The ecology, distribution, and abundance of midwater fishes of the Subarctic Pacific gyres

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Abstract

We describe the distribution and abundance of the midwater fish community, between 200 m and 500 m, in the North Pacific. The main area of interest was the Subarctic Pacific gyres, but we include species from the Bering Sea and the Sea of Okhotsk. There were 196 species identified in each gyre, 38 of which were common to both gyres. The most abundant species belong to the family Myctophidae and the most ecologically important myctophid probably is *Stenobrachius leucopsarus*. This species could have a biomass of approximately 21 million tonnes (t) in the Subarctic Pacific (including the Bering Sea and Sea of Okhotsk). *S. leucopsarus* is a small (about 8 cm maximum length) fish that lives up to 7 years. It is prey for a variety of other fishes, birds and mammals and may migrate into the mixing layer each evening where it feeds mainly on euphausiids and copepods.

The total abundance of midwater fishes appears to be large relative to total catches of other fish in the same areas. The vertical migratory behaviour of some of the residents provides a mechanism to transfer production out of the mixing layer. The movement into the surface layer by some fishes at night indicates that dynamic changes occur in the midwater community between the day and night, and the ecosystem dynamics in the surface layer are different in the day and in the night. This behaviour and the huge biomass relative to commercial species means that the dynamics of fish communities in the Subarctic Pacific are complex and need to be studied over a 24 hour period. The large biomasses may eventually attract commercial interest, thus it is important to establish international, cooperative programs now to learn more about the dynamics of these populations and the relationships with other species. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

In this report we consider the midwater fishes in the North Pacific that reside at depths between 200 m and 500 m. This corresponds to the upper portion of the mesopelagic layer which is usually considered to be between 200–1000 m, thus our deeper boundary is the base of the upper mesopelagic layer. This layer contains both a resident fauna and a transitional fauna that migrates vertically in response to diel changes in light. A component of this transitional fauna that is of critical importance to the ecosystems of the Subarctic Pacific is the deep scattering layer. This layer occurs at a depth interval of about 220 to 460 m. The species that migrate into the surface waters at night are frequently found within the deep scattering layer during the day and their migrations forms a trophic link between the surface mixing layer and the mesopelagic layer.

We identified 196 fish species in this habitat, but myctophids are dominant. There are also cephalopods (predominantly squids) and marine mammals that spend a portion of their day feeding at these depths. So little is known about many of the fish species that it is only possible to provide a very general overview of this midwater fish community. This report, therefore, identifies the key resident species and describes basic biological life histories for a few of them. Where possible, we examine trophic relationships by relating abundance and feeding habits to some of the important commercial fishes. We also identify potentially important relationships that might motivate research on midwater fishes in the Subarctic Pacific.

2. Species composition

Some of these 196 species (Table 1) have been reported only in areas adjacent to the Subarctic Pacific such as the Sea of Okhotsk and the Bering Sea. There is a lack of agreement on the taxonomy but it is beyond the scope of this study to review the nomenclature. The 196 species found belong to 59 families and 118 genera of which the family Myctophidae is the most diverse (Ahlstrom, 1959; Aron, 1962; Balanov & Il'Insky, 1992; Hart, 1973; Ivanov, 1997b; Neighbors & Nafpaktitis, 1982; Rass, 1954; Willis, Pearcy & Parin, 1988; Wisner, 1974). Myctophids are commonly known as lantern fishes because of their light producing organs. In general, mature myctophids range in length from 7 cm to 20 cm and have longevity of 3 to 10 years. Other prominent families include the Bathylagidae (deepsea smelts), the Gonostomiidae (lightfishes), and the Macrouridae (grenadiers).

There are also a number of species such as the Pacific lamprey, *Lampetra tridentata*, which although are not common, may play an important role in the midwater ecosystem. *L. tridentata* is a modern representative of a group of jawless fishes that have changed very little over their past 300 million years of anadromous and freshwater life histories. In some rivers, adults of this lamprey exceed 75 cm in length when they return to spawn after spending about two years in the ocean feeding on other inhabitants of the midwater community, such as pollock and chinook salmon. In the western Bering Sea, this species is not rare, and teeth marks have been found on the bodies of pollock, Greenland turbot, Pacific halibut, Kamchatka flounder, and arrow-tooth flounder. Another species of particular interest is *Anotopterus pharao* (the daggertooth). This fish has a wide distribution, throughout the North Pacific Ocean. Nagasawa, Ueno, Myers and Welch (1993) reported that 79 daggertooths were caught in surface gillnets from spring to fall of 1971 to 1991, throughout the North Pacific Ocean. More than 20 daggertooths were captured in bottom trawls made in Pacific waters off the northern Kuril Islands and southeastern Kamchatka during 1992–1998. Little is known about the life history of this fish, but it is believed to be an important predator of salmon as it moves into the surface waters to feed. Slash-mark wounds on one side of the backs of salmon implicate *A. pharao* as a predator of these fish in the Sea of Okhotsk and in the north Pacific off of the northern Kuril Islands (Radchenko & Semenchenko, 1996). Radchenko and Semenchenko (1996) also reported predation of juvenile salmon by daggertooth in these waters. Estimates of abundance and daily ration led them to conclude that daggertooth have a noticeable effect on the population of juvenile salmon as they pass through the Pacific waters off the Kuril Islands. In the coastal waters off British Columbia, 5 to 12% of adult sockeye have been reported to bear the slash marks in some years (Gilhousen, 1989; Henderson, McKinnell & Margolis, 1990 in Welch, Margolis, Henderson & McKinnell, 1991). Although a daggertooth may reach an average length of 85 cm (up to 146 cm), their small cross-sectional diameter of only 5 cm imparts a snake-like appearance to this fish. Specimens caught off of Kamchatka and the Kuril Islands ranged in length from 84 to 123 cm, and the several that were analyzed further were all found to be immature and had empty stomachs. *A. pharao* reportedly regurgitates its stomach contents, therefore, information about its

Table 1
Species of midwater fishes reported to inhabit the 100–500m depth layer of the Subarctic North Pacific
Ocean and adjacent seas

Family	Genus	Species	Region
Alepisauridae	*Alepisaurus*	*occulapius*	SO
		ferox	All
Alepocephalidae	*Alepocephalus*	*sp.*	WTZ
	Bajacalifornia	*megalops*	BS,SO
	Rouleina	*attrita*	BS
		squamilatera	SO
Ammodytidae	*Ammodytes*	*hexapterus*	BS,ESA,ETZ,SO,WSA
Anarhichadidae	*Anarrhichthys*	*ocellatus*	ESA,ETZ
Anoplogasteridae	*Anoplogaster*	*cornuta*	ETZ,SO
Anotopteridae	*Anotopterus*	*pharao*	BS,ANT,ATL,ESA,ETZ,SO,WSA
Apogonidae	*Howella*	*brodiei*	ETZ
Argentinidae	*Argentina*	*sialis*	ETZ
	Nansenia	*candida*	BS,ESA,ETZ,WSA
Aulopidae	*Aulopus*	*damasi*	SO
Bathylagidae	*Bathylagus*	*berycoides*	ETZ
		milleri	BS,ESA,ETZ,SO,WSA,WTZ
		ochotensis	BS,ESA,ETZ,SO,WSA,WTZ
		pacificus	BS,ESA,ETZ,WSA,WTZ
		wesethi	ESA,ETZ
	Leuroglossus	*schmidti*	BS,ESA,ETZ,SO,WSA,WTZ
		stilbius	BS ESA,ETZ
	Melanolagus	*bericoides*	WSA
Bathymasteridae	*Bathymaster*	*signatus*	BS,ESA,ETZ,WSA
Bramidae	*Brama*	*japonica*	BS,ESA,ETZ,WSA,WTZ
Bythitidae	*Thalassobathia*	*pelagica*	BS
Caristiidae	*Caristius*	*macropus*	ESA,ETZ,WTZ
Ceratiidae	*Ceratias*	*holboelli*	BS,WSA
Cyclopteridae	*Aptocyclus*	*ventricosus*	BS,SO
Gadidae	*Theragra*	*chalcogramma*	BS,ESA,ETZ,WSA
Gasterosteidae	*Gasterosteus*	*aculeatus*	BS,ESA,ETZ,WSA,WTZ
Gigantactinidae	*Gigantactis*	*elsmani*	SO
		macronema	WTZ

Table 1
(continued)

Family	Genus	Species	Region
Gonostomiidae	*Cyclothone*	*acclinidens*	CC,ESA,ETZ
		alba	ETZ,WTZ
		atraria	BS,ESA,ETZ,SO,WSA,WTZ
		pallida	BS,ESA,ETZ,WSA,WTZ
		pseudopallida	BS,ESA,ETZ,WSA,WTZ
		signata	BS,CC,ESA,ETZ,WSA,WTZ
	Gonostoma	*gracile*	BS,ESA,ETZ,SO,WSA,WTZ
Hexagrammidae	*Pleurogrammus*	*monopterygius*	BS,ESA,ETZ
Icosteidae	*Icosteus*	*aenigmaticus*	BS,ESA,ETZ,SO,WSA
Idiacanthidae	*Idiacanthus*	*astrosomus*	CC,ESA,ETZ
Lampridae	*Lampris*	*guttatus*	ESA,ETZ,WSA
Liparididae	*Nectoliparis*	*pelagicus*	BS,ESA,ETZ,SO,WSA,WTZ
	Paraliparis	*sp.*	BS,SO
Louvaridae	*Louvarus*	*imperialis*	ETZ
Macrouridae	*Albatrossia*	*pectoralis*	BS,ESA,ETZ,SO,WSA,WTZ
	Coryphaenoides	*acrolepis*	BS,SO,WSA
		angustifrons	BS
		cinereus	BS,ESA,ETZ,SO,WSA,WTZ
		clarki	BS
		filifer	BS, ESA,ETZ,WSA
		firmisquamis	BS
		lepturus	BS
		suborbitalis	BS
Malacosteidae	*Aristostomias*	*scintillans*	BS,ESA,ETZ,SO,WTZ
	Malacosteus	*niger*	BS
Melamphaeidae	*Melamphaes*	*lugubris*	BS,ESA,ETZ,SO,WSA,WTZ
		nycterinus	BS
		parvus	ETZ
		simus	ETZ,WTZ
		suborbitalis	SO
	Poromitra	*crassiceps*	BS,CC,ESA,ETZ,SO,WSA,WTZ
	Scopeloberyx	*robusta*	BS,ESA,ETZ,WSA,WTZ
	Scopelogadus	*bispinosus*	ETZ
Melanostomiidae	*Bathophilus*	*flemingi*	ESA,ETZ
	Leptostomias	*gladiator*	WSA
	Opostomias	*mitsuii*	ETZ,WTZ
	Pachystomias	*microdon*	BS,ETZ
	Tactostoma	*macropus*	BS,ESA,ETZ,SO,WSA,WTZ
Moridae	*Antimora*	*microlepis*	BS,ESA,ETZ
		rostrata	ETZ

Table 1
(*continued*)

Family	Genus	Species	Region
	Halargyreus	*johnsonii*	BS,SO
	Laemonema	*longipes*	BS,SO,WSA,WTZ
Myctophidae	*Ceratoscopelus*	*townsendi*	CC,ESA,ETZ,WTZ
		warmingii	ETZ,WSA
	Diaphus	*anderseni*	BS,ESA,ETZ
		gigas	WSA
		kuroshio	ETZ,WTZ
		metopoclampus	WSA
		perspicillatus	ETZ,WTZ
		rafinesqueii	ETZ,WTZ
		theta	BS,ESA,ETZ,SO,WSA,WTZ
	Diogenichthys	*atlanticus*	ETZ,WTZ
		laternatux	ETZ
	Dorsadena	*yaquinae*	ETZ
	Electrona	*rissoi*	ESA,ETZ,WSA,WTZ
	Hygophum	*atratum*	ETZ
		reinhardti	ESA,ETZ
	Lampadena	*luminosa*	WSA
		urophaos	ETZ,WSA
		yaquinae	WSA
	Lampanyctus	*acanthurus*	WSA
		fernae	ETZ
		idostigma	ETZ
		jordani	BS,ESA,ETZ,SO,WSA,WTZ
		mexicanus	ETZ
		niger	ETZ
		parvicauda	ETZ
		regalis	BS,CC,ESA,ETZ,SO,WSA,WTZ
		ritteri	BS,CC,ESA,ETZ
		simulator	ETZ
		steinbecki	WTZ
		tenuiformis	ETZ,WSA
	Myctophum	*asperum*	WSA
		margaritatum	ETZ
		nitidulum	ETZ
	Notolychnus	*valdiviae*	ETZ
	Notoscopelus	*elongatus*	ETZ
		japonicus	ESA,WSA,WTZ
		resplendens	ETZ,WSA
	Parvilux	*ingens*	ETZ
	Protomyctophum	*crockeri*	ESA,ETZ,WTZ
		thompsoni	BS,ESA,ETZ,SO,WSA,WTZ
	Stenobrachius	*leucopsarus*	BS,ESA,ETZ,SO,WSA,WTZ
		nannochir	BS,ESA,ETZ,SO,WSA,WTZ
	Symbolophorus	*californiensis*	ESA,ETZ,WSA,WTZ
		evermanni	WTZ

Table 1
(*continued*)

Family	Genus	Species	Region
	Tarletonbeania	*crenularis*	BS,ESA,ETZ,WSA,WTZ
		taylori	ETZ,WSA,WTZ
	Triphoturus	*nigrescens*	ETZ
Nemichthydae	*Avocettina*	*bowersi*	ESA,ETZ
		infans	BS,ESA,ETZ,SO,WSA
	Nemichthys	*scolopaceus*	ESA,ETZ,WSA,WTZ
Neoscopelidae	*Scopelengys*	*tristis*	BS
Nettastomatidae	*Venefica*	*tentaculata*	SO
Notosudidae	*Ahliesaurus*	*brevis*	WSA
	Scopelosaurus	*adleri*	BS,SO,WSA
		harryi	BS,ESA,ETZ,SO,WSA
Oneirodidae	*Bertella*	*idiomorpha*	BS,ESA,ETZ
	Dolopichthys	*longicornis*	ETZ
	Oneirodes	*bulbosus*	BS,ESA,ETZ,SO,WSA
		thompsoni	BS,ESA,ETZ,SO,WSA
Ophidiidae	*Bassozetus*	*compressus*	ETZ
		zenkevitchi	WSA
Opisthoproctidae	*Bathylychnops*	*exilis*	ESA,ETZ
	Dolichopteryx	*sp.*	BS,ETZ,SO,WSA
	Macropinna	*microstoma*	BS,ESA,ETZ,SO,WSA
	Opisthoproctus	*soleatus*	ETZ
	Winteria	*telescopa*	WSA
Oreosomatidae	*Allocyttus*	*verrucosus*	BS,ESA,WSA
Osmeridae	*Mallotus*	*villosus*	BS,ESA,ETZ
Paralepidae	*Arctozenus*	*rissoi*	WSA
	Lestidiops	*ringens*	ESA,ETZ,WSA,WTZ
		sphyraenopsis	WSA
	Magnisudis	*atlantica*	WSA
	Notolepis	*rissoi*	BS,ESA,ETZ,SO
	Paralepis	*atlantica*	ESA,ETZ,SO
Percichthyidae	*Howella*	*parini*	WSA
Petromyzontidae	*Lampetra*	*tridentatus*	BS,ESA,ETZ
Photichthyidae	*Ichthyococcus*	*elongatus*	ETZ,WTZ
		elegans	WSA
	Vinciguerria	*lucetia*	ETZ
		nimbaria	ETZ,WTZ
		poweriae	ETZ
Pleuronectidae	*Reinhartius*	*matsuurae*	BS,SO

Table 1
(*continued*)

Family	Genus	Species	Region
Psychrolutidae	*Malacocottus*	*sp.*	BS,SO,WSA
Pterothrissidae	*Leptodephalus*	*sp.*	WSA
Scomberescocidae	*Cololabis*	*saira*	CC,BS,ESA,ETZ,WSA,WTZ
Scopelarchidae	*Benthalbella*	*dentata*	BS,ESA,ETZ,SO,WSA,WTZ
		linguidens	ESA,ETZ,WSA,WTZ
Scorpaenidae	*Sebastes*	*crameri*	BS,ESA,ETZ
		entomelas	BS,ESA,ETZ
		flavidus	ESA,ETZ
	Sebastolobus	*altivelis*	BS,ESA,ETZ
		macrochir	BS,WSA
Searsidae	*Holtbyrnia*	*innesi*	BS,SO,WSA
	Maulisia	*argipalla*	BS,ETZ
	Sagamichthys	*abei*	ANT,BS,ESA,ETZ,WSA,WTZ
Serrivomeridae	*Serrivomer*	*sector*	ETZ,WSA
Squalidae	*Somniosus*	*pacificus*	BS,ESA,ETZ,SO
	Squalus	*acanthius*	BS,ESA,ETZ
Sternoptychidae	*Argyropelecus*	*aculeatus*	ETZ
		affinis	CC,ESA,ETZ
		hemigymnus	ETZ,WTZ
		lychnus	ESA,ETZ,WW
		sladeni	CC,ESA,ETZ,WTZ
	Danaphos	*oculata*	ESA,ETZ
	Polyipnus	*matsubarai*	WSA
	Sternoptyx	*diaphana*	CC,ESA,ETZ,WSA
		obscura	ETZ,WTZ
Stomiidae	*Macrostomias*	*longibarbatus*	ETZ
Syngnathidae	*Sygnathus*	*griseolineatus*	ETZ
Trachipteridae	*Desmodema*	*lorum*	ETZ,WSA
	Trachipteris	*altivelis*	ESA,ETZ
		iris	WSA
		ishikawai	WSA
Trichiuridae	*Aphanopus*	*arigato*	ESA,WSA
	Benthodesmus	*tenuis*	WSA,WTZ

feeding habits has been scanty, but recently predation on salmon has been confirmed by observations of specimens found attached by their teeth to prey fish (Welch et al., 1991).

Table 1
(*continued*)

Family	Genus	Species	Region
Zaproridae	*Zaprora*	*silenus*	BS,ESA,ETZ,WSA
Zoarcidae	*Bothrocarichthys*	*microcephalus*	SO,WSA
	Lycodapus	*mandibularis*	BS,ESA,ETZ
	Lycogramma	*brunnea*	BS,SO
		solatovi	BS,ESA,ETZ,SO
	Lycogrammoides	*nigrocaudatus*	SO
		schmidti	SO

Adapted from Ahlstrom, 1959; Aron, 1962; Bailey & Robison, 1986; Balanov & Il'Insky, 1992; Frost & McCrone, 1979; Hart, 1973; Ivanov, 1997b; Rass, 1954; Willis, 1984; Willis et al., 1988; Wisner, 1974). Antarctic Ocean, ANT; Atlantic Ocean, ATL; Bering Sea, BS; California Current, CC; Eastern Subarctic, ESA; Eastern Transition Zone, ETZ, Sea of Okhotsk, SO; Western Subarctic, WSA

3. Abundance estimates and distribution of myctophids

There are 48 species unique to the western Subarctic Pacific gyre, 13 to the eastern, and 38 species in common (Table 2). The most abundant are the myctophids *Stenobrachius leucopsarus, Diaphus theta, Protomyctophum thompsoni*, and *Stenobrachius nannochir*. The bathylagid, *Leuroglossus schmidti* and the chauliodontid *Chauliodus macouni* are common species representing other families in this region (Fig. 1).

Abundance and biomass estimates of the various species are very approximate at best and often not much better than informed speculation. Nevertheless, the estimates tend to be made by knowledgeable biologists and are worth reporting. A number of studies contain information on the distribution and relative abundance of fishes in the midwater community. The following is a brief review of some of these reports and a more detailed account of a few common species. In this paper abundance estimates are based on numbers of individual fish, whereas biomass is measured by weight of fish.

Aron (1962) sampled the eastern North Pacific using 1 and 2 m Isaac-Kidd midwater trawls (IKMT). For the most part, tows were at night from the surface down to 400 m, with only a few daylight hauls for comparison. *S. leucopsarus* represented 71% of the number of fish in catches in the eastern Subarctic Pacific; *D. theta*, 15%, and *Tarletonbeania crenularis, 8%*.

Taylor (1967) presents data from a cruise in July 1965, off the Queen Charlotte Islands beyond the continental shelf near 133°W; 52°N: 135°W; 53°N. Hauls were made using a large German Engel trawl, developed for midwater trawling of herring. Daytime hauls were made at 230 to 595 m depth and night hauls were made at 90 to 320 m depth. A total of 8 myctophid species comprised 79 to 87% of the total number of fish caught, chauliodontids made up 6 to 9%. In daytime hauls *D. theta* was the most abundant species comprising 37% of the catch, *P. thompsoni* was the second most abundant at 29%, and *S. leucopsarus* constituted 21% of the catch. *C. macouni* was the next most abundant species at 9%. In night-time hauls, the same

Table 2
Midwater fishes found in the eastern and western Subarctic North Pacific gyres, and some species restricted to each

Western	Common	Eastern
*Lampanyctus jordani	*Stenobrachius leucopsarus	*Lampanyctus ritteri
*Bathylagus milleri	*Protomyctophum thompsoni	*Tarletonbeania crenularis
*Cyclothone alba	*Diaphus theta	*Ceratoscopelus townsendi
*Tarletonbeania taylori	*Stenobrachius nannochir	Bathylagus flemingi
*Nectoliparus sp.	*Electrona rissoi (E. arctica)	Bathylagus wesethi
Ceratoscopelus warmingii	*Symbolophorus californiensis	Leuroglossus stilbius
Sebastolobus macrochir	*Bathylagus ochotensis	Avocettina bowersi
Desmodema lorum	*Chauliodus macouni	Sebastolobus altivelis
Leptostomias gladiator	Chauliodus sloani	Danaphos oculata
Notoscopelus resplendens	*Leuroglossus schmidti	Idiacanthus astosomus
Melanolagus bericoides	*Gonostoma gracile	Aristostomias scintillans
Servivomer sp.	*Lampanyctus regalis	Argyropelecus affinis
Polyipnus matsubarai	*Cyclothone atraria	Argyropelecus sladeni
Diaphus gigas	*Notoscopelus japonicus	
Diaphus metopoclampus	Theragra chalcogramma	
Lampris guttatus	Nansenia candida	
Lampadena luminosa	*Bathylagus pacificus	
Lampadena urophaos	Aptocyclus ventricosus	
Lampadena yaquinae	Gastrosteus aculeatus	
Lampadena acanthurus	*Benthalbella dentata	
Lampadena tenuiformis	Cyclothone signata	
Myctophum asperum	Nectoliparus pelagicus	
Nemicthys scolopaceus	Corphaenoides acrolepis	
Ahliesaurus brevis	Corphaenoides pectoralis	
Scopelosaurus adleri	*Melamphaes lugubris	
Scopelosaurus harryi	*Poromitra crassiceps	
Oneirodes bulbosus	Avocettina infans	
Bassozetus zenkevitchi	Macropinna microstoma	
Dolichopteryx sp.	Lestidium ringens	
Winteria telescopa	Protomyctophum crockeri	
Arctozenus rissoi	Benthalbella linguidens	
Howella parini	Steroptyx diaphana	
Ichthyococcus elongatus	*Cyclothone pallida	
Holtbyrnia innesi	*Cyclothone pseudopallida	
Sagamichthys abei	Tactostoma macropus	
Malacottus sp.	Alepisaurus ferox	
Trachipteris altivelis	Anotopterus pharao	
Trachipteris ishikawai	Lampetra tridentata	
Zaprora silenus		
Brama japonica		
Laemonema longipes		
Caristius macropus		
Bothrocarichthys microcephalus		
Icichthys lockington		
Chiasmodon niger		
Pseudoscopelus scriptus		
Artediellichthys nigripinnis		
Icosteus aenigmaticus		

* Indicates the species that we consider to be most abundant, from the information provided in the various studies.
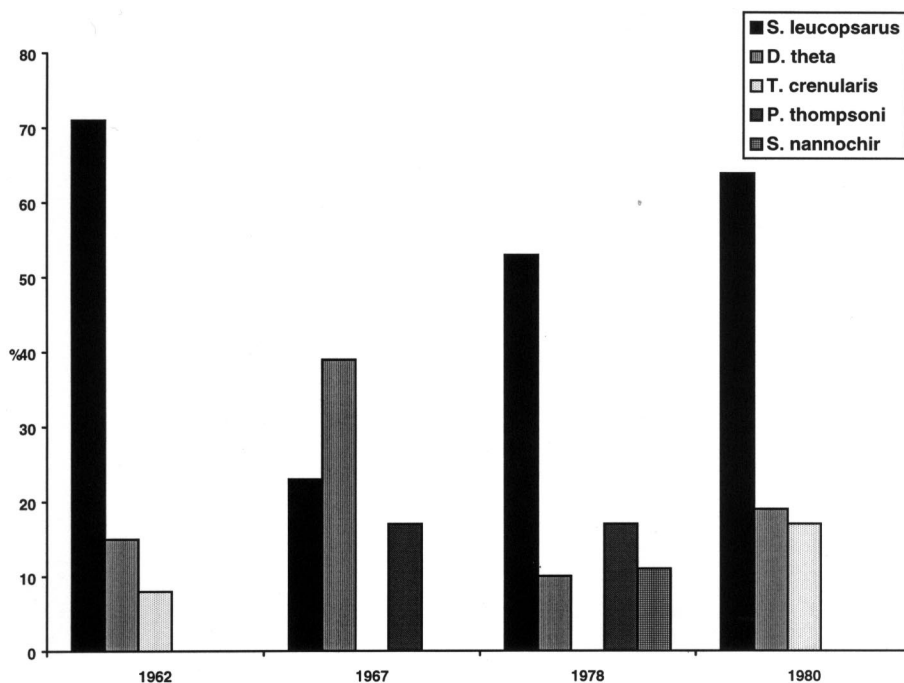
Fig. 1. Abundance of the most common midwater fishes in the eastern North Pacific. Adapted from Aron (1962); Frost and McCrone (1979); Taylor (1967) and Willis and Pearcy (1980)

species were most abundant. *D. theta* again was the most abundant species comprising 39% of the hauls, *S. leucopsarus* comprising 23%, *P. thompsoni* at 17%, and *C. macouni* at 6%. At night, 81% of the *D. theta* were caught in the 90 to 230 m depth interval, while *S. leucopsarus* and *P. thompsoni* were spread throughout the 90 to 320 m depth interval. Bathylagids *(Bathylagus milleri* and *B. ochotensis)* and argentinids *(Nansenia candida)* comprised some 19% of the catch at 510 to 595 m depth during the day, and 6% of the catch at 230 to 320 m depth at night. Taylor (1967) reported that abundances were unlike any of the others reviewed here, because they are the only records in which *D. theta* was more abundant than *S. leucopsarus*.

Taylor (1968) related these catches of midwater fishes to correspond to three different sound scattering layers, which were detected during the day at 220–230 m, 330–400 m, 185 and 90 m. The main scattering layer at 220–230 m was dominated by myctophids with gas filled swim bladders, while in deeper layers there were species lacking swim bladders, like bathylagids, argentinids, stomiatoids, and melamphids, and myctophids with fat-filled swim bladders such *as S. leucopsarus*.

Frost and McCrone (1979) used a modified Tucker trawl (rectangular mouth of 4 m^2) to collect fish from the surface to 460 m at two stations in the eastern Subarctic North Pacific. All sampling stations included day and night sample series. The average percentage of the four most abundant species was: *S. leucopsarus*, 52.8%; *P. thompsoni*, 17.2%; *S. nannochir*, 10.8%; and *D. theta*, 9.9%. Estimates of combined

biomass in numbers of fish, based on regression equations relating dry body weight and body length, varied from 0.85g fish/m^2 in 1973, to 1.24g/m^2 in 1974, to 0.61/m^2 in 1975, in the water column from the surface to 385–460 m. The mean abundance of all fishes captured during the three year period ranged from 0.78 to 1.61 fish/m^2.

Willis and Pearcy (1980) used a large-mouthed pelagic trawl, with a frontal area of 50 m^2 made of 19 mm stretch mesh to sample stations 110–120 km off Newport, Oregon (44°40′N, 125°35′–125°40′W). Sampling took place during both night and day, between 295 and 360 m depth, from June 30 to July 22, 1976 and July 30 to Aug 01, 1977. Only those tows in which > 40 individuals were caught are considered. The density of midwater fish was 8 individuals per 10^{-5}/m^3 filtered seawater or about 52 fish per hectare, based on depth of 4300 m. The percentages of the dominant fish species ranged from 42 to 86% for *S. leucopsarus*, 3 to 35% for *D. theta*, and 11 to 23% for *T. crenularis*.

Willis, Pearcy and Parin (1988) collated data from various sources relating to fish catches from the midwaters of the Pacific Ocean north of 40°N, between 1951 and 1981 (Table 3). Their sources included data from Oregon State University, University of Tokyo, Hokkaido University, Scripps Institution of Oceanography, University of Washington, Fisheries and Oceans Canada, Soviet Academy of Sciences. The data originated from 761 tows using IKMTs, of 1.8, 2.4, and 3.0 m. width. The rank order of numerical abundance of dominant species was shown for the Alaska Gyre and Western Subarctic. An important observation from this study was the high per-

Table 3
Relative abundance of fishes (number of individuals) in the midwater communites of the Alaska Gyre (AG) and the Western Subarctic Pacific (WSA)

Species	Overall				< 500m		> 500m	
	AG rank	%	WSA rank	%	AG rank	WSA rank	AG rank	WSA rank
S. leucopsarus	1	34	1	26	1	1	3	3
S. nannochir	2	21	2	25	5	4	1	1
P. thompsoni	3	12	5	8	2	3	5	6
C. atraria	4	9	3	16	–	–	2	2
C. macouni	5	7	6	4	4	5	4	5
D. theta	6	6	4	10	3	2	8	4
T. crenularis	7	3	–	1	6	7	–	–
B. pacificus	8	1	8	3	–	8	7	7
P. crassiceps	9	1	–	< 1	–	–	6	–
T. macropus	10	1	–	< 1	7	–	–	–
L. schmidti	–	1	7	4	8	6	–	8
L. jordani	–	< 1	9	1	–	10	–	9
G. gracile	–	< 1	10	1	–	9	–	10
B. ochotensis	–	< 1	–	< 1	9	–	–	–
M. lugubris	–	0	–	0	10	–	–	–
B. dentata	–	0	–	0	–	–	10	–

Adapted from Willis et al., 1988

centage of the biomass that was contributed by *S. leucopsarus, S. nannochir, D. theta*, and *P. thompsoni. S. leucopsarus*, however, consistently stands out as being widely distributed and extremely abundant.

Inventories of fishes of the upper mesopelagic layer have been compiled by Becker and Borodulina (1978), Willis et al. (1988) and Parin, Fedorov, Borodulina and Becker (1995). These lists of fishes include all the species found, including those known to be atypical for mesopelagic waters. A total of 84 species belonging to 66 genera and 37 families is recorded from the observed depth layer. Eleven additional species which occur in the 0–50 m layer can be added to the list of mesopelagic fishes in Table 2:

A. fimbria (Pallas)
Bertella idiomorpha (Pietsch)
Cryptopsarus couesi (Gill)
Lagocephalus lagocephalus (Linnaeus)
Nealotus tripes (Johnson)
Opostomias c.f. *mitsuii* (Imai)
Photonectes albipennis (Doberlein)
Psenes pellucidus (Lutken)
Tetragonurus cuvieri (Risso)
Thamnaconus modestus (Gunther)
Thyrsitoides marleyi (Fowler)

The majority of families of mesopelagic fishes (70%) in the region are represented by only 1–2 species (Balanov & Il'Insky, 1992; Balanov & Radchenko, 1995), whereas the Myctophidae and Bathylagidae are represented by 20 and 6 species, respectively. Twenty-five mesopelagic fish comprise a group of 'typical' species which occur at > 50% (Table 4). If co-occurrences in all areas are considered this group is reduced to just 5 species: *D. theta, S. leucopsarus, P. thompsoni, C. macouni*, and *L. schmidti*.

There were seasonal changes in the species composition and abundance of the dominant mesopelagic fishes in the Pacific waters off Kamchatka and the Kuril Islands. As a consequence of the ocean circulation and mixing, residents in the two domains mix, forming a mixed assemblage of species. In the fall and winter, species characteristic of the Subarctic Pacific (e.g. *L. schmidti, B. pacificus, T. crenularis)* and endemics of the Sea of Okhotsk (e.g. *Bothrocaricthys microcephalus*) also occurred there, in addition to residents typical of the northern transitional zone between the subtropic and subpolar gyres (e.g. *Symbolophorus californiensis, N. candida*) and tropic-subtropic species (e.g. *Ceratoscopelus warmingi, Trachipterus isikawai, Brama japonica)*.

In the summer of 1992, numbers of species almost doubled (from 39 to 68) in the mesopelagic layer of the southern Kuril Island area in comparison with the fall and winter of 1991. About 80% of this increase resulted from invasion by tropic-subtropic species of the transitional zone, many of which (30%) were myctophids. The mesopelagic fishes make up very productive communities in Russian waters. Estimates of fish abundance in the 200–1000 m layer vary from 2.8–6.9 t/km^2

Table 4

'Typical' midwater fishes of upper mesopelagic zone in the Russian EEZ in the North Pacific. Values are the percentages in which the species occured more than 50% of the time in a series of tows in each of three areas near the Kuril Islands in 1991, one area in 1992 and two areas off Kamchatka in 1991. The + indicates the number of areas where the incidence in the total number of tows exceeded 50%. The percentage is the average for the areas in which the incidence exceeded 50%. A 0 percentage indicates that the species was captured in less than 50% of the tows in an area

Species	Kuril Islands areas % incidence			Kamchatka areas % incidence	
Diaphus theta	97	+ + +	100	85	+ +
Stenobrachius leucopsarus	95	+ + +	100	96	+ +
Tarletonbenia crenularis	90	+ + +	82	0	
Chauliodus macouni	61	+ + +	100	79	+ +
Leuroglossus schmidti	59	+ + +	73	84	+ +
Bathylagus ochotensis	73	+	73	84	+ +
Protomyctophum thompsoni	68	+ + +	91	83	+ +
Bathylagus milleri	53	+	64	76	+ +
Stenobrachius nanochir	0		64	70	+
Bathylagus pacificus	0		0	70	+
Lampanyctus jordani	0		100	85	+ +
Arctozenus rissoi	52	+ +	73	57	+
Lestidiops ringens	75	+	0	0	
Aptocyclus ventricosus	50	+	0	79	+
Scopelosaurus harryi	60	+	0	57	+
Scopelosaurus adleri	0		0	65	+
Tactosoma macropus	60	+	73	0	
Gogostoma gracile	0		100	0	
Lampanyctus regalis	0		55	65	+
Benthalbella linguidens	0		64	0	
Benthalbella dentata	0		73	0	
Ceratoscopelus warmingii	0		64	0	
Symbolophorus californiensis	0		91	0	
Melaphaes lugubris	0		0	69	+ +
Laemonema longipes	64	+	0	0	

(Tseitlin, 1986; Gjøsaeter & Kawaguchi, 1980). A recent assessment of midwater fish abundance in the Bering and Okhotsk Seas based on detailed trawl surveys (Balanov & Il'Insky, 1990, 1992; Balanov, 1995; Il'Insky, 1995), resulted in biomass estimated of mesopelagic fishes (200–1000 m) ranging from 16.3 to 33.4 t/km^2 in Okhotsk Sea and from 9.0 to 24.4 t/km^2 in the Bering Sea.

In the fall and winter of 1991, the total mesopelagic fish biomass in the 200–500 m layer of Russian Pacific waters was estimated to be 1.07×10^7 metric t, a mean of 11.2 t/km^2 (ranging from 4.6 to 19.2 t/km^2). Biomass was highest in the two oceanic areas (18.7 and 19.2 t/km^2 respectively), slightly less near the Kuril Islands (16.8 t/km^2) and substantially less off Kamchatka area (6.4 t/km^2) (Table 5).

In Pacific waters around the Kuril waters the most abundant mesopelagic species were myctophids (85.8–94.7%) and bathylagids (5.2–11.6%) (Table 6) as was the

Table 5

Total biomass (10^3 metric t and t/km^2) of midwater fishe s in the Pacific Ocean of the Russian Exclusive Economic Zone (200–500 m layer). Areas 1 and 3 are oceanward. Note only area 3 shows two seasons. Ivanov, pers com

Kuril areas												Kamchatka areas					
1 (Nov.–Dec.,1991)		2 (Nov.–Dec.,1991)		3 (Nov.–Dec.,1991)		3 (Aug., 1992)		5 (Nov.–Dec.,1991)		6 (Nov.–Dec.,1991)	
10^3 t	t/km^2	10^3 t	t/km^2	10^3 t	t/km^2	10^3 t	t/km^2	10^3 t	t/km^2	10^3 t	t/km^2
4302	17.8	1492	16.8	2474.2	18.3	3178	23.5	639	4.1	1757	6.4

case in the Pacific waters off Kamchatka (74.6–85.2% and 11.3–19.1% respectively). In rank order of abundance, *D. theta* was first (43.8–74.5%), *S. leucopsarus*—second (11.9–43.5%) and *L. schmidti*—third (4.0–9.2%) in all areas off Kuril Islands. These three species contributed 92.4–94.3% of the total fish biomass. A similar situation was observed in Kamchatka waters, where *S. leucopsarus* was the most abundant (57.8%), *S. nannochir* second (10.4%), and *B. ochotensis* third (6.9%), while *D. theta* and *L. schmidti* were relatively scarce (6.5 and 6.1%).

In general, the domination of fish biomass by *D. theta* and *S. leucopsarus* is a distinctive feature of the mesopelagic ichthyofauna in Russian Pacific waters in comparison to the Okhotsk and Bering Seas (Balanov & Il'Insky, 1992). These two myctophids, which undertake vertical migration to the surface each night (Lapko & Ivanov, 1993; Lapko, 1995), are undoubtedly very important components of the epipelagic layer as well (0–200 m).

In the summer of 1992, mesopelagic fish abundance in the southern Kuril Island area increased by 1.3 times and reached 23.5 t/km^2, compared to fall–winter 1991. Myctophids were the most abundant family in both periods (88.9% in November–December 1991 and 82.8% in August 1992). The increase in fish abundance in summer was a result of immigration of tropic and subtropic species (15 species) and fishes of the transition zone (7 species).

If it is assumed that in the Pacific waters the total stock of the mesopelagic fishes is dispersed equally between the layers at 200–500 and 500–1000 m (Balanov, 1995), then the total concentration in the 200–1000 m layer looks to be the highest off the Kuril Islands at 20–47 t/km^2 and considerably less off Kamchatka 8.2–13.2 t/km^2. Although the information presented here relates only to the upper mesopelagic layer, following the assumption of Balanov (1995), the total fish biomass in the 200–1000 m layer can be estimated at 20–24 $\times$ 10^6 t in Russian Pacific waters.

Balanov and Il'Insky (1992) determined the biomass of common species and families in the Sea of Okhotsk and western part of the Bering Sea, and compared the two regions (Table 7). Their estimates are based on trawling surveys (mouth opening of 3500 m^2) that were conducted from 23 May to 1 July 1989 in the western part of the Bering Sea, and from 7 to 31 August 1989 in the Sea of Okhotsk. Horizontal hauls were made with a variable depth trawl in the 500–200 m layer and also at

Table 6
Biomass (thousand metric tonnes and %) of the dominant species of fishes of the upper mesopelagic layer in the Pacific Ocean of the Russian EEZ (layer 200–500 m)

Species	Kuril areas								Kamchatka areas			
	1 (Nov.–Dec., 1991)		2 (Nov.–Dec.,1991)		3 (Nov.–Dec., 1991)		3 (Aug., 1992)		5 (Nov.–Dec., 1991)		6 (Nov.–Dec., 1991)	
	10^3 t	%	10^3 t	%	10^3 t	%	10^3 t	%	10^3 t	%	10^3 t	%
D. theta	2012.5	46.8	1036.2	69.5	1840.5	74.5	1207.6	38	41.6	6.5	729	41.4
S. leucopsarus	1871.1	43.5	204	13.7	296.2	11.9	867.6	27.3	369.4	57.8	707.5	40.3
S. nannochir	–	–	15.8	1.1	+	+	25.4	0.8	66.4	10.4	47.5	2.7
L. schmidti	173.2	4	136.7	9.2	166.3	6.7	146.2	4.6	38.6	6.1	103.2	5.9
T. crenularis	110.4	2.6	17.1	1.2	37.2	1.5	3.2	0.1	+	+	0.5	+
B. milleri	36.7	0.8	16	1.1	16.4	0.7	85.8	2.7	21.5	3.4	47.4	2.7
L. jordani	24.6	0.6	20.1	1.3	18	0.7	206.6	6.5	9.8	1.5	40.5	2.3
S. californiensis	–	–	–	–	0.3	+	114.4	3.6	–	–	–	–
P. thompsoni	17.2	0.4	2.2	0.1	7.2	0.3	41.3	1.3	1.4	0.2	15.8	0.9
B. ochotensis	13.7	0.3	14.5	0.9	21.9	0.9	60.4	1.9	44.4	6.9	10.3	0.6
B. pacificus	6.2	0.1	5.9	0.4	3.2	0.1	+	+	17.3	2.7	36.7	2.1
L. longipes	1.8	+	2.1	0.1	3.2	0.1	117.6	3.7	+	+	–	–
Other	34.1	0.8	21.1	1.4	63.2	2.6	301.9	9.5	28.5	4.5	19	1.1
Total	4301.5	100	1491.7	100	2474.2	100	3177.9	100	638.9	100	1757.4	100

Table 7
Percent biomass of midwater fish in the Sea of Okhotsk and Bering Sea

Family	Species	% Biomass	
		Sea of Okhotsk	Bering Sea
Myctophidae		4.5	47.1
	S. leucopsarus	0	37.6
	S. nannochir	4.2	7.9
Bathylagidae		86.8	33.8
	L. schmidti	74.8	6.4
	B. ochotensis	10.0	5.3
	B. pacificus	0	12.0
	P. milleri	0	10.3
Macrouridae		1.1	3.6
Chauliodontidae		0	4.6
	C. macouni	0	4.6
Zoarcidae		6.2	0
	L. schmidti	3.0	0
	B. microcephalus	2.3	0
Cyclopteridae		0	2.8
Scopelosauridae		0	2.4
Other		1.4	5.8
	Other	5.7	15.9
TOTAL Biomass of mesopelagic fish		14.608×10^6 t	5.921×10^6 t
DENSITY		16.3 g/m^2	9.0 g/m^2

Adapted from Balanov and Il'Insky (1992).

1000–500 m, where possible. Bathylagids, mainly *L.schmidti*, dominated the biomass of mesopelagic fish in the Sea of Okhotsk, but in the Bering Sea contributed rather less to the biomass of mesopelagic fish than did myctophids. Myctophids contributed only the third largest percentage in the Sea of Okhotsk, less than the zoareids and much less than the bathylagids. In the Bering Sea the fish community was radically different, myctophids, predominantly *S. leucopsarus*, made up the greatest portion of the biomass, bathylagids were the second largest portion and zoareid were almost absent. The estimate of 20.5×10^6 t for the combined biomass of mesopelagic fishes in the Okhotsk and Bering Seas exceeds the biomass estimate of 16×10^6 made by Gjøsaeter and Kawaguchi (1980) for the Northwest Pacific (Table 8).

Il'Insky and Gorbatenko (1994) compared the biomasses of various species of mesopelagic fish in the Sea of Okhotsk between 1987 and 1989 (Table 9). The two surveys included in this comparison took place in June–August 1987 and August 1989. Oblique trawls were made at 500–200 m depth and also at 1000–500 m depth where possible, using a commercial trawler (PT/TM 119/620) towing a net with a mouth 70 m high and 80 m wide, and 12 mm mesh size. The total biomass in 1989 was less than 1987, but the relative abundances of species were approximately the same, except for *L. schmidti*.

Table 8
Estimates of midwater fish abundances in the North Pacific Ocean (Gjøsaeter & Kawaguchi, 1980), showing the composite density (g/m^2) and biomass

Region	Species	Density	Total Biomass
Northeast Pacific Subarctic	S. leucopsarus D. theta T. crenularis	4.5 g/m^2	15 t $\times$ 10^6
Transitional	S. leucopsarus D. theta P. crockeri	3.6 g/m^2	12 t $\times$ 10^6
Northwest Pacific Subarctic	S. nannochir S. leucopsarus D. theta	6.5 g/m^2	16 t $\times$ 10^6
Kuroshio System	D. atlanticus B. suborbitale D. kuroshio G. gracile C. atraria V. nimbaria	5.2 g/m^2	21 t $\times$ 10^6

Table 9
Estimated biomass (10^6 t) of mesopelagic species in the Sea of Okhotsk

Species	1987	1989	AVG.
L. schmidti	20.02	11.81	15.92
B. ochotensis	3.01	1.58	2.30
S. nannochir	2.09	0.67	1.38
B. microcephalus	0.88	0.72	0.80
Ly. schmidti	0.49	1.97	1.23
B. milleri	0.20	0.11	0.16
B. pacificus	0.27	0.19	0.23
S. leucopsarus	0.28	0.08	0.18
L. longipes	0.14	0.01	0.08
A. ventricosus	0.02	0.06	0.04
others	0.40	0.06	0.23
Total	27.80	17.26	22.55

From Il'Insky and Gorbatenko (1994)

Il'Insky (1995) compared the biomass and percentage composition of the various species in the mesopelagic fish community in different regions of the North Pacific. Trawl details were not given, but the data source is the same at that used by Il'Insky and Gorbatenko (1994). In the Bering Sea mesopelagic fish community biomass is dominated by *S. leucopsarus*, followed by *B. pacificus*, and thirdly by walleye pollock, *T. chalcogramma*. *S. leucopsarus* also dominated the mesopelagic biomass in

the waters off of the east coast of Kamchatka, with *D. theta* and *S. nannochir* being equal second most abundant, and *T. chalcogramma* at a close fourth. However, in the southern Kuril Island region, *D. theta* dominated the biomass, *S. leucopsarus* was second, *Lampanyctus jordani* came a distant third in terms of biomass. *Bathylagus pacificus, T. chalcogramma* and *S. nannochir* were not recorded.

Estimates of the total fish biomass in the mesopelagic zone of the Sea of Okhotsk between 12 and 30 million t fluctuated during the period of the study (Il'Insky, 1995). The Sea of Okhotsk can be distinguished from neighbouring regions by the dominant species occupying the mesopelagic zone. While *L. schmidti* dominated the biomass (42–66%) in the Sea of Okhotsk, *S. leucopsarus* and *D. theta* were dominant in the adjacent Pacific regions. *Bathylagus ochotensis* contributed 7–10% of the biomass in the Sea of Okhotsk, but $< 5\%$ in the neighbouring regions.

As noted earlier, when the first mesopelagic survey of the western and central Bering Sea was conducted in 1989, Balanov and Il'Insky (1992) uprated the biomass estimate of *S. leucopsarus* to 2.22×10^6 t. In 1990, estimates based on data collected using a specialized trawl were 17.7×10^6 t, but this was considered to be an overestimate because of the better catching of the specialized trawl. The estimate was adjusted using a catchability coefficient, which gave a new estimate of 6.3×10^6 t which was more in line with the 1989 value.

In 1994, Radchenko (pers. com.) extrapolated the results to estimate the total biomass in the whole Bering Sea. Biomass of *S. leucopsarus* was estimated to be about 12.7×10^6 t in the 1980s and about 14.3×10^6 t in the 1990s. Radchenko suggested that the increase was related to a decline in predation by walleye pollock, whose numbers were lower in the 1990s.

Despite the fragmented source of data, there are some impressive consistencies in observations. The ten dominant species of mesopelagic fishes in the different regions in the North Pacific Ocean contribute 60 to 90% of mesopelagic fish biomass (Gjøsaeter & Kawaguchi, 1980; Balanov & Radchenko, 1995). The most abundant planktivorous mesopelagic fishes in the North Pacific Ocean are:

> small-finned lanternfishes (*S. leucopsarus* and *S. nannochir*)
> *D. theta*
> the Taylor's lanternfish (*T. crenularis*)
> the northern smoothtongue *(L. schmidti)* and
> the pop-eyed blacksmelt *(Bathylagus (Lipolagus) ochotensis)*

(Balanov & Il'Insky, 1992; Balanov, 1995; Frost & McCrone, 1979; Parin, 1961; Willis & Pearcy, 1982; Willis et al., 1988).

S. leucopsarus is both abundant and widely distributed throughout the Subarctic Pacific. Seldom was any other species of myctophid more abundant. The estimates of total biomass of this one myctophid species are huge relative to the commercial catches of species such as walleye pollock, and to the average total annual marine fish landings globally from all of the oceans from 1990 to 1995, approximately 75×10^6 t. Only in the Sea of Okhotsk was *S. leucopsarus* substantially less abundant than other midwater species. However, in the Sea of Okhotsk, the bathylagical *L. schmidti* is exceptionally abundant, with a biomass about 5 times the estimated

biomass of walleye pollock in the summers of 1987 and 1989 (Il'Insky & Gorbatenko, 1994). Species such as *D. theta, T. crenularis, P. thompsoni*, and *S. nannochir* are commonly found throughout the Subarctic Pacific and are also abundant.

It is clear that the midwater community contains a small number of species that are extremely abundant compared to abundances of some familiar commercial species such as salmon and walleye pollock. The biomass estimates are approximate, but they are huge. The species are small and relatively short lived, indicating that there must be frequent and continued replacement of adults. The mesopelagic community may be analogous to the familiar small pelagic species found in coastal waters which we know are vital components of the food chains that support important commercial species. The particular life histories of the midwater fishes that undergo daily vertical migrations into the surface mixing layer at night, indicate that the Subarctic Pacific ecosystems are complex and that the trophodynamics will be different between day and night. Thus studies of these ecosystems must cover the full 24 hour period. It also means that sampling equipment must perform similarly by day and by night. The difficulties of understanding how these species interact and affect the trophodynamics of other species in the ecosystem, investigators need to be cautious when studying the dynamics of a single species such as Pacific salmon. For example, attempts to link changes in plankton abundance with variations in the abundance of a particular salmon species may not be assessing a direct relationship. In addition to the intrinsic scientific interest in learning more about the dynamics of these high seas fish communities, it seems inevitable that some day these species will become valuable commercially. Their biomasses are so large compared to the stocks of present commercial species that any discovery of commercial importance, such as a particular oil, combined with an appropriate technology for harvesting them will result in the development of experimental fisheries. In recognizing this possibility, international cooperative programs must be established to learn more about their population dynamics and their relationships with other fishes such as salmon, and marine mammals and birds, so that the baseline for their sustainable exploitation can be created.

4. Stenobrachius leucopsarus

The dominant species in the midwater community of the Subarctic Pacific gyres and associated areas is unquestionably, *S. leucopsarus*. There are several common names for this species, but here we use 'northern lanternfish', the common name given to this species by the American Fisheries Society (1991) and Hart (1973). The common name 'smallfin lanternfish' was used by Clemens and Wilby (1961) and Musienko (1970).

4.1. Distribution and abundance

The northern lanternfish is endemic to the boreal waters of the Pacific Ocean (Kulikova, 1960; Parin, 1961, 1983). Although it has not been extensively studied,

it is the most thoroughly investigated mesopelagic fish species of the northern Pacific (Bolin, 1956; Pearcy, Lorz & Peterson, 1979; Willis & Pearcy, 1980, 1982; Karatay-eva, Pavlov & Stygar, 1986; Willis et al., 1988). It occurs from the Pacific coast of Japan (38°N) to southern California (30°N), including deep water of the Sea of Okhotsk, Bering Sea, and Gulf of Alaska, and Pacific waters off the Kuril Islands and Kamchatka, British Columbia, Washington, Oregon and California (Kulikova, 1960; Clemens & Wilby, 1961; Parin, 1979; Novikov, 1971; Becker, 1983; Eschme-yer, Herald & Hammann, 1983; Masuda, Amaoka, Araga, Uyeno & Yoshino, 1984). In the Bering Sea its distribution is limited to the deep water; in the north to 62°N (Becker, 1967; Balanov, 1995; Nagasawa, Nishimura, Asanuma & Marubayashi, 1997) and in the south to 44–47°N (Becker, 1983). Its frequency of occurrence in catches and its abundance increases in the northwestern Pacific from south to north (Table 10). The northern lanternfish has its greatest abundance in the Bering Sea,

Table 10
Frequency of occurrence (%) and biomass (thousand t) of northern lanternfish in northwestern Pacific, presented as a range of values, with the average value shown in brackets; the total does not include the epipelagic zone of the Pacific waters off Kamchatka and lower mesopelagic zone of the Pacific waters off the Kuril Islands

Depth, m	Years	Frequency of occurrence % Range and (average)	Biomass, thousand t. Range and (average)	Source
Western Bering Sea				
0–200	1986–90	3.8–31.2 (16.5)	360.0–400.0 (380.0)	Radchenko, 1994
200–500	1989–90	100	5338.3–6863.0 (6326.0)	Balanov, 1995; Balanov & Radchenko, 1995
500–1000	1989–90	100	917.6–7091.8 (3028.4)	Balanov, 1995; Balanov & Radchenko, 1995
Pacific waters off Kamchatka				
200–500	1991–92	95.7–96.4 (96.1)	369.4–707.5 (538.5)	Ivanov, 1997a
Pacific waters off Kuril Islands				
0–200	1986–95	0–42.7 (24.2)	0–289.5 (135.3)	Ivanov, 1997b
200–500	1991–92	84.6–100 (96.2)	204.0–1871.1 (809.7)	Ivanov, 1997a
South part of the Sea of Ohkotsk				
0–200	1981–94	0–30.5 (6.6)	0.3–7.0 (3.7)	Lapko, 1996
200–500	1990–91	51.0–68.4 (59.7)	?	Balanov & Radchenko, 1995
500–1000	1990–91	84.6–95.5 (90.9)	?	Balanov & Radchenko, 1995
500–1000	1990	82.6	24.5	Balanov & Orlov pers. com.
200–1000	1987–89	?	80.0–280.0 (180.0)	Il'Insky & Gorbatenko, 1994
Total in the northwestern Pacific Ocean			**13059.1**	

where it dominates the biomass and abundance not only of fishes, but also all other nektonic species (Balanov & Il'Insky, 1992; Balanov, 1995).

Willis et al. (1988) reviewed the literature and catch data from a variety of sources available from 1951 to 1981. Their results were compiled from data from 761 oblique tows using midwater trawls (IKMTs) with 1.8, 2.4, and 3.0 m horizontal openings from the surface down to 4000 m. IKMTs are unsuitable for quantitatively estimating myctophid abundance but they do indicate the geographical range of the species. *S. leucopsarus* was described as being one of the species found throughout, and unique to, the Subarctic Pacific and the Bering Sea, as well as being the most common and best studied of Subarctic mesopelagic species. Other common fishes of the midwater zone of these waters are *S. nannochir, B. ochotensis, B. pacificus, B. milleri, C. macouni, Cyclothone atraria, C. pallida,* and *L. schmidti. S. leucopsarus* is found in abundance north of 45°N, but decreases in abundance and frequency of occurrence to the south in the eastern Subarctic, particularly in shallow water. *S. leucopsarus* is numerically dominant in all regions except for the western transition zone, where it is replaced by *D. theta*. This results both from an increase in the abundance of *D. theta* and *C. atraria*, as well as a decrease in the abundance of *S. leucopsarus*. *S. leucopsarus* was also the most abundant species in all shallow tows (< 500m), except in the western transition zone, but dominated the deep tows in only one region, the Bering Sea. Even in the deep tows though, *S. leucopsarus* still ranked in the top 4 most abundant species.

S. leucopsarus appears to be less abundant in the western than in the eastern part of the Pacific (Parin & Fedorov, 1981; Willis et al., 1988). The eastern biomass estimate is based on larval samples in coastal waters off California, in the CalCOFI area (Gulland, 1971). Otherwise the relative abundance of mesopelagic fishes is greater in western Subarctic Pacific than in the eastern part (Gjøsaeter & Kawaguchi, 1980). In the late 1950s, the biomass of *S. leucopsarus* in the eastern sector was estimated to be about 300 thousand metric t and 34.9% of total estimated biomass of myctophids. In Pacific waters off the Kuril Islands (Table 10), an area comparable in size to the CalCOFI area, the overall biomass of northern lanternfish is three times greater than in waters off California. Thus the assumptions by Parin & Fedorov (1981) and Willis et al. (1988) of larger northern lanternfish biomass in the eastern Pacific Ocean may not be correct.

4.2. Vertical migration

The northern lanternfish occurs in the upper layers of the ocean from the surface to depths possibly in excess of 2000 m (Grinols, 1965; Makushok, 1970; Matarese, Kendall, Blood & Vinter, 1989). It is one of the major elements of sound scattering layers (Barham, 1957; Pearcy & Mesecar, 1971; Taylor, 1968; Lapko & Ivanov, 1993) (see page 61). Many authors have described their vertical diel migrations (Pearcy & Laurs, 1966; Pearcy, Krygier, Mesecar & Ramsey, 1977; Frost & McCrone, 1979; Pearcy et al., 1979; Childress, Taylor, Cailliet & Price, 1980; Willis & Pearcy, 1980, 1982; Parin & Fedorov, 1981; Becker, 1983; Cailliet & Ebeling, 1990; Radchenko, 1991; Balanov & Radchenko, 1995; Lapko, 1995, 1996).

Pearcy (1964) and Paxton (1967) found concentrations of northern lanternfish in Oregonian and Californian waters moved between depths of 20–30 m at night, and 600–700 m in day time. In the Bering Sea the densest concentrations occur at 220–500 m in the open sea, and 300–500 m over the continental slope (Balanov & Radchenko, 1995). The diurnal range of their vertical migrations was 70–100 m. According to Gorbatenko and Il'Insky (1991) only 11% of individuals making diurnal migrations up to the surface were *S. leucopsarus*. Vertical migrations also are related to age. According to Willis and Pearcy (1980, 1982) fishes of length 15–20 mm (age 0) are the most abundant in depth range 400–480 m during the day time and are non-migrants. Those of length 30 to 40 mm (age 1) usually occur at depths of about 300 m by day and migrate up into the upper 30 m layer at night. Specimens with lengths of 50–60 mm (age 2–3) stayed subthermocline at night at 75–90 m, (i.e. beneath the age 1 group). The eldest fishes 70–80 mm (age 3 +) inhabited the same depths as the age group 0 fish, 400–800 m during the daytime and usually did not migrate above 200 m at night.

Frost and McCrone (1979) investigated the vertical distribution, diel vertical migration and abundance of some of the meospelagic fishes in the eastern Subarctic Pacific ocean, or more specifically, the Alaskan gyre. Their data were collected during three summertime cruises to Station P (950°N; 145°W) from July to August of 1973 and July to August of 1975, and to Station Q (51°N; 137°W) in July 1974. Night and day series of stratified samples were taken with a multiple net (Tucker trawl) at depths of 385 and 460 to 0 m. Just four myctophid species comprised 87% of the total fish catch; two of which, *S. leucopsarus* and *D. theta*, undertake diel vertical migrations. The other two species, *P. thompsoni* and *S. nannochir*, showed only slight vertical shifts in their distributions between day and night. Each of the species tended to be stratified vertically according to age (or size), with larger individuals taken progressively deeper. Two micronektonic crustaceans, *Euphausia pacifica* and *Sergestes similis*, were also undergoing diel vertical migrations. Hauls taken just after sunset showed an association between *S. leucopsarus, D. theta*, and *E. pacifica*, and the upward shift of a single coherent sound-scattering layer (12 kHz). The migrations of *S. similis* lagged behind that of *S. leucopsarus*. During both day and night, the distribution of *P. thompsoni* corresponded to a single deep non-migratory sound-scattering layer. Myctophid standing stock and abundance were high at 0.37 g dry wt/m^2 and 0.9 fish/m^2, respectively.

The maximum concentrations of the myctophids in single hauls in the deep sound scattering layer during the day and at the surface (0 to 55 m) at night was often > 100 fish/1000 m^3. The maximum concentration at the surface at night was 365 fish/1000 m^3, and by day 874 fish/1000 m^3 at a depth of 327–333 m. Frost and McCrone (1979) suggest that their data demonstrate that myctophids are more abundant by up to an order of magnitude in the open Subarctic Pacific than off the coast of Oregon (Pearcy et al., 1977). However, we note that it is difficult to compare data collected using different gear. The concentration of myctophids described by Pearcy and Laurs (1966) was also much higher than that described by Pearcy et al. (1977). Frost and McCrone (1979) suggest that these differences may be due to year to year variability rather than discrepancies in sampling.

Table 11
Age of northern lanternfish in various regions of the North Pacific Ocean

Age groups and total length, mm						Source
1	2	3	4	5	6	
32	50	68	78			Bolin, 1956
–	49.6	61.8	76.7	86.2	89.2	Kulikova, 1957[a]
30.3	48.1	62.8	77.2	84.7	–	Kulikova, 1957[b]
32	50	66	72	76	–	Fast, 1960
23	41	59	–	–	–	Smocker and Pearcy, 1970

[a]Observed data, [b]Fitted data.

4.3. Age and growth

The age of northern lanternfish has been determined using otoliths (Kulikova, 1957; Smocker & Pearcy, 1970; Childress et al., 1980) and length-frequency analysis (Bolin, 1956; Fast, 1960; Smocker & Pearcy, 1970). The results of both methods are comparable (Table 11). According to Smocker and Pearcy (1970), the asymptotic length (L) is 85 mm, whereas Childress et al. (1980) observed it to be 98.1 mm and Kulikova (1957) estimated it to be 111 mm. Fishes with a length about 120 mm are thought to be of an age of about 10–12 years (Balanov, 1995), but such ages have not been validated. The size composition of this species is similar throughout the various regions of the North Pacific Ocean (Fig. 2).

The prevalence of large-sized fishes and lack of juveniles under 30 mm is characteristic of feeding areas (southern Sea of Okhotsk and Bering Sea). Males appear to be slightly longer than females. Thus, in the Bering Sea the average length of males was 90.2 mm and of females was 88.5 mm. In the Sea of Okhotsk males averaged 88.1 mm and females 85.5 mm. Maximum known length of northern lanternfish from the Bering Sea is 125–130 mm (Gorbatenko & Il'Insky, 1991; Balanov, 1995). Body weights of northern lanternfish from the Bering Sea (79.8% weighing 7–11 g) and Sea of Okhotsk (65.7% weighing 6–12 g) varies from 2 to 32 g.

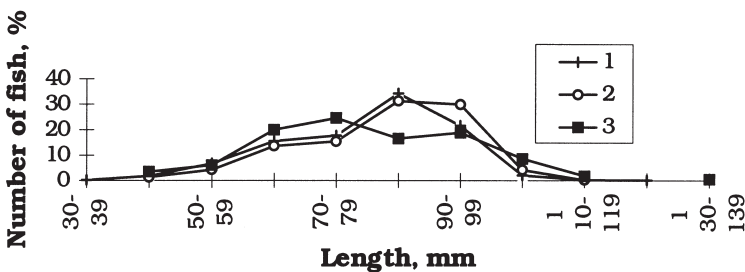Fast (1960) considered *S. leucopsarus* larvae to be identifiable at about 3 mm

Fig. 2.   Size composition of the northern lanternfish in autumn–winter of 1990 (1, western Bering Sea, 200–500 m; 2, western Bering Sea, 500–1000 m; 3, Sea of Okhotsk, 500–1000 m)

standard length (SL). The slender, elongated larvae expanded to a more fusiform shape at 10 mm, and metamorphosis was initiated at 10 mm. Scale formation was not completed until after metamorphosis, but some scales were laid down around the photophores of the larvae prior to metamorphosis. Larvae are reported to concentrate at 30 to 40 m depth, but occurred down to 100 m (Ahlstrom, 1959; Fast, 1960). Metamorphosis occurs at about 18 mm SL (Fast, 1960; Ahlstrom, 1959; Pertseva-Ostroumova, 1964; Smocker & Pearcy, 1970). Fast (1960) described a two-way ontogeotic vertical migration of *S. leucopsarus* which started when metamorphosing larvae of approximately 10 mm SL rapidly migrate into deeper water and then as juveniles slowly return to shallower waters (200–300 m). The migration carried larvae to depths of 500 to 500 m where older individuals of this species were less abundant. The complex nature of ontogenic vertical migrations of bathypelagic fishes was discussed by Taaning (1918, in Fast, 1960), Bertelsen (1951, in Fast, 1960), and Ahlstrom (1959). This early development of larvae is timed, apparently, to avoid areas occupied by potential predators.

Bolin (1956) carried out length-frequency examinations on hundreds of specimens to determine growth of *S. leucopsarus* in Monterey Bay, California. He showed that along the central coast of California, the average size of *S. leucopsarus* after the first year was 32 mm, after the second year it was 50 mm, and after the third year it was 68 mm. The largest specimen he collected was 78 mm SL. Bolin (1956) believed that the lack of a fourth year class indicated that the maximum age of this species in these waters was four years.

By following one year class from 1951 to 1955, Fast (1960) determined the maximum life expectancy to be 5 years. Upon determining that only 1% of the catch consisted of fish older than three years, Fast (1960) proposed a 'cataclysmic' decrease in the population of *S. leucopsarus* after the third year.

4.4. Reproduction

The reproduction of the northern lanternfish remains an inadequately investigated aspect of its life history. There are no observations of northern lanternfish spawning in the western part of their distribution. Balanov (1995) caught females with mature gonads in Pacific waters off the Kuril Islands. It is probable that northern lanternfish spawn in the Pacific waters over a wide zone stretching from off northern Japan and Kuril Islands to California, and are limited by the Subarctic front to the south and by Pacific waters of Aleutian current to the north (Balanov, 1995).

Fast (1960) described the difficulties in differentiating the sexes of individuals less than 50 mm SL, and noted that no distinguishing external characteristics were evident in the juveniles. Therefore, neither sex ratios nor growth rates can be differentiated between the sexes. Grey (1955) observed embryonated eggs and spermatozoa in the genital tracts of a female of a related species, *Lampanyctus cuprarius*, that indicates that this species may have internal fertilization; but the existence of internal fertilization has not been confirmed for *S. leucopsarus*. Fast (1960) described females greater than 50 mm SL as containing maturing ova (> 0.45 mm in diameter).

Smocker and Pearcy (1970) considered ova to be mature at 0.60 mm, and found these generally in females greater than 65 mm SL.

Off Oregon this species matures at 65 mm after 4 years (Smocker & Pearcy, 1970), and after 3 years off California (Fast, 1960). Analysis of the oocyte size, gonad condition, and peaks in abundance of larvae and juveniles showed that off Oregon gonad maturation begins in October, and the spawning occurs between December and March (Smocker & Pearcy, 1970). Off California, spawning occurs over a more extended period from November to August according to Fast (1960), but Wang (1981) reported a much shorter spawning season from December to February.

Fast (1960) assumed that each individual spawns only once per season but that the season might last for nine months, since larvae smaller than 6 mm SL were found in Monterey Bay, California from November through August. The author also concluded that individuals only spawned once in their lifetime and related this to a substantial decrease in the population size at the end of the third year. Smocker and Pearcy (1970), who found gravid females in the oceanic waters off Oregon from December through March, postulated a shorter spawning season than Fast (1960). Paxton (1967) described a shorter spawing season in the winter in San Pedro Bay of southern California, ascribing its brevity to the higher summer temperatures. Since no eggs of *S. leucopsarus* have been distinguished in plankton tows the precise determination of the spawning season remains speculative (Trumble, 1973).

4.5. Trophic relationships—general

Brodeur (1988) reviewed the literature on the trophic interactions of the dominant epipelagic fishes and produced a generalized food web for the Subarctic Pacific and the transition zone to the south. We have adapted his approach and have proposed a food web for *S. leucopsarus* (Fig. 3). The importance of this species as a prey item for other species is unknown, but it seems likely that this abundant fish is important in the population dynamics of other species.

About 30–40 prey species have been found in stomachs of the dominant mesopelagic fishes in the North Pacific Ocean. Copepods showed the highest species diversity among food organisms (Paxton, 1968; Pearcy et al., 1977; Gordon, Nishida & Nemoto, 1985; Balanov, Gorbatenko & Gorelova, 1994; Balanov, Gorbatenko & Efimkin, 1994). Little selectivity was noted in the diet of most species. In the family Myctophidae, feeding habits of *S. leucopsarus* have been extensively studied and in all areas, it mainly consumes copepods, amphipods, and euphausiids (Table 12). In the Bering Sea, its most important prey species are *Thysanoessa longipes, Neocalanus cristatus, Eucalanus bungii,* and *Pareuchaeta japonica* (Balanov, 1994; Balanov et al., 1994; Balanov, 1995). In Pacific waters off North America, prey include *Euphausia pacifica, Neocalanus* spp*., C. plumchrus, Metridia lucens, Parathemisto pacifica,* and *Hyperia galba* (Tyler & Pearcy, 1975; Pearcy et al., 1979; Cailliet & Ebeling, 1990), whereas off Japan the most abundant prey are *T. longipes, Gaidius variabilis, Metridia pacifica,* and *Pleurogramma* spp. (Gordon et al., 1985).

The stomach contents of *S. leucopsarus* collected from San Pedro Basin, California, in most cases, contained only one species of prey, although the type of prey
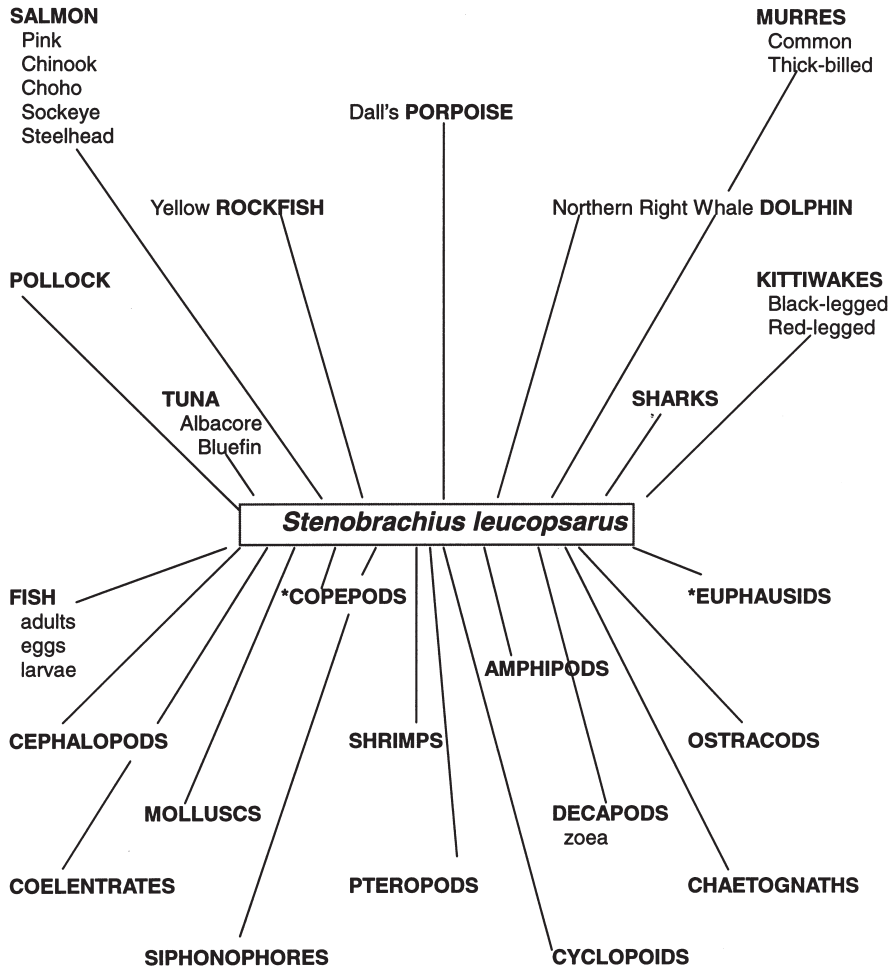
SALMON
Pink
Chinook
Choho
Sockeye
Steelhead

MURRES
Common
Thick-billed

Dall's **PORPOISE**

Yellow **ROCKFISH**

Northern Right Whale **DOLPHIN**

POLLOCK

KITTIWAKES
Black-legged
Red-legged

TUNA
Albacore
Bluefin

SHARKS

Stenobrachius leucopsarus

FISH
adults
eggs
larvae

***COPEPODS**

***EUPHAUSIDS**

AMPHIPODS

CEPHALOPODS

SHRIMPS

OSTRACODS

MOLLUSCS

DECAPODS
zoea

COELENTRATES

PTEROPODS

CHAETOGNATHS

SIPHONOPHORES

CYCLOPOIDS

Fig. 3. Food web of the Northern lanternfish *S. leucopsarus* in the Subarctic North Pacific Ocean. * Primary food item recorded in analyses of stomach contents.

varied among stomachs (Paxton, 1967). The selective feeding of small fish was exclusively on crustaceans, while fish > 60 mm also preyed on other fish as well. Individuals appeared to eat large quantities of a single species at a time; one stomach was found to contain 19 undigested euphausids, which may indicate the fish were feeding in the net. Stomachs were found to contain food both at night and day so feeding may continue throughout the day (Paxton, 1967). However, if individuals consume large amounts of food all at once, feeding is likely to be infrequent as the fish do not grow to large sizes.

Collard (1970) studied stomach contents of eastern Pacific midwater fishes collected in trawls. He analysed the contents of 1087 specimens belonging to 42 species. A variety of crustaceans, primarily copepods and euphausiids, comprised 95% of the

Table 12
Percent composition of major prey items for northern lanternfish, *S. leucopsarus*, in different areas of the
North Pacific by weight (1,2,4) and frequency of occurrence (3)

Prey Name	California[1]	Hokkaido[2]	Kuril Islands[3]	Bering Sea[4]
Euphausiacea	33.6	17.5	36.5	35.4
Copepoda	32.2	73.9	38.1	49.2
Amphipoda	–	4.3	7.9	4.9
Ostracoda	13.4	4.3	3.5	1.9
Crustacean debris	12.2	–	–	–
Chaetognatha	–	–	1.8	0.7
Coelenterata	–	–	0.4	3.2
Ctenophora	–	–	11.6	0.3
Miscellaneous Prey	7.4	–	0.2	3.4

Stomach content data are given according to: 1—Cailliet and Ebeling, 1990; 2—Gordon et al., 1985; 3—
Ivanov, 1997a (only epipelagic zone); 4—Balanov et al., 1994; Balanov et al., 1994.

diet of all specimens with identifiable stomach contents. The stomach contents were
identifiable in 42% of the stomachs of 486 specimens of *S. leucopsarus* sampled.
Analysis showed that these fish were predominantly feeding on copepods alone
(34%), euphausids alone (30%), or a mix of copepods and euphausids together (4%).
Seasonal differences were observed in the diet, and may have resulted either from
seasonal variations in zooplankton abundance and availablility, or from seasonal dif-
ferences in foraging activity. The frequency of Crustacea in the diet varied intersea-
sonally: copepods eaten ranged from 55% in spring to 6% in summer; euphausids
from 24% in spring to 61% in summer. In the fall and winter a greater variety of
food items were taken. There were size related or ontogenic changes in diet as a
larger variety of prey organisms occurred in the diets of larger fish. It appears that
S. leucopsarus is not a specific feeder, but rather it takes whatever prey is available
at any time or in any place. In his investigation of the diel vertical migration and
feeding behaviour of some mesopelagic fishes collected on summer cruises in 1973,
1974, and 1975. McCrone (1981) also described the trophic relationships of mesopel-
agic fishes in the eastern Subarctic Pacific ocean as being remarkably simple. He
found *S. leucopsarus* was feeding primarily on crustaceans, with little change in diet
throughout the year and without a distinct feeding chronology (Cailliet & Ebeling,
1990). When euphausids were abundant they dominated the diet, as was also
observed by Collard (1970).

Cailliet and Ebeling (1990) investigated the feeding habits of *S. leucopsarus* off
southern California, in the Santa Barbara and Santa Cruz basins, and compared them
with those of another common, but non-vertically migrating, midwater fish. They
proposed that *S. leucopsarus* is adapted to feeding by grasping and to eating larger,
faster and more elusive prey than is the suction feeder *L. stilbius*. Furthermore, *S.
leucopsarus* is better adapted to eat the more varied food resources offshore, and its
vertical migrations allow it to exploit the food-rich epipelagic waters at night.
According to Cailliet and Ebeling (1990), the alimentary morphology of this species
indicates that it feeds sporadically on small quantities of larger prey.

5. Trophic relationships of midwater fishes

Myctophids in general have been reported to eat copepods, euphausids, ostracods, mollusks, fish eggs and larvae, chaetognaths, larval and adult decapod shrimp, insects, siphonophores, tunicates, annelids, sipunculid and nemertine larvae, pycno-gonids, and foraminifera (Cailliet & Ebeling, 1990). Thus it would appear that in general myctophids and *S. leucopsarus* in particular are trophic generalists but exhibit a preference for crustaceans.

The feeding habits of another of the common myctophid species, *Diaphus theta*, has received less attention. In the Pacific waters off Kamchatka, North America, and Japan, the diet of this species consisted predominantly of euphausiids, copepods, and amphipods; the most abundant prey species *were E. pacifica, M. lucens, Metridia okhotensis*, and *Parathemisto pacifica* (Tyler & Pearcy, 1975; Gordon et al., 1985; Sobolevsy & Senchenko, 1996). In the stomachs of *T. crenularis* taken in the same areas, predominantly contained *E. pacifica, M. lucens, N. plumchrus, N. cristatus* and *Candacia columbiae* (Tyler & Pearcy, 1975; Kawamura & Fujii, 1988).

The stomach contents of *S. nannochir* (Table 13), commonly contained calanoid copepods in all regions. The most frequent copepod species *were N. cristatus, P. japonica, G. variabilis,* and *P. pacifica* (Gordon et al., 1985; Balanov et al., 1994; Balanov, 1995). Only in the mesopelagic zone of the Sea of Okhotsk does this mycto-phid also consume euphausiids, amphipods, and small decapods in considerable amounts (up to 10–20% of the total ration) (Il'Insky & Gorbatenko, 1994).

In the family *Bathylagidae (Microstomatidae)*, the most abundant species in the North Pacific are *L. schmidtii* and *B. ochotensis*. These species are ubiquitous in the North Pacific, and they dominated the biomass of mesopelagic fishes in of the Sea of Okhotsk (Balanov & Il'Insky, 1992; Il'Insky & Gorbatenko, 1994).

Jelly-fish, ctenophores, and larvaceans occur in the diets of both *L. schmidti* and *B. ochotensis* in the Bering Sea and the Pacific waters of Japan. The diet of *L. schmidti* consisted primarily of euphausiids and copepods (Gorbatenko & Il'Insky, 1991; Balanov, 1994; Balanov et al., 1994; Balanov et al., 1994). Similarly, in the Sea of Okhotsk, *L. schmidti* was consuming mostly euphausiids and amphipods (to 45% of the ration), and jelly-fish are abundant in stomachs of *B.ochotensis*, (Il'Insky & Gorbatenko, 1994).

Myctophids generally have large mouths, relatively few serrated gill rakers, well developed stomachs, and short intestines. This implies they are adapted to consume actively-moving prey such as copepods and euphausiids. Deepsea smelts, in contrast, have small mouths, dense, flat gill rakers, small stomachs, and long digestive tracts. These fishes are generally adapted to consume slow-moving gelatinous species such as jelly-fish, larvaceans, ctenophores and pteropods, etc. (Gorelova & Kobylyanskiy, 1985; Cailliet & Ebeling, 1990; Balanov et al., 1994; Balanov et al., 1994).

L. schmidti feeds actively at night in the epipelagic zone. In the epipelagic area of the Bering Sea and the Sea of Okhotsk the concentrations of euphausiids and amphipods are sufficiently large for *L. schmidti* to consume large numbers in both areas (Balanov et al., 1994; Balanov et al., 1994; Il'Insky & Gorbatenko, 1994).

Small prey items (less than 3.0 mm), in the stomachs of fishes in the mesopelagic

Table 13
Diet composition and percent by weight for the most abundant mesopelagic fishes in the Bering Sea (0–500m). For each species the percentage of major taxa (bold) and minor taxa are shown

Food item	Fish species			
	S. leucopsarus	*S. nannochir*	*L. schmidti*	*B. ochotensis*
EUPHAUSIACEA	**35.4**	**0.5**	**18.2**	**1.7**
Thysanoessa longipes	34.3	0.5	13.1	1.7
Other euphasiacea	1.1	–	5.1	–
COPEPODA	**49.2**	**83.5**	**15.7**	**8.1**
Neocalanus cristatus	17.1	50.1	7.4	3.1
N. plumchrus	2.9	4.5	0.3	0.5
Eucalanus bungii	7.6	3.0	15.1	–
Gaetanus intermedius	6.1	4.1	0.9	2.4
Pareuchaeta japonica	11.5	3.3	0.4	0.4
Candacia columbiae	1.5	3.2	0.1	–
Metridia pacifica	1.9	12.6	1.0	1.4
Other copepoda	0.6	2.7	0.5	0.3
AMPHIPODA	**4.9**	**0.4**	**7.5**	**1.5**
Parathemisto pacifica	3.8	0.1	5.4	1.4
Other amphipoda	1.1	0.3	2.1	0.1
CHAETOGNATHA	**0.7**	**1.3**	**1.8**	**0.3**
Parasagitta elegans	0.7	1.3	1.8	0.3
PTEROPODA	–	–	**2.7**	**0.1**
Limacina helicina	–	–	1.7	–
Clione limacina	–	–	1.0	0.1
OSTRACODA	**1.2**	**0.6**	**1.1**	**0.3**
APPENDICULARIA	+	**0.6**	**8.3**	**37.6**
Oikopleura labradoriensis	+	0.6	8.3	37.6
COELENTERATA	**3.2**	**8.9**	**24.4**	**35.2**
CTENOPHORA	**0.3**	–	**5.2**	**6.2**
POLYCHAETA	**0.6**	–	**0.9**	**0.7**
DECAPODA	**4.2**	**1.7**	**1.9**	**0.7**
HETEROPODA	–	–	**1.9**	+
GASTROPODA	–	–	**0.1**	**3.6**
CEPHALOPODA	**0.3**	–	**0.1**	**2.4**
NUDIBRANCHIA	–	–	**0.2**	**1.6**

zone include *Oikopleura labradoriensis, Gaetanus intermedius, Metridia pacifica, Conchoecia* sp. Mid-sized prey (3.0–11.0 mm) include *N. cristatus, P. japonica, Clione limacina*. The largest (18–30 mm) organisms consumed are polychaetes and euphusiids (Table 14).

Most of the common mesopelagic fishes of the Bering Sea exhibit well-defined feeding rhythms related to the vertical migrations of both the fish and their zooplankton prey. Species tend to show two peaks of stomach fullness: one at night between 2200 and 0400 hrs and the other during the day between 1000 and 1600 hrs. In the layers at 0–200 and 200–500 m, high stomach fullness, maximal content of fresh food, and minimal proportion of empty stomachs were found during these feeding times (Balanov, 1994; Balanov et al., 1994; Balanov et al., 1994). The predominance

Table 14
Frequency of occurrence (%) of the different sized prey in stomachs of abundant mesopelagic fishes in the Western part of the Bering Sea

Fish species and layer studied	n*	Size class, mm			
		< 3.0	3.1–10.0	10.1–20.0	> 20.0
0–200 m					
S. leucopsarus	50	36.0	46.0	10.0	8.0
L. schmidtii	35	17.1	40.0	25.8	17.1
200–500 m					
S. leucopsarus	84	28.6	58.3	7.1	6.0
S. nannochir	41	29.3	65.9	4.8	–
L. schmidti	75	29.3	34.7	24.0	12.0
B. ochotensis	40	55.0	37.5	–	7.5
500–1000 m					
S. leucopsarus	71	14.1	70.4	12.7	2.8
S. nannochir	23	–	78.3	13.1	8.7
L. schmidti	9	38.4	61.6	–	–
B. ochotensis	19	42.1	42.1	15.8	–

n*—total number of fish

of freshly ingested prey, the low proportion of digested food and pronounced feeding periodicity indicates that both the epipelagic (0–200 m) and the upper mesopelagic (200–500) zones provide trophic resources for the common midwater fishes of the North Pacific Ocean (Balanov et al., 1994; Balanov et al., 1994). Some species of mesopelagic fishes feed predominantly in the deeper mesopelagic zone (500–1000 m). In this layer, fish stomachs contained zooplankton species which were not found in the diets of fish from the epipelagic and the upper mesopelagic zones.

There is a general pattern of seasonal change in the predominant prey species taken by all mesopelagic fishes of the North Pacific. Copepods predominated in fish stomachs in winter, late spring, and summer, whereas euphausiids become dominant in late summer and autumn (Adams, 1979; Pearcy et al., 1979; Gordon et al., 1985; Balanov, 1994, 1995; Balanov et al., 1994; Balanov et al., 1994; Sobolevsy & Senchenko, 1996). In the Bering Sea, in spring and summer copepods (primarily *N. cristatus*) dominate the diets of myctophids both in the epipelagic (0–200 m) and the upper mesopelagic (200–500 m) zones. In autumn and winter, *N. cristatus*, which undertakes a seasonal migration to overwinter in deep water, is predominantly found in the stomachs of fish from the upper and lower (500–1000 m) mesopelagic zones (Balanov et al., 1994; Balanov et al., 1994; Sobolevsky, Sokolovskaya, Balanov & Senchenko, 1996).

The diets of mesopelagic fish collected from different layers and in different seasons match the vertical distribution patterns and seasonal migrations of the dominant copepods and euphausiids in the North Pacific Ocean. It is known that in late summer and autumn *N. cristatus* and *E. bungii* migrate from the surface layers where they

dominate in spring and summer to the mesopelagic zone. *P. japonica, M. pacifica*, and *G. intermedius* belong to a group of interzonal plankters and are the most common in the mesopelagic layer (Vinogradov, 1954; Brodskiy, 1957; Vinogradov & Arashkevich, 1969; Vinogradov, 1968; Marlow & Miller, 1975; Sekigushi, 1975; Markaseva & Razzhivin, 1982). Euphausid biomass is high during the autumn when they form dense aggregations in the epipelagic zone which coincides with when they become dominant in the diets of the mesopelagic fishes (Ponomareva, 1990). Amphipods also from large concentrations in surface waters at this time (Vinogradov, 1968) and also feature as important prey items of mesopelagic fishes feeding in the epipelagic zone (Tyler & Pearcy, 1975; Adams, 1979; Pearcy et al., 1979; Balanov et al., 1994; Sobolevsky et al., 1996).

Mesopelagic fishes transfer and redistribute energy and organic matter as a consequence of their migratory and feeding behaviour within the epipelagic and mesopelagic zones of the Bering Sea, and perhaps throughout the entire Subarctic North Pacific. There are two major trophic pathways along which this energy shift may take place. A first passes from the most abundant zooplankton species (*N. cristatus, T. longipes, E. pacifica*) to *S. leucopsarus*, and thence to squid, *C. macouni* and other mesopelagic zone predators. This pathway has a generalized 'downward' direction and conforms to the concept of the transfer of energy and matter from the enriched surface waters to oligotrophic deep pelagic waters of the world oceans (Vinogradov, 1968; Parin, 1968; Willis & Pearcy, 1982). A second pathway passes from *S. leucopsarus, D. theta, L. schmidti* to walleye pollock, salmons, dophins and whale in a general 'upward' direction, allowing epipelagic animals to use indirectly the rich resources of the mesopelagic zone. The same is true for tropical and subtropical areas, where some epipelagic tuna, sword-fish and sharks feed mainly in the lower epipelagic and upper mesopelagic zones on the permanent residents, squids and barracudinas, which in their turn eat migrating midwater fishes (Parin, 1968, 1988).

The northern lanternfish is a food item not only for various epi- and mesopelagic predators, but also for many bottom fishes in the outer shelf, meso- and bathybenthal. It has been found in stomachs of cetaceans (Fitch & Brownell, 1969), albacore, *Thunnus alalunga* and bluefin tuna, *Thunnus thynnus* (Pinkas, Oliphant & Iverson, 1971), salmon (Shimada, 1948; Clemens & Wilby, 1961; Brodeur, Lorz & Pearcy, 1987; Lapko, 1994; Nagasawa, Nishimura, Asanuma & Marubayashi, 1996), and walleye pollock, *T. chalcogramma* (Lapko, 1994). Sometimes they are a major component in the diet. For example, off Oregon and Washington, they comprise up to 15.2% of stomach contents of chinook salmon, *Oncorynchus tschawytscha* (Brodeur et al., 1987). The daily consumption of northern lampfish by walleye pollock and salmon in the Sea of Okhotsk during the summer period in the second half of the 1980s was estimated at 1.51 thousand metric t (Lapko, 1994). In the mesopelagial the northern lanternfish is consumed by walleye pollock, Pacific viperfish *Chauliodus macouni*, wearyfish *Scopelosaurus adleri*, pacific dreamer *Oneirodes bulbosus*, and Thompson dreamer *O. thompsoni*, northern pearleye, *Benthalbella dentata*, red squid *Berryteuthis magister* (Borodulina, 1972; Il'Insky & Gorbatenko, 1994; Balanov, 1994; Balanov, Pitruk & Orlov, 1994; Balanov, 1995). In the mesopelagic zone of the Sea of Okhotsk, northern lanternfish make up 0.9% of walleye

pollock's daily ration (Il'Insky & Gorbatenko, 1994) and in the mesopelagic of the Bering Sea, it constitutes 43.6% of the stomach contents of Pacific viperfish, 28.2% of wearyfish, 5.2% of walleye pollock 14.4% of red squid, and 70.0% of Pacific dreamers (Balanov, 1994, 1995). The amount consumed annually by predatory nekton is estimated to be about 2270 thousand metric t: 15.2% by pacific viperfish, 4.9% by wearyfish, 22.6% by walleye pollock, 33.3% by red squid, 14.1% by euryphagous squids, 3.0% by nectophagous squids, and 6.9% by other mesopelagic predators. Over the outer shelf and continental slope, northern lanternfish are eaten by benthic and bentho-pelagic fishes including spiny dogfish, *Squalus acanthias* (Hubbs, 1917), rockfishes of the genus *Sebastes* (Eigenmann & Eigenmann, 1890; Starks & Morris, 1907; Pereyra, Pearcy & Carvey, 1969; Yang, 1993), greenland turbot *Reinchardtius hippoglossoides*, (Lang, Livingston, Pacunsky, Parkhurst & Yang, 1991; Lang & Livingston, 1996; Orlov, 1997a, b), walleye pollock and sablefish, *Anoplopoma fimbria* (Yang, 1993) and Atka mackerel, *Pleurogrammus monopterygius* (Orlov, 1997c, d). Northern lanternfish are also found in stomachs of Kamchatka flounder *Antherestes evermanni*, whiteblotched skate, *Bathyraja maculata* and Matsubara skate, *B. masubarai*, Pacific ocean perch, *Sebastes alutus*, and greypurple sculpin, *Gymnacanthus detrisus* in the Pacific waters off the North Kurils and Southeast Kamchatka, and also the giant grenadier, *Albatrossia pectoralis*, shortraker rockfish, *S. borealis*, Alaska skate, *B. parmifera* and Pacific sleeper shark, *Somniosus pacificus* in the Bering Sea.

Mesopelagic fishes, in general, provide a major component of the diet of such species as the walleye pollock and squid *Berryteuthis magister*, making up 7 to 14% respectively of the diet of these species in the Bering sea (Radchenko, 1994; Shuntov, Volkov, Temnukh & Dulepova, 1993; Balanov, 1995).

5.1. Trophic relationships with marine mammals

Midwater fishes, primarily of the families Myctophidae and Bathylagidae, may comprise up to 90% of the diet of at least four of the species of marine mammals occurring in the Subarctic Pacific. Northern fur seals (*Callorhinus ursinus*) and Dall's porpoise (*Phocoenoides dalli*) are year-round residents of the Subarctic Pacific and its gyres. Pacific white-sided dolphin (*Lagenorhychus obliquidens*) and northern right whale dolphin (*Lissodelphis borealis*) are abundant seasonally. Most information on the diets of marine mammals is based on animals collected in nearshore waters over the continental shelf where their diet may be appreciably different from offshore regions. The marine mammal diet information summarized here is based primarily on hard parts of prey found in stomachs of animals that have either been commercially exploited or have been taken as by-catch in commercial fishing operations in the Subarctic Pacific Ocean. Collection periods for stomach samples ranged from the mid-1950s through the early 1990s.

Myctophid fishes are prominent in the diet of northern fur seals during their pelagic phase (year-round for ages 1–3, and from October through May for age 4 and above). Despite seasonal and annual variations in overall stomach contents, *Diaphus* sp. and *Notoscopelus japonicus* consistently dominated the stomach volumes of 2800 seals

collected from the transitional regions between the Oyashio and Kuroshio currents (Wada, 1971). Similarly, Walker and Jones (1991) reported that myctophid fishes made up 78% of species ingested by a sample of 21 northern fur seals taken by the North Pacific high seas driftnet fishery. Sixty-five percent of the prey from this sample were *Symbolophorus* sp. However, Walker and Jones (1991) cautioned that their samples may have been biased by the seals consuming red flying squid (*B. magister*) which also eat myctophid fishes (Sinclair, 1991). Recent satellite data and dive records collected from adult male northern fur seals within the Gulf of Alaska and Western Subarctic Gyre systems show the diving depths vary throughout the day following a pattern that would be expected if they are seeking out vertically migrating midwater prey (Loughlin, Ingraham, Baba and Robson, personal communication).

In a diet study based on 457 individual Dall's porpoises, Crawford (1981) found that the most common prey species were *P. thompsoni, D. theta,* and *Stenobrachius* sp. In fact, nearly every one of the 33 species of fishes identified were myctophids, 82% of specimens were non-migrating *P. thompsoni*. A more recent collection (n = 32) (available at the National Marine Mammal Laboratory, Seattle Washington) reaffirm the overriding dominance of myctophid fish (78% of total prey by number) in the diet of Dall's porpoise, the species including *Electrona risso, D. theta, P. thompsoni,* and *L. jordani*.

Sixty seven of the 72 (93%) of northern right whale dolphins examined by Walker and Jones (1991) had eaten myctophid fishes, and 81% of the total number of prey remains identified were from mesopelagic fishes, primarily Myctophidae (68%) and secondly Bathylagidae (10%). The myctophid species that comprised 7% of total prey number and higher in Walker and Jones (1991) were *Ceratoscopelas* sp*., D. theta, L. jordani, N. japonicus*, and *Stenobrachius* sp.

Studies of the partitioning of diet by size or by foraging in discrete locations have not been conducted for any of the marine mammals discussed here with the exception of northern fur seals (Sinclair, Loughlin & Pearcy, 1994). However, Pacific white-sided dolphin and northern right whale dolphin often travel together and have diets which are similar in species composition. Mesopelagic fishes compose 92% of total prey species consumed by Pacific white-sided dolphin (Walker & Jones, 1991), and 79% are myctophids which were found in 79% of the dolphins examined (n = 33). The myctophid species in this sample were mostly *Ceratoscopelas sp., Diaphus gigas, Diaphus sp.,* and *Symbolophorus* sp. As in the northern right whale dolphin, Bathylagidae comprised 11% of the total prey ingested by Pacific white-sided dolphin. Kajimura, Fiscus and Stroud (1980) reported that Pacific white-sided dolphins also consume the myctophid, *S. californiensis*.

Squids are the most abundant food of the Northern right whale dolphin. However, of the 17 fish species that have been identified in stomach contents, myctophids (8 or 9 species) and bathylagids were common (Leatherwood & Walker, 1979). Fitch and Brownell (1969) studied 152 otoliths taken from the stomach of a single animal off California. The myctophids they identified included *D. theta, L. urophaos, L. ritteri, S. leucopsarus, Triphoturus mexicanus* and unidentified species, but 97% of the otoliths belonged to just 4.

Ninety percent of the stomach contents of Dall's porpoises by volume were squid,

primarily gonatid squids but they are also taking 33 species of epi- and mesopelagic fishes (Crawford, 1981), and 94% of the mesopelagic fish were myctophids; and over 82% were *P. thompsoni*; also found were *D. theta, Stenobrachius* sp., *L. jordani*, and the bathylagids, *B. pacificus* and *B. milleri*.

The Steller's sea lion (*Eumetopias jubatus*) feeds primarily at night. Calkins and Pitcher (1982), in Kajimura and Laughlin (1988) recorded mesopelagic fishes as four of the five top-ranked prey but these were not listed amongst the 10 top ranking prey species by Pitcher (1980). The northern elephant seal *(Mirounga angustirostris)* are known to move to deep waters to feed.

5.2. Trophic relationships with seabirds

We include a brief summary of the feeding consumption of myctophids by seabirds to show that these midwater fishes are also important components of their diets. Sanger and Ainley (1988) reviewed the literature on the feeding ecology of seabirds in the oceanic Subarctic North Pacific Ocean. Most of the common species of Subarctic seabirds feed within a half-meter of the sea surface, but Alcids (murres, auklets, puffins) are all able to dive to depths of at least 40–50 m to feed. In the Subarctic current, tufted puffins (*Fratercula cirrhata*) eat northern smooth-tongues (*L. stilbius*) and Atka mackerel (*P. monopterigius*). Sooty shearwaters (*Puffinus griseus*) prey heavily on fish, particularly Pacific saury (*Cololabis saira*) in the central Subarctic. Short-tailed shearwaters (*Puffinus tenuirostris*) eat mainly squid and some euphausids and fish in the western Subarctic. In different areas of the Subarctic north Pacific, fish represented from 38% to 100% of the diet by weight of *P. tenuirostris*. The main of fish identified were Atka mackerel in the East Kuriles, Western Subarctic Gyre and the Alaskan Stream, and myctophids in the Western Subarctic Gyre.

Thick-billed murres (*Uria lomvia*) which probably account for a significant portion of the avian biomass in the western part of the north Pacific in winter, have been caught in fishing gear at depths of 72 m in the North Atlantic. Throughout the Pacific they eat both squid and fish, with fish making up to 37% of numbers. Fish identifiable to species were Atka mackerel in birds from the East Kurile area, the myctophids *S. nannochir* and *T. crenularis* in birds from the Western Subarctic Gyre, and *S. leucopsarus* from the Subarctic current. In the western Aleutian Islands Springer, Piatt and Van Vliet (1996) recorded the occurrence of northern lanternfish in the diets of the following sea birds: black-legged kittiwakes (*Rissa tridactyla*), red-legged kittiwakes (*Rissa brevirostris*), common murre *(Uria aalge)*, and thick-billed murre. Shearwaters are capable of diving to at least 20 m depth, and murres to well over 100 m. The three species of North Pacific puffins (*Fratercula* sp.) are probably able to dive as deep as their north Atlantic congener (60 m). Thus, migrating midwater fishes are important components in the diet of marine birds and may be a factor in the population dynamics of some species.

5.3. The deep scattering layer

The deep scattering layer or DSL was discovered in 1942 by Eyring, Christensen and Raitt, the University of California, Division of War Research, and is now recog-

nised as being a prominent feature in midwater. DSLs were subsequently described in the Atlantic Ocean (Hersey & Moore, 1948), the Pacific Ocean (Dietz, 1948), and in the Indian Ocean, Mediterranean and Red Seas (Tchernia, 1950). In 1951, G.H. Tucker presented fathograms recorded by the U.S. Navy Electronics Laboratory of the San Diego Trough which clearly showed two distinct layers; a surface scattering layer at 0–55 m and a deeper scattering layer with a daytime depth of 180–360 m over a sounding of 440 m. The deeper scattering layer migrated from daytime depths to the surface 100 m at sunset and decended again at sunrise. Analysing biological collections made concurrently with sound-scattering recordings, Tucker (1951) concluded that the upper more diffuse layer was correlated with a denser population of euphausids, while the deeper and more intense scattering was correlated with fishes, mainly of the family Myctophidae.

Marshall (1951) presented evidence that the DSLs are produced by the sound waves reverberating off the swim bladder of mesopelagic fishes. The most common and abundant species of fishes captured in deep-water nets were species of Gonostomatidae, Sternoptychidae, and Myctophidae. Nearly all of the species have gas filled swim-bladders which, throughout their life cycles, have dimensions that result in them scattering sound over a range of frequencies commonly used in echo-sounders. Many of these species undergo diurnal vertical migrations synchronised with the movements of the DSL. During the day they are concentrated between 274 and 823 m, the usual day-time limits of the DSL.

Off the continental slope near the Queen Charlotte Islands, Taylor (1968) reported that in summer the most intense, clearly defined and persistent layer was at 220–230 m, with other less intense layers occurring at 330–400, 185, and 90 m. The main and deep layers were shallower in the fall. In the main scattering layer, 94% of the fish caught were myctophids with well-developed swim bladders. However, both *D. theta* and *S. leucopsarus*, as adults, have fat-invested swim bladders and so will not scatter the sound, although they contributed approximately 85% of the fish catch. Nearly 90% of the fish lacking swim bladders were taken below the main scattering layer, and including all the argentinids and dragonfish *Tactostoma macropus*, 83% of the viperfish, *C. macouni*, and 89% of the 'other' species, which were mainly melamphids.

Frost and McCrone (1979) reported that in the Eastern gyre of the Subarctic North Pacific that there is a single diffuse, sound scattering layer at a depth of 275 to 375 m by day. A second sound scattering layer was evident during the day from 100 m to the surface. A single layer migrated up from the deep layer twilight at about 2130 hr joining the surface layer within half of an hour, and then returned to the deep non-migrating layer at first light at about 0530 hr. The dominant species caught in this region were the myctophids *S. leucopsarus, D. theta*, and *P. thompsoni*, the chauliodontid *C. macouni,* the euphausid *E. pacifica,* and the shrimp *S. similis.* The depth of the scattering layer by day corresponded with the main depth ranges of *E. pacifica*, *D. theta, P. thompsoni* and smaller size classes of *S. leucopsarus. E. pacifica* was unlikely to have contributed to either the deep or migratory scattering layer since the population never reached concentrations high enough to be effective scatterers of 12 kHz sound, even though it was 5 times more abundant than all the myctophid

fishes combined. No other potential sound scattering organisms that were sampled consistently had their centres of abundance between 275–400 m in the daytime. Note some siphonophore species have gas-filled floats and are known to vertically migrate, but they aregrossly underestimated by nets. The abundance of the three species of myctophid in the 300–400 m layer averaged 136 fish/10 000 m^3. The vertical distribution and diel vertical migration of *D. theta, E. pacifica* and small and medium size classes (less than 80 mm) of *S. leucopsarus* were synchronised with the migrating DSL. S. *similis* also undertook diel vertical migrations to near the surface but the timing of its migration did not coincide with the movements of the DSL. *P. thompsoni* was strongly correlated in its distribution with the depth of the non-migratory portion of the deep sound-scattering layer. The large size-class of *S. leucopsarus* was rare and broadly distributed from 450–50 m. *C. macouni* exhibited some diel vertical migration but it was contained in the deep layers and its main layer of occurrance probably extended below the level of sampling.

6. Conclusion

The midwater fish community in the Subarctic Pacific contains a variety of species, but only a small number of which are extremely abundant. The biology and life histories of some of these fishes have been studied in the open ocean ecosystems, but in general their ecological linkages with the commercially important fish species such as Pacific salmon, and with the marine mammals are poorly known. Myctophids in general and *S. leucopsarus* in particular, are abundant species with short life spans. Their abundance and behaviour indicate that they are important components of these midwater ecosystems. *S. leucopsarus* appears to a keystone species analogous to the role played by key inshore prey species such as Pacific herring, and sand lance. It is probable that this one myctophid species is either a direct or indirect prey food source for many commercially important species. Their abundance is likely to fluctuate naturally as observed for other species such as sardines (Kawasaki & Omori, 1988) and salmon (Beamish & Boullon, 1993). If such fluctuations occur, they can be expected to have knock-on effects on associated species. Hence it is no longer acceptable to ignore the midwater species when establishing fishing strategies or when responding to our responsibilites as stewards of our marine ecosystems. Even in the absence of pressures to maintain commercial fisheries, there should be sufficient intrinsic scientific curiosity within the community of biologists around the North Pacific to assess the impact these fishes have on other animals. Ecosystem models that fail to incorporate these fishes will fail to simulate the open ocean ecosystems adequately. It is clear from the literature that the epipelagic zone functions totally differently between the day and night, because of the migrations of the midwater community. Thus, any studies of these ocean ecosystems will have to ensure that representative sampling occurs over a 24 hour period. Hopefully the developing understanding of the need to move from single species thinking and management to ecosystem thinking and management will also provide both resources and encouragment to understand more about the midwater community of the Subarctic Pacific gyres.

7. References

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