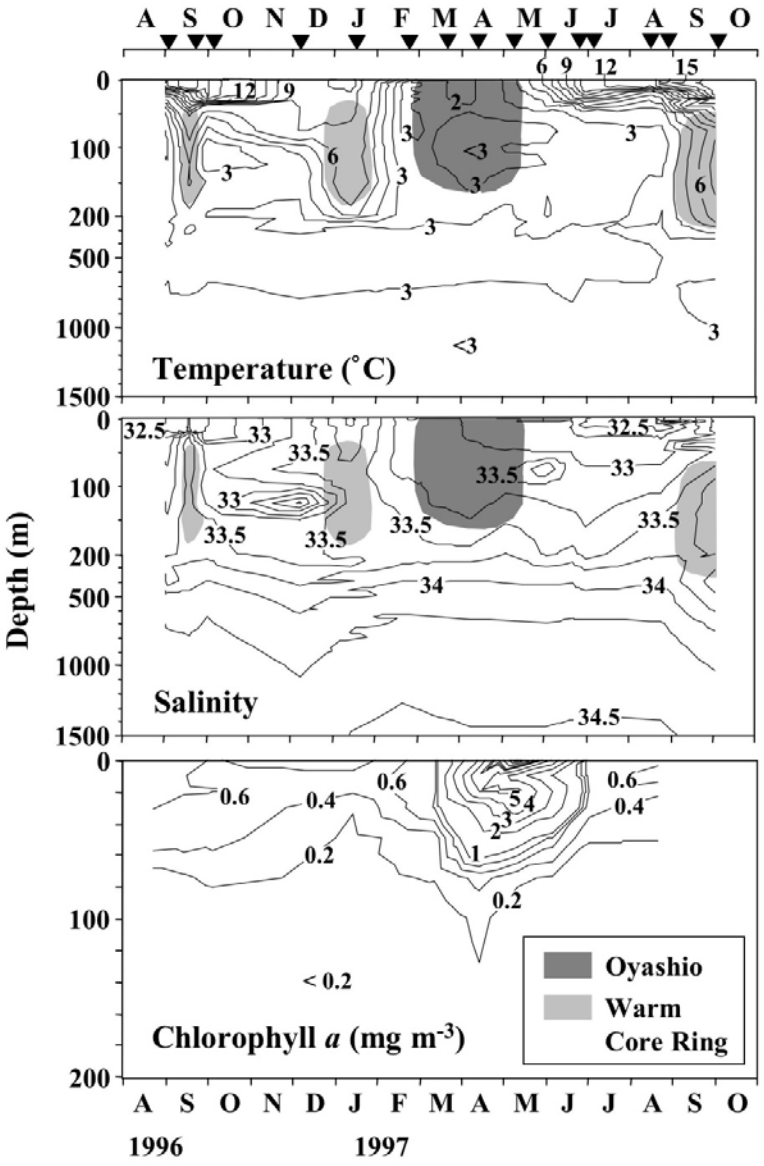
Group	Species	B (mgC m^{-2}) 0-250m	B (mgC m^{-2}) 0-2000m	(%)	Annual P:B	(M: $\times10^{-3}$Kcal)	Annual P (mgC m^{-2})
Copepods	*Neocalanus cristatus*	**790.5**	**2454**[1)]	**29.9**	**5.0**[15)]		**12270**
	Neocalanus plumchrus	**306**	**1206.5**[1)]	**14.7**	**5.2**[15)]		**6274**
	Neocalanus flemingeri	**103**	**479.5**[1)]	**5.8**	**5.3**[15)]		**2541**
	Eucalanus bungii	**360**	**1322**[2)]	**16.1**	**5.6**[16)]	**2.90**	**7403**
	Metridia pacifica	**256**	**533**[3)]	**6.5**	**6.2**[17)]		**3305**
	Metridia okhotensis	**34**	**305**[3)]	**3.7**	**5.7**[16)]	**2.85**	**1739**
	Pleuromamma scutullata	**0**	**55.5**[4)]	**0.7**	**6.0**[16)]	**2.43**	**333**
	Gaidius variabilis	**0**	**110.5**[5)]	**1.3**	**5.8**[16)]	**2.65**	**641**
	Heterorhabdus tanneri	***0***	***41***[4)]	***0.5***	***5.9***[16)]	***2.59***	***242***
	Paraeuchaeta elongata	***0***	***105***[6)]	***1.3***	***3.2***[16)]	***13.0***	***336***
	Paraeuchaeta rubra	***0***	***71.5***[6)]	***0.9***	***2.8***[16)]	***20.0***	***200***
	Paraeuchaeta birostrata	***0***	***154***[6)]	***1.9***	***2.3***[16)]	***32.0***	***354***
	Oncaea/Triconia spp.	0	80[7)]	1.0			
	Oithona spp.	100	100[8)]	1.2			
Chaetognaths	***Sagitta elegans***	***108.5***	***108.5***[9)]	***1.3***	***3.3***[16)]	***12.4***	***358***
	Eukrohnia hamata	***0***	***449***[9)]	***5.5***	***4.6***[16)]	***4.92***	***2065***
	Eukrohnia bathypelagica	***0***	***137.5***[9)]	***1.7***	***4.6***[16)]	***4.92***	***633***
	Eukrohnia fowleri	0	29[9)]	0.4			
Amphipods	***Themisto pacifica***	***31***	***31***[10)]	***0.4***	***9.1***[10)]		***282***
	Themisto japonica	***19.5***	***19.5***[10)]	***0.2***	***11.6***[10)]		***226***
	Primno abyssalis	***0***	***17.5***[10)]	***0.2***	***2.1***[10)]		***37***
	Cyphocaris challengeri	***0***	***36.5***[10)]	***0.4***	***4.5***[10)]		***164***
Ostracods	*Discoconchoecia pseudodiscophora*	0	33[11)]	0.4			
	Orthoconchoecia haddoni	0	45.5[11)]	0.6			
	Metaconchoecia skogsbergi	0	8.5[11)]	0.1			
Coelenterates	***Aglantha digitale***	***93***	***93***[12)]	***1.1***	***8.7***[17)]		***809***
Euphausiids	*Euphausia pacifica, Thysanoessa* spp.	**154**	**154**[13)]	**1.9**	**6.4**[18)]		**986**
Appendicularians	*Oikopleura* spp.	31	31[14)]	0.4			
TOTAL		2396.5	8221	100			41199

1) Kobari and Ikeda (2000)
2) Shoden (2000), Appendix 2
3) Padmavati (2002), Appendix 2
4) Yamaguchi and Ikeda（2000a)
5) Yamaguchi and Ikeda（2000b)
6) Yamaguchi and Ikeda（2001)
7) Nishibe and Ikeda (2004)
8) Kaneko (2005), Appendix 2
9) Nishiuchi (1999), Nishiuchi and Ikeda (unpublished data), Appendix 2
10) Yamada et al. (2002), Yamada and Ikeda (2006)
11) Kaeriyama and Ikeda (2002)
12) Takahashi and Ikeda (2006)
13) Okazaki and Ikeda (unpublished), Appendix 2
14) Shichinohe (2000). Appendix 2
15) Kobari et al. (2003)
16) $\log_{10}(P/B) = -0.34\log_{10}M - 0.16$ (Banse and Mosher,1980)
17) Ikeda (unpublished)



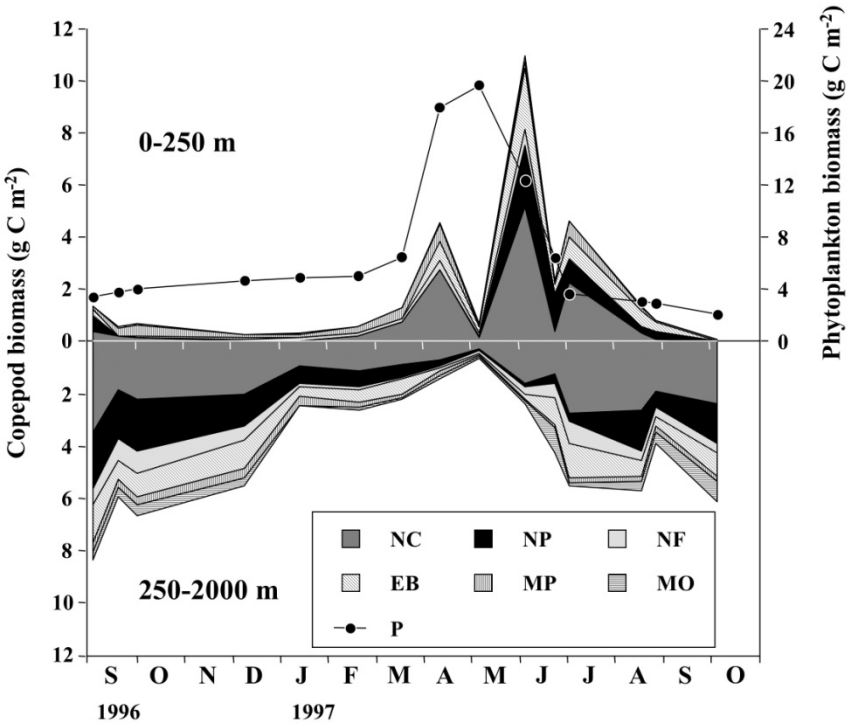
Ikeda et al. Fig. 1

Fig. 1. Current systems (arrowed) and the Oyashio region (shaded) in the western subarctic Pacfic Ocean. Locations of Site H, A3 and KNOT are superimposed



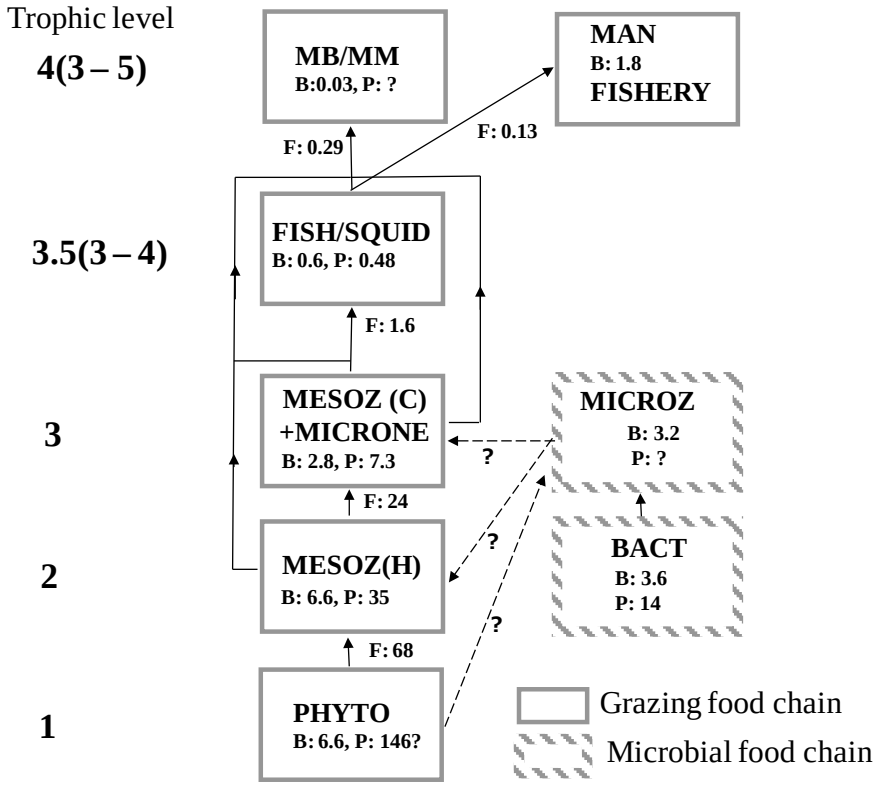
Ikeda et al. Fig.2

Fig. 2. Seasonal changes in temperature (top), salinity (middle) and chlorophyll a (bottom) at Site H in the Oyashio region. Incidences of the Oyashio and effects of Warm Core Rings are shown in (a) and (b). Note different depth scale in (c). Solid triangles on abscissa denote sampling dates.



Ikeda et al. Fig. 3

Fig. 3. Seasonal changes in the biomass of large/medium-sized copepods in the two depth strata (0-250 and 250-2000 m) at Site H in the Oyashio region. Concomitant changes in phytoplankton biomass (closed circles) are superimposed in the 0-250 m panel. Copepod abbreviations; NC=*Neocalanus cristuatus*, NP=*Neocalanus plumchrus*, NF=*Neocalanus flemingeri*, EB=*Eucalanus bungii*, MP=*Metridia pacifica*, MO=*Metridia okhotensis*.



Ikeda et al. Fig.4

Fig. 4. Schematic presentation of trophic structure (including grazing and microbial food chains) of the oceanic ecosystem in the Oyashio region, as expressed by its biomass (annual mean) distribution (B: g C m^{-2}) and carbon flow through the grazing food chain based on annual production (P: g C m^{-2} y^{-1}). Figures alongside the arrows denote annual consumption (F: g C m^{-2} y^{-1}). Human biomass density (MAN) on Japanese islands and fishing impacts (FISHERY) are superimposed in the top right panel for comparison. For detailed figures see text.

Appendix 1. Biomass of heterotrophic bacteria at Site H during May-December 2002. Unit: mgC m^{-3} (Matsunaga and Yamaguchi, unpublished). See text for details.

Depth	19-May-02	7-Jun-02	13-Jul-02	9-Aug-02	9-Oct-02	18-Dec-02
0	14.7	11.15	14.42	23.36	10.35	3
5	14.91	11.83	12.03	21.67	23.12	5.42
10	15.58	12.61	12.42	19.85	15.78	8.09
20	22.17	11.37	15.13	16.81	13.66	4.14
30	15.9	23.76	14.6	11.83	19.96	4.75
40	10.38	8.29	6.99	8.42	6.75	5.36
50	7.79	7.09	7.17	7.97	5.73	4.72
75	5.71	4.52	5.58	5.69	4	4.54
100	4.73	4.06	3.81	3.7	3.04	2.24
125	4.45	3.93	4.84	3.81	3.36	3.65
150	4.48	3.2	3.42	3.44	2.84	5.45
200	2.83	2.95	2.49	3.49	2.6	3.96
300	3.41	2.45	1.93	3.48	1.78	3.05
400	3.06	2.51	0.97	1.99	1.64	2.2
500	1.17	1.13	0.73	1.83	1.04	0.98
750	1.01	0.9	0.55	1.03	1	1.56
1000	1.21	0.68	0.52	0.86	0.96	1.46
1250	1.02	1.08	0.48	0.72	0.87	1.03
1500	0.76	1.57	0.36	0.54	0.71	0.64
1750	0.93	1.37	0.45	0.54	0.68	0.74
2000	0.59	1.19	0.2	0.3	0.53	0.77
2250	0.31	0.65	0.21	0.34	0.5	0.48
2500	0.69	0.69	0.15	0.27	0.3	0.56
2750	0.3	0.7	0.19	0.38	0.3	0.31
3000	0.5	0.18	0.34	0.37	0.4	0.29
0-3000 (mgC m^{-2})	4220	4318	2591	3705	3362	3703

Appendix 2. Biomasses integrated over 0-2000 m of copepods [*Eucalanus bungii* (Shoden, 2000), *Metridia pacifica* and *M. okhotensis* (Padmavali, 2002), and *Oithona* spp. (Kaneko, 2005)], chaetognaths [*Sagitta elegans*, *Eukrohnia fowleri*, *E. bathypelagica*, and *E. hamata* (Nishiuchi and Ikeda, unpublished)], euphausiids (Okazaki and Ikeda, unpublished) and *Oikopleura* spp. (Schinohe, 2000) at Site H during September 1996-October 1997. Unit: mg DM m^{-2} (0-2000 m). ND: not determined. See text for details.

Date	*E. bungi*	*M. pacifica*	*M. okhotensis*	*Oithona* spp.	*S. elegans*	*E. fowleri*	*E. bathypelagica*	*E. hamata*	Euphausiids	*Oikopleura* spp
4-Sep-96	3471	994	630	282	600	75	175	1150	61.9	28.85
19-Sep-96	1430	1109	891	ND	175	0	200	525	17.7	582.51
2-Oct-96	1933	1506	821	ND	550	0	150	975	11.2	228.92
8-Dec-96	2288	1134	607	392	175	0	225	1500	9.4	40.61
13-Jan-97	866	906	184	ND	75	0	175	400	5.8	0.24
20-Feb-97	1042	723	328	ND	175	50	250	450	33.5	0.07
17-Mar-97	1362	945	186	ND	75	100	300	625	19.4	0.24
11-Apr-97	1854	1624	325	76	250	0	250	950	13	0.2
7-May-97	650	157	300	ND	175	0	175	525	10.6	0.54
4-Jun-97	5081	630	692	ND	725	0	350	1075	45.9	7.76
23-Jun-97	2751	591	1869	ND	250	0	225	1350	22.8	0.61
2-Jul-97	4336	1633	180	ND	475	200	400	1275	123	0.44
17-Aug-97	2388	660	800	ND	175	50	325	850	315	70.31
26-Aug-97	1344	689	855	ND	100	150	225	750	33.3	24.41
5-Oct-97	1893	504	1580	131	75	0	225	950	18.1	329.7

1

Appendix 3. Biomasses of micronektonic decapods and mysids (Kanazawa and Ikeda, unpublished) and micronektonic fishes (Yokokura and Yamaguchi, unpublished) at Site H during August 2002-August 2003. D/N: Day and Night samples were combined to calculate means. Unit: g WM m^{-2} (0-1000 m). See text for details.

Dates	Day/Night	Decapods	Mysids	Fishes
9-Aug-02	D/N	3.55	2.58	1.51
9-Oct-02	D/N	8.59	1.95	7.44
11-Feb-03	D	4.54	4.83	7.44
13-Mar-03	N	2.82	7.88	8.96
11-May-03	D/N	4.66	3.15	2.67
21-May-03	D/N	2.57	1.75	5.61
4-Jun-03	D	5.28	1.16	2.59
15-Jun-03	D	1.32	0.54	3.8
28-Jun-03	D	2.28	0.97	1.94
23-Aug-03	N	8.55	1.23	8.15

2

3