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MICRONEKTON OF THE NORTH PACIFIC

PICES Working Group 14 Final Report

Edited by

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1. Introduction

Micronekton are relatively small, but actively swimming, organisms ranging in size (2–10 cm) between plankton, which mostly drift with the currents, to the larger nekton, which have the ability to swim freely without being overly affected by currents. Although many micronektonic species can be found close to shore or near the sea bottom, we consider only those that occur in the pelagic realm mainly at the edge of, or beyond, the continental shelves. Many diverse taxonomic groups include micronektonic forms but the principal groups we examine in this report include cephalopods (small species and juvenile stages of large oceanic species), crustaceans (including large euphausiids, pelagic decapods, and mysids), and fishes (mainly mesopelagic species and juveniles of pelagic nekton). Although not generally fished commercially because of their relatively small size, micronekton represent a critical, but poorly understood, intermediate trophic link between the meso and macrozooplankton, and the higher trophic levels, including fishes, seabirds, and marine mammals. Many studies have shown that micronektonic species are a primary food source for a wide variety of harvested nektonic species. Unfortunately, micronekton are poorly sampled in most field studies due to their ability to avoid standard plankton sampling gear and their extrusion through the mesh of larger fish trawls.

Diel vertical migration of micronekton has been shown to contribute significantly to the rapid vertical transport of organic material from epipelagic to mesopelagic zones, referred to as the biological pump (Hidaka *et al.*, 2001 and references therein). Through this biological pump, carbon fixed as living organic matter plus anthropogenic substances such as insecticides, butyltin and PCBs are transported to deep-sea ecosystems. Myctophids have been suggested as particularly good monitors of deep-sea pollution because they encounter a variety of water masses (of different origin) during their substantial diel vertical migrations (Takahashi *et al.*, 2000).

1.1 Working Group History

A need was identified within the PICES community, especially among the ecosystem modelers, for a synthesis of the available information on micronekton in the North Pacific. In response, a theme session was held during the 1997 PICES Annual Meeting in Pusan, Korea, which brought together a large number of micronekton experts within the North Pacific region. It was at that time that a proposal was put forth to the Biological Oceanography Committee (BIO) to establish a PICES working group to assimilate knowledge of micronekton and their sampling in the North Pacific. This led to the formation of Working Group 14 (WG 14) on “Effective Sampling of Micronekton to Estimate Ecosystem Carrying Capacity” in 1998. Although organizational meetings were held at PICES Annual Meetings in 1998 in Fairbanks, U.S.A. and 1999 in Vladivostok, Russia, there were difficulties getting co-chairmen and members to attend these meetings. Membership for the Working Group was finalized in 2000, and the Working Group met for the first time at PICES IX in Hakodate, Japan. Subsequent Working Group meetings were held during PICES Annual Meetings in 2001, in Victoria, Canada, and 2002, in Qingdao, China, and an intersessional meeting was held in winter of 2002, in Honolulu, U.S.A. Initial summaries of the sampling conducted by each member nation were contained in a report presented at the PICES/CoML/IPRC workshop on “Impact of Climate Variability on Observation and Prediction of Ecosystem and Biodiversity Changes in the North Pacific” held in Honolulu in March 2001 (Brodeur, 2001a) and have been included in this report as Appendix Tables.

Prior to the 2000 Annual Meeting in Hakodate, the Working Group co-sponsored a symposium entitled “Advanced Techniques of Sampling Gear and Acoustic Surveys for Estimation of Fish Abundance and Behavior” which has since been published electronically (Iida, 2003). During the 2002 PICES Annual Meeting in Qingdao, three members of the Working Group (Drs. John

Dower, Richard Brodeur and Orio Yamamura) organized a special theme session on "The Importance of Biophysical Coupling in Concentrating Marine Organisms around Shallow Topographies". Many of these papers dealt primarily with micronekton and were useful in preparing this report. Several of the papers presented during this symposium were subsequently submitted to a special volume of Journal of Marine Systems and were published in 2004 (Dower and Brodeur, 2004).

The following report synthesizes what is known about the distribution and trophic relationships of micronekton in the North Pacific Ocean and adjacent seas, with a summary of the present state of sampling of these organisms. The report is not meant to be all-inclusive but merely to synthesize important aspects based on the literature and the knowledge of the Working Group, and to identify key knowledge gaps that should be filled in the coming years.

2. Species Composition and Distribution Patterns Related to Water Masses

2.1 Mesopelagic Fishes

2.1.1 Dominant families

In the subarctic and transitional regions, fishes of the families Myctophidae and Microstomatidae are the most abundant in terms of number and biomass, accounting from 80% to more than 90% of total micronektonic fish catch, while in the subtropical waters, Myctophidae, Gonostomatidae, and Phosichthydae comprise most of the total catch (Gjøsaeter and Kawaguchi, 1980; Beamish *et al.*, 1999). Although occasionally found in deep fjords or inland seas (*e.g.*, Mason and Phillips, 1985; Abookire *et al.*, 2002), the vast majority of micronektonic species are found along the continental or insular slope regions, and around the seamount areas of the North Pacific. Slope water species are mainly myctophids and sternoptychids which occur adjacent to insular or continental shelves and seamounts in the transition, subtropical and tropical regions. Considering these family compositions, we reviewed the common species of these two families in the subarctic and transitional waters, three families in the subtropical waters, and two families in the slope waters of the North Pacific. Rare species of taxonomic interest were not treated in this report because of their low biomass.

2.1.2 Large-scale feeding and/or spawning migration or expatriation?

When examining the distribution of these families, the most remarkable feature is that, with the exception of a few species (see Table 2.1), most of the subarctic waters are not utilized as spawning grounds. For example, all of the myctophids hitherto classified as subarctic species (based on adult distribution) spawn in warmer transitional waters including the Transition Domain and Transition Zone and Subtropical waters (see Fig. 5.1). In the case of *Notoscopelus japonicus*, a typical transitional water species found off Japan, its spawning ground is located in the upstream region of the Kuroshio Current off southern Japan, and the larvae are transported northward to the transitional waters off northern Japan (Sassa *et al.*, 2004a). The larvae of *Lipolagus ochotensis,* the adults of which are common in the Bering Sea, also occur in the subtropical waters of the Kuroshio and in the warm waters of the California Current (Moser *et al.*, 1993; Moser and Ahlstrom, 1996; Sassa *et al.*, 2004a). Although it has never been studied in detail, scattered evidence suggests that some micronektonic mesopelagic fishes may undertake spawning and feeding migrations of up to 1000 km (Sassa *et al.*, 2004a). Balanov and Il'insky (1992) estimated that there were about 2.8 million tons of myctophid and 0.31 million tons of *Lipolagus ochotensis* biomass in the Bering Sea. Their larvae are known to occur in the California Current region, the Transition Domain and Alaska Current waters in the eastern North Pacific, as well as in the transition and Kuroshio regions of the western North Pacific (Fig. 2.1; Abookire *et al.*, 2002; Moser and Ahlstrom, 1996; Funes-Rodríguez *et al.*, 2000; Zahuranec, 2000). However, it is not known whether this biomass represents a feeding migratory population in the Bering Sea or expatriation from elsewhere. Absence or very low density of their larvae in the Alaska Current and Alaskan Stream regions does not explain the abundance of adults in the Bering Sea. Exact knowledge is essential on this type of large-scale migration, or expatriation, in order to understand the productivity and fluctuation of populations of each micronekton species since the significance of myctophids as food for salmonids and squids has been suggested (Nagasawa *et al.*, 1997). Considering these possibilities, we reviewed the distribution patterns of both larvae and juvenile–adult specimens after metamorphosis (hereafter cited as adults) to identify the spawning ground of each species in the North Pacific, and to discuss expatriation, since previous reviews were restricted only to adults.

2.1.3 Definition of water masses

As the distribution patterns of micronektonic mesopelagic fish are well correlated with physical oceanographic structures, species composition was described with respect to the different water masses defined here. The distributions of adult specimens of common species are well known, based on the several comprehensive reviews and studies, as subsequently described. However, knowledge of larval micronekton distributions is very limited because of the difficulty in identifying many of the early life stages. We selected typical areas (Tables 2.1–2.3) where both larval and adult distributions were fairly well described in the main water masses and current systems hitherto designated. Oceanographic terminology (*e.g.*, current systems, gyres, domains, and water masses) adopted in the following description of species distributions are based on Favorite *et al.* (1976) unless otherwise stated. Their definitions, and physical oceanographic features and relationships with mesopelagic fish zoogeography are described in the next section.

(1) Subarctic Waters (SAW)

Bering and Okhotsk Seas

These two geographically semi-enclosed areas (Table 2.1) correspond to the Bering Sea Gyre, the Bering Sea Current system, the Okhotsk Sea Gyre and the Okhotsk Kurile Current system, as defined by Favorite *et al.* (1976).

Oyashio Waters (OyW) and Western Subarctic Waters (WSAW)

The Oyashio Current is a southward branch of the outflow of the Okhotsk Kurile Current and is well distinguished from the western Transitional Domain waters by the Oyashio Front (OyF), which has been defined by the 5°C isotherm and 33.4 isohaline at 100 m depth off Japan (Kawai, 1972). The OyF extends eastward along approximately 40°N latitude before turning northward to join the Subarctic Current near 45°N and 155°E. The WSAW in Table 2.1 includes the Western Subarctic Gyre with its related current systems and the Subarctic Current System west of 170°E. Favorite *et al.* (1976) proposed that the 4°C isotherm at 100 m depth serve as a boundary between waters of the Subarctic Current System and Transition Domain. This boundary almost coincides with the OyF in the west, since the 4° and 5°C isotherms are almost identical in this region.

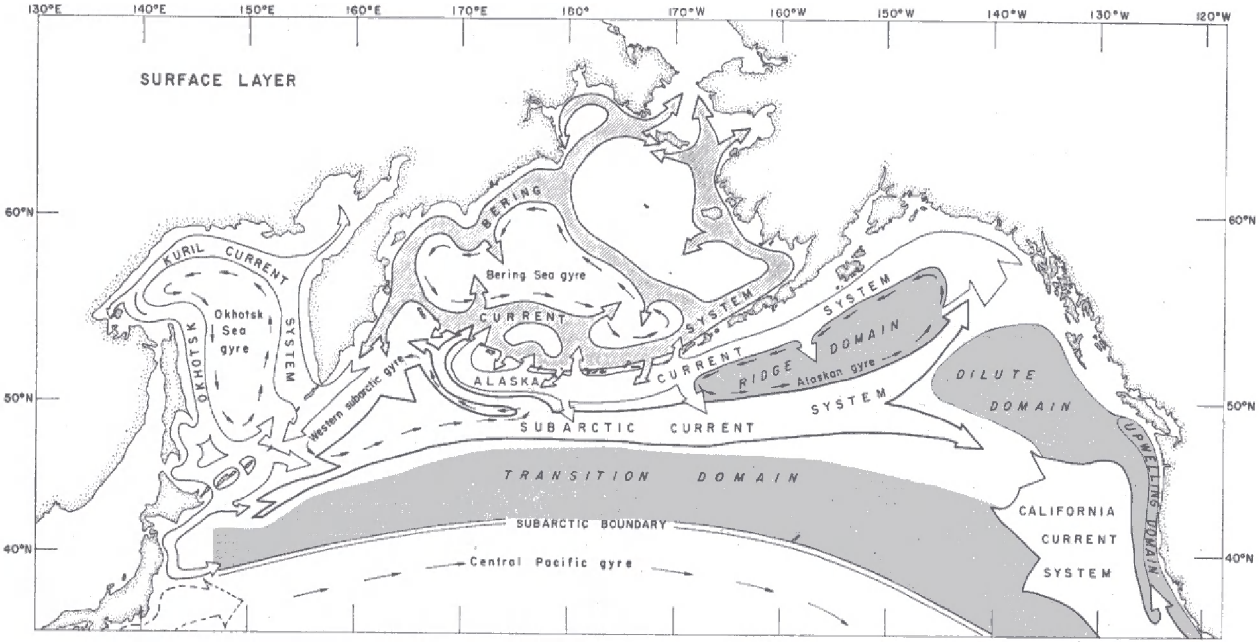


Fig. 2.1 Large-scale near surface circulation of the subarctic North Pacific Ocean. (from Favorite *et al.*, 1976)

Eastern Subarctic Waters (ESAW)

The ESAW correspond with the eastern parts of both the Subarctic Current System and the Ridge Domain. Associated with the northward shift of the 4° and 5°C isotherms at 100 m depth east of 140°W (Fig. 14 of Favorite *et al.*, 1976), the southern limit of the ESAW shifts northward in the eastern North Pacific due to the effect of the warmer Alaska Current which flows northward along the west coast of North America and becomes the Alaskan Stream.

(2) Transition Domain (TrD), Transition Zone (TrZ) and California Current System

The TrD has been defined as the zone between the Subarctic Boundary (SAB) and the southern boundary of the Subarctic Current System (Fig. 2.1) characterized by 4–5°C isotherm at 100 m depth. Pearcy (1991) recognized the "Transition Zone" as the zone between the SAB and the Subtropical Front and named the area, including both the Transition Zone and Transition Domain, the "transition region". Roden (1991) reviewed the dynamic aspects of the transition region (mainly in the Central Pacific), excluding the California Current and Oyashio–Kuroshio confluence regions, and defined the TrZ, a Subarctic Frontal Zone to the north, and a Subtropical Frontal Zone to the south, based on the frontal structures of salinity and temperature. He indicated that the southern limit of the Subarctic Frontal Zone is best defined by the surfacing of the 33.8 isohaline. This means that his Subarctic Frontal Zone is not exactly the TrD previously designated, since the southern limit of the latter was defined by the surfacing of the 34.0 isohaline (Favorite *et al.*, 1976). However, the two areas are almost identical since the positions of the 33.8 and 34.0 isohalines are usually quite close. A recent study in the western North Pacific revealed that the SAB is the key front for defining the spawning grounds of mesopelagic fishes in transitional areas (Sassa, 2001; Sassa *et al.*, 2004b). Considering the biological importance and the spatio-temporal stability of the SAB, as shown in Fig. 34 of Favorite *et al.* (1976), we hereafter adopt the terminology of Favorite *et al.* (1976) and Pearcy (1991).

In the North Pacific west of 155°E longitude, the waters between the OyF and Kuroshio Front (KuF) have been called by various terms, such as transition waters, Transition Zone, or Ku-Oy mixing zone. The problem is that the above terms often include the waters of both the TrD and TrZ, which are located on both sides of the SAB, since the SAB is always located between the OyF and KuF. This ambiguous terminology, used to describe the transition water zoogeography, seems to have resulted in considerable confusion in scientific discussion. Considering the significance of the SAB as the boundary of larval and adult distributions of mesopelagic and harvested fish (Mishima, 1981; Sassa *et al.*, 2004b), descriptions based on the exact distinction of the above water masses are necessary in the western North Pacific.

Transition Domain

The TrD is continuous from Japan to North America (Fig. 2.1). The southern boundary of the TrD is well denoted by the SAB and its location is both seasonally and annually stable, corresponding well with that of the 34 isohaline at both the surface and 100 m depth due to the vertical orientation of the 34 isohaline (Fig. 34 of Favorite *et al.*, 1976). The SAB is located around 41°N in the western part of the TrD (extending eastward to 160°W), and then gradually turns southward to join the offshore region of the California Current System. The northern boundary of the TrD is denoted by the OyF (determined by the 5°C isotherm at 100 m depth) in the area west of approximately 155°E (Kawai, 1972; Susana and Sugimoto, 1998). East of about 155 °E, the 4°C isotherm at 100 m depth denotes its northern boundary. East of 160°W, however, the northern boundary is delimited by the "Dilute Domain", denoted by the small salinity difference (<2 psu) in the upper 100 m depth from the surrounding water masses (Favorite *et al.*, 1976). As this salinity difference does not affect mesopelagic fish distribution (LeBrasseur, 1970), the Dilute Domain was included in the eastern TrD in the present description of mesopelagic fish zoogeography (Table 2.1). The same is true for the Upwelling Domain from California to British Columbia, although upwelling is known to affect the offshore–inshore larval distributions off

Oregon (Richardson and Pearcy, 1977). In other words, the TrD in this review expands northward into the Alaska Current, and also southward, to merge into the California Current regions where transitional and subarctic water mesopelagic fishes dominate (Table 2.1). The obvious temperature difference between the cold Subarctic Waters (SAW) of the Subarctic Current and the warmer TrD waters of the Alaska Current was shown in the upper 1000-m layer by Favorite *et al.* (1976). The warm TrD nature of the Alaska Current gradually decreases northward toward the Alaskan Stream region since mesopelagic fish larvae, which are abundant in the California Current region, also decrease northward. In the western Pacific off Japan, the TrD waters can be as narrow as 10–20 km, and sometimes indiscernible because of the strong southward intrusion of the Oyashio, but become more obvious east of 155°E.

Transition Zone

In the area west of approximately 170°E, the TrZ is located between the SAB and KuF and its eastward extension (Subtropical Front) as defined by the 15°C isotherm and 34.6 isohaline at 100 m near 37–38°N. The Subtropical Front is deflected southward by current–topography interactions with the Emperor Seamount chain near 170°E (Roden, 1991), becoming diffuse southward to 30°N. No discernable front associated with the Kuroshio is observed in the central North Pacific east of the Emperor Seamount chain. The Subtropical Convergence is located mainly around 30°N, but is also recognizable around 25°N in the western North Pacific. Therefore, the Subtropical Frontal Zone defined by Roden (1991) is used to define the southern TrZ boundary in the central North Pacific. Near 160°W, the northern boundary of the TrZ (= SAB) is gradually deflected southeastward, reaching the area near 30°N and 130°W where it merges into the offshore region of the California Current.

California Current System

As stated in the TrD section, the eastern TrD expands southeastward, together with one branch of the Subarctic Current, the upper 250 m of which turns southeast near 150°E to merge into the California Current System, although this is "an overly simplified description of flow in one of the most important regions" (Favorite *et al.*, 1976). This current system borders the subtropical Eastern North Pacific Central Waters to the west and the eastern Pacific Tropical Waters to the south. From the viewpoint of mesopelagic fish zoogeography, the California Current waters (at least its colder shoreward side) show no remarkable differences from the eastern TrD waters north of the SAB, although the subtropical central water and the eastern Tropical Pacific components also occur in its western offshore and southern boundary regions, respectively. Both larvae and adults of most subarctic and transitional water microstomatids and myctophids are abundant off California (Moser and Smith, 1993b).

(3) Subtropical Domain or Subtropical Waters (STD or STW)

In the area west of approximately 170°E, the STW correspond to waters of the Kuroshio Current, the Kuroshio Extension and their related warm-core rings and streamers dispatched northward into the TrZ across the KuF. The northern boundary corresponds with the KuF, and its eastward extension is denoted by the 15°C isotherm and 34.6 isohaline at 100 m depth near 36–37°N. In the central North Pacific, a northern border is denoted by the sharp subtropical salinity front around 32°N in which 34.6–35.0 isohalines are embedded (Roden, 1991). These waters have been often called Eastern North Pacific Central Waters, and border the eastern TrZ to the north and the California Current System to the east.

(4) Slope Waters

Slope water species belonging to shelf-edge assemblages occur in transition and subtropical waters over continental and insular slopes (*e.g.*, the Kuroshio Current and transition region off Japan, off Hawaii, the Emperor Seamount region, and off southern California) (Table 2.3). They also occur in the tropical slope waters of the Indo-Pacific region, but are absent in subarctic waters (except for its southernmost areas).

2.1.4 Species composition

Typical species compositions of both larvae and adults are summarized by water mass in Tables 2.1 to 2.3. After metamorphosis, juveniles (especially *Stenobrachius leucopsarus*, *Diaphus theta*, *Protomyctophum thompsoni* and *Lipolagus ochotensis*) are considered adults. The zoogeographic species groups listed in Tables 2.1 and 2.2 are based on the adult distributions as presently known (Rass, 1954; Parin, 1961, 1988; Aron, 1962; Pearcy, 1964; Pearcy *et al.*, 1979b; Ahlstrom, 1969; Parin and Fedorov, 1981; Bekker, 1967, 1983; Willis, 1984; Willis *et al.*, 1988; Balanov and Il'Insky, 1992; Beamish *et al.*, 1999). Species identified in Tables 2.1 and 2.2 as "transpacific" are those that are distributed in both the western and eastern sides of the subarctic, transitional and subtropical waters. Adult and larval distribution patterns in the transition region of the Central Pacific are restricted (Norcross *et al.*, 2003). The distribution patterns of each species group are as follows.

(1) Subarctic–Transition Water species

<u>Transpacific Subarctic–Transition Water (SAW–TrW) species</u>

Adults of this group are known to be widely distributed in the eastern, central and western subarctic and transition waters, including both the TrZ and TrD, and California Current waters, and partly extend their distribution into the Bering and Okhotsk Seas (Table 2.1). However, their larval distributions are centered in the transition and California Current waters. In the western Pacific, larval *Stenobrachius leucopsarus*, *Diaphus theta* and *Nannobrachium regale* are restricted mainly to the TrZ waters, while the larvae of *Stenobrachius nannochir* and *Protomyctophum thompsoni* occur in TrD waters, and are frequently found in the northern boundary area of the TrZ (Sassa, 2001; Sassa *et al.*, 2004a). The larvae of *Leuroglossus schmidti* occur in the western and eastern SAW and Bering Sea (Sobolevsky and Sokolovskaya, 1996; Dunn, 1983) and the southern Okhotsk Sea (Savinykh, pers. observ.). Although *L. schmidti* larvae were sometimes recorded in the California Current north of 35°N (Moser *et al.*, 1994), it has not been recorded near Oregon, indicating that spawning occurs mainly in subarctic waters north of 50°N.

In the eastern Pacific, the greatest number of larvae in this group is distributed mainly in the TrD and the California Current region north or northeast of the SAB (Moser *et al.*, 1993, 1994; Moser and Smith, 1993a,b; Norcross *et al.*, 2003). However, the number of larval species decreases northward from Oregon (Richardson and Pearcy, 1977; Richardson *et al.*, 1980; Doyle *et al.*, 2002) to the Alaskan Gyre systems (LeBrasseur, 1970; Dunn and Naplin, 1974; Frost and McCrone, 1979). Norcross *et al.* (2003) examined larval fish distributions from vertically stratified tows along a north–south transect at 158°W in winter and found four species of myctophids in the Subarctic Domain (we note that their Subarctic Domain south of 50°N (stations NH17-27) is identified as the TrD according to the definition in this review, and so their results agree with the findings of the present evaluation). The larvae of four species, *S. leucopsarus, P. thompsoni, L. schmidti,* and *Tarletonbeania crenularis*, occur in the Alaskan Gyre systems including the Alaska Current, Alaska Stream, Ridge Domain, and Subarctic Current waters (Table 2.1). Nishimura *et al.* (1999) reported juvenile *S. leucopsarus* of 22 mm SL (*i.e.*, just after metamorphosis) in the southeastern Bering Sea, indicating that larval transport probably occurred from the south through the Alaska Stream. In midwater trawling in the eastern Bering Sea, Sinclair and Stabeno (2002) caught high numbers of Microstomatidae (mainly *L. schmidti, Bathylagus pacificus* and *Pseudobathylagus milleri*) and Myctophidae (*S. leucopsarus* and *S. nannochir*). The distribution patterns of these adults and larvae raise the question of whether most of the huge mesopelagic fish biomass in the SAW, especially in the Bering and Okhotsk Seas, represents expatriate or feeding/migratory populations, since Balanov and Il'Insky (1992) estimated the biomass of myctophids to be approximately 2.8 million tons in the Bering Sea.

Table 2.1 Occurrence of adults and larvae of the subarctic and transitional water fishes belonging to Myctophidae and Microstomatidae in the northern North Pacific.

Species	Western Transition Waters				SAW										California Current and Eastern TD Waters					
	TrZ Waters		TrD Waters		Oyashio		WSAW		Bering		Okhotsk		ESAW#		California Current		Oregon		Alaska Current	
	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae
Transpacific SAW-TrW species																				
Myctophidae																				
Stenobrachius leucopsarus	A	L	A	–	A	–	A	–	A	(?)	A	–	A	(L)	A	L	A	L	A	L
Stenobrachius nannochir	A	(L)	A	L	A	–	A	–	A	–	A	–	A	–	(A)	–	A	–	A	L**
Diaphus theta	A	L	A	(L)	A	(L)	A	–	A	–	A	–	A	–	A	L	A	–	A	L**
Protomyctophum thompsoni	A	L	A	L	A	(L)	A	–	A	–	A	–	A	(L)	A	L	A	L	A	L
Nannobrachium regale	A	(L)*	A	–	A	–	A	–	A	–	A	–	A	(L)	A	L	A	L	A	(L)
Microstomatidae																				
Lipolagus ochotensis	A	–	A	–	A	–	A	–	A	–	A	–	A	–	A	L	A	L	A	(L)
Pseudobathylagus milleri	A	L	A	L	A	(L)	A	–	A	–	A	–	A	–	A	L	A	L	A	–
Bathylagus pacificus	A	L	A	L	A	L	A	–	A	–	–	–	A	–	A	L	A	L	A	(L)
Leuroglossus schmidti	A	L	A	L	A	L	A	L	A	L	A	(L)	A	L	A	(L)	A	–	A	L
Transpacific TrW species																				
Myctophidae																				
Protomyctophum crockeri	A	–	–	–	–	–	–	–	–	–	–	–	–	–	A	L	A	L	–	–
Symbolophorus californiensis	A	L	A	–	(A)	–	(A)	–	–	–	–	–	(A)	–	A	L	A	–	–	–
Western SAW and TrW species																				
Myctophidae																				
Tarletonbeania taylori	A	(L)	A	L	A	–	A	–	–	–	–	–	–	–	–	–	–	–	–	–
Lampanyctus jordani	A	(L)	A	L	A	–	A	–	A	–	A	–	A	–	(A)	–	–	–	–	–
Notoscopelus japonicus	A	–	A	–	A	–	(A)	–	–	–	–	–	(A)	–	–	–	–	–	–	–
Diaphus gigas	A	–	A	–	(A)	–	(A)	–	–	–	–	–	–	–	–	–	–	–	–	–
Microstomatidae																				
Melanolagus bericoides	–	–	–	–	A	–	A	–	–	–	–	–	–	–	–	–	–	–	–	–
Eastern SAW or TrW species																				
Myctophidae																				
Tarletobeania crenularis	–	–	–	–	–	–	–	–	A	–	–	–	A	(L)	A	L	A	L	A	L
Nannobrachium ritteri	–	–	–	–	–	–	–	–	A	–	–	–	(A)	–	A	L	A	(L)	A	(L)
Microstomatidae																				
Melanolagus bericoides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	A	–	A	–	–	–
Bathylagidae wesethi	–	–	–	–	–	–	–	–	–	–	–	–	A	–	A	L	A	–	A	–
Leuroglossus stilbius	–	–	–	–	–	–	–	–	A	–	–	–	A	–	A	L	A	–	A	–

Table 2.1 Continued

Note: Species are grouped according to their adult distributions hitherto reported.

includes Ridge Domain (RD) and Subarctic Current (SAC).

A and (A) indicate common and rare occurrence of adults, respectively; L indicates common larval occurrence; (L) denotes larval occurrence in the marginal waters adjacent to the main spawning water mass defined by the larval occurrence; (?) indicates that the larva is not yet described; dash indicates no previous record.

* Restricted to waters east of *ca.* 160°E; ** south of 50°N along 158°E in the eastern Transitional Domain waters (*sensu* Favorite *et al.*, 1976 after Norcross *et al.*, 2003).

TrZ = Transitional Zone, TrD = Transitional Domain, SAW = subarctic waters, WSAW = western subarctic waters, ESAW = eastern subarctic waters, TrW = transition waters

Transpacific Transitional Water (TrW) species

Two species, *Symbolophorus californiensis* and *Protomyctophum crockeri*, occur in both the eastern and western Pacific TrW, although their populations may be discontinuous. Adults of this group show transpacific distribution in the transitional region including both the TrD and TrZ, and sometimes enter the southern edge of the SAW. In the western Pacific, larvae of *S. californiensis* occur only in TrZ waters south of the SAB, while in the eastern Pacific, their larvae are common in both the TrD and California Current regions (Moser *et al.*, 1993; 2001; Sassa, 2001; Norcross *et al.*, 2003; Sassa *et al.*, 2004b).

Western Subarctic–Transitional Water (SAW–TrW) species

Adults of this species group are distributed in the SAW, TrD and TrZ of the western Pacific west of about 175°E (Table 2.1, Sassa *et al.*, 2002b). Occasional records from the eastern Pacific are likely due to infrequent transport by the Subarctic Current System. *Lampanyctus jordani* extends its distribution into the Bering and Okhotsk Seas (Kulikova, 1960). Of the five species in this group, the larvae of *Tarletonbeania taylori* and *Lampanyctus jordani* occur in the TrD waters and northern TrZ close to the SAB. However, *Notoscopelus japonicus* larvae occur in the western STW of the Kuroshio region off southern Japan, which suggests a large-scale spawning migration of this species on the order of 1,000 kilometers (Sassa *et al.*, 2004b). Larvae of *Diaphus gigas* and *Melanolagus bericoides* have not yet been described. It has been pointed out that *D. gigas* might actually be oversized senile expatriates of the subtropical water species *D. perspicillatus* (Kawaguchi and Shimizu, 1978).

Eastern Subarctic–Transitional Water (SAW–TrW) species

Adults of five species (*T. crenularis, Nannobrachium ritteri, Melanolagus bericoides, Bathylagus wesethi*, and *Leuroglossus stilbius*) occur in both the California Current and TrD waters off Oregon (Table 2.1) and several have extended distributions through the Alaska Current region into the Bering Sea. Larvae of all but *M bericoides* occur in the California Current region (Moser *et al.*, 1993, 1994; Doyle *et al.*, 2002), while two occur off Oregon (Richardson and Pearcy, 1977; Richardson *et al.*, 1980) up to the Alaskan Current (LeBrasseur, 1970). Only one species (*T. crenularis*) occurs in the Alaskan Stream region off Kodiak Island (Dunn and Naplin, 1974; Norcross *et al.*, 2003) and none have been reported from the Bering Sea. Larvae of *B. bericoides* are abundant in the tropical and subtropical eastern Pacific but rare in the California Current sampling region (Moser and Ahlstrom, 1996).

Variability in use of the Transition Zone (TrZ) and Transition Domain (TrD) as spawning grounds

In the eastern North Pacific, the TrZ waters south or southwest of the SAB are mainly dominated by adults of the subtropical central water species (Willis, 1984), while the TrZ of the western Pacific is dominated by the subarctic and transitional water species (Sassa *et al.*, 2004a). The larvae of transpacific SAW and TrW species which occur in the TrZ in the western Pacific are distributed in TrD and California Current regions in the eastern Pacific (Table 2.1), that is, the use of western Pacific TrZ waters as spawning grounds of both subarctic and transitional water species seems to be replaced by the use of TrD and California Current waters north or northeast of the SAB in the eastern Pacific (Table 2.1). This northward shift of spawning grounds crossing the SAB is probably explained by the warmer temperature of the TrD in the upper 300 m layer. The long-term mean temperatures at 125 m and 300 m depth are 2–3°C and 3–5°C higher, in summer and winter respectively, in the eastern TrD than in the western part (Fig. 35 of Favorite *et al.*, 1976).

(2) Tropical–Subtropical species

Transpacific Subtropical–Tropical Water (STW–TW) species

Common species belonging to the three most abundant families (in terms of both biomass and abundance) are listed in Table 2.2. Based on larval occurrence, all of these species are thought to spawn in the Subtropical Central Gyre (Clarke, 1973, 1987; Loeb, 1979a,b, 1980, 1986; Norcross *et al.*, 2003) and the Kuroshio waters (Ozawa, 1986a,b; Sassa, 2001; Sassa *et al.*, 2002a, 2004b,c). In the western North Pacific, both adults and larvae rarely occur in the TrD, although they are occasionally found in the TrZ south of the SAB where they are probably related to the dynamic interaction between Kuroshio and Oyashio waters (*e.g.*, warm streamers and warm-core rings). In the North Pacific east of about 150°W, the distribution of subtropical central water species extends eastward into the warmer offshore region of the California Current System where they have been collected in offshore California Cooperative Oceanic Fisheries Investigations (CalCOFI) samples (Moser and Alhstrom, 1996; Moser *et al.*, 1987, 1993, 1994, 2001). They do not, however, occur in the colder waters off Oregon (Richardson and Pearcy, 1977; Richardson *et al.*, 1980). In general, gonostomatid larvae are found more commonly in warmer waters than myctophid larvae, and both are absent from the colder TrD. However, adults of non-vertically migrating gonostomatids, such as *Cyclothone* spp., extend northward into SAW. The deepest dweller, *Cyclothone atraria*, is distributed in the Bering and Okhotsk Seas, while *C. pallida* and *C. pseudopallida* occur in the Bering Sea (Beamish *et al.*, 1999; Sinclair and Stabeno, 2002).

Western Tropical and Subtropical Water (WTW and WSTW) species

Both the adults and larvae of three myctophid species (*Diaphus kuroshio, D. garmani,* and *D. perspicillatus*) and one gonostomidid (*Sigmops gracile*) are distributed in the Kuroshio and Western North Pacific Central Waters, and enter partly into the TrZ in association with warm core rings and warm streamers from the Kuroshio Front (Table 2.2). Only adult *S. gracile* extend their distribution into the TrD, and farther north into the Bering and Okhotsk Seas (Beamish *et al.*, 1999; Sinclair and Stabeno, 2002).

Table 2.2 Occurrence of the common mesopelagic micronektonic fishes belonging to Myctophidae, Gonostomatidae, and Phosichthydae in the subtropical and tropical waters of the North Pacific.

Species	Western Tropical and Subtropical				Western Transition				Eastern Subtropical and Tropical				California Current Region		Eastern Transition Waters off Oregon	
	W. Central Pacific Waters		Kuroshio Current Waters		Transition Zone Waters		Transition Domain Waters		Eastern Pacific Tropical Waters		Eastern N. Pacific Central Waters					
	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae
Transpacific STW or TW species																
Myctophidae																
Notolychnus valdiviae	A	L	A	L	(A)	(L)	–	–	A	L	A	L	A	(L)	–	–
Notoscopelus resplendens	A	L	A	L	(A)	(L)	–	–	A	L	A	L	A	(L)	–	–
Ceratoscopelus warmingii	A	L	A	L	A	L	–	–	–	–	A	L	–	–	–	–
Lobianchia gemellari	A	L	A	L	(A)	(L)	–	–	(A)	–	A	L	(A)	–	–	–
Lampadena luminosa	A	L	A	L	A	L	–	–	A	L	A	L	–	–	–	–
Lampadena urophaos	A	L	A	L	(A)	(L)	–	–	–	–	A	L	A	L	–	–
Lampanyctus alatus	A	L	A	L	(A)	(L)	–	–	A	L	A	L	–	–	–	–
Lampanyctus steinbecki	A	L	A	L	(A)	(L)	–	–	A	L	A	L	–	–	–	–
Diogenichthys atlanticus	A	L	A	L	(A)	(L)	–	–	A	L	A	L	A	L	–	–
Centrobranchus brevirostris	A	L	A	L	(A)	–	–	–	A	L	A	L	–	–	–	–
Hygophum reinhardti	A	L	A	L	(A)	(L)	–	–	A	L	A	L	A	(L)	–	–
Hygophum proximum	A	L	A	L	–	–	–	–	A	L	A	L	(A)	(L)	–	–
Symbolophorus evermanni	A	L	A	L	(A)	–	–	–	A	L	A	L	–	–	–	–
Myctophum nitidulum	A	L	A	L	(A)	(L)	–	–	A	L	A	L	A	(L)	–	–
Myctophum asperum	A	L	A	L	(A)	(L)	–	–	–	–	A	L	–	–	–	–
Benthosema suborbitale	A	L	A	L	(A)	(L)	–	–	A	L	A	L	(A)	(L)	–	–
Gonostomatidae																
Cyclothone acclinidens	A	L	A	L	–	–	–	–	A	L	A	L	A	L	–	–
Cyclothone alba	A	L	A	L	A	(L)	(A)	–	–	–	A	L	–	–	–	–
Cyclothone pseudopallida	A	L	A	L	A	(L)	(A)	–	A	L	A	L	A	L	(A)	–
Cyclothone pallida	A	L	A	L	A	(L)	(A)	–	A	L	A	L	A	L	(A)	–
Cyclothone atraria	A	L	A	L	A	(L)	A	–	A	L	A	L	(A)	–	(A)	–
Sigmops elongatum	A	–	A	–	(A)	–	–	–	A	L	A	L	(A)	–	–	–
Gonostoma atlanticum	A	L	A	L	(A)	–	–	–	A	L	A	L	–	–	–	–
Phosichthydae																
Vinceguerria nimbaria	A	L	A	L	(A)	(L)	–	–	–	–	A	L	–	–	–	–
Vinceguerria poweriae	A	L	A	L	–	–	–	–	–	–	A	L	A	L	–	–

Table 2.2 Continued

Species	Western Tropical and Subtropical				Western Transition				Eastern Subtropical and Tropical				California Current Region		Eastern Transition Waters off Oregon	
	W. Central Pacific Waters		Kuroshio Current Waters		Transition Zone Waters		Transition Domain Waters		Eastern Pacific Tropical Waters		Eastern N. Pacific Central Waters					
	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae
Western STW or TW species																
Myctophidae																
Diaphus kuroshio	A	L	A	L	(A)*	(L)**	–	–	–	–	–	–	–	–	–	–
Diaphus garmani	A	L	A	L	(A)	(L)	–	–	–	–	–	–	–	–	–	–
Diaphus perspicillatus	A	L	A	L	(A)	(L)	–	–	–	–	–	–	–	–	–	–
Gonostomatidae																
Sigmops gracile	A	L	A	L	A	(L)	(A)	–	–	–	–	–	–	–	–	–
Eastern STW or TW species																
Myctophidae																
Triphoturus mexicanus	–	–	–	–	–	–	–	–	A	L	–	–	A	L	–	–
Ceratoscopelus townsendi	–	–	–	–	–	–	–	–	A	L	–	–	A	L	–	–
Diogenichthys laternatus	–	–	–	–	–	–	–	–	A	L	–	–	A	L	–	–
Gonostomatidae	–	–														
Cyclothone signatha	–	–	–	–	–	–	–	–	A	L	(A)	–	A	L	A	–
Phosichthydae																
Vinceguerria lucetia	–	–	–	–	–	–	–	–	A	L	–	–	A	L	–	–

Note: Kuroshio Current waters include the Kuroshio Extension waters. STW = subtropical waters, TW = tropical waters (see text for definition of water masses.)

A and (A) indicate common and rare occurrence of adults, respectively.

L indicates common larval occurrence and (L) denotes larval occurrence in the marginal waters adjacent to the main spawning water mass defined by the larval occurrence; dash indicates no previous record.

Table 2.3 Distribution patterns of slope water species belonging to the families Myctophidae and Sternoptychidae endemic to the slope waters off Japan, Hawaiian Islands, and southern California.

Species	off Japan		off Hawaii		Emperor Seamount		off California	
	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae
Myctophidae								
Myctophum orientale	A	L	–	–	–	–	–	–
M. selenops	–	–	A	L	–	–	–	–
M. brachygnathos	A	?	A	L	–	–	–	–
Benthosema pterotum	A	L	–	–	–	–	–	–
B. panamense	–	–	–	–	–	–	A	L
B. fibulatum	A	?	A	L*	A	?	–	–
Diaphus suborbitalis	A	?	–	–	–	–	–	–
D. trachops	–	–	A	?	–	–	A	–
D. chrysorhynchus	A	?	A	?	A	?	–	–
D. adenomus	A	?	A	?	A	?	–	–
D. watasei	A	?	–	–	–	–	–	–
Idiolychnus urolampus	A	?	A	?	A	?	–	–
Sternoptychidae								
Maurolicus japonicus	A	L	A**	–	A	L	–	–
M. imperatorius	–	–	–	–	A	L	–	–

*Boehlert and Mundy (1993) record only, with no description; **Parin and Kobyliansky (1993).
A and L denote the occurrence of adults and larvae, respectively.
Dash indicates no previous record of the species, and a question mark indicates that the larva is not yet described.

Eastern Tropical and Subtropical Water (ETW and ESTW) species

Both the adults and larvae of five species (*Triphoturus mexicanus*, *Ceratoscopelus townsendi, Diogenichthys laternatus, Cyclothone signatha* and *Vinceguerria lucetia* occur in the eastern Tropical Pacific and southern California Current region, but are absent in the Eastern North Pacific Central Waters (Table 2.2). Adults of *C. signatha* extend their distribution into the Bering Sea and are distributed in both eastern and western subarctic waters with a sharp westward decrease in abundance (Beamish *et al.*, 1999), which is probably due to transport by the Alaska Current and Alaska Stream.

(3) Slope Water species

Fishes of this group form local high-density schools and serve as important prey of higher trophic levels resident in slope regions. Their productivity is believed to be very high, reflecting the generally high productivity of shelf-edge or slope waters. No slope water species are found in the subarctic regions. Common species are listed in Table 2.3. Ten species occur from the Japanese slope waters, all of which have their distribution centers in the subtropical and tropical waters off central Japan to the Southeast Asian Seas in the Indo-Pacific regions (Kawaguchi, 1977; Kawaguchi and Shimizu, 1978; Gjøsaeter and Kawaguchi, 1980; Zhenran, 1983). Of these ten species, six (*Myctophum brachygnathos, Benthosema fibulatum, Diaphus chrysorhynchus*, *D. adenomus*, *Idiolychnus urolampus* and *Maurolicus japonicus*) also occur in the Hawaiian slope waters (Wisner, 1976; Reid *et al.*, 1991), and five species are known from the Emperor Seamount region (Kodolov and Gavrilov, 1980). Furthermore, Japanese and Hawaiian slope waters are inhabited by two sibling species (*i.e.*, *Myctophum orientale–M selenops* and *Diaphus suborbitale–D. trachops*) although the status of these as species remains controversial. *Maurolicus* had long been a monospecific genus represented only by *M muelleri*, but has recently been divided into 15 species occupying mainly slope waters throughout the world (Parin and

Kobyliansky, 1993), although some parts of their separation are still controversial. The biomass of *M. imperatorius* is substantial (Boehlert *et al.*, 1994; Sassa *et al.*, 2002b). The distribution of the same, or closely related, sibling species in the slope waters off Japan, Hawaii and the Emperor Seamount areas would be a result of transport by the Kuroshio Current and its extension. *Benthosema panamense,* off California, is closely related to *B. pterotum,* which occurs off Japan, and is one of the two slope water species presently known from the California Current region (Wisner, 1976). No mesopelagic fishes have been recorded from the Yellow Sea (Yoon, unpubl. data).

2.2 Crustacean Micronekton

The larger species of euphausiids, mesopelagic shrimps and mysids rank next to the myctophids in terms of micronekton biomass in oceanic waters (Aizawa and Marumo, 1967; Blackburn, 1968; Blackburn *et al.*, 1970; Omori, 1974a,b; Maynard *et al.*, 1975; Pearcy, 1976; Pearcy *et al.*, 1977; Hopkins and Lancraft, 1984; Nishikawa *et al.*, 2001). Nicol (2003) believes that considering the juvenile and adult euphausiids (larvae fit well in the conventional definition of plankton) as part of the plankton is one of the major impediments to the more general understanding of the biology and ecology of all species. Although larger euphausiids behave as micronekton, historically they have been studied as zooplankton, using techniques developed for animals which are orders of magnitude smaller than them.

2.2.1 Euphausiids

Euphausiids comprise the bulk of the micronekton community at most Northeast Pacific continental shelf and upper continental slope locations. The distribution and biology of Pacific euphausiids has been thoroughly described (Brinton, 1962; Ponomareva, 1963, 1990; Nemoto, 1966; Mauchline and Fisher, 1969; Gopalakrishnan, 1974; Brinton, 1975; Mauchline, 1980; Nicol and Endo, 1997; Brinton *et al.*, 2000; Everson, 2000). Fifty-six of the 86 known euphausiid species have been recorded in the North Pacific (20 to 60°N). About 48 of these species are found along the Asiatic coast and 53 of them along North American coast, but most have transpacific distributions (Table 2.4). The neritic species restricted to the western North Pacific are *Euphausia nana* (endemic), *Pseudeuphauisa sinica* (endemic), and *P. latifrons*; the species restricted to the eastern North Pacific are the neritic *Nyctiphanes simplex*, the tropical species *Euphausia distinguenda, E. eximia*, *E. lamelligera*, and *Nematoscelis gracilis* (endemic in the eastern Tropical Pacific, but having a temporal northward intrusion up to California (31°N) during warming episodes) (Baker *et al.*, 1990; Brinton *et al.*, 2000). The overall distribution range for several rare species is difficult to determine because relatively little information has been obtained for meso and bathypelagic euphausiids. For example, *Thysanopoda minyops* was described in 1987 in the California and Central Pacific regions (Brinton, 1987), and only on two other occasions has it been recorded again, most recently south of Madagascar (Casanova, 1996). *Thysanoessa spinifera* has most of its distribution in the eastern Pacific but has also been recorded in the north (50–60°N) as far as 170°E, perhaps as expatriates. Species of the genera *Bentheuphausia* and *Thysanopoda* are primarily mesopelagic and bathypelagic. Some giant individuals (total length from 120–150 mm) are considered completely nektonic, and usually display cosmopolitan or circumglobal distributions due to the absence of physico–chemical barriers to their movements (Nemoto *et al.*, 1977). However, along the continental shelf of both continents only a few species (usually no more than three, and including at least one neritic species) dominate in the abundance and biomass of those ecosystems. The maximum total length of epipelagic euphausiids in the North Pacific ranges from 7–65 mm, and 17 species reach a maximum total length usually between 20–30 mm. Most species of the genus *Thysanopoda* are usually larger than 32 mm (Baker *et al.*, 1990). However, the two species of *Pseudeuphausia,* most of the species in the genus *Stylocheiron,* and some species in the genera *Euphausia, Thysanoessa, Nematoscelis,* and *Nyctiphanes* (26 species) are all generally ≤18 mm and are, therefore, considered primarily planktonic. It is interesting to note that smaller euphausiid species, like other pelagic crustaceans, tend to be distributed in lower latitudes.

Table 2.4 List of euphausiids distributed in the North Pacific (>20°N) showing the range of latitudes recorded along the western or eastern North Pacific (Baker *et al.*, 1990; Brinton *et al.*, 2000).

Species (alphabetically ordered)	Species Authorship	Reproductive Strategy	Maturation Size (mm)	Maximum Size (mm)	Maximum Life Expectancy (y^{-1})	Western Pacific (°N)	Eastern Pacific (°N)
Bentheuphausia amblyops	G.O. Sars, 1885	Broadcast		50		< 60	< 60
Euphausia brevis	Hansen, 1905	Broadcast		10		< 40	< 40
Euphausia diomideae	Ortmann, 1884	Broadcast		16		< 40	< 30
Euphausia distinguenda	Hansen, 1908	Broadcast		15		absent	< 30
Euphausia eximia	Hansen, 1911	Broadcast		30		absent	< 40
Euphausia gibboides	Ortmann, 1893	Broadcast		26		30-50	20-50
Euphausia hemigibba	Hansen, 1910	Broadcast		14		< 40	< 40
Euphausia lamelligera	Hansen, 1911	Broadcast		11		absent	< 30
Euphausia mutica	Hansen, 1905	Broadcast		12		< 40	< 40
Euphausia nana	Brinton, 1962	Broadcast		12	< 1	20-40	absent
Euphausia pacifica	Hansen, 1911	Broadcast	12	25	<1.5 to > 2	30-60	20-60
Euphausia paragibba	Hansen, 1910	Broadcast		14		absent?	<30
Euphausia recurva	Hansen, 1905	Broadcast		14		< 40	< 40
Euphausia similis	G. O. Sars, 1883	Broadcast		26		<40	absent
Euphausia tenera	Hansen, 1905	Broadcast		9		< 40	< 30
Nematobrachion boopis	Calman, 1896	Broadcast ?		25		< 50	< 40
Nematobrachion flexipes	Ortmann, 1893	Broadcast ?		23		< 40	< 60
Nematobrachion sexspinosum	Hansen, 1911	Broadcast ?		25		< 40	< 30
Nematoscelis atlantica	Hansen, 1910	Sac spawner		15		< 40	< 40
Nematoscelis difficilis	Hansen, 1911	Sac spawner	17	26	< 2	30-50	20-60
Nematoscelis gracilis	Hansen, 1910	Sac spawner		16		absent	< 30
Nematoscelis microps	G.O. Sars, 1883	Sac spawner		20		< 50	< 40
Nematoscelis tenella	G.O. Sars, 1883	Sac spawner		20		< 40	< 40
Nyctiphanes simplex	Hansen, 1911	Sac spawner	8.8	16	< 1	absent	< 50
Pseudeuphausia latifrons	G.O. Sars, 1883	Sac spawner		16		< 40	absent
Pseudeuphausia sinica	Wang and Chen, 1963	Sac spawner		16		30-40	absent
Stylocheiron abbreviatum	G.O. Sars, 1883	Sac spawner		17		< 40	< 40
Stylocheiron affine	Hansen, 1910	Sac spawner		9		< 40	< 40
Stylocheiron carinatum	G.O. Sars, 1883	Sac spawner		12		< 40	< 40
Stylocheiron elongatum	G.O. Sars, 1883	Sac spawner		18		< 50	< 40
Stylocheiron longicorne	G.O. Sars, 1883	Sac spawner		12		< 50	< 60
Stylocheiron maximum	Hansen, 1908	Sac spawner		30		< 50	< 60
Stylocheiron microphthalma	Hansen, 1910	Sac spawner		7		< 40	< 30
Stylocheiron robustum	Brinton, 1962	Sac spawner		18		< 40	< 30
Stylocheiron suhmi	G.O. Sars, 1883	Sac spawner		7		< 40	< 40
Tesarabrachion oculatum	Hansen, 1911	Sac spawner?		26		30-60	30-60
Thysanoessa gregaria	G.O. Sars, 1883	Broadcast		17		20-50	20-50
Thysanoessa inermis	Kroyer, 1846	Broadcast	14	32	2.0	> 40	> 40
Thysanoessa inspinata	Nemoto, 1963	Broadcast		18		30-50	30-50
Thysanoessa longipes	Brandt, 1851	Broadcast	14	30	3.0	30-60	40-60
Thysanoessa parva	Hansen, 1905	Broadcast		11		30-40	20-30
Thysanoessa raschi	M Sars, 1864	Broadcast	14	25	2.0	> 30	> 40
Thysanoessa spinifera	Holmes, 1900	Broadcast	20	38	2.0	50-60	20-70
Thysanopoda acutifrons	Holt and Tattersal, 1905	Broadcast	35	50	2.0	30-50	30-60
Thysanopoda aequalis	Hansen, 1905	Broadcast		19		< 40	30-60
Thysanopoda astylata	Brinton, 1975	Broadcast		18		absent?	< 40
Thysanopoda cornuta	Illig, 1905	Broadcast		120		30-50	20-60
Thysanopoda cristata	G.O. Sars, 1883	Broadcast		65		< 30	< 40
Thysanopoda egreria	Hansen, 1905	Broadcast		62		< 20	20-50
Thysanopoda minyops	Brinton, 1987	Broadcast		124		absent?	30-40
Thysanopoda monocantha	Ortmann, 1893	Broadcast		32		< 40	< 40
Thysanopoda obtusifrons	G.O. Sars, 1883	Broadcast		23		< 40	< 40
Thysanopoda orientalis	Hansen, 1910	Broadcast		38		< 40	< 40
Thysanopoda pectinata	Ortmann, 1893	Broadcast		44		< 40	< 40
Thysanopoda spinicauda	Brinton, 1953	Broadcast		150		30-40	30-40
Thysanopoda tricuspidata	Milne-Edwards, 1837	Broadcast		25		< 40	< 30

Note: There are endemic species that are distributed only on one side of the North Pacific (absent), but several rare species have been significantly undersampled. Therefore, it is unclear whether these species really have restricted longitudinal distribution or are mostly oceanic species (absent?).

The dominant micronektonic euphausiids along the North American continental margin include *Euphausia pacifica* and *Thysanoessa spinifera* (essentially the entire latitudinal range from the Aleutian Islands to the northern part of Baja California), *T. inermis* and *T. raschi* (mostly north of 50°N), and *T. inspinata* and *T. longipes* (north of 40°N). Several species are largely confined to continental margin regions. *Nyctiphanes simplex* usually occurs south of 30°N along Baja California and Gulf of California, where close to the coast this single species accounts about 95% of the euphausiid biomass (Gómez-Gutiérrez, 1995; Gómez-Gutiérrez *et al.*, 1995; Lavaniegos, 1994, 1995). This species has been reported as far north as 46°N during 1982–83 (Brodeur, 1986) and in Canadian waters at 48°54′N during 1997–98 (Tanasichuk and Cooper, 2002), which were both extreme warming episodes (El Niño). Four additional species are either primarily (*T. inermis* and *T. spinifera*) or entirely (*T. raschi* and *N. simplex*) restricted to the continental shelf and closely adjoining deep oceans in more northern areas. Although the remaining species have much broader distributions, extending westward long distances into or across the Pacific, their highest abundance and biomass are often found along the continental shelf break and slope.

It is important to note that *E. pacifica* is, by far, the best studied euphausiid in the North Pacific, comparable with *Meganyctiphanes norvegica* in the Atlantic and *Euphausia superba* in the Antarctic. *Euphausia pacifica* has been extensively studied in most aspects of its biology and ecology, including morphology, ontogenesis, fecundity, egg and larval development, hatching mechanisms, feeding, growth, respiration, carbon utilization, excretion, swimming behavior, diel vertical migration, as prey of higher trophic predators, parasitism, population dynamics, distribution and abundance, secondary productivity, and evolution (Lasker, 1966; Smiles and Pearcy, 1971; Brinton, 1962, 1976; Johnson and Brinton, 1963; Ross, 1981; Ross *et al.*, 1982; Suh *et al.*, 1991; Iguchi and Ikeda, 1994, 1999; Iguchi *et al.*, 1993; Tanasichuk 1998a; Yamamura *et al.*, 1998; Croll *et al.*, 1998; Ju and Harvey, 2002; Taki *et al.*, 2002; Feinberg *et al.*, 2003; De Robertis, 2002a,b; De Robertis *et al.*, 2003a,b; Gómez-Gutiérrez, 2003b). This large information base, plus its ecological importance, makes *E. pacifica* an excellent species for modeling studies (De Robertis, 2002a; Goldthwait, 2004).

Euphausiid species richness increases substantially from nearshore to oceanic areas along the western and eastern Pacific coasts, usually with an abrupt increase immediately seaward of the shelf break (Gómez-Gutiérrez *et al.*, 2005). Zoogeography, vertical distribution, and speciation of euphausiids in the Pacific Ocean are well summarized by Brinton (1962, 1967, 1975) and Gopalakhrisnan (1974). Brinton *et al.* (2000) summarized information concerning all 86 euphausiid species found worldwide and provided maps of their zoogeographic distributions, including eco-phenotypes or "form" distributions. Net tows (Brinton, 1962) and baleen whale gut contents (Kawamura, 1982) provide similar pictures of large-scale distributional zonation. The latitudinal pattern generally follows the distribution of currents and water masses, while species richness decreases progressively with increasing latitude (Brinton, 1962; Johnson and Brinton, 1963). For example, along the North American coast, the number of species decreases from 30–32 between 28° and 36°N, to 17 species at 46°N, 10–12 species between 52° and 56°N, and only two species at 77°N. From north to south, the sequence of dominant oceanic species is *Thysanoessa longipes* and *T. raschi* (subarctic gyres, especially their northern portions), *E. pacifica* (subarctic gyres and TrZ, but most abundant along the boundary between the two), and *Nematoscelis difficilis* and *T. gregaria* (northern transitional, oceanic distribution centered along about 40°N). Local population densities are usually lower, by a factor of 2 to 10, than along the continental margin (Brinton, 1962) but because of the much larger total area, the open ocean populations account for the majority of total euphausiid biomass (Brinton *et al.*, 2000). Siegel (2000b) reviewed values for abundance and biomass of euphausiids, including *E. pacifica*, *N difficilis*, *T. longipes*, and *T. spinifera* in the North Pacific, estimated from net tows or acoustics.

The TrZ is between subarctic and central populations in the mid-Pacific and between subarctic and equatorial populations in the California Current System. From the euphausiid zoogeography perspective, this is regarded as a biogeographical zone because it harbors: (1) endemic species like *N. difficilis* (35–45°N), (2) bi-subtropical species, which are limited by the North Pacific to the belt that occurs on each side of the tropics (but not within them), such as *Thysanoessa gregaria* or *Thysanopoda acutifrons*, and (3) maximum densities or regions of dominance of certain species having broader total ranges, like *Euphausia gibboides*. This region changes in extension according to climatic variability at different ecological and geological time scales (Brinton, 1962). The TrZ pattern does not fit well into a hypothetical water mass–population species distribution scheme (Johnson and Brinton, 1963). Features such as rings and recirculation cells near the western edge of these domains may act to maintain seed populations against the flow which can then supply the rest of the TrZ. The system of fronts and eddies that characterize the TrZ is thought to be made up of zones of episodically enhanced productivity and might, therefore, represent an environment with high carrying capacity patches (Olson and Hood, 1994). Those populations would then supply individuals upstream to the average flow in counter-rotating eddies.

On the western side of the North Pacific, the same basic latitudinal pattern of species richness is observed, but the distribution of certain species (*e.g.*, *T. longipes* and *T. inermis*) is displaced somewhat farther southward. The main differences in species composition are that *N. simplex* is absent on the western side, *T. spinifera* is mostly distributed in the eastern side with a eastern distribution limit of 70°E restricted between 50° and 60°N, and *Euphausia nana*, *E. similis*, *Pseudeuphausia latifrons* and *P. sinica* occur within the North Pacific only in the Kuroshio Current and adjoining regions. In the Okhotsk Sea, *T. longipes* and *T. inermis* are relatively abundant, followed by *T. raschi*. *Euphausia pacifica* is found only in the southern part of the Okhotsk Sea (Ponomareva, 1963). In the Japan/East Sea, ten species of euphausiids have been recorded (Endo and Komaki, 1979), but most of these are transported into the southern part of the Japan/East Sea by the warm Tsushima Current. The exceptions are *E. pacifica* (dominant over all areas), *T. longipes* (offshore waters), and *T. inermis* and *T. raschi* (neritic waters), which are all dominant species in the northern part of the Japan/East Sea.

In the Kuroshio Current region, including the East China Sea, 49 species of euphausiids have been recorded. *Euphausia nana* and *P. latifrons* are the major species on the continental shelf side in the East China Sea, while *E. nana* and *E. similis* dominate off southern Japan (Hirota, 1995). Hong (1969) reported ten species of euphausiids in Korean waters, including *E. pacifica*, *E. nana*, *P. latifrons*, *E. mutica*, *E. recurva*, *E. similis*, *E. tenera*, *T. longipes*, *Stylocheiron ăffine*, and *S. carinatum*. The first three of these were the dominant species, while the latter were associated mainly with the influx of the Tsushima Current and observed only sporadically.

The NAGA Report of Brinton (1975) does not include information from Korea and the Yellow Sea, showing the distributions of all the euphausiids southward and off the east coast of Japan, due to lack of sampling in those areas. Further studies like Suh (1990) recorded *Pseudeuphausia sinica* for the first time in the coastal waters of southwestern Korea. Cai (1986) collected 15 species in the southern Yellow Sea and the East China Sea, among which *E. pacifica*, *E. nana*, *P. sinica*, and *P. latifrons* were the most abundant species. *Euphausia pacifica* and *E. nana* dominated during spring and summer, *E. nana* and *P. latifrons* in autumn, and *E. pacifica* and *P. sinica* dominated in winter. In the central and eastern Yellow Sea, four species of euphausiids have been recorded, including *E. pacifica*, *E. sanzoi*, *P. latifrons* and *S. ăffine* (Yoon *et al.*, 2000). *Euphausia pacifica* dominated the euphausiid community throughout the year, representing in some locations within its distribution range more than 95% of the total. *Pseudeuphausia latifrons* was observed intermittently in the eastern coastal area along the Korean Peninsula, and in the southeastern area, *E. sanzoi* and *S. ăffine* were rarely collected, their temporal distribution seemingly related to the influx of the East China Sea water into the Yellow Sea. The distribution of adult *E. pacifica* was determined exclusively by temperature while larval distribution was affected by both temperature and chlorophyll *a* concentration. The seasonal appearance of Yellow Sea Cold Bottom Water seemed to regulate the distribution of *E. pacifica*. Interestingly, *E. pacifica* of the Yellow Sea showed genetic differences from its congeners of the East (Japan) Sea and the California Current (Yoon, unpubl. data).

2.2.2 Mysids and decapods

Among the non-euphausiid crustaceans, large-scale distribution patterns have been analyzed for pelagic decapods (Krygier and Wasmer, 1988) and mysids (Mauchline, 1980; Krygier and Murano, 1988). Recent studies have compared species diversity, zoogeography, and vertical distribution of these groups in four geographic regions of the North Pacific (Nishikawa *et al.*, 2001; Toczko *et al.*, unpubl. MS).

Mysids have been shown to be particularly abundant in neritic regions and commonly dominate estuaries and shallow regions where they play an important role as a key link between benthic and pelagic systems in neritic food chains (Mauchline, 1980; Wortham-Neal and Price, 2002). Thus, few species can be considered truly micronektonic. Dominant species include *Gnathophausia gigas*, *Boreomysis californica*, and *Eucopia girmaldii* (Krygier and Wasmer, 1988; Toczko *et al.*, MS). Mysid biomass is highest (and diversity lowest) in the Bering Sea, while biomass and diversity are similar in both the western and eastern subarctic. Dominant decapod crustaceans include *Hymenodora frontalis*, *H. gracilis*, *Sergestes similis*, and *Bentheogennema borealis* which comprise about 80% of the total biomass and number of nektonic pelagic decapods (Krygier and Wasmer, 1988; Toczko *et al.*, unpubl. MS). Peak biomass of decapods occurs in the western subarctic Pacific, but is not significantly different from the eastern subarctic Pacific, and is associated with warm temperatures and high chlorophyll *a* concentrations. Species diversity is highest in the eastern subarctic and lowest in the Bering Sea. Wicksten (2002) provides zoogeographic distribution information for 43 species of midwater shrimp in the Northeast Pacific Ocean. She notes that the midwater shrimps generally have much broader distributions and a lower level of endemism than do demersal shrimp species. Aizawa (1974) and Krygier and Wasmer (1988) described 27 and 31 species of pelagic decapods, respectively, from the western subarctic Pacific, most belonging to the families Sergestidae and Penaeidae. Eight species were described as trans-subarctic. In addition, Aizawa (1974) reported no distinct seasonal biomass fluctuations in his trawl samples, collected from 1964 to 1968. A literature review by Krygier and Murano (1988) reported the distribution of 31 species of pelagic mysids in the subarctic North Pacific (from a total of 56 mysid species), 11 of which were described as cosmopolitan in distribution. From all the mysids recorded in the North Pacific, 29 species are restricted to the Northeast Pacific, nine are cosmopolitan, eight are circumpolar, and six are common to the northern North Pacific. Kikuchi and Nemoto (1986) collected 88 species of pelagic shrimps at just seven stations off the coast of Japan, which suggests a higher diversity in the western Pacific Ocean than elsewhere.

In the southern part of the California Current System, the pelagic crab *Pleuroncodes planipes* (Galatheidae) forms very high concentrations (>30 individuals m^{-3} and an estimated biomass of about 7.8×10^5 metric tons) along the Baja California peninsula, and extends its northward distribution during El Niño events (Smith, 1985; Aurioles-Gamboa, 1992; Thompson *et al.*, 1993; Gómez-Gutiérrez *et al.*, 2000). During the strong El Niño of 1997–1998, several mass strandings of this crustacean were observed along central California (Gómez-Gutiérrez, unpubl. data). This is perhaps the only benthopelagic galatheid species of sufficient abundance to be considered a key trophic species in upwelling regions, with the potential to support a commercial fishery in the North Pacific for biotechnological applications in aquaculture and human food additives.

2.3 Cephalopod Micronekton

Zoogeographical patterns of pelagic micronektonic cephalopods in the North Pacific can be determined from a collection of regional studies. For the marginal seas around the basin rim (Nesis 1973), cephalopod fauna have been reported for waters in the Northwest Pacific and around Japan (Okutani, 1968; Kubodera and Furuhashi, 1987; Okutani *et al.*, 1987; Ivanov, 1997; Shevtsov and Mokrin, 1998), the Bering Sea (Jefferts, 1988; Radchenko, 1992; Sinclair *et al.*, 1999), the Okhotsk Sea (Lapko, 1995), the subarctic (Okutani *et al.*, 1988; Kubodera and Jefferts, 1984), the Northeast Pacific and Gulf of Alaska (Jefferts, 1983, 1988), and the eastern Pacific, including the California Current System (Young, 1972; Okutani, 1974; Savinykh, 1999). In the central North Pacific Gyre, cephalopods occupying subtropical waters in the vicinity of the Hawaiian Islands (Berry, 1912; Young, 1978), and the subarctic–subtropical TrZ and associated frontal systems have been documented (Seki, 2001). For convenience, we present individual species distributions under the appropriate familial classification below.

For most of the cephalopod families encountered in the micronekton, it is the juvenile and subadult forms that are typically represented in net sampling, and in the diets of higher-level predators. For example, in boreal waters juvenile and subadult forms of the family Gonatidae dominate the cephalopod component of the micronekton (Jefferts, 1988) and represent key forage species for numerous fishes, seabirds, and marine mammals (Okutani *et al.*, 1988; Pearcy *et al.*, 1988). Young squid of the family Ommastrephidae play a similar role in the pelagic subtropical central and eastern Pacific (Harrison and Seki, 1987; Seki, 1993; Young and Hirota, 1998; Bower *et al.*, 1999). Alternatively, in all tropical, subtropical, and transitional waters of the North Pacific, squids of the families Enoploteuthidae and Pyroteuthidae are generally the most abundant and frequent components of the micronekton squid fauna. With most adults attaining dorsal mantle lengths (DML) <60 mm, all stages of development, from paralarvae to adult, are common in the micronekton.

2.3.1 Family Enoploteuthidae

Seventeen enoploteuthid squid species from four genera inhabit the various regions of PICES interest; these include five species of *Enoploteuthis*, five species of *Abralia*, seven *Abraliopsis*, and one *Watasenia*. The taxonomy and biogeography of the species in this diverse family are detailed by McGowan and Okutani (1968), Burgess (1982, 1991), Riddell (1985), Tsuchiya (1993), Tsuchiya and Okutani (1988, 1990), Young (1972) and Young and Harman (1985). In the case of *Abraliopsis*, we adopt the nomenclature and reference to the squid species reported in Young (1978). Two species, *Abraliopsis felis* and *Watasenia scintillans* are, in particular, key components of the respective ecosystems that they occupy.

In the central North Pacific, *A. felis* is the most common and abundant micronektonic squid. Latitudinally, it occurs from the boreal waters of the Subarctic Domain to waters through the TrZ to the southern limits of the Subtropical Frontal Zone but is completely absent in the Subtropical Domain (Seki, 2001). Zonally, *A. felis* is found in the Japan/East Sea and exhibits a continuous distribution across the basin to the California Current. However, this species is uncommon in the western Pacific Ocean (Ivanov, 1997), whereas it is dominant (56% of the total cephalod biomass) in the California Current (Savinykh, 1999). Attaining a maximum size of about 60 mm DML, a general shift was observed in its size frequency distribution, from slightly larger squid being taken in the more northern provinces to smaller sizes taken in the south, particularly across the SAB (Seki, 2001). Two other species of *Abraliopsis*, *A. pacificus* and *Abraliopsis* sp. *A* are principally subtropical species, but have distributions extending through the Subtropical Front into the southern TrZ. The remaining species of *Abraliopsis* are restricted to subtropical waters.

Enoploteuthis chunii is common in shelf waters between 23° and 40°N latitudes around Japan and in western Pacific waters west of 160°E longitude (Tsuchiya, 1993) and is also occasionally found in the central North Pacific within the nominal bounds of the TrZ. The other *Enoploteuthis* species, *E. higginsi, E. jonesi*, and *E. reticulata*, occur only in subtropical waters to the south of the Subtropical Frontal Zone. *Enoploteuthis higginsi* is widely distributed in the tropical Indo-Pacific, but not in the eastern Pacific (Tsuchiya, 1993). *Enoploteuthis reticulata* is considered to be a pan-tropical to subtropical Indo-Pacific species, and the most widespread species among the genus *Enoploteuthis* (Tsuchiya, 1993). *Enoploteuthis jonesi* is distributed in the Central Pacific, Hawaiian waters, and equatorial regions (Burgess, 1982), and is believed to be a mesopelagic boundary species (Bower *et al.*, 1999; Seki, 2001).

Several species of *Abralia* are thought to exhibit varying degrees of topographic fidelity. *Abralia multihamata* and *A. andamanica* are occupants of the shelf waters of Japan north to Sagami Bay (Tsuchiya, 1993) and the adult *A. trigonura* is recognized as a member of the Hawaiian mesopelagic boundary community (Reid *et al.*, 1991; Bower *et al.*, 1999). *Abralia similis* is found in the western TrZ, while *A. astrosticta* occurs in the warm waters of the subtropical Northwest and Central Pacific. Around Hawaii, evidence suggests that *A. astrosticta* is also associated with the ocean bottom.

Watasenia scintillans is the most abundant enoploteuthid in the western TrZ and it undertakes feeding migrations into the northwestern Japan/East Sea (Shevtsov and Mokrin, 1998), the southern Okhotsk Sea, and Pacific waters off the Kuril Islands (Ivanov, 1997). Recent Russian studies have shown that the proportion of the total nekton biomass in the western TrZ made up by *W. scintillans* can vary dramatically, from as high as approximately 40% in November 2001 to as low as about 1% in July 2002.

2.3.2 Family Gonatidae

Squids of the family Gonatidae are cold water species (Okutani *et al.,* 1988) and account for the majority of cephalopods in the subarctic Pacific. Seventeen species of Gonatidae are found as juveniles and subadults in regions of PICES interest.

Across the subarctic Pacific, species such as *Gonatus onyx*, *G. madokai*, *Gonatus* sp. *A.*, *Gonatopsis borealis*, and *Berryteuthis magister* dominate the squid micronekton. However, all members of the family Gonatidae do not occur uniformly across the subarctic Pacific. *Gonatus middendorffi*, *Eogonatus tinro*, *Gonatopsis makko*, and *G. okutanii* are found principally in the western subarctic. Restricted to the eastern subarctic are *Gonatus berryi*, *G. pyros*, *G. californiensis*, *G. ursabrunae*, *G. oregonensis*, and *Berryteuthis anonychus* (Okutani *et al.*, 1988). In the Bering Sea, *Eogonatus tinro*, *Gonatopsis borealis,* and *B. magister* are the dominant species (Sinclair and Stabeno, 2002). *Gonatopsis borealis* has the most extensive north–south distribution, extending well into the TrZ near the subtropics (Young, 1972; Seki, 2001).

2.3.3 Family Onychoteuthidae

Squids of the family Onychoteuthidae are taken throughout the subarctic through to the subtropical Pacific, with the most abundant, and frequently encountered, belonging to the genus *Onychoteuthis*. Five species of *Onychoteuthis* are presently recognized in the North Pacific: *O. borealijaponica*, *O. compacta*, *Onychoteuthis* sp. *B*, sp. *C*, and sp. *D* (Kubodera *et al.*, 1998; Seki, 2001). With the exception of *O. borealijaponica*, which is commonly found in higher latitudes, and *Onychoteuthis* sp. *D*, a TrZ endemic, most *Onychoteuthis* species tend to be found in tropical and subtropical waters of the world oceans (Seki, 2001).

Young *O. borealijaponica* have been caught in the temperate, northern TrZ waters, and southward along the California Current; adults tend to occupy waters farther to the north of the SAB. *Onychoteuthis* sp. *D* is found throughout the subarctic–subtropical TrZ but appears to be limited to the north by the SAB. The length frequency distributions of the two transitional–temperate *Onychoteuthis* species show clear latitudinal trends, with larger animals being collected at higher latitudes (Seki, 2001). This trend for *O. borealijaponica* supports the south spawning–north feeding migration pattern proposed by Kubodera (1986). Distribution trends observed for *Onychoteuthis* sp. *D* suggest a similar and spatially complementary pattern.

Onychoteuthis compacta and *Walvisteuthis cf. rancureli* are found throughout the region from waters adjacent to the Hawaiian Ridge into the TrZ. *Onychoteuthis* sp. *C* was captured only at sampling stations positioned closest to the Hawaiian Archipelago Islands, and has been designated as an island-associated species (Bower *et al.*, 1999). *Onychoteuthis* sp. *B*, sp. *C* and *Onykia carriboea* have been reported only from the subtropics; all specimens have been paralarval and/or juvenile forms of the respective species.

2.3.4 Family Pyroteuthidae

Like the Enoploteuthidae, members of the Pyroteuthidae appear in the micronekton throughout their ontogenetic development from paralarvae to adult. Four species (from two genera) of Pyroteuthidae are found in the North Pacific: *Pyroteuthis addolux*, *Pterygioteuthis giardi*, *P. microlampas*, and *P. gemmata*. *Pyroteuthis addolux* is the only species of the genus that occurs in the North Pacific, although its considerable meridianal range leads one to wonder whether more than one species is present. *Pterygioteuthis giardi* and *P. microlampas* are two of the three species of this genus occurring in the North Pacific, the other being *P. gemmata* which, in the North Pacific, occupies waters in the eastern Pacific off the southern coast of California. Detailed taxonomic descriptions for all three species are presented in Riddell (1985).

The extensive distribution currently recognized for *P. addolux* stretches latitudinally from subtropical waters south of the Hawaiian Islands through the TrZ and bounded to the north by the Subarctic Boundary (Jefferts, 1988; Seki, 2001), and westward into the California Current. *Pyroteuthis addolux* collected at more southerly stations have tended to be slightly smaller than those sampled farther north, however, there have been no obvious differences in systematic characters of individuals from extremes of the range.

Pterygioteuthis giardi and *P. microlampas* are similar in size and both are frequently caught in small numbers throughout the Subtropical Domain although their distributions appear to be bounded to the north by the Subtropical Front in the California Current (Savinykh, 1999).

2.3.5 Other cephalopods

A number of other species warrant mention when discussing the cephalopod component of the North Pacific micronekton. As adults, squids of the family Ommastrephidae, particularly *Ommastrephes bartramii* and *Todarodes pacificus*, are among (if not the most) commercially important North Pacific squid resources, and represent keystone species in the ecosystems that they inhabit (Murata, 1990). However, the role of these species, as juveniles in the micronekton, is poorly understood. On the other hand, *Sthenoteuthis oualaniensis* appears nearly ubiquitous in the subtropical open ocean waters and is a key ecosystem component as a predator of micronekton, and as the primary prey for seabirds, fishes, and cetaceans (Young and Hirota, 1998).

During large-scale faunal surveys in the central North Pacific, *Chiroteuthis calyx* (family Chiroteuthidae), *Mastigoteuthis pyrodes* (family Mastigoteuthidae), *Galiteuthis phyllura*, *Taonius borealis*, and *Megalocranchia abyssicola* (family Cranchiidae) were among the most numerically abundant cephalopods in the TrZ to the subarctic; *Cranchia scabra* (family Cranchiidae) was most abundant in the subtropics (Seki, 2001). Unlike the squid species mentioned thus far, these species are generally characterized by weak musculature, are neutrally buoyant, and are readily sampled in deeper water during the day.

3. Vertical Distribution Patterns

3.1 Mesopelagic Fishes

3.1.1 Significance of diel vertical migration

The most remarkable biological and ecological feature of mesopelagic fishes is their diel vertical migrations (DVM). Despite this feature, there remain considerable gaps in our knowledge of species-specific patterns. This information is needed in order to understand the feeding habits of these species, their impact on zooplankton biomass, their role as prey of other large nektonic animals, and their life history strategies. DVM in this report is defined as a diel vertical migration between the mesopelagic and epipelagic zones.

DVM has been regarded as an upward feeding migration from the mesopelagic zone into the productive epipelagic zone. However, nighttime feeding in the epipelagic zone is also an adaptive response to escape from visual epipelagic predators such as larger fishes, squids, sea birds, and marine mammals (although the light organs of many micronektonic fishes might actually increase their vulnerability at night). From the viewpoint of ecosystem research, the ecological importance of mesopelagic fishes in oceanic ecosystems is of interest because of the huge biomass of vertical migratory species. Non-migrants such as genus *Cyclothone* (Gonostomatidae) and *Stenobrachius nannochir* (Myctophidae) can also represent considerable mesopelagic biomass. Their ecological significance, however, may be lower than that of the vertical migrants since, based on their restricted daily ration, their productivity is believed to be extremely low (Moku *et al.*, 2000).

3.1.2 DVM patterns

Most myctophids and some sternoptychids (genus *Maurolicus*) and phosichthyds (genus *Vinceguerria*) do not initiate DVM until after metamorphosis from larvae to juveniles. Recently, the migration patterns of some common myctophids have been documented from the transitional waters of the western North Pacific (Watanabe *et al.*, 1999). According to their criteria, DVM patterns are categorized into five types (Fig. 3.1). The first two types include the migrants in which day and night habitat depths are usually separated. Slope water species show both vertical and horizontal migration to the shallow coastal waters at night (Reid *et al.*, 1991).

Type 1. Surface migrant

Fishes of this group are commonly collected at the surface by nighttime neuston net sampling (Ogawa, 1961; Kawaguchi *et al.*, 1972; Watanabe and Kawaguchi, 2003b) or dip-netting from the side of a ship. They are rarely collected in oblique tows or by neuston nets towed from the stern. Observations at sea suggest that they are good swimmers and sometimes jump into the air to escape predation by squids. Their abundance has almost certainly been underestimated because of their ability to escape from the ship's bow wave or wake. Moreover, the lower limit of their nighttime depth range is not well known, making it even more difficult to estimate their biomass.

Type 2. Midwater migrant

Members of this group rarely occur in neuston samples, but are common in samples taken at night in the epipelagic zone below 15–20 m depth. Their DVM patterns are not well depicted in relation to physical oceanographic structures at the species level. It is possible that ecological factors, such as resource partitioning, may be a key factor controlling their DVM patterns.

Type 3. Semi-migrant

In this group, part of the population often remains at depth at night, resulting in a bimodal vertical distribution. This type of behavior is known only from *Stenobrachius leucopsarus* and *Leuroglossus schmidti,* which are most abundant in the SAW and TrW (Paxton, 1967a; Pearcy *et al.*, 1977; Frost and McCrone, 1979; Watanabe *et al.*, 1999). In the Bering Sea, both species are known to cease DMV during winter, suggesting a trade-off between prey abundance in the epipelagic zone and the energy cost for DVM.

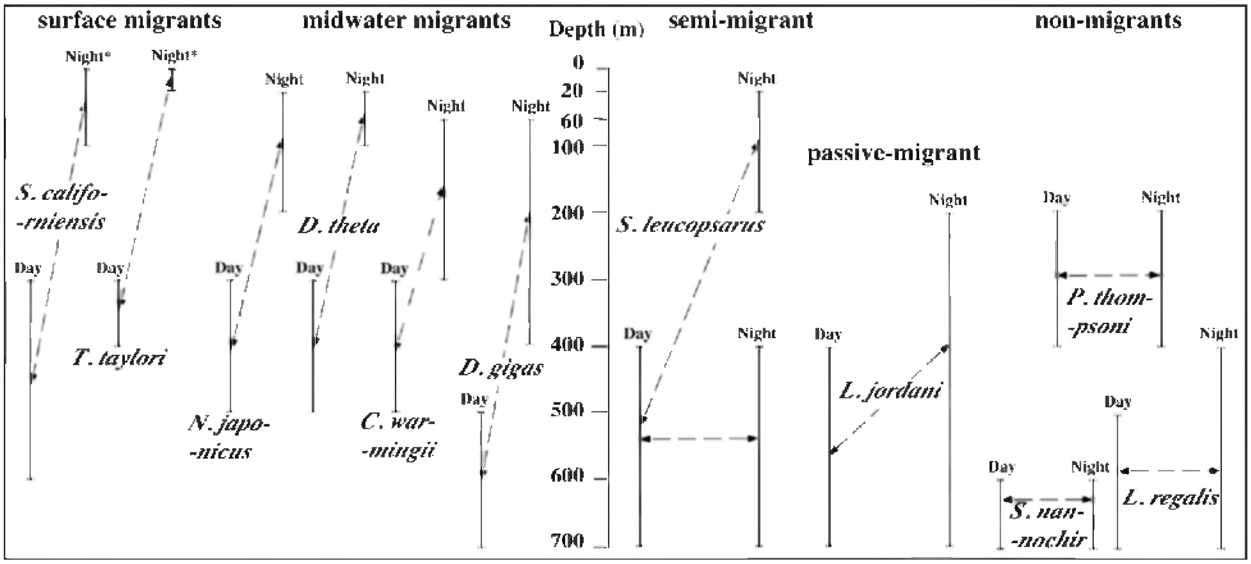


Fig. 3.1 Diel vertical migration patterns of myctophid fishes in transitional waters of the western North Pacific off Japan. (taken from Watanabe *et al.*, 1999) The layers in which more than 75% of the total catch was recorded are indicated as the habitat depth; * denotes surface migrants according to Ogawa (1961) and Kawamura and Fujii (1988).

Type 4. Passive-migrant

The upper limit of distribution expands upward at night in this group, probably as a result of following vertically migrating prey, such as euphausiids. There is no clear day–night habitat separation for this type.

Type 5. Non-migrant

After metamorphosis from larva to juvenile, the fishes of this group stay in the same depth range both day and night, although juveniles tend to be distributed in shallower depths. Off California, *N. regalis* of 31–118 mm SL are known to undertake DVM between the 50–100 m and 700–750 m depth layers (Paxton, 1967b), while a non-migratory population in the western Pacific is composed of the specimens larger than 140 mm SL, suggesting that the change in DVM pattern with growth is probably related to a shift in prey size (Watanabe *et al.*, 1999).

The vertical migratory myctophids include both eurythermal and stenothermal species. Surface migrants are usually eurythermal, adapting to the wide range of temperatures from surface to the mesopelagic zone, while midwater-migrants, semi-migrants, and non-migrants are restricted to the narrower temperature range (Fig. 3.2; Watanabe *et al.*, 1999). DVM patterns of the common species listed in Tables 2.1, 2.2, and 2.3 are summarized in Table 3.1, based on present knowledge, although the patterns are often modified by physical factors, such as water temperature and light. In the western TrZ, it is known that warm-core rings and streamers derived from the Kuroshio waters crossing the Kuroshio Front depress the nighttime migration depth of subarctic and TrW species (Watanabe *et al.*, 1999). These results suggest a possible seasonal change in the DVM patterns in those regions where marked seasonal temperature change is expected and/or ice covers the sea surface (*e.g.*, the Bering and Okhotsk Seas). No seasonal variations in vertical distributions and migrations have been detected for any species in the eastern Pacific TrW (Pearcy and Laurs, 1966). The distribution and DVM patterns in comparable water masses are known to be similar for SAW and TrW species between the eastern and western Pacific TrW (Paxton, 1967a; Pearcy *et al.*, 1977; Watanabe *et al.*, 1999). Biological factors such as prey availability may also be important in defining DVM patterns, especially in highly productive areas (*e.g.*, slope waters and over seamounts, such as those found in the Bering Sea) during winter, when the most of the zooplankton biomass is concentrated in the layer deeper than 100 m depth.

DVM within the lower mesopelagic zone below 500 m depth has been suggested for some species that are considered non-migrants or passive migrants in Table 3.1 (Willis and Pearcy, 1980; Willis and Pearcy, 1982), but detailed analysis of this migration remains for future study.

3.1.3 Ontogenetic change in DVM patterns

In general, the depth range of DVM is known to shift deeper with age in species, such as *S. leucopsarus*, *Diaphus theta* and *Protomyctophum thompsoni* (Frost and McCrone, 1979). Juveniles are known to occur at shallower depth layers, compared to adults, during the daytime (Clarke, 1973). For some species like *Nannobrachium regale*, *Sigmops gracile*, *S. elongatum*, and probably most species of *Lampadena*, the juveniles initially undergo active DVM. As they get older, however, DVM behavior gradually ceases. All myctophid, gonostomatid and bathylagid larvae are distributed in the epipelagic zone prior to metamorphosis. Most known species of myctophids (at least 15 species in the subtropical western Pacific and three species in the eastern North Atlantic) undergo metamorphosis in the mesopelagic zone between 300–900 m depth (Badcock and Merrett, 1976; Loeb, 1979a; Clarke, 1973; Sassa, 2001), with the exceptional of some species of myctophids in the genus *Diaphus*, which are reported to start DVM from the metamorphosis stage (Sassa, 2001).

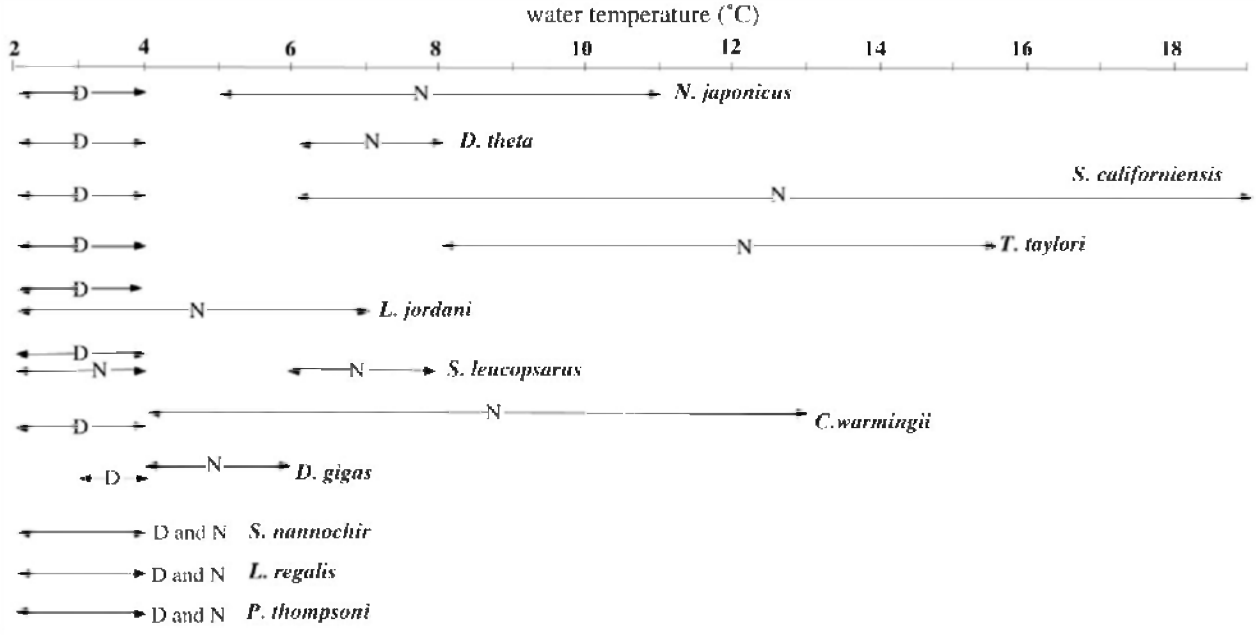


Fig. 3.2 Temperature ranges of the daytime (D) and nighttime (N) habitats of 11 myctophid species off Japan (Watanabe *et al.*, 1999). Surface migrants (*Symolophorus californiensis* and *Tarletonbeania taylori*) are very eurythermal and the temperature difference between the day and night habitats is 14–17°C, while nonmigratory species such as *Stenobrachius nannochir* and *L. regalis*) are very stenothermal and found in water at 2–4°C throughout the day.

Table 3.1 Diel vertical migration (DVM) patterns of the common mesopelagic fishes belonging to the families Myctophidae, Gonostomatidae, Sternoptychidae, Phosichthydae, and Bathylagidae in the North Pacific Ocean.

DVM Pattern	Subarctic and Transitional Water Species	Subtropical and Tropical Water Species	Slope Water Species
Surface migrants	Myctophidae *Tarletonbeania taylori* *Tarletonbeania crenularis* *Symbolophorus californiensis*	Myctophidae *Myctophum nitidulum* *Myctophum asperum* *Myctophum spinosum* *Hygophum reinhardti* *Hygophum proximum* *Centrobranchus brevirostris* *Symbolophorus evermanni*	Myctophidae *Myctophum orientale* *Myctophum brachygnathos* *Myctophum selenops*
Midwater migrants	Myctophidae *Diahus theta* *Nannobrachium regale* (<140 mm SL only) *Notoscopelus japonicus* Bathylagidae *Lipolagus ochotensis* *Leuroglossus schmidti* *Leuroglossus stilbius*	Myctophidae *Notolychnus valdiviae* *Notoscopelus resplendens* *Ceratoscoperus warmingi* *Ceratoscoperus townsendi* *Lobianchia gemellari* *Diaphus schmidti* *Diaphus fulgens* *Diaphus kuroshio* *Diaphus perspicillatus* *Lampadena luminosa* *Lampadena urophaos* *Lampanyctus alatus* *Lampanyctus steinbecki* *Triphotrus mexicanus* *Notoscopelus caudispinosus* *Bolinichthys photothorax* *Benthosema suborbitale* *Diogenichthys atlanticus* *Diogenichthys laternatus* Bathylagidae *Dolycholagus longirostris* Gonostomatidae *Gonostoma atlanticum* *Sigmops elongatum* Phosichthydae *Vinceguerria nimbaria* *Vinceguerria poweriae*	Myctophidae *Diaphus adenomus* *Diaphus chrysorhynchus* *Diaphus watasei* *Diaphus suborbitalis* *Diaphus gigas* *Diaphus trachops* *Benthosema pterotum* *Benthosema panamense* *Benthosema fibulatum* *Idiolychnus urolampus* Sternoptychidae *Maurolicus japonicus* *Maurolicus imperatorius*
Semi-migrants	Myctophidae *Stenobrachius leucopsarus* *Lampanyctus ritteri* Microstomatidae *Leuroglossus schmidti*		
Passive migrants	Myctophidae *Lampanyctus jordani* Microstomatidae *Lipolagus ochotensis*	Gonostomatidae *Sigmops gracile*	
Non-migrants	Myctophidae *Stenobrachius nannochir* *Protomyctophum crockeri* *Protomyctophum thompsoni* Microstomatidae *Pseudobathylagus milleri* *Bathylagus pacificus*	Gonstomatidae *Cyclothone* (all species)	

3.2 Crustacean Micronekton

The massive pan-oceanic DVM of the zooplankton and micronekton community is one of the most prominent characteristics in the short-term biomass variability in the pelagic ecosystem. Considerable debate has taken place about the ultimate (long-term) and proximate (immediate) factors controlling this behavior. The most generally accepted hypothesis is that DVM is a trade-off between food intake and risk of predation by planktivorous fish. Euphausiids occupy poorly illuminated habitats during the day to reduce the probability of detection and attack by visual predators, but at the cost of decreased net energy gain. Thus, smaller, less vulnerable euphausiids should ascend into food-rich surface waters earlier and descend later than larger, more conspicuous organisms (De Robertis, 2002a,b; De Robertis *et al.*, 2003a). However, daytime predation mortality may not be negligible. Myctophids are mesopelagic low-light-adapted predators, and they may prey on euphausiids during the day when the euphausiids reach deeper waters. Euphausiids are particularly exposed to top predators when they form surface swarms during the day, apparently associated with reproduction. This is particularly noteworthy for *Thysanoessa spinifera* in central California (Smith and Adams, 1988) and *Nyctiphanes simplex* in the Gulf of California, although surface swarms also have been observed along the Pacific coast of Baja California (Gendron, 1992). Surface swarms have been reported for *Euphausia pacifica* (Kotori, 1995) and *E. nana* (Hanamura *et al.*, 2001) in Japan, however, Endo *et al.* (1985) did not associate reproduction with the surface swarms of *E. pacifica* in the Japan/East Sea.

The early ontogenetic, vertical distribution is partially dependent on the euphausiid reproductive strategy. In broadcast spawners, the initial locations (maximum spawning depth) of newly produced eggs should be identical to those of their mothers at the moment of spawning, but only for a short period (perhaps few hours) due to extensive female DVM. The eggs behave as passive, sinking particles. The overall result is an imperfect match between cross-shelf distributions of euphausiid eggs and mature females which, in coastal waters, may cause a cross-shelf age segregation with the bulk of larvae standing stock distributed near the coast, and most of the juveniles and adults distributed far offshore (Gómez-Gutiérrez *et al.*, 2005). For sac-spawning species, the mismatch of larvae distribution *versus* juvenile and adult distribution occurs after hatching because the embryos develop inside the ovigerous sac (Gómez-Gutiérrez, 2003a). Currently, most juvenile and adult euphausiids are considered macrozooplankton or micronekton which drift with the currents; these crustaceans are capable of migrating hundreds of meters vertically during circadian cycles (Nicol, 2003). The DVM of euphausiids is regulated by complex behavioral patterns modulated by a suite of potential exogenous (*e.g.*, light, temperature, gravity, oxygen, mixing layer, prey and predators, and inter- and intra-specific competition) and endogenous factors (*e.g.*, sex, age, physiology, biological rhythms, and metabolism rates). Because different euphausiid life stages have different vertical distribution patterns and swimming capabilities, they are also expected to have distinct zonation patterns. This is particularly evident in nearshore regions where coastal spawning areas and juvenile recruitment are significantly separated by intense larval drift and local current circulation (Gómez-Gutiérrez *et al.*, 2005).

Euphausiids are completely planktonic as larvae, but become micronektonic when they are juveniles and adults (Nicol, 2003). Euphausiids undergo DVM as juveniles and adults, moving close to surface during the night to feed in the productive euphotic zone before migrating back down to deeper waters during the day (Ponomareva, 1963; Brinton, 1967; Brinton and Wyllie, 1976; Youngbluth, 1976). The best studied euphausiid species is probably *E. pacifica,* the subject of a considerable number of publications on its distribution range, most of which were recently summarized by De Robertis (2002a,b), De Robertis *et al.* (2003a), and Nakagawa *et al.* (2003). The vertical range of DVM in this species varies with size and water clarity, but is typically more than 100 m depth (Brinton, 1967). Over continental shelves, daytime depth may be at or very near the seabed, which poses additional sampling problems. This near bottom biomass concentration of *E. pacifica* and *N. simplex* along the west coast of Baja California has also been recognized as an important food source for demersal predators (Robinson and Gómez-Gutiérrez, 1998a), and may represent an important link between epibenthic and pelagic communities. Iguchi and Ikeda (2004) reported the vertical distribution, population structure, and life history of *Thysanoessa longipes* in the central Japan/East Sea. This species is present throughout a broad bathymetric layer (<1000 m depth) with peak abundance at 30–300 m during the night and 150–500 m during the day. This species shows a clear trend of larger specimens occurring at deeper depths. In the western Pacific, long-distance vertical migrants, the *Euphausia* species, showed clear nocturnal feeding habits. The non-migrant and short-distance vertical migrants, the *Stylocheiron* and *Pseudeuphausia* species, did not exhibit clear diurnal feeding rhythms. Layers at which maximum stomach fullness of the *Nematoscelis* and *Stylocheiron* species occurred were both the epipelagic and mesopelagic zones, whereas maximum stomach fullness of the *Euphausia* species occurred only in the epipelagic zone. In the *Euphausia* species, the depth of high stomach fullness corresponded to the maximum chlorophyll layer (Hirota and Nemoto, 1990).

Horizontal spatial distribution is intensely patchy at a variety of scales. At somewhat larger scales (1–10 km cross-shore, 10–100 km alongshore), there is a clear association of high euphausiid biomass with bathymetric edges, and with shelf-edge currents and upwelling plumes. Very dense swarms (abundances $>10^3$ m^{-3}), with a diameter about 10–100 m, are occasionally observed at the sea surface during daylight, providing highly aggregated feeding opportunities for predators that can visually detect them.

Although there is no evidence that any euphausiid species consistently exhibits a reverse DVM pattern (*i.e.*, up by day, down by night), several species do regularly form daytime surface aggregations for behavioral, feeding, and reproductive purposes. For example, in the western Pacific (Japan/East Sea) *E. pacifica* commonly forms dense daytime surface swarms that facilitate the commercial exploitation of this species, while daytime surface swarms of *E. pacifica* are less common along the North American coast (Nicol and Endo, 1997). However, daytime surface swarms have been commonly observed in highly abundant neritic euphausiids like *T. spinifera*, *Pseudeuphausia latifrons* and *N. simplex* (Smith and Adams, 1988; Gendron, 1992; Wilson *et al.*, 2001, 2003). Euphausiids can swim at speeds ranging from 1 to 4 cm s^{-1} (Lasker, 1966), but dense scattering layers of *E. pacifica* and *N simplex* migrate at speeds ranging between only 0.3 and 0.7 cm s^{-1} (Robinson and Gómez-Gutiérrez, 1998a). The swimming behavior of euphausiids (either as individuals or as swarms) makes them particularly difficult to sample, and to understand the ultimate driving forces of the DVM in a given location (Brinton, 1967; Nicol, 2003).

Like myctophids, mesopelagic shrimps and mysids are categorized into migratory and non-migratory groups based on their DVM patterns (Foxton, 1970a,b; Aizawa, 1974; Omori, 1974a; Heffernan and Hopkins, 1981; Krygier and Pearcy, 1981; Kikuchi and Omori, 1985; Krygier and Murano, 1988; Toczko *et al.*, unpubl. MS). With the exception of the epipelagic penaeid decapod *Sergestes similis*, the dominant decapod and mysid species are mesopelagic and are only rarely found above 400 m during the day or night. The biology and ecology of shrimps of the genus *Sergestes,* including growth, morphology, feeding, larval and postlarval development, DVM, and population dynamics (Pearcy and Forss, 1969; Nemoto, 1970; Judkins and Fleminger, 1972; Walters, 1976; Frost and McCrone, 1979; Omori, 1979; Omori and Gluck, 1979; Cowles, 2001) are among the most well known and studied. Much less is known about the biology of other pelagic decapod species in the North Pacific. Maynard *et al.* (1975), in a study of micronektonic standing stock in the upper 1200 m off Hawaii, showed that total penaeids (mostly sergestids), caridean shrimps, and myctophid fishes have abundances of 1.3, 0.3, and 0.8 m^{-2}, respectively, confirming their importance as micronekton. Although some species occupy the entire mesopelagic zone down to 1500 m depth, others are restricted to the upper 500 m of the water column (Wicksten, 2002). In the eastern North Pacific, two major components of the micronekton are euphausiids and decapod shrimps, chiefly *E. pacifica* and *Sergestes similis*; both species are conspicuous diel vertical migrators

(Frost and McCrone, 1979). Samples collected in horizontal hauls immediately following sunset showed that three migratory species, the two migratory myctophids, and *E. pacifica*, were closely associated with the single migratory sound-scattering layer (12 kHz); *S. similis* lagged the ascent of the migratory scattering layer.

In the southern part of the California Current System, the pelagic red crab *Pleuroncodes planipes* has three main life phases: (1) a planktonic phase during its zoea-through-galathea stage (analogous to the megalop stage for brachyuran), (2) an obligate pelagic phase during the first year of life as a juvenile and adult, and (3) a flexible pelagic–benthic phase for animals older than 2 years (Boyd, 1967; Aurioles-Gamboa, 1992; Gómez-Gutiérrez and Sánchez-Ortíz, 1997). However, the diel vertical distribution of the red crab seems to be quite adaptive and flexible, with their DVM patterns being associated with daily food availability, allowing them to move suddenly (< 1 h) from the seafloor to rich food layers near the surface (Robinson and Gómez-Gutiérrez, 1998b), or with local currents, where they must actively swim vertically in the column layer to maintain themselves for long diurnal periods close to large concentrations of food (Robinson and Gómez-Aguirre, 2004).

3.3 Cephalopod Micronekton

Many oceanic cephalopods appear to undergo DVM which enable them to maximize the breadth of their trophic niche while simultaneously minimizing risks from predation in the upper photic layers of the water column. Like most vertical migrators, squid ascend towards the ocean surface at dusk and return to deeper waters at dawn. In subtropical waters around Hawaii, Young (1978) reported that about 60% of cephalopod species underwent DVM.

For species in the PICES region, Roper and Young (1975) reported that *Abraliopsis felis* undergoes a DVM of more than 300 m off the coast of California, ascending from a mean daytime depth of 450 m to a mean nighttime depth of 100 m. Similarly, other enoploteuthids and pyroteuthids in the subtropics appear to vertically migrate (Roper and Young, 1975). However, no evidence of any diel movement for *Watasenia scintillans* has been observed off Japan (Yamamura *et al.*, 1993a). To the north, most of the eurybathic gonatids (including most *Gonatus* species, *Gonatopsis borealis* and *Berryteuthis anonychus*) exhibit DVM from daytime depths of 400–800 m to nighttime depths of generally shallower than 400 m, *e.g.*, *G. borealis* (Roper and Young, 1975), *B. anonychus* (Pearcy and Voss, 1963), *G. californiensis*, *G. madokai*, *G. ursabrunae,* and *G. oregonensis* (Jefferts, 1983).

4. Biomass Patterns

4.1 Micronektonic Fish

In the western subarctic Pacific waters, the biomass of micronektonic fish ranges from 4.5 to 6.5 g m^{-2} wet weight as measured by bridle-free micronekton nets such as Isaacs-Kidd Midwater Trawl (IKMT) and Rectangular Midwater Trawl (RMT) nets (Table 4.1). Ocean Research Institute (ORI)-net sampling usually results in a smaller biomass, possibly due to the avoidance effect generated by the bridles. Commercial-sized trawls usually yield biomass estimates that are up to an order of magnitude higher because of their increased efficiency for sampling larger micronekton, such as *Lampadena, Nannobrachium, Lampanyctus,* and other large mesopelagic fishes.

Biomass levels in the Okhotsk and Bering Seas are about the same as in the subarctic waters, but the composition is quite different at the family level, with bathylagids being dominant in these marginal seas, and myctophids dominating in the open subarctic. Biomass in the eastern subarctic and transitional areas tends to be lower than in the western regions although, at present, the only comparable sampling by similar gear types in the same season has been that of Nishikawa *et al.* (2001), based on RMT-8 sampling from each gyre.

In the Kuroshio region, biomass is higher along the shoreward side of the current axis (2.4 ± 0.8 *vs.* 1.6 ± 0.4 g m^{-2} wet weight), likely reflecting higher productivity as a result of interactions with coastal shelf waters (Table 4.1). Biomass estimates from different sized gears (*e.g.*, ORI net *vs.* IKMT) do not show substantial differences as observed in the subarctic, probably because of the smaller size spectrum of subtropical species, and due to the increase in proportion of gonostomatids, which are less active swimmers than myctophids. Clarke (1973) reported 0.3 g m^{-2} wet weight for myctophids in the Eastern North Pacific Central Waters, which would be comparable to roughly the 1.6 ± 0.4 g m^{-2} (wet weight) present in offshore areas of the Kuroshio Current, when this dominance of gonostomatids is considered. No reliable estimates of mesopelagic fishes made by commercial trawls are currently available for the subtropical North Pacific, although Hidaka *et al.* (2003) report biomass and taxonomic composition of diel migratory myctophids, together with other micronektonic animals, such as squids, shrimps and euphausiids, based on commercial-size trawl sampling.

In the case of shelf-edge or slope water species, dense aggregations are often formed at night along the shelf edge which could perhaps be best estimated by acoustics. At present, there are no biomass estimates available, with the exception of those for *Maurolicus japonicus*, in the Japan/East Sea. Ohshimo (1998) acoustically estimated the biomass of *M. japonicus* at the shelf edge of the Japan/East Sea to be 3.0 g m^{-2} wet weight.

Decadal changes in the relative abundance of surface migratory myctophid fishes in the Kuroshio region, in relation to fluctuations of Kuroshio transport volume, were studied from 1957 to 1994 (Watanabe and Kawaguchi, 2003b). These studies show substantial interannual variability and decadal-scale trends in some species (Fig. 4.1).

Table 4.1 Comparison of biomass estimates based on various sampling gear in the typical water masses in the subarctic, transitional, and subtropical North Pacific Ocean.

Area	Biomass Wet Weight (g/m^2)	Sampling Gear Mouth Opening	Day/Night	Sampling Depth (m)	Sampling Month	Dominant Families	Reference
Western subarctic							
average	2.5 ± 1.1	ORI-net, 2m^2	N	0–1000	May–Nov.	My, Go, Ste, Ph	Gjøsaeter and Kawaguchi (1980)
average	6. 5	IKMT-10 ft, *ca.* 10 m^2	N	0–1000	May–Nov.	My, Go	Gjøsaeter and Kawaguchi (1980)
48°N, 165°E	4. 5	RMT-8, 8 m^2	D	0–1000	July, 1997	My, Go	Nishikawa *et al.* (2001)
average	16	Trawl, 3500 m^2	N	0–200	June, 1989	My, Ba	Karedin (1998)
off Kamchatka	6.4	Trawl, 3500 m^2	D, N	200–500	Nov.–Dec., 1991	My, Ba	Ivanov (1997)
off Kurile Islands	16.8	Trawl, 3500 m^2	D, N	200–500	Nov.–Dec., 1991	My, Ba	Ivanov (1997)
Western transition							
off Japan	18.5 ± 4.7	Trawl, 490 m^2	D	0–700	July, 1995	My only	Watanabe *et al.* (1999)
Central subarctic							
48°N, 177°E	5. 4	RMT-8, 8 m^2	D	0–1000	July, 1997	My, Go	Nishikawa *et al.* (2001)
average	10.0	Trawl, 3500 m^2	N	0–200	July, 1989	My	Karedin (1998)
Eastern subarctic							
Stn. P (50°N,145°W)	1.7–2.3	Tucker Trawl, 4 m^2	N	0–500	July–Aug., 1973–75	My only	Frost and McCrone (1979)
Stn. P (50°N,145°W)	3. 3	RMT-8, 8 m^2	D	0–1000	July, 1997	My, Go	Nishikawa *et al.* (2001)
Stn. Q (51°N,137°W)	1. 2	Tucker Trawl, 4 m^2	N	0–500	July-Aug., 1973–75	My only	Frost and McCrone (1979)
average	4. 5	IKMT-10 ft, 10 m^2	D	0–1000	May–Nov.	My, Go, Ste, Ph	Gjøsaeter and Kawaguchi (1980)
average	7–15	Trawl, 3500 m^2	N	0–200	Aug.–Sept., 1989	My	Karedin (1998)
Eastern transition							
off Oregon	3. 6	IKMT-6 ft, *ca.* 3.5 m^2	N	0–1000	seasonal average	My, Sto	Pearcy and Laurs (1966)
California Current	1.4	Trawl, 3500 m^2	N	0–125	Dec. 1988–Jan., 1989	My, Ba	Savinykh (1999)

Table 4.1 Continued

Area	Biomass Wet Weight (g/m^2)	Sampling Gear Mouth Opening	Day/Night	Sampling Depth (m)	Sampling Month	Dominant Families	Reference
Bering Sea							
central	4. 5	RMT-8, 8 m^2	D	0–1000	July, 1997	My, Mic, Go	Nishikawa *et al.* (2001)
western, central	9.0–24.4	Trawl, 3500 m^2	D, N	200–1000	May–July, 1989	My, Mic, Go	Beamish *et al.* (1999)
western, central	0.9	Trawl, 3500 m^2	N	0–200	Oct.–Nov., 1990	My, Ba	Karedin (1998)
Okhotsk Sea							
average	16.3–33.4	Trawl, 3500 m^2	D, N	200–1000	Aug., 1989	Mic, Zo, My	Beamish *et al.* (1999)
average	0.16	Trawl, 3500 m^2	N	0–200	Nov. 1989–Jan.,1990	My, Ba	Karedin (1998)
average	16.3–33.4	Trawl, 3500 m^2	N	0–50	Aug.–Sept., 1994	My, Ba, Zo	Radchenko *et al.* (1997)
Western Subtropical							
Kuroshio waters							
area west of the axis	2.4 ± 0.8	ORI-net, 2 m^2	D, N	0–*ca.* 1000	Apr., 1965	Go, My, Ste, Ph	Kawaguchi (1973)
area west of the axis	2.8 ± 0.7	IKMT-10 ft, *ca.* 10 m^2	D, N	0–ca.1400	Sept., 1991	Go, My, Ste, Ph	Miya *et al.* (1995)
area east of the axis	1.6 ± 0.4	ORI-net, 2 m^2	D, N	0–*ca.* 1000	Apr., 1965	Go, My, Ste, Ph	Kawaguchi (1973)
Central Subtropical							
off Hawaii	0. 32	IKMT-6, 10 ft, 3.5,10 m^2 Cobb trawl, *ca.* 100 m^2	D, N	0–*ca.* 1200	seasonal average	My only	Clarke (1973)
Emperor Seamounts	142	Trawl, 3500 m^2	D, N	0–400	Mar.–Nov.	Ste	Karedin (1998)
Japan/East Sea							
south of 40° N	3. 0	Echo sounder, 50 kHz	D, N	0–200	May–June, 1993–95	*Maurolicus japonicus*, only	Ohshimo (1998)

IKMT = Isaacs-Kidd Midwater Trawl, RMT = Rectangular Midwater Trawl, ORI = Ocean Research Institute.

My = Myctophidae, Ba = Bathylagidae, Go = Gonostomatidae, Mic = Microstomatidae, Ste = Sternoptychidae, Sto = Stomiidae, Ph = Phosichthydae, Zo = Zoarcidae.

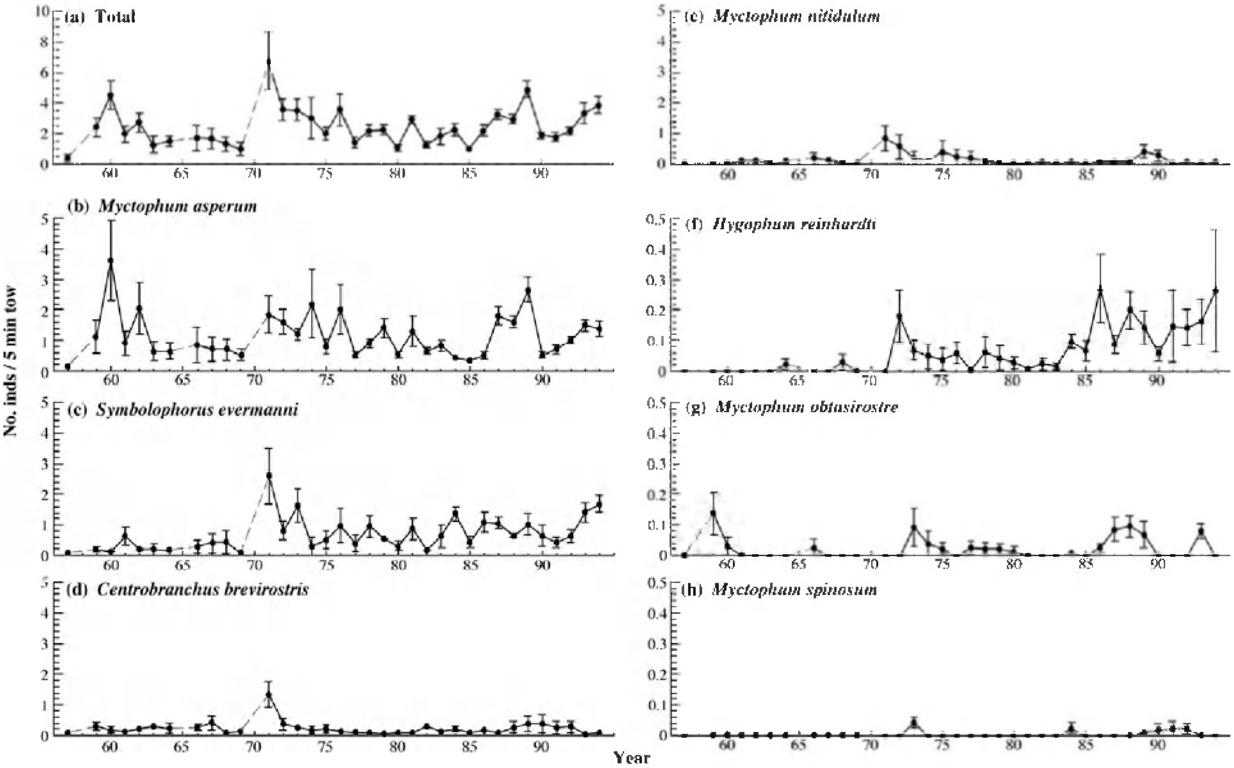


Fig. 4.1 Annual fluctuation in the average catches of juveniles (age 0+) (SL < 40 mm) of the surface migratory myctophid species in the Kuroshio region over 35 years, from 1957 to 1994. Bars indicate standard error.

5. Life History

5.1 Fish Micronekton

5.1.1 Age and growth

Life history information (*i.e.*, age, growth and fecundity) on mesopelagic fishes accumulated until the mid-1990s has been reviewed by Gjøsaeter and Kawaguchi (1980) and Beamish *et al.* (1999). Since then, with the exception of some new information on the growth of *Diaphus theta* and early growth rates based on daily increments of otoliths, no remarkable advances have been made in the northern North Pacific. Therefore, we summarize here the available knowledge accumulated over the past 25 years, mainly in subarctic and subtropical regions, and include the Antarctic waters.

Validations of daily growth otolith increments of myctophids have been conducted for six species: *Benthosema suborbitale, Diaphus dumerilii, D. theta, D. kapalae, Lepidophanes guentheri,* and *Myctophum asperum* (Table 5.1), suggesting the possibility that these daily increments would be universally observed, at least among vertically migrating myctophids. In general (as seems to be the case for most fish species), the otolith increments of myctophids are clearly discernible during larval and juvenile stages, but become harder to read following metamorphosis. Linkowski (1991) also cautions that the otoliths of many myctophids are characterized by multiple primordia, further complicating the ability to obtain accurate age estimates in young specimens.

Based on the validated daily increments, together with traditional reading of annual otolith rings, growth rates were studied for both early and adult stages (Table 5.1). Based on increment width in the larval zone, larval growth rates are known to increase with age prior to metamorphosis in the subarctic *Stenobrachius leucopsarus* and three subtropical myctophid species (Gartner, 1991b; Methot, 1981), although growth is linear for both larval and juvenile stages in *D. theta* (Moku *et al.*, 2001). As expected, the larval periods of subarctic species are much longer than those of tropical and subtropical species (Table 5.1). In most cases, growth rates are highest during the early juvenile stage (*i.e.*, just after metamorphosis), when DVM is initiated, and rates subsequently decrease as the fish get older. Sexual differences in growth rates have been reported for *Electrona antarctica*, with a higher rate for females than for males (Table 5.1).

Lunar periodicity in daily otolith increment formation has been reported for surface migratory *Myctophum asperum* and *M nitidulum*, in which growth rate is slower at full moon, probably due to depression of the upper limit of the migration depth during a full moon (Giragosov and Ovcharov, 1992; Hayashi *et al.*, 2001a). However, in the case of four species of *Hygophum,* growth rates are highest during the full moon (Linkowski, 1996), probably because these species migrate up to the productive warm surface layers only during a full moon night.

Gjøsaeter and Kawaguchi (1980) and Beamish *et al.* (1999) reviewed the age of maturity and lifespan of myctophids. Generally, in tropical and subtropical waters, small-sized myctophids (less than ~ 40 mm SL) mature one year after hatching, while medium-sized species can take 2–4 years to mature. As expected, maturity usually occurs 1–2 years later in subarctic waters than in subtropical and tropical waters. Deeper dwelling species, and those found farther north, also tend to have older age of maturity. In the Bering Sea and Okhotsk Sea, myctophids such as *S. leucopsarus and D. theta* grow to an extraordinary size, probably due to expatriation or feeding migrations.

In general, spawning frequency usually ranges from 1 to approximately 4 years, with an increase in fecundity with body size. An acute decrease in catch is observed in the larger size range after spawning; lifespan is, therefore, thought to coincide with the age of the largest spawners. The lifespan of larger-sized myctophids in the subarctic, subtropical and transitional waters is presently unknown, and remains a topic for future study.

Table 5.1 Age and growth-related information on mesopelagic fishes accumulated from the last 25 years from the subtropical, subarctic, and Antarctic waters of the world oceans.

Species	Growth Rate (mm BL/d)	Growth Curve	Larval Period (d)	Lifespan (yr)	Geographic Area	Reference
Subtropical and tropical species						
Benthosema pterotum	–	power equation	*ca.* 30	–	western Arabian Sea	Gjøsaeter (1987)
Benthosema fibulatum	–	power equation	30–40	–	western Arabian Sea	
Benthosema suborbitale	0.10–0.20	Von Bertalanffy	*ca.* 40	*ca.* 1	Gulf of Mexico	Gartner (1991a,b)
Lepidophanes guentheri	0.19–0.29	Von Bertalanffy	*ca.* 30	–	Gulf of Mexico	Gartner (1991a,b)
Diaphus dumerilii	0.19–0.35	Von Bertalanffy	*ca.* 30	*ca.* 2	Gulf of Mexico	Gartner (1991a,b)
Diaphus kapalae	0.23–0.25	–	*ca.* 38	–	southern Coral Sea	Suthers (1996)
Diaphus suborbitalis	0.35	Von Bertalanffy	53	< 1	equatorial Indian Ocean	Prut'tko (1987)
Diaphus vanhoeffeni	0.21	Von Bertalanffy	24	< 1	central Eastern Atlantic	Boltachev *et al.* (1993)
Myctophum asperum	0.20–0.32	–	–	–	western North Pacific	Hayashi *et al.* (2001b)
Myctophum nitidulum	0.33	Von Bertalanffy	60	< 1	tropical Atlantic	Gigarosov and Ovcharov (1992)
Ceratoscopelus maderensis	0.05–0.23	Von Bertalanffy	–	*ca.* 2	eastern North Atlantic	Linkowski *et al.* (1993)
Ceratoscopelus warmingii male	–	power equation	–	< 1	eastern North Atlantic	Linkowski *et al.* (1993)
female	–	linear equation	–	> 1	eastern North Atlantic	Linkowski *et al.* (1993)
Ceratoscopelus warmingii	0.045	Von Bertalanffy	*ca.* 30	< 1	tropical Indian Ocean	Tsarin (1994)
Subarctic Pacific species						
Diaphus theta (larva and juvenile)	0.13–0.14	linear equation	59–80	–	western transition Pacific	Moku *et al.* (2001)
Diaphus theta	–	power equation	–	5–6	western subarctic Pacific	Ivanov and Lapko (1994)
Stenobrachius leucopsarus	0.11–0.28	–	–	–	California Current region	Methot (1981)
Stenobrachius leucopsarus	–	–	*ca.* 70	–	Bering Sea	Nishimura *et al.* (1999)
Subarctic Atlantic species						
Protomyctophum arcticum	–	linear equation	–	1–1.25	eastern North Atlantic	Kawaguchi and Mauchline (1982)
Benthosema glaciale	–	estimated curve	–	3–4	eastern North Atlantic	Kawaguchi and Mauchline (1982)
Lampanyctus macdonaldi	–	estimated curve	–	7–8	eastern North Atlantic	Kawaguchi and Mauchline (1982)
Antarctic species						
Electrona antarctica	0.05–0.07	linear equation	30–47	*ca.* 3.5	Scotia Sea (58–62°S)	Greely *et al.* (1999)

Dashes indicate no information.

Studies of the three vertically non-migrant species of *Cyclothone* that co-occur in Sagami Bay, on the east coast of Japan (*C. alba*, *C. pseudopallida*, and *C. atraria*), reveal some interesting life history differences. Miya and Nemoto (1991) showed that adult size, age-at-maturity, age-at-reproduction, number of spawning cycles, and fecundity all increased with depth. Thus, *C. alba* (which occurs from 300–500 m depth) reaches maturity at age 1–2 years (at length 16–20 mm) and spawns only once, with mature females producing about 250 eggs. In contrast, *C. pseudopallida* (at depths of 400–600 m) matures at age 2–3 years (at length 20–30 mm), spawns at least two times, with mature females producing about 600 eggs. The deepest species, *C. atraria* (which occurs from 400 to >1000 m), matures at age 3–4 years (at length 22–40 mm) and spawns at least twice, with mature females producing about 1000 eggs. Miya and Nemoto (1991) suggest that this vertical gradient in life history characteristics reflects the decrease in food supply with depth, and that the larvae of the deeper species experience higher mortality rates than those in shallower waters. Interestingly, similar vertical gradients in life history characteristics have been shown to exist among *Cyclothone* assemblages elsewhere in the North Pacific, including the Hawaiian Islands (Maynard *et al.*, 1975; Maynard, 1982) and off the coast of southern California (DeWitt, 1972).

5.1.2 Production

As a considerable amount of knowledge on growth rate and age has been previously obtained, estimates of productivity, including the P/B (annual production to mean annual biomass) ratio should be possible for the dominant subarctic species, and much easier to estimate for subtropical and tropical species with a 1-year lifespan. Despite this, such studies are presently lacking.

5.1.3 Reproduction

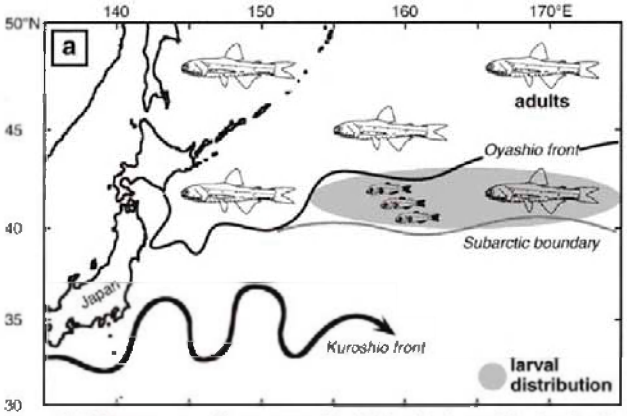
Information on the spawning season of mesopelagic fishes has recently been estimated from the seasonal occurrence of larvae for subarctic, transitional and subtropical species in the California Current region (Moser *et al.*, 1993a,b, 1994, 2001), and the western North Pacific (Sassa, 2001; Sassa *et al.*, 2004a,b; Moku *et al.*, 2003), which supplements the previous reviews by Gjøsaeter and Kawaguchi (1980) and Beamish *et al.* (1999). In the eastern Gulf of Mexico, reproductive patterns (including sex ratio, oocyte development, sizes at sexual maturity, spawning season, fecundity related to size, and spawning strategies) were determined for the seven numerically dominant myctophid species (Gartner, 1993). *Myctophum nitidulum, M affine*, and *M. asperum* are known to spawn all year round, with their peak spawning periods segregated. Their fecundities have also been reported, based on the histological observation of gonads (Oven, 1985). Similar year-round spawning is also reported for *Diaphus suborbitalis* in the tropical Indian Ocean (Lisovenko and Prut'ko, 1986).

Spawning migrations of myctophid and microstomatid fishes are reported for the subarctic and transitional species such as *Notoscopelus japonicus, Symbolophorus californiensis, D. theta* and *Lipolagus ochotensis*, based on their larval distribution patterns (Fig. 5.1; Moku *et al.*, 2003; Sassa *et al.*, 2004a,b).

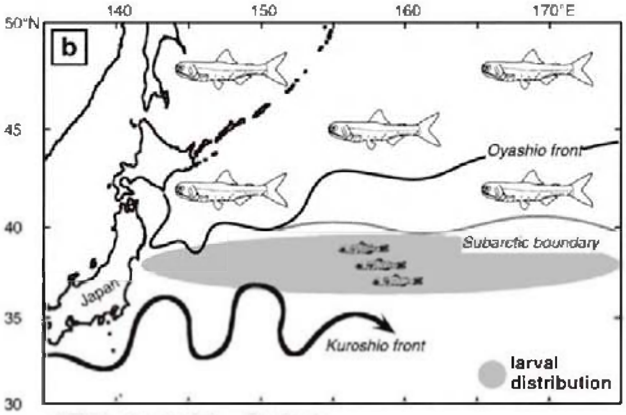
Fecundities have been reported for subtropical and tropical *Benthosema fibulatum, B. pterotum,* and *B. suborbitale* (Gjøsaeter, 1981; Hussain and Ali-Khan, 1987), for subarctic Atlantic *B. glaciale, Protomyctophum arcticum,* and *Lampanyctus macdonaldi* (Kawaguchi and Mauchline, 1982), and for *Lampanyctodes hectoris* and *Maurolicus muelleri* in the southern South Pacific (Young *et al.*, 1987). It seems remarkable that fecundities are known for only a handful of species from a few genera or species belonging to shelf-edge (slope water) species. Generally, mature female myctophids are rarely collected, which has resulted in a restricted knowledge of their fecundity. Spawning behaviors in the field, including the possible formation of dense spawning aggregation at depths, remain for future studies, since inactive spermatozoa have been reported in *L. hectoris* and *Diaphus danae* in the southern Pacific off Tasmania (Young *et al.*, 1987).

5.1.4 Mortality

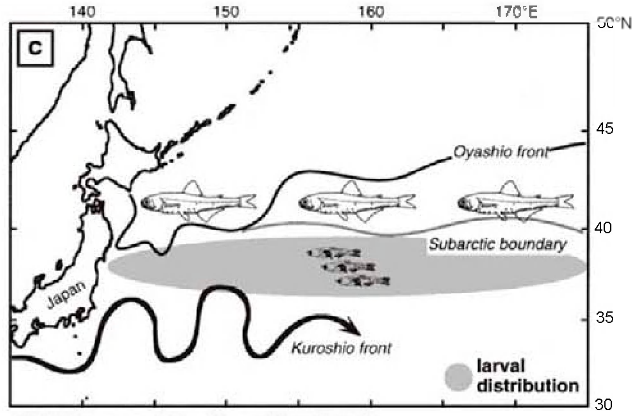
Available information concerning the mortality of mesopelagic fishes has been restricted to only a few studies, due largely to an insufficient number of aged specimens. Annual mortality of *Benthosema glaciale* has been estimated to be 83% in the northwestern Atlantic (Halliday, 1970), but only 52% (z = 0.74) in Norwegian waters (Gjøsaeter, 1973), indicating a highly variable mortality rate within the same species inhabiting different zoogeographical regions. Young *et al.* (1988) estimated the annual mortality rate of *Lampanyctodes hectoris* to be 79%. Gjøsaeter (1981) reported the instantaneous mortality rate (z) of 0.8 for *Notoscopelus kroeyeri*. All the above estimates should be considered tentative, however, since they are based mainly on the age composition of samples collected by gears with considerable sampling bias related with fish size. In this regard, the establishment of a set of standard sampling gears capable of collecting a wide size range (~15–150 mm SL) of mesopelagic fishes is recommended as a subject for future study.



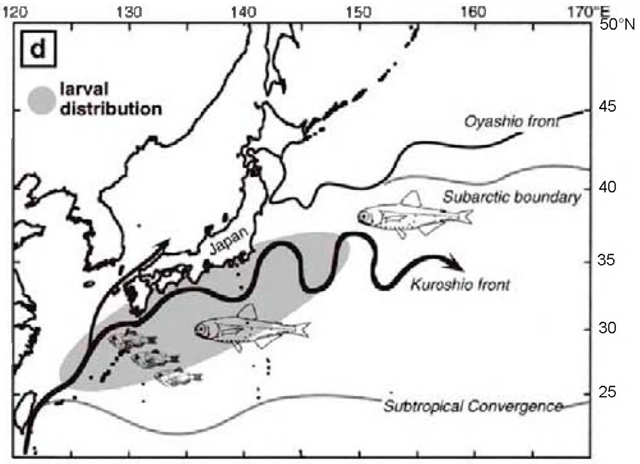
NTW-group—*S. nannochir*, *T. taylori*, and *L. jordani*



STW-group (1)—*D. theta*



STW-group (2)—*S. californiensis*



Kuroshio-group—*M. asperum* and *D. garmani*

Fig. 5.1 Diagrams showing possible spawning migration patterns of (a) the northern transition water group, *Stenobrachius nannochir*, *Tarletonbeania taylori*, and *Lampanyctus jordani*, (b) the southern transition water group (1) *Diaphus theta*, (c) the southern transition water group (2) *Symbolophorus californiensis*, and (d) the Kuroshio group, *Myctophum asperum* and *Diaphus garmani*, based on the relationship between the horizontal distribution pattern of larvae, juveniles, and adults, and the three oceanic fronts in the western North Pacific. (from Sassa *et al.*, 2004) The transition region of the western North Pacific functions as spawning or nursery grounds for not only commercial epipelagic fishes, but also for various subarctic, transitional, and subtropical myctophid fishes.

5.2 Crustacean Micronekton

Most euphausiid taxa (approximately 71%, 7 genera and 61 species out of a total of 11 genera and 86 species) are broadcast spawners (Brinton *et al.*, 2000). Epipelagic euphausiid life cycles from the North Pacific range from 1 to 3 years (compared with 4 to 7 years for the Antarctic krill, *Euphausia superba*); the subtropical species usually have a shorter lifespan (<1 year) than temperate species, but Arctic species, and meso and bathypelagic euphausiids, may have longer lifespans than epipelagic euphausiids, and with relatively little latitudinal variation in the lifespan (Nemoto *et al.*, 1977; Ross *et al.*, 1982; Lavaniegos, 1992; Ross and Quetin, 2000; Iguchi and Ikeda, 2004). Ross and Quetin (2000) reviewed the reproduction of euphausiids, with emphasis on species of commercial value, all of which exhibit a broadcast spawning strategy. They did not include estimates of the fecundity of sac-spawning species in their review, some of which, like *Pseudeuphausia latifrons* (southwestern Pacific <40°N) and *Nyctiphanes simplex* (southern section of the California Current System and Gulf of California), or *Nematoscelis difficilis* (North Pacific TrZ) (Brinton, 1962), are dominant in several ecosystems. However, several other sac-spawning species, like *Nematoscelis* spp. and *Stylocheiron* spp. seem to be significantly less abundant in the North Pacific. *Nematoscelis difficilis* produces egg sacs containing up to 560 eggs fem^{-1} (Nemoto *et al.*, 1972), similar to other North Pacific broadcast spawning species, but *N. simplex* usually produces ovigerous sacs smaller than 61 eggs fem^{-1} (Gendron, 1992; Lavaniegos, 1995). Euphausiids show latitudinal gradients in both duration and timing of reproduction (Feinberg and Peterson, 2003). Generally, earlier and longer spawning seasons occur at lower latitudes, with the timing and duration of spawning of coastal species often synchronized to the period of elevated food production (Ross and Quetin, 2000). At the highest latitudes, and in the coldest waters, first maturation may require two growing seasons, for example, *Thysanoessa longipes* becomes mature at the age of 2 years and spawns at 20–28 mm total length, and individuals who have spawned might survive for a third year (Nemoto, 1957; Iguchi and Ikeda, 2004). In Arctic latitudes, *T. inermis* and *T. raschi* have a short spawning season (<2 months) in spring or early summer, whereas in subarctic latitudes these same species (in addition to *Euphasia pacifica*) typically have spawn over 3 to 6 months between March and September. In temperate regions reproduction of *E. pacifica* and *N simplex* seems to occur throughout the year, with periods of higher spawning activity during summer or fall (Brinton, 1976; Lavaniegos, 1995; Ross and Quetin, 2000). For most species, reproduction is generally concentrated in spring, and it is recognized that most euphausiids spawn several times during each reproductive season. *Thysanoessa longipes*, in the central Japan/East Sea, reproduces over only a limited period during the year, between April and May, and although this species has a relatively long lifespan for the North Pacific (~3 years), females reach maturity in 2 years (Iguchi and Ikeda, 2004). At mid-latitudes (approximately 35–55°N), reproductive maturity is usually at several months (6 months for *N simplex* and 9 months for *E. pacifica*), but some older and larger individuals are often present in the population (Lavaniegos, 1992, 1995; Feinberg *et al.*, 2003; Gómez-Gutiérrez, 2003b). These larger individuals are the most "micronektonic" in size (>20 mm) and avoidance capability (Brinton, 1967; Hovekamp, 1989). Reproduction remains concentrated in spring and early summer, but additional summer cohorts are often detectable in size-frequency histograms (*e.g.*, Brinton, 1976, Lavaniegos, 1995; Gómez-Gutiérrez *et al.*, 1996). Individual growth slows or ceases during the winter, then resumes the following spring. Most studies suggest a maximum population biomass in early autumn, following the summer growing season. At lower latitudes (<35°N), growth and reproduction are less clearly seasonal, and appear to be more closely tied to upwelling events and the resulting shorter-term variation in food supply (Ross and Quetin, 2000; Feinberg and Peterson, 2003). Siegel (2000a) and Siegel and Nicol (2000) summarized information on krill population parameters in the world oceans, including lifespan, growth, mortality, and production. Drawing on these data sources, the life history (growth and age, production, reproduction, and mortality) of euphausiids in the North Pacific is depicted below.

Feinberg and Peterson (2003), and references therein, summarized several studies about the timing of the spawning season for the euphausiids, primarily *E. pacifica* and *Thysanoessa spinifera*, in the North Pacific. The spawning period of these species, and probably of most temperate species, is seasonally limited. This implies that there is one cycle of ovarian maturation and regression per year, though it is possible to have several broods of eggs during the reproductive season (Ross and Quetin, 2000). Durations of spawning season greatly vary regionally and temporally; even for the same population there is considerable year-to-year variability both in spawning season duration and intensity of reproduction. *Euphausia pacifica*, in the coastal waters off California and Oregon, reproduces from March to around mid-October, but the main reproductive peak is between May and August (Smiles and Pearcy, 1971; Brinton 1976). In Toyama Bay, Japan, however, the spawn of *E. pacifica* grows actively only for the first half of the year due to the high thermal regime in the upper layers, and low food supply in the latter half of the year (Iguchi and Ikeda, 1994, 1999).

The average brood size of *E. pacifica* populations from Puget Sound, Washington (Ross *et al.*, 1982), Toyama Bay (Iguchi and Ikeda, 1994; 1999) and from the Oregon coast (Gómez-Gutiérrez, 2003b), are not significantly different. However, the maximum brood sizes are significantly larger for the Oregon population (599 eggs fem^{-1}) in comparison with Toyama Bay (296 eggs fem^{-1}) and Puget Sound (258 eggs fem^{-1}). Along the Oregon coast the maximum brood size recorded for *T. spinifera* is considerably larger (859 eggs fem^{-1}) than for *E. pacifica*, but the average brood size is not significantly different. *Thysanoessa spinifera* spawns primarily in spring and early summer during upwelling events and at depths between 50 and 150 m depth (Feinberg and Peterson, 2003; Gómez-Gutiérrez, 2003b). The average interbrood period of *E. pacifica* under laboratory conditions is 6.5 days, but there is a large female-to-female variability (1 to 27 days), reflecting the difficulty in estimating fecundity in this species (Feinberg *et al.*, 2003; Gómez-Gutiérrez, 2003b). The estimation of the interbrood period to calculate the fecundity of *T. spinifera* has been unsuccessful because mature females collected in the field and incubated in the laboratory spawn only once even if they are provided the same experimental conditions as those for *E. pacifica*, which may spawn several times after collection. In addition, it has been difficult to estimate the interbrood period of *T. spinifera* using the proportion of ripe females, by the method reported by Ross *et al.* (1982), because most of the specimens analyzed were associated with degenerate gonads, although the cause of this is still unknown (Gómez-Gutiérrez, 2003b).

In the southern part of the California Current System, *N. simplex* spawns during spring and summer, with a second spawning of lower intensity occurring in fall. This species has multiple brood production within a reproductive season (~ 3 spawning events with brood sizes < 61 eggs fem^{-1}), averaging about 2% of the total secondary production (body growth, exuvia) (Gendron, 1992; Lavaniegos, 1995; Gómez-Gutiérrez, 1995; Gómez-Gutiérrez *et al.*, 1996). However, Gómez-Gutiérrez and Robinson (2005) reported the interbrood period of *N. simplex* ranged between 7 and 15 days at 16–18°C. This interbrood period is about one-fourth to half of what was previously assumed for this species, suggesting a significant underestimation of the fecundity of this species. In the western Pacific, *Pseudeuphasia latifrons* reproduces throughout the year and histological studies show continuous oogenesis and spermatogenesis, suggesting multiple spawnings with average brood sizes of 83 eggs fem^{-1} (Wilson *et al.*, 2003). In the South China Sea, *P. latifrons* peak reproduction, indicated by larvae, takes place during, and immediately following, the northeast monsoon season when adults are also at their maximum abundance (Brinton, 1975).

Spawning of the deep sea *Thysanopoda* species is poorly known but may occur repeatedly at certain intervals. These species produce large eggs, possibly an adaptation to a deep-sea environment where food is scarce (Nemoto *et al.*, 1977). The fecundity (even brood size) for most of the species from oceanic populations is completely unknown. The same is true for most vital rates, such as growth, molting, and feeding.

Walters (1976) described the ecology of 20 species of sergestid shrimps off the coast of Hawaii. He found that spawning occurs mainly in the spring, but may also occur year round, during an average lifespan of 1 year, and similar to lifespans reported off Oregon (Pearcy and Forss, 1969). Fecundity is difficult to measure since sergestids spawn their eggs directly into the water, rather than carry them on appendages like Caridean shrimp or mysids.

Wittmann (1984) summarized the reproduction and duration of marsupial development for more than 40 species of mysids from different latitudes. Temperature was the most important factor responsible for variations in development times; egg size had a much smaller effect. Incubation times were inversely related to temperature and ranged from 8 days at 30°C to 180 days at 3°C. Because the larvae hatch has a completely formed juvenile stage, the number of eggs that can be accommodated in the oostegite is relatively lower (usually < 30 embryos) than that seen in sac-spawning euphausiids (Gómez-Gutiérrez, 2003a; Gómez-Gutiérrez and Robinson, 2005). The mysid larvae are regularly oriented, with the anterior ends pointing posteriorly and dorsal surfaces facing the ventral surface of the female, as an adaptation to package the greatest number of larvae in the least amount of space, as well as to prevent premature displacement of young from the brood pouch (Wortham-Neal and Price, 2002).

5.2.1 Age and growth

Embryonic development of the eggs of broadcast spawners is, on average, 35 hours (11°C) for *E. pacifica* and *T. spinifera,* 40 hours for the sac-spawning species *N. difficilis* along the Oregon coast (Gómez-Gutiérrez, 2002, 2003a,b), and 72 hours (16°C) for *N. simplex* from the waters around the southwestern part of the Baja California peninsula (Gómez-Gutiérrez and Robinson, 2005). Results have shown that larval development time (larvae to juveniles), measured under laboratory conditions for *E. pacifica* (Ross, 1981; Feinberg *et al.*, 2003), is delayed about 45 days at 12°C and 68 days at 8°C, and for *Nyctiphanes simplex*, about 58 days at 14°C (Lavaniegos, 1992). Euphausiids grow throughout their lifespan and molt every 3 to 8 days; the molting process depends mostly on the temperature, but not on the amount of food eaten (Lasker, 1966). Several laboratory and field studies indicate that body shrinkage is common, and in Antarctic krill, could possibly be an over-wintering mechanism for reducing metabolic demand when food is scarce (Hosie and Ritz, 1989; Dalpadado and Ikeda, 1989; Nicol, 2000; Shin and Nicol, 2002). In the North Pacific, the only species that has been observed for shrinkage is *E. pacifica* (along the California coast), which can survive periods of abnormally high temperatures (such as El Niño events) by shrinking between molts, even if food is plentiful (Marinovic and Mangel, 1999). The authors also note a high degree of individual variability in growth rates. This complicates the accurate estimation of age and growth rates, using conventional cohort analysis. However, even with its inherent limitations, cohort analysis remains the most practical way to estimate field growth rates in recent publications (Lavaniegos, 1995; Gómez-Gutiérrez *et al.*, 1996; De Silva-Davila and Palomares-García, 1998; Iguchi and Ikeda, 2004). Concentration of lipofuscin, a metabolic by-product that accumulates with age, shows a linear association with age (from specimens spawned and reared under laboratory conditions), but not with total length, in which there is a high individual variability in *E. pacifica* and *T. spinifera* (Ju and Harvey, 2002). Maximum age and growth patterns of *E. pacifica* have been investigated for some local populations in the North Pacific and have been shown to vary regionally. The maximum age ranges from 6–8 months (southern California) to 2+ years (northwestern Pacific) (Brinton, 1976; Siegel, 2000a), and mean daily growth rates range from 0.000 (no growth) to 0.096 mm d^{-1}, with large seasonal and interannual differences (Siegel and Nicol, 2000). The prolonged maximum age and low growth rate are believed to be due to low water temperatures in the winter and depletion of their food supply (mainly phytoplankton).

The growth pattern of *T. longipes* was studied off Kamchatka Peninsula (Nemoto, 1957), the west coast of British Columbia, Canada (Fulton and LeBrasseur, 1984), and on Yamoto Rise, central Japan/East Sea (Iguchi and Ikeda, 2004). For the Kamchatka population (group A in Nemoto, 1957), sexual differences in growth rate (higher in females) were observed, and spawning occurred at the age of 2+ years. The daily growth rates of the population off the west coast of Canada were 0.015 mm, or 0.28% of wet weight. Samples from the central Japan/East Sea included at least three cohorts consisting of individuals aged 0+, 1+, and 2+. Fitting a von Bertalanffy growth equation to mean body length-at-age indicated that maximum body length is reached 3 years after hatching (Iguchi and Ikeda, 2004). The maximum ages of *T. inermis* around the Aleutian Islands and *T. spinifera* off British Columbia were 2 to 3+ years (Siegel, 2000a). In the southeastern Bering Sea, the daily growth rate of the populations of *T. inermis* and *T. raschi* was estimated to be about 2% of dry weight (Smith, 1991).

Measurements of euphausiid growth rates are lacking for all bathypelagic and mesopelagic species, and for most of the euphausiids in the Central Pacific. Most growth rates are calculated from cohort analysis of juveniles and adult stages because development times of larvae from nauplius-to-furcilia stages (<1 month), estimated under laboratory conditions, are typically much shorter than the frequency of zooplankton sampling. Even relatively high frequency sampling programs (*e.g.*, biweekly) are not suitable for tracking cohorts in order to estimate larval growth rates of *E. pacifica* and *T. spinifera* (Feinberg and Peterson, 2003). Thus, growth rate estimation of euphausiid larvae must be made from laboratory incubations (Ross, 1981; Lavaniegos, 1992).

5.2.2 Production

Production of crustaceans is defined as the sum of growth increments of the individuals pertaining to one population, eggs and molts included, during a period of time (Ritz and Hosie, 1982; Lavaniegos, 1995; Iguchi and Ikeda, 1999). Most estimates of euphausiid production are derived using body growth from cohort analysis, but eggs and molts are much less frequently studied (Hosie and Ritz, 1983). Lasker (1966) estimated that the egg production from a broadcast spawner (*E. pacifica*) accounts for 15% of the total secondary productivity, and Lavaniegos (1995) reported that the total secondary production for a sac spawner (*N. simplex*), is partitioned as 75% for body growth, 23% for molts, and 2% for egg production. The annual P/B ratio derived from the growth of *E. pacifica* was investigated in the waters off southern California (Lasker, 1966), in Saanich Inlet, British Columbia (Heath, 1977), off Oregon (Mauchline, 1977), off British Columbia (Tanasichuk 1998a), and in Toyama Bay, southern Japan/East Sea (Iguchi and Ikeda, 1999). The annual P/B ratio is highly variable among these regional populations: 2.6 for Saanich Inlet (re-calculated), 8.7 off Oregon, 11.0 (range 6.4–16.7) off British Columbia (calculated from Table 4 in Tanasichuk, 1998a), and 3.8 for Toyama Bay.

Such regional variations within the same species are due to differences in growth rates and patterns during their 1-year life cycle, and have also been reported for *N. simplex* living in western (P/B ratio = 12.7, Lavaniegos, 1995) and southwestern waters of Baja California peninsula (7.0, Gómez-Gutiérrez *et al.*, 1996). De Silva-Dávila *et al.* (2002) reported that variability of P/B ratios of *N. simplex* along Baja California during February 1994 does not exhibit a simple latitudinal trend as would be expected (15.3 at Bahía Vizcaíno (28.5°N), 21.2 at Punta Abreojos (26°N), and 16.1 at Bahía Magdalena (24.5°N)), but higher productions are typically found in upwelling regions associated with topographic prominences. The P/B ratios of this species could be strongly biased if the population is not completely sampled (for example, by including mostly daytime samples that are biased for larvae and juveniles), leading to unusually high P/B values (De Silva-Dávila and Palomares-García, 1998).

The annual P/B ratio of *T. spinifera* off British Columbia was reported to be 19.5 (range 11.1–35.0, Tanasichuk, 1998b). However, P/B ratios are highly dependent on the method of sampling (size-bias), preservation (preserved versus dry weight from fresh animals), the size frequency distribution of the samples (number of euphausiids measured), and frequency of the sampling to estimate growth rates. High P/B ratios (>20) are usually reported in studies where larvae and juveniles dominate the population composition, perhaps resulting in overestimates of the overall population P/B ratio. Because relatively recent experimental estimations of instantaneous growth rates have reflected the *in situ* nutritional history of the previous intermolt period (Ross *et al.*, 2000), the development of new and better egg production incubation techniques (Ross and Quetin, 2000), and the physiological capability of the euphausiid to shrink under a relatively wide range of environmental conditions, it is expected that future studies will use more carefully the information from cohort analysis and avoid assuming *a priori* the euphausiid's vital rates to estimate euphausiid secondary productivity.

5.2.3 Reproduction and early life history

The reproductive patterns and population fecundity of euphausiids has been thoroughly described by Ross and Quetin (2000). However, this review includes mostly broadcast spawning species subject to fishery activity. Siegel (2000a) has reviewed the development of euphausiid larvae. In the North Pacific, however, the bulk of information on reproduction is restricted to *E. pacifica* (Feinberg and Peterson, 2003). The timing and duration of spawning in *E. pacifica* is flexible, and a link between the spring bloom, or period of upwelling, and the length and intensity of spawning has been suggested (Ross and Quetin, 2000). Hatching success of *E. pacifica* is high (>96%) in the temperature range of 1–20°C, but falls to 70% at 22°C, and only to 1.1% at 25°C (Iguchi and Ikeda, 1994). Comparison of three broadcast spawning species (*E. pacifica*, *T. spinifera*, and *T. inspinata*) and one sac spawning species (*N. difficilis*) indicates that all have similar egg developmental rates and hatching times (<40 hours) at the same temperature (11°C) (Gómez-Gutiérrez, 2002, 2003a,b). The assumption that the developmental time of eggs for *N. simplex* is 30 days (Lavaniegos, 1995) is perhaps an overestimation, particularly in regions with higher temperatures (15–21°C). Thus, the total fecundity of this species (33 mg m^{-2} yr^{-1}) may be substantially underestimated. Gómez-Gutiérrez and Robinson (2005) observed an interbrood period of *N. simplex*, ranging between 7 and 16 days under shipboard incubations (16°C), in the southern part of Baja California, and found that it was significantly smaller than the interbrood period assumed by Lavaniegos (1995). This indicates that the fecundity of this species was underestimated by between ¼ and ½ of the expected value obtained from direct observation of the interbrood period. Thus, whereas Lavaniegos (1995) calculated that egg production contributed about 2% of the total secondary productivity, using the recently observed interbrood periods, egg production would be expected to contribute about 7% of the total secondary productivity of this species.

The hatching success of species inhabiting the North Pacific has been studied in *E. pacifica*, and most recently in *T. spinifera*, and may be attributed not only to high female-to-female variability, but may also be partly due to temperature (Iguchi and Ikeda, 1994; Gómez-Gutiérrez, 2002). Gómez-Gutiérrez (2002, 2003b) observed hatching mechanisms of three broadcast spawning euphausiids (*E. pacifica, T. spinifera*, and *T. inspinata*) and a sac spawning species (*N. difficilis*) off Oregon. Delayed egg hatching schedules in broadcast spawning species were promoted by low temperatures (<8°C), and both early and delayed egg hatching times were associated with relatively lower hatching success and brood size compared to eggs that hatched at a normal larvae stage (first nauplius stage (N1) for broadcast and metanauplius (MN) for sac spawning species).

5.2.4 Mortality

Euphausiid mortality rates estimated from field samples are scarce. For *E. pacifica* in the North Pacific, mortality ranges from z = 0.4 to 8.7, depending on developmental stage and region (Siegel 2000a). In southern California waters, Brinton (1976) reported an average survivorship of 16% during the 1-month furcilia larval phase, 67% for juveniles (6–9 mm), and 60–64% for young adults (9–18 mm). Egg mortality is expected to be higher for broadcast spawners than for sac spawners due post-spawning predation, losses to the seabed (caused by egg sinking), and transport by currents to unfavorable areas. There are no quantitative estimates of egg mortality in the field. However, the mortality of *E. pacifica* embryos has been associated with malformation during the development of the embryo (15% of individuals), protozoan parasitism (5%), and failure of embryos to hatch (2%) (Gómez-Gutiérrez, unpubl. data). Only recently has it become recognized that euphausiids have a considerable flexibility in their hatching mechanism. Gómez-Gutiérrez (2002, 2003a,b) and Gómez-Gutiérrez and Robinson

(2005) reported that broadcast spawner (*E. pacifica*, *Thysanoessa spinifera* and *T. inspinata*) and sac spawner (*Nematoscelis difficilis* and *Nyctiphanes simplex*) species have different hatching mechanisms and different patterns of hatching success.

Gómez-Gutiérrez *et al.* (2003) reported a mass mortality of *E. pacifica* by an apostome parasitoid ciliate in the California Current System in the summer of 2001. The epizootic character of the observed euphausiid mortality challenges the widely held notion that mortality in pelagic organisms can be attributed primarily to predation and starvation. Because these parasitoid ciliates have been recorded in other euphausiids in the Bering Sea (*T. inermis*) and off the Oregon–Washington coasts (*T. spinifera*, *T. gregaria*), and because of the difficulty in detecting the infected euphausiids in preserved samples, it is therefore suspected that this kind of infection may occur in other euphausiids from the North Pacific as well. In March 2004, an apostome parasitoid ciliate that infected and killed the most abundant euphausiid (*Nyctiphanes simplex*) of the southern part of the California Current System and the Gulf of California was discovered (Gómez-Gutiérrez and Robinson, 2004). This is the first observation of a ciliate parasitoid infection in a sac-spawning euphausiid species. Preliminary observations suggest those parasitoid ciliates may compete for the same resource (euphausiids) with more conventional stenophagous euphausiid predators like the blue whale *Balaenoptera musculus*, whale shark *Rhincodon typus*, mantas *Mobula japonica* and *Mobula thurstoni*), and juvenile stages of squids (*Dosidicus gigas*). Other parasites, although they do not kill euphausiids, may significantly affect their health. For example, the helminth *Anasakis simplex*, which infects *T. raschi* (Hays *et al.*, 1998), has also been observed in *E. pacifica* and *N simplex* (Gómez-Gutiérrez, pers. observ.) occupying most of the carapace and abdomen space, and it is believed that euphausiids are the intermediate host of this kind of parasite. The Dajidae parasites that infect *Stylocheiron* and *Nematoscelis* species in the California Current System and South China Sea have also been noted; they apparently castrate their host and can infect euphausiids even in juvenile stages (Shields and Gómez-Gutiérrez, 1996; Gómez-Gutiérrez and Shields, 1998).

5.3 Cephalopod Micronekton

Life history characteristics common to pelagic squids include early and/or semelparous breeding, rapid growth, a short lifespan, little overlap of generations, and vulnerability to environmental variables (Boyle and Boletsky, 1996).

5.3.1 Age and growth

It is generally held that cephalopods are fast growing animals which reproduce once and then die (semelparous). Usually, most species do not live longer than one year. Few studies have been conducted on age and growth for species in the PICES region. The lifespan of *Watasenia scintillans* has been estimated to be between 12–13 months for females and 11–12 months for males (Hayashi, 1993). *Onychoteuthis borealijaponica* has been reported to have a lifespan of 1 year (Murata and Ishii, 1977), but only a fraction of this occurs in the micronekton. Insight into the growth of enoploteuthin squids might be extracted from statolith-based age and growth studies on pelagic young (paralarvae) *Abralia trigonura* in Hawaiian waters, where they grew exponentially at a rate of 5.9% mantle length (ML) d^{-1} for approxiamtely 40 days post-hatching, while post-paralarvae exhibited slower growth (Bigelow, 1992). Statolith microstructural analysis and exponential growth models suggest that growth in length was similar (0.80% ML d^{-1}) for male and female *Onychoteuthis borealijaponica*, while increase in weight was higher for females (1.9% WT d^{-1}) than for males (1.4% WT d^{-1}) (Bigelow, 1994). Yatsu (2000) presented estimates of age and growth for the ommastrephid species *O. bartramii*, *Symplectoteuthis oualaniensis*, and *Dosidicus gigas*, based on statolith microstructure. Relationships between ML and age were exponential during early life stages, and almost linear for subadults and adults.

5.3.2 Production

No production estimates for cephalopod micronekton are available.

5.3.3 Reproduction and early life history

Reproduction in cephalopods has been comprehensively reviewed in Mangold (1987). Pelagic squids that dominate the micronektonic cephalopods are "semelparous" but there also appears to be a very high degree of flexibility in "semelparity", ranging from one exhaustive spawning followed by death, to repeated egg-laying episodes that resemble "iteroparity". Lack of nidamental glands (which help to produce egg masses) in enoploteuthins suggests that these squids release eggs singly (surrounded only by oviducal jelly) rather than in clumped masses (Young and Harman, 1985; Young *et al.*, 1985). Oceanic squid generally have planktonic young (paralarvae) which are typically confined to the near-surface waters (0–200 m); paralarval squid spend an unknown length of time in the plankton and then typically descend to an adult habitat in the mesopelagic (400–1200 m) or bathypelagic (>1200 m) zone.

5.3.4 Mortality

Natural mortality, which includes catastrophic and post-spawning mortality, predator-prey related deaths, and cannibalism is difficult to quantify in the field. For short-lived animals, such as pelagic cephalopods, estimations of natural mortality become even more subjective and, at present, are nonexistent for micronektonic cephalopods.

6. Ecological Relations

Much of the following section on feeding is based on the review by Moku and Hidaka (2002). Since the term "micronekton" was proposed to express the animal groups between plankton and nekton in terms of swimming ability (Marshall, 1954), their ecological roles in the oceanic ecosystems have been stressed and recognized as important to trophically connect zooplankton with carnivorous nekton, mainly because of their potential huge biomass. Micronekton includes larger-sized crustaceans, such as euphausiids, shrimps, and mysids, small fishes and squids, most of which dwell in the mesopelagic zone and are diel vertical migrants.

All large oceanic fishes and squids of substantial commercial value also pass through a micronektonic stage during their early life history stages. In this regard, scientific interests have been raised regarding the potential for competition between "true" micronekton and the juveniles or adults of commercial fishes. As competitors, vertically migrating micronekton are considered to merit future study because of their high abundance and productivity depending on diel feeding migration to the euphotic zone. Knowledge of the dynamic aspects of their feeding habits, however, has been restricted due to lack of quantitative sampling methods. Here, we review the existing literature for North Pacific populations, as well as for populations in other oceans, in order to extract the key points directing future studies.

6.1 Feeding Habits

There are several methodological difficulties in quantitatively assessing the food habits of mesopelagic organisms. A recurring problem is that of post-capture ingestion in the codend of most nets (Hopkins and Baird, 1975; Lancraft and Robison, 1980). In a comparison of the feeding habits of net-caught *Sergestes similis* with those collected in albacore stomachs, Judkins and Fleminger (1972) found strong evidence for codend feeding on fish scales, copepods, and euphausiids. Thus, caution must be exercised when considering the diets of these midwater species collected in lengthy trawls. Another problem is the potential for regurgitation of stomach contents, especially for fish with swim bladders, brought up from the deep ocean. This is likely to lead to underestimates of daily ration and potential bias in diet composition.

6.1.1 Fish micronekton

Considerable knowledge has accumulated on the feeding habits of micronekton, but in many cases these analyses have been qualitative rather than quantitative. Myctophid fishes are always one of the most abundant groups of micronektonic animals in the world oceans (Maynard *et al.*, 1975; Hopkins and Lancraft, 1984). As expected (given their propensity for DVM behavior), studies of myctophid feeding patterns suggest increased feeding at night. Up to 40 prey species have been found in stomachs of the abundant planktivorous mesopelagic fishes in the North Pacific Ocean. Copepods show the highest species diversity among prey organisms (Paxton, 1968; Pearcy *et al.*, 1979a; Adams, 1979; Gordon *et al.*, 1985; Balanov *et al.*, 1994, 1995a). Owing to their large mouths, relatively scarce and serrated gill rakers, well-developed stomach, and short intestine, myctophids consume predominantly actively-moving prey (copepods, euphausiids, *etc.*), whereas deep-sea smelts (bathylagids) which have a small mouth, dense and flat gill rakers, weakly-developed stomach, and long digestive tract are generally adapted to consume slow-moving animals such as jellyfish, larvaceans, ctenophores, and pteropods (Gorelova and Kobylanskiy, 1985; Ebeling and Cailliet, 1990; Balanov *et al.*, 1994).

The main prey taxa of myctophids are crustacean zooplankton, such as copepods, euphausiids, amphipods, and ostracods (Hopkins and Gartner, 1992; Gartner *et al.*, 1997; Moku *et al.*, 2000). Some specialized genera or species, however, are known to select their prey or broaden their prey animal groups. For example, species of the genus *Centrobranchus* are specialists that feed on gelatinous plankton such as pteropods and appendicularians (Gorelova, 1977; Hopkins and Gartner, 1992), while fishes in the genus *Ceratoscopelus* feed not only on crustaceans but also on appendicularians, salps and ichthyoplankton, and occasionally even on large diatoms (Duka, 1987; Kinzer and Schulz, 1985; Robison, 1984).

In the family Myctophidae, feeding habits have been extensively studied for *Stenobrachius leucopsarus*, one of the most common mesopelagic fishes in the North Pacific. In all areas, this species consumes mainly copepods, amphipods, and euphausiids. In the Bering Sea, the most important prey species are the euphausiid *Thysanoessa longipes,* and the copepods *Neocalanus cristatus, Eucalanus bungii*, and *Paraeuchaeta elongata* (Balanov, 1994; Balanov *et al.*, 1994). In the Pacific waters off North America, *Euphausia pacifica, Calanus* spp., *Neocalanus plumchrus, Metridia lucens, Themisto pacifica*, and *Hyperia galba* are their main prey (Tyler and Pearcy, 1975; Pearcy *et al.*, 1979a; Ebeling and Cailliet, 1990). In the Pacific waters off northern Japan, the major prey are *E. pacifica, T. longipes, M. pacifica,* and *N. plumchrus* (Gordon *et al.*, 1985; Moku *et al.*, 2000).

In the stomachs of *Stenobrachius nannochir*, calanoid copepods predominate. The most frequently consumed copepod species are *N. cristatus, P. elongata, Gaidius variabilis*, and *P. pacifica* (Gordon *et al.*, 1985; Balanov *et al.*, 1994; Moku *et al.*, 2000). This species consumes euphausiids, amphipods, and small decapods in considerable quantities (up to 10–20% of the total ration) only in the mesopelagic zone of the Okhotsk Sea (Il'insky and Gorbatenko, 1994).

In the North Pacific waters off Kamchatka, off North America, and off northern Japan, the bulk of the diet of *Diaphus theta* consists of euphausiids, copepods, and amphipods; the predominant prey items are *E. pacifica, Metridia lucens, M okhotensis*, and *Themisto pacifica* (Tyler and Pearcy, 1975; Gordon *et al.*, 1985; Moku *et al.*, 2000). In the stomachs of *Tarletonbeania crenularis* in the same areas, the predominant species are the euphausiid *E. pacifica,* and the copepods *M lucens, N plumchrus, N. cristatus*, and *Candacia columbiae* (Tyler and Pearcy, 1975; Kawamura and Fujii, 1988).

Among fishes of the family Microstomatidae, the most abundant species in the North Pacific are *Leuroglossus schmidti* and *Lipolagus ochotensis*. These species are found throughout the entire North Pacific, and in the mesopelagic zone of the Okhotsk Sea, they occupy the dominant position among the mesopelagic fishes (Balanov and Il'insky, 1992; Il'insky and Gorbatenko, 1994). Medusae, ctenophores, and larvaceans are dominant components in the diet of both species in the Bering Sea and the Pacific waters off northern Japan. For *L. schmidti*, euphausiids and copepods constitute the greater part of the ration (Gorbatenko and Il'insky, 1992; Balanov, 1994; Balanov *et al.*, 1994). In the Okhotsk Sea, *L. schmidti* consumes predominantly euphausiids and amphipods. Gelatinous zooplankton are most prevalent in the diet of *L. ochotensis* (Il'insky and Gorbatenko, 1994). *Leuroglossus schmidti* actively feeds on euphausiids, amphipods, or copepods at night in the epipelagic zone (0–200 m), whereas jellyfish and other soft-bodied animals prevail in stomachs of this species in the upper mesopelagic zone (200–500 m) (Balanov *et al.*, 1994, 1995a). Thus, it appears that *L. schmidti* feeds as a typical myctophid in the epipelagic region and as a typical deep-sea smelt in the upper mesopelagic region. Apparently, the concentration of prey organisms in the epipelagic area of the Bering Sea is sufficient for *L. schmidti* (which is adapted to feed on slow-moving organisms) to consume them in large numbers (Balanov *et al.*, 1994). The same is true for the mesopelagic zone of the Okhotsk Sea where euphausiids and amphipods are abundant enough to contribute substantially to the diet of *L. schmidti* (Il'insky and Gorbatenko, 1994).

In early studies, most myctophids were usually characterized as "opportunistic" feeders that filtered water with well-developed gill rakers (Marshall, 1979). However, more recent studies have revealed evidence of resource partitioning (by both species and by size) for many species, together with habitat segregation by species and size (Merrett and Roe, 1974; Clarke, 1980; Hopkins and Gartner, 1992; Moku *et al.*, 2000; Watanabe *et al.*, 2002). This difference in results is due mainly to the recent development of discrete-depth sampling methods and the collection of sufficiently large sample sizes at higher spatial and temporal resolution. Recently, resource partitioning has also been recognized for larval myctophid fish communities (Sabates and Saiz, 2000; Sassa and Kawaguchi, 2004).

In the subarctic and transitional regions, seasonal changes in species composition and biomass of the epipelagic zooplankton are due to the vertical migrations of crustaceans, especially copepods such as *Neocalanus*, related to their ontogenetic vertical migration and diapause in summer (Miller *et al.*, 1984; Batchelder, 1985; Odate, 1994; Kobari and Ikeda, 1999). This change in zooplankton assemblage is reflected in prey species composition of the subarctic and TrZ myctophids. For example, the occurrence ratios of euphausiids in myctophid stomachs are known to vary with the seasonal change in euphausiid abundance (Collard, 1970; Cailliet and Ebeling, 1990; Balanov *et al.*, 1995a). There is a seasonal change in the general pattern of dominant prey species in stomachs of the most abundant mesopelagic fishes in the North Pacific. Copepods predominate in winter, later spring, and summer, whereas euphausiids are the dominant group in late summer and autumn (Adams, 1979; Pearcy *et al.*, 1979; Gordon *et al.*, 1985; Cailliet and Ebeling, 1990). In the Bering Sea in spring and summer, copepods (primarily *N. cristatus*) are dominant in the diet of myctophids both in the epipelagic (0–200 m) and in the upper mesopelagic (200–500 m) zones. In autumn and winter, *N cristatus* is predominantly found in the stomachs of fish from the upper and lower (500–1000 m) mesopelagic zones (Balanov, 1994; Balanov *et al.*, 1995a).

However, tropical and subtropical myctophids seem to show no clear seasonal change in their prey composition, presumably reflecting the low seasonality in zooplankton community and biomass at lower latitudes (Dalpadado and Gjøsaeter, 1988). The knowledge of seasonal and regional changes in prey species related with change of zooplankton community is restricted and spatio-temporally fragmental (North Pacific: Collard, 1970; Cailliet and Ebeling, 1990; Bering Sea: Balanov *et al.*, 1995a,b; Atlantic: Gjøsaeter, 1973; Indian Ocean: Dalpadado and Gjøsaeter, 1988).

Ontogenetic changes in feeding habits and prey size are readily apparent in most mesopelagic fishes. Generally, copepods dominate as prey (with a size shift from nauplii to copepodite stages with growth from larvae to adults), and later are partly replaced with larger crustaceans, such as euphausiids. However, most myctophids continue to consume copepods of various sizes throughout their life, although their relative importance decreases among the larger-sized myctophids (*e.g.*, those reaching 10 cm or more) that begin feeding on small squids and fishes (Gjøsaeter, 1973; Hopkins and Baird, 1985; Kinzer, 1977; Clarke, 1980; Hopkins and Gartner, 1992). Recently, the feeding habits of two dominant myctophid larvae, *Diaphus garmani* and *Myctophum asperum*, were studied in the transition region of the western North Pacific. The former depends mainly on appendicularian houses and copepod nauplii, while the latter feeds mainly on ostracods and polychaetes. It was concluded that competition for prey among these myctophid larvae and co-existing Japanese anchovy larvae is unlikely because of diet and habitat depth segregation (Sassa and Kawaguchi, 2004).

The diel feeding habits of myctophids are closely related with their vertical migration patterns. In the tropical and subtropical waters, they show clear feeding periodicity, feeding mainly at night in the epipelagic zone (Baird *et al.*, 1975; Clarke, 1978; Kinzer and Schulz, 1985; Watanabe *et al.*, 2002; Fig. 6.1). In the subarctic, transitional, upwelling and slope water areas (where considerable zooplankton biomass is distributed in the mesopelagic zone), many myctophids feed both at night and during the daytime (Paxton, 1967a; Samyshev and Schetinkin, 1971; Young and Blaber, 1986; Moku *et al.*, 2000). The few studies on the feeding periodicity of *S. leucopsarus* in the North Pacific have revealed no pronounced rhythms in food consumption. Based on the diel distribution of different stages of food digestion and stomach fullness, it has been reported that this species feeds mainly in the morning and at night, although the possibility of feeding during the daytime cannot totally be ruled out (Tyler and Pearcy, 1975; Ebeling and Cailliet, 1990). Most of the common mesopelagic fishes of the Bering Sea exhibit well-defined feeding rhythms related to the vertical migrations of both fish and zooplankton.

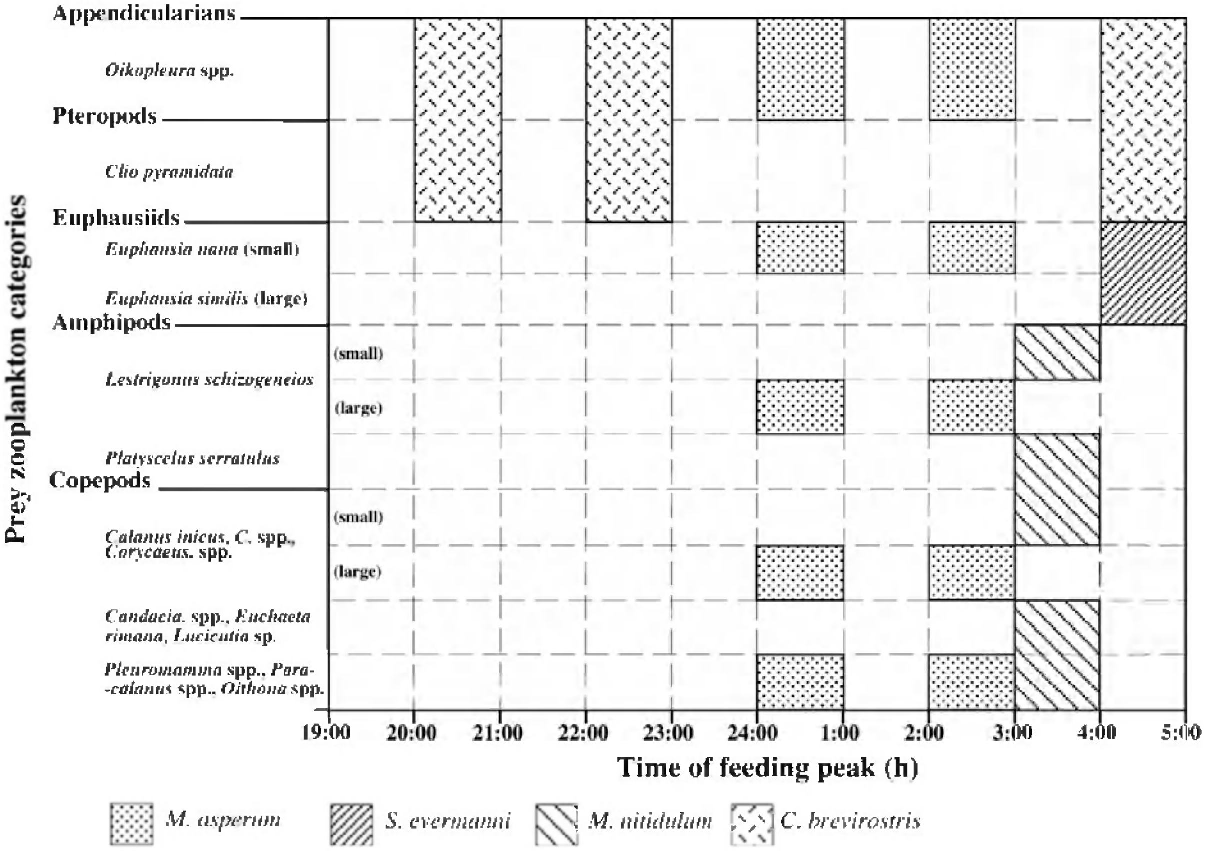


Fig. 6.1 Relationship among the main prey categories, their sizes, and feeding peaks for four juvenile surface migratory myctophid fishes, *Myctophum asperum*, *Symbolophorus evermanni*, *Myctophum nitidulum*, and *Centrobranchus brevirostris* in the Kuroshio region of the western North Pacific.

Many species show two peaks of stomach fullness: one at night between 2200 and 0400 h in the epipelagic zone (0–200 m) and another during the day between 1000 and 1600 h in the upper mesopelagic zone (200–500 m). High stomach fullness, maximal content of fresh food, and minimal proportion of empty stomachs were found during these consumption periods. In the 500–1000 m layer, no distinct rhythm of food consumption was found, although digested food prevailed in the stomachs of fish in this layer and the proportion of empty stomachs was highest (Balanov, 1994; Balanov *et al.*, 1994; Balanov *et al.*, 1995a,b). Pronounced feeding periodicity has been reported for *S. leucopsarus* and *D. theta* off northern Japan (Moku *et al.*, 2000). Existing knowledge on the feeding habits of non-migratory mesopelagic stomiatoid fishes is currently restricted to those occurring in Hawaiian waters (Clarke, 1982).

Recently, an interdecadal change (between 1964–1999) in the diet of a surface-migrating myctophid (*Myctophum nitidulum*) was reported in the Kuroshio region (Watanabe and Kawaguchi, 2003a). These authors pointed out that predation on Japanese sardine larvae by *M. nitidulum* occurred during the peak period of the sardine stock from 1976–1990, and they estimated that 0.24 (± 0.14) to 0.52 (± 0.31) sardine larvae per meter cubed were consumed by *M. nitidulum* every night in January and February during these years.

6.1.2 Crustacean micronekton

Many studies using a variety of methods have tried to quantify the diets of euphausiids. Since the food entering the euphausiid stomach has already been thoroughly masticated by the mandibles, identification of gut contents is extremely difficult, with the exception of copepod mandibles. Mauchline (1967) reviewed the morphology of feeding appendages of all the genera of euphausiids, separating genera typically carnivorous (*Nematoscelis*, *Nematobrachion*), with larger space among setae of the feeding appendages, to genera that are mostly herbivores, with dense setae along the periopods (*Nyctiphanes*). More specifically, Mauchline and Fisher (1969) have reviewed early studies of food items of euphausiids, which included some common North Pacific euphausiid species *E. pacifica*, *T. longipes*, *T. inermis*, and *T. raschi* and divided their feeding modes into three classes: (1) those which eat diatoms, dinoflagellates and tintinnids filtered from the water by mouthparts, (2) those which feed on zooplankton, and (3) those which feed on detrital material obtained from bottom sediments. The stomach contents of three bathypelagic giant *Thysanopoda* are usually dominated by copepods, chaetognaths, and in less proportion, by euphausiids, amphipods, mysids, and pelagic shrimps (Nemoto, 1977). He considered that *Thysanopoda egregia* is the most voracious euphausiid, preying on micronektonic fishes, and even oceanic squid larva. Strong solitary spines and setae that are typical of carnivorous euphausiids are found along the inner side of the stomach wall. There are no clusters of spines, such as those found in the stomach walls of typically herbivorous euphausiids. Hamner (1988) reviewed the filtering mechanisms of the genus *Euphausia*, describing that the thoracic appendages of particle-feeding euphausiids bear long, anteriorly-directed setae forming a filter basket (closed basket). This fills from the front, beneath the antennae, when the legs are opened. During opening, the filter surface is covered by the exopods (outer legs) to keep water from moving in through the screen.

In the North Pacific, knowledge on the feeding habits of euphausiids is restricted mainly to *E. pacifica* because this species has received considerable attention in order to understand its role in organic matter transfer in marine ecosystems. Examination of the gut contents of *E. pacifica* larvae (calyptopis stage), using scanning electron microscopy, revealed a diet composed entirely of amorphous organic detritus, crustacean remains, and inorganic particles (Suh *et al.*, 1991). As for the adults, comparative morphology of the feeding basket and gut of five species in the North Pacific suggested that *E. pacifica* is more adapted to herbivorous feeding (Mauchline, 1967; Suh and Choi, 1998). However, Ohman (1984) reported that *E. pacifica* is omnivorous, based on laboratory experiments in which they were fed different prey types (diatoms and copepods), and found that copepods seemed to be the less preferred prey item. He also noted, however, that this species switched easily from herbivory to carnivory, according to the relative food availability. Off eastern Japan, copepods proved to be the most important food item in terms of carbon, suggesting that *E. pacifica* does, indeed, switch its feeding behavior (suspension feeding on phytoplankton and raptorial feeding on small copepods) according to the ambient phytoplankton abundance (Nakagawa *et al.*, 2001; Taki *et al.*, 2002).

In addition to these traditionally well known main food items, it is known that *E. pacifica* can also feed on marine snow (particles > 0.5 mm diameter) with relatively high efficiency, even when other sources of food are provided (Dilling *et al.*, 1998; Dilling and Brzezinski, 2004), and probably also feeds on protozoans (Stoecker and Capuzzo, 1990). Dilling and Brzezinski (2004) developed a new ingenious method to track food sources by labeling the frustules of aggregated *Nitzschia angularis* cells with different naturally occurring, but rare, stable isotopes of silicon (^{30}Si and ^{29}Si). *Euphausia pacifica* consumed both aggregates and dispersed cells, even when more cells were made available in dispersed form than in aggregated form. This suggests that aggregates may, indeed, be a food source for euphausiids in the field, even when dispersed cells are relatively abundant. Marine snow is a significant sinking source of carbon, from the pelagic realm to deeper layers of the ocean, and euphausiids are capable of fragmenting a single aggregate of marine snow into multiple, smaller aggregates by fluid stress created around the appendages during swimming, thus significantly reducing marine snow sinking rates and decreasing the carbon loss from the highly productive epipelagic layer (Dilling and Alldredge, 2000; Goldthwait *et al.*, 2004). However, Ponomareva *et al.* (1974) was perhaps the first to develop experiments for the determination of the assimilability of algae and bacteria (n = 7) in euphausiids (tropical species *Euphausia diomedeae*, *Thysanopoda tricuspidata* and *E. brevis*), recording that feeding rates of euphausiids on phytoplankton and bacteria were very low. According to the authors, *E. diomedae* consumes bacteria aggregated on particles in larger amounts than single cells, and its rates of assimilation of phytoplankton and bacteria are fairly high.

Finally, *E. pacifica*, and several other euphausiid species from the region, may also be one of the most important predators on the early stages of anchovy (eggs and yolk-sac larvae) off southern California (Theilacker and Lasker, 1973; Theilacker *et al.*, 1986; Theilacker *et al.*, 1993). Similarly, *T. spinifera* and *T. inermis* have been shown to be important predators on the early stages of walleye pollock in the Gulf of Alaska (Bailey *et al.*, 1993; Brodeur and Merati, 1993).

Bargu *et al.* (2003) reviewed the effect of toxic phytoplankton on euphausiids, reporting that the smaller *E. pacifica* has bigger weight-specific ingestion and higher filtration rates than the larger *T. spinifera,* but both feed at similar rates from toxic and non-toxic *Pseudo-nitzschia* phytoplankton. They did not observe an immediate effect by toxic *Pseudo-nitzschia* on both species. However, like in copepods, it is expected that toxic phytoplankton should affect primarily the brood size and/or hatching success of euphausiid embryos rather than cause mortality of the juveniles or adults.

The daytime feeding activity of *E. pacifica* in northeastern Japan is low even when food organisms are abundant in the top 50 m of the ocean. Thus, the feeding rhythm of this species is explained by decreased feeding activity during the day, rather than by reduced food availability (Nakagawa *et al.*, 2003). Hu (1978) reported a strong relationship between vertical migration patterns and diet in four species of mesopelagic euphausiids in Oahu, Hawaii. *Thysanopoda aequalis* and *T. monocantha*, which are strong diel vertical migrators, showed a marked increase in stomach weight at night when exposed to a relatively large diel change in prey density. *Thysanopoda pectinata*, a moderate vertical migrator, showed constant stomach weight throughout day and night, while *Nematobrachion sexspinous*, a weak or non-migrator, showed increased stomach weight during the day, presumably with small change in prey density. The most abundant prey in the stomach of these euphausiids were copepods, microplankton, euphausiids, decapods, chaetognaths and, rarely, fish larvae. Similar patterns have been observed for other mesopelagic and epipelagic euphausiids in the California Current System (Brinton, 1967).

Micronektonic shrimp masticate their prey into pieces with mandibular teeth, which has presented a barrier to attempts to conduct quantitative studies of their feeding habits. This feeding behavior is also common with squids. Micronektonic shrimp consume a wide variety of prey compared to pelagic mysids or euphausiids (Table 6.1). Although they feed mainly on crustaceans (such as copepods), migratory shrimp species have also been found to consume diatoms, protozoans, chaetognaths, and even small fish (Foxton and Roe, 1974; Heffernan and Hopkins, 1981; Nishida *et al.*, 1988; Flock and Hopkins, 1992; Toczko, unpubl. data). Non-migrant micronektonic shrimps generally feed on amorphous particulate organic material derived from living organisms in the water column (Walters, 1976; Nishida *et al.*, 1988; Flock and Hopkins, 1992). As stated for myctophids, only the migratory species actively consume zooplankton in the epipelagic zone (Omori, 1969; Foxton and Roe, 1974; Donaldson, 1975 Walters, 1976; Heffernan and Hopkins, 1981) and are thought to contribute to the dynamics of the oceanic ecosystems because of their high abundance and productivity.

The diets of pelagic mysids are poorly known compared to other pelagic crustaceans (Table 6.1), but they are believed not only to feed mainly on crustaceans (euphausiids and copepods), but are also known to feed on coelenterates (Toczko *et al.*, unpubl. data).

Table 6.1 Previous studies on feeding patterns for decapods, euphausiids, and mysids.

	Decapods	Mysids	Euphausiids	Unidentified Crustaceans	Copepods	Fish	Coelentrates	Chaetognaths	Mollusca	"green detritus"	Marine Snow (?)	Cannibals	Foraminiferans & radiolarians	Tintinnids	Amphipods	Ostracods	Coccolithophores	Limacina	Diatoms	Authors*
Decapods																				
Gennadas			X		X					X										1, 5, 6, 9
Bentheogennema	X			X	X	X	X	X			X		X	X						6, 4, 10
Sergia	X		X		X	X					X		X		X	X				1, 2, 5, 10
Sergestes		X	X	X	X		X			X	X		X	X	X	X				2, 4, 5, 8, 9, 10, 13
Acanthephyra	X	X	X	X	X	X		X			X		X		X	X				4, 5, 9, 10
Systellaspis	X	X	X	X	X	X	X					X	X							4, 5, 9, 10
Pasiphaea			X	X	X			X			X									10, 13
Notostomus	X	X	X				X													4
Hymenodora	X	X	X	X	X		X	X			X		X	X	X					4, 10
Physetocharis					X			X		X	X					X				9, 10
Euphausiids																				
Euphausia				X	X			X		X	X		X	X	X	X	X		X	7, 11, 12, 14
Thysanoessa				X	X			X	X	X			X	X	X	X	X		X	7, 11, 12
Tessarabrachion				X					X				X							7
Stylocheiron				X						X									X	7, 11
Thysanopoda				X		X	X	X	X	X			X	X					X	7, 11
Bentheuphausia				X			X	X					X	X					X	7, 11
Nematoscelis				X				X		X			X	X	X				X	7
Nematobrachion				X		X		X					X		X				X	7, 11
Mysids																				
Gnathophausia																				3, 5, 7
Eucopia			X	X	X		X						X							3, 5, 7
Boreomysis				X															X	3, 5, 7
Dactylambylops																				7
Meterythrops																				3, 5, 7
Pleurerythrops																				7

Feeding is described to genus level.

*List of authors below corresponds to numbers in right-hand column. (modified from Toczko *et al.*, unpubl. MS)

1 - Mincks *et al.* (2000)	6 - Heffernan and Hopkins (1981)	11 - Mauchline and Fisher (1969)
2 - Flock and Hopkins (1992)	7 - Mauchline (1980)	12 - Ponomareva (1963)
3 - Krygier and Murano (1988)	8 - Omori and Gluck (1979)	13 - Renfro and Pearcy (1966)
4 - Nishida *et al.* (1988)	9 - Foxton and Roe (1974)	14 - Dilling *et al.* (1998)
5 - Roe (1984)	10 - Omori (1974a)	

6.1.3 Cephalopod micronekton

In general, cephalopods are active, fast-moving predators. To support this life-history strategy, *i.e.*, fast growth, short lifespan, and semelparous reproduction, cephalopods are voracious predators and feed on a wide range of prey which enables them to maintain both high growth and metabolic rates (Boucher-Rodoni and Boucaud-Camou, 1987). Morphologically, cephalopods possess an extraordinary set of adaptations to facilitate prey handling and enable opportunistic feeding (Rodhouse and Nigmatullin, 1996).

6.2 Estimating the Impact of Micronekton Predation on Zooplankton

Estimating the impact of micronekton predation on zooplankton is essential to understanding the dynamics of energy flow from mesozooplankton to higher trophic levels in oceanic ecosystems because of the huge amount of micronekton biomass and their intermediate size range. As stated above, quantitative studies on the feeding habits of micronektonic squids and shrimps are difficult due to mastication of prey, and species-specific feeding behaviors. For example, some squid, such as *Todarodes pacificus*, sever the head of fish prey and feed only on the body. Some deep-sea squid have been shown to feed only on fish viscera (K. Kawaguchi, pers. observ.).

Among the micronekton, myctophids are believed to be the most important consumers of crustacean zooplankters, and act as competitors for prey with small pelagic fishes (such as sardine, anchovy, and saury) and the juveniles of various larger-sized oceanic fishes, such as tuna and salmon.

6.2.1 Predation by micronektonic fish

Estimates of daily rations have been compiled for several species, based on analyses of diel changes in their stomach contents (Baird *et al.*, 1975; Clarke, 1978; Hopkins and Baird, 1985; Dalpadado and Gjøsaeter, 1988; Gorbatenko and Il'inskii, 1992; Pakhomov *et al.*, 1996; Moku *et al.*, 2000; Watanabe *et al.*, 2002). As the estimation methods differed between studies, direct comparison among species is difficult. In general, however, the values obtained ranged from about 0.1 to 4.5% of body weight per day, in dry weight (Table 6.2). All of the early studies dealt with the tropical and subtropical species since they feed mainly in the upper productive layer at night (which makes estimating evacuation time easier than for subarctic and transitional species). For the subarctic and transitional species (Table 2.1), feeding behaviors have been actively studied in the eastern North Pacific since the late 1960s (Paxton, 1967a; Collard, 1970; Borodulina, 1972; Tyler and Pearcy, 1975; Pearcy *et al.*, 1979a; Moku *et al.*, 2000).

Some subarctic myctophid species are active feeders both day and night, which hinders the estimation of their daily ration (because of the lack of a diel feeding rhythm). However, in the early 1990s, Gorbatenko and Il'inskii (1992) estimated the rations of two *Stenobrachius* species in the subarctic waters of the Bering Sea (Table 6.2). In the western North Pacific, prey species analyses were made for the SAW and TrW species in the 1980s (Gordon *et al.*, 1985; Kawamura and Fujii, 1988). Moku *et al.* (2000) examined the feeding habits and diel feeding chronology of the most abundant subarctic myctophids: *Stenobrachius leucopsarus* (typical Type 3 semi-migrant swimming up to the 20–200 m layer at night; for the migration pattern, see subsection 3.1.2), *Diaphus theta* (typical Type 2 midwater migrant swimming up to the 20–100 m layer), and *S. nannochir* (typical Type 5 non-migrant) during summer in the transitional waters of the western North Pacific. They estimated daily rations to be 3.3, 1.8, and 0.14% of dry body weight, respectively. The value for the typical diel vertical migrant is the highest, followed by the semi-migrant, and then the non-migrant, suggesting that the strongest feeding impact on epipelagic zooplankton would be from vertical migrants.

Once daily rations have been obtained, the feeding impact of micronektonic fish on zooplankton can be calculated using the estimated zooplankton and myctophid biomass. In this regard, it is urgent to develop a set of reliable sampling methods that allow the above estimates to be calculated. In the eastern Gulf of Mexico, Hopkins and Gartner (1992) estimated that myctophids consume about 2% of the mesozooplankton biomass in the upper 200 m every night. In the Southern Ocean,

Table 6.2 Daily rations of myctophid fishes in percent of body weight based on worldwide literature.

Species	Daily Ration (%)	Region	Reference
Benthosema pterotum	4.5[a]	Indian Ocean	Dalpadado and Gjøsaeter (1988)
Diaphus taaningi	0.8[a]	Cariaco Trench	Baird *et al.* (1975)
Diaphus theta	3.3[a]	western North Pacific	Moku *et al.* (2000)
Hygophum proximum	5.7[a]	central Pacific	Clarke (1978)
Lampanyctus alatus	2–4[b]	Gulf of Mexico	Hopkins and Baird (1985)
Stenobrachius leucopsarus	1.1[c]	Bering Sea	Gorbatenko and Il'inskii (1992)
Stenobrachius leucopsarus	1.8[a]	western North Pacific	Moku *et al.* (2000)
Stenobrachius nannochir	1.0[c]	Bering Sea	Gorbatenko and Il'inskii (1992)
Stenobrachius nannochir	0.14[a]	western North Pacific	Moku *et al.* (2000)
4 species (antarctic and subantarctic)	0.24–3.92[a]	Southern Ocean	Pakhomov *et al.* (1996)
8 species (temperate and subtropical)	0.23–4.4[a]	Southern Ocean	Pakhomov *et al.* (1996)

[a]dry weight basis; [b]ash-free dry weight basis; [c]wet weight basis

myctophids are estimated to feed on 5 to 20% of zooplankton biomass standing stock in the upper 300-m layer every day (Pakhomov *et al.*, 1999). In the Kuroshio region, Watanabe *et al.* (2002) estimated that the four species of surface-migratory myctophids (Fig. 6.1) consumed 0.9–10.1% (usually 1–4%) of the zooplankton biomass in the upper 150 m each night during 1971–1984 (although they likely underestimated the biomass of active zooplankters, like euphausiids and amphipods, since their data were collected with vertical North Pacific standard plankton (NORPAC) net tows).

Assuming a P/B ratio of 7% per day for copepods in the Southern Ocean, Pakhomov *et al.* (1999) estimated that the most dominant myctophid species, *Electrona carlsbergi*, would consume 1.3 to 16.8% of daily copepod production per day. If the maximum biomass for *E. carlsbergi* observed by Filin *et al.* (1991) is adopted, the daily consumption ratios calculated would be 54 to 77% of the daily copepod production. The above estimates in the Southern Ocean would be low since they were based on the assumption that sampling efficiency of myctophids by the trawl was 100%.

Using the biomass of the diel migrant myctophid estimated by Watanabe *et al.* (1999) for the western transitional region, Moku and Hidaka (2002) estimated a daily feeding rate of the myctophids in the upper 200 m to be 32 mg C m^{-2} day^{-1}. This feeding impact accounts for 110–290% of the zooplankton production (or 1.9–5.1% of the zooplankton biomass) reported in the study area by Ikeda and Motoda (1978) and Odate (1994). However, these values should probably be considered underestimates since many of the surface-migratory myctophids, especially those in the genera *Symbolophorus* and *Tarletonbeania,* were not effectively collected by the stern trawl used. Estimates of zooplankton biomass were based upon vertical NORPAC net tows, and should also be considered an underestimate for the larger crustaceans, such as euphausiids and amphipods (due to their ability to avoid smaller nets) that may be important prey items.

6.3 Predators

Euphausiids, mesopelagic fishes, and other micronekton are pivotal components of marine ecosystems. They play important roles due to their substantial biomass, widespread and ubiquitous occurrence, and intermediate body sizes between mesozooplankton and larger nektonic organisms. In addition, their unique DVM behavior means that they also play an indispensable role in transporting organic material between the productive euphotic, and less productive, mesopelagic zones. The diets of many important predators in the North Pacific have been effectively analyzed by morphology of otoliths for fishes (Ohizumi *et al.*, 2001) and beaks for squids (Kubodera and Furuhashi, 1987). Endo *et al.*

(2000) summarized the role of euphausiids, mainly *Euphausia pacifica,* in the marine food webs for Japan, Canada and the Antarctic waters, including the demersal and pelagic environments. A summary of the diets of major predators is presented by area in Table 6.3. The following sections are organized by major predator groupings.

6.3.1 Cephalopods

Limited data are available on cephalopods in the PICES area. Watanabe *et al.* (2004) found substantial numbers of myctophid otoliths in the stomachs of the flying squid *Ommastrephes bartramii* caught in the transitional zone of the northwestern North Pacific (NWP) (35–39°N, 155–175°30′E), and they were identified as *Symbolophorus californiensis, Protomyctophum thompsoni, Ceratoscopelus warmingii*, and *Electrona rissoi.* The authors also found other micronekton, such as euphausiids and small squids of both subarctic and TrD origin. Yamamura (unpubl. data) examined stomachs of the Japanese common squid *Todarodes pacificus* and found this species preyed on *Euphausia pacifica,* unidentified myctophids, and firefly squid *Watasenia scintillans.*

6.3.2 Elasmobranchs

The ingestion of euphausiids and micronekton has been recorded only from relatively small-sized shark species. Baba *et al.* (1987) examined diets of the three species of dogfish sharks (family Squalidae) from central Japan waters and found firefly squids *W. scintillans* and *Enoploteuthis chunii* in all three. Tanasichuk *et al.* (1991) identified the euphausiids *T. spinifera* and *E. pacifica* from the stomachs of spiny dogfish caught near Vancouver Island, British Columbia, whereas Yamamura and Kubodera (unpubl. data) found three common species of myctophids from dogfish caught in the Oyashio–Kuroshio Transition area. The blue shark *Prionace glauca* also ingests euphausiids, along with myctophids, in the Gulf of Alaska and NWP, in spite of its relatively large body size (LeBrasseur, 1966; Kono, 1983). In the central North Pacific, Seki (1993) reported that small micronektonic myctophids and gonatid squids dominated the diet of young blue sharks (<65 cm precaudal length). Watanabe and Kubodera (unpubl. data) identified beaks of *Gonatus onyx* and *Taonius pavo*, ingested by blue sharks in the NWP. *Rhincodon typus* and *Mobula japonica* and *M. thurstoni* feed almost exclusively on swarms of the subtropical euphausiid *N. simplex* in the southern part of the California Current System.

6.3.3 Osteichthyes

The salmonids, especially in their adult phase in the open North Pacific, can be considered primarily as micronektonic feeders on euphausiids, fishes, and squids (Brodeur, 1990). Steelhead trout, which migrate to the ocean from fresh water, depend chiefly on micronekton and euphausiids. Pearcy *et al.* (1988) identified three species of euphausiids, fishes, and squids from the stomachs of steelhead collected in the Gulf of Alaska, whereas Kono (1983) found two species of squids in steelhead from the NWP. They pointed out that euphausiids were more important as prey when primary productivity was locally high due to upwelling and cyclonic circulation near the center of the Alaskan Gyre and Ridge Domain.

Chum salmon have unique food habits among the Pacific salmon in that they depend more upon gelatinous plankton and pteropods. Despite this, Pearcy *et al.* (1988) identified two myctophids, *Protomyctophum thompsoni* and *Stenobrachius leucopsarus* (which do not undertake diurnal vertical migration), suggesting that chum salmon feed at depths > 200 m during the day.

Masou salmon, endemic to the eastern Pacific, are known to persist over the continental shelf during its oceanic migration, where they feed chiefly on micronekton. Yamamura (unpubl. data) found that masou salmon off southeastern Hokkaido Island ingest euphausiids *Diaphus theta* and *W. scintillans*. Andrievskaya (1958) found that euphausiids *T. longipes, T. inermis, T. spinifera*, and *E. pacifica* were the most important prey item (~ 25%) for sockeye salmon in three out of six areas in the NWP, whereas no micronekton were found in their guts. Euphausiids were also important for juvenile sockeye salmon off Oregon and Washington, accounting for >15% in weight of the total diet (Brodeur and Pearcy, 1990).

Pink salmon have diverse diets, including both euphausiids and micronekton. Gorbatenko and Chuchukalo (1989) found that pink salmon from the Okhotsk Sea ingested *T. longipes* and *T. spinifera*, but that they constituted only 8.2% in wet weight (WW) of the total diet.

In the coastal area of the California Current, Brodeur and Pearcy (1990) found that euphausiids (mainly *E. pacifica*) represented >50% WW of the total diet of juvenile coho salmon. Pearcy *et al.* (1988) found that the major prey of coho salmon were gonatid squids in the Subarctic Current region, whereas euphausiids and myctophids were also important in the Alaskan Current and the Ridge Domain of the Gulf of Alaska. Juvenile coho in the California Current area fed chiefly (>70%) on fishes, but due to the shallow coastal distribution, myctophids constituted only trace amounts (<0.1%), whereas euphausiids (*E. pacifica* and *T. spinifera*) accounted for about 10% of the diet (Brodeur and Pearcy, 1990). Chinook salmon are piscivorous in their coastal phase, depending less on mesozooplankton, compared with other *Oncorhynchus* spp. Brodeur and Pearcy (1990) reported that juvenile coho in the California Current coastal area fed mainly (88%) on fishes, whereas euphausiids accounted for <5%. In their oceanic phase, chinook salmon depend mainly upon squids such as *Gonatus* and *Berrytheuthis* (Pearcy *et al.*, 1988).

Gadiform fishes are the most important predators of euphausiids and micronekton in continental shelf and slope areas. Brown hakeling, *Physiculus maximowiczi,* and threadfin hakeling, *Laemonema longipes,* are dominant species over the upper shelf and upper slope, respectively. Both depend primarily on euphausiids and micronekton in the Oyashio and Oyashio–Kuroshio Transition. Yamamura and Inada (2001) identified at least two, seven, and three species of micronektonic shrimp, fish and squids, respectively, from the stomachs of threadfin hakeling in the Oyashio–Kuroshio Transition.

The diet of walleye pollock has been studied extensively throughout the North Pacific Ocean, however, most studies are seasonal and cover only limited ontogenetic stages of the pollock life history. The exceptions are the studies by Dwyer *et al.* (1987) and Mito *et al.* (1999) in the eastern Bering Sea, which were exceptionally comprehensive, covering entire ontogenetic stages and seasons. Euphausiids were more important as prey during spring and summer, and for small-sized fishes. Mito *et al.* (1999) revealed a geographic variation in pollock diet in which euphausiids were more important in the southeastern Bering Sea than in the northeastern and southern Aleutian Basin. Yoshida (1994) studied the diet of pelagic pollock caught commercially in the central Bering Sea, although only three species of *Thysanoessa* and no *E. pacifica* were found. A recent study of walleye pollock diets by Yamamura *et al.* (2002) in the Oyashio is noteworthy in terms of both sample size and fidelity in prey identification. They found that euphausiids were important prey throughout the year for juvenile (<200 mm SL) pollock, except during spring, when they fed chiefly on the copepod, *Neocalanus cristatus. Euphausia pacifica* was the predominant species consumed, accounting for >80% of euphausiids ingested. Although >20 species of micronekton were identified, *D. theta* and *W. scintillans* were most important, with two *Lampanyctus* spp. being of secondary importance. In the Japan/East Sea, pollock dependence on euphausiids (mainly *T. longipes*) was low during April and October 1993 (<16%), but generally high (>70%) during April 1994 (Kooka *et al.*, 1997). In the Gulf of Alaska, the only feeding data available are for age-0 pollock. Brodeur (1998) found age-0 pollock ingested four species of *Thysanoessa* and *Euphasia.* This study also examined prey selection and revealed that age-0 pollock showed an extensive preference for euphausiids. The importance of micronektonic organisms as a food source for demersal fishes that live on the continental slope has been well known; Yamamura *et al.* (1993a) reported predation on the micronektonic squid *Watasenia scintillans* by 13 species off the coast of Japan.

Table 6.3 Main predators of various micronektonic groups found in each geographic area.

Predator Common Name	Predator Scientific Name	Area	Euphausiids	Shrimp	Fish	Squid	Reference
Cephalopods							
Flying squid	*Ommastrephes bartrami*	NWP			Sca, Ptom, Cwa, Eri	Gbe, Goy, Gpy, Gmi, Ban, Gbo, Hdo	Watanabe *et al.* (2004)
			unid.		Diap	Wsc	Naito *et al.* (1977)
Firefly squids	*Watasenia scintillans*	J/ES	Epa				Hayashi and Hirakawa (1997)
Japanese common squid	*Todarodes pacificus*	OY	Epa		Myct	Wsc	Yamamura (unpubl. data)
Elasmobranchs							
Fuji-kujira shark	*Etmopterus lucifer*	OYKT	unid.	Ssi, Acan	Dth, Ljo, Njp, Cwa	Ech, Wsc	Baba *et al.* (1987); Yamamura (unpubl. data)
	E. unicolor	OYKT			unid.	Ech, Wsc	Baba *et al.* (1987)
	Centroscyllium ritteri	OYKT	unid.		Diap	Ech, Wsc	Baba *et al.* (1987)
Spiny dogfish	*Squalus acanthias*	NEP	Tsp, Epa				Tanasichuk *et al.* (1991)
		OYKT		Ssi	Dth, Ljo, Njp	Wsc, Ech	Yamamura (unpubl. data)
Blue shark	*Prionace glauca*	NWP	Epa		Myct		Kono (1983)
		NWP			Sca	Gpy, Goy	Watanabe and Kubodera (unpubl. data)
		GOA	unid.		Myct		LeBrasseur (1966)
Osteichthyes							
Herring	*Clupea pallasii*	OY, OYKT	Epa				Yamamura *et al.* (1998)
	C. harengus	NEP	Epa, Tsp				Robinson (2000)
		GOA	Epa, Tra				Coyle and Paul (1992)
Sardine	*Sardinops melanostictus*	OYKT	Epa				Yamamura (unpubl. data)
Capelin	*Mallotus villosus*	EBS	Tra				Naumenko (1986)
		GOA	unid. egg				Coyle and Paul (1992)
Steelhead trout	*Oncorhynchus mykiss*	GOA	Tlo, Tsp, Epa		Nem, Ste, Tcr	Gon, Gmi, Gbo, Ban	Pearcy *et al.* (1988)
		NWP				Gmi, Ban	Kono (1983)
Masou salmon	*O. masou*	OY	unid.		Dth	Wsc	Yamamura (unpubl. data)
Sockeye salmon	*O. nerka*	GOA	Tlo, Tsp, Tim, Epa		Nem, Ptom, Sle, Sna		Pearcy *et al.* (1988)
		NWP	Tim, Tlo, Tsp, Epa		Lri		Andrievskaya (1958)
		CC	Epa, Tsp				Brodeur and Pearcy (1990)
Pink salmon	*O. gorbuscha*	GOA	Tlo, Tsp, Epa		Sle, Sna, Tcr	Gon, Gmd, Gmi, Ban	Pearcy *et al.* (1988)
		NWP	Epa		Myct		Kono (1983
		OK	Tlo, Tsp				Gorbatenko and Chuchukalo (1989)
		NWP	Tlm, Tlo, Tsp, Epa		Lri	Gon, Ban	Andrievskaya (1958); Kono (1983)
Chum salmon	*O. keta*	GOA	Tlo, Tsp, Epa		Pth, Sna, Lri	Gonat	Pearcy *et al.* (1988)
		OK	Tlo, Tsp				Gorbatenko and Chuchukalo (1989)
		NWP	Tim, Tlo, Tsp, Epa		Lri, Sle	Gonat	Andrievskaya (1958); Kono (1983)
		CC	Epa, Tsp				Brodeur and Pearcy (1990)
Coho salmon	*O. kisutch*	GOA	Tlo, Tsp, Epa		Sle, Sna, Lri, Tcr	Gon, Gmd, Gmi, Gbo, Ban	Pearcy *et al.* (1988)
		NWP	Tlo			Gmi, Ban	Kono (1983)
Coho (juvenile)		CC	Epa, Tsp				Brodeur and Pearcy (1990)

Table 6.3 Continued

Predator Common Name	Predator Scientific Name	Area	Euphausiids	Shrimp	Fish	Squid	Reference
Chinook salmon	*O. tshawytscha*	GOA			Sna	Gon, Ber	Pearcy *et al.* (1988)
		NWP	Tlo			Ban	Kono (1983)
Chinook (juvenile)		CC	Epa, Tsp				Brodeur and Pearcy (1990)
Pacific saury	*Cololabis saira*	NWP	unid.				Odate (1977)
Pacific hake	*Merluccius productus*	CC	Epa, Tsp		Myct		Brodeur et al. (1987); Tanasichuk *et al.* (1991)
Brown hakeling	*Physiculus maximowiczi*	OY	Epa	Ssi	Mmu, Njp, Dth		Yamamura and Inada (2001); Yamamura *et al.* (1998)
Threadfin hakeling	*Leamonema longipes*	OY, OYKT	Epa, Esi, Tlo	Ssi, Bbo	Lsh, Boc, Bmi, Ljo, Lre, Dth, Paral	Wsc, Ech, Gbo	Yamamura and Inada (2001); Yamamura *et al.* (1998)
Pacific cod	*Gadus macrocephalus*	OY, OYKT	Epa	Ssi, Bbo	Mmu, Dth, Ljo, Lre, Lni	Wsc	Yamamura and Inada (2001); Yamamura *et al.* (1998; 1993b)
Walleye pollock	*Theragra chalcogramma*	OY	Epa, Tlo, Tin	Ssi, Bbo	Lsh, Loc, Pmi, Bpa, Ljo, Lre, Dia, Dth, Myc, Mas, Tta, Sca	Wsc, Bma, Goy, Gmk	Yamamura *et al.* (2002)
		GOA	Epa,Tim,Tsp,Tlo				Brodeur (1998)
		J/ES	Epa, Tlo, Tin		Mmu		Kooka *et al.* (1997)
		OK	Epa, Tra, Tim, Tlo		Myct	Gon	Gorbatenko and Chuchukalo (1989)
		EBS	unid.		Myct		Dwyer *et al.* (1987); Mito *et al.* (1999)
Pacific pomfret	*Brama japonica*	NWP	unid.		Myct, Paral		Wada and Murata (1985)
		NWP	Epa		Tar, Paral	Gma, Gbe, Ban	Kono (1983)
		NWP,NEP				Gbo	Watanabe and Kubodera (unpubl.)
		GOA	Gonat		Tcr		Pearcy *et al.* (1993)
Chub mackerel	*Scomber japonicus*	NWP	Epa, Tlo, Ndi			Gon	Kono (1983)
		CC	Epa				Brodeur *et al.* (1987)
Skipjack tuna	*Katsuwonus pelamis*	NWP	Esi, Ndi			Enop	Iizuka *et al.* (1989); Kono (1983)
Albacore tuna	*Thunnus alalunga*	NWP	Epa		Myct, Paral	Abf, Gon, Gbo	Kono (1983)
		NWP			Mmu	Gbo	Watanabe and Kubodera (unpubl. data)
Hairtail	*Trichiurus haumela*	YS	unid.				Wei (1980)
Atka mackerel	*Pleurogrammus monopterygius*	NWP	unid.		Ptom, Sle, Sna, Boc, Lsh, Ggr		Orlov (1997d)
Yellowtail rockfish	*Sebastes flavidus*	NEP	Epa, Tsp, Tlo	Ssi	Sle, Dth, Tcr, Sca, Pcr, Aac	Gon, Abf	Brodeur and Pearcy (1984)
Canary rockfish	*S. pinniger*	NEP	Epa, Tsp	Ssi	Sle, Tcr		Brodeur and Pearcy (1984)
Ocean perch	*S. alatus*	NEP	Epa, Tsp	Ssi			Brodeur and Pearcy (1984)
Splitnose rockfish	*S. diploproa*	NEP	Epa, Tsp	Ssi	Sle		Brodeur and Pearcy (1984)
Darkblotched rockfish	*S. crameri*	NEP	Epa, Tsp	Ssi			Brodeur and Pearcy (1984)
Arrowtooth flounder	*Atheresthes stomias*	EBS	Tra, Tim				Yang and Livingston (1986)
Kamchatka flounder	*A. evermanni*	EBS	Tra, Tim				Yang and Livingston (1986)
Greenland halibut	*Reinhardtius hippoglossoides*	EBS	Tim		Sle, Lst	Gop, Gon	Yang and Livingston (1988)

Table 6.3 Continued

Predator Common Name	Predator Scientific Name	Area	Euphausiids	Shrimp	Fish	Squid	Reference
SEABIRDS							
Bonin petrel	*Pterodroma hypoleuca*	EQP			Ster, Myct		Harrison *et al.* (1983)
Bluwer's petrel	*Bulweria bulwerii*	EQP			Ster, Myct		Harrison *et al.* (1983)
Sooty shearwater	*Puffinus griseus*	NP	unid.		Myct	Ban	Shiomi and Ogi (1992)
		CC	Tsp			Gon, Obj	Chu (1984)
Short-tailed shearwater	*P. tenuirostris*	EBS	Tlo, Tra				Ogi (1980a); Ogi *et al.* (1980)
Leach's storm-petrel	*Oceanodroma leucorhoa*	OY	Epa, Tlo, Tim				Watanuki (1985)
Common murre	*Uria aalge*	EBS	Tra, Tlo				Ogi and Tsujita (1973)
Thick-billed murre	*U. lomvia*	NP	Tim, Tlo		Myct	Ban, Gbo	Ogi (1980b)
Cassin's auklet	*Ptychoramphus aleuticus*	NEP	Tsp, Tlo, Tra, Epa, Ndi	Ppa			Gaston and Jones (1998); Vermeer (1981); Vermeer *et al.* (1985)
		CC	Epa, Tsp, Ndi, Nsi				Ainley *et al.* (1996a)
Parakeet auklet	*Cyclorhynchus psittacula*	NEP, EBS	Tim, Tra				Gaston and Jones (1998)
		BS	Tim		Myct		Hunt *et al.* (1998)
Least auklet	*Aethia pusilla*	GOA	Thys				Hunt and Harrison (1990)
		EBS	Thys				Springer and Roseneau (1985)
Tufted puffin	*Fratercula cirrhata*	NWP	unid.		Lst		Ogi (1980a,b)
Marbled murrelet	*Brachyramphus marmoratus*	NEP	Tsp, Epa				Sealy (1975)
Ancient murrelet	*B. antiquus*	NEP	Epa, Tsp, Tlo				Sealy (1975); Vermeer *et al.* (1985)
Crested auklet	*Aetia cristatella*	GOA	Thys				Bédard (1969)
		BS	Tim, Tsp				Hunt *et al.* (1998)
Whiskered auklet	*A. pygmaea*	NEP	Tim				Gaston and Jones (1998)
PINNIPEDS							
Northern fur seal	*Callorhinus ursinus*	NEP			Myct	Gonat	Perez and Bigg (1986)
		GOA				Gonat	Perez and Bigg (1986)
		EBS				Gbo	Perez and Bigg (1986)
		EBS			Myct, Lsc	Bma, Gbo	Sinclair *et al.* (1994)
		OY			Njp, Diap	Wsc	Wada (1971)
Ringed seal	*Phoca hispida*	EBS	Thys				Lowry *et al.* (1980)
			unid.				Lowry *et al.* (1980)
Spotted seal	*P. vitulina*	OK	Tim				Goto (1999)
Ribbon seal	*P. fasciata*	OK			Ljo		Goto (1999)
Elephant seal	*Mirounga angustirostris*	NEP, CC				Gon, Gop	Condit and Le Boeuf (1984)
California sea lion	*Zalophus californianus*	CC			Myct		Lowry *et al.* (1990)
Steller sea lion	*Eumetopias jubatus*	GOA				Gon	Pitcher (1981)

Table 6.3 Continued

Predator Common Name	Predator Scientific Name	Area	Euphausiids	Shrimp	Fish	Squid	Reference
CETACEANS							
Baleen whales							
Blue whale	*Balaenoptera musculus*	NWP	Tim, Nema				Tomilin (1967)
		NP	Tlo, Tsp, Tim, Epa				Nemoto (1959); Kawamura (1982); Smith and Adams (1988); Croll *et al.* (1998)
		OY	Epa				Nemoto (1959)
Bryde's whale	*B. edeni*	NWP, OY	Epa, Tim		Dth, Tta, Vni		Tamura and Fujise (unpubl.)
		NP	Epa, Esi, Tim, Ndi	Ssi	Mmu, Vni		Kawamura (1982)
Fin whale	*B. physalus*	BS	Tim				Hollis (1939)
		GOA	Epa, Tim, Tsp				Nemoto and Kasuya (1965)
		BS	Tsp				Hollis (1939)
		WBS	Tim				Rice (1977)
		NP	Epa, Tra, Tim,Tsp, Tlo, Tlo, Ndi	Ssi	Mmu, Vni, Tta		Kawamura (1973); Kawamura (1982)
		OK	Epa, Tra, Tim, Tlo, Tra				Nemoto (1959)
		OY	Epa				Nemoto (1959)
Minke whale	*Balaenoptera acutorostrata*	NWP	Epa, Tim, Tin, Tlo				Tamura et al. (1998)
		OK	Ep, Tlo, Tra, Tim				Nemoto (1959)
		OY	Epa				Nemoto (1959)
Humpback whale	*Megaptera novaeangliae*	BS	Tsp				Hollis (1939)
		WBS	Tim				Rice (1977)
		NP	Tlo, Tsp				Nemoto (1959)
		OY	Epa				Nemoto (1959)
Sei whale	*Balaenoptera borealis*	NP	Epa, Tgr, Tim, Tlo, Tsp, Ndi, Ngr	Ssi	Tta, Mmu		Kawamura (1973); Kawamura (1982)
		OY	Ep, Tim, Tlo				Nemoto (1959)
		EQP	Tgr		Mmu, Mas	Gon	Nishimoto (1952)
Northern Pacific right whale	*Eubalaena japonica*	OY	Epa				Nemoto (1959)
Toothed whales							
Baird's beaked whale	*Berardius bairdii*	OY, NWP			Sca, Dth, Mas, Sle, Ljo, Cwa	Gon, Ech, Ale, Hce, Hme, Hpf, Lre	Isoda (2000)
Sperm whale	*Physeter macrocephalus*	OYKT				Gbo, Gon	Kawakami (1976)
		NWP				Ale, Gfa, Gbe,Gmk, Goc, Csc	Kawakami (1980)
		BS, GOA				Gfa, Gbo, Gma, Goc	Okutani and Nemoto (1964)
		OYKT				Ale, Gma, Goc, Csc	Okutani (1976)
		NWP				Ech, Ale, Gbe, Gpy, Gmi, Hdo, Hco, Hme	Tamura and Fujise (unpubl. data)

Table 6.3 Continued

Predator Common Name	Predator Scientific Name	Area	Euphausiids	Shrimp	Fish	Squid	Reference
CETACEANS (cont.)							
Toothed whales (cont.)							
Dall's porpoise	*Phocoenoides dalli*	OK			Loc, Ptom, Sna, Lre, Ljo, Dth	Gmi, Gmd, Gbo, Gmk	Ohizumi (1998)
		NWP			Ptom, Eri, Sca, Njp, Cwa, Sle, Ljo, Dth	Afe, Gon, Gbe, Gbo	Ohizumi (1998); Ohizumi *et al.* (2003)
		OK			Lsc, Cwa, Sten, Lre	Wsc, Gon, Gma	Walker (1996)
Northern right whale dolphin	*Lissodelphis borealis*	NWP			Lsc, Cwa, Dgi	Ech, Gbo	Mori (1989)
Pacific white-sided dolphin	*Lagenorhynchus obliquidens*	NWP			Njp, Cwa, Dgi	Wsc, Afe, Gbe, Gpy	Mori (1989)
Pantropical spotted dolphin	*Stenella attenuata*	NWP			Cwa	Gon, Gpy, Ech, Afe	Mori (1989)
Striped dolphin	*S. coeruleoalba*	KCA		Bbo	Nem, Dgi, Diap, Ljo		Miyazaki (1973)
Risso's dolphin	*Grampus griseus*	NWP			Sev, Nre, Mmu	Ech, Ale, Hco, Lre	Isoda (2000)
Bottlenose dolphin	*Tursiops truncatus*	NWP			Sle	Wsc	Mori (1989)
Common dolphin	*Delphinus delphis*	NWP			Lsc, Boc, Iel, Eri, Njp, Cwa, Sle, Dgi, Ljo, Dth	Gon, Gbe, Gpy, Ech, Wsc, Abf	Mori (1989)
		NWP			Lsc, Mmu, Tta, Ptom, Sca, Mas, Njp, Llu, Lur, Cwa, Sle, Dgi, Lre, Ljo, Dth	Gon, Gbe, Gpy, Gmi, Ech, Wsc	Ohizumi *et al.* (1998)

BS = Bering Sea, CC = California Current, EBS = eastern Bering Sea, EQP = Equatorial Pacific, GOA = Gulf of Alaska, KCA = Kuroshio Current area, NP = North Pacific, NEP = Northeast Pacific, NWP = Northwest Pacific, OK = Okhotsk Sea, OY = Oyashio region, OYKT = Oyashio/Kuroshio Transition area, J/ES = Japan/East Sea, WBS = western Bering Sea, YS = Yellow Sea

Euphausiids

Epa	*Euphausia pacifica*
Esi	*Euphausia similis*
Ndi	*Nematoscelis difficilis*
Nsi	*Nematoscelis gracilis*
Nem	*Nematoscelis* sp.
Ppa	*Pasiphaea pacifica*
Tgr	*Thysanoessa gregaria*
Tim	*Thysanoessa inermis*
Tlo	*Thysanoessa longipes*
Tra	*Thysanoessa raschii*
Tsp	*Thysanoessa spinifera*
Thys	*Thysanoessa* sp.

Decapod crustaceans

Acan	*Acanthephyra quadrispinosa*
Bbo	*Bentheogenemma borealis*
Ssi	*Sergestes similis*

Fish

Aac	*Argyropelachus aculeatus*
Boc	*Bathylagus ochotensis*
Bmi	*Bathylagus milleri*
Cwa	*Ceratoscopelus warmingii*
Cal	*Cyclothone alba*
Diap	*Diaphus* sp.
Dgi	*Diaphus gigas*
Dku	*Diaphus kuroshio*
Dth	*Diaphus theta*
Eri	*Electrona rissoi*
Ggr	*Gonostoma gracile*
Iel	*Ichthyococcus elongatus*
Llu	*Lampadena luminosa*
Lur	*Lampadena urophaos*
Ljo	*Lampanyctus jordani*
Lni	*Lampanyctus niger*
Lre	*Lampanyctus regalis*
Lri	*Lampanyctus ritteri*
Lsh	*Leuroglossus schmidti*
Lst	*Leuroglossus stibilius*
Mmu	*Maurolicus muelleri*
Myct	Myctophids (unid.)
Mas	*Myctophum asperum*
Nem	*Nemichthys* sp.
Njp	*Notoscopelus japonicus*
Paral	Paralepidids (unid.)
Pcr	*Protomyctophum crockeri*
Ptom	*Protomyctophum thompsoni*
Ste	*Stenobrachius* sp.
Sle	*Stenobrachius leucopsarus*
Sna	*Stenobrachius nannochir*
Sca	*Symbolophorus californiensis*
Ster	Sternoptychidae
Tar	*Tarletonbeania* sp.
Tcr	*Tarletonbeania crenularis*
Vni	*Vinciguerria nimbaria*

Cephalopods

Ale	*Ancistrocheirus lesueuri*
Abf	*Abraliopsis felis*
Ban	*Berryetuthis anonychus*
Ber	*Berryteuthis* sp.
Bma	*Berryteuthis magister*
Csc	*Cranchia scabra*
Gonat	Gonatiids (unid.)
Gon	*Gonatus* sp.
Gbe	*Gonatus berryi*
Gfa	*Gonatus fabricii*
Gmd	*Gonatus madokai*
Gmi	*Gonatus middendorffi*
Gpy	*Gonatus pyros*
Gbo	*Gonatopsis borealis*
Goy	*Gonatus onyx*
Gmk	*Gonatopsis makko*
Gop	*Gonatopsis* sp.
Goc	*Gonatopsis octopedatus*
Enop	Enoploteuthidae
Ech	*Enoploteuthis chunii*
Hpf	*Helicocranchia pfefferi*
Hce	*Histoteuthis celataria*
Hco	*Histoteuthis coronainermis*
Hdo	*Histoteuthis dofleini*
Hme	*Histoteuthis meleagroteuthis*
Lre	*Licranchia reinhardti*
Obj	*Onychoteuthis borealijaponicus*
Tpa	*Taonius pavo*
Wsc	*Watasenia scintillans*

Diets of five rockfishes (*Sebastes* spp.) studied by Brodeur and Pearcy (1984) at the shelf break off Oregon showed that all depended primarily on euphausiids, especially *E. pacifica.* The heavy ingestion of euphausiids was attributed to fact that the migration of euphausiids to daytime depths typically found in the open ocean was restricted by the shelf at their study sites, and thus euphausiids were trapped in close proximity to near-bottom predators. Of the five species examined, yellowtail rockfish exhibited relatively high dependence (>15% by weight) on micronektonic fishes. Pereyra *et al.* (1969) and Bosley *et al.* (2004) found that yellowtail rockfish in Astoria Canyon consumed mainly euphausiids and mesopelagic prey (*S. leucopsarus* and *Pasiphae*) advected into the canyon from deep water. Yang and Livingston (1986, 1988) examined diets of two species of *Atheresthes* flounders and Pacific halibut. All three were primarily piscivorous, but also ingested euphausiids to some extent. Halibut also consumed *S. leucopsarus* and *L. schmidti*.

Simplified food webs that include micronekton have been constructed by Brodeur (1988), Pearcy (1991) and Brodeur *et al.* (1999), based on reviews of dietary studies for both the Subarctic and Transition Zone of the open North Pacific (Fig. 6.2). Food habits of pelagic fishes migrating across the Subarctic Boundary, such as Pacific pomfret (*Brama japonica*), skipjack tuna (*Katsuwonus pelamis*) and albacore tuna (*Thunnus alalunga*), were studied extensively by Kono (1983). He found that euphausiids and gonatid squids were important prey, along with pelagic forage fishes, such as Pacific sardine and anchovy. Myctophids, however, were far less important in their diets. The diets of Pacific pomfret in the Gulf of Alaska consisted of many micronektonic squid (mostly Gonatidae), euphausiids, and some myctophids such as *Tarletonbeania crenularis* (Pearcy *et al.*, 1993).

6.3.4 Seabirds

This topic has been reviewed extensively for the subarctic Pacific region by PICES Working Group 11 on Consumption of Marine Resources by Marine Birds and Mammals (Hunt *et al.*, 2000) and will, therefore, be only briefly considered in this review. In Hawaiian waters, Harrison *et al.* (1983) examined the diets of Bonin and Bluwer's petrels and found that both species depend primarily on fish, including sternoptychids and myctophids. Although shearwaters are one of the most abundant oceanic birds, information on their food habits is very limited. Shiomi and Ogi (1992) examined diets of sooty shearwaters in the North Pacific and reported that they are primarily piscivorous and rarely ingest euphausiids (<1% WW). Off northern California, midwater squids (*Gonatus* sp. and *Onychoteuthis borealijaponicus*) were important prey for sooty shearwaters, along with anchovy and rockfishes, (Chu, 1984). Ogi (1980a) examined stomachs of short-tailed shearwaters in the Okhotsk and Bering Seas, and the North Pacific, and found that euphausiids, (especially *T. raschii*) were important only in the eastern Bering Sea. Storm petrels and auklets are primarily planktivorous, reflecting their relatively small body size. Hunt *et al.* (1998) compared least, crested, and parakeet auklets along with the biophysical sampling near the Aleutian Islands, and found a well-partitioned foraging pattern in which only the crested auklet foraged upon euphausiids upwelled on the upstream side of a pass. Murrelets show mixed diets of mesozooplankton and fishes, but no midwater fishes and squids were reported as prey. In California during the pre-breeding season, and after the onset of upwelling, euphausiids (*E. pacifica* and *T. spinifera*) and juvenile rockfish (*Sebastes* spp.) became prevalent in the diet of murres. Diets were least diverse during the breeding season because of the dominance of rockfish, especially among murres foraging in mid- and outer-shelf habitats. Other important prey were also significant for commercial or sport fishing: *Engraulis mordax* and *Clupea harengus* in coastal waters, *Merluccius productus* and *Loligo opalescens* in mid- and outer-shelf waters. These results support a hypothesis that diet varies as a function of where murres forage. Hence, if the most characteristic prey of one habitat disappears, murres switch foraging areas, bringing a switch in diet. Owing to environmental changes in the region, murres may be losing the option of prey switching as a strategy to maintain an adequate intake of food (Ainley *et al.*, 1996b).

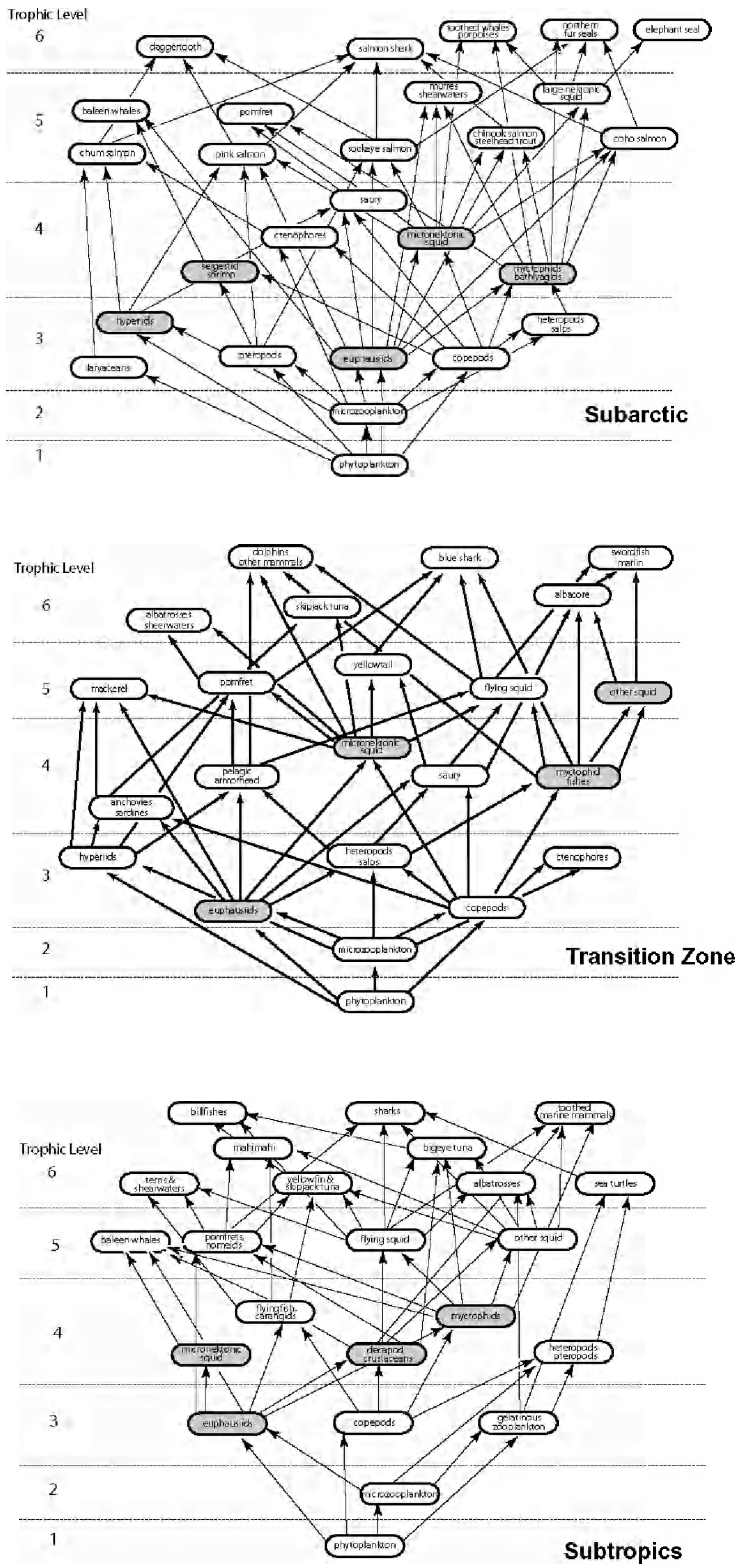


Fig. 6.2 Structure of North Pacific Ocean food webs. (from Brodeur *et al.*, 1999)

The diet of a planktivore, the Cassin's auklet *Ptychoramphus aleuticus*, in the Gulf of the Farallones, California, is strongly associated with the local climate and food availability. During the non-upwelling period, auklets fed on the small, energetically inferior, oceanic euphausiid *E. pacifica*, but following the spring transition, the auklets switched to small, juvenile fish (mostly *Sebastes* spp.) until these had grown too large for capture (Ainley *et al.*, 1996a). Thereafter, the auklets switched to the larger and energetically more valuable euphausiid, *T. spinifera*, which had become available upon the onset of upwelling. This general pattern was repeated each year, although some between-year variability among ancillary prey was evident. The decrease in the prevalence of *T. spinifera* in the diet fed to chicks from 1971 to 1991 is consistent with decreased intensity of upwelling in the region, as is the reduction in numbers of auklets in the region over the same period (Ainley *et al.*, 1996a).

6.3.5 Pinnipeds

Among the pinnipeds, the diets of northern fur seals have been studied most extensively. Perez and Bigg (1986) organized a data set on a substantial number (*n* = 18,404) of fur seal stomachs and revealed that they are primarily piscivorous and feed opportunistically. In their data set, myctophids occurred only in the northern California Current, and gonatiid squids were relatively important (30%) in the eastern Bering Sea. Northern fur seals in the Oyashio–Kuroshio Transition fed primarily on *Notoscopelus japonicus, Diaphus* spp. (probably *D. theta* and *D. kuroshio*) (Wada, 1971) and *W. scintillans*, along with threadfin hakeling, schooling pelagic fishes, and Japanese common squid.

Among the Pacific phocid seals, ringed seals depend on relatively small-sized animals including amphipods, euphausiids, and fishes (King, 1983). Lowry *et al.* (1980) found that euphausiids account for <3% of the diet, whereas saffron cod and shrimp were more important. Other seals feed primarily on fish on an opportunistic basis. Goto (1999) examined the stomach contents of spotted and ribbon seals along the Okhotsk Sea coast of Hokkaido Island and found *T. inermis* and *Lampanyctus jordani*, respectively. Elephant seals and Steller sea lions also prey mainly on relatively large-sized fish and cephalopods, so the ingestion of micronekton is very limited.

6.3.6 Cetaceans

Baleen whales

Only studies from the period of pelagic whaling have been available for reconstructing the diets of baleen whales. In the North Pacific a few species, including the blue whale *Balaenoptera musculus* depend primarily on euphausiids (Kawamura, 1982; Smith and Adams, 1988; Croll *et al.*, 1998). Other species such as fin, humpback, sei, and minke whales are basically piscivorous, and prey opportunistically upon abundant fish and squid (T. Tamura, pers. comm.). The available literature deals mostly with euphausiids ingested by whales, and includes *E. pacifica* and four species of *Thysanoessa* that were commonly consumed in the Gulf of Alaska, Bering Sea, Okhotsk Sea, and Oyashio Current area. Kawamura (1973, 1982) reported diets of sei and Bryde's whales, and identified *Maurolicus muelleri, Vinciguerria nimbaria*, and *Tarletonbeania taylori* as prey items. Recently, Tamura and Fujise (unpubl. data) studied minke whale diets in the North Pacific Ocean and found that the bulk (81%) of the diet was composed of saury *Cololabis saira*. Although *E. pacifica, T. inermis, T. inspinata*, and *T. longipes* were also identified, their total contribution was only around 5% of the diet.

Acevedo-Gutiérrez *et al.* (2002) concluded that the blue whale forages in relatively small areas (<1 km^2) and foraging lasts for more than one dive, indicating that euphausiids do not disperse. The high energetic cost of lunge-feeding confine them to short durations of submergence, and to areas with dense euphausiid aggregations, like the hot spots in frontal zones described by Etnoyer *et al.* (2004). Thus, because of their limited foraging time under water, these whales may be particularly vulnerable to perturbations in prey abundance.

According to Croll *et al.* (1998), the diving behavior of foraging blue whales is correlated to the distribution and density of euphausiid aggregations. These whales showed a stereotypical pattern, diving consistently and directly down to

150–200 m in the water column and performing a series of 1–4 min, 20–30 m vertical excursions on each dive, feeding exclusively upon euphausiids in proportions significantly different from the composition of euphausiids in net samples. Thus, blue whales concentrate their foraging activity on deeper layers of euphausiids during the day. Analysis of whale fecal samples revealed that blue whales in Monterey Bay, California, fed primarily upon *T. spinifera* (80% ± 22.6%) and *E. pacifica* (13% ± 26.4%); other euphausiids accounted for only 7% (±4.7%) of their diet. Euphausiid species composition within net samples collected during the same period consisted of 30.17% (±34.95%) *T. spinifera*, 68.32% (±34.75%) *E. pacifica*, and 1.51% (±2.56%) other species. They reported for the first time, an estimate of the magnitude of prey densities for large rorquals feeding on euphausiid patches having densities up to 4,400 individuals m^{-3} on the shelf-break of Monterey Canyon (Croll *et al.*, 1998). Thus, blue whales appear to be seeking out extremely dense aggregations of zooplankton to meet their metabolic needs (minimum required approximately 50 individuals m^{-3}). The annual migratory movements of California blue whales likely reflect seasonal patterns in productivity in other foraging areas (Etnoyer *et al.*, 2004). The authors recognized particularly the relevance of persistent thermal oceanic fronts in the North Pacific in the blue whale distribution and residence time; specifically, they showed how blue whales migrate from central California waters to the oceanic thermal front southwest of the Baja California peninsula (~23°N), considered a critical hot spot habitat for this species. This frontal zone, with persistence of more than 9 months, is considered a hot spot for the entire Northeast Pacific (Malakoff, 2004), but Etnoyer *et al.* (2004) reported such thermal fronts are rare, located in only 1% of the total area of the North Pacific Ocean. Regions with different seasonal upwelling patterns, and euphausiid species with different life history traits, will show temporal differences in peak euphausiid abundance. Due to their high total prey requirements, California blue whales likely migrate seasonally between dense, ephemeral euphausiid patches that appear in southern/central California waters in the summer and fall, the Gulf of California in the winter, and the central Baja California Pacific coast in the spring.

Toothed whales

Diets of toothed cetaceans are characterized by a diverse spectrum of prey items, with a typical individual containing >5 prey categories in its stomach. Recently, Japanese scientists have conducted extensive studies of the food habits of toothed whales, revealing the diversity and significance of micronektonic animals in diets. For instance, Ohizumi (1998) and Ohizumi *et al.* (2003) examined the stomach contents of Dall's porpoise from many areas of the North Pacific Ocean and presented geographical variation in species composition of micronektonic fishes. In the Oyashio Current, *N. japonicus, D. theta, L. jordani*, and *P. thompsoni* were predominant. Although *D. theta* was important throughout the North Pacific Ocean, other predominant species changed by subarea. Finally, the importance of *D. theta* was replaced by *S. leucopsarus* in the Bering Sea. They also identified >15 species of cephalopods from the stomach contents. Robison and Craddock (1983) found that Fraser's dolphins feed on micronektonic mesopelagic fishes. Sperm whales have been known for their preference for squids, and more than 20 species of midwater squids have been identified from the stomachs of sperm whales. Interestingly, no euphausiids have been found in the stomachs of toothed whales to date.

6.3.7 Human consumption

Some fisheries on myctophids have been carried out in the past and some restricted local consumption of myctophid fishes have also been reported (Gjøsaeter and Kawaguchi, 1980). Although the qualities of lipids and protein of myctophid fishes have been shown not to differ much from those of commercial fishes, the non-migratory species have wax and are therefore, not suitable for human consumption (Seo *et al.*, 1996, 1998; Saito and Murata, 1996). Euphausiids, mostly *Euphausia pacifica,* are currently consumed by people in Russia and Japan. Japan alone had an average annual catch of around 60,000 t between 1986 and 2000; about 6–7% was used for human consumption and for bait in sport fishing (Ichii, 2000). The euphausiid fishery is also developed in Canada and United States for aquaculture and the aquarium pet food industry (human consumption, negligible), with catches ranging from 40 to 580 t between 1983 and 1995.

6.4 Predation Rate

Only a few attempts have been made to estimate the consumption of euphausiids and micronekton by any particular group of fishes. Brodeur *et al.* (1992) estimated food consumption of juvenile coho and chinook salmon in the California Current area during the summers of 1981 to 1984, using both field data and bioenergetic modeling methods. Since juveniles of both species fed primarily on fishes, the estimated daily consumption of euphausiids was only about 0.13 kg km^{-2}. By calculating fractions of prey consumed daily by predators, they concluded that "food limitation" is unlikely for salmon during normal years. Of the 87 species examined for stomach contents, Yamamura *et al.* (1998) found that 24 species, representing >90% of the fish biomass, were highly dependent on *E. pacifica*, and the maximum consumption rate by the entire fish assemblage was estimated to be 7.52 kg km^{-2} d^{-1}. Although no estimates of euphausiid abundance were available, they noted that the annual estimate of consumption by the demersal fish community represented 15–64% of the commercial catch of *E. pacifica*, and concluded that euphausiid fisheries would have a considerable impact on demersal fish assemblages.

Robinson (2000) estimated euphausiid consumption by the seven most abundant fish species on the continental shelf off southwestern Vancouver Island for the month of August, from 1985 to 1997. The fish community during August was estimated to consume an average of 124 t km^{-2}, and Pacific hake and herring accounted for 60% and 30%, respectively, of the euphausiid consumption.

Yamamura and Inada (2001) evaluated the contribution of micronekton to the total diet of demersal fish assemblages in Oyashio–Kuroshio Transition. From 1989 to 1992, the average contribution of micronekton during May and November was estimated to be 35.7% and 35.5%, respectively. Although no consumption estimate was available directly from Yamamura and Inada (2001), the demersal fish assemblage in the deep layer (300–500 m) was estimated to consume 22.8 kg km^{-2} daily during May 1991, applying the parameters used in Yamamura *et al.* (1998).

Recently, Yamamura (2004) estimated the prey consumption rates of walleye pollock in the coastal Oyashio Current area using an age-structured trophodynamic model. The average annual consumption of euphausiids (mainly *E. pacifica*), fish micronekton, and small squid (mainly *W. scintillans*) by adult walleye pollock was estimated to be 22.2 ± 5.3 g m^{-2} yr^{-1}, 6.3 ± 1.6 g m^{-2} yr^{-1} and 3.0 ± 0.6 g m^{-2} yr^{-1}, respectively. Remarkably, all of these consumption estimates outstripped standing stock and annual production. He concluded that these prey are supplemented by active migration and passive transport from more oceanic areas.

Although no attempt has been made to estimate euphausiid/micronekton consumption by specific seabirds or marine mammals, total prey consumption during summer has been estimated for some regions of North Pacific (Hunt *et al.*, 2000). Zooplankton consumption rates by seabirds during the summer (92 days) in the eastern Bering Sea and Gulf of Alaska were high (55 and 44 t km^{-2}, respectively). Of these, more than half would be represented by euphausiids. Consumption estimates for marine mammals are shown in Table 6.4. It should be noted that 13.7 t of micronekton were consumed daily in the Kamchatka and Kuril Islands area. The greatest portion of the consumption was attributed to Dall's porpoise, northern right whales, and Pacific white-sided dolphins. Other areas of heavy summer consumption of micronekton (exceeding 20 t km^{-2}) included the western transition region, the Okhotsk Sea, and the Kuroshio/Oyashio Current regions. Based on substantial sampling throughout the North Pacific and the Bering Sea, Ohizumi *et al.* (2003) estimated that Dall's porpoises, alone, would consume approximately 4.7% to 6.5% of the biomass of mesopelagic fishes in the subarctic Pacific Ocean, and may account for almost a third of the mortality of micronekton in the region. They suggested that myctophids are a major energy pathway leading to Dall's porpoises in the subarctic Pacific.

Table 6.4 Food consumption (t km^{-2}) by marine mammals in PICES subregions during summer (122 days). (after Hunt *et al.*, 2000)

Region	Crustacean zooplankton	Small Squid	Mesopelagic Fishes
Western Transition	1.7	19.2	25.3
Kamchatka and Kuril Islands	65.3	897.2	779.6
Okhotsk Sea	22.3	13.3	9.9
Kuroshio/Oyashio Current	0.2	31.0	13.4
Western Bering Sea and Basin	4.1	2.6	1.4
Western subarctic	0.0	0.5	0.2
Japan/East Sea	2.4	1.0	0.3

6.5 Ecosystem Perspectives

The food webs leading to and from micronekton in the open North Pacific regions, including the subarctic, transition, and subtropical regions, have been summarized by Brodeur *et al.* (1999) and Seki and Polovina (2001) (see Figure 6.2). The aforementioned studies have revealed (usually qualitatively rather than quantitatively) that prey–predator relationships between micronekton and mesozooplankton, especially crustaceans, are one of the key processes in oceanic food webs. To further understand this process, the feeding behaviors of micronekton (including feeding chronology, prey selectivity, and daily ration) should be studied not only in fish but also in squids, euphausiids, and shrimps. In particular, the feeding ecology of micronektonic squid should be stressed in order to understand rate processes of the oceanic marine food web, since squid are known to grow substantially faster than fish (due to their shorter life cycles and higher secondary productivity rates).

In the transition and subarctic waters, the mesozooplankton community is dominated by copepods of the genera *Neocalanus* and *Eucalanus*, both of which undergo extended ontogenetic vertical migrations (Miller *et al.*, 1984; Miller and Clemons, 1988; Tsuda *et al.*, 1999; Kobari and Ikeda, 1999). Due to their seasonal vertical migration, during which most of the year is spent overwintering at depth, the vertical structure of the prey environment experienced by micronektonic animals would change spatio-temporally, probably also causing changes in micronekton feeding behaviors. However, knowledge on the seasonality of micronekton feeding is extremely limited for all taxonomic groups. Interestingly, the extent to which diel migratory micronekton in the subarctic Pacific utilize (or rely on) overwintering layers of these large calanoids (*e.g.*, *Neocalanus* spp.) as a food source is also unknown. The depth range occupied by these overwintering layers (approximately 400–1200 m) overlaps the vertical distribution of both migrant and non-migrant myctophids species. This topic certainly warrants future study, as these deep overwintering layers occur throughout the subarctic Pacific and represent a large portion of the annual secondary production in the region.

6.6 Interactions between Micronekton and Shallow Topographies

Micronekton often show concentrations well above the background levels in several types of pelagic hot spot environments that are associated with abrupt topographies (Dower and Brodeur, 2004; Genin, 2004). Boehlert and Mundy (1993) reported that the ichthyofauna of seamounts and oceanic islands are typically dominated by myctophid larvae. Despite this, only a very few species of micronekton (*e.g.*, *Maurolicus muelleri*) are known to spawn over shallow topographies. The apparent enrichment of myctophid (and other) larvae over such topographies likely occurs via physical concentration in Taylor cones, through bottom-trapping during DVM behavior (*e.g.*, Genin *et al.*, 1994; Genin, 2004; Wilson and Boehlert, 2004), or via other topographically generated flows (see Roden, 1987; Rodgers, 1994).

There is evidence that micronektonic species occasionally form a mesopelagic boundary community that interacts with the slope regions of shallow topographies (*e.g.*, seamounts, oceanic islands, and continental slopes) and are often called a "slope water community" or "shelf-edge community". Reid *et al.* (1991) documented one such mesopelagic boundary community around Hawaii in which six micronektonic fish species (which together comprised 90% of the micronekton community) occurred at depths of 400–700 m on the island slope. These same species, however, were virtually absent at the same depths even a few kilometers offshore. The species in question were also reported to undergo diel horizontal migrations upslope to depths as shallow as 50–250 m. These communities may be represented by patches with a horizontal extent of several kilometers (Benoit-Bird and Au, 2003). Reid *et al.* (1991) state that similar mesopelagic boundary communities have been reported occasionally from continental slopes and may, in fact, be a global phenomenon. Similar mesopelagic boundary communities (slope water communities) have been commonly observed from continental or insular slopes in tropical and subtropical waters of the Indo-West Pacific region (Kawaguchi, 1976; Reid *et al.*, 1991).

There is also reason to suspect that seamounts and oceanic islands may represent local hot spots for the feeding and growth of non-boundary community micronekton, particularly in oligotrophic regions. Rissik and Suthers (2000) and Suthers (1996) reported that, relative to background conditions, post-larvae and late juveniles of *Diaphus kapalae* and various *Myctophum* spp. exhibited significantly higher levels of gut fullness, recent growth rates (based on otolith microstructure), and better condition (based on RNA:DNA ratios) in the flow-disturbed region downstream of an island in the South Pacific. Such behavior may also be expected to occur in the oligotrophic North Pacific, which is replete with shallow seamounts.

Submarine canyons are another environment where micronekton may be aggregated due to convergent flows on steep topography (Genin, 2004). Canyons along the west coast of North America show enhanced concentrations of micronekton, especially euphausiids, relative to other shelf or slope environments, and frequently contain elevated biomass of higher trophic level predators feeding on these abundant and predictable food sources (Pereyra *et al.*, 1969; Schoenherr, 1991; Mackas *et al.*, 1997; Brodeur, 2001b). Based on an analysis of currents and stable isotope composition of plankton and fish, Bosley *et al.* (2004) determined that rockfishes in Astoria Canyon off the Columbia River, Oregon were feeding on primarily mesopelagic prey of offshore origin, which was confirmed by diet analysis.

7. Sampling Considerations

7.1 Net Trawling

The merits and shortcomings of many different gear types for sampling micronekton have been discussed at length in reports and publications arising from the SCOR Working Group on Methods of Sampling Micronekton (Pearcy, 1975; 1981). We will briefly review some of the major findings of that Working Group and discuss new developments in the intervening period. Wiebe and Benfield (2003) have recently traced the history, and summarized the state of the art, with respect to sampling both zooplankton and micronekton, and discuss at length some alternatives to net sampling, including optical and acoustic methodologies. Net gear can be classified into either non-closing nets or opening/closing nets of various sizes and designs. Watkins *et al.* (2000) summarized the most usual sampling methods used to collect euphausiids, and Nicol (2003) reported the need to develop new methods for those organisms, such as euphausiids that are in between macrozooplankton and micronekton.

7.1.1 Sampling gears

Biomass estimates of micronektonic or mesopelagic fishes have been attempted with various sampling gears, such as an ORI-net (a large conical plankton net of 2 m^2 mouth opening), 6 ft-IKMT (Isaacs-Kidd midwater trawl, 3.5 m^2 mouth opening), 10 ft-IKMT (~10 m^2), large Tucker Trawl (4 m^2), Methot Trawl (5 m^2), RMT-8 (8 m^2), Cobb Trawl (~100 m^2), and, more recently, commercial-sized midwater trawls with mouth openings of 400–3500 m^2 (Table 4.1). The depth coverage of the sampling varies greatly in the literature, so in most cases biomass is expressed as weight per unit sea surface area in the 0–1000 m layer at night or the 200–1000 m layer (mesopelagic zone) during the daytime.

Although estimates made with micronekton nets, such as the ORI-net, 6 ft-IKMT, 10 ft-IKMT and RMT-8 tend to increase with the mouth area, the differences between them are within a factor of 2 to 3. As shown in Table 4.1, however, biomass estimates from commercial trawls are significantly larger (usually an order of magnitude larger) than those from so-called "micronekton nets" with mouth areas less than 10 m^2. It has been shown that larger myctophids, ranging from 10 to 20 cm SL (such as *Lampadena*, *Lampanyctus* and *Nannobrachium*), are very common in commercial trawl catches. These large "nektonic myctophids" are rarely collected by normal micronekton nets and, even when they are collected, they are not usually categorized as micronekton, but rather as an accidental catch since they tend to bias the biomass estimate of typical "micronektonic fishes".

The filtering volume of a large commercial trawl is several hundred times larger than that of a micronekton net due to both its large mouth and higher towing speed, 2–2.5 m s^{-1} (4–5 knots). This high catchability of large trawl nets has revealed the presence of large micronektonic animals, including fishes and squids, which span the gap both in size and swimming ability between "micronekton" and "nekton", as conventionally recognized. Thus, sampling targets are different between these two types of sampling gears, with one covering typical micronektonic animals less than 10 cm in total body length while the other targets micronekton in the 10–20 cm range.

It should also be noted that micronektonic fish biomass is different from mesopelagic fish biomass. In most Russian literature based on commercial-sized trawls, biomasses were estimated for mesopelagic fishes, including the above-mentioned larger-sized micronekton, including large myctophids, bathylagids, stomiids, and paralepidids (Beamish *et al.*, 1999). The difference in estimates between the above mentioned two different sized types of gears would be larger in the subarctic and transition regions than in the tropical and subtropical waters, since larger-sized mesopelagic fishes are more common in cold waters (*e.g.*, the mean size of mesopelagic animals is smaller and the range is narrower in warmer waters than in cold waters).

7.1.2 Sampling of surface migratory myctophids

It is known that surface migrant myctophids (Table 3.1) are not collected effectively with sampling gears deployed from the stern of the vessel due to the disturbance from the ship's wake. To avoid the ship's wake, neuston net sampling should be conducted from the side of the ship, but the effects of the bow wave, and bridles and towing wire from the side beam, are also potential problems. Effects of bridles and towing wire on net avoidance of surface migrant myctophids were studied, based on the comparison between the catches of a conical plankton net and bridle-free neuston net. These studies revealed that *Myctophum asperum*, a typical surface migrant (of 28–29.9 mm size range) in the Kuroshio Current, avoided a bridle-towed net (mouth size, 2 m^2) around 20 times more effectively compared with the bridle-free neuston net of much smaller mouth size (0.24 m^2) (Watanabe, 1998; Watanabe and Kawagwuchi, 1999). They also showed that *M. asperum* > 30 mm SL were rarely collected by the bridle-towed net, but larger specimens up to 42 mm SL were collected by the bridle-free neuston net. The neuston net is designed to be towed from its side otter board, so no bridle, towing wire, or ropes are present in front of the net mouth, and thus, it is capable of sampling outside of the ship's wake. However, its handling in rough seas is compromised due to the instability of the otter board, which responds to the rough sea surface. At present, there are no suitable sampling gears to estimate densities of surface migrant myctophids, in spite of their considerable biomass, and their importance as prey in the oceanic surface ecosystem at night. Towing commercial-sized trawls in their daytime habitat would be promising but visual avoidance of the net is likely, since their daytime habitat is in the upper mesopelagic zone.

7.1.3 Commercial-sized trawl sampling

The merits of commercial-sized trawls are their high catch rate and high towing speed, although small mesh cannot be adopted for an entire trawl net because of its high resistance. The use of fine mesh cod-end (5–12 mm mesh) makes commercial trawls effective for determining qualitative characters or relative abundance of micronekton, in spite of the disadvantage owing to escape through the larger mesh near the net mouth. The visual threat by the large mesh would be effective for good swimmers to prevent extrusion through the mesh. Recent studies based on large trawls revealed a large amount of "nektonic micronekton" biomass in the mesopelagic zone (Beamish *et al.*, 1999; Watanabe *et al.*, 1999). It should be noted that commercial-sized midwater trawl catches have shown a remarkably different picture from that of the traditionally adopted micronekton nets, like IKMT and RMT, in terms of size spectrum and species composition. Although the previous studies adopted 10–15% as a catch rate, based on empirical knowledge, critical studies of their sampling efficiency are limited, but will be required in order to know the absolute standing stock of micronekton.

7.1.4 Sampling of euphausiids and pelagic decapods

Brinton (1967) demonstrated that adult euphausiids exhibit active net avoidance, particularly to nets with bridles, and during daytime sampling. *Euphausia pacifica* seems to have different regional DVM patterns that may affect its catchability. In Japan, surface daytime aggregations facilitate the catch of relatively high densities, whereas in the eastern Pacific, those daytime surface aggregations seem to be less frequent (Nicol and Endo, 1997). Nets with large mouth areas and black mesh nets, like the BIONESS or the MOCNESS, substantially increase the efficiency of catches in regions with moderate and high densities of euphausiids. However, in tropical and suptropical environments, and perhaps in the oligotrophic Central Pacific, where euphausiids typically have lower densities than in high productive coastal environments, daytime net avoidance may be increased, leading to underestimates of the populational abundance. Wilson *et al.* (2003) used light traps to attract and collect the neritic euphausiid *Pseudeuphasia latifrons* in Western Australia, collecting densities several orders of magnitude larger than with conventional nets. Wiebe *et al.* (2004) have recently suggested that the escape avoidance of euphausiids can be partly overcome by equipping MOCNESS systems with large strobe lights. Working in the Southern

Ocean, they found that strobing increased the total euphausiid biomass captured by a factor of about 1.5. Moreover, the increased biomass resulted mainly from having captured about twice as many adult euphausiids (15–60 mm length) as compared to a MOCNESS without strobing. Differences in abundance of euphausiids also are common when net samples are compared with abundance estimated from acoustic data. Omori (1983) compared various methods (small and large net trawling, underwater photography, larval abundance, and predator consumption) to estimate the abundance of micronekton sergestid shrimp. Gómez-Gutiérrez and Robinson (2005) used a 1-m ring with black mesh net with a codend 70 cm long and 25 cm wide, equipped with a commercial underwater video camera (Ikelite), a commercial diver underwater light, and a microcat Seabird CTD to collect epibenthic swarms of the subtropical euphausiid *Nyctiphanes simplex* in the southern part of Baja California. The catch efficiency was high enough to collect up to 80 kg of *N. simplex* adults in a 15-minute trawl. The simultaneous *in situ* observations of swarming behavior and sampling of the specimens is a promising method to study euphausiids in the field. Sampling method is critical to estimate euphausiid abundance. Nicol (1986) compared densities of the North Atlantic euphausiid *Meganyctiphanes norvegica* surface swarms using three different methods: bag-sampler estimating densities up to 41,000 euphausiids m^{-3}; photographic methods estimating densities up to 770,000 euphausiids m^{-3}, and plankton net which gave numbers that never exceeded 6 euphausiids m^{-3}. The same is true for significant differences in the abundance, including comparisons of several orders of magnitude, when euphausiid abundance is estimated acoustically and by standard zooplankton nets (Watkins *et al.*, 2000). This is particularly interesting because *E. pacifica*, *Thysanoessa spinifera*, *P. latifrons* and *N simplex* in the North Pacific commonly form daytime surface swarms that usually are out of acoustic detection (by the near-field effect) and net avoidance makes it particularly difficult to estimate reliable *in situ* standing stock.

7.2 Acoustic Sampling

7.2.1 Acoustic theory and usage

The local intensities of trophic interactions within the micronekton community, and of trophic interactions between the micronekton and either fish or plankton, are, in general, proportional to the products of their local concentrations. These concentrations are very patchy, varying by several orders of magnitude. The development and application of remote sensing for examination of biological and physical variables at a variety of scales is critical to the identification and quantification of specific biological oceanographic processes influencing populations and species composition in marine ecosystems. Quantitative acoustics is one such remote sensing technology. Although applied mainly for the purposes of fisheries management and stock assessment, its ability to estimate the biomass of planktonic, micronektonic and nektonic organisms at fine scales makes it an important research tool in modern biological oceanography. The basic principles of sound scattering by zooplankton and nekton have been described (Holliday, 1980; Greene and Wiebe, 1990; Smith *et al.*, 1992; MacLennan and Simmonds, 1992; Watkins *et al.*, 2000; Foote and Stanton, 2000). Much of the information presented here can be found in the above references. The application of acoustic techniques to biological oceanography involves three primary tasks:

1. Collection and standardization of the acoustic measurements (obtaining an accurate measurement of acoustic backscatter from a volume of water or an individual target),
2. Target identification (knowing what type of target(s) produced the backscatter), and
3. Based on the above knowledge, scaling of the acoustic measurements to abundance or biomass of the target population(s) present in each acoustically-sampled volume.

The first step (acoustic calibration) is essentially an engineering problem of quantifying the electrical response of a particular system (oscillator, transducer, receiver, and data logger) for a known acoustic target strength at a known range. Although commercial echo sounder suppliers can carry out thorough calibrations of system components before delivery, regular follow-up field calibrations with a standard target are recommended, and are essential if components are interchanged. Soule *et al.* (1995) showed that evidence of bias in estimates of target strength obtained with a split-beam echo sounder were due to problems in the software algorithms detected during tank-tested calibration experiments. Once the data have been collected, the detailed information they provide on the spatial distribution of sound scattering intensity must be converted to some measure of abundance or biomass to be of use in biological research. This is done in the second and third steps (target identification and calculation of biomass estimates from acoustic backscatter intensity). The two are inter-related. Different biological targets have different target-strength characteristics that are functions of their body type (density and compressibility contrast relative to the surrounding seawater, presence or absence of "hard" parts, presence or absence of gas bubbles), their size, their orientation (if body shape is not isotropic), the acoustic frequencies used, and the position of the target relative to the axis of the acoustic beam, and the abundance and neighbor-to-neighbor distance of the organisms that sometimes make it difficult to discriminate single targets. The problems of target identification and conversion from target strength to animal abundance or biomass density also differ, depending on whether one or multiple targets are present in the resolved range interval along the acoustic beam.

In general, a wide range of target types is present in a given survey domain. The conversion factors are, therefore, highly sensitive to misinterpretation if the size, shape, orientation, and composition of the targets is unknown or incorrect (Stanton *et al.*, 1996). Using a dual-beam acoustical system, Wiebe *et al.* (1990) measured the target strengths of a variety of zooplankton and micronekton ranging in size from large copepods to shrimp, and found target strengths ranging from –93 to –43 db animal^{-1}, a range equivalent to five orders of magnitude. Such a broad range of possible sound scattering intensity by potential targets necessarily implies the potential for large errors in the conversion of acoustic data to estimates of abundance and biomass. Therefore, much effort has been devoted to the development of techniques to accurately scale acoustic data to the abundance or biomass of the target species. For example, the development of multiple-beam technology has improved substantially the measurement of individual target strengths of the organisms. Dual-beam and split-beam systems can determine the target strength of the sound scattering organisms by measuring the position of the target in the sound cone relative to the acoustic axis. If the position of the target is known, then the beam pattern can be used to normalize the return for each target relative to the reflected intensity at the acoustic axis. If a sufficient number of measurements are made on targets over a broad size category, an empirical model of target strength against target size can be generated using regression analysis (*e.g.*, Foote and Traynor, 1988; Traynor, 1996). The results of the empirical model may then provide backscatter values for each size category in the study area. However, a limitation of this approach is that each target must be resolved individually, which requires very fine spatial resolution of the ensonified volumes in some cases.

An alternative approach is to measure the total return from all targets within the resolved sampling volume, and solve for a biomass *versus* target spectrum, assuming a matrix of average target strength for each target type at each acoustic frequency. The fundamental assumption governing quantitative acoustics is that the total scattering intensity from a given volume of water is equal to the sum of the scattering by each individual randomly-distributed target within the volume. However, the target strength of an individual target is a function of its physical aspect relative to the direction of the incident sound wave, density, and reflection characteristics of the organisms. When converting relative signal intensity to absolute abundance or biomass, it is assumed that the animals are randomly distributed within the insonified volume, and that a sufficient number of measurements will produce an unbiased mean value of volume backscatter. In this case, the acoustic return is measured as backscatter intensity per unit volume of water, rather than per unit target, and the calculation of return per unit biomass density is usually based on empirical or theoretical models of target strength *versus* acoustic frequency.

Sound scattering models use the characteristics of the target to compute backscatter for any user-selected frequency. The development of analytical sound scattering models is a complex problem in applied physics, and beyond the scope of this discussion. However, once an adequate model has been developed, it can be used to predict the backscatter intensity for any target that conforms to the limitations of the model. A variety of models has been developed for fluid-filled spheres and prolate spheroids, straight and bent cylinders, and even for fish (Anderson, 1950; Stanton, 1989; Horne and Clay, 1998). Fluid-filled organisms include taxa such as copepods and euphausiids (and, by analogy, mysids and pelagic decapods). They are weak sound scatterers and often contribute only a minor component of the total sound scattering intensity. Elastic scatterers have a reflectivity value roughly 100 times higher than the fluid-filled targets (Stanton *et al.*, 1994), and include shelled organisms such as thecate pteropods. Although fish and siphonophores with gas bladders have the highest reflection coefficient, it is important to note their morphological features vary with species. For example, some myctophid species have a well-inflated swimbladder and strong backscatter, others have atrophied (or fat-filled) swimbladders and weak backscatter (Butler and Pearcy, 1972; Neighbors, 1992; Yasuma *et al.*, 2003). Mesopelagic fishes are known to have various types of gas bladders, from completely absent to lipid or gas-filled types, not only by species, but also by growth stages, suggesting specific and ontogenetic changes in target strength (Butler and Pearcy, 1972; Neighbors and Nafpaktitis, 1982). Analytical sound scattering models are continually undergoing refinement as experimental data accumulate and the technology improves (Stanton *et al.*, 1998; Stanton and Chu, 2000; Horne and Clay, 1998).

Sound scattering models have been used with multiple frequencies to estimate the size distribution of acoustic targets (Holliday and Pieper, 1980; Pieper and Holliday, 1984; Greenlaw and Johnson, 1983; Costello *et al.*, 1989; Pieper *et al.*, 1990; Ressler *et al.*, 2005). The multifrequency technique is based on the relationship between backscatter and frequency. This technique exploits the difference in target strength relative to frequency in order to estimate the size distribution of targets from volume scattering data. A fundamental condition of the multifrequency inverse method is that the ratio of the target size to the acoustic frequencies must span the transition from Rayleigh to geometric scattering (Holliday and Pieper, 1995). Unfortunately, the Rayleigh–geometric transition zone for many large targets falls below the frequency of most commercial transducers (Horne and Jech, 1999). In addition, the number of size categories in the acoustic record can often exceed the number of frequencies available for the survey. In such cases, the inversion algorithm may not converge to a unique or reliable solution.

Back-scattering models, with up to 21 frequencies, have been used to estimate zooplankton size distribution (Costello *et al.*, 1989; Pieper *et al.*, 1990). The equipment required to simultaneously collect data at 21 frequencies is complex and cost-prohibitive for most studies. In addition, such equipment has a short effective detection range due to the high absorption of sound at high frequencies. It cannot be towed beside the vessel but must be lowered on a hydrographic wire with the vessel stationary, or towed on an undulating vehicle in order to obtain the depth distribution of the targets. It therefore lacks the sampling density possible with a towed transducer array. Nevertheless, when the size composition of the targets is very diverse, multiple high frequency sampling may be the only way to obtain reliable acoustic density estimates.

In practice, few acoustic studies have a sufficient number of frequencies to completely characterize the size distribution and species composition of the sound scattering targets. Nevertheless, if the micronektonic community is dominated by only a few species and size categories, as usually happens in nearshore pelagic environments, acoustic systems with one or two frequencies may be sufficient to characterize the abundance and distribution of the target animals. In the western North Pacific, for example, a two-frequency (38 and 120 kHz) method is available for distinguishing *E. pacifica* from other crustaceans (Miyashita and Aoki, 1999). In such cases, backscatter can be scaled with concurrently collected net samples (using regression analysis) or by applying target strength corrections from the literature, or from model calculations (Coyle, 1998; Coyle *et al.*, 1992; Coyle and Cooney, 1993; Macaulay *et al.*, 1995). With multiple frequencies and target types, canonical correlation may help identify and scale acoustic data to net data (Coyle and Hunt, 2000).

The above approach assumes that net samples are a reliable measure of the density of organisms detected by the sounder, in other words, that net avoidance is negligible. However, since sound scattering can also result from a number of sources other than animals retained by a net, correlation analysis with net samples will not always produce statistically usable results. Fish, for example, may completely mask the weaker acoustic signals from crustaceans, resulting in an underestimation of crustacean biomass where the fish and crustaceans overlap (Coyle and Pinchuk, 2002). If scattering from fish is mistaken for scattering from crustaceans, a large overestimate of crustacean abundance or biomass will result. In general, correlation cannot help in scaling acoustic data in cases where the net sampling tools are assumed to be non-quantitative. Even in those cases where significant results are observed, the correlations may not be the direct result of sound scattering by taxa from the nets. Thus, using a combination of hydroacoustic techniques, underwater video camera, and several types of nets during survey could provide enough evidence to identify the main organisms responsible for most of the backscattering recorded by the echo sounder. Comparison of the correlating frequencies, as identified by canonical loadings, with measured and model predictions of volume scattering at those frequencies, can help expose such correlations. Even where correlations are considered genuine, the researcher must ultimately use experience and judgement to decide the degree of correlation required to usefully describe the distribution and biomass of a given target taxa. While a given set of correlation coefficients may adequately scale the data on some transects, they may produce unacceptable results on other transects where the species composition or sampling conditions are different.

A substantial number of studies have applied acoustics to survey the distribution and estimate the abundance of micronektonic organisms in the North Pacific, and a complete review of these is beyond the scope of this report. Many of the earlier studies were aimed at examining the diel distribution and migration patterns of the ubiquitous sound scattering layers in the North Pacific. Some of these early studies are presented in Farquhar (1970) and Andersen and Zahuranec (1977). Regional observations of mesopelagic fish in Oregon waters (Pearcy *et al.*, 1977; Kalish *et al.*, 1986), in the Central Pacific (Benoit-Bird and Au, 2003), western North Pacific (Yasuma, 2004), Bering Sea (Yasuma, 2004), Japan/East Sea (Hamano and Uchida, 1992; Hamano *et al.*, 1992; Noda and Moriwaki, 1996; Ohshimo, 1998), as well as elsewhere in the Pacific Ocean (Koslow *et al.*, 1997) are provided.

Numerous studies of pelagic crustacean (mainly euphausiid) distributions determined with higher frequencies are also available from throughout the North Pacific Ocean (Pieper, 1979; Pieper *et al.*, 1990; Coyle and Cooney, 1993; Mackas *et al.*, 1997; Miyashita *et al.*, 1997, 1998; Swartzman *et al.*, 1999; Gómez-Gutiérrez *et al.*, 2000; Ressler *et al.*, 2005).

7.3 Video Observations (Submersible and ROV)

Our ability to directly observe the distribution, ecology, and behavior of mesopelagic organisms has progressed greatly since the first observations of myctophid fishes during bathysphere dives off Bermuda (Beebe, 1935). Barham (1963, 1972) described the composition and behavior of a mesopelagic community in a sound scattering layer off southern California, based on observations from 50 dives in a variety of submersibles. He noted that different mesopelagic fishes showed different types of behavior which he was able to classify as "active" (residing in shallower waters) and "inactive" (residing in deeper waters). Backus *et al.* (1968) examined scattering layers using the *ALVIN* submersible in the North Atlantic and found them to be composed of dense aggregations of a single species of myctophid (*Ceratoscopelus madrensis*). Dense aggregations of myctophids, cephalopods, and sergestids were observed off Cape Hatteras, U.S.A. in the Atlantic by Milliman and Manheim (1968). Robison (1983) examined associations of myctophids with other mesopelagic organisms in Monterey Bay, California. More recently, Auster *et al.* (1992) made underwater observations in canyons south of New England, U.S.A. using the *Johnson Sea-Link* submersible, and described multispecies associations of myctophids, other fishes, euphausiids, sergestids, and ctenophores. The authors suggest that this behavior reduces predation on these myctophids and helps them locate common prey. Another type of anti-predator behavior has been described by Robison (1999) who noted that elongate fish and other midwater organisms assume a circular shape to mimic medusae and other unpalatable prey. Finally, Hunt and Lindsay (1999) observed midwater fauna off Japan, using both submersibles and unmanned Remotely Operated Vehicles (ROVs) and observed 11 species of midwater fishes, although their emphasis in this study was primarily on gelatinous zooplankton.

The use of scientific submarine and ROV technology has substantially improved our ability to learn about micronekton behavior, feeding habits, and predation–prey interactions that are impossible to obtain using nets, optic and/or acoustic devices (Wiebe and Benfield, 2003). Using these technologies has also enabled researchers to collect specimens virtually intact for physiological and taxonomic studies. Submarine and ROV technology can be also applied to acoustic systems as well as video systems (Sawada *et al.*, 2004; Takahashi *et al.*, 2004), and observations of deep-sea organisms will be able to provide more quantitative information by combining these systems. Relatively inexpensive video camera systems that can be deployed as any regular CTD or plankton/nekton net can significantly increase our understanding of schooling of fish and swarming behavior of pelagic crustaceans.

8. Summary of Present State of Knowledge

8.1 Fish Micronekton

The present knowledge of micronektonic mesopelagic fishes in the North Pacific can be summarized as follows:

1. Taxonomic problems are mostly resolved, particularly for the common species that are regarded as being ecologically important because of their high abundance.
2. Larval taxonomy is almost established for the common species in the subarctic, transitional and subtropical waters, with the exception of the genera *Diaphus* and *Lampanyctus*, but there are relatively few scientists familiar with their identification.
3. Egg taxonomy is not established for most of the mesopelagic fishes. Myctophid eggs have been described for only 3 of about 230 species in the world oceans, which has limited our understanding of myctophid spawning seasons and grounds. Development of a new sampling gear is necessary since plankton nets have not been effective at collecting their fragile eggs.
4. Using a genetic approach would contribute to the confirmation of not only both established and ambiguous larval and adult taxonomy, but would also help to differentiate between different populations of this widely distributed fish group.
5. Zoogeographic distribution patterns are mostly depicted for adults, but are not yet determined for many larvae, which cause difficulties in separating expatriate populations from feeding populations that migrate into subarctic waters, including the Bering and Okhotsk Seas.
6. Diel vertical migration patterns have been studied for the subarctic and transitional water species. Ontogenetic changes in migration depth, especially from juveniles to adults, have been reported, but this subject needs to be examined further.
7. Knowledge of spawning behaviors, including spawning depth, timing, and schooling behaviors within spawning aggregations is almost totally lacking at present.
8. Life history studies are restricted to several dominant species. Parameters for production, mortality, and reproduction are needed but are hard to obtain due to the lack of suitable sampling methodology and seasonal data, especially during winter in subarctic waters.
9. Knowledge of the ecological roles of these fishes in oceanic ecosystems is restricted to feeding habits of several dominant species in the North Pacific. Daily rations, feeding impact on zooplankton biomass, predators and predation rates have been studied for several transitional and subarctic species. Generally, spatio-temporal habitat segregation, through different DVM patterns and resource partitioning, appears to be very common in the micronektonic fish community.
10. Marine mammals (such as fur seals and porpoises), seabirds, large pelagic and benthic fishes, and squids are all known to be predators of mesopelagic micronekton, but this information is scattered in the literature on stomach content analysis of various predatory animals. The relatively soft fragile body of most mesopelagic fishes may have caused an underestimate of the importance of micronektonic fishes in many predator diets.
11. The nutritional values of myctophid fishes have been studied in terms of their protein and lipid quality, and most species have been found to be not so different from those of other epipelagic fishes, including commercially exploited species. Wax ester is contained in several vertically non-migratory or semi-migratory species.
12. Quantitative biomass estimates are restricted to only a few species because an effective quantitative sampling technique has not yet been established. It is known that commercial-sized trawl nets are more effective than traditional micronekton nets, but quantitative evaluation of these larger trawls is needed. We suggest that once this

evaluation method, including the use of acoustics, has been established, biomass estimates at species level would be possible, based upon the discrete depth sampling in the habitat of each species.

8.2 Crustacean Micronekton

The present knowledge of micronektonic mesopelagic crustaceans in the North Pacific can be summarized as follows:

1. In terms of body size and sampling considerations, more of the euphausiid and mysid species fall between the range of macrozooplankton and micronekton than the other, more stereotypic, micronektonic taxa (*e.g.*, myctophids, small squids, and pelagic decapod shrimps). Epipelagic adult euphausiid total length is usually 1–3 cm, but mesopelagic species range between 3–12 cm total length. Both juveniles and adults can be caught with conventional meso-zooplankton nets, but capture efficiency can be low (especially in daylight). Recent studies recommend that fast trawls and larger net mouths should replace conventional plankton nets when the main goal is to catch euphausiids.
2. Trophic niche is often species- and location-specific, but the most abundant North Pacific euphausiids are omnivorous (on large-celled phytoplankton) and carnivorous (on juvenile and adult mesozooplankton). However, it was recently discovered that euphausiids feed actively on marine snow (> 0.5 mm) even when other sources of food are available, and that they can also actively fragment marine snow, perhaps playing a significant biological agent in the biogeochemical cycle of particulate organic carbon.
3. Taxonomy and identification of late juveniles and adults of euphausiids, mysids, and pelagic decapods are well established at the genus and species level, as are the large-scale zoogeographic patterns.
4. Taxonomy and identification of eggs and larvae for broadcast spawning species, required to estimate spawning areas, intensity, and duration, as well as larval recruitment, are needed. Species-level identification of earlier larval stages is possible for some of the most abundant and ecologically-important North Pacific euphausiid species, but expertise in taxonomy and published identification guides for about half of the euphausiid species is critically lacking. Of the 56 euphausiid species distributed in the North Pacific, the biometry of the eggs of only 20 species has been measured. Because all mysid species are sac-spawning, the spawning areas, intensity, and duration are theoretically easier to study but there is relatively little information about their spawning in the North Pacific.
5. Life history strategies (maturation rate, seasonal timing and frequency of reproduction, and feeding type) and larval developmental sequences can be quite variable within a species (even in the same population), and may be cued by local environmental conditions. The variability of age structure dynamics, multiple spawning with overlap of generations, and body shrinkage during unfavorable conditions complicates traditional models for the interpretation of growth, mortality, and secondary production rates.
6. Most detailed time series observations of feeding, growth, development, and metabolic rates have been from nearshore sub-populations, even for species with trans-pacific ranges. The reproductive strategy (broadcast or sac-spawning) for species of the genera *Nematobrachion* and *Tessarabrachion* is still unknown.
7. Spatial distributions are extremely patchy in the three-dimensional scale. Most of the North Pacific euphausiid species undergo significant DVM as juveniles and adults (range 50–300 m, variable with age, species, location, season, and year-to-year). Typical layer thickness is 5–20 m. At least in continental margin regions, the locations of strong horizontal aggregations are correlated with bathymetric slopes and with current patterns, and daytime scattering layers may interact with the benthic boundary layer, or

remain occasionally as daytime surface aggregations for feeding and reproductive purposes.

8. Because of their patchy spatial distribution and their relatively substantial swimming capabilities, spatially-intensive and high-resolution sampling methods are needed to quantify distributions and total stock size. The most common method is a combination of acoustic-backscatter mapping of scattering layer extent and intensity, supplemented by targeted net sampling. Considerable work has been done on the development of euphausiid target strength models. Most models agree to about a factor of 2 to 3 in their biomass estimates. However, there remains significant uncertainty due to effects of body orientation and interference from strong acoustic targets with similar depth distribution (*e.g.*, pteropods and siphonophores). Optical and acoustic information can extract behavioral information not easily obtained with conventional net sampling, such as the velocity of DVM, size, compactness, and density of the euphausiid aggregations. Swimming and swarming behavior of euphausiids and mysids can be studied using underwater video cameras to better understand the social association among members of the same aggregation.
9. Euphausiids are the primary and preferred prey for a large number of North Pacific finfish, squid, pelagic decapods, seabirds, and marine mammal species.
10. Spawning areas and duration of the spawning seasons are relatively well known for only a few of the dominant euphausiid species (*Euphasia pacifica*, *Nyctiphanes simplex*, *Thysanoessa inermis*, *T. spinifera*, and *T. raschi*) but more research is needed for other species particularly in the Transitional Zone and Transitional Domain areas.
11. Although *Euphausia pacifica*, *E. nana*, *Thysanoessa longipes*, *T. raschi*, and *T. spinifera* are part of a relatively small-scale fishery in Japan, United States, and Canada using dip or trawl nets, there is a lack of reliable estimates of the standing stock and vital rates of these euphausiids in the North Pacific. It is necessary to study the dynamics of their populations, secondary productivity, and the ecological impact of this pelagic component to set precautionary catch limits in order to avoid short-term, or permanent damage, to natural population levels of their predators as has been the situation for the Antarctic krill, *Euphausia superba* (Hewitt *et al.*, 2002).

8.3 Cephalopod Micronekton

The present knowledge of micronektonic cephalopods in the North Pacific can be summarized as follows:

1. As with most micronekton, much of what we know about cephalopods in the North Pacific centers on the common, generally coastal, species that have been identified as ecologically important and/or are highly abundant, thereby facilitating obtaining samples. Away from coastal waters (*i.e.*, open oceans), our knowledge of virtually all aspects of this group diminishes considerably.
2. For many of the cephalopod families encountered in the micronekton, it is the juvenile and subadult forms that are typically represented in net sampling and which are found in the diets of higher-level predators. As expected, species-specific life history and ecological information for these developmental stages are even more difficult to come by than what is available for the adults.
3. Particularly lacking are data on the life history and ecological relationships of the neutrally buoyant cephalopods (*e.g.*, Histioteuthidae and Cranchiidae).

9. Recommendations

On the whole, a large amount of data on the biological features of micronekton has been accumulated over the last few decades and it should not be too difficult to fill the remaining gaps in the near future from the standpoint of fisheries oceanography. We are only now beginning to understand how micronekton populations vary over longer time scales that may relate to climate change (Brodeur *et al.*, 2003; Watanabe and Kawaguchi, 2003b). These preliminary results strongly suggest close dynamic interactions among climate change, physical oceanographic variability, and epipelagic-mesopelagic marine ecosystems.

The next step towards developing our knowledge of this huge biomass in the oceanic ecosystems should be the establishment of quantitative sampling techniques to accurately assess their distribution and abundance patterns. This will also greatly contribute to quantitative sampling of juvenile fishes of the commercially important species, which is essential for predicting their stock fluctuations. Based on the consideration mentioned above, we would, therefore, recommend that the following studies be conducted toward gear development:

1. Quantification of the extrusion rate through the mesh of commercial-sized trawl related by various sized micronekton using underwater cameras, videos, or by fine mesh nets attached to the outside of the trawl to catch the extruded animals;
2. Development of a reliable neuston net (A bridle-free neuston net is preferable.) that could be towed simultaneously with the trawl along the side of a ship;
3. Development of a micronekton net for discrete depth sampling of smaller-sized micronekton (<5–7 cm), such as RMT-8, MOCNESS, and Tucker Trawl, which should be towed in combination with the quantitatively established large trawl;
4. Development of opening/closing bridleless pop-up nets to sample in deep water or from ships without the ability to deploy large trawls;
5. Expansion of visual techniques using towed or mobile cameras systems and comparison of the species composition and densities obtained from these methods to those from net systems presently being used.

As a result of the recommendations of this working group, PICES formed an Advisory Panel of the Micronekton Sampling Intercalibration Experiment in 2002 to plan a cruise (or several cruises) to compare micronekton sampling gears and other quantifying technologies, such as acoustics and visual sampling methods, similar to that done in the Atlantic Ocean utilizing mainly plankton gears (Wiebe *et al.*, 2002). The Advisory Panel will oversee planning and implementation of the field program and dissemination of the results to the scientific community.

10. References

Abookire, A.A., Piatt, J.F. and Speckman, S.G. 2002. A nearsurface, daytime occurrence of two mesopelagic fish species (*Stenobrachius leucopsarus* and *Leuroglossus schmidti*) in a glacial fjord. Fish. Bull. U.S. **100**: 376–380.

Acevedo-Gutiérrez, A., Croll, D.A. and Tershy, B.R. 2002. High feeding cost limit dive time in the largest whales. J. Exp. Biol. **205**: 1747–1753.

Adams, A.E. 1979. The food habits, age, and growth of three midwater fishes (*Stenobrachius leucopsarus, S. nannochir*, and *Leuroglossus schmidti*) from the southeastern Bering Sea. M.S. Thesis, University of Alaska, Fairbanks, 302 pp.

Ahlstrom, E.H. 1969. Mesopelagic and bathypelagic fishes in the California current region. Coop. Oceanic Fish. Invest. Rep. **13**: 39–44.

Ainley, D.G., Spear, L.B. and Allen, S.G. 1996a. Variation in the diet of Cassin's auklet reveals spatial, seasonal, and decadal occurrence patterns of euphausiids off California, USA. Mar. Ecol. Prog. Ser. **137**: 1–10.

Ainley, D.G., Spear, L.B., Allen, S.G., Ribic, C.A. 1996b. Temporal and spatial patterns in the diet of the common murre in California waters. Condor **98**: 691–705.

Aizawa, Y. 1974. Ecological studies of micronektonic shrimp (Crustacea, Decapoda) in the western North Pacific. Bull. Ocean Res. Inst. Univ. Tokyo **6**: 1–84.

Aizawa, Y. and Marumo, R. 1967. Vertical distribution of zooplankton and micronekton biomass in the Sagami Bay, Central Japan. Info. Bull. Plankt. Japan **14**: 1–7. (in Japanese with English abstract)

Andersen, N.R. and Zahuranec, B.J. (*Editors*) 1977. Oceanic sound scattering prediction. Plenum Press, 859 pp.

Anderson, V.C. 1950. Sound scattering from a fluid sphere. J. Acoust. Soc. Am. **22**: 426–431.

Andrievskaya, L.D. 1958. The food of Pacific salmon in the northwestern Pacific Ocean (Pitanie Tikhookeanskikh lososei v severo-zapadnoi chasti Tikhovo okeana). Fish. Res. Bd. Can. Translation Series **182**: 12.

Aron, W. 1962. The distribution of animals in the Eastern North Pacific and its relationship to physical and chemical conditions. J. Fish. Res. Bd. Can. **19**: 271–314.

Auster, P.J., Griswold, C.A., Youngbluth, M.J. and Bailey, T.G. 1992. Aggregations of myctophid fishes with other fauna. Env. Biol. Fishes **35**: 133–139.

Aurioles-Gamboa, D. 1992. Inshore-offshore movements of pelagic red crabs *Pleuroncodes planipes* (Decapoda, Anomura, Galatheidae) off the Pacific coast of Baja California Sur, Mexico. Crustaceana **62**: 71–84.

Baba, O., Taniuchi, T. and Nose, Y. 1987. Depth distribution and food habits of three species of small squaloid sharks off Chosi. Bull. Japan. Soc. Sci. Fish. **53**: 417–424.

Backus, R.H., Craddock, J.E., Haedrich, R.H., Shores, D.L., Teal, J.M., Wing, A.S., Mead, G.W. and Clark, W.D. 1968. *Ceratoscopelus maderensis*: peculiar sound-scattering layer identified with this myctophid fish. Science **160**: 991–993.

Badcock, J. and Merrett, N.R. 1976. Midwater fishes in the North Atlantic – I. Vertical distribution and associated biology in 30N, 23W, with developmental notes on certain myctophids. Prog. Oceanogr. **7**: 3–58.

Bailey, K.M., Brodeur, R.D. Merati, N. and Yoklavich, M.M. 1993. Predation on walleye pollock (*Theragra chalcogramma*) eggs and yolk-sac larvae by crustacean invertebrates in the western Gulf of Alaska. Fish. Oceanogr. **2**: 30–39.

Baird, R.C., Hopkins, T.L. and Wilson, D.F. 1975. Diet and feeding chronology of *Diaphus taaningi* (Myctophidae) in the Cariaco Trench. Copeia **2**: 356–365.

Baker, A. de C., Boden, P. and Brinton, E. 1990. A practical guide to the euphausiids of the world. Natural History Museum Publications. London, pp. 96.

Balanov, A.A. 1994. Feeding habits of the most abundant mesopelagic fishes in the Bering Sea. Vopr. Ikhtiol. **34**: 252–259.

Balanov, A.A. and Il'Insky, E.N. 1992. Species composition and biomass of mesopelagic fishes in the Sea of Okhotsk and the Bering

Sea. J. Ichthyol. **32**: 85–93.

Balanov, A.A., Gorbatenko, K.M. and Gorelova, T.A. 1994. Diurnal feeding dynamics of mesopelagic fishes in the Bering Sea during summer. J. Ichthyol. **34**: 85–99.

Balanov, A.A., Gorbatenko, K.M. and Efimkin, A.Y. 1995a. Foraging dynamics of mesopelagic fishes in the Bering Sea during summer and autumn. J. Ichthyol. **35**: 65–77.

Balanov, A.A., Gorbatenko, K.M. and Efimkin, A.Y. 1995b. Diurnal feeding dynamics of mesopelagic fishes in the Bering Sea during autumn. Biol. Mor. **21**: 125–131. (in Russian)

Bargu, S., Marinovic, B., Mansergh, S. and Silver, M.V. 2003. Feeding resposes of krill to the toxin-producing diatom *Pseudo-nitzschia*. J. Exp. Mar. Biol. Ecol. **284**: 87–104.

Barham, E.G. 1963. Deep scattering layer migration and composition: observations from a diving saucer. Science **151**: 1399–1403.

Barham, E.G. 1972. Deep-sea fishes: lethargy and vertical orientation. pp. 100–118. *In* Proceedings of an International Symposium on Biological Sound Scattering in the Ocean. *Edited by* G.B. Farquhar. Maury Center for Ocean Science Rep. 6.

Batchelder, H.P. 1985. Seasonal abundance, vertical distribution, and life history of *Metridia pacifica* (Copepoda: Calanoida) in the oceanic subarctic Pacific. Deep-Sea Res. **32**: 949–964.

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

Bédard, J. 1969. Feeding of the least, crested, and parakeet auklets around St. Lawrence Island, Alaska. Can. J. Zool. **47**: 1025–1050.

Beebe, W. 1935. Half Mile Down. Duell, Sloan and Pearce, New York, 344 pp.

Bekker, V.E. 1967. Luminescent anchovies: family Myctophidae. pp. 145–181. *In* Biology of the Pacific Ocean. Vol. 7, Book III. *Edited by* T.S. Rass. Tokyo, Ratisu. (In Japanese,translated from Russian)

Bekker, V.E. 1983. Myctophid fishes of the world ocean. Moscow, Nauka, 248 pp.

Benoit-Bird, K.J. and Au, W.W.L. 2003. Spatial dynamics of a nearshore, micronekton sound-scattering layer. ICES J. Mar. Sci. **60**: 899–913.

Berry, S.S. 1912. The Cephalopoda of the Hawaiian Islands. Bull. Bur. Fish., Washington, DC **32**: 255–362.

Bigelow, K.A. 1992. Age and growth in paralarvae of the mesopelagic squid *Abralia trigonura* based on daily growth increments in statoliths. Mar. Ecol. Prog. Ser. **82**: 31–40.

Bigelow, K.A. 1994. Age and growth of the oceanic squid *Onychoteuthis borealijaponica* in the North Pacific. Fish. Bull. U.S. **92**: 13–26.

Blackburn, M. 1968. Micronekton of the eastern tropical Pacific Ocean: family composition, distribution, abundance, and relations to tuna. Fish. Bull. **67**: 71–115.

Blackburn, M., Laurs, R.M., Owen, R.W. and Zeitzschel, B. 1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. Mar. Biol. **7**: 14–31.

Boehlert, G.W. and Mundy, B.C. 1993. Ichthyoplankton assemblages at seamounts and oceanic islands. Bull. Mar. Sci. **53**: 336–361.

Boehlert, G.W., Wilson, C.D. and Mizuno, K. 1994. Populations of the sternoptychid fish *Maurolicus muelleri* on seamounts in the Central North Pacific. Pac. Sci. **48**: 57–69.

Boltachev, A.R., Gigarosov, V.A. and Tsarin, S.A. 1993. Distribution, age, growth, life cycle, and production patterns of *Diaphus vanhoeffeni*. Tr. Inst. Oceanologii RAN. **128**: 257–270.

Borodulina, O.D. 1972. Materials on the feeding of predatory mesopelagic fishes of the high seas. Vop. Ikhtyol. **12**: 757–768.

Bosley, K.L., Lavelle, J.W., Brodeur, R.D., Wakefield, W.W., Emmett, R.L., Baker, E.T. and Rehmke, K.M. 2004. Biological and physical processes in and around Astoria Submarine Canyon, Oregon, USA. J. Mar. Syst. **50**: 21–37.

Boucher-Rodoni, R. and Boucaud-Camou, E. 1987. Feeding and digestion. pp. 85–108. *In* Cephalopod Life Cycles – Vol. II. *Edited by* P.R. Boyle, Academic Press, London.

Bower, J.R., Seki, M.P., Young, R.E., Bigelow, K.A., Hirota, J. and Flament, P. 1999. Cephalopod paralarvae assemblages in

Hawaiian waters. Mar. Ecol. Prog. Ser. **185**: 203–212.

Boyd, C.M. 1967. Benthic and pelagic habitats of the red crabs *Pleuroncodes planipes*. Pac. Sci. **21**: 394–403,

Boyle, P.R. and Boletsky, S.V. 1996. Populations: definitions and dynamics. *In* The role of cephalopods in the world's oceans. *Edited by* M.R. Clarke. Phil. Trans. R. Soc. Lond. B **351**: 985–1002.

Brinton, E. 1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr. **8**: 51–270.

Brinton, E. 1967. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. **12**: 451–483.

Brinton, E. 1975. Euphausiids of Southeast Asian waters. Scientific results of marine investigations of the South China Sea and Gulf of Thailand. Naga Report **4**: 1–287.

Brinton, E. 1976. Population biology of *Euphausia pacifica* off southern California. Fish. Bull. U.S. **74**: 733–762.

Brinton, E. 1987. A new abyssal euphausiid, *Thysanopoda minyops*, with comparisons of eye size, photophores, and associated structures among deep-living species. J. Crust. Biol. **7**: 636–666.

Brinton, E. and Wyllie, J.G. 1976. Distributional atlas of euphausiid growth stages off southern California, 1953 through 1956. Calif. Coop. Ocean. Fish. Invest. Atlas **24**: 1–289.

Brinton, E., Ohman, M.D., Townsend, A.W., Knight, M.D. and Bridgeman, A.L. 2000. Euphausiids of the World Ocean, World Biodiversity Database CD-ROM Series, Springer Verlag, New York.

Brodeur, R.D. 1986. Northward displacement of the euphausiid *Nyctiphanes simplex* Hansen to Oregon and Washington waters following the El Niño event of 1982–83. J. Crust. Biol. **6**: 686–692.

Brodeur, R.D. 1988. Zoogeography and trophic ecology of the dominant epipelagic fishes in the northern North Pacific. Bull. Ocean Res. Inst. **26**: 1–27.

Brodeur, R.D. 1998. Prey selection by age-0 walleye pollock, *Theragra chalcogramma*, in nearshore waters of the Gulf of Alaska. Envir. Biol. Fishes **51**: 175–186.

Brodeur, R.D. 1990. A synthesis of the food habits and feeding ecology of salmonids in marine waters of the North Pacific. FRI-UW-9016, Fisheries Research Institute, Univ. Washington, Seattle, 38 pp.

Brodeur, R.D. 2001a. Micronekton data sets in the North Pacific. pp. 86–90. *In* Impact of Climate Variability on Observation and Prediction of Ecosystem and Biodiversity Changes in the North Pacific. *Edited by* V. Alexander, A. Bychkov, P. Livingston, and S.M. McKinnell. PICES Sci. Rep. No. 18, 210 pp.

Brodeur, R.D. 2001b. Habitat-specific distribution of Pacific Ocean perch (*Sebastes alutus*) in Pribilof Canyon, Alaska. Cont. Shelf Res. **21**: 207–224.

Brodeur, R.D. and Merati, N. 1993. Predation on walleye pollock (*Theragra chalcogramma*) eggs in the Western Gulf of Alaska: the roles of vertebrate and invertebrate predators. Mar. Biol. **117**: 483–493.

Brodeur, R.D. and Pearcy, W.G. 1984. Food habits and dietary overlap of some shelf rockfishes (genus *Sebastes*) from the northeastern Pacific Ocean. Fish. Bull. **82**: 269–293.

Brodeur, R.D. and Pearcy, W.G. 1990. Trophic relations of juvenile Pacific salmon off the Oregon and Washington coast. Fish. Bull. U.S. **88**: 617–636.

Brodeur, R.D., Lorz, H.V. and Pearcy, W.G. 1987. Food habits and dietary variability of pelagic nekton off Oregon and Washington, 1979-1984. NOAA Tech. Rep., NMFS **57**: 1–32.

Brodeur, R.D., Francis, R.C. and Pearcy, W.G. 1992. Food consumption of juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tschawytscha*) on the continental shelf off Washington and Oregon. Can. J. Fish. Aquat. Sci. **49**: 1670–1685.

Brodeur, R.D., McKinnell, S., Nagasawa, K., Pearcy, W.G., Radchenko, V. and Takagi, S. 1999. Epipelagic nekton of the North Pacific Subarctic and Transition Zones. Prog. Oceanogr. **43**: 365–397.

Brodeur, R.D., Pearcy, W.G. and Ralston, S. 2003. Abundance and distribution patterns of nekton and micronekton in the Northern

California Current Transition Zone. J. Oceanogr. **59**: 515–535.

Burgess, L.A. 1982. Four new species of squid (Oegopsida: *Enoploteuthis*) from the central Pacific and a description of adult *Enoploteuthis reticulata*. Fish. Bull. U.S. **80**: 703–734.

Burgess, L.A. 1991. Squids of the genus *Abralia* (Cephalopoda) from the central equatorial Pacific with a description of *Abralia heminuchalis*, new species. Bull. Mar. Sci. **49**: 113–136.

Butler, J.L. and Pearcy, W.G. 1972. Swimbladder morphology and specific gravity of myctophids off Oregon. J. Fish. Res. Bd. Can. **29**: 1145–1150.

Cai, B.-G. 1986. The distribution of the Euphausiacea in the Huanghai Sea and East China Sea. Oceanology **25**: 140–146

Cailliet, G.M. and Ebeling, A.W. 1990. The vertical distribution and feeding habits of two common midwater fishes (*Leurogrossus stilbius* and *Stenobrachius leucopsarus*) off Santa Barbara. CalCOFI Rep. **31**: 106–123.

Casanova, B. 1996. Crustacea Euphausiacea: Euphausiids from the south-west tropical Pacific Ocean (New Caledonia, Wallis and Futuna Islands, Indonesia). Functional morphology and biogeography. Musorstom Cruises Reports, Vol. 15. Mémoires du Muséum national d'Histoire naturelle (France). Paris. Editions du Museum, Paris (France), **168**: 167–195.

Chu, E.W. 1984. Sooty shearwater off California: diet and energy gain. pp. 64–71. *In* Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. *Edited by* D.N. Nettleship, G.A. Sanger and P.F. Springer. Min. Supply and Services, Ottawa.

Clarke, T.A. 1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull. U.S. **71**: 401–434.

Clarke, T.A. 1978. Diel feeding patterns of 16 species of mesopelagic fishes from Hawaiian waters. Fish. Bull. U.S. **76**: 495–513.

Clarke, T. A. 1980. Diets of fourteen species of vertically migrating mesopelagic fishes in Hawaiian waters. Fish. Bull. U.S. **78**: 619–640.

Clarke, T.A. 1982. Feeding habits of stomiatoid fishes from Hawaiian waters. Fish. Bull. U.S. **80**: 287–304.

Clarke, T.A. 1987. The distribution of vertically migrating fishes across the central equatorial Pacific. Biol. Oceanogr. **4**: 47–81.

Collard, S.B. 1970. Forage of some eastern Pacific midwater fishes. Copeia **2**: 348–354.

Condit, R. and Le Boeuf, B.J. 1984. Feeding habits and feeding grounds of the northern elephant seal. J. Mammol. **65**: 281–290.

Costello, J.H., Pieper, R.E. and Holliday, D.V. 1989. Comparison of acoustic and pump sampling techniques for the analysis of zooplankton distribution. J. Plankt. Res. **11**: 703–709.

Cowles, D.L. 2001. Swimming speed and metabolic rate during routine swimming and simulated diel vertical migration of *Sergestes similis* in the laboratory. Pac. Sci. **55**: 215–226.

Coyle, K.O. 1998. *Neocalanus* scattering layers near the western Aleutian Islands. J. Plankt. Res. **20**: 1189–1202.

Coyle, K.O. and Cooney, R.T. 1993. Water column sound scattering and hydrography around the Pribilof Islands, Bering Sea. Cont. Shelf Res. **13**: 803–827.

Coyle, K.O. and Hunt, Jr., G.L. 2000. Seasonal differences in the distribution, density and scale of zooplankton patches in the upper mixed layer near the western Aleutian Islands. Plankt. Biol. Ecol. **47**: 31–42.

Coyle, K.O. and Paul, A.J. 1992. Interannual differences in prey taken by capelin, herring and red salmon relative to zooplankton abundance during the spring bloom in a southeast Alaskan embayment. Fish. Oceanogr. **1**: 294–305.

Coyle, K.O. and Pinchuk, A.I. 2002. The abundance and distribution of euphausiids and zero-age pollock on the inner shelf of the southeast Bering Sea near the Inner Front in 1997–1999. Deep-Sea Res. II **49**: 6009–6030.

Coyle, K.O., Hunt, G.L., Jr., Decker, M.B. and Weingartner, T.J. 1992. Murre foraging, epibenthic sound scattering and tidal advection over a shoal near St. George Island, Bering Sea. Mar. Ecol. Prog. Ser. **83**: 1–14.

Cowles, D.L. 2001. Swimming speed and metabolic rate during routine swimming and simulated Diel Vertical Migration of *Sergestes* *similis* in the laboratory. Pac. Sci. **55**: 215–226.

Croll, D.A., Tershy, B.R., Hewitt, R.P., Demer, D.A., Fiedler, P.C., Smith, S.E., Armstrong, W., Popp, J.M., Kiekhefer, T., Lopez, V.R., Urban, J. and Gendron, D. 1998. An integrated approach to the foraging ecology of marine birds and mammals. Deep-Sea Res. II **45**: 1353–1371.

Dalpadado, P. and Gjøsaeter, J. 1988. Feeding ecology of the lanternfish *Benthosema pterotum* from the Indian Ocean. Mar. Biol. **99**: 555–567.

Dalpadado, P. and Ikeda, T. 1989. Some observations on moulting, growth and maturation of krill (*Thysanoessa inermis*) from the Barents Sea. J. Plankt. Res. **11**: 133–139.

De Robertis, A. 2002a. Size-dependent visual predation risk and timing of vertical migration: an optimizing model. Limnol. Oceanogr. **45**: 1838–1844.

De Robertis, A. 2002b. Small-scale spatial distribution of the euphausiid *Euphausia pacifica* and overlap with planktivorous fishes. J. Plankt. Res. **24**: 1207–1220.

De Silva-Dávila, R. and Palomares-García, R. 1998. Unusual larval growth production of *Nyctiphanes simplex* in Bahía de La Paz, Baja California, México. J. Crust. Biol. **18**: 490–498.

De Silva-Dávila, R., Palomares-García, R., Martínez-López, A. and Carballido-Carranza, M.A. 2002. Standing stock of *Nyctiphanes simplex* in the southern region of the California Current System. J. Plankt. Res. **24**: 1057–1066.

De Robertis, A., Schell, C. and Jaffe, J.S. 2003a. Acoustic observations of the swimming behavior of the euphausiid *Euphausia pacifica* Hansen. ICES J. Mar. Sci. **60**: 885–898.

De Robertis, A., Ryer, C.H., Veloza, A. and Brodeur, R.D. 2003b. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Can. J. Fish. Aquat. Sci./J. Can. Sci. Halieut. Aquat. **60**: 1517–1526.

DeWitt, F.A. 1972. Bathymetric distributions of two common deep-sea fishes, *Cyclothone acclinidens* and *C. signata*, off southern California. Copeia **1972**: 88–96.

Dilling, L. and Alldredge, A.L. 2000. Fragmentation of marine snow by swimming macrozooplankton: A new process impacting carbon cycling in the sea. Deep-Sea Res. I **47**: 1227–1245.

Dilling, L. and Brzezinski, M.A. 2004. Quantifying marine snow as a food choice for zooplankton using stable silicon isotope tracers. J. Plankt. Res. **26**: 1105–1114.

Dilling, L., Wilson, J., Steinberg, D. and Alldredge, A. 1998. Feeding by the euphausiid *Euphauisa pacifica* and the copepod *Calanus pacificus* on marine snow. Mar. Ecol. Prog. Ser. **170**: 189–201.

Donaldson, H.A. 1975. Vertical distribution and feeding of sergestid shrimp (Decapoda: Natantia) collected near Bermuda. Mar. Biol. **31**: 37–50.

Dower, J.F. and Brodeur, R.D. 2004. The role of biophysical coupling in concentrating marine organisms around shallow topography. J. Mar. Syst. **50**: 1–2.

Doyle, M.J., Mier, K.L., Busby, M.S. and Brodeur, R.D. 2002. Regional variations in springtime ichthyoplankton assemblages in the Northeast Pacific Ocean. Prog. Oceanogr. **53**: 247–281.

Duka, L.A. 1987. Feeding of *Ceratoscopelus warmingii* (Myctophidae) in the tropical Atlantic. J. Ichthyol. **28**: 89–95.

Dunn, J.R. 1983. Development and distribution of the young of northern smoothtongue, *Leuroglossus schmidti* (Bathylagidae), in the northeast Pacific, with comments on the systematics of the genus *Leuroglossus* Gilbert. Fish. Bull. U.S. **81**: 23–39.

Dunn, J.R. and Naplin, N.A. 1974. Fish eggs and larvae collected from waters adjacent to Kodiak Island, Alaska, during April and May, 1972. NWFC MARMAP Survey I, Rep. No. 12, 61 pp.

Dwyer, D.A., Bailey, K.M. and Livingston, P.A. 1987. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special reference to cannibalism. Can. J. Fish. Aquat. Sci. **44**: 1972–1984.

Ebeling, A.W. and Cailliet, G.M. 1990. The vertical distribution and feeding habits of two common midwater fishes (*Leuroglossus* *stilbius* and *Stenobrachius leucopsarus*) off Santa Barbara. CalCOFI Rep. **31**: 106–123.

Endo, Y. and Komaki, Y. 1979. Larval stage of euphausiids with descriptions of those of *Thysanoessa longipes* Brandt. Bull. Japan Sea Res. Lab. **30**: 97–110.

Endo, Y., Hanamura, Y. and Taniguchi, A. 1985. In situ observations on surface swarming *Euphausia pacifica* in Sendai Bay in early spring with special reference to their biological characteristics. Bull. Mar. Sci. **37**: 764 pp.

Endo, Y., Tanasichuk, R. and Everson, I. 2000. Role of krill in marine food webs. pp. 182–200. *In* Krill: Biology, Ecology and Fisheries. *Edited by* I. Everson, Fish and Aquatic Resources Series 6, Blackwell Science, London.

Etnoyer, P., Canny, D., Mate, B. and Morgan, L. 2004. Persistent pelagic habitat in the Baja California to Bering Sea (B2B) ecoregion. Oceanography. **17**: 90–101.

Everson, I. (*Editor*). 2000. Krill: Biology, Ecology and Fisheries. Fish and Aquatic Resources Series 6, Blackwell Science, London, 372 pp.

Farquhar, G.B. (*Editor*) 1970. Proceedings of an international symposium on biological sound scattering in the ocean. Maury Center for Ocean Science, Washington, DC, 629 pp.

Favorite, F., Dodimead, A.J. and Nasu, K. 1976. Oceanography of the subarctic Pacific region, 1960–1971. Bull. Int. North Pacific Fish. Comm. **33**: 1–187.

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

Feinberg, L.R., Gómez-Gutiérrez, J., Shaw, T. and Peterson, W.T. 2003. Vital rates for *Euphausia pacifica* off the Oregon coast, compared with populations around the North Pacific. Third International Zooplankton Production Symposium. 20–23 May 2003 at Gijon, Spain, 189 pp.

Filin, A.A., Gorchinsky, K.V. and Kiseleva, V.M. 1991. Biomass of myctophids in the Atlantic sector of the Southern Ocean as estimated by acoustic surveys. Sel. Sci. Pap. Sci. Comm. Cons. Antarct. Mar. Liv. Resour. SC-CAMLL-SSP/7: 417–431.

Flock, M.E. and Hopkins, T.L. 1992. Species composition, vertical distribution, and food habits of the sergestid shrimp assemblage in the eastern Gulf of Mexico. J. Crust. Biol. **12**: 210–223.

Foote, K.G. and Stanton, T.K. 2000. Acoustical methods. pp. 223–258. *In* Krill: Biology, Ecology and Fisheries. *Edited by* I. Everson, Fish and Aquatic Resources Series 6, Blackwell Science, London.

Foote, K.G. and Traynor, J.J. 1988. Comparison of walleye pollock target strength estimates determined from in situ measurements and calculations based on swimbladder form. J. Acoust. Soc. Am. **83**: 9–17.

Foxton, P. 1970a. The vertical distribution of pelagic decapods (Crustacea: Natantia) collected on the SOND cruise 1965. I. The Caridea. J. Mar. Biol. Assoc. U.K. **50**: 939–960.

Foxton, P. 1970b. The vertical distribution of pelagic decapods (Crustacea: Natantia) collected on the SOND cruise 1965. II. The Penaeidea and general discussion. J. Mar. Biol. Assoc. U.K. **50**: 961–1000.

Foxton, P. and Roe, S.J. 1974. Observations on the nocturnal feeding of some mesopelagic decapod crustacea. Mar. Biol. **28**: 37–49.

Frost, B.W. and McCrone, L.E. 1979. Vertical distribution, diel vertical migration, and abundance of some mesopelagic fishes in the eastern subarctic Pacific Ocean in summer. Fish. Bull. U.S. **76**: 751–770.

Fulton, J. and LeBrasseur, R. 1984. Euphausiids of the continental shelf and slope of the Pacific coast of Canada. La mer **22**: 268–276.

Funes-Rodríguez, R., Flores-Coto, C., Esquivel-Herrera, A., Fernández-Alamo, M.A. and Gracia-Gasca, A. 2002. Larval fish community structure along the best coast of Baja California during and alter the El Niño event (1983). Bull. Mar. Sci. **70**: 41–54.

Gartner, J.V., Jr. 1991a. Life histories of three species of lanternfishes (Pisces: Myctophidae) from the eastern Gulf of Mexico. I. Morphological and microstructural analysis of sagittal otoliths. Mar. Biol. **111**: 11–20.

Gartner, J.V., Jr. 1991b. Life histories of three species of lanternfishes (Pisces: Myctophidae) from the eastern Gulf of Mexico. II. Age and growth patterns. Mar. Biol. **111**: 21–27.

Gartner, J.V., Jr. 1993. Patterns of reproduction in the dominant lanternfish species (Pisces: Myctophidae) of the eastern Gulf of Mexico, with a review of reproduction among tropical-subtropical Myctophidae. Bull. Mar. Sci. **52**: 721–750.

Gartner, J.V., Jr., Crabtree, R.E. and Sulak, K.J. 1997. Feeding at depth. pp. 115–193. *In* Deep-Sea Fishes. *Edited by* D.J. Randall and A.P. Farrell, Academic Press, London.

Gaston, A.J. and Jones, I.L. 1998. The Auks. Oxford Univ. Press, Oxford. 260 p.

Gendron, D.L. 1992. Population structure of daytime surface swarms of *Nyctiphanes simplex* (Crustacea: Euphausiacea) in the Gulf of California. Mar. Ecol. Progr. Ser. **87**: 1–6.

Genin, A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. J. Mar. Syst. **50**: 3–20.

Genin, A., Greene, C., Haury, L., Wiebe, P., Gal, G., Kaartvedt, S., Meir, E., Fey, C. and Dawson, J. 1994. Zooplankton patch dynamics – daily gap formation over abrupt topography. Deep-Sea Res. I **41**: 941–951.

Gigarosov, V.Ye. and Ovcharov, O.P. 1992. Age and growth of the lantern fish *Myctophum nitidulum* (Myctophidae) from the tropical Atlantic. Vopr. Ikhtiol. **32**: 61–68. (English translation, J. Ichthyol. **32**: 34–42).

Gjøsaeter, J. 1973. The food of the myctophid fish, *Benthosema glaciale* (Reinhardt), from western Norway. Sarsia **52**: 53–58.

Gjøsaeter, J. 1981. Life history and ecology of the myctophid fish *Notoscopelus kroeyeri* from the north-east Atlantic. Fisk Dir. Skr. (Ser. Havunders.) **17**: 133–152.

Gjøsaeter, H. 1987. Primary growth incements in otoliths of six tropical myctophid species. Biol. Oceanogr. **4**: 359–382.

Gjøsaeter, J. and Kawaguchi, K. 1980. A review of the world resources of mesopelagic fish. FAO Fish. Tech. Paper **193**: 1–151.

Goldthwait, S., Yen, J., Brown, J. and Alldredge, A. 2004. Quantification of marine snow fragmentation by swimming euphausiids. Limnol. Oceanogr. **49**: 940–952.

Gómez-Gutiérrez, J. 1995. Distribution patterns, abundance and population dynamics of the euphausiids *Nyctiphanes simplex* and *Euphausia eximia* in the west coast of Baja California, México. Mar. Ecol. Prog. Ser. **119**: 63–76.

Gómez-Gutiérrez, J. 2002. Hatching mechanism and delayed hatching of the eggs of three broadcast spawning euphausiid species under laboratory conditions. J. Plankt. Res. **24**: 1265–1276.

Gómez-Gutiérrez, J. 2003a. Hatching mechanism and accelerated hatching of the eggs of a sac-spawning euphausiid *Nematoscelis difficilis*. J. Plankt. Res. **25**: 1397–1411.

Gómez-Gutiérrez, J. 2003b. Comparative study of the population dynamic, secondary productivity, and reproductive ecology of the euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* in the Oregon upwelling region. Ph.D. Dissertation, College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR.

Gómez-Gutiérrez, J. and Robinson, C.J. 2004. Parasitoid ciliates (Apostomatida: Colliniidae: *Collinia*) infecting the subtropical euphausiid *Nyctiphanes simplex* in the southern part off Baja California, México. CalCOFI conference, San Diego, USA, November 15–18, 2004.

Gómez-Gutiérrez, J. and Robinson, C.J. 2005. Embryonic, early larval development time, hatching mechanism and interbrood period of the sac-spawning euphausiid *Nyctiphanes simplex* Hansen. J. Plankt. Res. **27**: 279–295.

Gómez-Gutiérrez, J. and Sánchez-Ortíz, O.C. 1997. Larval drift and population structure of the pelagic phase of *Pleuroncodes planipes* (Simpson) (Crustacea: Galatheidae) off the southwest coast of Baja California, México. Bull. Mar. Sci. **61**: 305–326.

Gómez-Gutiérrez, J. and Shields, J. 1998. Range extension for *Oculophryxus bicaulis* Shields and Gómez (Isopoda, Dajidae) in the South China Sea. Crustaceana **71**: 167–170.

Gómez-Gutiérrez, J., Palomares-García, R. and Gendron, D. 1995. Community structure of the euphausiids populations along the west coast of Baja California, México during the weak ENSO 1986–87. Mar. Ecol. Prog. Ser. **120**: 41–51.

Gómez-Gutiérrez, J., Silva, R.D. and Lavaniegos, B.E. 1996. Growth production of the euphausiid *Nyctiphanes simplex* on the coastal shelf off Bahía Magdalena, Baja California Sur, México. Mar. Ecol. Prog. Ser. **138**: 309–314.

Gómez-Gutiérrez, J., Domínguez-Hernández, E., Robinson, C.R. and Arenas-Fuentes, V. 2000. Hydroacoustical evidence of autumn-inshore residence of the red crab *Pleuroncodes planipes* in Punta Eugenia, Baja California, Mexico. Mar. Ecol. Progr. Ser. **208**: 283–291.

Gómez-Gutiérrez, J., Peterson, W.T., DeRobertis, A. and Brodeur, R.D. 2003. Mass mortality of krill caused by parasitoid ciliates. Science **301**: 339.

Gómez-Gutiérrez, J., Peterson, W.T. and Miller, C.B. 2005. Cross-shelf life-stage segregation and community structure of the euphausiids off central Oregon (1970–1972). Deep-Sea Res. II **52**: 289–315.

Gopalakrishnan, K. 1974. Zoogeography of the genus *Nematoscelis* (Crustacea, Euphausiacea) Fish. Bull. **4**: 1039–1074.

Gorbatenko, K.M. and Il'inskii, E.N. 1992. Feeding behavior of the most common mesopelagic fishes in the Bering Sea. J. Ichthyol. **32**: 52–60.

Gorbatenko, K.M. and Chuchukalo, V.I. 1989. Feeding and daily food consumption of Pacific salmon of the genus *Oncorhynchus* in the Okhotsk Sea. J. Ichthyol. **29**: 143–151.

Gordon, J.D., Nishida, M.S. and Nemoto, T. 1985. The diet of mesopelagic fish from the Pacific coast of Hokkaido, Japan. J. Oceanogr. **41**: 89–97.

Gorelova, T.A. 1977. Some characteristics of the nutrition of the young of nictoepipelagic and mesopelagic lantern fish (Pisces, Myctophidae). Oceanology **17**: 220–222.

Gorelova, T.A. and Kobylanskiy, S.G. 1985. Feeding habits of deepwater fish of the Bathylagidae. Vopr. Ikhtiol. **25**: 264–274. (in Russian)

Goto, Y. 1999. Feeding ecology of steller sea lion, ribbon and spotted seal in Hokkaido Island, northern Japan. Ph.D. Dissertation, Hokkaido University, Hakodate, 180 pp.

Greely, T.M., Gartner, J.V., Jr. and Torres, J.J. 1999. Age and growth of *Electrona antarctica* (Pisces: Myctophidae), the dominant mesopelagic fish of the Southern Ocean. Mar. Biol. **133**: 145–158.

Greene, C.H. and Wiebe, P.H. 1990. Bioacoustic oceanography: New tools for zooplankton and micronekton research in the 1990s. Oceanography **3**: 12–17.

Greenlaw, C.F. and Johnson, R.K. 1983. Multiple-frequency acoustical estimation. Biol. Oceanogr. **2**: 227–252.

Halliday, R.G. 1970. Growth and vertical distribution of the glacier lanternfish, *Benthosema glaciale*, in the northwestern Atlantic. J. Fish. Res. Bd. Can. **27**: 105–126.

Hamano, A. and Uchida, K. 1992. Target strength measurement of sternoptychid fish, *Maurolicus muelleri*, using 88 kHz quantitative echo sounder. Bull. Japan. Soc. Fish. Oceanogr. **56**: 283–293.

Hamano, A., Uchida, K. and Takeda, Y. 1992 Sorting echoes of sternoptychid fish, *Maurolicus muelleri*, from quantitative sounder echograms with verification by midwater trawl. Bull. Japan. Soc. Fish. Oceanogr. **56**: 295–308.

Hamner, W.M. 1988. Biomechanic of filter feeding in the Antarctic krill *Euphausia superba*: review of past work and new observations. J. Crust. Biol. **8**: 149–165.

Hanamura, Y., Kamizono, M. and Katayama, S. 2001. Surface swarm and shore stranding of the euphausiid *Euphausia nana* in the Seto Inland Sea, Japan. Bull. Fish. Environ. Inland Sea. **3**: 47–51.

Harrison, C.S. and Seki, M.P. 1987. Trophic relationships among tropical seabirds at the Hawaiian Islands. pp. 305–326. *In* Seabirds: Feeding Ecology and Role in Marine Ecosystems. *Edited by* J.P. Croxall, Cambridge University Press, Cambridge.

Harrison, C.S., Hida, T.S. and Seki, M.P. 1983. Hawaiian seabird feeding ecology. Wildl. Monogr. **85**: 71 pp.

Hayashi, A. 1993. Growth and maturation of the firefly squid, *Watasenia scintillans* (Berry), in Toyama Bay and adjacent waters of the Sea of Japan. pp. 571–585. *In* Recent Advances in Cephalopod Fisheries Biology. *Edited by* T. Okutani, R.K. O'Dor, and T. Kubodera.

Hayashi, S. and Hirakawa, K. 1997. Diet composition of the firefly squid, *Watasenia scintillans,* from Toyama Bay, southern Japan Sea. Bull. Japan Sea Natl. Fish. Res. Inst. **47**: 57–66.

Hayashi, A., Kawaguchi, K., Watanabe, H. and Ishida, M. 2001a. Daily growth increment formation and its lunar periodicity in otoliths of the myctophid fish *Myctophum asperum*

(Pisces: Myctophidae). Fish. Sci. **67**: 811–817.

Hayashi, A., Watanabe, H., Ishida, M. and Kawaguchi, K. 2001b. Growth of *Myctophum asperum* (Pisces: Myctophidae) in the Kuroshio and transitional waters. Fish. Sci. **67**: 983–984.

Hays, R., Measures, L.N. and Hout, J. 1998. Euphausiids as intermediate hosts of *Anasakis simplex* in the St. Lawrence estuary. Can. J. Zool. **76**: 1226–1235.

Heath, W.A. 1977. The ecology and harvesting of euphausiids in the Strait of Georgia. Ph.D. Thesis, Univ. of British Columbia, 187 pp.

Heffernan, J.J. and Hopkins, T.L. 1981. Vertical distribution and feeding of the shrimp genera *Gennadas* and *Bentheogennema* (Decapoda: Penaeidea) in the eastern Gulf of Mexico. J. Crust. Biol. **1**: 461–473.

Hewitt, P.R., Watkins, J.L., Naganobu, M., Tshernyshkov, P., Brierley, A.S., Demer, D.A., Kasatkina, S., Takao, Y., Goss, C., Malyshko, A., Brandon, M.A., Kawaguchi, S., Siegel, V., Trathan, P.N., Emery, J.H., Everson, I. and Miller, D.G.M. 2002. Setting a precautory catch limit for Antarctic krill. Oceanography **15**: 26–29.

Hidaka, K., Kawaguchi, K., Murakami, M. and Takahashi, M. 2001. Downward transport of organic carbon by diel migratory micronekton in the western equatorial Pacific: its quantitative and qualitative importance. Deep-Sea Res. I **48**: 1923–1939.

Hidaka, K., Kawaguchi, K., Tanaka, T., Takahashi, M. and Kubodera, T. 2003. Biomass and taxonomic composition of micronekton in the western tropical-subtropical Pacific. Fish. Oceangr. **12**: 112–125.

Hirota, Y. 1995. The Kuroshio. Part III. Zooplankton. Oceanogr. Mar. Biol. Ann. Rev. **33**: 151–220.

Hirota, Y. and Nemoto, T. 1990. Relationship between feeding and vertical distribution of euphausiids in the western Pacific Ocean. Bull. Plankt. Soc. Japan/Nihon Purankuton Gakkaiho **36**: 127–135.

Holliday, D.V. 1980. Use of frequency diversity for marine biological measurements. pp. 423–460. *In* Advanced concepts in ocean measurements for marine biology. *Edited by* F.P. Diemer *et al.*, Univ. South Carolina Press, Columbia, SC.

Holliday, D.V. and Pieper, R.E. 1980. Volume scattering strengths and zooplankton distributions at acoustic frequencies between 0.5 and 3 MHz. J. Acoust. Soc. Am. **67**: 135–146.

Holliday, D.V. and Pieper, R.E. 1995. Bioacoustical oceanography at high frequencies. ICES J. Mar. Sci. **52**: 279–296.

Hong, S.Y. 1969. The euphausiid crustaceans of Korean waters. pp. 291–300. *In* The Kuroshio. *Edited by* J.C. Marr, Univ. Hawaii Press.

Hopkins, T.L. and Baird, R.C. 1975. Net feeding in mesopelagic fishes. Fish. Bull. U.S. **73**: 908–914.

Hopkins, T.L. and Baird, R.C. 1985. Aspects of trophic ecology of the mesopelagic fish *Lampanyctus alatus* (Family Myctophidae) in the eastern Gulf of Mexico. Biol. Oceanogr. **3**: 285–313.

Hopkins, T.L. and Gartner, J.V., Jr., 1992. Resource-partitioning and predation impact of a low-latitude myctophid community. Mar. Biol. **114**: 185–197.

Hopkins, T.L. and Lancraft, T.M. 1984. The composition and standing stock of mesopelagic micronekton at 27°N 86°W in the eastern Gulf of Mexico. Contrib. Mar. Sci. **27**: 143–158.

Horne, J.K. and Clay, C.S. 1998. Sonar systems and aquatic organisms: matching equipment and model parameters. Can. J. Fish. Aquat. Sci. **55**: 1296–1306.

Horne, J.K. and Jech, J.M. 1999. Multi-frequency estimates of fish abundance: constraints of rather high frequencies. ICES J. Mar. Sci. **56**: 184–199.

Hosie, G.W. and Ritz, D.A. 1983. Contribution of moulting and eggs to secondary production in *Nyctiphanes australis* (Crustacea: Euphausiacea). Mar. Biol. **77**: 215–220.

Hosie, G.W. and Ritz, D.A. 1989. Body shrinkage in the sub-tropical euphausiid *Nyctiphanes australis* G.O. Sars. J. Plankt. Res. **11**: 595–598.

Hovekamp, S. 1989. Avoidance of nets by *Euphausia pacifica* in Dabob Bay. J. Plankt. Res. **11**: 907–924.

Hu, V.J.H. 1978. Relationships between vertical migration and diet in four species of euphausiids. Limnol. Oceanogr. **23**: 296–306.

Hunt, G.L., Jr. and Harrison, N.M. 1990. Foraging habitat and prey taken by least aulkets at King Island, Alaska. Mar. Ecol. Prog. Ser. **5**: 141–150.

Hunt, G.L., Jr., Russell, R.W., Coyle, K.O. and Weingartner, T. 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. Mar. Ecol. Prog. Ser. **167**: 241–259.

Hunt, G.L., Jr., Kato, H. and McKinnell, S.M. 2000. Predation by marine birds and mammals in the Subarctic North Pacific Ocean. PICES Sci. Rep. No. 14, 165 pp.

Hunt, J.C. and Lindsay, D.J. 1999. Methodology for creating an observational database of midwater fauna using submersibles: results from Sagami Bay, Japan. Plankt. Biol. Ecol. **46**: 75–87.

Hussain, S.M. and Ali-Khan, J. 1987. Fecundity of *Benthosema 'fibulatum* and *Benthosema pterotum* from the northern Arabian Sea. Deep-Sea Res. **34**: 1293–1299.

Ichii, T. 2000. Krill harvesting. pp. 228–261. *In* Krill: Biology, Ecology and Fisheries. *Edited by* I. Everson, Fish and Aquatic Resources Series 6, Blackwell Science, London.

Iida, K. 2003. Proceedings of the International Symposium on Advanced Techniques of Sampling Gear and Acoustical Surveys for Estimation of Fish Abundance. (Electronic proceedings available from Hokkaido University, Hakodate, Japan.)

Iguchi, N. and Ikeda, T. 1994. Experimental study on brood size, egg hatchability and early development time of the euphausiid *Euphausia pacifica* from Toyama Bay, Southern Japan Sea. Bull. Japan Sea. Natl. Fish. Res. Inst. **44**: 49–57.

Iguchi, N. and Ikeda, T. 1999. Production, metabolism and P:B ratio of *Euphausia pacifica* (Crustacea: Euphausiacea) in Toyama Bay, southern Japan Sea. Plankt. Biol. Ecol. **46**: 68–74.

Iguchi, N. and Ikeda, T. 2004. Vertical distribution, population structure and life history of *Thysanoessa longipes* (Crustacea: Euphausiacea) around Yamato Rise, central Japan Sea. J. Plankt. Res. **26**: 1015–1023.

Iguchi, N., Ikeda, T. and Imamura, A. 1993. Growth and life cycle of an euphausiid crustacean (*Euphausia pacifica* Hansen) in Toyama Bay, Southern Japan Sea. Bull. Japan Sea. Natl. Fish. Res. Inst. **43**: 69–81.

Iizuka, K., Asano, M. and Naganuma, A. 1989. Feeding habits of skipjack tuna (*Katsuwonus pelamis* L.) caught by pole and line and the state of young skipjack tuna distribution in the tropical seas of the western Pacific. Bull. Tohoku Reg. Fish. Res. Lab. **51**: 135–155.

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

Il'insky, E.N. and Gorbatenko, K.M. 1994. Basic trophic relations of mesopelagic necton in the Sea of Okhotsk. Izv. TINRO **116**: 91–104. (in Russian)

Isoda, T. 2000. Study on feeding habits in two forms of short-finned pilot whale (*Globicephala macrorhynchus*) and Risso's dolphin (*Grampus griseus*) in the Pacific coast of Japan. M.S. Thesis, Tokai Univ., Shimizu, 30 pp.

Ivanov, O.A. 1997. Composition and biomass of the fishes and cephalopods of the Kuril and Kamchatka waters of the Pacific Ocean. J. Ichthyol. **37**: 147–158.

Ivanov, O.A. and Lapko, V.V. 1994. Size and age characteristics of the mesopelagic fish *Diaphus theta* (Myctophidae) in the south Kurile region. Russ. J. Mar. Biol. **20**: 148–152.

Jefferts, K. 1983. Zoogeography and systematics of cephalopods of the northeastern Pacific Ocean. Ph.D. Dissertation, Oregon State University, Corvallis, OR, 291 pp.

Jefferts, K. 1988. Zoogeography of cephalopods from the northeastern Pacific Ocean. Bull. Ocean Res. Inst., Univ. Tokyo **26**: 123–157.

Johnson, M.W. and Brinton, E. 1963. Biological species, water masses and currents. pp. 381–414. *In* The Sea, Vol. 2. *Edited by* M.N. Hill, Interscience Publ., New York.

Ju, S. and Harvey, R.D. 2002. Determination of age structure, nutritional status and potential for trophic transfer in the *Euphausia pacifica* and *Thysanoessa spinifera* using multiple organic tracers. Ocean Sciences Meeting 2002. American Society of Limnology and

Oceanography, 11–15 February 2002, Honolulu, Hawaii. p. 43.

Judkins, D.C. and Fleminger, A. 1972. Comparison of foregut contents of *Sergestes similis* obtained from net collections and albacore stomachs. Fish. Bull. U.S. **70**: 217–223.

Kalish, J.M., Greenlaw, C.F., Pearcy, W.G. and Holliday, D.V. 1986. The biological and acoustical structure of sound scattering layers off Oregon. Deep-Sea Res. **33**: 631–653.

Karedin, Ye.P. 1998. Resources of the northern Pacific mesopelagic fishes. Izvestia TINRO-Centre **124**: 391–416.

Kawaguchi, K. 1973. Biology of *Gonostoma gracile* (Gonostomatidae) II. Geographical and vertical distribution. J. Oceanogr. Soc. Japan **29**: 113–120.

Kawaguchi, K. 1976. Geographical distribution of myctophid fishes (family Myctophidae) in the northern North Pacific. Bull. Japan. Soc. Fish. Oceanogr. **29**: 58–59.

Kawaguchi, K. 1977. Micronektonic community – Community of myctophid fishes (Myctophidae) in Suruga Bay, central Japan. pp. 235–268. *In* Communities and Production in the Sea. *Edited by* S. Nishizawa, R. Ishida and T. Kawasaki, Kouseisha-Kouseikaku, Tokyo. (in Japanese)

Kawaguchi, K. and Mauchline, J. 1982. Biology of myctophid fishes (family Myctophidae) in the Rockall Trough, northeastern Atlantic Ocean. Biol. Oceanogr. **1**: 337–373.

Kawaguchi, K. and Shimizu, H. 1978. Taxonomy and distribution of the lanternfishes, genus *Diaphus* (Pisces, Myctophidae) in the western Pacific, eastern Indian Oceans and the southeast Asian Seas. Bull. Ocean Res. Inst. Univ. Tokyo **10**: 1–145.

Kawaguchi, K., Ikeda, H., Tamura, M. and Ueyanagi, S. 1972. Geographical distribution of surface-migrating myctophid fishes (genus *Myctophum*) in the tropical and subtropical Pacific and Indian Oceans. Bull. Far Seas Fish. Res. Lab. **6**: 23–37.

Kawai, H. 1972. Hydrography of the Kuroshio and Oyashio. pp. 129–321. *In* Physical Oceangraphy, II. Kaiyokagaku Kiso Koza (Fundamentals of Oceanography). *Edited by* M. Iwashita, Y. Komaki, T. Hoshiai, S. Horibe and J. Masuzawa, Tokai Univ. Press, Tokyo. (in Japanese)

Kawakami, T. 1976. Squids found in the stomach of sperm whales in the Northwestern Pacific. Sci. Rep. Whales Res. Inst. **28**: 145–151.

Kawakami, T. 1980. A review of sperm whale food. Sci. Rep. Whales Res. Inst. **32**: 199–218.

Kawamura, A. 1973. Food and feeding of sei whales caught in the waters south of 40 N in the North Pacific. Sci. Rep. Whales Res. Inst. **25**: 219–236.

Kawamura, A. 1982. Food habits and prey distributions of three rorqual species in the North Pacific Ocean. Sci. Rep. Whales Res. Inst. **34**: 59–91.

Kawamura, A. and Fujii, F. 1988. Forage of the mesopelagic fishes, *Symbolophorus californiensis* (Eigenmann and Eigenmann) and *Tarletonbeania taylori* Mead caught in gill nets in the northwestern North Pacific Ocean. Bull. Ocean Res. Inst., Univ. Tokyo **26**: 143–159.

Kikuchi, T. and Nemoto, T. 1986. List of pelagic shrimps (Crustacea, Decapoda) from the Western North Pacific. Bull. Biogeogr. Soc. Japan **41**: 51–59.

Kikuchi, T. and Omori, M. 1985. Vertical distribution and migration of oceanic shrimps at two locations off the Pacific coast of Japan. Deep-Sea Res. **32**: 837–851.

King, J. 1983. Seals of the World. Oxford Univ. Press, Oxford, 240 pp.

Kinzer, J. 1977. Observation on feeding habits of mesopelagic fish *Benthosema glaciale* (Myctophidae) off NW Africa. pp. 381–392. *In* Oceanic Sound Scattering Prediction. *Edited by* W.R. Anderson, and B.J. Zahuranec, Plenum Press, New York.

Kinzer, J. and Schultz, K. 1985. Vertical distribution and feeding patterns of midwater fish in the central equatorial Atlantic—I. Myctophidae. Mar. Biol. **85**: 313–322.

Kobari, T. and Ikeda, T. 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.

Kodolov, L.S. and Gavrilov, G.M. 1980. Species composition of the family Melanostomiidae

(Osteichthyes) on the Emperor Sea Mountains. Izv. TINRO **104**: 163–167.

Kono, N. 1983. Distributional patterns and prey organisms of pelagic fishes occurring in the subarctic Pacific region in the summer. M.S. Thesis, Hokkaido Univ., Hakodate, 142 pp.

Kooka, K., Takatsu, T., Kamei, Y., Nakatani, T. and Takahashi, T. 1997. Food habits of walleye pollock inhabiting the mesopelagic zone in the northern Japan Sea in spring and autumn. Nippon Suisan Gakkaishi **63**: 537–541.

Koslow, J.A., Kloser, R.J. and Williams, A. 1997. Pelagic biomass and community structure over the mid-continental slope off southeastern Australia based upon acoustic and midwater trawl sampling. Mar. Ecol. Prog. Ser. **146**: 21–35.

Kotori, M. 1995. An incidence of surface swarming of *Euphausia pacifica* off the coast of western Hokkaido, Japan. Bull. Plankt. Soc. Japan **42**: 80–84.

Krygier, E.E. and Murano, M. 1988. Vertical distribution and zoogeography of oceanic mysids from the northeastern Pacific Ocean. Bull. Ocean Res. Inst. **26**: 109–122.

Krygier, E.E. and Pearcy, W.G. 1981. Vertical distribution and biology of pelagic decapod crustaceans off Oregon. J. Crust. Biol. **1**: 70–95.

Krygier, E.E. and Wasmer, R.A. 1988. Zoogeography of pelagic shrimps (Natantia: Penaeidea and Caridea) in the North Pacific Ocean (with synopses and keys to the species of the Subarctic and Transitional Zones). Bull. Ocean Res. Inst. **26**: 43–98.

Kubodera, T. 1986. Relationships between abundance of epipelagic squids and oceanographic-biological environments in the surface waters of the Subarctic Pacific in summer. Bull. Int. N. Pac. Fish. Comm. **47**: 215–228.

Kubodera, T. and Furuhashi, M. 1987. A manual concerning species assessment of squid and myctophids found in stomach contents. Northern Ocean Boundary Ecosystem Model Dev. Task, Data Suppl. Rep. Spec. Vol., Japan Fisheries Agency, 65 pp.

Kubodera, T. and Jefferts, K. 1984. Distribution and abundance of the early life stages of squid, primarily Gonatidae (Cephalopoda, Oegopsida), in the northern North Pacific. Bull. Natl. Sci. Mus., Ser. A **10**: 165–193.

Kubodera, T., Piatkowski, U., Okutani, T. and Clarke, M.R. 1998. Taxonomy and zoogeography of the family Onychoteuthidae (Cephalopoda: Oegopsida). *In* Systematics and Biogeography of Cephalopods, Vol. II. *Edited by* N.A. Voss, M. Vecchione, R.B. Toll and M.J. Sweeney, Smithsonian Contr. Zool. **586**: 277–291.

Kulikova, E.B. 1960. The lampanyctids (genus *Lampanyctus*) of the Far Eastern seas and of the northwestern part of the Pacific Ocean. Trudy Instituta Okeanologii SSSR **31**: 166–204.

Lancraft, T.M. and Robison, B.H. 1980. Evidence of post-capture ingestion by midwater fishes in trawl nets. Fish. Bull. U.S. **77**: 713–715.

Lapko, V.V. 1995. The role of squids in the Sea of Okhotsk communities. Okeanologia **35**: 737–742.

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

Lavaniegos, B.E. 1992. Growth and larval development of *Nyctiphanes simplex* in laboratory conditions. CalCOFI Rep. **33**: 162–171.

Lavaniegos, B.E. 1994. Dispersion and development patterns in larvae of *Nyctiphanes simplex* (Euphausiacea) in the upwelling region off Baja California. Mar. Ecol. Progr. Ser. **106**: 207–225.

Lavaniegos, B.E. 1995. Production of the euphausiid *Nyctiphanes simplex* in Bahia Vizcaíno western Baja California. J. Crust. Biol. **15**: 444–453.

LeBrasseur, R.J. 1966. Stomach contents of blue shark (*Prionace glauca* L.) taken in the Gulf of Alaska. J. Fish. Res. Bd. Can. **21**: 861–862.

LeBrasseur, R.J. 1970. Larval fish species collected in zooplankton samples from the northeastern Pacific Ocean, 1956–1959. Fish. Res. Bd. Can. Tech. Rep. 175, 47 pp.

Linkowski, T.B. 1991. Otolith microstructure and growth-patterns during the early life-history of lanternfishes (Family Myctophidae). Can. J. Zool. **69**: 1777–1792.

Linkowski, T.B. 1996. Lunar rhythms of vertical migrations coded in otolith microstructure of

North Atlantic lanternfishes, genus *Hygophum* (Myctophidae). Mar. Biol. **124**: 495–508.

Linkowski, M.B., Radtke, R.L. and Lenz, P.H. 1993. Otolith microstructure, age and growth of two species of *Ceratoscopelus* (Osteichthyes: Myctophidae) from the eastern North Atlantic. J. Exp. Biol. Ecol. **167**: 237–260.

Lisovenko, L.A. and Prut'ko, V.G. 1986. Reproductive biology of *Diaphus suborbitalis* (Myctophidae) in the equatorial part of the Indian Ocean. 1. Nature of oogenesis and type of spawning. Vopr. Ikhtiol. **4**: 619–629.

Loeb, V.J. 1979a. Vertical distribution and development of larval fishes in the north Pacific central gyre during summer. Fish. Bull. U.S. **77**: 777–739.

Loeb, V.J. 1979b. Larval fishes in the zooplankton community of the North Pacific Central Gyre. Mar. Biol. **53**: 173–191.

Loeb, V.J. 1980. Patterns of spatial and species abundance within the larval fish assemblage of the North Pacific Gyre during late summer. Mar. Biol. **60**: 189–200.

Loeb, V.J. 1986. Importance of vertical distribution studies in biogeographic understanding: Eastern Tropical Pacific vs. North Pacific central gyre ichthyoplankton assenblages. pp. 171–181. *In* Pelagic Biogeography. *Edited by* A.C. Pierrot-Bults, S. van der Spoel, B.J. Zahuranec and R.K. Johnson, UNESCO Tech. Paper Mar. Sci.

Lowry, L.F., Frost, K.J. and Burns, J.J. 1980. Variability in the diet of ringed seals, *Phoca hispida,* in Alaska. Can. J. Fish. Aquat. Sci. **37**: 2254–2261.

Lowry, M.S., Stewart, S.B., Heath, C.B., Yochem, P.K. and Francis, J.M. 1990. Seasonal and annual variability in the diet of California sea lions *Zalophus californianus* at San Nicolas Island, California, 1981–86. Fish. Bull. U.S. **89**: 331–336.

Macaulay, M.C., Wishner, K.F. and Daly, K.L. 1995. Acoustic scattering from zooplankton and micronekton in relation to a whale feeding site near Georges Bank and Cape Cod. Cont. Shelf Res. **15**: 509–537.

Mackas, D.L., Kieser, R., Saunders, M., Yelland, D.R., Brown, R.M. and Moore, D.F. 1997. Aggregations of euphausiids and Pacific hake (*Merluccius productus*) along the outer continental shelf off Vancouver Island. Can. J. Fish. Aquat. Sci. **54**: 2080–2096.

MacLennan, D.N. and Simmonds, E.J. 1992. Fisheries Acoustics. Chapman and Hall, London, 325 pp.

Malakoff, D. 2004. New tools reveal treasures at Ocean Hot Spots. Science **304**: 1104–1105.

Mangold, K. 1987. Reproduction. pp. 157–200. *In* Cephalopod Life Cycles, Vol. II, Comparative reviews. *Edited by* P.R. Boyle, Academic Press, London.

Marinovic, B. and Mangel, M. 1999. Krill can shrink as an ecological adaptation to temporally unfavorable environments. Ecology Lett. **2**: 338–343.

Marshall, N.B. 1954. Aspects of Deep Sea Biology. Hutchinson, London, 380 pp.

Marshall, N.B. 1979. Development in Deep-Sea Biology. Blandford, London, 566 pp.

Mason, J.C. and Phillips, A.C. 1985. Biology of the bathylagic fish (*Leuroglossus schmidti*) in the Strait of Georgia, British Columbia, Canada. Can. J. Fish. Aquat. Sci. **42**: 1144–1153.

Mauchline, J. 1967. Feeding appendages of the Euphausiacea (Crustacea). J. Zool. Lond. **153**: 1–43.

Mauchline, J. 1977. Growth and moulting of Crustacea, especially euphausiids. pp. 401–422. *In* Oceanic sound scattering prediction. *Edited by* N.R. Andersen and B.J. Zahuranec, Plenum Press, New York.

Mauchline, J. 1980. The biology of mysids and euphausiids. Adv. Mar. Biol. **18**: 1–681.

Mauchline, J. and Fisher, L.R. 1969. The biology of euphausiids. Adv. Mar. Biol. **7**: 1–454.

Maynard, S.D. 1982. Aspects of the biology of mesopelagic fishes of the genus *Cyclothone* in Hawaiian waters. Ph.D. Thesis, Univ. of Hawaii, 257 pp.

Maynard, S.D., Riggs, F.V. and Walters, J.F. 1975. Mesopelagic micronekton in Hawaiian waters: faunal composition, standing stock, and diel vertical migration. Fish. Bull. U.S. **73**: 726–736.

McGowan, J.A. and Okutani, T. 1968. A new species of enoploteuthid squid, *Abraliopsis* (*Watasenia*) *felis*, from the California Current. Veliger **11**: 72–79.

Merrett, N.R. and Roe, H.S.J. 1974. Patterns and selectivity in the feeding of certain mesopelagic fishes. Mar. Biol. **28**: 115–126.

Methot, R.D., Jr. 1981. Spatial covariation of daily growth rates of larval northern anchovy, *Engraulis mordax*, and northern lampfish, *Stenobrachius leucopsarus*. Rapp. P.-v. Reun. Cons. int. Explor. Mer **178**: 424–431.

Miller, C.B. and Clemons, M.J. 1988. Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. Prog. Oceanogr. **20**: 293–313.

Miller, C.B., Frost, B.W., Batchelder, H.P., Clemons, M.J. and Conway, R.E. 1984. Life history of large, grazing copepods in a subarctic Ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the northeast Pacific. Prog. Oceanogr. **13**: 201–243.

Milliman, J.D. and Manheim, F.T. 1968. Observations in deep-scattering layers off Cape Hatteras, U.S.A. Deep-Sea Res. **15**: 505–507.

Mincks, S.L., Bollens, S.M., Madin, L.P., Horgan, E., Butler, M., Kremer, P.M. and Craddock, J.E. 2000. Distribution, abundance, and feeding ecology of decapods in the Arabian Sea, with implications for vertical flux. Deep-Sea Res. II **47**: 1475–1516.

Mishima, S. 1981. On the passing over of subtropic fishes to the subarctic region in the summer season. Res. Inst. North Pacific Fish., Hokkaido Univ. Spec. Vol., pp. 105–119.

Mito, K., Nishimura, A. and Yanagimoto, T. 1999. Ecology of groundfishes in the eastern Bering Sea, with emphasis on food habits. pp. 537–580. *In* Dynamics of the Bering Sea. *Edited by* T.R. Loughlin and K. Ohtani, Univ. Alaska Grant, Fairbanks, AK.

Miya, M. and Nemoto, T. 1991. Comparative life histories of the mesopelagic and bathypelagic fishes of the genus *Cyclothone* (Pisces, Gonostomatidae) in Sagami Bay, central Japan. Deep-Sea Res. **38**: 67–89.

Miya, M., Yamaguchi, M. and Okiyama, M. 1995. Midwater fishes off the Pacfic coast of Boso Peninsula, central Japan: Species Composition, Abundance, Biomass, and Zoogeographic Affinities. Japan. J. Ichthyol. **42**: 237–248.

Miyashita, K. and Aoki, I. 1999. Acoustic measurements of zooplankton using a dual frequency echo sounder. Mar. Ecol. Prog. Ser. **180**: 105–109.

Miyashita, K., Aoki, I., Seno, K., Taki, K. and Ogishima, T. 1997. Acoustic identification of isada krill, *Euphausia pacifica* Hansen, off the Sanriku coast, north-eastern Japan. Fish. Oceanog. **6**: 266–271.

Miyashita, K., Aoki, I., Asami, T., Mori, H. and Taki, K. 1998. Study on acoustical estimation of distribution and abundance of isada krill *Euphausia pacifica* Hansen off the Sanriku and off the Joban, northern Japan. J. Korean Soc Fish. Resources **1**: 128–135.

Miyazaki, N. 1973. Food of *Stenella caeruleoalba.* Sci. Rep. Whales Res. Inst. **25**: 265–275.

Moku, M. and Hidaka, K. 2002. Predation on zooplankton by micronekton. Bull. Plankt. Soc. Japan **49**: 52–60.

Moku, M., Kawaguchi, K., Watanabe, H. and Ohno, A. 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.

Moku, M., Ishimaru, K. and Kawaguchi, K. 2001. Growth of larval and juvenile *Diaphus theta* (Pisces: Myctophidae) in the transitional waters of the western North Pacific. Ichthyol. Res. **48**: 385–390.

Moku, M., Tsuda, A. and Kawaguchi, K. 2003. Spawning season and migration of the myctophid fish *Diaphus theta* in the western North Pacific. Ichthyol. Res. **50**: 52–58.

Mori, K. 1989. Study on feeding habits of dolphins in North Pacific. M.S. Thesis, Tokai Univ., Shimizu, 41 pp.

Moser, H.G. and Ahlstrom, E.H. 1996. Myctophidae; Lanternfishes. *In* The early stages of fishes in the California Current Region. *Edited by* H.G. Moser, La Jolla, California, CalCOFI Atlas 32, 180 pp.

Moser, H. G. and Smith, P.E. 1993a. Larval fish assemblages and oceanic boundaries. Bull. Mar. Sci. **53**: 283–289.

Moser, H.G. and Smith, P.E. 1993b. Larval fish assemblages of the California Current region and their horizontal and vertical distributions across a front. Bull. Mar. Sci. **53**: 645–691.

Moser, H.G., Smith, P.E. and Eber, L.E. 1987. Larval fish assemblages in the California

Current region, 1954–1960, a period of dynamic environmental change. CalCOFI Rep. **28**: 97–127.

Moser, H.G., Charter, R.L., Smith, P.E., Ambrose, D.A., Charter, S.R., Meyer, C.A., Sandknop, E.M. and Watson, W. 1993. Distributional atlas of fish larvae and eggs in the California current region: taxa with less than 1000 total larvae, 1951 through 1984. CalCOFI Atlas 31, 233 pp.

Moser, H.G., Charter, R.L., Smith, P.E., Ambrose, D.A., Charter, S.R., Meyer, C.A., Sandknop, E.M. and Watson, W. 1994. Distributional atlas of fish larvae in the California Current region: taxa with 1000 or more total larvae, 1951 through 1984. CalCOFI Atlas 32, 181 pp.

Moser, H.G., Charter, R.L., Smith, P.E., Ambrose, D.A., Watson, W., Charter, S.R. and Sandknop, E.M. 2001. Distributional atlas of fish larvae and eggs in the Southern California Bight region: 1951–1998. CalCOFI Atlas 34, 166 pp.

Murata, M. 1990. Oceanic resources of squids. Mar. Behav. Physiol. **18**: 19–71.

Murata, M. and Ishii, M. 1977. Some information on the ecology of the oceanic squid, *Ommastrephes bartrami* (Lesueur), and *Onychoteuthis borealijaponicus* Okada, in the Pacific Ocean off Northeastern Japan. Bull. Hokkaido Reg. Fish. Res. Lab **42**: 1–23. (in Japanese with English abstract)

Nagasawa, K., Nishimura, A., Asanuma, T. and Marubayashi, T. 1997. Myctophids in the Bering Sea: distribution, abundance, and their significance as food for salmonids. pp. 337–350. *In* Forage Fishes in Marine Ecosystems, Alaska Sea Grant College Program Rep. No. 97-10, Fairbanks, AK.

Nakagawa, Y., Endo, Y. and Taki, K. 2001. Diet of *Euphauisa pacifica* Hansen in Sanriku waters off northeastern Japan. Plankt. Biol. Ecol. **48**: 68–77.

Nakagawa, Y., Endo, Y. and Sakisaki, H. 2003. Feeding rhythm and vertical migration of *Euphauisa pacifica* in coastal waters of north-eastern Japan during Fall. J. Plankt. Res. **25**: 633–644.

Naito, M., Murakami, K. and Kobayashi, T. 1977. Growth and food habits of oceanic squids (*Ommastrephes bartrami, Onychoteuthis borealijaponica, Berryteuthis magister* and *Gonatopsis borealis*) in the western Subarctic Pacific region. Univ. Hokkaido, Res. Inst. North Pacific, Spec. Vol., pp. 339–351.

Naumenko, E.A. 1986. Daily feeding rhythm and ration of the capelin, *Mallotus villosus socialis* (Osmeridae), in the southeastern Bering Sea during winter. J. Ichthyol. **27**: 158–161.

Neighbors, M.A. 1992. Occurrence of inflated swimbladders in five species of lanternfishes (family Myctophidae) from waters off southern California. Mar. Biol. **114**: 355–363.

Neighbors, M.A. and Nafpaktitis, B.G. 1982. Lipid compositions, water contents, swimbladder morphologies and buoyancies of nineteen species of midwater fishes (18 Myctophids and 1 Neoscopelid). Mar. Biol. **66**: 207–215.

Nemoto, T. 1957. Food of baleen whales in the northern Pacific. Sci. Rep. Whales Res. Inst. **12**: 33–89.

Nemoto, T. 1959. Prey of baleen whales with reference to whale movement. Sci. Rep. Whales Res. Inst. **14**: 149–290.

Nemoto, T. 1966. *Thysanoessa* euphausiids, comparative morphology, allomorphosis and ecology. Sci. Rep. Whales Res. Inst. **20**: 109–155.

Nemoto, T. 1970. Feeding pattern of baleen whales in the ocean. pp. 241–252. *In* Marine Food Chains. *Edited by* J.H. Steele, Oliver and Boyd, Edinburgh.

Nemoto, T. 1977. Food and feeding structures of deep-sea *Thysanopoda* euphausiids. *In* Oceanic Sound Scattering Prediction. *Edited by* N.R. Andersen, and B.J. Zahuranec, Proceedings of a symposium conducted by the Ocean Science and Technology Division of the Office of Naval Research held in Monterey, Calif. Nov. 10–14, 1975, 859 pp.

Nemoto, T. and Kasuya, S. 1965. Foods of baleen whales in the Gulf of Alaska of the North Pacific. Sci. Rep. Whales Res. Inst. **19**: 45–51.

Nemoto, T., Kamada, K. and Hara, K. 1972. Fecundity of an euphausiid crustacean, *Nematoscelis difficilis*, in the North Pacific Ocean. Mar. Biol. **14**: 41–47.

Nemoto, T. Brinton, E. and Kamada, K. 1977. Reproduction and growth of deep-sea

Thysanopoda euphausiids. Bull. Plankt. Soc. Japan. **24**: 36–43.

Nesis, K.N. 1973. Patterns of distribution of cephalopods in the North Pacific. pp. 213–239. *In* Multidisciplinary Investigations of the Continental Slope of the Gulf of Alaska Area. *Edited by* Z.A. Filatova, Trudy Instituta Okeanologii, P.P. Shirshov, 91, Akad. Nauk SSSR, Moscow. (in Russian)

Nicol, S. 1986. Shape, size and density of daytime surface swarms of the euphausiid *Meganyctiphanes norvegica* in the Bay of Fundy. J. Plankt. Res. **8**: 29–39.

Nicol, S. 2000. Undesrtanding krill growth and aging: the constribution of experimental studies. Can. J. Fish. Aquat. Sci. **57**: 168–177.

Nicol, S. 2003. Living krill, zooplankton and experimental investigations: a discourse on the role of krill and their experimental study in marine ecology. Mar. Fresh. Behav. Physiol. **36**: 191–205.

Nicol, S. and Endo, Y. 1997. Krill fisheries of the world. FAO Fish. Tech. Paper 367, 100 pp.

Nishida, S., Pearcy, W.G. and Nemoto, T. 1988. Feeding habits of mesopelagic shrimps collected off Oregon. Bull. Ocean Res. Inst. Univ. Tokyo **26**: 99–108.

Nishikawa, J., Nishida, S., Moku, M., Hidaka, K. and Kawaguchi, K. 2001. Biomass, abundance, and vertical distribution of micronekton and large gelatinous zooplankton in the Subarctic Pacific and the Bering Sea during the summer of 1997. J. Oceanogr. **57**: 361–375.

Nishimura, A., Nagasawa, K., Asanuma, T., Aoki, H. and Kubota, T. 1999. Age, growth and feeding habits of lanternfish, *Stenobrachius leucopsarus* (Myctophidae), collected from near-surface layer in the Bering Sea. Fish. Sci. **65**: 11–15.

Noda, K. and Moriwaki, S. 1996. Acoustic survey of distribution and abundance of micronektonic fish, *Maurolicus muelleri,* in the southwestern Japan Sea. Bull. Japan. Soc. Fish. Oceanogr. **60**: 1–6. (in Japanese, with English abstract)

Norcross, B.L., McKinnell, S.M., Frandsen, M., Musgrave, D.L. and Sweet, S.R. 2003. Larval fishes in relation to water masses of the Central North Pacific Transitional Areas, including the shelf break of West-Central Alaska. J. Oceanogr. **59**: 445–460.

Odate, K. 1977. On the feeding habits of the Pacific saury, *Cololabis saira* (Brevoort). Bull. Tohoku Reg. Fish. Res. Lab. **38**: 75–88.

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 abstract)

Ogawa, T. 1961. Study on the fishes of the family Myctophidae in the north-eastern sea area along the Pacific coast of Japan. Part I. Species and distribution. Bull. Tohoku Reg. Fish. Res. Lab. **19**: 81–89.

Ogi, H. 1980a. The pelagic feeding ecology of the short-tailed shearwater *Puffinus tenuirostris* in the subarctic Pacific region. J. Yamashina Inst. Ornithol. **12**: 157–182.

Ogi, H. 1980b. The pelagic feeding ecology of thick-billed murres in the North Pacific, March-June. Bull. Fac. Fish. Hokkaido Univ. **31**: 50–72.

Ogi, H. and Tsujita, T. 1973. Preliminary examination of stomach contents of murres (*Uria* spp.) from the eastern Bering Sea and Bristol Bay, June–August, 1970 and 1971. Japan. J. Ecol. **23**: 201–209.

Ogi, H., Kubodera, T. and Nakamura, K. 1980. The pelagic feeding ecology of the short-tailed shearwater *Puffinus tenuirostris* in the Subarctic Pacific region. J. Yamashita Inst. Ornithol. **12**: 157–182.

Ohizumi, H. 1998. Feeding ecology of Dall's porpoises. Ph.D. Thesis, Univ. of Tokyo, Tokyo, 152 pp.

Ohizumi, H., Yoshioka, M., Mori, K. and Miyazaki, N. 1998. Stomach contents of common dolphins (*Delphinus delphis*) in the pelagic western North Pacific. Mar. Mam. Sci. **14**: 835–844.

Ohizumi, H., Watanabe, H., Moku, M. and Kawahara, S. 2001. Identification of otoliths of the 36 myctophid fish species in the western North Pacific. Kaiyou to Seibutu (Sea and Marine Organisms) **23**: 626–637.

Ohizumi, H., Kuramochi, T., Kubodera, T., Yoshioka, M. and Miyazaki, N. 2003. Feeding habits of Dall's porpoises (*Phocoenoides dalli*) in the Subarctic North Pacific and the Bering Sea basin and the impact of predation on mesopelagic micronekton. Deep-Sea Res. I **50**: 593–610.

Ohman, M.D. 1984. Omnivory by *Euphausia pacifica*: the role of copepod prey. Mar. Ecol. Prog. Ser. **19**: 125–131.

Ohshimo, S. 1998. Distribution and stomach contents of *Maurolicus muelleri* in the Sea of Japan (East Sea). J. Korean Soc. Fish. Res. **1**: 168–175.

Okutani, T. 1968. Studies on early life history of decapodan Mollusca – III. Systematics and distribution of larvae of decapod cephalopods collected from the sea surface on the Pacific Coast of Japan, 1960–65. Bull. Tokai Reg. Fish. Res. Lab. **55**: 9–57.

Okutani, T. 1974. Epipelagic decapod cephalopods collected by micronekton tows during the EASTROPAC expeditions, 1967–1968. Bull. Tokai Reg. Fish. Res. Lab. **80**: 29–118.

Okutani, T. 1976. Squids eaten by sperm whales caught off Joban district, Japan, during January–February, 1976. Bull. Tokai Reg. Fish. Res. Lab. **87**: 67–113.

Okutani, T. and Nemoto, T. 1964. Squids as the food of sperm whales in the Bering Sea and Alaskan Gulf. Sci. Rep. Whales Res. Inst. **18**: 111–127.

Okutani, T., Masaru, T. and Horikawa, H. 1987. Cephalopods from continental shelf and slope around Japan. Japan Fish. Res. Conserv. Assn., Tokyo, Japan, 194 pp.

Okutani, T., Kubodera, T. and Jefferts, K. 1988. Diversity, distribution and ecology of gonatid squids in the subarctic Pacific: a review. Bull. Ocean Res. Inst., Univ. Tokyo **26**: 159–192.

Olson, D.B. and Hood, R.R. 1994. Modelling pelagic biogeography. Progr. Oceanogr. **34**: 161–205.

Omori, M. 1969. The biology of a sergestid shrimp, *Sergestes lucens* Hansen. Bull. Ocean Res. Inst., University of Tokyo 4, 83 pp.

Omori, M. 1974a. The biology of pelagic shrimps in the ocean. Adv. Mar. Biol. **12**: 233–324.

Omori, M. 1974b. Shrimps. pp. 151–171. *In* Marine Plankton. *Edited by* R. Marumo, Univ. of Tokyo Press, Tokyo. (in Japanese)

Omori, M. 1979. Growth, feeding and mortality of larval and early postlarval stages of the oceanic shrimp *Sergestes similis* Hansen. Limnol. Oceanogr. **24**: 273–288.

Omori, M. 1983. Abundance assessment of micronektonic sergestid shrimp in the ocean. Biol. Oceanogr. **2**: 199–210.

Omori, M. and Gluck, D. 1979. Life history and vertical migration of the pelagic shrimp *Sergestes similes* off the southern Californian coast. Fish. Bull. U.S. **77**: 183–198.

Orlov, A.M. 1997a. Role of fishes in predator diets of the Pacific slope of the Northern Kuril Islands and Southeastern Kamchatka. pp. 209–229. *In* Forage fishes in marine ecosystems. Alaska Sea Grant College Program. Publication 97-01, Fairbanks, AK.

Orlov, A.M. 1997b. Ecological characteristics of the feeding of some Pacific predatory fish of South-East Kamchatka and Northern Kuril Islands. Rus. J. Aquat. Ecol. **6**: 59–74.

Orlov, A.M. 1997c. On feeding of Atka greenling *Pleurogrammus monopterygius* in the Pacific waters of Northern Kurile Islands. Vopr. Ikhtiol. **37**: 196–201.

Orlov, A.M. 1997d. Mesopelagic fishes as prey of Atka mackerel (*Pleurogrammus monopterygius*, Hexagrammidae, Scorpaeniformes) off the Northern Kuril Islands. pp. 323–335. *In* Forage fishes in marine ecosystems. Alaska Sea Grant College Program Report No. 97-01, Fairbanks, AK.

Oven, L.S. 1985. Comparative analysis of reproductive biology of some lantern fishes (Myctophidae) from the tropical zone of the Atlantic Ocean. Vopr. Ikhtiol. **2**: 226–236.

Ozawa, T. 1986a. Early life history of the family Myctophidae in the ocean off southern Japan. pp. 114–187. *In* Studies on the Oceanic Ichthyoplankton in the Western North Pacific. *Edited by* T. Ozawa, Kyushu Univ. Press, Hukuoka.

Ozawa, T. 1986b. The larvae of three Japanese species of the gonostomatid genus *Gonostoma*. pp. 68–73. *In* Studies on the Oceanic Ichthyoplankton in the Western North Pacific. *Edited by* T. Ozawa, Kyushu Univ. Press, Hukuoka.

Pakhomov, E.A., Perissinotto, R. and McQuaid, C.D. 1996. Prey composition and daily rations of myctophid fishes in the Southern Ocean. Mar. Ecol. Prog. Ser. **134**: 1–14.

Pakhomov, E.A., Perissinotto, R. and Froneman, P.W. 1999. Predation impact of carnivorous macrozooplankton and micronekton in the

Atlantic sector of the Southern Ocean. J. Mar. Syst. **19**: 47–64.

Parin, N.V. 1961. The distribution of deep-sea fishes in the upper bathypelagic layer of the Subarctic waters of the northern Pacific Ocean. Trudy Institute Okeanologica Akademy Nauk SSSR **45**: 359–378. (translation by Bureau of Commercial Fisheries)

Parin, N.V. 1988. Fish of the open ocean. Marine Science, 272 pp.

Parin, N.V. and Fedorov, V.V. 1981. Comparison of deepwater pelagic ichthyofaunas of northwestern and northeastern Pacific Ocean. pp. 72–78. *In* Biology of Larger Depth of the Pacific Ocean. Vladivostok.

Parin, N.V. and Kobyliansky, S.G. 1993. Review of the genus *Maurolicus* (Sternoptychidae, Stomiiformes), with re-establishing validity of five species considered junior synonyms of *M. muelleri* and descriptions of nine new species. Russian Acad. Sci. **128**: 69–107.

Paxton, J.R. 1967a. Biological note on southern California lanternfishes (family Myctophidae). Calif. Fish Game **53**: 214–217.

Paxton, J.R. 1967b. A distributional analysis for the lanternfishes (family Myctophidae) of the San Pedro Basin, California. Copeia **2**: 422–440.

Paxton, J.R. 1968. Biological notes on southern California lanternfishes (family Myctophidae). Calif. Fish Game **53**: 214–217.

Pearcy, W.G. 1964. Some distributional features of mesopelagic fishes off Oregon. J. Mar. Res. **22**: 83–102.

Pearcy, W.G. (*Editor*). 1975. Workshop on problems of assessing populations of nekton. Office of Naval Research Rep. ACR 211, 26 pp.

Pearcy, W.G. 1976. Seasonal and inshore-offshore variations in the standing stocks of micronekton and macrozooplankton off Oregon. Fish. Bull. U.S. **74**: 70–80.

Pearcy, W.G. (*Editor*) 1981. SCOR Symposium on methods of sampling micronekton. Biol. Oceanogr. **2**: 1–456.

Pearcy, W.G. 1991. Biology of the transition region. pp. 39–55. *In* Biology, Oceanography, and Fisheries of the North Pacific transition zone and subarctic frontal zone. *Edited by* J.A. Wetherall. NOAA Tech. Rep. NMFS 105.

Pearcy, W. and Forss, C. 1969. The oceanic shrimp *Sergestes similis* off the Oregon coast. Limnol. Oceanogr. **14**: 755–765.

Pearcy, W.G. and Laurs, R.M. 1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. **13**: 153–165.

Pearcy, W.G. and Voss, G.L. 1963. A new species of gonatid squid from the northeastern Pacific. Proc. Biol. Soc. Wash. **76**: 105–112.

Pearcy, W.G., Krygier, E.E., Mesecar, R. and Ramsey, F. 1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res. **24**: 223–245.

Pearcy, W.G., Lorz, H.V. and Peterson, W. 1979a. Comparison of the feeding habits of migratory and non-migratory *Stenobrachius leucopsarus* (Myctophidae). Mar. Biol. **51**: 1–8.

Pearcy, W.G., Nemoto, T. and Okiyama, M. 1979b. Mesopelagic fishes of the Bering Sea and adjacent Northern North Pacific. J. Oceanogr. Soc. Japan **35**: 127–135.

Pearcy, W.G., Brodeur, R.D., Shenker, J.M., Smoker, W.W. and Endo, Y. 1988. Food habits of Pacific salmon and steelhead trout, midwater trawl catches and oceanographic conditions in the Gulf of Alaska, 1980–1985. Bull. Ocean Res. Inst. **26**: 29–78.

Pearcy, W.G., Fisher, J.P. and Yoklavich, M.M. 1993. Biology of the Pacific Pomfret (*Brama japonica*) in the North Pacific Ocean. Can. J. Fish. Aquat. Sci. **50**: 2608–2625.

Pereyra, W.T., Pearcy, W.G. and Carvey, F.E., Jr. 1969. *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Board Can. **26**: 2211–2215.

Perez, M.A. and Bigg, M.A. 1986. Diet of northern fur seal, *Callorhinus ursinus,* off western North America. Fish. Bull. U.S. **84**: 957–971.

Pieper, R.E. 1979. Euphausiid distribution and biomass determined acoustically at 102 kHz. Deep-Sea Res. **26A**: 687–702.

Pieper, R.E. and Holliday, D.V. 1984. Acoustic measurements of zooplankton distribution in the sea. J. Cons. int. Explor. Mer **41**: 226–238.

Pieper, R.E., Holliday, D.V. and Kleppel, G.S. 1990. Quantitative zooplankton distributions from multifrequency acoustics. J. Plankt. Res.

12: 433–441.

Pitcher, K.W. 1981. Prey of the steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fish. Bull. U.S. **79**: 467–472.

Ponomareva, L.A. 1963. Euphausiids of the North Pacific: their distribution and ecology. Academy of Sciences in the USSR Institute of Oceanology, Moscow. (translation by the Israel Program for Scientific Translations 1966). U.S. Department of the Interior and the National Science Foundation, 154 pp.

Ponomareva, L.A. 1990. Biology of Euphausiids of the World's Oceans. Akademii Nauka USSR, Moskva (USSR), 213 pp.

Ponomareva, L.A., Tsikhon-Lukanina, E.A. and Sorokin, Y. 1974. Consumption of phytoplankton and bacteria by tropical euphausiids. Life activity of pelagic communities in the ocean tropics based on data of the 44th Cruise of the R/V *Vityaz*, 1973, pp. 166–171.

Prut'ko, V. G. 1987. Age and growth of *Diaphus suborbitalis* (Myctophidae) from the equatorial part of the Indian Ocean. J. Ichthyol. **28**: 14–23.

Radchenko, V.I. 1992. The role of squids in the Bering Sea pelagic ecosystem. Oceanologia. **32**: 1093–1101.

Radchenko, V.I., Mel'nikov, I.V., Volkov, A.F., Semenchenko, A.Y., Glebov, I.I. and Mikheev, A.A. 1997. Environmental conditions and composition of plankton and nekton in epipelagic layer of the southern Sea of Okhotsk and adjacent Pacific waters in summer. Russian J. Mar. Biol. **23**: 15–25.

Rass, T.S. 1954. Deep-sea fish of far eastern seas of the USSR. Zoologicheskii Zhurnal **33**: 1312–1324. (translation by the Israel Program for Scientific Translations)

Reid, S.B., Hirota, J., Young, R.E. and Hallacher, L.E. 1991. Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. Mar. Biol. **109**: 427–440.

Renfro, W.C. and Pearcy, W.G. 1966. Food and feeding apparatus of two pelagic shrimps. Fish. Res. Bd. Can. **23**: 1971–1975.

Ressler, P.H., Brodeur, R.D., Peterson, W.T., Pierce, S.K., Vance, P.M., and Barth, J.A. 2005. Spatial distribution of euphausiid aggregations in the northern California Current during August 2000. Deep-Sea Res. II **52**: 89–108.

Rice, D.W. 1977. Synopsis of biological data on the sei whale and Bryde's whale in the Eastern North Pacific. Rep. Int. Whale Comm. Special Rep. **1**: 92–97.

Richardson, S.L. and Pearcy, W.G. 1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull. U.S. **75**: 125–145.

Richardson, S.L., Laroche, J.L. and Richardson, M.D. 1980. Larval fish assemblages and associations in the north-east Pacific Ocean along the Oregon coast, winter–spring 1972–1975. Estuar. Coastal Mar. Sci. **11**: 671–699.

Riddell, D.J. 1985. The Enoploteuthidae (Cephalopoda: Oegopsida) of the New Zealand region. N.Z. MAF Fish. Res. Bull. 27, 51 pp.

Rissik, D. and Suthers, I.M. 2000. Enhanced feeding by pelagic juvenile myctophid fishes within a region of island-induced flow disturbance in the Coral Sea. Mar. Ecol. Prog. Ser. **203**: 263–273.

Ritz, D.A. and Hosie, D.W. 1982. Production of the euphausiid *Nyctiphanes australis* in Storm Bay, South-Eastern Tasmania. Mar. Biol. **68**: 103–108.

Robinson, C.J. and Gómez-Gutiérrez, J. 1998a. Daily vertical migration of dense scattering layers related to shelf-break area in the northwest coast of Baja California, México. J. Plankt. Res. **20**: 1679–1697.

Robinson, C.J. and Gómez-Gutiérrez, J. 1998b. The red-crab bloom of the west coast of Baja California, México. J. Plankt. Res. **20**: 2009–2016.

Robinson, C.J. and Gomez-Aguirre, S. 2004. Tidal stream use by the red crab *Pleuroncodes planipes* in Bahia Magdalena, Mexico. J. Exp. Mar. Biol. Ecol. **308**: 237–252.

Robinson, C.L.K. 2000. The consumption of euphausiids by the pelagic fish community off southwestern Vancouver Island, British Columbia. J. Plankt. Res. **22**: 1649–1662.

Robison, B.H. 1983. Midwater biological research with the WASP ADS. Mar. Tech. Soc. J. **17**: 21–27.

Robison, B.H. 1984. Herbivory by the myctophid fish *Ceratoscopelus warmingii*. Mar. Biol. **84**: 119–123.

Robison, B.H. 1999. Shape change behavior by mesopelagic animals. Mar. Fresh. Behav. Physiol. **32**: 17–25.

Robison, B.H. and Craddock, J.E. 1983. Mesopelagic fishes eaten by Fraser's dolphin, *Lagenodelphis hosei*. Fish. Bull. U.S. **81**: 283–289.

Roden, G.I. 1987. Effect of seamounts and seamount chains on ocean circulation and thermohaline structure. pp. 335–354. *In* Seamount Islands and Atolls. *Edited by* B.H. Keating, P. Fryer, R. Batiza and G.W. Boehlert, Geophysical Monograph. Washington, AGU.

Roden, G.I. 1991. Subarctic-subtropical transition zone of the North Pacific: Large-scale aspects and mesoscale structure. pp. 1–38. *In* Biology, oceanography, and fisheries of the North Pacific transition zone and subarctic frontal zone. *Edited by* J.A. Wetherall, NOAA Tech. Rep. NMFS 105.

Rodgers, A.D. 1994. The biology of seamounts. Adv. Mar. Biol. **30**: 306–350.

Rodhouse, P.G. and Nigmatullin, C.M. 1996. Role as consumers. *In* The role of cephalopods in the world's oceans. *Edited by* M.R. Clarke, Phil. Trans. R. Soc. Lond. B **351**: 1003–1022.

Roe, H.S.J. 1984. The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 2. Vertical migrations and feeding of mysids and decapod crustacea. Prog. Oceanogr. **13**: 269–318.

Roper, C.F.E. and Young, R.E. 1975. Vertical distribution of pelagic cephalopods. Smithsonian Contrib. Zool. **209**: 1–51.

Ross, R.M. 1981. Laboratory culture and development of *Euphausia pacifica*. Limnol. Oceanogr. **26**: 235–246.

Ross, R. and Quetin, L. 2000. Reproduction in Euphausiacea. pp. 150–181. *In* Krill: Biology, Ecology and Fisheries, *Edited by* I. Everson, Fish and Aquatic Resources Series 6, Blackwell Science, London.

Ross, R.M., Daly, K.L. and English, T.S. 1982. Reproductive cycle and fecundity of *Euphausia pacifica* in Puget Sound, Washington. Limnol. Oceanogr. **27**: 304–314.

Ross, R.M., Quetin, L.B., Baker, K.S., Vernet, M., and Smith, R.C. 2000. Growth limitation in young *Euphausia superba* under field conditions. Limnol. Oceanogr. **45**: 31–43.

Sabatés, A. and Saiz, E. 2000. Intra and interspecific variability in prey size and niche breadth of myctophiform fish larvae. Mar. Ecol. Prog. Ser. **201**: 261–271.

Saito, H. and Murata, M. 1996. The high content of monoene fatty acids in the lipids of some midwater fishes: family Myctophidae. Lipids **31**: 757–763.

Samyshev, E.Z. and Schetinkin, S.V. 1971. Feeding patterns of some species of Myctophidae and *Maurolicus muelleri* caught in the sound-dispersing layers in the northwestern African area. Ann. Biol. **28**: 212–215.

Sassa, C. 2001. Ecological study of myctophid fish larvae and juveniles in the western North Pacific. Ph.D. Thesis, Aquatic Biological Science, Graduate School of Agricultural Life Science, University of Tokyo, 274 pp. (in Japanese)

Sassa, C., Moser, H.G. and Kawaguchi, K. 2002a. Horizontal and vertical distribution patterns of larval myctophid fishes in the Kuroshio Current region. Fish. Oceanog. **11**: 1–10.

Sassa, C., Kawaguchi, K., Kinoshita, T. and Watanabe, C. 2002b. Assemblages of vertical migratory mesopelagic fish in the transitional region of the western North Pacific. Fish. Oceanogr. **11**: 193–204.

Sassa, C., Kawaguchi, K., Oozeki, Y., Kubota, H. and Sugisaki, H. 2004a. Distribution patterns of larval myctophid fishes in the transition region of the western North Pacific. Mar. Biol. **144**: 417–428.

Sassa, C., Kawaguchi, K. and Mori, K. 2004b. Late winter larval mesopelagic fish assemblage in the Kuroshio waters of the western North Pacific. Fish. Oceanogr. **13**: 121–133.

Sassa, C., Kawaguchi, K., Hirota, Y. and Ishida, M. 2004c. Distribution patterns of larval myctophid fish assemblages in the subtropical-tropical waters of the western North Pacific. Fish. Oceanogr. **13**: 267–282.

Sassa, C. and Kawaguchi, K. 2004. Larval feeding habits of *Diaphus garmani* and *Myctophum asperum* (Pisces: Myctophidae) in the transiton region of he western North Pacific. Mar. Ecol. Prog. Ser. **278**: 279–290.

Savinykh, V.F. 1999. Nektonic community of the epipelagic zone of the Californian convergence region in winter. J. Ichthyol. **39**: 29–42.

Sawada, K., Takao, Y., Takahashi, H., Abe, K., Okumura, T., Kobayashi, A. and Sugimoto, M. 2004. Development of an acoustic-optical system (J-QUEST) for fisheries surveys 1 – Acoustic system. Tech. Rep. Natl. Res. Inst. Fish. Eng. **26**: 23–33. (in Japanese)

Schoenherr, J.R. 1991. Blue whales feeding on high concentrations of euphausiids around Monterey Submarine Canyon. Can. J. Zool. **69**: 583–594.

Sealy, S.G. 1975. Feeding ecology of the ancient and marbled murrelets near Langara Island, British Columbia. Can. J. Zool. **53**: 418–433.

Seki, M.P. 1993. The role of the neon flying squid, *Ommastrephes bartramii*, in the North Pacific pelagic food web. pp. 207–215. *In* Symposium on biology, distribution, and stock assessment of species caught in the high seas driftnet fisheries in the North Pacific Ocean. *Edited by* J. Ito *et al.*, Bull. Int. N. Pac. Fish. Comm. 53.

Seki, M.P. 2001. Distribution patterns of pelagic cephalopods through the Subarctic and Subtropical Frontal Zones in the central North Pacific. M.S. Thesis, University of Hawaii, Honolulu, Hawaii, 102 pp.

Seki, M.P. and Polovina, J.J. 2001. Food webs: ocean gyre ecosystems. pp. 1959–1965. *In* Encyclopedia of Ocean Sciences. *Edited by* J.H. Steele, K.K. Turekian, and S.A. Thorpe, Academic Press, San Diego, CA.

Seo, H.-S., Endo, Y., Fujimoto, K., Watanabe, H. and Kawaguchi, K. 1996. Characterization of lipids in myctophid fish in the subarctic and tropical Pacific Ocean. Fish. Sci. **62**: 447–453.

Seo, H.-S., Endo, Y., Muramoto, K., Fujimoto, K., Moku, M. and Kawaguchi, K. 1998. Amino acid composition of proteins in myctophid fishes in the subarctic and tropical Pacific Ocean. Fish. Sci. **64**: 652–653.

Shevtsov, G.A. and Mokrin, N.M. 1998. Cephalopods from the Japan Sea, Russian EEZ, in summer-fall. Izv. TINRO. **123**: 191–206.

Shields, D.J. and Gómez-Gutiérrez, J. 1996. *Oculophryxus bicaulis* a new genus and species of Dajid isopod parasitic on the euphausiid *Stylocheiron affine* Hansen. Int. J. Parasit. **26**: 261–268.

Shin, H-C. and Nicol, S. 2002. Using the relationship between eye diameter and body length to detect the effects of long-term starvation on Antarctic krill *Euphausia superba.* Mar. Ecol. Prog. Ser. **239**: 157–167.

Shiomi, K. and Ogi, H. 1992. Feeding ecology and body size dependence on diet of the sooty shearwater, *Puffinus griseus,* in the North Pacific. Proc. Natl. Inst. Polar Res. Symp. Polar Biol. **5**: 105–113.

Siegel, V. 2000a. Krill (Euphausiacea) life history and aspects of population dynamics. Can. J. Fish. Aquat. Sci. **57**: 130–150.

Siegel, V. 2000b. Krill (Euphausiacea) demography and variability in abundance and distribution. Can. J. Fish. Aquat. Sci. **57**: 151–167.

Siegel, V. and Nicol, S. 2000. Population parameters. pp. 103–149. *In* Krill: Biology, Ecology and Fisheries. *Edited by* I. Everson, Fish and Aquatic Resources Series 6, Blackwell Science, London.

Sinclair, E.H. and Stabeno, P.J. 2002. Mesopelagic nekton and associated physics of the southeastern Bering Sea. Deep-Sea Res. II **49**: 6127–6145.

Sinclair, E., Loughlin, T. and Pearcy, W. 1994. Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. Fish. Bull. U.S. **92**: 144–156.

Sinclair, E., Balanov, A.A., Kubodera, T., Radchenko, V.I. and Fedorets, Y.A. 1999. Distribution and ecology of mesopelagic fishes and cephalopods. pp. 485–508. *In* Dynamics of the Bering Sea. *Edited by* T.R. Loughlin and K. Ohtani, Univ. of Alaska Press, Fairbanks, AK.

Smiles, M.C. and Pearcy, W.G. 1971. Size, structure and growth of *Euphausia pacifica* off the Oregon coast. Fish. Bull. U.S. **69**: 79–86.

Smith, P.E. 1985. A case history of an anti-Niño transition plankton and nekton distribution and abundances. pp. 121–142. *In* El Niño North: Niño effects in the eastern subarctic Pacific Ocean. *Edited by* W.S. Wooster and L.F. David, Washington Sea Grant, Seattle, WA.

Smith, S.M. 1991. Growth, development and distribution of the euphausiids *Thysanoessa raschi* (M. Sars) and *Thysanoessa inermis*

(Kroyer) in the southeastern Bering Sea. Polar Res. **10**: 461–478.

Smith, S.E. and Adams, P.B. 1988. Daytime surface swarms of *Thysanoessa spinifera* (Euphausiacea) in the Gulf of the Farallones, California. Bull. Mar. Sci. **42**: 76–84.

Smith, S.L., Pieper, R.E., Moore, M.V., Rudstam, L.G., Green, C.H., Zamon, J.E., Flagg, C.N. and Williamson, C.E. 1992. Acoustic techniques for the in situ observation of zooplankton. Arch. Hydrobiol. Beih. Ergebn. Limnol. **36**: 23–43.

Sobolevsky, Ye.I. and Sokolovskaya, T.G. 1996. Development and distribution of the young of northern smoothtongue (*Leuroglossus schmidti*) in the northwest Pacific Ocean and western Bering Sea. pp. 257–263. *In* Ecology of the Bering Sea: A Review of Russian Literature. *Edited by* O.E. Mathisen and K.O. Coyle, Alaska Sea Grant Rep. No. 96-01, Fairbanks, AK.

Soule, M., Barange, M. and Hampton, I. 1995. Evidence of bias in estimates of target strength obtained with a split-beam echo-sounder. ICES J. Mar. Sci. **52**: 139–144.

Springer, A.M. and Roseneau, D.G. 1985. Copepod-based food webs: auklets and oceanography in the Bering Sea. Mar. Ecol. Prog. Ser. **21**: 229–237.

Stanton, T.K. 1989. Simple approximate formulas for backscattering of sound by spherical and elongate objects. J. Acoust. Soc. Am. **86**: 1499–1510.

Stanton, T.K. and Chu, D. 2000. Review and recommendations for the modelling of acoustic scattering by fluid-like elongated zooplankton: euphausiids and copepods. ICES J. Mar. Sci. **57**: 793–807.

Stanton, T.K., Wiebe, P.H., Chu, D., Benfield, M.C., Scanlon, L., Martin, L. and Eastwood, R.L. 1994. On acoustic estimates of zooplankton biomass. ICES J. Mar. Sci. **51**: 505–512.

Stanton, T.K., Chu, D. and Wiebe, P.H. 1996. Acoustic scattering characteristics of several zooplankton groups. ICES J. Mar. Sci. **53**: 289–295.

Stanton, T.K., Chu, D. and Wiebe, P.H. 1998. Sound scattering by several zooplankton groups. II. Scattering models. J. Acoust. Soc. Am. **103**: 236–253.

Stoecker, D.K. and Capuzzo, J.M. 1990. Predation on protozoa: its importance to zooplankton. J. Plankt. Res. **12**: 891–908.

Swartzman, G., Brodeur, R.D., Napp, J.M., Hunt, G.L., Demer, D. and Hewitt, R. 1999. Spatial proximity of age-0 walleye pollock (*Theragra chalcogramma*) to zooplankton near the Pribilof Islands, Bering Sea, Alaska. ICES J. Mar. Sci. **56**: 545–560.

Suh, H.-L. 1990. *Pseudeuphausia sinica* (Euphausiacea, Crustacea): A new record from the Korean waters. Bull. Korean Fish. Soc. **23**: 65–67.

Suh, H.-L. and Choi, S.-D. 1998. Comparative morphology of the feeding basket of five species of *Euphausia* (Crustacea, Euphausiacea) in the western North Pacific, with some ecological considerations. Hydrobiol. **385**: 107–112.

Suh, H.-L., Toda, T. and Terazaki, M. 1991. Diet of calyptopes of the euphausiids *Euphausia pacifica* in the Yellow Sea. Mar. Biol. **111**: 45–48.

Susana, S.T. and Sugimoto, T. 1998. Spreading of warm water from the Kuroshio Extension into the perturbed area. J. Oceanogr. **54**: 257–271.

Suthers, I.M. 1996. Spatial variability of recent otolith growth and RNA indices in pelagic juvenile *Diaphus kapalae* (Myctophidae): an effect of flow disturbance near an island? Mar. Freshwater Res. **47**: 273–282.

Takahashi, H., Sawada, K., Takao, Y., Abe, K., Machida, K. and Sugimoto, M. 2004. Development of an acoustic-optical system (J-QUEST) for fisheries surveys 2 – Optical system. Tech. Rept. Natl. Res. Inst. Fish. Eng. **26**: 35–45. (in Japanese)

Takahashi, S., Tanabe, S. and Kawaguchi, K. 2000. Organochlorine and butyltin residues in mesopelagic myctophid fishes from the western North Pacific. Environ. Sci. Technol. **34**: 1161–1166.

Taki, K., Tsubo, J., Nakagawa, Y. and Endo, Y. 2002. Diet of *Euphausia pacifica* in southeastern Hokkaido and Joban waters off northeastern Japan. Bull. Japan. Soc. Fish. Oceanogr. **66**: 155–163. (in Japanese)

Tamura, T., Fujise, Y. and Shimazaki, K. 1998. Diet of minke whales *Balaenoptera acutorostrata* in the northwestern part of

North Pacific in summer 1994 and 1995. Fish. Sci. **64**: 71–76.

Tanasichuk, R.W. 1998a. Interannual variations in the population biology and productivity of *Euphausia pacifica* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. Mar. Ecol. Prog. Ser. **173**: 163–180.

Tanasichuk, R.W. 1998b. Interannual variations in the population biology and productivity of *Thysanoessa spinifera* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. Mar. Ecol. Prog. Ser. **173**: 181–195.

Tanasichuk, R.W. and Cooper, C. 2002. A northern extension of the range of the euphausiid *Nyctiphanes simplex* into Canadian Waters. J. Crust. Biol. **22**: 206–209.

Tanasichuk, R., Ware, D.M., Shaw, W. and McFarlane, G.A. 1991. Variations in diet, daily ration, and feeding periodicity of Pacific hake (*Merluccius productus*) and spiny dogfish (*Squalus acanthias*) off the lower west coast of Vancouver Island. Can. J. Fish. Aquat. Sci. **48**: 2118–2128.

Theilacker, G.H. and Lasker, R. 1973. Laboratory studies of predation by euphausiid shrimps on fish larvae. International Symposium on the Early Life History of Fish, Oban, U.K., 17 May 1973.

Theilacker, G.H., Kimball, A.S. and Trimmer, J.S. 1986. Use of an ELISPOT immunoassay to detect euphausiid predation on larval anchovy. Mar. Ecol. Progr. Ser. **30**: 127–131.

Theilacker, G.H., Lo, N.H.C. and Townsend, A.W. 1993. An immunochemical approach to quantifying predation by euphausiids on the early stages of anchovy. Mar. Ecol. Prog. Ser. **92**: 35–50.

Thompson, B., Tsukada, D. and Laughlin, J. 1993. Megabenthic assemblages of coastal shelves, slopes, and basins off southern California. Bull. South. Calif. Acad. Sci. **92**: 25–42.

Toczko, S., Nishikawa, J. and Nishida, S. Community structure and diversity of micronektonic crustaceans in the subarctic Pacific in summer, 1997. Unpubl. MS. Available from Ocean Research Institute, University of Tokyo.

Traynor, J.J. 1996. Target-strength measurements of walleye pollock (*Theragra chalcogramma*) and Pacific whiting (*Merluccius productus*). ICES J Mar. Sci. **53**: 253–258.

Tsarin, S.A. 1994. Age, growth and some production patterns of *Ceratoscopelus warmingii* (Myctophidae) in the topical zone of Indian Ocean. Vopr. Ikhtiol. **34**: 234–242.

Tsuchiya, K. 1993. Distribution and zoogeography of the family Enoploteuthidae in the Northwest Pacific. pp. 571–585. *In* Recent Advances in Cephalopod Fisheries Biology. *Edited by* T. Okutani, R.K. O'Dor and T. Kubodera.

Tsuchiya, K. and Okutani, T. 1988. Subgenera of *Enoploteuthis*, *Abralia*, and *Abraliopsis* of the squid Family Enoploteuthidae. Bull. Natl. Sci. Mus., Tokyo, Ser. A. **14**: 119–136.

Tsuchiya, K. and Okutani, T. 1990. *Abraliopsis pacificus*, a new species of the squid family Enoploteuthidae from the northwest Pacific. Bull. Natl. Sci. Mus., Tokyo, Ser. A. **16**: 47–60.

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

Tyler, H.R., Jr. and Pearcy, W.G. 1975. The feeding habits of three species of lanternfishes (family Myctophidae) off Oregon, USA. Mar. Biol. **32**: 7–11.

Vermeer, K. 1981. The importance of plankton to Cassin's auklets during breeding. J. Plankt. Res. **3**: 315–329.

Vermeer, K., Fulton, J.D. and Sealy, S.G. 1985. Differential use of zooplankton prey by ancient murrelets and Cassin's auklets in the Queen Charlotte Islands. J. Plankt. Res. **7**: 443–459.

Wada, K. 1971. Food and feeding habit of northern fur seals along the coast of Sanriku. Bull. Tokai Reg. Fish. Res. Lab. **64**: 1–37.

Wada, T. and Murata, M. 1985. Distribution and biological characteristics of pomfret, *Brama japonica* Hilgendorf, in the Pacific Ocean off northern Japan. Bull. Hokkaido Natl. Fish. Res. Inst. **50**: 1–12.

Walters, J.F. 1976. Ecology of Hawaiian sergestid shrimps (Penaeidea: Sergestidae). Fish. Bull. U.S. **74**: 799–836.

Watanabe, H. 1998. Ecological study of surface migratory myctophid fishes in the Kuroshio and its adjacent regions. Ph.D. Thesis, University of Tokyo, 151 pp.

Watanabe, H. and Kawaguchi, K. 1999. The effect of towing bridles on net avoidance by micronektonic fishes in night time neuston sampling. Bull. Jpn. Soc. Fish. Oceanogr. **63**: 1–15.

Watanabe, H. and Kawaguchi, K. 2003a. Decadal change in the feeding habits of the surface migratory myctophid fish, *Myctophum nitidulum*, in the Kuroshio region of the western North Pacific: Predation on sardine larvae by myctophids. Fish. Sci. **69**: 716–721.

Watanabe, H. and Kawaguchi, K. 2003b. Decadal change in abundance of surface migratory myctophid fishes in the Kuroshio region from 1957 to 1994. Fish. Oceanogr. **12**: 100–111.

Watanabe, H., Moku, M., Kawaguchi, K., Ishimaru, K. and Ohno, A. 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., Kawaguchi, K. and Hayashi, A. 2002. Feeding habits of juvenile surface-migratory myctophid fishes (family Myctophidae) in the Kuroshio region of the western North Pacific. Mar. Ecol. Prog. Ser. **236**: 263–272.

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

Watanuki, Y. 1985. Food of breeding Leach's storm-petrels (*Oceanodroma luecorhoa*). Auk **102**: 884–886.

Watkin, J., Macaulay, M. and Everson, I. 2000. Sampling krill. pp. 8–39. *In* Krill: Biology, Ecology and Fisheries. *Edited by* I. Everson, Fish and Aquatic Resources Series 6, Blackwell Science, London.

Wei, C. 1980. Food and feeding habits of hairtail (*Trichiurus haumela* Forskaal) from the Yellow Sea. Mar. Fish. Res. **1**: 49–57.

Wicksten, M.K. 2002. Midwater decapods of the Northeastern Pacific. pp. 127–144. *In* Contributions to the Study of East Pacific Crustaceans. *Edited by* M.E. Hendrickx. Unidad Academica Mazatlan.

Wiebe, P.H. and Benfield, M.C. 2003. From the Hensen net toward four-dimensional biological oceanography. Prog. Oceanogr. **56**: 7–136.

Wiebe, P.H., Green, C.H., Stanton, T.K. and Burczynski, J. 1990. Sound scattering by live zooplankton and micronekton: Empirical studies with a dual-beam acoustical system. J. Acoust. Soc. Am. **88**: 2346–2360.

Wiebe, P.H., Groman, R.C. and Allison, M.D. (*Editors*). 2002. ICES/GLOBEC Sea-going workshop for intecalibration of plankton samplers. ICES Coop. Res. Rep. 250, 25 pp.

Wiebe, P.H., Ashjian, C.J., Gallager, S.M., Davis, C.S., Lawson, G.L. and Copley, N.J. 2004. Using a high-powered strobe light to increase the catch of Antarctic krill. Mar. Biol. **144**: 493–502.

Willis, J.M. 1984. Mesopelagic fish faunal regions of the Northeast Pacific. Biol. Oceanogr. **3**: 167–185.

Willis, J.M. and Pearcy, W.G. 1980. Spatial and temporal variations in the population size structure of three lanternfishes (Myctophidae) off Oregon, USA. Mar. Biol. **57**: 181–191.

Willis, J.M. and Pearcy, W.G. 1982. Vertical distribution and migration of fishes of the lower mesopelagic zone off Oregon. Mar. Biol. **70**: 87–98.

Willis, J.M., Pearcy, W.G. and Parin, N.V. 1988. Zoogeography of midwater fishes in the Subarctic Pacific. Bull. Ocean Res. Inst. Univ. Tokyo **26**: 79–142.

Wilson, C.D. and Boehlert, G.W. 2004. Interaction of ocean currents and resident micronekton at a seamount in the central North Pacific. J. Mar. Syst. **50**: 39–60.

Wilson, S.G., Pauly, T. and Meekan, M.G. 2001. Daytime surface swarming by *Pseudeuphausia latifrons* (Crustacea, Euphausiacea) off Ningaloo reef, Western Australia. Bull. Mar. Sci. **68**: 157–162.

Wilson, S.G., Meekan, M.G., Carleton, J.H., Stewart, T.C. and Knott B. 2003. Distribution, abundance and reproductive biology of *Pseudeuphausia latifrons* and other euphausiids on the southern North West Shelf, Western Australia. Mar. Biol. **142**: 369–379.

Wisner, R.L. 1976. The taxonomy and

distribution of lanternfishes (family Myctophidae) of the eastern Pacific Ocean. Navy Ocean Res. and Develop. Act Rep. 3.

Wittmann, K.J. 1984. Ecophysiology of marsupial development and reproduction in Mysidacea (Crustacea). Oceanogr. Mar. Biol. Ann. Rev. **22**: 393–428.

Wortham-Neal, J.L. and Price, W.W. 2002. Marsupial developmental stages in *Americamysis bahia* (Mysida: Mysidae). J. Crust. Biol. **22**: 98–112.

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

Yamamura, O., Inada, T. and Shimazaki, K. 1993a. Predation on firefly squid *Watasenia scintillans* by demersal fishes off Sendai Bay, North Japan. pp. 633–639. *In* Recent advances in cephalopod fisheries biology. *Edited by* T. Okutani, R. K. O'Dor and T. Kubodera, Tokai Univ. Press, Tokyo.

Yamamura, O., Watanabe, K. and Shimazaki, K. 1993b. Feeding habits of Pacific cod, *Gadus macrocephalus*, off eastern Hokkaido, north Japan. Proc. Natl. Inst. Polar Res. Symp. Polar Biol. **6**: 44–54.

Yamamura, O., Inada, T. and Shimazaki, K. 1998. Predation on *Euphausia pacifica* by demersal fishes: predation impact and influence of physical variability. Mar. Biol. **132**: 195–208.

Yamamura, O. and Inada, T. 2001. Importance of micronekton as food of demersal fish assemblages. Bull. Mar. Sci. **68**: 13–25.

Yamamura, O., Honda, S., Shida, O. and Hamatsu, Y. 2002. Diets of walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan: ontogenetic and seasonal variations. Mar. Ecol. Prog. Ser. **238**: 187–198.

Yang, M.S. and Livingston, P.A. 1986. Food habits and diet overlap of two congeneric species *Atheresthes stomias* and *Atheresthes evermanni,* in the eastern Bering Sea. Fish. Bull. U.S. **82**: 615–623.

Yang, M.S. and Livingston P.A. 1988. Food habits and daily ration of Greenland halibut, *Reinhardtius hippoglossoides,* in the eastern Bering Sea. Fish. Bull. U.S. **86**: 675–690.

Yasuma, H., Sawada, K., Ohshima, T., Miyashita, K. and Aoki, I. 2003. Target strength of mesopelagic lanternfishes (family Myctophidae) based of swimbladder morphology. ICES J. Mar. Sci. **60**: 584–591.

Yasuma, H. 2004. Studies on the acoustical biomass estimation of myctophid fishes. Ph.D. Thesis, Aquatic Biological Science, Graduate School of Agricultural Life Science, University of Tokyo, 237 pp. (in Japanese)

Yatsu, A. 2000. Age estimation of four oceanic squids, *Ommastrephes bartramii, Dosidicus gigas, Sthenoteuthis oualaniensis*, and *Illex argentinus* (Cephalopoda, Ommastrephidae) based on statolith microstructure. Japan Agr. Res. Quart. **34**: 75–80.

Yoon, W.D., Cho, S.H., Lim, D., Choi, Y.K. and Lee, Y. 2000. Spatial distribution of *Euphausia pacifica* (Euphausiacea: Crustacea) in the Yellow Sea. J. Plankt. Res. **22**: 939–949.

Yoshida, H. 1994. Food and feeding habits of pelagic walleye pollock in the central Bering Sea in summer, 1976–1980. Sci. Rep. Hokkaido Fish. Exp. Stn. **45**: 1–35.

Young, J.W. and Blaber, S.J.M. 1986. Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. Mar. Biol. **93**: 147–156.

Young, J.W., Blaber, S.J.M. and Rose, R. 1987. Reproductive biology of three species of midwater fishes associated with the continental slope of eastern Tasmanina, Australia. Mar. Biol. **95**: 323–332.

Young, J.W., Bulman, C.M., Blader, S.J.M. and Wayte, S.E. 1988. Age and growth of the lanternfish *Lampanyctodes hectoris* (Myctophidae) from eastern Tasmania, Australia. Mar. Biol. **99**: 569–576.

Young, R.E. 1972. The systematics and areal distribution of pelagic cephalopods from the seas off Southern California. Smithsonian Contrib. Zool. **97**: 1–159.

Young, R.E. 1978. Vertical distribution and photosensitive vesicles of pelagic cephalopods from Hawaiian waters. Fish. Bull. U.S. **76**: 583–615.

Young, R.E. and Harman, R.F. 1985. Early life history stages of enoploteuthin squids (Cephalopoda: Teuthoidea: Enoploteuthidae) from Hawaiian waters. Vie Milieu **35**: 181–201.

Young, R.E. and Hirota, J. 1998. Review of the ecology of *Sthenoteuthis oualaniensis* near the Hawaiian Archipelago. *In* Large Pelagic Squids. *Edited by* T. Okutani, Japan Marine Fishery Resources Research Center, Tokyo.

Young, R.E., Harman, R.F. and Mangold, K.M. 1985. The common occurrence of oegopsid squid eggs in near-surface oceanic waters. Pac. Sci. **39**: 359–366.

Youngbluth, M.J. 1976. Vertical distribution and diel vertical migration of euphausiids in the central region of the California Current. Fish. Bull. U.S. **74**: 925–936.

Zahuranec, B.J. 2000. Zoogeography and systematics of the lanternfishes of the genus *Nannobrachium* (Myctophidae: Lampanyctini). Smithsonian Contrib. Zool. **607**: 1–69.

Zhenran, C. 1983. Studies on the lantern fishes (Myctophidae) from the central waters of the South China Sea (I). South China Sea Institute of Oceanography, Academia Sinica, pp. 199–216. (in Chinese with English abstract)

11. Appendices

Table A11.1 Micronekton sampling programs by Japan since 1980.

Organization	Principal Investigator	Area studied	No. of Sampling Times a Year	Years Sampled	Sampling Gear Used	Main Purpose of Study	Micronekton Sampled
SNFRI (JFA)	S. Ohshimo	W Japan Sea	1	1993-1995	midwater trawl and acoustic	SSE, jack mackerel and sardine	*Maurolicus japonicus* (*muelleri*)
SNFRI (JFA)	S. Ohshimo	E Eastern China Sea	2	1997-present	midwater trawl and acoustic	SSE, jack mackerel and sardine	*Diaphus regani*
TNFRI (JFA)	H. Sugisaki	off Pacific coast of N Honshu	4	1998-present	MOCNESS 4 m^2, MOHT net	micronekton	N/S
HU (HNFRI (JFA))	K. Miyashita (H. Honda)	off Pacific coast of NE Honshu and Hokkaido	2	1996-present	Acoustic (EK500)	walleye pollock	N/S (*Diaphus theta, Lampanyctus jordani, Stenobrachius leucopsarus*)
HU (Tottori Pref.)	K. Miyashita	Japan Sea	N/A	N/A	KFC1000 (38, 70 kHz), KFC3000 (38, 120 kHz)	N/A	*Maurolicus japonicus* (*muelleri*)
TNFRI (JFA) (HU)	D. Kitagawa (K. Uchikawa)	off Pacific coast of NE Honshu	1	1995–present	bottom trawl	sampling for bottom fishes	*Diaphus watasei,* *Diaphus theta,* *Lampanyctus jordani*
HNFRI (JFA)	K. Nagasawa, A. Nishimura	Bering Sea Basin and Shelf	1	1989–1991, 1994	acoustics, midwater trawl	horizontal and vertical distribution of mesopelagic fishes	*Theragra chalcogramma,* *Stenobrachius leucopsarus*
ORI (NFRI (JFA))	T. Kikuchi (YNU)	off Pacific coast of Honshu	1	1981–1984	KOC-net, KMT-net	radioactivities of marine organisms	mesopelagic shrimps
ORI (JAMARC)	K. Kawaguchi	off Pacific coast of N Honshu	1	1994–1996	midwater trawl	micronekton	N/S
TNFRI	K. Taki	37°–41°N, 142°–145°E	4	1997–present	130 cm Ring net, 1 m^2 MOCNESS	ecology of euphausiids	Euphausiids
TNFRI	H. Sugisaki	36°–42°N, 141°–147°E	1	1998–present	130 cm Ring net, 1 m^2 MOCNESS	food availability for *Cololabis saira*	N/S
HNFRI	A. Tsuda	39°–43°N, 145°–147°E	6	1988–present	Bongo	ecology of zooplankton	N/S
HU	Y. Sakurai, K. Uchikawa	NW Pacific Ocean (155°E, 175.30°E)	1	1995, 1997–2000	beam trawl (5 m^2)	ecology of micronekton and zooplankton	N/S
ORI	K. Kawaguchi	Subarctic Pacific, Bering Sea	1	1997	RMT 8+1, IKMT	community structure of zooplankton and micronekton	Myctophids, shrimps, squids, zooplankton

Table A11.2 Micronekton sampling programs by Russia since 1980.

Organization	Principal Investigator	Area studied	No. of Sampling Times a Year	Years Sampled	Sampling Gear Used	Main Purpose of Study	Micronekton Sampled
TINRO	A. Balanov, V. Radchenko	western Bering Sea	1	1989, 1990	midwater trawl	mesopelagic ecosystem surveys	Bathylagidae, Myctophidae
TINRO	E. Ill'insky, V. Lapko	Okhotsk Sea	1	1989–1991	midwater trawl	mesopelagic ecosystem surveys	Bathylagidae, Myctophidae
TINRO	E. Ill'insky, V. Lapko	Okhotsk Sea	1	1998–1999	midwater trawl	epipelagic ecosystem surveys	
TINRO	O. Ivanov	east of Kamchatka, Kuril Islands	1	1987, 1989, 1991–1995	acoustics, midwater trawl	scattering layer identification	Myctophids, Cephalopods
TINRO	V. Savinykh	NW Pacific, Transition, Subtropical	1	1990–1991	midwater trawl	epipelagic ecosystem surveys	
TINRO	V. Savinykh	California Current	1	1988–1989	midwater trawl	epipelagic ecosystem surveys	*Ceratoscopelus,* Cephalopods
TINRO	E. Karedin	North Pacific and Gulf of Alaska	1	1989	midwater trawl	epipelagic ecosystem surveys	

Table A11.3 Micronekton sampling programs by People's Republic of China since 1980.

Organization	Principal Investigator	Area studied	No. of Sampling Times a Year	Years Sampled	Sampling Gear Used	Main Purpose of Study	Micronekton Sampled
YSFRI	Q. Tang, X. Jin, X. Zhoa	Bering Sea, Aleutian Basin	1	June–Aug. 1993	acoustic (EK-400), midwater trawl	acoustic and trawl survey	*Stenobrachius,* Bathylagids

Table A11.4 Micronekton sampling programs by the United States since 1980.

Organization	Principal Investigator	Area studied	No. of Sampling Times a Year	Years Sampled	Sampling Gear Used	Main Purpose of Study	Micronekton Sampled
NMFS/SWFSC Honolulu	G. Boehlert/M. Seki	Southeast Hancock Seamount	1	summer 1984, winter 1985	1.8 m IKMT	micronekton fauna around seamounts	myctophids
NMFS/SWFSC Honolulu	C. Wilson	Southeast Hancock Seamount	2	summer 1987 to fall 1998	1.8 m IKMT	interaction of currents and micronekton	*Maurolicus, Gnathophausia*
NMFS/SWFSC Honolulu	J. Polovina	Hawaiian Archipelago	1 to 2	April 1988, June, October 1999	100 m^2 small mesh rope trawl	examine lobster larvae distribution	*Panularis phyllosoma*
NMFS/SWFSC Honolulu	J. Polovina	Hawaiian Archipelago	3	January, July, October 1991	140 m^2 small mesh Cobb trawl	examine lobster larvae distribution	*Panularis phyllosoma*
NMFS/SWFSC Honolulu	W. Matsumoto/ M. Seki	Subarctic Frontal and Transition Zone	1	August 1993	140 m^2 small mesh Cobb trawl	distribution and abundance of flying squid	*Ommastrephes bartramii*
NMFS/SWFSC Honolulu	M. Seki	Subarctic Frontal and Transition Zone	1	March–April 1992	140 m^2 small mesh Cobb trawl	examine micronekton in relation to oceanic fronts	mesopelagic fishes and squids
NMFS/SWFSC Honolulu	M. Seki	Subarctic Frontal and Transition Zone	1	August 1991	140 m^2 small mesh Cobb trawl	examine micronekton in relation to oceanic fronts	mesopelagic fishes and squids
NMFS/SWFSC Tiburon	S. Ralston	California Current off Central California	3	May–June 1983–2001	140 m^2 small mesh Cobb trawl	examine juvenile fishes in relation to ocean conditions	*Sebastes*
NMFS/AFSC Seattle	R. Brodeur/ M. Wilson	eastern Bering Sea around Pribilof Islands	1	September 1994–1999	140 m^2 small mesh Cobb trawl	examine juvenile fishes in relation to tidal fronts	*Theragra chalcogramma*
NMFS/AFSC Seattle	R. Brodeur/ M. Wilson	eastern Bering Sea around Pribilof Islands	1	September 1994–1999	Methot or IKMT trawl	examine juvenile fishes in relation to tidal fronts	*Theragra chalcogramma*
NMFS/AFSC Seattle/ Hokkaido University	R. Brodeur/ Y. Sakurai/N. Shiga	eastern Bering Sea shelf near Pribilof Islands	1	July 1995–2001	Methot beam trawl	examine shelf distribution of micronekton	*Theragra chalcogramma*
NMFS/AFSC Seattle	E. Sinclair/ T. Loughlin	eastern Bering Sea, Unimak Pass, Pribilof Canyon	1	May 1999-2000	Aleutian wing trawl with fine liner	examine habitat of mesopelagic fish and squid	*Stenobrachius, Bathylagus*
NMFS/AFSC Seattle	C. Wilson/ R. Brodeur	California Current from Washington to California	1	July–September 1995, 1998, 2001	Methot trawl	mesopelagic taxa causing acoustic backscatter	*Stenobrachius, Diaphus,* euphausiids
Oregon State University	W. Pearcy/ R. Brodeur	oceanic Gulf of Alaska	1	July 1980–1985	1.8 m IKMT and RMT	examine prey of adult salmon	mesopelagic fishes and squids

King, J.R. (Ed.) 2005. Report of the Study Group on the Fisheries and Ecosystem Responses to Recent Regime Shifts. **PICES Sci. Rep. No. 28**, 162 pp.

Jamieson, G. and Zhang, C.-I. (Eds.) 2005. Report of the Study Group on Ecosystem-Based Management Science and its Application to the North Pacific. **PICES Sci. Rep. No. 29**, 77 pp.

Brodeur, R. and Yamamura, O. (Eds.) 2005. Micronekton of the North Pacific. **PICES Sci. Rep. No. 30**, 115 pp.