

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

(Part 2)

By

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Geographic distribution of species and size classes of the family Gonatidae

All members of the family Gonatidae do not occur uniformly across the Subarctic Pacific; we have here attempted to demonstrate the geographic distribution of each species and its size classes.

Gonatus berryi seems to be limited to the eastern portion of the northern North Pacific and the southernmost Bering Sea (Figs. 4A–C). No individuals were taken further west than 176°E. Adolescents (>20 mm DML) occurred over the entire range, but the larvae (<10 mm DML) occurred only in nearshore waters off the American coast. Post-larval individuals occurred at both limits of the distribution, off the American coast and south of the central Aleutians. This type of distribution suggests a spawning area localized in the California Current.

Gonatus pyros showed a distribution very similar to that of *G. berryi*, limited to the central and eastern portions of the northern North Pacific (Figs. 5A–C). *Gonatus pyros* occurred more frequently than *G. berryi*, but again the easternmost limit was about 174°E. Larval individuals (<10 mm DML) again occurred only near the American coast, while adolescents (>20 mm) and post-larval individuals occurred over a broader area, possible evidence again of a California Current spawning area.

Gonatus californiensis was limited to waters of the California Current system of the eastern North Pacific (Figs. 6A–B). Post-larvae and adolescents were collected in very low numbers.

Gonatus ursabrunae and *G. oregonensis* also had eastern northern North Pacific distributions very similar to that of *Gonatus pyros*, although *G. oregonensis* was limited to an area off the coast of Oregon (Figs. 7–8). The numbers of individuals were too few to allow further conclusions.

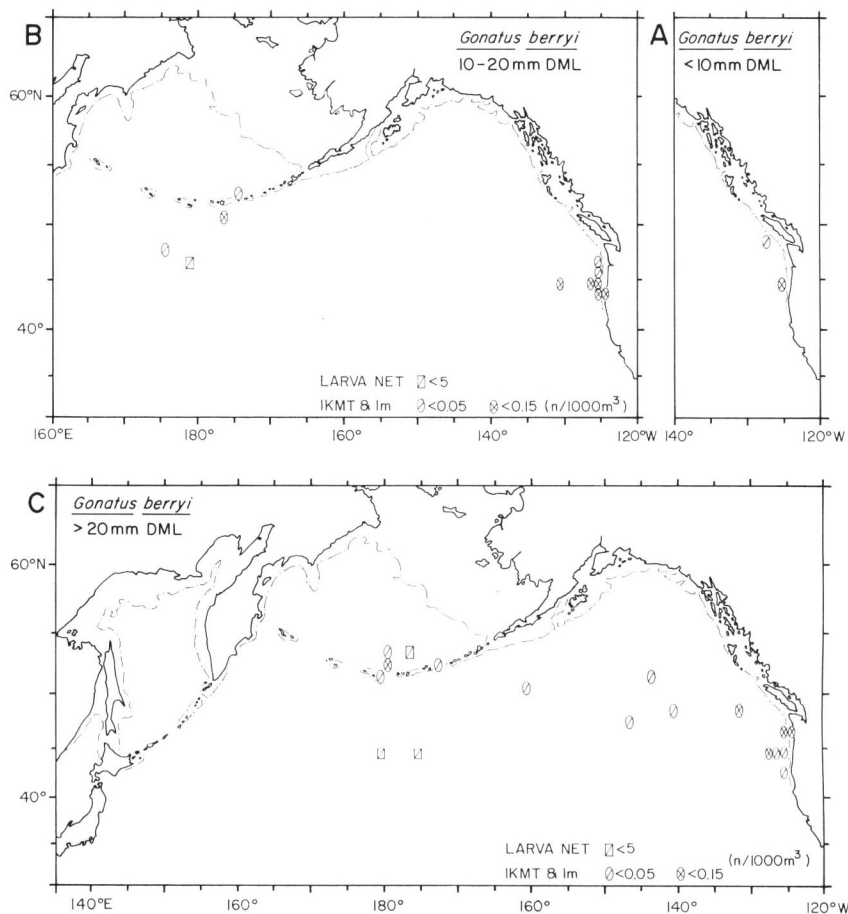


Fig. 4. Frequency of *Gonatus berryi*, by size. A; <10 mm DML, B; 10–20 mm DML, C; >20 mm DML.

A group of species with western northern North Pacific distributions included *Gonatus middendorffi*, *Gonatopsis octopedatus* and *Gonatopsis* type A KUBODERA. The range of *Gonatus middendorffi* is mostly included between 160°E and 170°W, although some larval individuals (<10 mm DML) were recorded off Hokkaido and the southern Kuriles (Figs. 9A–C). Larvae were never taken in the Bering Sea, and adolescents (>30 mm DML) only occasionally, but post-larvae were frequently abundant there. The two species of *Gonatopsis* were taken only in the Sea of Okhotsk, off southwestern Kamchatka (Fig. 10).

The remaining Gonatidae are divisible into two broadly-distributed Subarctic groups: those which were rarely or never caught in the Sea of Okhotsk, and those which occurred there routinely. Among the first group are *Gonatus* type A KUBODERA and OKUTANI 1981b, *Gonatopsis borealis* and *Berryteuthis anonychus*. *Gonatus* type A,

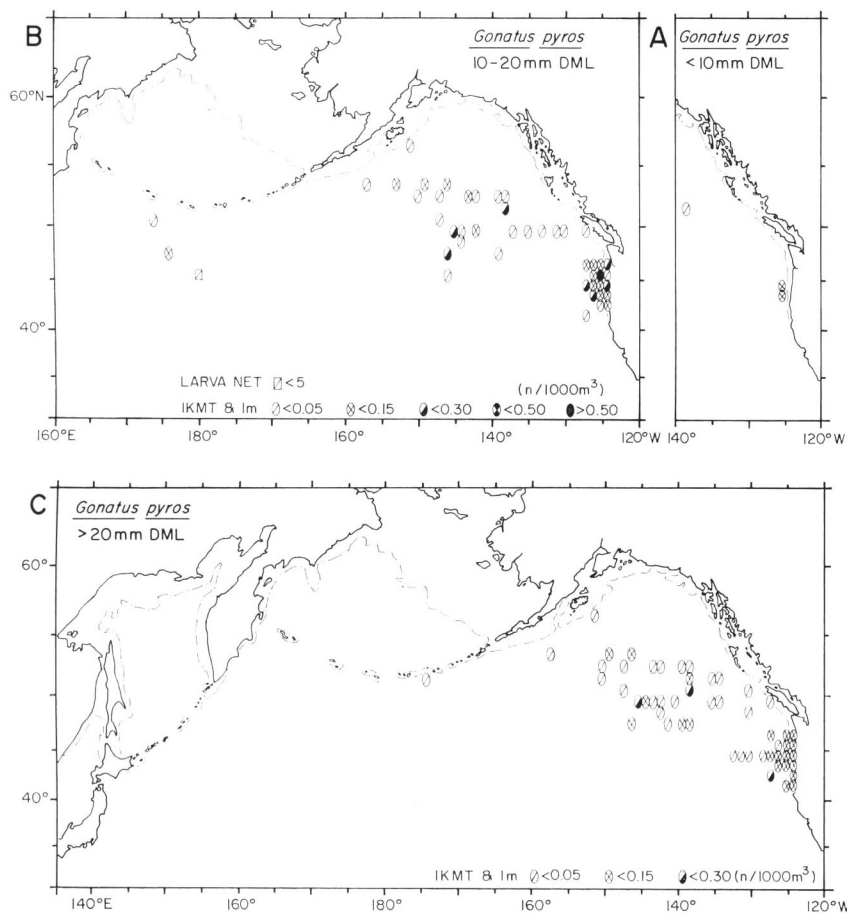


Fig. 5. Frequency of *Gonatus pyros*, by size. A; <10 mm DML, B; 10–20 mm DML, C; >20 mm DML.

although very rarely taken in the Sea of Okhotsk (Figs. 11A–B), seemed to be much more frequent in the western North Pacific than in the east. Larvae (<10 mm DML) and post-larvae (10–18 mm) commonly occurred over the deeper portions of the Bering Sea, south and southwest of the Aleutians, and south of the Kuriles. Animals in both size ranges occurred in the Gulf of Alaska and off the American coast, although the smaller group was somewhat more frequent and abundant off the Oregon and Washington coasts.

Gonatopsis borealis occurred across the northern North Pacific; the rare Okhotsk occurrences were of large (>30 mm DML) individuals (Figs. 12A–C). Relative to the other size classes, larvae (<10 mm) were especially abundant in the Bering Sea and south of the western Aleutians. The distributions of larvae and post-larvae were otherwise very similar. The general lack of adolescent captures is probably related to an

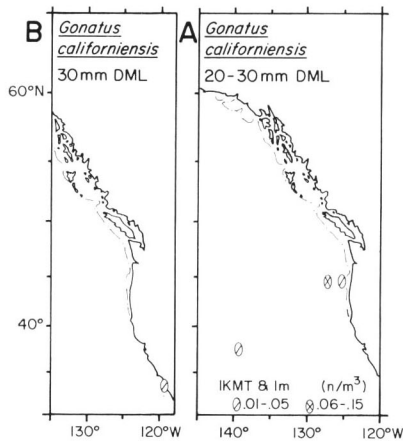


Fig. 6. Frequency of *Gonatus californiensis*, by size. A; 20-30 mm DML, B; >30 mm DML.

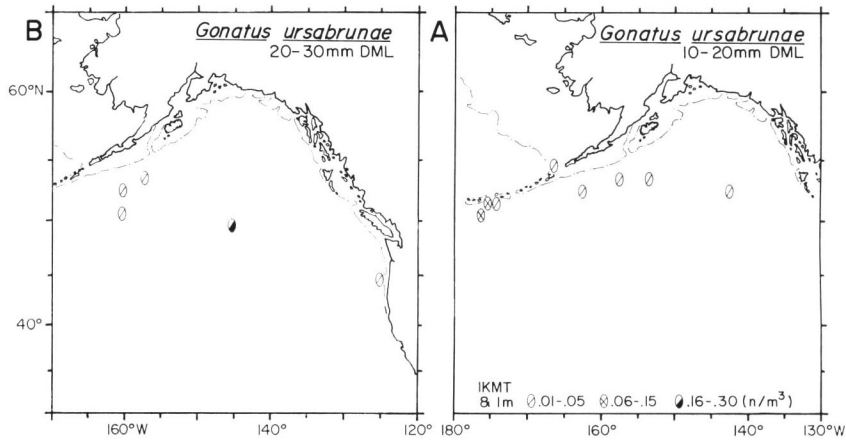


Fig. 7. Frequency of *Gonatus ursabrunae*, by size. A; 10-20 mm DML, B; 20-30 mm DML.

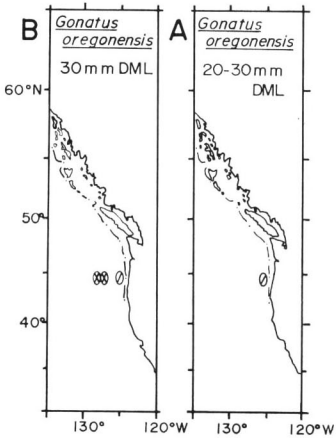


Fig. 8. Frequency of *Gonatus oregonensis*, by size. A; 20-30 mm DML, B; >30 mm DML.

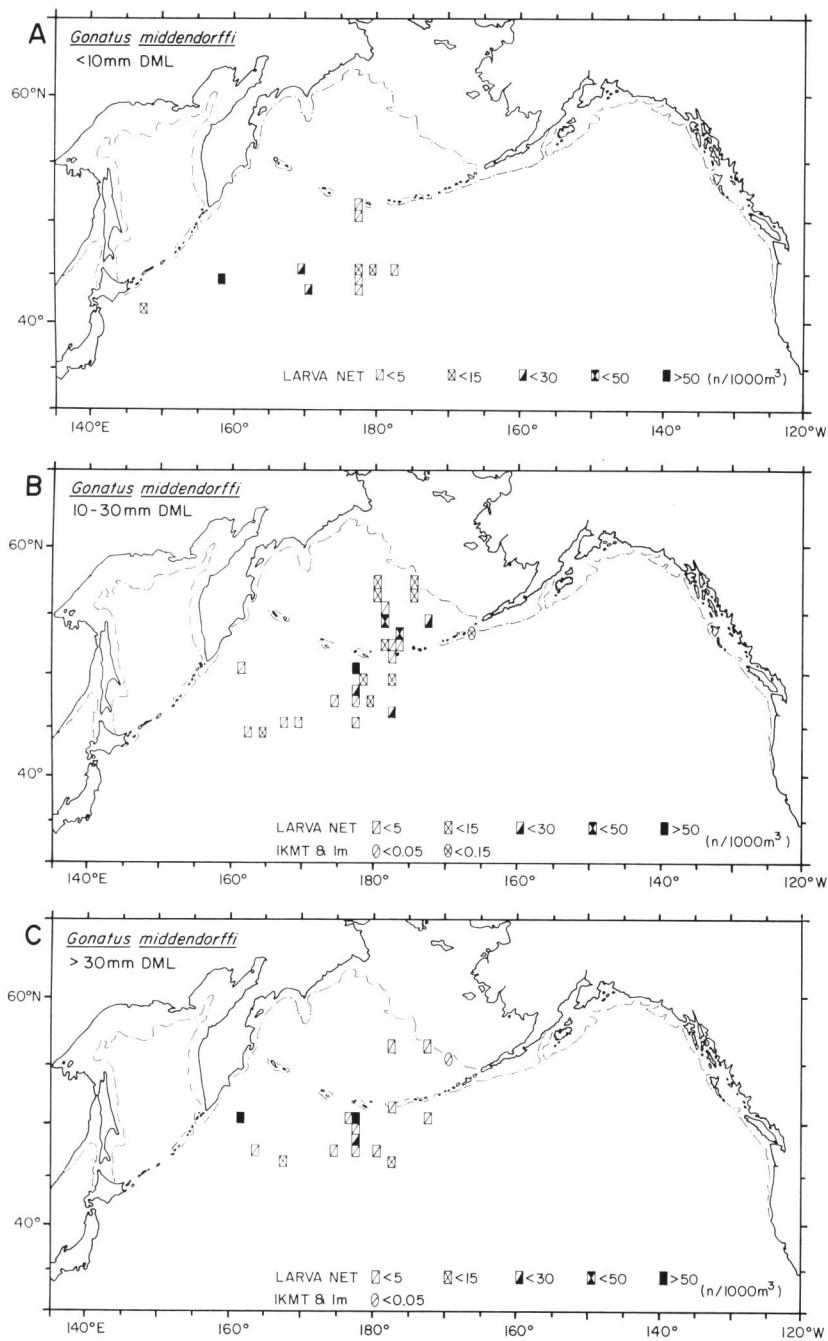


Fig. 9. Frequency of *Gonatus middendorffi*, by size. A; <10 mm DML, B; 10–30 mm DML, C; >30 mm DML.

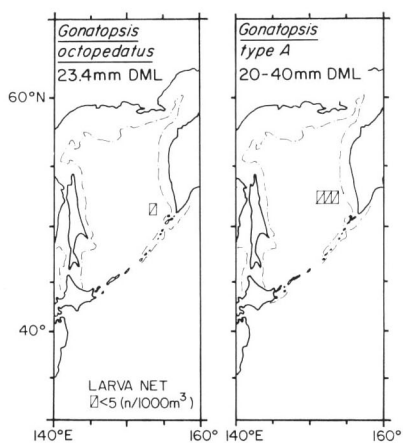


Fig. 10. Occurrence of *Gonatopsis octopedatus* and frequency of *Gonatopsis* type A, 20-40 mm DML.

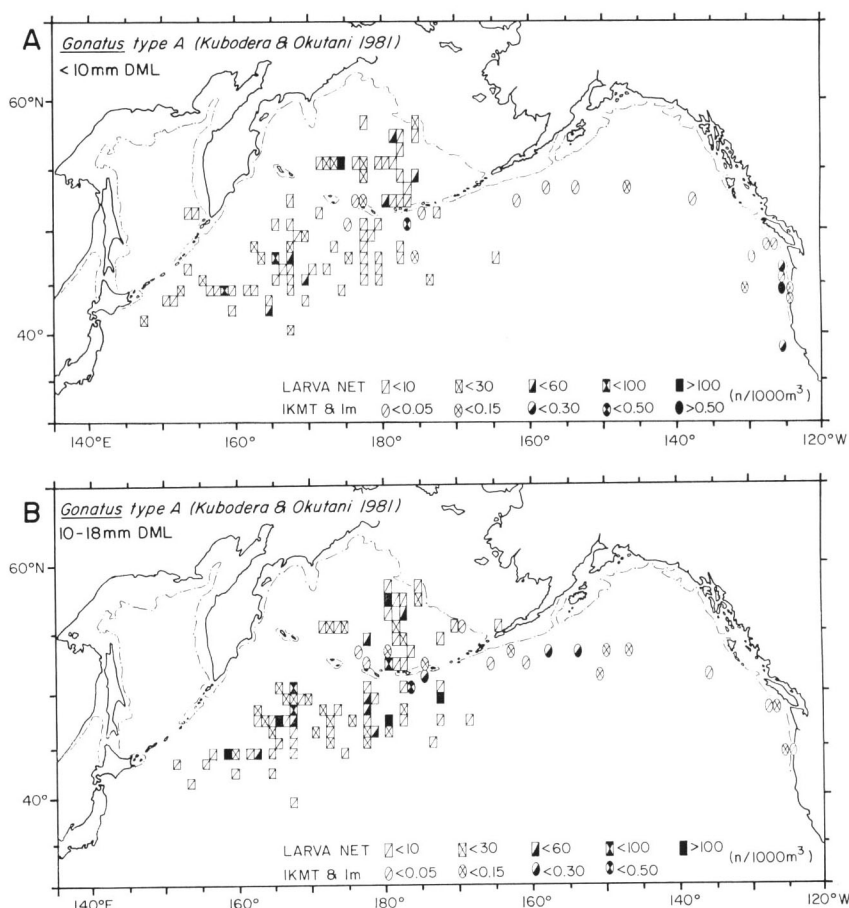


Fig. 11. Frequency of *Gonatus* type A, by size. A; <10 mm DML, B; 10-18 mm DML.

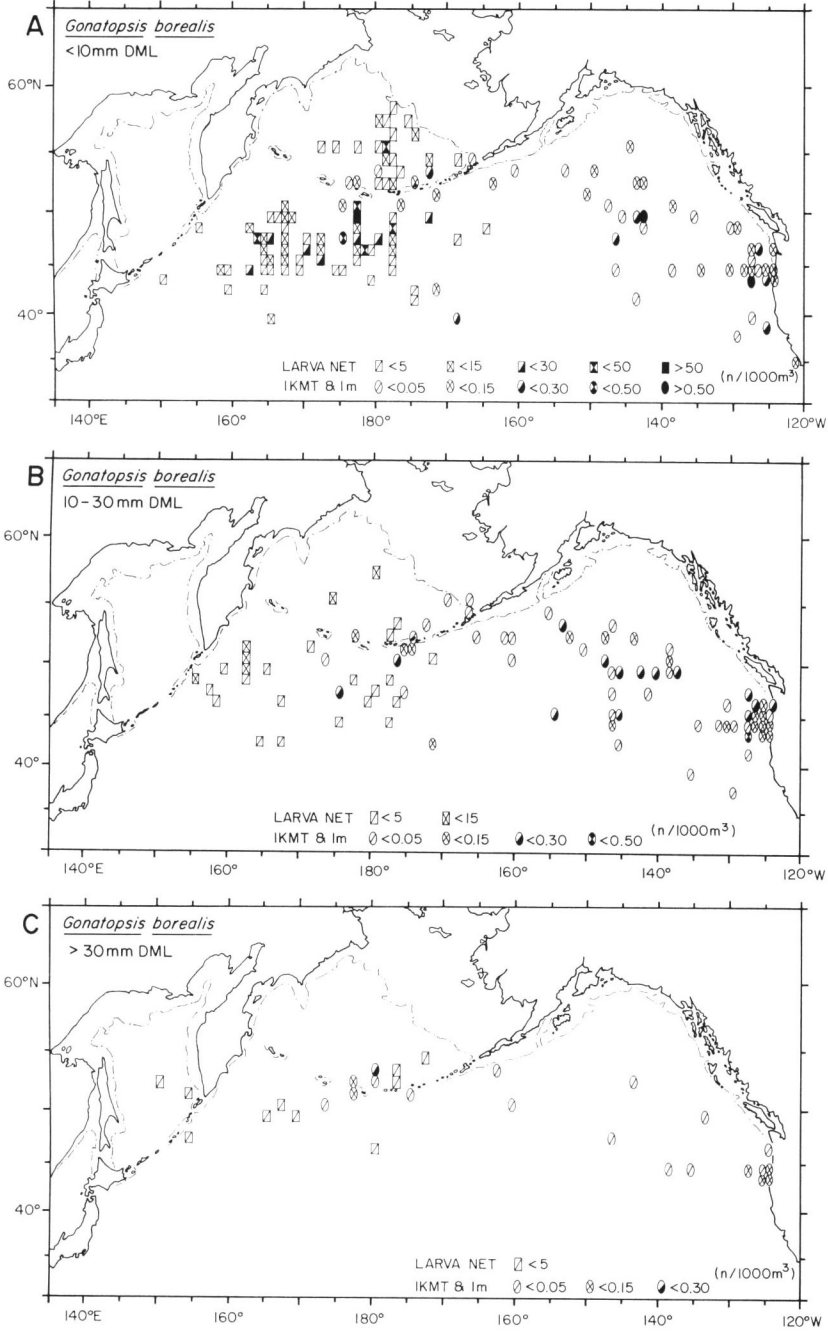


Fig. 12. Frequency of *Gonatopsis borealis*, by size. A; <10 mm DML, B; 20-30 mm DML, C; >30 mm DML.

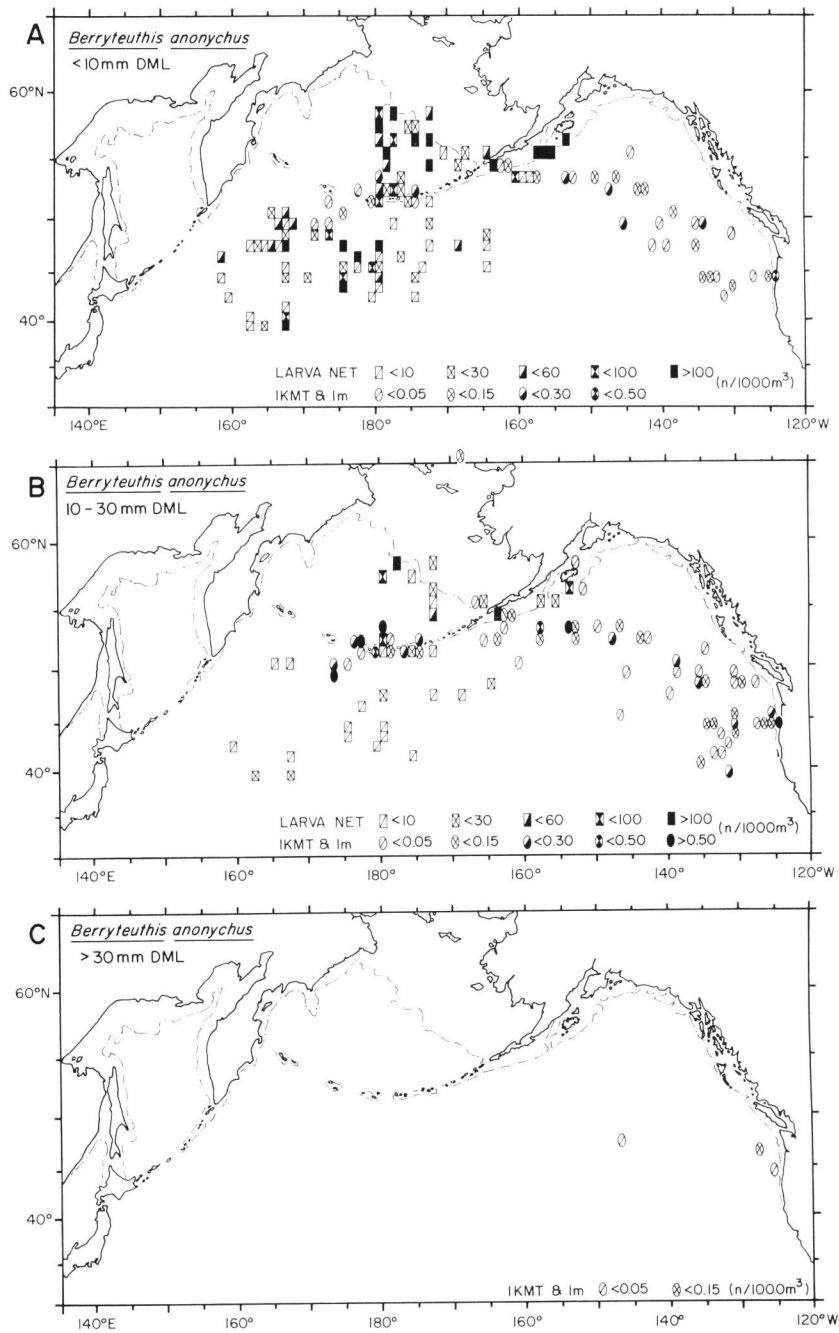


Fig. 13. Frequency of *Berryteuthis anonychus*, by size. A; <10 mm DML, B; 10–30 mm DML, C; >30 mm DML.

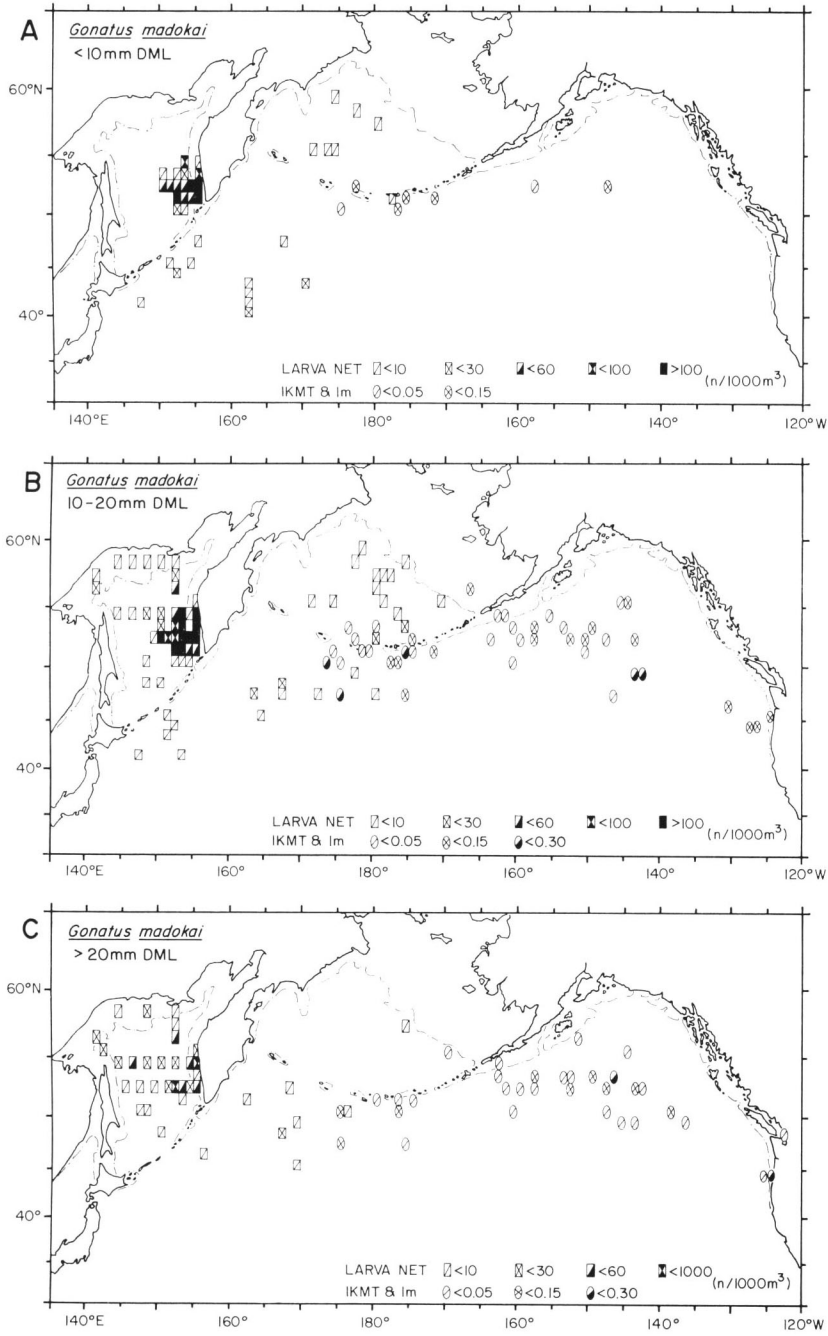


Fig. 14. Frequency of *Gonatus madokai*, by size. A; <10 mm DML, B; 10–20 mm DML, C; >20 mm DML.

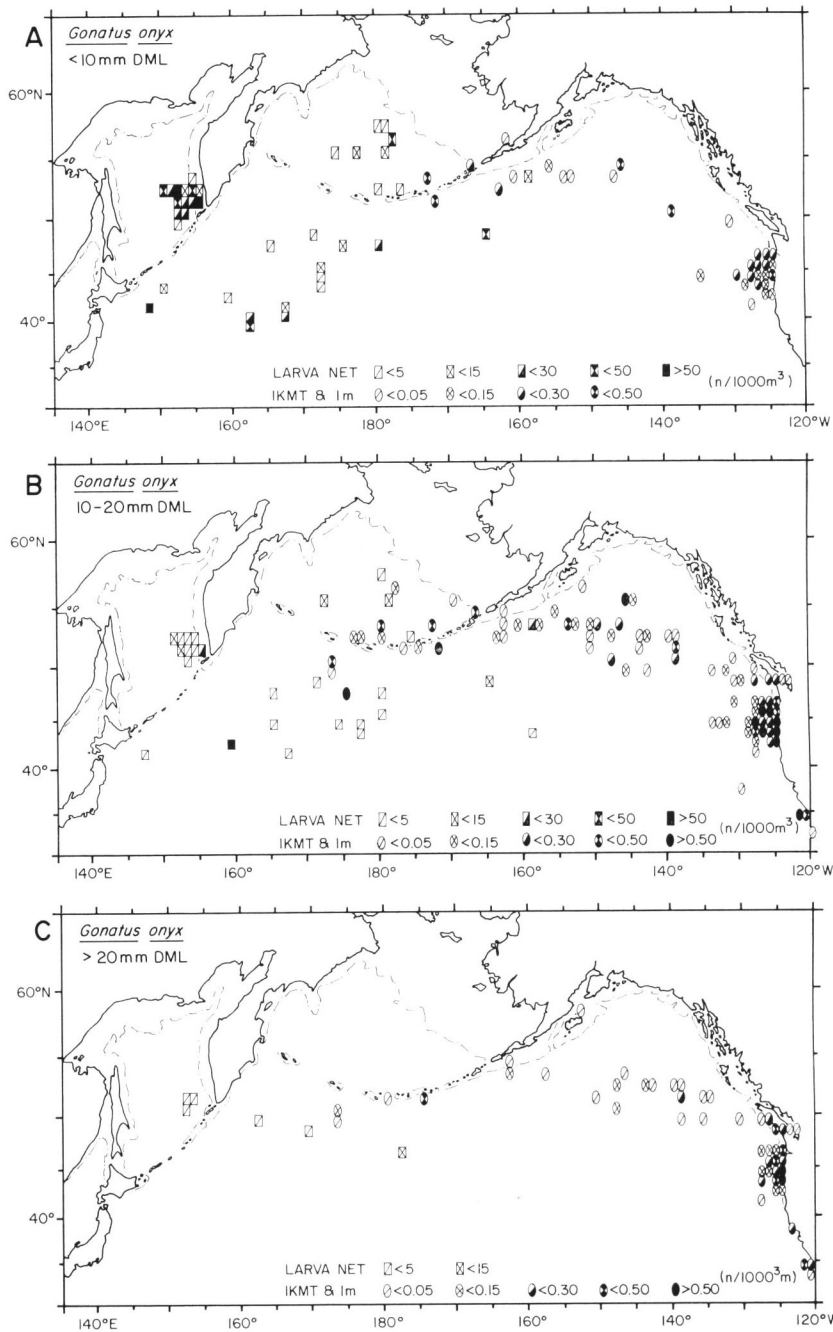


Fig. 15. Frequency of *Gonatus onyx*, by size. A; <10 mm DML, B; 10-20 mm DML, C; >20 mm DML.

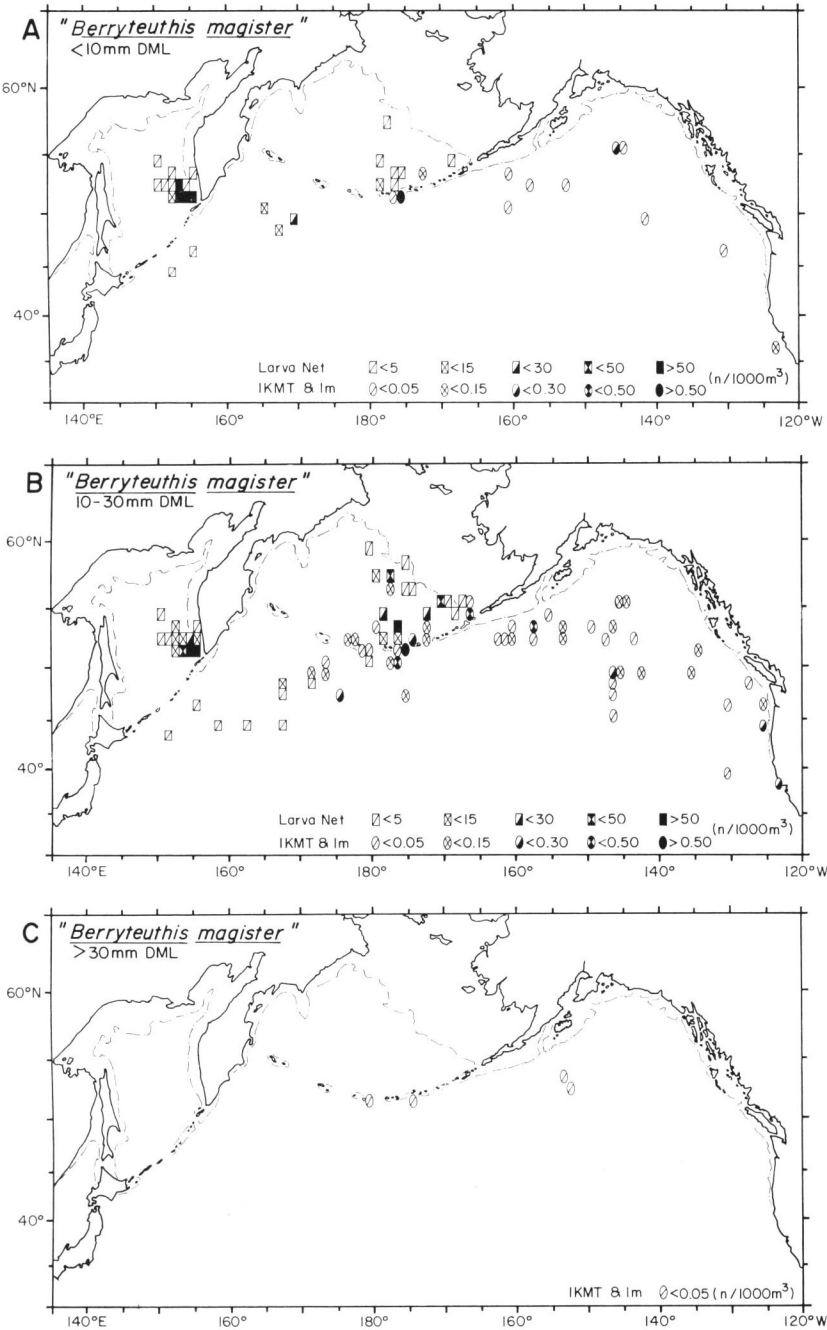


Fig. 16. Frequency of "*Berryteuthis magister*", by size. A; <10 mm DML, B; 10–30 mm DML, C; >30 mm DML.

ability to avoid the sampling gear.

The larvae (<10 mm DML) and post-larvae (10–30 mm) of *Berryteuthis anonychus* were abundant across the northern North Pacific, especially in the Bering Sea (Figs. 13A–C). This species was much less abundant off the coast of the United States and British Columbia than was *G. borealis*. Adolescents (>30 mm) were very rare, again probably because of net avoidance. A tendency for the larvae to be more abundant and frequent than post-larvae in the area south of the western Aleutians and in the Bering Sea is evident in the distributions of both these species.

The remaining species occurred across the northern North Pacific and were frequently taken in the Sea of Okhotsk. *Gonatus madokai*, although found across the Subarctic, was obviously more abundant in the northwestern Pacific (Figs. 14A–C). This species was very rare in the California Current system. Maximum abundances for all size groups occurred in the Sea of Okhotsk, although occasional high catches occurred south of the Aleutians and Gulf of Alaska. Post-larvae (10–20 mm DML) and adolescents (>20 mm) had somewhat broader distributions than larvae.

Gonatus onyx also occurred across the northern North Pacific, including the southern Sea of Okhotsk and Bering Sea (Figs. 15A–C). Peak abundance of the larvae (<10 mm DML) occurred in the southeastern Sea of Okhotsk and off the American coast. Post-larvae (10–20 mm) had a somewhat more extensive distribution in the eastern North Pacific. Adolescents were absent from the Bering Sea and rare in the Sea of Okhotsk, but were generally less abundant, again suggesting net avoidance.

“*Berryteuthis magister*” was broadly distributed across the northern North Pacific, occurring in both the Okhotsk and Bering seas (Figs. 16A–C). Abundance maxima for larvae (<10 mm DML) and post-larvae (10–30 mm) occurred in the southeastern Okhotsk Sea and southcentral Bering Sea. Post-larvae occurred more frequently than either other size class. The lack of large individuals is probably attributable to net avoidance.

*Seasonal and geographic occurrence of various
life stages in the family Gonatidae²⁾*

Gonatus berryi, although fairly abundant in the IKMT samples, was only rarely taken by Larva net (Fig. 17). Larvae were present from May to November in the eastern North Pacific, and adolescent animals from late May to January. Post-larvae were present essentially year round. The numbers of individuals collected were too low to allow any meaningful statistical analysis of growth or spawning period, although peak catches of larvae occurred in June and August, and of post-larvae in November.

Gonatus pyros was taken only once by Larva net, but was the second most abundant *Gonatus* in the eastern North Pacific IKMT samples (Fig. 18). Larvae were very infrequent, but occurred in widely separated months: February, June, July, and September.

2) We wish to emphasize that year round collections were available only from the IKMT-metre net samples from waters off Oregon.

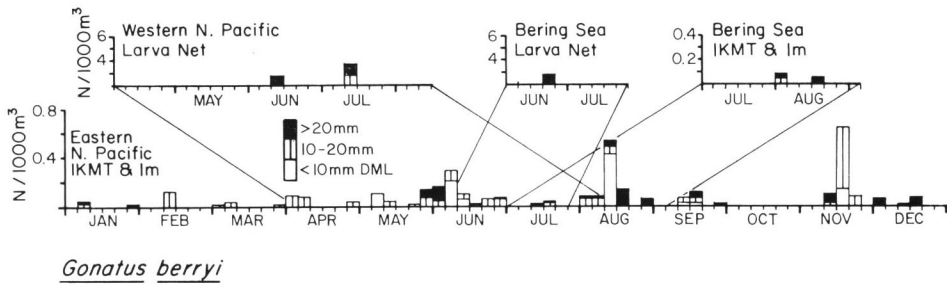


Fig. 17. Seasonal and geographic occurrence of various size classes of *Gonatus berryi*.

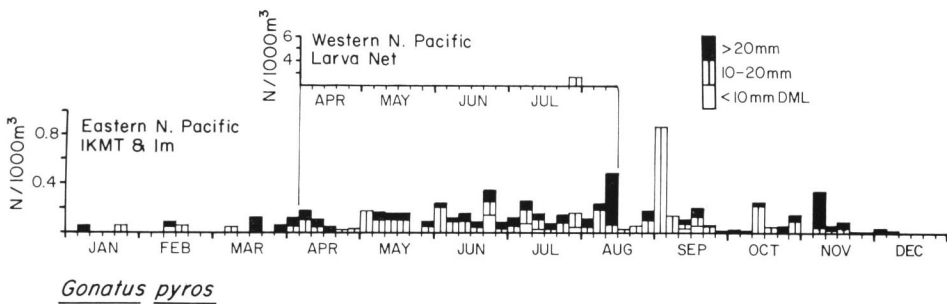


Fig. 18. Seasonal and geographic occurrence of various size classes of *Gonatus pyros*.

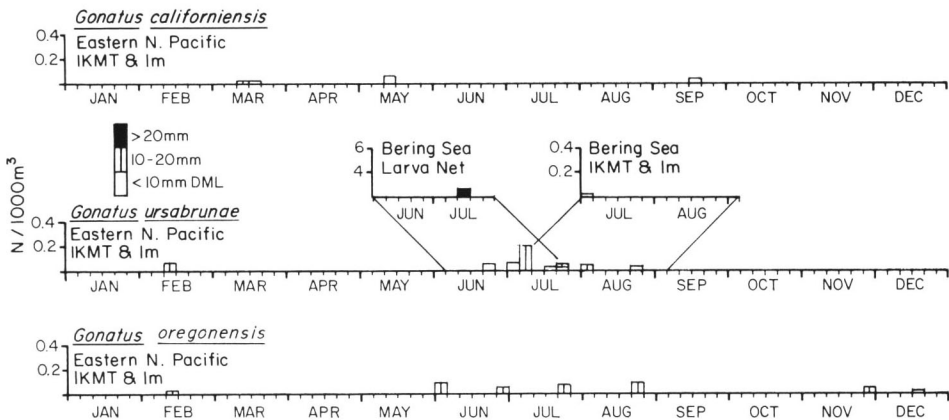


Fig. 19. Seasonal and geographic occurrences of various size classes of *Gonatus californiensis*, *Gonatus ursabrunae* and *Gonatus oregonensis*.

ber. Post-larvae were present throughout the year, but showed peak abundances from late spring to late summer. Adolescents were present in every month; high abundances occurred in August and November.

Gonatus californiensis was rare, occurring only in eastern North Pacific IKMT samples (Fig. 19). Larvae were collected in March, May, and September, and post-

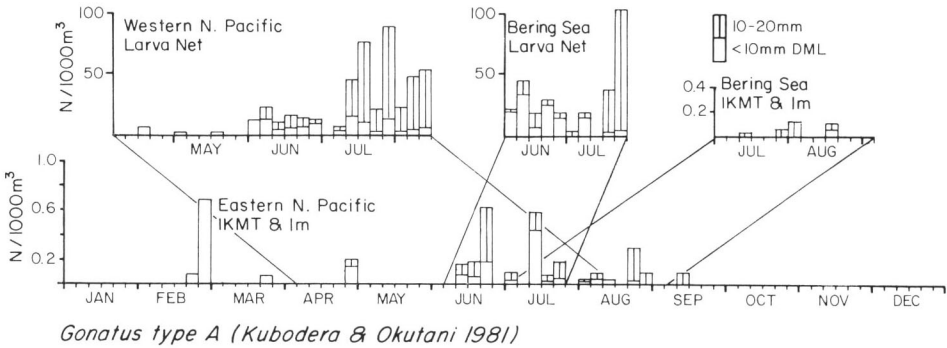


Fig. 20. Seasonal and geographic occurrence of various size classes of *Gonatus* type A Kubodera and Okutani 1981b.

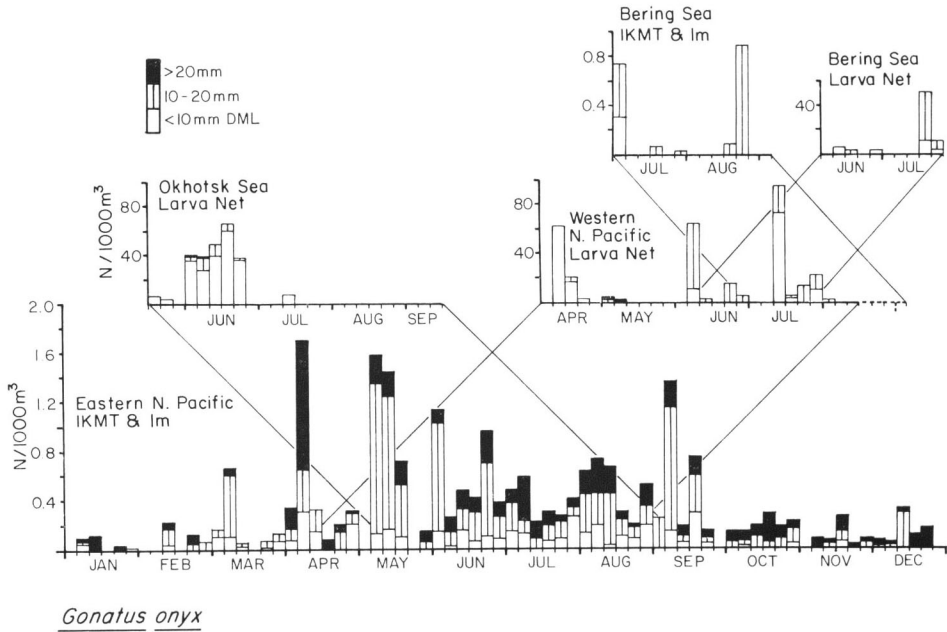


Fig. 21. Seasonal and geographic occurrence of various size classes of *Gonatus onyx*.

larvae in March.

Gonatus ursabrunae was taken in the eastern North Pacific and Bering Sea, both by IKMT and Larva net (Fig. 19). Larvae and post-larvae were collected primarily during the late June to early August period; the only Larva net sample was of an adolescent in July. Low abundances prevent any further conclusions.

Gonatus oregonensis was taken only in the eastern North Pacific (Fig. 19). The only larval collection was made in December; post-larvae were sampled in February, June, July, and August. Low abundances preclude any further conclusions.

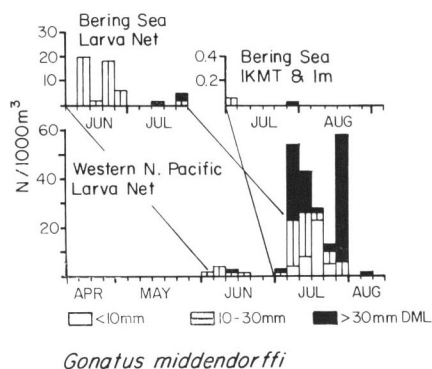
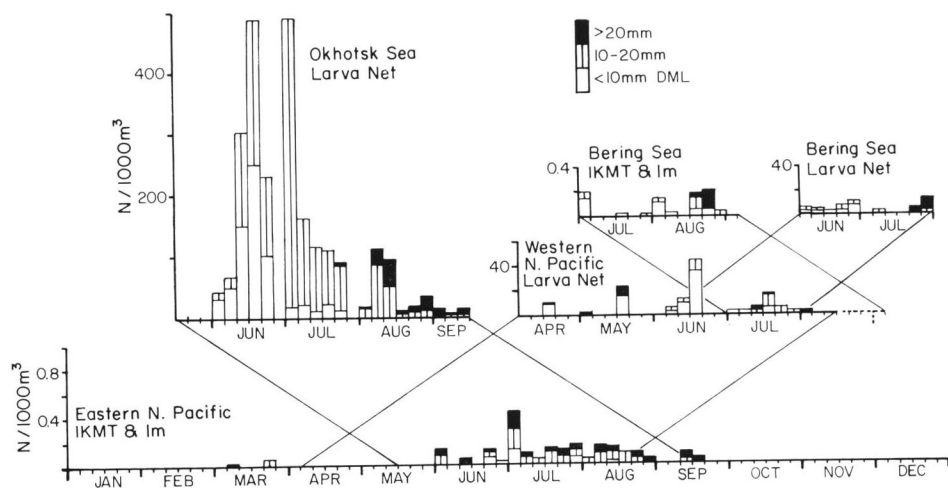


Fig. 22. Seasonal and geographic occurrence of various size classes of *Gonatus middendorffi*.

Gonatus type A KUBODERA and OKUTANI was taken across the Subarctic Pacific with both gear types (Fig. 20). The year-round samples showed high larval abundances both in February and during the summer; post-larvae were present primarily during summer months. The western Pacific Larva net samples show an increasing abundance of post-larvae during early to mid-summer. The Bering Sea samples show a decreasing abundance of larvae during this period, accompanied by an increasing abundance of post-larvae. No adolescents were collected. These data are suggestive of a spring hatching period, with growth from the larval to post-larval stage (which is probably not fully vulnerable to the sampling gear) during early to mid-summer in the Bering Sea and northwestern Pacific.

Gonatus onyx was taken in all areas sampled (Fig. 21). The eastern North Pacific samples show the presence of larvae nearly year round. There is perhaps some indication that the samples have a greater proportion of post-larvae and adolescents than larvae during the later months of the year. Overall abundance falls off sharply at the onset of autumn, not to rise again until April. Larvae are abundant in the Okhotsk Sea in June, but apparently absent later in the summer. *Gonatus onyx* is only occasionally present in the western Pacific and Bering Sea, but when present, tends to be quite abundant. Very few adolescents were taken in these areas. The samples from later months tend to be composed more of post-larvae than larvae, relative to earlier sampling periods. The data do not suggest a synchronous or limited spawning or hatching period.

Gonatus middendorffi occurred primarily in the western Pacific samples; the only IKMT samples were from the Bering Sea in July (Fig. 22). The sample for this species is therefore limited to late spring and summer months. The Bering Sea samples show an apparent progression from post-larvae in June to adolescents in July. The western North Pacific samples show a rapid increase in frequency in July. Larvae are present in this area only during mid July. Post-larvae are present, but infrequent, during June, and show a rapid increase in availability during July. Adolescents are present primarily during July with very small catches during June and August. These limited



Gonatus madokai

Fig. 23. Seasonal and geographic occurrence of various size classes of *Gonatus madokai*.

data suggest a spawning or hatching period fairly well limited to a time immediately previous to July. With no data on growth rate for the larvae, we cannot pinpoint the precise hatching period, but it probably occurs in May or June.

Gonatus madokai also occurred throughout the sampling area, but is significantly more frequent in the western Pacific (Fig. 23). In the eastern North Pacific, this species is present in March and from June to September. Larvae occur only from late June to mid-August; post-larvae and adolescents were collected throughout the cited time span. In the western Pacific samples, larvae and adolescents were present from April to early August; post-larvae did not appear until early to mid-June. The Bering Sea samples show larvae and post-larvae from June through August, but adolescents are not present until late July and August. The Okhotsk Sea samples were abundant and showed a very clear pattern. Larvae first appeared in early June, and were present until late July. Post-larvae also first appeared in early June and rapidly increased in importance until tailing off in late August and September. Adolescents did not appear until late July but persisted until the end of the sampling period. This indicates a spawning/hatching period immediately prior to June. We cannot precisely identify this period in the absence of other data, but we think it likely occurs in early to late spring.

Gonatopsis type A KUBODERA was collected only by Larva net in the Sea of Okhotsk (Fig. 24). Post-larvae and adolescents were taken in June and July.

Gonatopsis octopedatus occurred only as adolescents in the Sea of Okhotsk during May (Fig. 24).

Gonatopsis borealis was taken in all areas sampled (Fig. 25). In the eastern Paci-

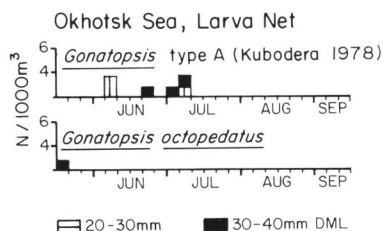
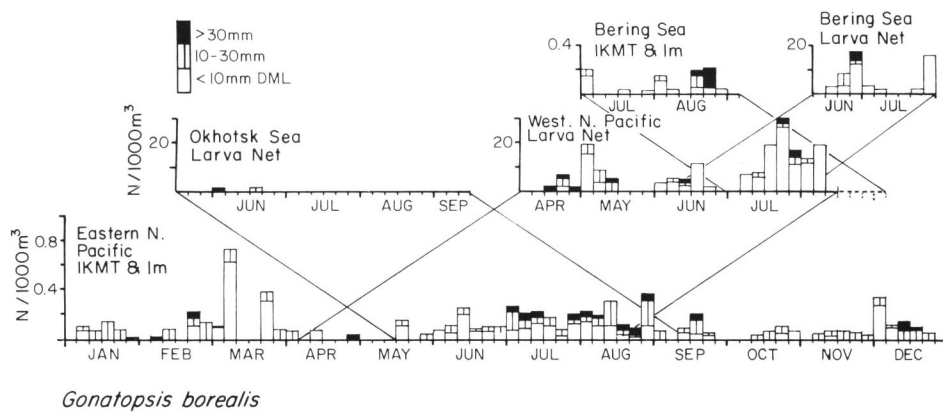


Fig. 24. Seasonal and geographic occurrences of various size classes of *Gonatopsis* type A Kubodera 1978 and *Gonatopsis octopedatus*.

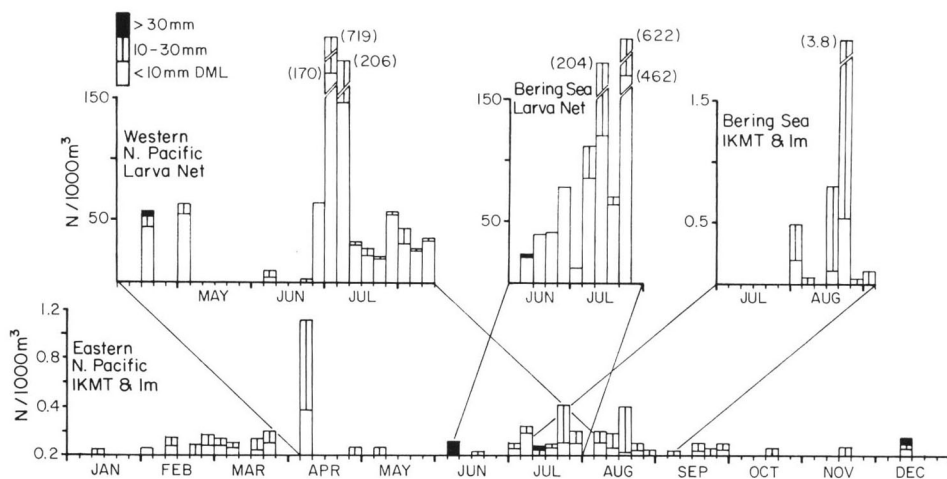


Gonatopsis borealis

Fig. 25. Seasonal and geographic occurrence of various size classes of *Gonatopsis borealis*.

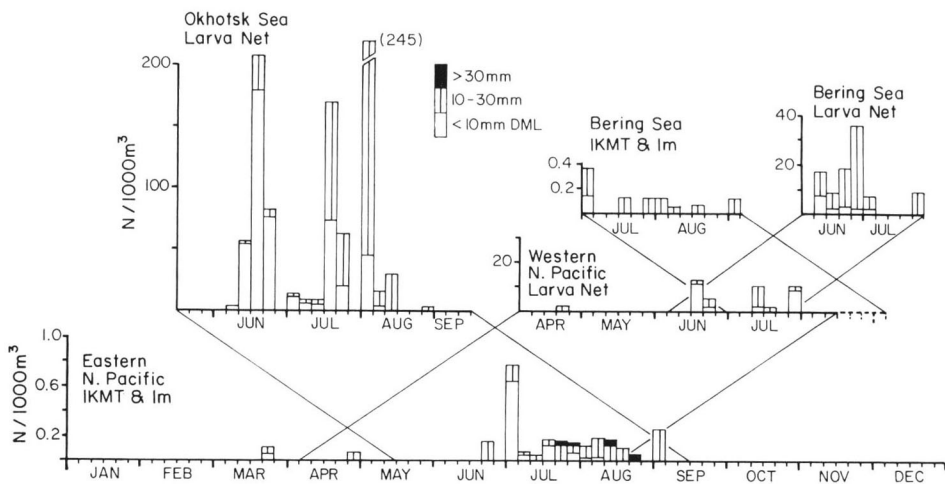
fic, larvae and post-larvae occurred year round, but adolescents seemed to be most frequent in mid to late summer, with perhaps a second peak in late winter. All size classes occurred during the months sampled in the western North Pacific, although there was an indication of greater frequency of larvae during July and early August. The Bering Sea samples were sparse: IKMT samples indicated only larvae and post-larvae during July, and all three size classes in August, while Larva net samples showed only larvae during July after taking all size classes during June. Post-larvae and adolescents occurred in the Sea of Okhotsk in June. There is thus little evidence for a synchronous or limited hatching period in this species.

Berryteuthis anonychus was taken in all sampling areas except the Sea of Okhotsk (Fig. 26). Adolescents were nearly absent from the samples, probably indicating good avoidance capability. In the eastern North Pacific, there is some indication of two abundance peaks, one from July to September, and another from February to April. The summer peak shows some tendency for post-larvae to become more frequent than larvae toward late August and September. The western North Pacific samples show very large frequencies of post-larvae during the first part of July. Larvae and post-larvae are present most consistently and frequently during late June and July. A



Berryteuthis anonychus

Fig. 26. Seasonal and geographic occurrence of various size classes of *Berryteuthis anonychus*.



"Berryteuthis magister"

Fig. 27. Seasonal and geographic occurrence of various size classes of *"Berryteuthis magister."*

similar pattern is seen in the Bering Sea Larva net samples, although the major peak is just a bit later in July. The Bering Sea IKMT samples show a major peak in late August. This pattern seems to indicate a successive spawning/hatching pattern across the Subarctic Pacific from west to east.

"Berryteuthis magister" was present in all areas sampled (Fig. 27). In the eastern North Pacific, it was present from late March to early September, but frequent only in summer. Larvae tended to be more abundant in early summer, and post-larvae and

adolescents to be more abundant in late summer. Adolescents were absent from all other areas. The western North Pacific samples were few, and were confined to April, June, and July. In the Bering Sea, post-larvae were much more frequent than larvae, and were present throughout the periods sampled (June to early September). This taxon was present in the Sea of Okhotsk from June to August. Earlier samples were primarily larvae, while later samples were dominated by post-larvae. The possible identification problem for this group of organisms clouds any conclusions. The general absence of adolescents may reflect either the identification problem—i.e., the larger animals are more easily identified as *G. tinro*, or something else, other than *B. magister*—or it may reflect the increased net avoidance ability of larger animals. However, the shift in dominance from larvae early in the summer to post-larvae late in the summer should reflect real growth in the group in question.

Growth estimation for Gonatus madokai in the Okhotsk Sea

Estimation of growth in the early period of life from field samples is often very difficult due to the addition of small individuals during the sampling period, avoidance and migration of large individuals from the sampling gear and area, and mixing with groups from different spawning areas and hatching periods.

In the present material, only *Gonatus madokai* exhibited characteristics which allowed a reliable estimation of growth rate in the early life stages. This species spawned in a localized area in the Sea of Okhotsk, had a relatively short hatching period, based on the short period of occurrence of larvae, and long period of occurrence with successive apparent changes from larval to adolescent stages. Figure 28 shows the serial size range and mean dorsal mantle length for each sampling day for Larva net samples in the Okhotsk Sea from 1 June to 6 September, 1976. The narrow size range of 7–12 mm DML in early June shifted to a larger and wider size range of 13–33 mm DML by early September, indicating growth during the sampling period. However, the addition of small individuals of about 7 mm DML seemed to continue from June to early July; the growth rate deduced from the mean size of each sampling day was thus considered to be an underestimate. Therefore the growth rate of *G. madokai* was calculated using the largest size of each sampling day.

An exponential growth curve best fits the data. With time in days as the abscissa (1 June at the origin) and DML in mm as the ordinate, the growth curve for *G. madokai* is:

$$Y = 9.1545 e^{0.0134X}$$

$$\text{or,} \quad \ln Y = \ln 9.1545 + 0.0134X \quad (\text{Fig. 29}).$$

$$(R=0.969, p<0.001, df=55)$$

Although no information is available for growth rates of early life stages of pelagic squid in the northern North Pacific, monthly growth rates for the closely related North Atlantic species *Gonatus fabricii* have been reported. NESIS (1965) estimated the month-

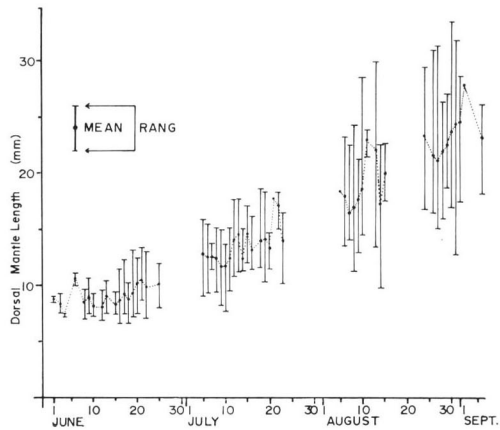


Fig. 28. Serial size variations in the early life stages of *Gonatus madokai* in the Okhotsk Sea in 1976.

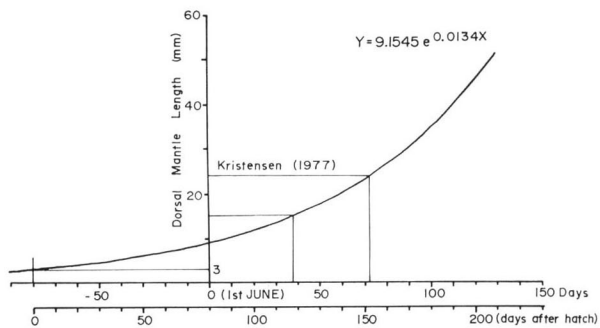


Fig. 29. Estimated growth curve of *Gonatus madokai* in the early life stages in the Okhotsk Sea, 1976.

ly growth rate of *G. fabricii* by comparing samples collected in July and August from different areas and years; he reported a growth rate of 11–12 mm per month. KRISTENSEN (1977) examined growth rate more precisely by considering the influence of addition of small individuals on changes of average ventral mantle length from month to month; he estimated 8 mm growth per 30 days. This monthly growth rate for *G. fabricii* is in good agreement with that for *G. madokai* in that size range (Fig. 29).

The size at which *Gonatus madokai* hatches is not known. KRISTENSEN (1977) roughly estimated that *Gonatus fabricii* in the North Atlantic hatched at about 3 mm ventral mantle length. This hatching size lies within the known size range for pelagic squid: 1 mm for *Todarodes pacificus* (HAMABE, 1962; OKIYAMA, 1965) to 5 mm for *Loligo bleekeri* (HAMABE, 1960). Assuming that the hatching size of *G. madokai* is similar to that for *G. fabricii*, individuals of 10 mm DML are probably about 3 months post hatching. Judging from the occurrence of small individuals, the hatching period

of *G. madokai* in the Okhotsk Sea is estimated as March to May with a peak in early April. The same estimate for *G. madokai* in the northern North Pacific suggests a hatching period from February to early June. Some large individuals (>70 mm DML) which were occasionally caught in April in the northwestern North Pacific (KUBODERA and OKUTANI, 1977) might be one year old. The size of the largest known specimen (Table 4) suggests that the life span of *G. madokai* is probably at least two years.

Discussion

Sampling programs

The data upon which conclusions in this paper are based derived from two rather different sampling programs. The northwestern Pacific program (Larva net) utilized gear which was fished in limited vertical strata and only during summer months and with different physical dimensions (mouth opening and mesh size) relative to the northeastern Pacific program (IKMTs). It is therefore reasonable to expect that these two programs would have sampled different segments of the cephalopod community. However, many of the differences can be related to a reduced ability of squids to avoid the larger (IKMT) nets. The IKMTs often captured larger individuals of certain species and more frequently captured the robust, fast-swimming species. Despite their differences in collection methods and incomplete seasonal coverage, these two extensive data sets are the only suitable ones extant and provide new and useful information on the distribution of cephalopods in the northern North Pacific.

Dominance of Gonatidae in the Subarctic Pacific

The pelagic cephalopod fauna of the Subarctic Pacific is dominated by the family Gonatidae. Data collected in all geographical areas and with both gear types show gonatids to be the dominant element. The family comprised over 90% of cephalopods collected in all areas and with both gear types, with the exception of California Current IKMT collections. That area is oceanographically and faunally complicated by the addition of subtropical elements, yet Gonatidae still account for about 50% of the individuals. Collections from the Bering and Okhotsk seas were nearly exclusively gonatids. JEFFERTS (1983a) showed similar patterns for data collected with many gear types in the northeastern Pacific.

This family is of great import to the diets of many other nektonic organisms, including other cephalopods, fishes, marine mammals, and birds (SASAKI, 1920; AKIMUSHKIN, 1955; OKUTANI and NEMOTO, 1964; PANINA, 1964; FISCUS *et al.*, 1965; ANTONELIS *et al.*, 1980; KAJIMURA *et al.*, 1980; FISCUS, 1982). Very little is known of the dietary habits of the Gonatidae themselves. Immature individuals of *Berryteuthis magister* have been shown to consume only Crustacea, while the adults eat only small

fish and squid (NAITO *et al.*, 1977b). *Gonatopsis borealis* only occasionally had identifiable food in the gut; material examined consisted exclusively of small fishes (NAITO *et al.*, 1977b).

Distribution and Abundance

Distribution patterns of species in the family Gonatidae show good correlation with oceanographic features (cf. DODIMEAD *et al.*, 1963; FAVORITE *et al.*, 1976 for general oceanographic review). The following groups were apparent from our data:

- 1) Pan-Subarctic Pacific species: *Gonatus onyx*, *G. madokai*, "*Berryteuthis magister*."
- 2) Species occurring throughout the Subarctic Pacific except for the Sea of Okhotsk: *Gonatopsis borealis*, *Gonatus* type A KUBODERA and OKUTANI 1981b.
- 3) Species occurring from the California Current to Alaskan Stream: *Gonatus berryi*, *G. pyros*, *Gonatus ursabrunae*.
- 4) California Current endemics: *Gonatus californiensis*, *Gonatus oregonensis*.
- 5) Western Subarctic endemics: *Gonatus middendorffi*.
- 6) Species localized in the Sea of Okhotsk: *Gonatopsis octopedatus*, *Gonatopsis* type A KUBODERA 1978.

The Sea of Okhotsk and California Current showed faunal and gonatid species composition much different from the other regions. Only Gonatidae were collected in the Sea of Okhotsk, with *Gonatus madokai* the dominant form, and the geographically limited *Gonatopsis octopedatus* and *Gonatopsis* type A KUBODERA 1978 also present. The California Current area was characterized by a large number of *Gonatus* species, including two endemics, *G. californiensis* and *G. oregonensis*. The relatively closed current system and winter ice cover in the Sea of Okhotsk is likely one factor which has resulted in the unique and limited cephalopod fauna. Habitat complexity in the form of a large transitional area between Subarctic and subtropical waters in the California Current is likely one source of the large number of *Gonatus* species in that region.

Species of the family Gonatidae were classified into four groups according to the geographical pattern of relative abundance of early life stages. The first group characteristically has a high larval abundance in near-shore oceanic waters: *Gonatus madokai*, *G. onyx*, and "*Berryteuthis magister*." Conversely, in the second group larval abundance is highest in offshore waters: *Gonatus* type A KUBODERA and OKUTANI 1981b, *G. middendorffi*, and *Gonatopsis borealis*. The third group shows an intermediate pattern, and contains only *Berryteuthis anonychus*. Larvae of the fourth group are rarely or never caught; most of the remaining species are included here.

Dispersal from the spawning and/or hatching area should occur between spawning and hatching, or hatching and the time (size) at which young animals become available to the sampling gear. The pattern of abundance for the first group is thought to reflect a pattern of spawning and hatching at narrowly restricted areas intimately con-

nected with the continental slope. Spawning and/or hatching of *Gonatus onyx* is thus estimated to occur along the continental slope from northern Japan to California; the waters off southwestern Kamchatka in the Sea of Okhotsk, along the eastern Aleutians and off Oregon are thought to be more important spawning areas. Early life stages of *Gonatus onyx* have been reported (as *Gonatus fabricii*) from off Sanriku to eastern Hokkaido (OKUTANI 1966, 1968a) and off southern California (OKUTANI and MCGOWAN, 1969). *Gonatus madokai* is also thought to have a large spawning/hatching ground off southwestern Kamchatka in the Sea of Okhotsk, and other small spawning areas from off Hokkaido through the Kuriles and Aleutians to the Pacific coast of North America. "*Berryteuthis magister*" seems to have a more restricted spawning/hatching area than the previous two species; waters off southwestern Kamchatka in the Sea of Okhotsk, in the eastern Aleutians, and along the continental slope in the Bering Sea are estimated to be among the more important spawning areas. According to NAITO *et al.* (1977a), large numbers of adult *Berryteuthis magister* (no identification difficulty) have been taken by bottom trawl fisheries along the continental slope between 200 and about 1000 m from northern Japan through the Kuriles and Aleutians and Okhotsk and Bering seas. Occurrence of larval "*Berryteuthis magister*" agrees well with the known adult distribution; however, the absence of adolescent individuals in the present material suggests ontogenetic migration of larger individuals into the adult nektobenthic habitat.

The pattern of the second group may indicate that spawning and/or hatching takes place broadly throughout pelagic waters of the Subarctic Pacific. *Gonatus* type A KUBODERA and OKUTANI 1981b and *Gonatopsis borealis* are therefore considered to have broad offshore spawning/hatching areas in the Subarctic Pacific, with the exception of the continental shelf area of the Bering Sea and the entire Sea of Okhotsk. The spawning area of *Gonatus middendorffi* seems to be restricted to pelagic waters of the western Subarctic. NAITO *et al.* (1977a) and KUBODERA *et al.* (1983) reported broad epipelagic distribution of adult *Gonatopsis borealis* in the northern North Pacific, Bering Sea, and Sea of Okhotsk. The occurrence of early life stages is nearly identical to the adult distribution; however, the absence of larvae in the Sea of Okhotsk suggests an absence of spawning activity by *G. borealis* in that area.

Berryteuthis anonychus showed a pattern of relative abundance intermediate between the first and second groups. This pattern may indicate that spawning and/or hatching is loosely connected with near-shore oceanic waters, and that larvae disperse toward oceanic waters. The waters along the continental slope from the central to southern Bering Sea and from the Aleutian Islands to the Pacific coast of the Alaskan Peninsula are estimated to encompass a large spawning/hatching area of *B. anonychus*. Young individuals have been reported from stomach contents of short-tailed shearwaters in the southern Bering Sea (OGI *et al.*, 1980), and have frequently been found in the stomach contents of coho salmon and Pacific pomfret in the central northern North Pacific (KUBODERA and SHIMAZAKI, unpublished), indicating an epipelagic habitat for this species. FISCUS (*in litt.*, 18 Sept 83) noted that *B. anonychus* has now

been identified from the stomach of Pacific fur seal (*Callorhinus ursinus*). Current difficulties with beak identification are probably a factor in the low number of records from predator stomachs.

The absence and/or rare occurrence of larvae of species in the last group may be attributable to differences between time and area of sampling and their hatching period and habitat. ROPER and YOUNG (1975), reporting vertical distribution of pelagic cephalopods off southern California, demonstrated that *Gonatus californiensis*, *G. pyros*, and *G. berryi* were distributed between 200 and 1200 m with an upward shift at night, but they did not appear in the upper 100 m layer even at night. Adult *Gonatopsis octopedatus* have additionally been reported from both coasts of northern Japan as well as from the southern Sea of Okhotsk (SASAKI, 1920; AKIMUSHKIN, 1963; OKIYAMA, 1970; OGATA *et al.*, 1973; OKUTANI *et al.*, 1976). However, the present material includes by far the smallest individual ever taken (about 23 mm DML); this and other occurrences of small individuals in the Sea of Okhotsk may be construed as evidence of reproduction by this species in that area.

Spawning and hatching periods

The period of occurrence and timing of the rapid increase in frequency and abundance of early developmental stages is here considered to be closely correlated with spawning period and peak hatching time. We have year-round samples only from waters off Oregon, and those samples were taken during several years, but we believe some general trends in abundance of young pelagic cephalopods are evident. Abundance of early life stages is low in winter and spring, rises rapidly in early summer, and declines gradually in autumn. The timing of the rapid increase varies by geographic area and among species. In the Bering and Okhotsk seas, the abundance of early life stages increases rapidly beginning in June. Larvae of *Berryteuthis anonychus* and *Gonatus* type A KUBODERA and OKUTANI 1981b account for this increase in the Bering Sea, and *Gonatus madokai*, *G. onyx*, and "*Berryteuthis magister*" in the Sea of Okhotsk. The rapid increase is delayed until July in the northwestern North Pacific, and is composed of larvae and post-larvae of *Gonatus* type A KUBODERA and OKUTANI 1981b, *Gonatus middendorffi*, *Gonatopsis borealis*, and *Berryteuthis anonychus*. Early life stages occur nearly year round off Oregon: larvae and post-larvae of *Gonatus onyx*, *Gonatus* type A KUBODERA and OKUTANI 1981b, and *Gonatopsis borealis* are abundant from April through the summer, and young of *Gonatus berryi*, *G. pyros*, and *G. onyx* show a small peak in late summer.

These regional differences in timing and pattern of abundance of young gonatids are likely associated with availability of appropriate food organisms. Larvae and post-larvae of most gonatid species have very similar external morphology, with small ovoid fins and a bell-shaped, thin-walled mantle, suggesting adaptation to planktonic life. They generally also have weak arms with undeveloped arm armatures and relatively robust tentacles, the clubs of which are not yet developed. The tentacle stalks bear

many minute (0.05–0.1 mm diameter) suckers on the oral surface, suggesting that the larvae and post-larvae depend on small food organisms such as nauplii or copepodites. The notable exception to this pattern is *Gonatus berryi*, which develops arm hooks at a very small size (under 10 mm DML). This species probably has a very different food supply.

The hatching period and peak hatching time for “normal” gonatid squid in the North Pacific is thus probably correlated with increasing abundances of crustacean larvae just after the spring phytoplankton bloom. This postulated relationship between regional differences of hatching period and increasing abundance of crustacean larvae is one of the more important areas for future research.

Growth rates in Subarctic Gonatidae

Growth rates for young of gonatid squid in the North Pacific have not been reported heretofore. Possible comparisons include growth rates of gonatids in the North Atlantic (KRISTENSEN, 1977) and of other taxa in the Subarctic Pacific. Growth rates have seldom been investigated for non-commercial species, or for young stages of any species, which further narrows the comparative possibilities. Growth rates have been derived for such commercially important species as *Todarodes pacificus*, but only for relatively large individuals.

Loligo opalescens, which is a neritic species ranging from southeastern Alaska to Baja California, hatches (in captivity) at a mean mantle length of 2.5 mm (HANLON *et al.*, 1979). Growth rate estimates range from 0.5 to 4.5 mm per month (HURLEY, 1976—for newly hatched animals) to 1.1 to 5.6 mm per month (HANLON *et al.*, 1979—also for newly hatched animals) to 7 mm per month (FIELDS, 1965—trawl caught individuals).

Estimates of growth rates of *Gonatus fabricii* in the North Atlantic range from 8 mm per month (KRISTENSEN, 1977—animals above about 20 mm DML) to 11–12 mm per month (NESIS, 1965—also for animals above about 20 mm DML). This species hatches at about 3 mm DML.

The growth curve derived here for *Gonatus madokai* is comparable to growth rates described for the above species. The presence of large individuals in April indicates overwintering, and the size of the largest known individuals leads us to postulate a life span of at least two years. *Gonatus madokai* likely hatches from March to May in the Sea of Okhotsk, and from February to early June in the northern North Pacific.

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