

# IDENTIFICATION, DISTRIBUTION AND RELATIVE ABUNDANCE OF PARALARVAL GONATID SQUIDS (CEPHALOPODA: OEGOPSIDA: GONATIDAE) FROM THE GULF OF ALASKA, 2001–2003

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## ABSTRACT

Paralarvae of the family Gonatidae were sampled in the Gulf of Alaska during spring 2001–2003. Taxonomic characters were determined to allow identification of the specimens to species. The dorsal head chromatophore pattern (DHCP) was the most robust character and allowed identification to species for the first time without requiring the removal and examination of the radula. Six different DHCPs were found among the six species in the study area. The 1140 specimens collected consisted of the following six species: *Berryteuthis anonychus* (759), *Berryteuthis magister* (71), *Gonatopsis borealis* (155), *Gonatus kantschaticus* (1), *Gonatus madokai* (4) and *Gonatus onyx* (143). The specimens had a size range of 3.0–20.63 mm dorsal mantle length with the majority of specimens smaller than 10 mm. All species showed an increasing trend in abundance from the shelf (0–200 m) to the slope (200–1000 m) to the basin (>1000 m) except *G. onyx* in 2001 and 2002. Wide variation in distribution and abundance was found for the four most abundant species; however, in general, *B. anonychus* was most abundant and widely distributed, followed by *Gonatopsis borealis*, *Gonatus onyx* and *B. magister*.

## INTRODUCTION

Fourteen families of Cephalopoda (Bolitaenidae, Chiroteuthidae, Cranchidae, Enoploteuthidae, Gonatidae, Histioteuthidae, Loliginidae, Octopodidae, Octopoteuthidae, Ommastrephidae, Onychoteuthidae, Opisthoteuthidae, Sepiolidae and Vampyroteuthidae) are present in the eastern North Pacific Ocean. Of these, the Gonatidae (order Oegopsida) has the most species and the greatest biomass (Nesis, 1997). Worldwide, 19 described species of the Gonatidae belong to four genera: *Berryteuthis*, *Eogonatus*, *Gonatus* and *Gonatopsis*. All are endemic to the North Pacific Ocean or Bering Sea, with the exception of three species of the genus *Gonatus*, two of which are found in the North Atlantic and one in the Southern Ocean.

The ecology of most gonatid squids, despite their species richness and large biomass, is relatively unknown. The adults are difficult to collect and all stages are difficult to identify, especially since many species of the family may co-occur in a relatively small area. Nevertheless they are important in the diets of many fishes, including Pacific salmon (*Oncorhynchus* spp.) and walleye pollock (*Theragra chalcogramma*), as well as marine mammals and seabirds (Nesis, 1997; Okutani, Kubodera & Jefferts, 1988; Radchenko, 1992). Gonatid squids, predominantly *Berryteuthis magister*, are fished commercially outside the US Exclusive Economic Zone (EEZ) by both Japanese and Russian fishers (Nesis, 1997). Although not a commercial fishery in the US, gonatid squids are frequently taken as bycatch in commercial fisheries. The extent to which the biomass of gonatid squids is affected by harvest, bycatch and predation is unknown due to the paucity of data on their biology and life history.

Estimating biomass for any squid species is notoriously difficult using conventional sampling techniques, such as trawling and fisheries acoustics (Vecchione, 1987). Mature squids can easily avoid or escape trawls and, because they typically aggregate only during spawning events (the locations of which are unknown for most species) their biomass cannot be accurately estimated using acoustic detection. In contrast, paralarval

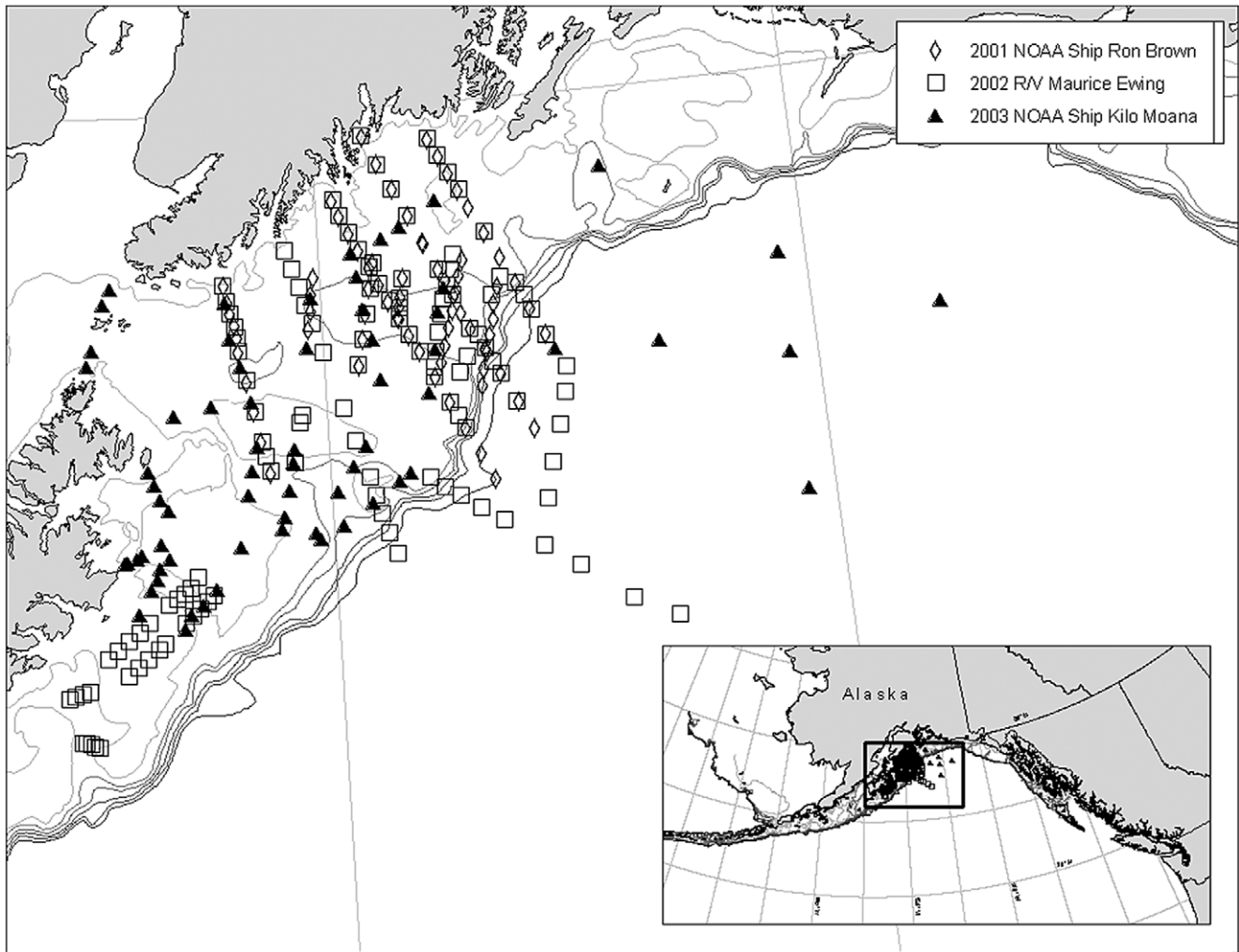
squids, while difficult to identify, have limited swimming ability and are relatively easy to collect. For these reasons, Vecchione (1987) and Bower *et al.* (1999) concluded that the most accurate method of sampling squids for estimating distribution and abundance is by paralarval collection. Unfortunately, accurate identification of small (<8 mm) gonatid paralarvae to species, or even genus in most cases, has not been possible. Identification keys for several species of this family have been published (Okutani *et al.*, 1988; Okutani & Clarke, 1992), but they rely on removal and examination of the radula for final identification, which is often neither definitive nor easy. Furthermore, Arkhipkin & Bizikov (1997) published a key on the identification of gonatid squids from the Bering Sea based on the morphology of their statoliths. However, the process of extraction is destructive to the specimen, the statoliths are difficult to extract, and the majority of specimens collected for this study were smaller than those on which the statolith key was based. The goals of this research are (1) to determine taxonomic characters to identify species of paralarval gonatid squids occurring in the Gulf of Alaska; (2) to estimate their distribution and abundance; and (3) to infer the timing and location of hatching.

## MATERIAL AND METHODS

Gonatid paralarvae were sampled from the northeastern Gulf of Alaska during late April to early June 2001 to 2003. Paralarvae were collected as bycatch in ichthyoplankton tows conducted by NOAA's Fisheries Oceanography Coordinated Investigations (FOCI) Program. Although the FOCI sampling area was geographically large, a small subset of cruises was chosen for this study based on the availability of multi-year sampling and presence of high numbers of gonatid paralarvae. Sampling was conducted from the NOAA ship *Ron Brown* (2001), the R/V *Maurice Ewing* (2002) and the NOAA ship *Kilo Moana* (2003). Dates of sampling were 13–23 May 2001, 22 May–10 June 2002 and 29 April–11 May 2003 (Fig. 1).

Sampling was conducted on the shelf, slope and basin each year of the study; however, sampling locations varied greatly among years. Sampling was least extensive in 2001, while in

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**Figure 1.** Map of sampling locations. Larger map represents area in black rectangle of smaller map.

2002 and 2003 the basin was examined to sample an annual offshore eddy, whose position changed between years. The maximum area sampled for all years was divided into a 50-km<sup>2</sup> grid to facilitate interannual comparison of distribution and abundance. Grid size was chosen to maximize the number of data points per cell while maximizing the resolution at which the data would be analysed. Because of the variability of sampling locations, interannual comparisons of distribution and abundance will be limited to those cells in the grid where sampling was conducted each year.

Samples were collected with a 60-cm bongo net (333- $\mu$ m mesh) towed double-obliquely to a maximum depth of either 300 m or 10 m off bottom at a vessel speed of 2 knots. Volume filtered was calculated from the revolutions of a calibrated flowmeter mounted in the middle of each net opening. The contents of the bongo net codend were fixed in a 5% buffered formalin seawater solution and later sorted for ichthyoplankton and cephalopods at the Sea Fisheries Institute's Plankton Sorting and Identification Center in Szczecin, Poland.

Cephalopod samples were sorted to family (Gonatidae, Cranchiidae and Octopodidae). Gonatid samples were then sorted into morphological groups based on a matrix of characters, including dorsal head chromatophore pattern (DHCP), relative arm and tentacle length, arm and tentacle armature and dorsal mantle chromatophore pattern. Specimens in these groups were organized into growth series such that the largest specimen was identifiable using published keys, thus allowing identification of

the entire growth series. In addition to specimens from the NOAA collection, the collections at the National Science Museum, Tokyo (NSMT), were used in the determination of characters of *Gonatus kamtschaticus* (Middendorff, 1849) since the NOAA collection contained too few specimens for taxonomic analysis. Abundance is presented as the number of each species collected per 100 m<sup>3</sup> seawater filtered at each station.

Abbreviations used are those recommended by Roper & Voss (1983) and are as follows: dorsal mantle length (DML) and fin width index (FWI).

## RESULTS

Gonatid paralarvae (Table 1) were the most abundant (97% of total) and widely distributed cephalopods collected. Of the pelagic squids commonly found in the Gulf of Alaska as

**Table 1.** Cephalopod paralarvae collected.

Year	Bolitaenidae	Cranchiidae	Gonatidae	Octopodidae	Total
2001	0	0	696	3	699
2002	1	4	226	2	233
2003	0	1	225	19	245
Total	1 (0.08%)	5 (0.42%)	1147 (97.45%)	24 (2.04%)	1177

adults (Cranchiidae, Onychoteuthidae, Gonatidae and Chroteuthidae), only gonatid and cranchiid paralarvae were collected in this study; gonatids comprised 99.6% of these. Of the 1147 gonatid paralarvae collected, 759 were *Berryteuthis anonychus* Percy & Voss, 1963, 71 *Berryteuthis magister* (Berry, 1913), 155 *Gonatopsis borealis* Sasaki, 1923, 1 *Gonatus kamtschaticus* (Middendorff, 1849), 4 *Gonatus madokai* Kubodera & Okutani, 1977, 143 *Gonatus onyx* Young, 1972 and 7 were unidentifiable specimens.

Gonatid paralarvae are very fragile and therefore susceptible to mechanical damage during sampling. Some specimens were crushed and dismembered during sampling but the most consistent damage incurred was mantle inversion. *B. anonychus*, *B. magister* and *Go. borealis* were particularly prone to this problem. Due to the lack of a rigid skeleton, the effects of fixation were dramatic. However, while some variation existed, the changes that occurred with fixation were consistent within species. Upon contact with 5% formalin or 70% ethanol, the proteins of the paralarval tissues bind together, causing the animal to become opaque and to shrink slightly. The effects of this constriction were most apparent on the mantle, where the deeper tissues shrank away from the epidermis, sometimes leaving a large gap between the two layers. The chromatophores on the head, arms, tentacles and mantle generally enlarged to their maximum size. Fins, arms and tentacles shrank such that the fins curled under the mantle and the arms and tentacles curled and intertwined. The fin attachment points of *Go. borealis* and *B. magister* pulled into the mantle slightly, compressing the specimen laterally.

The effects of fixation increased the potential for subsequent damage to the mantle epidermis and chromatophores. This, combined with trawl damage, made the use of mantle chromatophore patterns described here unreliable for three (*B. magister*, *G. madokai*, *G. onyx*) of the six species. Fixation or capture trauma (Arkhipkin & Bizikov, 1996) also typically caused the head to withdraw into the mantle, affording the head chromatophores some protection from mechanical damage during shipping and sorting. The effects of fixation on the remaining characters should be considered when assigning value to those characters for identification. Taxonomic characters previously published (Kubodera & Okutani, 1981; Okutani *et al.*, 1988; Okutani & Clarke, 1992) for gonatid paralarvae (tentacle armature and relative arm and tentacle length) were found to be either too variable or too susceptible to the effects of fixation and trawl damage to be reliable for identification. The identification of 1140 specimens from the study indicated that there was complete overlap in tentacle armature for five of the six species while the relative arm and tentacle length could not be used to distinguish between any of the species in the study area (Table 2). Characters used to identify fixed specimens, however, are not necessarily applicable to living specimens, because the effects of fixation and trawl damage are so dramatic.

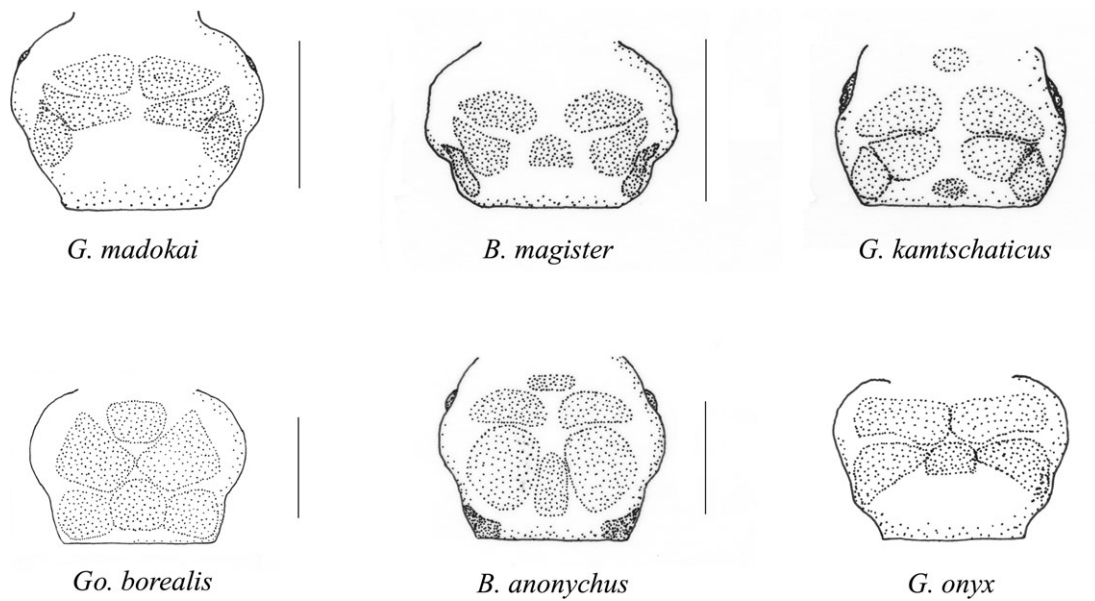
Of the four characters used to group unidentified specimens into species groups, the DHCP was most robust. Dorsal mantle chromatophore pattern was also a unique character among the six species; however, as mentioned previously, the mantle epidermis was too easily damaged for this to be a reliable character. The tentacle armature and relative arm and tentacle lengths were poor characters for the sizes of animals studied here.

*Taxonomy*

The six species of gonatids in the study area have six unique DHCPs. These form two basic types: Type I and Type II (Fig. 2). Type I has three tear-shaped chromatophores on each side (six total) that come to a point over each eye, while Type II has anterior-to-posterior rows of one-two-three chromatophores on the head. In the descriptions that follow, variations

**Table 2.** Character comparison of paralarvae. Asterisk indicates inclusion of specimens from NSMT.

Species	Number of specimens	DHCP	Dorsal mantle chromatophore no.	Relative arm / tentacle length	Tentacle armature
<i>B. anonychus</i>	759	Type II + 2	18–25	T > II > I > III > IV or T > I > II > III > IV	3–5; sparse to dense
<i>B. magister</i>	71	Type I + 1	20–25	T > II > I > III > IV or T > I > II > III > IV	5 or 6; dense
<i>Go. borealis</i>	155	Type II	6–10	T > II > I > III > IV or T > I > II > III > IV	4–6; dense
<i>G. kamtschaticus</i>	5*	Type I + 2	16	T > II > III > I > IV	Sucker buds
<i>G. madokai</i>	15*	Type I	14–18	T > II > III > I > IV	5; dense
<i>G. onyx</i>	143	Type II – 1	7	T > II > III > I > IV or T > I > II > III > IV	5 or 6; dense



**Figure 2.** Summary of DHCPS. The layout is arranged to facilitate comparison of patterns between species. Top row (left to right): Type I, Type I + 1, Type I + 2; bottom row: Type II, Type II + 2, Type II - 1. Scale bars: *Gonatus madokai* = 2.0 mm; *B. magister* = 2.0 mm; *Gonatus kamtschaticus* = 3.0 mm; *Gonatus borealis* = 1.0 mm; *B. anonychus* = 1.0 mm; *Gonatus onyx* = 2.0 mm.

of the basic DHCP will be given as either plus the number of chromatophores additional to the basic pattern or minus the number of chromatophores that are missing from the basic pattern. The patterns appear to remain constant throughout the paralarval period. The relative size of the chromatophores was not found to aid identification.

*Berryteuthis anonychus* (Fig. 3) has the Type II+2 DHCP (Fig. 2); the extra two chromatophores are located posterolaterally but are visible dorsally. The relative arm and tentacle lengths are  $T > II > I > III > IV$  or  $T > I > II > III > IV$ ; the third arm pair is not reduced (suckers with chitinous rings are present) in the size range studied (3.2–8.5 mm DML). Distally, the tentacles have three to five suckers per transverse row depending on the degree of constriction during fixation. The tentacular suckers are distributed evenly but vary from sparsely to closely spaced depending on fixation state. The mantle is muscular with an opening approximately equal to the head diameter; the head is always exposed. There are 16–25 dorsal mantle chromatophores. The fins are rectangular and small;  $FWI = 0.2$ . The radula has seven teeth per row.

At the largest size collected, 8.5 mm DML, the chromatophores of the head and mantle have begun to increase in number, but the DHCP is still discernible. The maximum tentacle length is shorter relative to maximum arm length and the tentacular armature is four or five per row, spaced closely and evenly. No differentiation of the tentacular club is discernible and no sucker buds are present.

In over 750 specimens of *B. anonychus* examined, the number of suckers per row on the tentacular club varied from three to five, appearing sparsely to closely spaced. An overlap of three to five sparsely to closely spaced suckers per row encompasses all species of the gonatid paralarvae included in the key published by Kubodera & Okutani (1981). This has been especially confusing for distinguishing *B. anonychus* and *G. kamtschaticus* paralarvae, which, according to that key, overlap in all characters except the number and organization of the suckers on the tentacular club and the teeth on the radula. With the wide variation in tentacular armature found here, the radula would need to be removed and examined for each specimen collected for positive identification, according to the previously published key.

The DHCP described here allows *B. anonychus* to be distinguished from *G. kamtschaticus* without the removal of the radula.

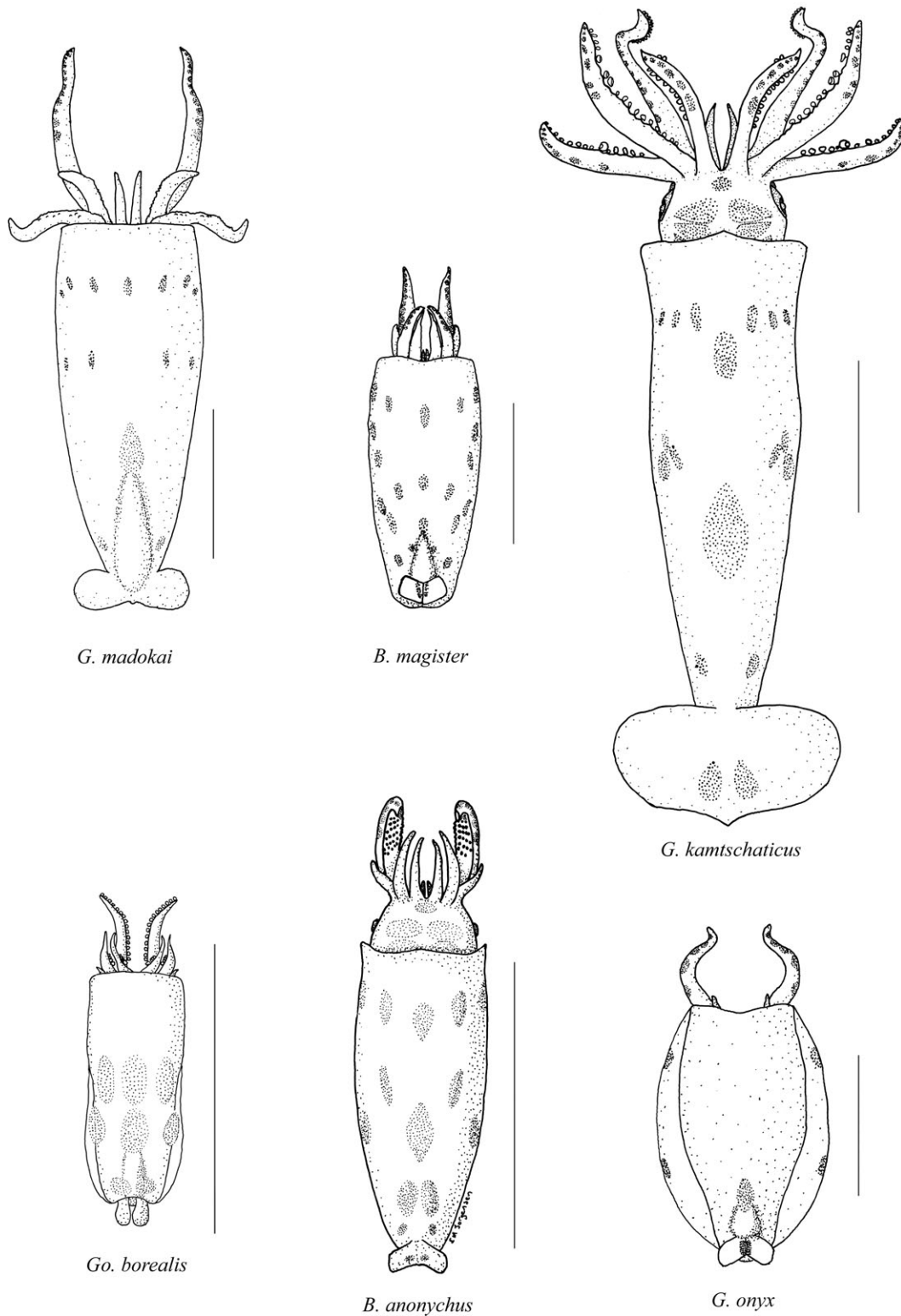
Perhaps most easily recognized by the abundance of mantle chromatophores, *B. anonychus* has a reliable DHCP, unique among the six species examined in this study. The pattern is most similar to that of *Go. borealis*, but differs in the location of two posterolateral chromatophores. The mantle of *B. anonychus* shrinks little during fixation so mantle chromatophores are often intact and can be used to supplement DHCP in identification.

*Berryteuthis magister* (Fig. 3) has the Type I+1 DHCP (Fig. 2); the extra chromatophore is located on the midline of the head. The relative arm and tentacle lengths are  $T > II > I > III > IV$  or  $T > I > II > III > IV$  or  $T > II > III > IV$ ; the third arm pair is not reduced in the size range studied (3.4–12.3 mm DML). The mantle is muscular with an opening much larger than the head; the head is always withdrawn. There are 20–25 dorsal mantle chromatophores. The tentacular suckers are evenly and closely spaced with five or six suckers per row. The fins are small;  $FWI < 0.2$ . The radula has seven teeth per row.

At the largest size collected, 12.3 mm DML, the DHCP was augmented by one small chromatophore over each eye. Change in mantle chromatophores is unknown because none of the larger specimens collected had an intact mantle epidermis. At approximately 11 mm DML, the tentacular club begins to differentiate; the distal portion has only sucker buds and is slightly broader than the proximal portion. The fin has become proportionally larger ( $FWI \sim 0.4$ ) and rounded.

The DHCP is most similar to that of *G. kamtschaticus*, except that the extra medial chromatophore in *G. kamtschaticus* is more posterior, whereas the extra chromatophore in *B. magister* is more anterior, located between the eyes. The mantle epidermis and chromatophores of *B. magister* are often torn away upon fixation, so mantle chromatophore patterns should not be relied upon for identification. However, when the mantle epidermis is intact, it contains over 20 chromatophores dorsally, making it the second most pigmented paralarva in this study, after *B. anonychus*.





**Figure 3.** Summary of whole animals. The layout corresponds to that of Fig. 2. Illustrations showing the head withdrawn into mantle are representative of that species and reflect the effects of fixation. Scale bars = 5.0 mm.

*Gonatopsis borealis* (Fig. 3) has the Type II DHCP (Fig. 2) throughout the size range collected (3.0–10.4 mm DML). Two chromatophores are located posterolaterally appearing very similar to those of *B. anonychus*; however, they are not visible in dorsal view as in *B. anonychus*. The relative arm and tentacle

lengths are  $T > II > I > III > IV$  or  $T > II = I > III > IV$ ; the third and fourth arm pairs are reduced until  $\sim 6$  mm DML. Distally, the tentacles have four to six evenly spaced suckers per row. The mantle is muscular with a mantle opening approximately equal to the head diameter; the head is often withdrawn.

There are six to ten dorsal mantle chromatophores. The fins are small; FWI < 0.2. The radula has seven teeth per row.

The mantle chromatophores can be used in conjunction with the DHCP to verify species identification, although the mantle epidermis is fragile and often damaged, especially in smaller sizes (<6 mm DML). In such cases, the laterally compressed mantle of *Go. borealis* is also a good character for distinguishing *Go. borealis* from *B. anonychus*, as the mantle of *B. anonychus* is consistently pointed posteriorly even after the specimen has been fixed.

A single juvenile specimen of *G. kamtschaticus* (Fig. 3) was collected from the study area and only a few have been identified from the entire collection; however, this species deserves mention here because it has often been confused with *B. anonychus*. *Gonatus kamtschaticus* has the Type I + 2 DHCP (Fig. 2), similar to that of *B. magister*. The extra two chromatophores are located medially on the head, one anterior at the base of the arms, the other posterior. The anterior chromatophore is very faint. The relative arm and tentacle lengths are III > II > T > I > IV. The distal portions of the tentacles have only sucker buds, arranged four per row. The mantle is firm and muscular with an opening equal to the head diameter; the head is typically exposed or only partially withdrawn into the mantle. There are 16 dorsal mantle chromatophores. The fins are large; FWI ~ 0.4. The radula has five teeth per row.

The DHCP of *G. kamtschaticus* is not known for certain in the paralarval stage. The only specimens available were at the juvenile stage, longer than 15 mm DML. The pattern is probably typical of the paralarval stage. However, the faint, medial chromatophore located anteriorly on the head may be a newly formed organ, which would give a paralarval pattern of Type I + 1. This latter pattern is most similar to that of *B. magister* and *G. madokai*. The mantle of *G. kamtschaticus* is more muscular and firm than either that of *B. magister* or *G. madokai* at juvenile sizes.

*Gonatus kamtschaticus* paralarvae have always been difficult to identify. Samples of paralarvae at NSMT labeled *G. middendorffi* [a junior synonym of *G. kamtschaticus* (Nesis, 1997)] were actually *B. anonychus*, based on head chromatophore pattern and radular tooth count. Their correct identification remained unknown because the tentacular armature of *G. kamtschaticus* does not differentiate into hooks until a DML of at least 30 mm, a size that is difficult to collect. Moreover, the tentacles of *B. anonychus* never develop hooks, so the two remain very similar in appearance throughout the paralarval and most of the juvenile stages. While both have a firm, muscular mantle, their head chromatophore patterns are very different, enabling identification.

*Gonatus madokai* (Fig. 3) has the Type I DHCP (Fig. 2). The relative arm and tentacle length is T > II > III > I > IV; the third arm pair is not reduced in the size range studied (6–12 mm DML). Distally, the tentacles have five evenly spaced suckers per row. The mantle is weak and loose with a mantle opening much larger than the diameter of the head; the head is always withdrawn. This species is especially susceptible to damage to the mantle epidermis after fixation and is often seen in collections with no mantle chromatophores because the entire mantle epidermis has been torn away. When intact, the mantle has as many as 18 dorsal and 28 ventral mantle chromatophores. The fins are small; FWI ~ 0.2. The radula has five teeth per row.

The DHCP of *G. madokai* is most similar to that of *B. magister* and *G. kamtschaticus* but can be distinguished because it lacks the extra medial chromatophore. *Gonatus madokai* also has a pointed posterior mantle, whereas fixed specimens of *B. magister* have a compressed mantle. Unlike the muscular, firm mantle of *G. kamtschaticus*, the mantle of *G. madokai* is weak and distended.

*Gonatus onyx* (Fig. 3) has the Type II–1 DHCP (Fig. 2). It lacks the single anterior medial chromatophore. The relative arm and tentacle lengths are T > II > III > I > IV or T > II > I > III > IV; the third arm pair is not reduced in the size range studied (5.3–17.1 mm DML). Distally, the tentacles have five or six suckers per row, closely and evenly spaced. Differentiation of the tentacular club begins at approximately 11 mm DML when the distal portion of the tentacle broadens and sucker buds begin to appear. The mantle is muscular and loose with an opening approximately equal in diameter to the head; the head is always withdrawn. This species has the most dramatic reaction to fixation of the six discussed here; the mantle shrinks away from the mantle epidermis to such an extent that the epidermis is attached only at the mantle opening and fin attachment. Most specimens were missing the mantle epidermis entirely. When intact, the mantle has only five chromatophores: two pairs of lateral chromatophores and a single dorsal chromatophore positioned near the fin. The fins are large; FWI ~ 0.5. The radula has five teeth per row.

When the mantle epidermis is intact this species may be distinguished from the other six species without referencing the DHCP because of the swollen shape of the mantle and the distinctive mantle chromatophore pattern. However, when the mantle epidermis is torn away this species looks similar to *B. magister*, so the DHCP should be used for identification.

A short identification key to the paralarval gonatids of the Gulf of Alaska is given below.

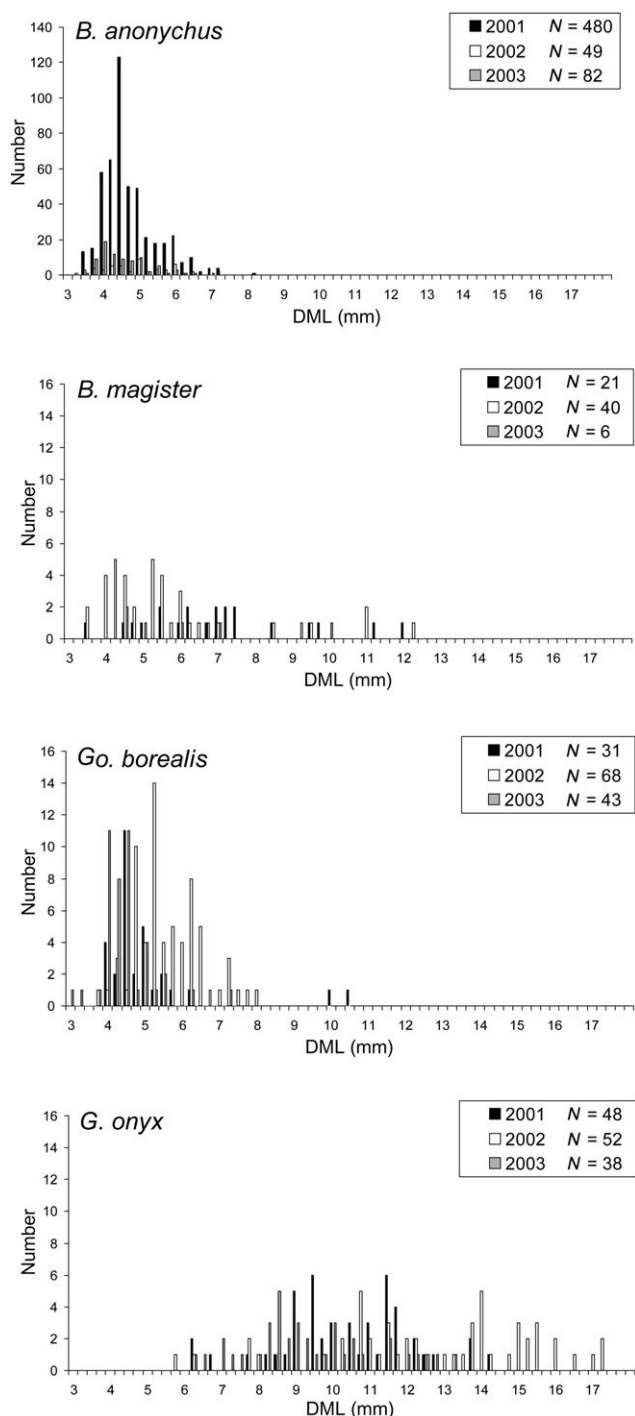
- 1a. DHCP is either Type I or Type II with no modification..... 2
- 1b. DHCP is a modification of either Type I or Type II ..... 3
- 2a. DHCP is Type I with no modification ..... *G. madokai*
- 2b. DHCP is Type II with no modification ..... *Go. borealis*
- 3a. DHCP is a modification of Type I ..... 4
- 3b. DHCP is a modification of Type II ..... 5
- 4a. DHCP is Type I + 1 ..... *B. magister*
- 4b. DHCP is Type I + 2 ..... *G. kamtschaticus*
- 5a. DHCP is Type II + 2 ..... *B. anonychus*
- 5b. DHCP is Type II – 1 ..... *G. onyx*

#### Distribution and abundance

During the 3 years of sampling, only four of the six species were collected consistently each year. The rarest species, *G. kamtschaticus*, was found at only a single station in 2002 while the second rarest, *G. madokai*, occurred at three stations in 2001 and one in 2003. Comparisons of distributions and abundance are therefore confined to the four most consistently collected species, *B. anonychus*, *B. magister*, *Go. borealis* and *G. onyx*. The distribution of each species was compared between day and night samples, but no diel pattern was apparent.

DMLs were recorded for each undamaged specimen (Fig. 4). *Berryteuthis anonychus* and *Go. borealis* had the narrowest range of lengths and smallest average length for each of the study years (Table 3). The average length and standard deviation did not vary significantly for *B. anonychus* between the 3 years of the study while those of *Go. borealis* were more variable. *Berryteuthis magister* had the next longest average length and a much greater range of lengths than *B. anonychus* and *Go. borealis*. *Berryteuthis magister* had an interannual variation in average DML of 1.2 mm while standard deviation of DML showed no interannual variation. *Gonatus onyx* had the longest average DML which was 1.5 to 2 times longer than that of *B. magister*. *Gonatus onyx* had interannual variations in DML of over 3 mm and wide variation in standard deviation.

The geographic distribution and abundance of each species showed large interannual variation. *Berryteuthis anonychus* had



**Figure 4.** Length-frequency distributions. Black columns represent data from 2001, white are 2002, grey are 2003.

the largest variation in distribution and abundance of the four species discussed here (Fig. 5). In 2001, 587 specimens of *B. anonychus* were collected. Sampling was conducted mostly on the shelf and each grid cell sampled was dominated by *B. anonychus* (Fig. 6). Although sampling was more intense the following 2 years, these abundances were not seen again. The number of specimens collected dropped to 49 in 2002 and only slightly recovered in 2003 to 123. In 2002, *B. anonychus* had abundances similar to the other three species in the study; however, the shelf region of the sampling area showed many fewer squid than in

2001 and 2003. In 2003, *B. anonychus* dominated most shelf and basin samples.

*Beryteuthis magister* showed a high interannual variation in abundance (Fig. 5); in 2001, 21 specimens were collected followed by 44 in 2002 and 6 in 2003. These specimens were mostly from over the shelf break or troughs though they were also collected over the basin in 2002. *Beryteuthis magister* was consistently the least abundant and had the narrowest distribution of all the species in the area (Fig. 6).

*Gonatopsis borealis* also showed a high interannual variation in abundance (Fig. 5); 32 specimens were collected in 2001, 69 in 2002 and 54 in 2003. It was only distributed over the shelf region in 2001, the year of lowest abundances; in 2002 and 2003 its distribution was primarily over the basin and shelf break (Fig. 6). In 2002, *Go. borealis* dominated most shelf break and basin samples while in 2003, its abundance was second to *B. anonychus*.

*Gonatus onyx* showed the least interannual variation in abundance (Fig. 5); 49 specimens were collected in 2001, 55 in 2002 and 39 in 2003. It was found over the shelf, shelf break and basin in all years. It was second least abundant in all years but had a broad distribution in 2002 and 2003 (Fig. 6).

In general, sampling in 2001 yielded the most gonatid paralarvae even though sampling was most restricted. Sampling in 2002 was the most extensive yet resulted in the fewest paralarvae, especially over the shelf. In 2003, the area sampled was broad but the number of stations was fewer than in 2002. Despite this, the abundance of paralarvae was similar to that of 2002. Unlike the 2002 distribution, 2003 samples yielded more paralarvae on the shelf.

The sampling region showed a high species diversity for Gonatidae with up to four species occurring in a single tow. The number of species collected increased from the shelf to the slope to the basin. This offshore increase was not due to increased tow times in deeper water, there was no correlation between volume filtered and species richness ( $R^2 = 0.19$  in 2001,  $R^2 = 0.46$  in 2002,  $R^2 = 0.19$  in 2003). The distribution and abundance of gonatid paralarvae were variable each year of the study, as was the species richness. The high gonatid species richness found in the area has likely been a factor in the difficulty identifying gonatid species in the past.

## DISCUSSION

Paralarval gonatids have been studied several times in the last 40 years, beginning with the work in the northern North Pacific by Okutani (1966) and Okutani & McGowan (1969) on the California Current, followed by Kubodera & Okutani (1981), Bublitz (1981), Kubodera & Jefferts (1984a, b) on the North Pacific and Okutani *et al.* (1988) on the subarctic Pacific. However, these efforts have all suffered from taxonomic difficulties. For example, Okutani & McGowan (1969) referred all gonatid paralarvae collected to *Gonatopsis fabricii*, thought at the time to be the only valid species, but now recognized as a species not found in their study area (Young, 1972). Kubodera & Okutani (1981) described as '*Gonatopsis middendorffi*' paralarvae found here to be *Beryteuthis anonychus* based on the presence of seven teeth on the radula instead of five and the head chromatophore pattern. The identification published by Kubodera & Okutani (1981) was also included in the summary by Okutani & Clarke (1992). The confusion surrounding '*G. middendorffi*' and *B. anonychus* shows that the characters other than the radula (tentacle armature, relative arm lengths, and mantle type) used for identification previously were not sufficient to distinguish the two species.

In addition, these works lacked observations of specimens smaller than 8 mm DML. Previously very small specimens were thought not to be identifiable to species (T. Kubodera,

**Table 3.** Dorsal mantle length (DML) (mm) statistics.

Year	Species	Average DML	StDev DML	Minimum DML	Maximum DML	N
2001	<i>B. anonychus</i>	4.7	0.8	3.3	8.2	480
2002	<i>B. anonychus</i>	4.8	0.9	3.2	6.3	49
2003	<i>B. anonychus</i>	4.5	0.7	3.5	6.8	82
2001	<i>B. magister</i>	6.9	2.1	3.5	11.8	20
2002	<i>B. magister</i>	5.7	2.2	3.4	12.3	40
2003	<i>B. magister</i>	6.1	2.2	4.3	10	6
2001	<i>Go. borealis</i>	5.0	1.5	4	10.4	31
2002	<i>Go. borealis</i>	5.3	0.9	3.3	7.7	68
2003	<i>Go. borealis</i>	4.4	0.7	3	7.1	43
2002	<i>G. kamtschaticus</i>	20.6	0.0	20.63	20.63	1
2001	<i>G. madokai</i>	9.2	3.0	6	12	3
2003	<i>G. madokai</i>	7.6	0.0	7.6	7.6	1
2001	<i>G. onyx</i>	10.4	2.1	6.1	17.14	49
2002	<i>G. onyx</i>	12.4	2.7	5.3	16.98	52
2003	<i>G. onyx</i>	9.3	1.8	6.2	13.1	38

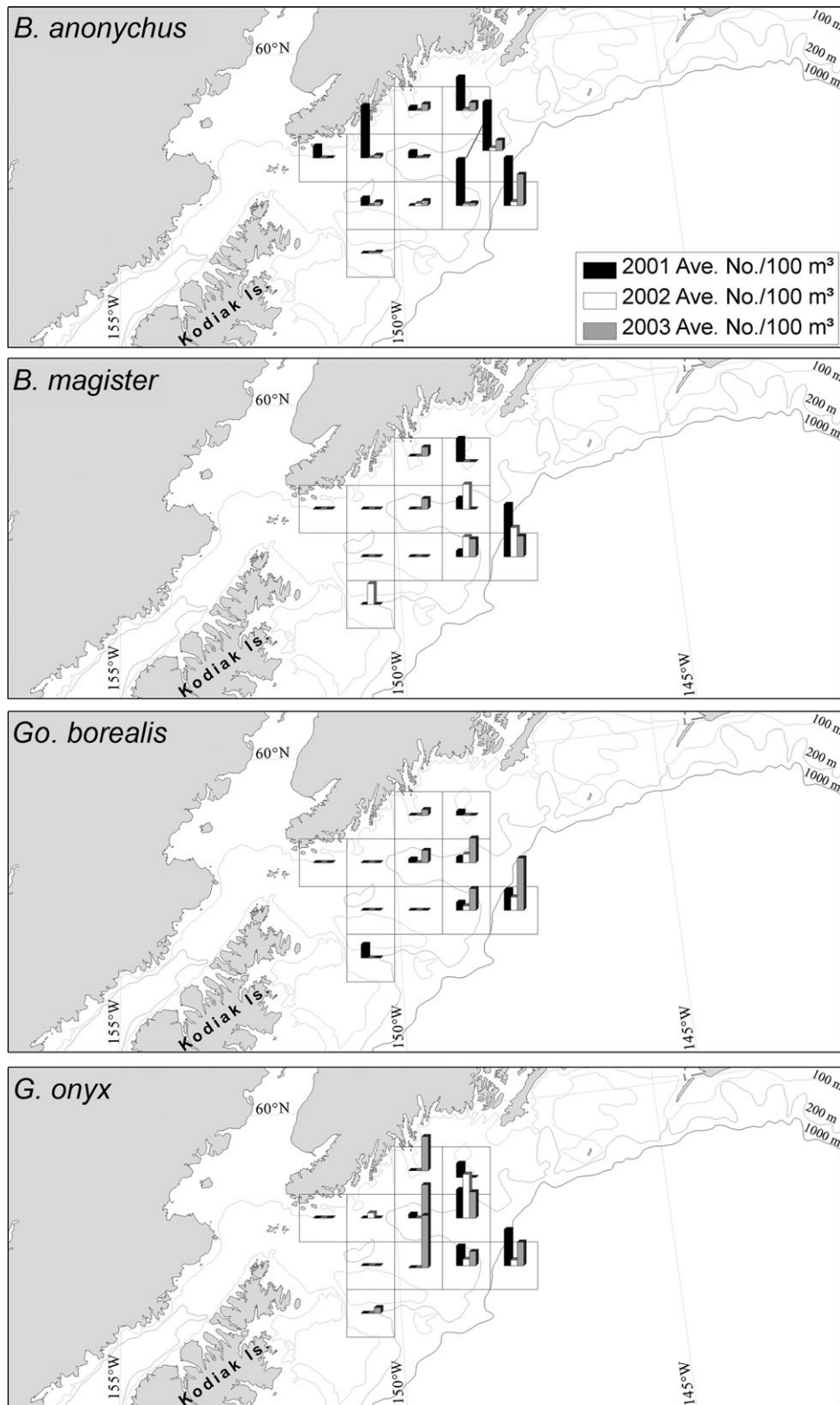
personal communication, 6 July 2004); however, it is the small paralarvae that are least able to avoid sampling gear and therefore offer the most unbiased information about the populations. The literature available to identify early juvenile specimens is difficult to employ due to the lack of descriptions of external characters. The four genera of Gonatidae are distinguished from each other by the number of teeth on the radula (*Eogonatus* and *Gonatus* have five per row, *Berryteuthis* has seven and *Gonatopsis* has five or seven), the presence or absence of tentacles in adults (*Berryteuthis*, *Eogonatus* and *Gonatus* have tentacles as adults, while *Gonatopsis* does not), and the armature of tentacles in adults (*Eogonatus* and *Berryteuthis* have suckers only, while *Gonatus* has suckers plus a varying number of hooks). However, there are seven species of *Gonatus*, two of *Berryteuthis* and potentially five species of *Gonatopsis*; therefore, robust external characters are needed to distinguish paralarvae of the majority of species. Furthermore, the tentacles of *Gonatopsis* are present until the animal reaches ~15 mm DML, making the presence or absence of tentacles a poor character for identification even among genera in paralarval specimens. Species of *Gonatus* are differentiated by the armature of the tentacular club, the development of which varies among species but is not recognizable in any species before 12 mm DML. Club armature is therefore not useful in distinguishing gonatid paralarvae.

Of all the characters examined for this study, the DHCP was most robust. The head chromatophore patterns described here enable differentiation of paralarval gonatid squids for the first time. In the literature on gonatid paralarvae, DHCPs had been recorded only once, by Okutani & McGowan (1969); however, at that time only one species of the Gonatidae, identified as *G. fabricii*, was included in the publication. No publication on gonatid paralarvae has mentioned the head chromatophores since; however, head chromatophores were found to be useful for identification of paralarval loliginids (Vecchione, 1982; Vecchione & Lipinski, 1995). Based on the head chromatophore patterns they outlined, Okutani & McGowan (1969) were describing *Gonatus onyx*, as also concluded by Young (1972). Harman & Young (1985), Young & Harman (1985) and Young, Harman & Mangold (1985) used mantle chromatophores extensively in their work with the paralarvae of the Ommastrephidae, Euploteuthidae and *Brachioteuthis* sp., respectively, and have proved their use in identifying species. However, the use of mantle chromatophores is not feasible with the collection, fixation and preservation methods commonly used for specimens such as those studied here.

Although the general timing and sampling area were similar in each of the 3 years of this study, the specific locations and dates were not identical; however, the distributions of length frequencies indicate that paralarvae were sampled at a similar age each year. Using Kristensen's (1983) growth rate of 8–9 mm per month [similar to that found by Arkhipkin & Bizikov (1997)], the relative ages of the populations can be estimated. Kristensen's monthly growth rate yields a daily growth rate of 0.27–0.3 mm. Since the maximum difference in average annual DML of *B. anonychus* was 0.3 mm, the estimated maximum age difference was approximately 1 day between the populations. Similarly, the interannual age difference in the population of *B. magister* was 4–4.5 days, for *Go. borealis* 3–4 days and for *G. onyx* 10–12 days. Arkhipkin & Bizikov (1997) calculated growth equations for five of the six gonatids discussed here; however, the estimated size at hatching was always larger and, in some cases, double the size of the smallest specimens collected in this study so their equations were not used to estimate ages of the specimens for this study. It does point out that the growth rate for very young gonatids must be faster than that of late paralarval to juvenile stages, making the interannual age differences, calculated above, conservative estimates.

The smallest *Go. borealis* collected was ~3 mm DML while the smallest *B. anonychus* and *B. magister* were ~3.5 mm, similar to the published hatching size of *G. fabricii* (Kristensen, 1983). The smallest *G. onyx* paralarvae collected in the study was over 5 mm however, a brooding female and hatchlings of *G. onyx* were collected by Seibel, Hochberg & Carlini (2000) and the hatchlings were 3.2–3.5 mm DML. The available evidence, therefore, suggests a similar hatching size for the four most commonly collected gonatid paralarvae in the study area. Based on this information, conclusions can be made on the relative hatching times of the species collected here. Because specimens of *B. anonychus* had the smallest size range and had the highest abundances of gonatid paralarvae sampled each year of the study, individuals were likely sampled very close to the area and time that they were hatched. Their small size indicates young animals and their high numbers indicate predation and starvation have not yet taken their toll. The discrepancy in abundance between years could be due to the difference in sampling time, response of the spawning adults to ocean conditions or fortuitously sampling the population of paralarvae in 2001 before the currents dispersed them. Specimens of *B. magister* were fewer and relatively larger than those of *B. anonychus*, indicating that they were likely hatched at some time before

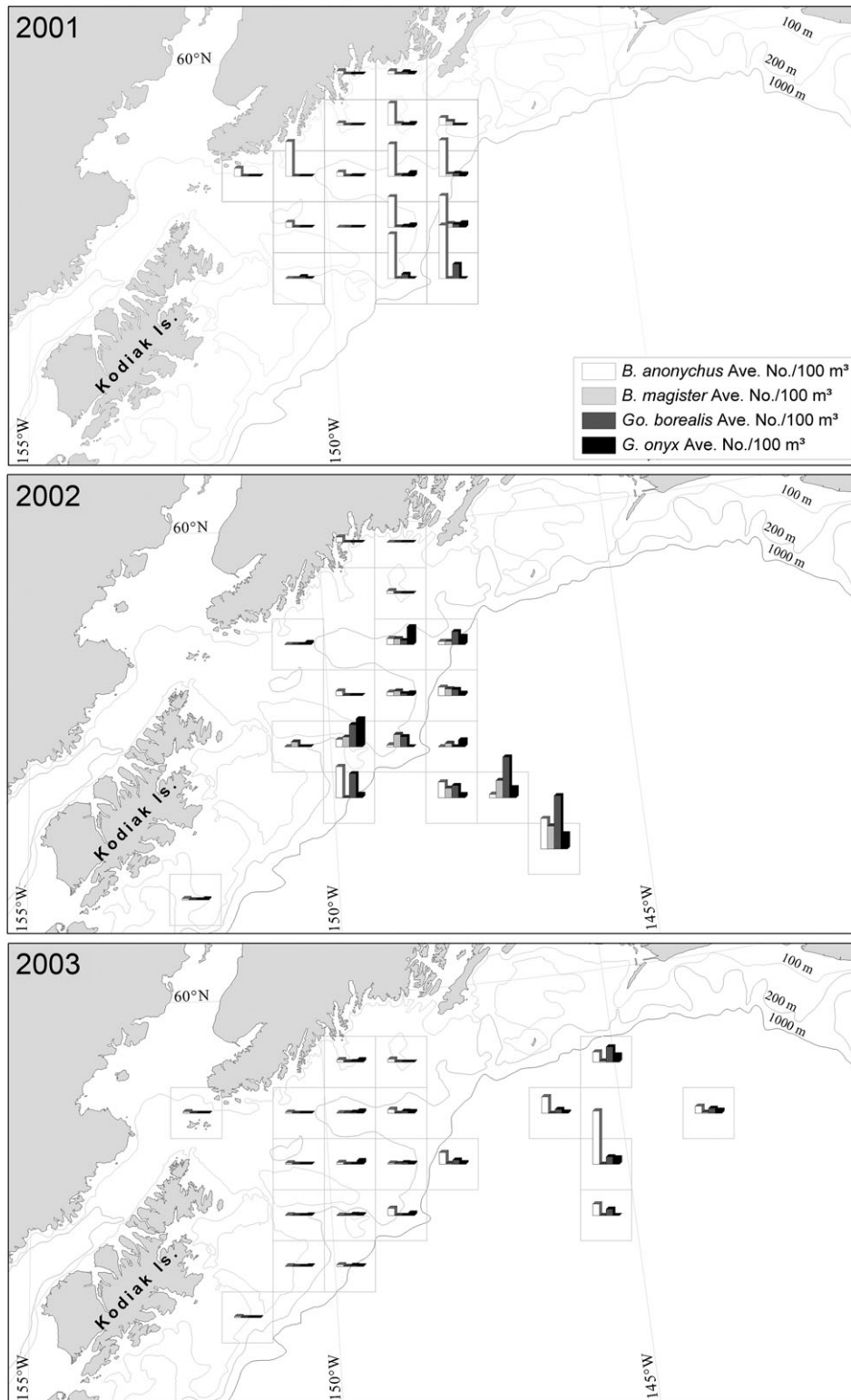




**Figure 5.** Interannual comparisons of relative abundances by species. Comparisons are limited to those grid cells that were sampled each year of the study. Grid size is 50 km<sup>2</sup>. The value associated with the tallest column varies for each map and represents the maximum average number of paralarvae collected: *B. anonychus* = 4.20 per 100 m<sup>3</sup>; *B. magister* = 0.45 per 100 m<sup>3</sup>; *Go. borealis* = 0.90 per 100 m<sup>3</sup>; *G. onyx* = 0.80 per 100 m<sup>3</sup>.

*B. anonychus*. The presence of small specimens mixed in with predominately larger specimens suggests a more prolonged hatching time. *Gonatopsis borealis* was also represented by relatively

small-sized animals and was the second most abundant species in the sampling area. Based on this, the hatching time of *Go. borealis* would be shortly before the time of sampling,



**Figure 6.** Distributions and relative abundances of each species. Grid size is 50 km<sup>2</sup>. The value associated with the tallest column varies for each map and represents the maximum average number of paralarvae collected: 2001 = 6.46 per 100 m<sup>3</sup>; 2002 = 2.00 per 100 m<sup>3</sup>; 2003 = 11.28 per 100 m<sup>3</sup>.

similar to that of *B. anonychus*. *Gonatus kamtschaticus* was represented by a single, large specimen. It is a muscular squid and, at the late paralarval stages, likely can avoid bongo nets. As a paralarva, it does not occur in the study area during early April to late May so it does not hatch in this area at this time.

Only four relatively large specimens of *G. madokai* were collected during the 3 year study, suggesting little hatching in this area at this time. The abundance of *G. onyx* ranked third behind *B. anonychus* and *Go. borealis*. Its size range was broader and started with larger-sized animals than those of *B. anonychus*,

*B. magister* and *G. borealis*. Therefore, *G. onyx* likely hatched before *B. anonychus*, *B. magister* and *Go. borealis*, and after *G. madokai*.

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