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Distribution and Abundance of the Early Life Stages of Squid, Primarily Gonatidae (Cephalopoda, Oegopsida), in the Northern North Pacific

(Part 1)

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Abstract

Cephalopods collected with micronekton nets in the Subarctic North Pacific are shown to be primarily young stages of the family Gonatidae. Regional and seasonal changes of abundance of cephalopods in the northern North Pacific are discussed. A pattern of low winter abundance with a rapid early summer increase and gradual autumn decrease is evident. Distribution patterns of species in the family Gonatidae show good correlation with large scale oceanographic features. The distribution types include pan-Subarctic forms of two kinds, including and excluding the Sea of Okhotsk; northeastern Pacific endemics; California Current endemics; western Subarctic endemics; and species localized within the Sea of Okhotsk. The Sea of Okhotsk and California Current showed distinctive faunal and gonatid species composition. Species of the family Gonatidae are classified into four groups according to the geographical pattern of relative abundance of the early life stages. One group shows high abundance in neritic waters, another in offshore waters, a third is intermediate, and larvae of the fourth group were rarely or never caught. The geographical area and timing of spawning or hatching are estimated for most gonatid species. A growth curve is derived for young individuals of *Gonatus madokai* in the Sea of Okhotsk.

Introduction

In the northern North Pacific, large numbers of small squid are occasionally caught with conventional micronekton and zooplankton samplers during the spring and summer months. These small squid are important components of the diets of salmonids (ANDRIEVSKAJA, 1958; ALLEN and ARON, 1959; ITO, 1964; LEBRASSEUR, 1966; UENO, 1969; MACHIDORI, 1972) and sea birds (OGI and TSUJITA, 1977; SANGER and BAIRD, 1977). Most of these small squid have been shown to be early life stages of squid in the family Gonatidae (OKUTANI, 1966; TAKEUCHI, 1972; SATO and

HIRAKAWA, 1976; OGI, 1980; OGI *et al.*, 1981), but little research has been directed at determining the specific identities of these young squid.

Most of the highly nektonic pelagic squid are planktonic during the early, post-hatching developmental stages. These young individuals have little avoidance capability; we have therefore assumed their sampled distribution and abundance to accurately reflect those in the ocean. The investigation of distribution and abundance of early life stages is an accepted technique for estimating those of the adults, which may be difficult to capture with conventional sampling gear. Geographic distribution, relative abundance, and seasonal occurrence of the early life stages are considered to be closely correlated to the spawning area, spawning period, and spawning behaviour of adults. The difficulty arises in specifically identifying the young stages. These early life stages have not yet developed many of the specific characters of the adult; specific identification of these small individuals is often extremely difficult if reliance is placed solely on the systematic characters of the adults.

During the 1960s OKUTANI examined the distribution and systematics of the early life stages of squid caught with zooplankton and micronekton samplers in the northwestern North Pacific (OKUTANI, 1966), and off the Pacific coast of northern Japan (OKUTANI, 1968a). OKUTANI and MCGOWAN (1969) examined those of the California Current, and discovered that the early life forms of gonatid squid were the dominant cephalopod faunal component. They tentatively classified them as species known at that time, and additionally described several other early stages which did not correspond with any known (adult) species. Incomplete knowledge of the systematics of the family Gonatidae made these early studies difficult and incomplete.

Systematic work on the family Gonatidae has greatly increased in the past few years (FIELDS and GAULEY, 1971; YOUNG, 1972; NESIS, 1972, 1973; KUBODERA and OKUTANI, 1977, 1981a; KRISTENSEN, 1981; BUBLITZ, 1981; and JEFFERTS, 1984); eight new species have been added to the family. These studies have greatly simplified the taxonomy of the early life stages. KUBODERA and OKUTANI (1981b) recently reexamined the early life stages of cephalopods from the northwestern North Pacific and gave detailed descriptions and an artificial key for their identification, in which eight species and one type of gonatid were included. JEFFERTS (1983) studied the zoogeography and systematics of cephalopods in the northeastern North Pacific and described some early life stages of gonatid squid from that area.

Although not all the early life stages of the family Gonatidae have yet been described, and some taxonomic confusion remains, both in the early stages and the adults (OKUTANI, pers. comm.; BUBLITZ, pers. comm.), we feel that the task has been so nearly accomplished that the present report is justified. In this study, we examine the distribution and family composition of the pelagic cephalopod fauna, and attempt to clarify the geographic distribution and seasonal changes of abundance and occurrence of the early life stages of gonatid squid in the entire northern North Pacific, based on samples collected with several kinds of nets. We discuss the probable spawning areas, spawning periods, and growth rates, and suggest areas for further research on the biology and ecology of gonatid squid in the northern North Pacific.

Materials and Methods

The samplers and sampling methods which provided the specimens and data for this study are broadly divisible into two categories. The samples examined by KUBODERA were collected with a Maruchi-A type net of NAKAI (1962), here termed "Larva net". It is a conical net 1.3 m in mouth diameter and 4.5 m in length. The anterior 3 m has mesh about 2.0 mm square and the remainder has mesh about 0.3 mm. A standardized collection with the larva net consisted of towing the net at the sea surface with two-thirds of the mouth submerged in the water for ten minutes at about two knots one hour after sunset. The sampling was therefore restricted to the uppermost one metre of the water column. Although the filtering rate of the net was not examined, it was assumed that all the water passing through the mouth was filtered (about 600 m^3/tow). In total, 650 Larva net tows were conducted by five Japanese Salmon Research Vessels (Fisheries Agency of Japan), and the *Oshoro-Maru* and *Hokusei-Maru*, training vessels of Hokkaido University, from mid-April to mid-September, 1975–1979. A total of 31,969 individual cephalopods was collected (Table 1A). The area investigated with the Larva net was mainly in the western sector of the northern North Pacific, north of 38°N, and in the Okhotsk and Bering

Table 1A. General collection data, Larva Net samples.

Year	Vessel	Area	Period	No. Samples	No. Cephalopods
1975	*Oshoro-Maru*	N.W. North Pacific	8 June –27 July	30	1391
		Bering Sea	13 June – 4 July	30	5365
	Oyashio-Maru	N.W. North Pacific	18 April –12 May	14	31
		Sea of Okhotsk	15 May –15 Sept.	51	5791
1976	*Oshoro-Maru*	N.W. North Pacific	8 June –29 July	11	147
		Bering Sea	14 June –25 July	28	128
	Oyashio-Maru	N.W North Pacific	15 April –22 May	24	105
		Sea of Okhotsk	15 May –12 Sept.	83	6705
	Hokusei-Maru	N.W. North Pacific	7 June –26 June	13	94
		Sea of Okhotsk	10 July –16 August	22	1015
	Habomai-Maru	N. W. North Pacific	17 April –18 May	53	243
		Bering Sea	9 June –17 July	81	690
1977	*Oyashio-Maru*	N.W. North Pacific	1 June – 1 August	48	1531
1978	*Oshoro-Maru*	N.W. North Pacific	9 July – 1 August	20	459
	Hokushin-Maru	N.W. North Pacific	9 July –29 July	14	465
	Iwate-Maru	N.W. North Pacific	3 July –29 July	22	307
	Hokuho-Maru	N.W. North Pacific	10 July –14 August	30	924
1979	*Oshoro-Maru*	N.W. North Pacific	6 June – 9 August	36	1369
		Bering Sea	10 July –25 July	14	3985
	Hokusei-Maru	N.W. North Pacific	14 July – 9 August	26	1224
Total				650	31969

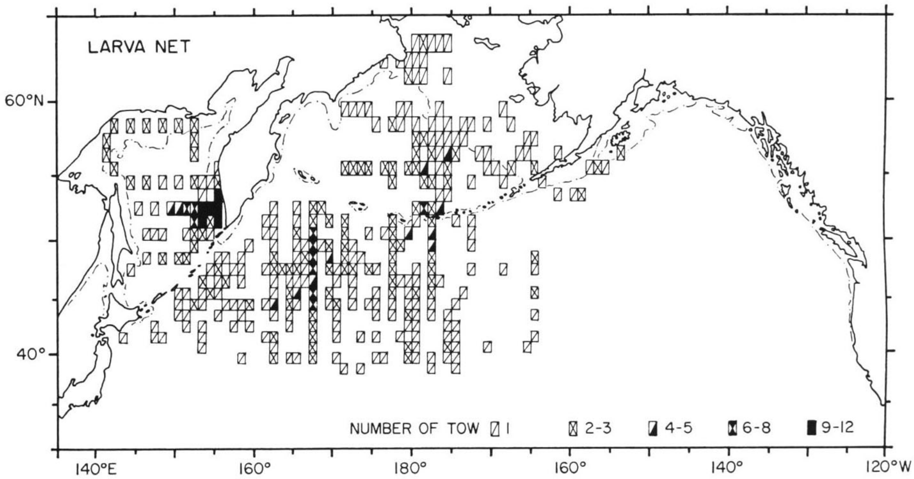

Fig. 1. Sampling area and intensity for Larva Net.

seas. Sampling was concentrated in the waters off the southern Kamchatka Peninsula in the Okhotsk Sea, between 44°N and 51°N and 162°E and 171°E in the northwestern North Pacific, and around Adak Island in the Aleutian Islands (Fig. 1).

The samples examined by JEFFERTS were collected with several different Isaacs-Kidd Midwater Trawls (IKMTs) and one metre ring nets. Four different sizes of IKMT were used (0.91 m, 1.83 m, 2.44 m, and 3.05 m depressor width), with cod ends of one metre ring nets or Multiple Plankton Samplers (MPS) (JEFFERTS, 1983). The MPS system allowed the collection of up to eight discrete depth samples during the course of one tow. Mesh size varied among the different pieces of gear, from about 0.6 mm at the rear to 3.2 mm at the front of the 0.91 m IKMT, to 3.2 mm and 5 mm in the larger IKMTs. These collections were conducted by Oregon State University (e.g., PEARCY, 1964), and the University of Washington (R/V *Brown Bear*) (ARON, 1958, 1962). The samples were collected between 1957 and 1980 at all times of the year. A total of 2239 hauls captured cephalopods; the number of individuals collected and examined was 16,489 (Table 1B). These positive hauls covered a broad expanse in the eastern sector of the northern North Pacific, north of about 30°N, extending into the Bering Sea, but were concentrated in the waters off Oregon (Fig. 2). The IKMTs were towed obliquely from the surface to various depths from 30 m to over 1000 m; some nets of the MPS fished only at depth, or from the surface to the sampling depth, or from depth to the surface. Details of the sampling protocol varied among the various research programs, but the nets were generally towed at 3 to 6 kts. Sampling occurred during daylight and nighttime hours. One metre ring nets were also used. They were fished vertically, obliquely, or attached to the wire above an IKMT. The volume of water filtered by each tow (or MPS net) was estimated with flow meters, or by calculation from mouth area of the net and distance towed, assuming

Table 1B. General collection data, IKMT and meter net samples.

Year	Vessel	Area	Period	No. positive hauls	No. Cephalopods
1957	*Brown Bear*	N.E. North Pacific	23 July –21 Sept.	101	664
		Bering Sea	3 Aug. –29 Aug.	19	456
1958	*Brown Bear*	N.E. North Pacific	30 June – 3 Oct.	301	1324
1959	*Brown Bear*	N.E. North Pacific	15 July –26 July	44	606
		Bering Sea	28 July – 2 Sept.	5	6
1960	*Brown Bear*	N.E. North Pacific	12 Mar. –24 Mar.	28	52
1961	*Acona*	N.E. North Pacific	13 June – 3 Dec.	49	372
	Kiska	N.E. North Pacific	28 Mar.	1	3
1962	*Acona*	N.E. North Pacific	9 Oct. –28 Dec.	119	788
1963	*Acona*	N.E. North Pacific	6 Oct. –14 Dec.	129	759
1964	*Acona*	N.E. North Pacific	2 Feb. –13 Dec.	107	739
1965	*Acona*	N.E. North Pacific	27 Jan. –20 Dec.	114	1267
1966	*Acona*	N.E. North Pacific	25 Jan. –14 June	20	172
	Yaquina	N.E. North Pacific	15 June –19 Dec.	73	812
		Bering Sea	3 July – 4 July	2	88
1967	*Yaquina*	N.E. North Pacific	13 Jan. –16 Nov.	100	1350
1968	*Yaquina*	N.E. North Pacific	7 Jan. – 7 Dec.	30	246
1969	*Yaquina*	N.E. North Pacific	18 Jan. –31 Oct.	149	1614
	Cayuse	N.E. North Pacific	28 June –24 Aug.	41	409
1970	*Yaquina*	N.E. North Pacific	13 Mar. –17 Nov.	42	219
	Cayuse	N.E. North Pacific	13 May – 1 Sept.	64	744
1971	*Yaquina*	N.E. North Pacific	2 April –21 July	79	499
1972	*Yaquina*	N.E. North Pacific	25 June – 5 Dec.	249	1264
1973	*Yaquina*	N.E. North Pacific	2 Mar. –25 July	94	492
1974	*Yaquina*	N.E. North Pacific	14 Sept. –24 Sept.	104	559
1975	*Yaquina*	N.E. North Pacific	25 May –16 Sept.	56	327
1976	*Wecoma*	N.E. North Pacific	16 April –19 Aug.	71	413
1977	*Wecoma*	N.E. North Pacific	8 Aug. –11 Aug.	43	130
1978	*Hakuho-Maru*	North Pacific	14 Aug.	2	87
		Bering Sea	15 July –29 July	3	26
Total				2239	16489

all water passing through the mouth was filtered.

All samples were fixed and preserved in 10% buffered formalin-seawater solution at sea. In the laboratories the samples were roughly sorted to major taxon (zooplankton, fish, cephalopods, etc.), and the cephalopods later identified to lowest possible taxon, measured (dorsal mantle length, DML), and enumerated. Individuals were generally counted on the basis of whole animals. However, if mantle-less heads, or clearly identifiable mantles were present, they were counted on the basis of heads plus excess mantles. Measurement of DML was generally made for all individuals in each species in the sample. However, when a large number of individuals of a single species was caught, a random subsample of 50 to 100 individuals was selected and measured. Individuals were also observed for development of the tentacular

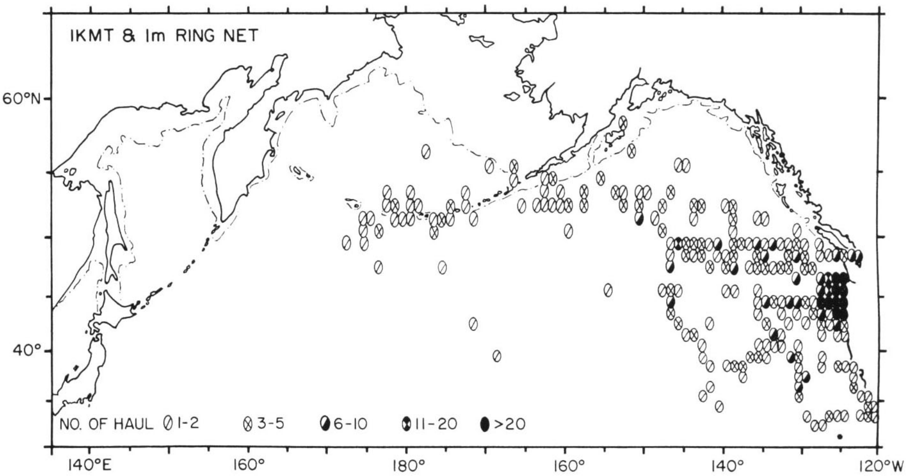

Fig. 2. Sampling area and intensity, IKMT and meter net.

club, club armatures, and arm armatures, in order to classify them into developmental stages.

Regional distributions and relative abundances of these cephalopods are here indicated as the average number of individuals per 1000 m^3 filtered (positive hauls only) in each one degree square. Due to the difference in sampling methods and net structures, the Larva net was up to two orders of magnitude more effective at capturing cephalopods than the IKMTs and ring nets. We therefore treated the two sample groups separately.

Results

Regional and seasonal changes of sampling area and relative abundance of cephalopods

Sampling area and intensity varied from year to year and month to month in the two sampling programs; the area investigated and the relative abundance of cephalopods are therefore presented by season and gear type for all years of the sampling program (Figs. 3A–F). Comparison of relative abundances between the Larva net samples and the IKMT and metre net samples is not statistically appropriate due to the differences of net construction and sampling protocol. Nevertheless, a general pattern of seasonal and regional changes in relative abundance can be seen.

During the January to March period (Fig. 3A) only positive hauls by IKMT and metre nets off Oregon (34–48°N, 124–143°W) were available. Abundance in most of the area investigated was less than 0.5 individuals per 1000 m^3. However, relatively high abundance was seen in waters slightly offshore (43–45°N, 127–134°W), where in some squares the value exceeded 0.5 individuals per 1000 m^3.

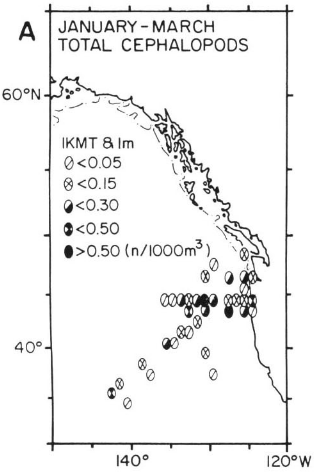

Fig. 3A. Relative abundance of cephalopods, January to March.

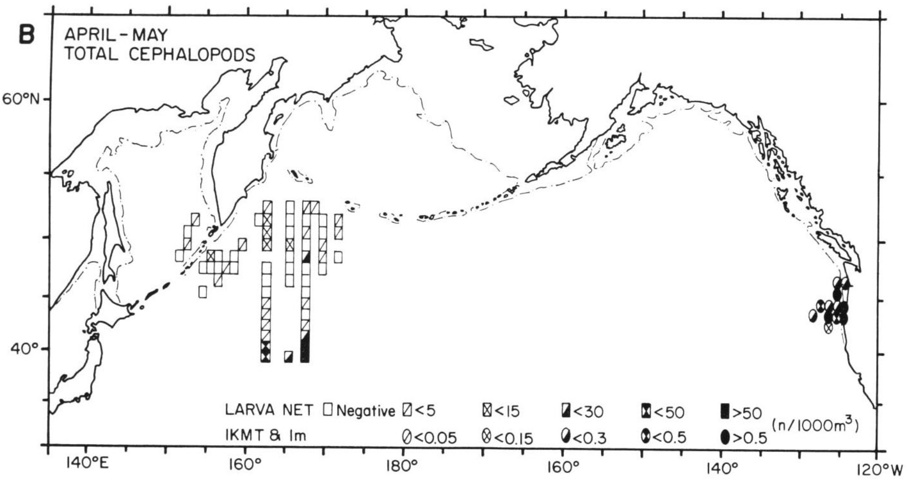

Fig. 3B. Relative abundance of cephalopods, April to May.

During the April to May period (Fig. 3B), positive IKMT and metre net hauls were concentrated in the waters off Oregon between 42°N and 46°N and 124°W and 128°W. The abundance of cephalopods increased slightly compared to the previous period and values above 0.5 individuals per 1000 m^3 were commonplace.

Larva net sampling during April and May was conducted mainly in the waters between 39°N and 52°N and 155°E and 173°E, in the western sector of the northern North Pacific and in the small area off the northern Kurile Islands within the Sea of Okhotsk (Fig. 3B). The relative abundance of cephalopods taken by Larva net was up to

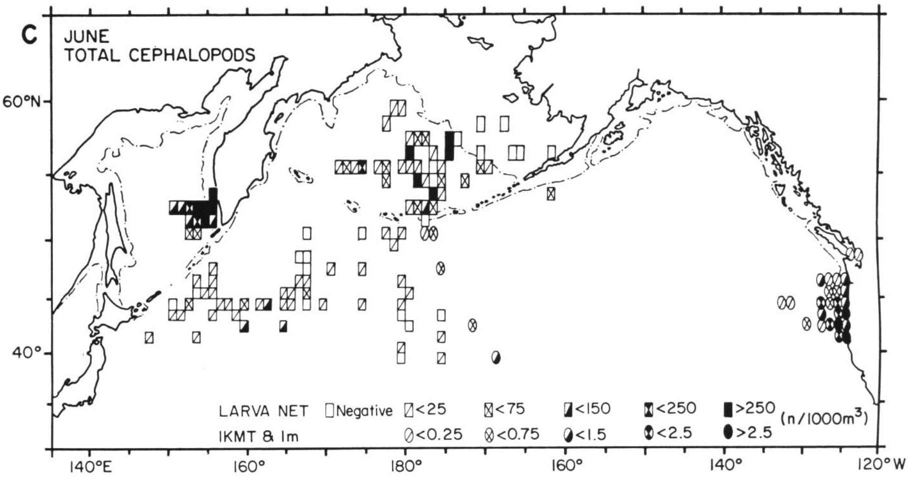

Fig. 3C. Relative abundance of cephalopods, June.

two orders of magnitude greater than that for IMKT and ring net. Cephalopods were relatively abundant in the waters south of 41°N, where some values exceeded 30 individuals per 1000 m^3. Most squares north of 41°N had fewer than 15 individuals per 1000 m^3 or none.

In June (Fig. 3C), positive IKMT and metre net hauls were again concentrated in the waters off Oregon and sparsely distributed in the central North Pacific between 44°N and 50°N and 168°W and 177°W. The abundance of cephalopods increased radically compared to the immediately previous period and tended to be higher in nearshore waters than in offshore waters. Due to the increase in abundance, scale values were multiplied by five. Most of the squares along the coast had abundances of more than 0.75 individuals per 1000 m^3.

Larva net research in June covered the area from 39°N to 51°N and 142°E to 175°W in the northern North Pacific, a large portion of the southern Bering Sea, and a portion of the waters off southern Kamchatka in the Okhotsk Sea. In the western sector of the northern North Pacific, cephalopods were again relatively abundant in the waters south of about 45°N, where some values exceeded 75 individuals per 1000 m^3. Most of the squares north of about 45°N had fewer than 25 individuals per 1000 m^3 or none. Compared to the northern North Pacific, cephalopods were extremely abundant in the Okhotsk and Bering seas. High abundance, over 250 individuals per 1000 m^3, occurred commonly in the waters off southern Kamchatka, and in the triangular area of the Bering Sea surrounded by the Aleutian Islands, 100-m isobath, and 180° meridian. No cephalopods were taken over the continental shelf in the Bering Sea.

In July, positive IKMT and metre net hauls were widely distributed along the west coast of the United States and Canada between 34°N and 50°N, and extended offshore to about 147°W between 38°N and 53°N, to the Gulf of Alaska, and west along

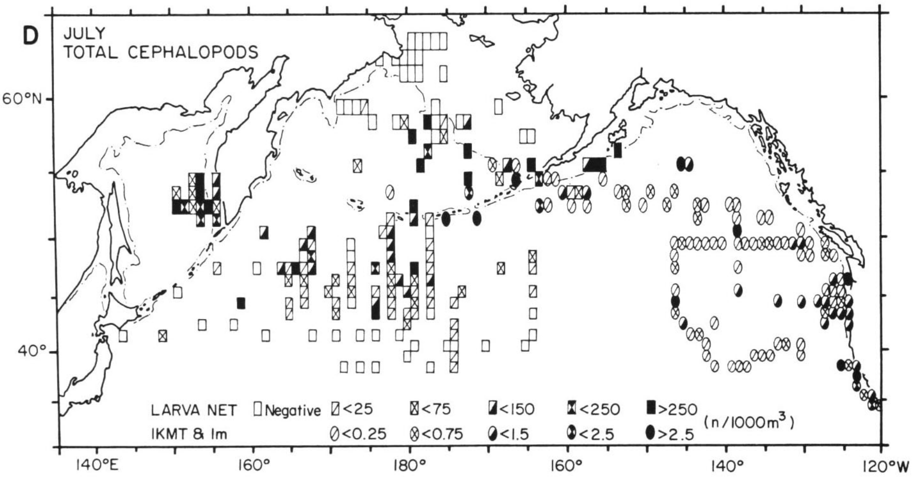

Fig. 3D. Relative abundance of cephalopods, July.

the Aleutians to about 180° (Fig. 3D). Abundance tended to be high in nearshore waters relative to offshore waters, especially off Oregon and California and off the Aleutians. Values above 1.5 individuals per 1000 m^3 were common in those areas inside the 200-m isobath. In offshore waters abundance was generally below 0.75 individuals per 1000 m^3, although somewhat higher values were noticed in waters north of about 42°–43°N.

Larva net sampling in July was conducted in a broad area of the western sector of the northern North Pacific between 38°N and 51°N and 143°E and 164°W, off portions of the Alaskan Peninsula, in the Bering Sea, and off southern Kamchatka in the Sea of Okhotsk. In the western sector of the northern North Pacific, the abundance of cephalopods increased radically over that of June to values exceeding 75 individuals per 1000 m^3. These high values were seen north of 43°N and off the Alaskan Peninsula. Few cephalopods were collected south of about 43°N. Cephalopods were again very abundant in the southern Sea of Okhotsk and in the above-mentioned triangular area of the Bering Sea, where abundances above 250 individuals per 1000 m^3 were commonplace. Again, no cephalopods were taken over the continental shelf in the Bering Sea.

During the August–September period (Fig. 3E), positive IKMT and metre net hauls were from a broad area west from the American coast to about 130°W between 33°N and 45°N, to about 160°W between 45°N and 50°N, and along the Aleutians to about 173°N. Cephalopod catches tended to decrease slightly over the entire area, but were again high in waters north of about 43°N (>0.75 individuals per 1000 m^3), and in the central Aleutian Islands (>2.5 individuals per 1000 m^3).

Fewer and more widely spaced Larva net tows were made during August and

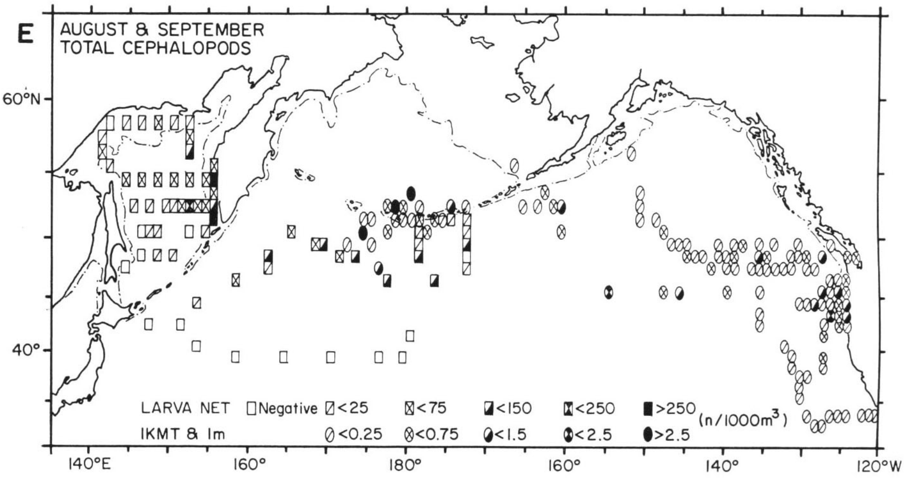

Fig. 3E. Relative abundance of cephalopods, August and September.

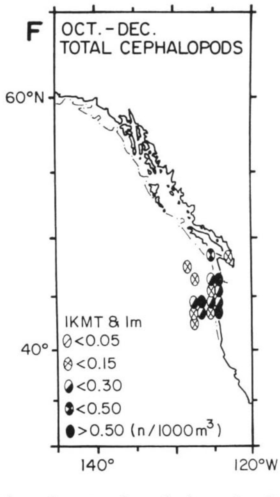

Fig. 3F. Relative abundance of cephalopods, October to December.

September in the northwestern Pacific; the area examined was between 38°N and 50°N and 147°E and 172°W. No investigations were made in the Bering Sea, but sampling in the Sea of Okhotsk was extensive. Cephalopod catches decreased slightly over the entire area relative to July, but were high in waters north of about 45°N. Few cephalopods were taken south of 45°N. Abundance was again high off southern Kamchatka, where values exceeded 150 individuals per 1000 m^3; most of the rest of the Sea of Okhotsk had values below 75 individuals per 1000 m^3.

During the October-December period (Fig. 3F) positive IKMT and metre net hauls were limited to a small area off the Pacific coast of North America between

42°N and 48°N and 123°W and 128°W. Due to the low abundance of cephalopods during this period, scale values were reduced by half an order of magnitude (thus the same as for the early months of the year). Cephalopods tended to be more abundant in nearshore waters; however, the research area was too small to allow conclusions about regional characteristics of relative abundance.

In general, cephalopod abundance in the northern North Pacific fluctuates seasonally, rising rapidly from a low in the winter and spring to a maximum in early summer. The summer maximum is persistent until a gradual autumn decline to the low winter levels. These seasonal changes, especially the time of rapid increase, vary slightly according to region in the North Pacific. As a rough estimate, the rapid increase begins in June in the Okhotsk and Bering seas and in July in the North Pacific north of about 42°–43°N. Waters south of 42°–43°N (transitional region) are sub tropical; cephalopods tend to be abundant there in the early part of the year.

Geographically, cephalopods are extremely abundant in the waters off southern Kamchatka in the Okhotsk Sea, in the triangular area of the Bering Sea surrounded by the Aleutian Islands, the 100-m isobath, and the 180° meridian, along the Pacific coast of the eastern Aleutian Islands and Alaskan Peninsula, and off Oregon.

Family composition of the samples

In order to present a general overview of the present material, the numerical and percentage composition of the cephalopods collected have been summarized by family, area, and gear type (Table 2). It is apparent that the dominant element is the family Gonatidae, in the samples collected with each gear type, and in each area investigated.

In the western sector of the northern North Pacific, 341 Larva net samplings provided 8290 individuals in six families, among which Gonatidae were the most abundant, comprising 93% of the catch. The remainder were Octopodidae (6.3%), Enoploteuthidae (0.6%), Bolitaenidae (0.1%), Octopoteuthidae (0.01%), and Onychoteuthidae (0.01%). In the eastern sector of the North Pacific, 15,969 individuals collected with IKMTs and ring nets were distributed among seventeen families. Gonatidae were again the most abundant, but accounted for only about 50% of the catch, followed by Chiroteuthidae (14.4%), Enoploteuthidae (12.5%), Bolitaenidae (9.3%), Cranchiidae (7.1%), Octopodidae (3.7%), Octopoteuthidae (1.4%), Onychoteuthidae (1.0%), and several other less numerically important families.

In the Bering Sea, 10,168 individuals were collected with the Larva net, and 520 individuals with IKMTs and ring nets. Gonatidae comprised over 99% of both sets of samples. A small number of Octopodidae accounted for the remainder of the Larva net samples; the rest of the IKMT samples were Cranchiidae.

All of the 12,496 individuals collected with the Larva net in the Okhotsk Sea belonged to the family Gonatidae.

The large number of families and lesser contribution of Gonatidae in the IKMT samples from the northeastern Pacific is at least in part attributable to the wide range of sampling depths and the mixed oceanographic character of sampling areas in the California Current. In general, the early life stages of gonatids are the dominant component of the pelagic cephalopod fauna available to micronekton samplers across the northern North Pacific, and especially so in the Bering and Okhotsk seas.

Geographic variation within the gonatid faunal component

Fourteen species and three genera were identified within the family Gonatidae (Table 3). Nine species belonged to the genus *Gonatus*, three to *Gonatopsis*, and two to *Berryteuthis*.

In the western sector of the northern North Pacific (Larva net samples), the most abundant taxon was *Berryteuthis anonychus*, accounting for 36.3% of the individuals collected, followed by *Gonatus* type A KUBODERA and OKUTANI 1981b (28.0%), unidentified Gonatidae (17.5%), *Gonatopsis borealis* (7.7%), *Gonatus middendorffi* (4.6%), *Gonatus onyx* (3.7%), and four other taxa accounting for less than two per cent each.

Berryteuthis anonychus was the most abundant species within both groups of samples in the Bering Sea, (Larva net—23.5%, IKMTs—47.0%). Other important taxa taken by Larva net included *Gonatus* type A KUBODERA and OKUTANI 1981b (9.2%), "*Berryteuthis magister*"[1] (2.2%), *Gonatus middendorffi* (2.1%), and four other less abundant taxa. The IKMT samples from the Bering Sea also collected *Gonatus onyx* (11.8%), *Berryteuthis magister* (9.2%), *Gonatopsis borealis* (5.6%), and *Gonatus* type A KUBODERA and OKUTANI 1981b (2.1%), and four other less abundant taxa.

In the eastern sector of the northern North Pacific (IKMTs and ring nets), *Gonatus onyx* was the most abundant taxon, accounting for 55.0% of the individuals, followed by unidentified Gonatidae (19.6%), *Gonatus pyros* (8.3%), *Gonatopsis borealis* (5.5%), *Berryteuthis anonychus* (4.9%), and seven other taxa each accounting for less than two per cent of the total.

The samples from the northeastern Pacific represent not one but several zoogeographic areas (JEFFERTS, 1983). The dominance of *Gonatus onyx* and *G. pyros* in these samples is due to their importance in the California Current, and not to their major importance across the Subarctic Pacific, although both species do occur some distance west of the California Current.

The dominant taxa in the Sea of Okhotsk were *Gonatus madokai* (74.9% of the individuals), "*Berryteuthis magister*" (12.7%), unidentified Gonatidae (6.5%), and *Gonatus onyx* (5.7%). Four other less abundant taxa were also collected.

The samples from the northwestern Pacific (except the Sea of Okhotsk) and the Bering Sea were in general very similar, with *Berryteuthis anonychus* of major im-

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1) "*Berryteuthis magister*" here refers to a complex of individuals which we believe may perhaps represent young individuals of *Gonatus* (*E.*) *tinro* as well as *B. magister*. We believe that the absence of *G. tinro* larvae in the samples may be related to an identification problem and/or a fundamental difference in distribution.

Table 2. Family composition of the samples, by geographical area and sampling method.

	Northern North Pacific				Bering Sea				Sea of Okhotsk	
	Larva net*		IKMT & meter**		Larva net		IKMT & meter		Larva net	
	N	%	N	%	N	%	N	%	N	%
Sepioidea										
Sepiolidae	—	—	7	0.04	—	—	—	—	—	—
Teuthoidea										
Gonatidae	7712	93.03	7960	49.84	10103	99.36	5.9	99.81	13511	100.00
Chiroteuthidae	—	—	2303	14.42	—	—	—	—	—	—
Enoploteuthidae	49	0.59	1999	12.52	—	—	—	—	—	—
Cranchiidae	—	—	1138	7.13	—	—	1	0.19	—	—
Octopoteuthidae	1	0.01	223	1.40	—	—	—	—	—	—
Onychoteuthidae	1	0.01	159	1.00	—	—	—	—	—	—
Histioteuthidae	—	—	64	0.40	—	—	—	—	—	—
Loliginidae	—	—	8	0.05	—	—	—	—	—	—
Ctenopterygidae	—	—	2	0.01	—	—	—	—	—	—
Mastigoteuthidae	—	—	3	0.02	—	—	—	—	—	—
Bathyteuthidae	—	—	3	0.02	—	—	—	—	—	—
Vampyromorpha										
Vampyroteuthidae	—	—	29	0.18	—	—	—	—	—	—
Octopoda										
Bolitaenidae	9	0.11	1485	9.30	—	—	—	—	—	—
Octopodidae	518	6.25	583	3.65	65	0.64	—	—	—	—
Ocythoidae	—	—	2	0.01	—	—	—	—	—	—
Cirrata	—	—	1	0.01	—	—	—	—	—	—
Total	8290		15969		10168		520		13511	
Total No. haul	341	—	—		153		—		156	
Total No. positive haul	234		2210		114		29		127	

*, mainly from western sector of the northern North Pacific; **, mainly from eastern sector of the northern North Pacific.

Table 3. Species composition of gonatid collections, by

	Northern North Pacific							
	Larva Net*				IKMT & meter**			
	N	%	P	%	N	%	P	%
Gonatidae								
Gonatus berryi	2	—	2	0.9	99	1.2	86	6.9
onyx	288	3.7	32	14.5	4381	55.0	839	67.7
pyros	1	—	1	0.5	662	8.3	369	29.7
californiensis	—	—	—	—	4	0.1	4	0.3
madokai	124	1.6	25	11.3	139	1.7	74	6.0
middendorffi	355	4.6	30	13.6	—	—	—	—
type A***	2161	28.0	104	47.1	110	1.4	45	3.4
ursabrunae	—	—	—	—	18	0.2	16	1.3
oregonensis	—	—	—	—	9	0.1	4	0.3
Gonatopsis borealis	593	7.7	84	38.0	435	5.5	307	24.7
octopedatus	—	—	—	—	—	—	—	—
type A****	—	—	—	—	—	—	—	—
Berryteuthis anonychus	2796	36.3	74	33.5	388	4.9	120	9.7
"magister"	45	0.6	13	5.9	153	1.9	67	5.4
Unidentified Gonatidae	1347	17.6	107	48.4	1562	19.6	523	42.1
Total	7712		221		7960		1241	

N, number of individuals; P, number of positive haul; *, mainly from western sector of the northern OKUTANI (1981b); ****, KUBODERA (1978); *"magister"*, see foot-note in text page 102.

portance in both areas. *Gonatus* type A and *Gonatus middendorffi* were also important in the two areas, with the exception of the IKMT Bering Sea samples, where *G. middendorffi* accounted for less than one per cent of the individuals.

Berryteuthis anonychus was also important in the eastern North Pacific, although the dominant organism was *Gonatus onyx*.

Size range and size class composition of species in the family Gonatidae

The present material (Table 4) included animals over most of the known size range for several species: from a minimum of about 5 mm DML to 94 mm DML for *Gonatus berryi*, 97 mm for *Gonatus onyx*, 66 mm for *Gonatus pyros* and 276 mm for *Gonatopsis borealis*. For species of greater adult size, the range covered in the samples included only early life stages: 6–72 mm for *Gonatus madokai*, 6–60 mm for *Gonatus middendorffi*, and 6–34 mm for "*Berryteuthis magister*". *Berryteuthis anonychus* probably is fairly small as an adult, but only younger individuals were collected, measuring 5–46 mm DML. *Gonatus* type A KUBODERA and OKUTANI 1981b was collected in both types of gear in large numbers but no individuals larger than 16 mm DML appeared. The other species were collected only in small numbers.

geographical area and sampling method.

Bering Sea								Sea of Okhotsk			
Larva Net				IKMT & meter				Larva Net			
N	%	P	%	N	%	P	%	N	%	P	%
1	—	1	0.9	5	1.0	4	13.8	—	—	—	—
68	0.7	10	9.0	61	11.8	10	34.5	769	5.7	39	30.7
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
53	0.5	18	16.2	8	1.5	7	24.1	10124	74.9	100	78.7
210	2.1	20	18.0	3	0.6	2	6.9	—	—	—	—
932	9.2	52	46.8	11	2.1	8	27.6	7	0.1	3	2.4
1	—	1	0.9	1	0.2	1	3.4	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
66	0.7	19	17.1	29	5.6	14	48.3	3	—	3	2.4
—	—	—	—	—	—	—	—	1	—	1	0.8
—	—	—	—	—	—	—	—	6	—	5	3.9
2373	23.5	29	26.1	224	47.0	14	48.3	—	—	—	—
225	2.2	29	26.1	48	9.2	19	65.5	1722	12.7	39	30.7
6179	61.1	53	47.7	109	21.0	10	34.5	879	6.5	36	28.3
10103		111		519		29		13511		127	

North Pacific; **, mainly from eastern sector of the northern North Pacific; ***, KUBODERA and

In order to give a general view of size composition, we divided each species into three size classes using the developmental stages described by KUBODERA and OKUTANI (1981b). The first size class is <10 mm DML, for all the species; this corresponds with the stage of KUBODERA and OKUTANI (1981b) which has as yet not developed any tentacular club, and is here termed "larval stage." The second size class is 10–20 mm DML for *Gonatus berryi*, *G. onyx*, *G. pyros*, *G. madokai*, *G. ursabrunae*, *Gonatus* type A KUBODERA and OKUTANI 1981b, and *Gonatopsis* type A KUBODERA 1978, and 10–30 mm DML for *Gonatus californiensis*, *G. middendorffi*, *G. oregonensis*, *Gonatopsis borealis*, *G. octopedatus*, *Berryteuthis anonychus*, and "*Berryteuthis magister*," and roughly coincides with the stage of KUBODERA and OKUTANI (1981b) which has developed minute sucker buds on the tentacular club. It is here termed "postlarval stage." The third size class is >20 mm or >30 mm DML, according to the groups described above. In this "adolescent stage" most of the specific adult characters are recognizable. The size frequency of each species is summarized according to gear type in Table 4.

In general, Larva Net samples consisted mainly of individuals in larval and postlarval stages, while IKMT and metre net samples included postlarval and adolescent stages. The IKMT probably has a higher sampling efficiency for larger individuals than the Larva net due to a larger mouth opening and mesh size and higher

Table 4. Size composition of gonatid collections, by sampling method.

	Gear	N	Size Range (mm)	KLS (mm)	Size Class Composition (mm) <10 N	%	10–20 or 10–30 N	%	>20 or >30 N	%
Gonatidae										
Gonatus berryi	L.N	3	13–30	119	0	—	1*	33	2	67
	IKMT	104	6–94		15	14	54*	52	35	34
onyx	L.N	1152	6–26	98	925	80	222*	19	4	1
	IKMT	4442	2–97		430	10	2549*	57	1463	33
pyros	L.N	1	14	66	0	—	1*	100	0	—
	IKMT	662	7–66		8	1	286*	43	368	56
californiensis	IKMT	4	24–72	112	0	—	3**	75	1	25
madokai	L.N	10301	6–72	329	3547	34	6248*	61	506	5
	IKMT	147	7–60		9	6	77*	52	61	41
middendorffi	L.N	565	6–60	296	153	27	233**	41	179	32
	IKMT	3	11–20		0	—	2**	67	1	33
type A	L.N	3100	8–16	16	824	27	2276**	73	0	—
	IKMT	121	4–16		51	42	70*	58	0	—
ursabrunae	L.N	1	30	30	0	—	0*	—	1	100
	IKMT	19	12–29		0	—	9*	47	10	53
oregonensis	IKMT	9	24–48	48	0	—	5**	56	4	44
Gonatopsis borealis	L.N	662	5–60	480	604	91	44**	7	14	2
	IKMT	464	4–276		134	29	303**	65	27	6
octopedatus	L.N	1	23	200	0	—	1**	100	0	—
type A	L.N	6	18–40	40	0	—	3*	50	3	50
Berryteuthis anonychus	L.N	5169	5–30	150	4539	88	630**	12	0	—
	IKMT	632	5–46		123	19	504**	80	5	1
"magister"	L.N	1992	7–34	335	1216	61	776**	39	0	—
	IKMT	201	6–34		27	13	170**	85	4	2

KLS; known largest size; *G. berryi*, *G. onyx*, *G. pyros*, *G. californiensis*; Young 1972; *G. madokai*, Kubodera and Okutani 1977; *G. middendorffi*, Kubodera and Okutani 1981a; *G. borealis*, Okutani and Satake 1978; *G. octopedadus*, Okutani *et al.* 1976; *B. anonychus*; Okutani 1968b; *B. magister*, Naito *et al.* 1977; *, 10–20 mm; **, 10–30 mm.

towing speed. This trend is evident in samples of *Gonatus onyx*, *G. madokai*, and *Gonatopsis borealis*. However, the abrupt decline in abundance of adolescent *Gonatopsis borealis* seems to have been affected by net avoidance by larger individuals. Although large numbers of small individuals in larval and postlarval stages were captured by both gear types, adolescents of *Gonatus* type A Kubodera and Okutani 1981b, *Berryteuthis anonychus*, and "*B. magister*" were seldom captured even with IKMTs. The absence of larger individuals in these species might also be attributable to net avoidance. However, ontogenetic migration from the sampling area or depth stratum might also be a factor. (To be continued.)