Abstract—The stomach contents of the minimal armhook squid (*Berryteuthis anonychus*) were examined for 338 specimens captured in the northeast Pacific during May 1999. The specimens were collected at seven stations between 145–165°W and 39–49°N and ranged in mantle length from 10.3 to 102.2 mm. Their diet comprised seven major prey groups (copepods, chaetognaths, amphipods, euphausiids, ostracods, unidentified fish, and unidentified gelatinous prey) and was dominated by copepods and chaetognaths. Copepod prey comprised four genera, and 86% by number of the copepods were from the genus *Neocalanus*. *Neocalanus cristatus* was the most abundant prey taxa, composing 50% by mass and 35% by number of the total diet. *Parasagitta elegans* (Chaetognatha) occurred in more stomachs (47%) than any other prey taxon. Amphipods occurred in 19% of the stomachs but composed only 5% by number and 3% by mass of the total prey consumed. The four remaining prey groups (euphausiids, ostracods, unidentified fish, and unidentified gelatinous prey) together composed <2% by mass and <1% by number of the diet. There was no major change in the diet through the size range of squid examined and no evidence of cannibalism or predation on other cephalopod species.

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Diet of the minimal armhook squid (*Berryteuthis anonychus*) (Cephalopoda: Gonatidae) in the northeast Pacific during spring

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The squid family Gonatidae plays an important role in the ecosystems of the North Pacific. In the Sea of Okhotsk, the annual production of gonatid squids is more than half that of fish production (Lapko, 1996), and in the western and central Bering Sea, gonatid production is thought to exceed that of the dominant fish families (Radchenko, 1992). In the subarctic North Pacific, the gonatids are an important link in the pelagic food web (Brodeur et al., 1999). To better understand the food web in the North Pacific and the processes influencing the production of gonatid squids in this region, information is needed on the feeding behavior of these squids.

The minimal armhook squid (*Berryteuthis anonychus*) (also known as the "smallfin gonate squid" [Roper et al., 1984]) is a small gonatid (maximum mantle length=150 mm) distributed mainly in the northeast Pacific (Roper et al., 1984; Bower et al., 2002). It is a major prey for fishes, squids, seabirds, and marine mammals (Ogi et al., 1980; Pearcy et al., 1988; Pearcy, 1991; Kuramochi et al., 1993; Pearcy et al., 1993; Ohizumi et al., 2003) but is not targeted by any fishery. Despite the importance of *B. anonychus* in the food web of the subarctic North Pacific, the only published reports on its feeding behavior are two abstracts in the Russian literature (Lapshina, 1988; Didenko, 1990). In this article, we provide further information on the feeding behavior of *B. anonychus* by describing the diet of a wide size range of squid collected from the northeast Pacific during late spring.

Methods

Berryteuthis anonychus was collected during a United States National

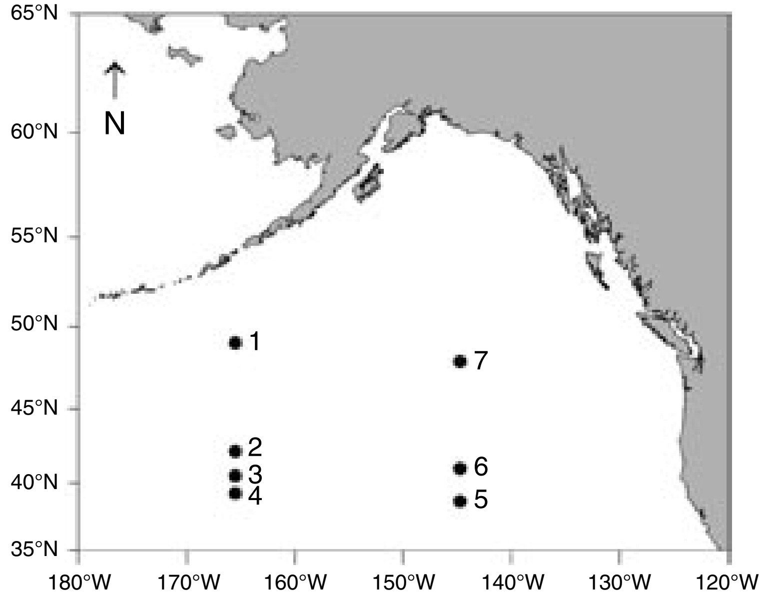

Figure 1

Sampling stations in the northeast Pacific where *Berryteuthis anonychus* were collected during May 1999. Numbers indicate station numbers.

Marine Fisheries Service (NMFS) survey of salmon in the northeast Pacific (Carlson et al., 1999; Bower et al., 2002). Samples were collected during 6–17 May 1999 at seven stations between 145–165°W and 39–49°N (Fig. 1). At each station, a midwater trawl modified to fish at the surface was towed for 1 hour. The trawl was 198 m long and had hexagonal mesh in its wings and body, and a 1.2-cm mesh liner was used in the codend. Trawling speeds were 7–9 km/h, and the average net dimensions while fishing were 16 m vertical spread and 45 m horizontal spread.

Squid samples were frozen on board to −20°C and preserved in 50% isopropyl alcohol in the laboratory. The mantle length (ML) of each squid was measured to the nearest 0.1 mm, and each squid was weighed to the nearest 0.01 g. The stomach contents of 338 squid (167 males, 144 females, 27 undetermined) ranging in ML from 10.3 to 102.2 mm (Fig. 2) were examined under a stereomicroscope. A total of 359 squid were collected during the survey (Bower et al., 2002), but 21 of these specimens were either damaged or lost, and thus excluded from our analyses. Most prey items were fragmented; therefore prey identification was usually based on diagnostic body parts as described in Brodsky (1950), Miller (1988), Baker et al. (1990), and Vinogradov et al. (1996), and by comparison with zooplankton specimens collected in the same area. The prey items were counted and weighed to the nearest 0.01 mg. These wet mass measurements presumably underestimated the initial wet masses because mass loss occurs in invertebrate samples preserved in isopropyl alcohol (e.g., Howmiller, 1972), and it was assumed all prey taxa were equally affected by the preservation. The numbers of individuals of each

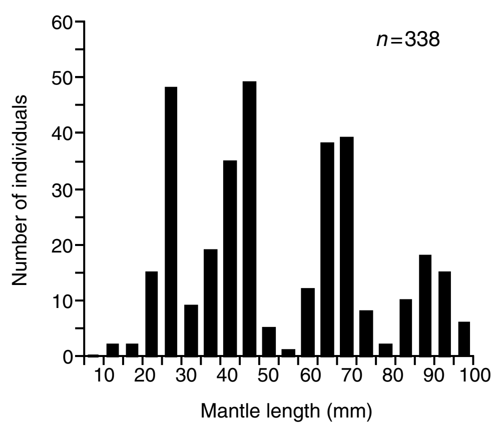

Figure 2

Length-frequency distribution for *Berryteuthis anonychus*.

prey taxon were estimated from the numbers of prey parts, such as copepod mandibles, amphipod heads and chaetognath seizing hooks. Because of the difficulty in distinguishing the copepods *Neocalanus plumchrus* and *N. flemingeri*, they were grouped as a single taxon, *N. plumchrus+flemingeri*. Some calanoid copepods that could not be identified to genus level were identified as either a “specialized form” or a “generalized form”; characters of the specialized form included appendages that were greatly enlarged or strongly developed with chelae, spines on the posterior corners of the terminal thoracic segment,

Table 1

Numbers of *Berryteuthis anonychus* stomachs with identifiable prey remains, without identifiable remains, and without remains from the northeast Pacific. Station numbers refer to those shown in Figure 1.

Station no.	With identifiable remains	Without identifiable remains	Without remains	Total
1	25	0	0	25
2	29	19	45	93
3	33	0	2	35
4	12	1	2	15
5	51	9	6	66
6	44	18	16	78
7	26	0	0	26
Total	220	47	71	338

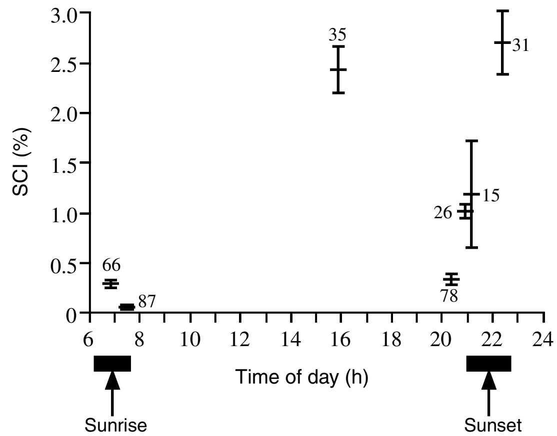

Figure 3

Mean stomach contents index (SCI) of *Berryteuthis anonychus* collected in the northeast Pacific during May 1999 at different times of day. SE = standard error of the mean. Numbers indicate squid sample size for each sampling.

and an asymmetrically swollen genital segment. The generalized form included calanoid copepods of the *Calanus* type that did not share any of these characters.

A stomach-contents index (SCI, %) was calculated as *SCI*=(*wet mass of total stomach contents*/*wet body mass*)×100. For each prey taxon, the percentages by number (*N*) and wet mass (*WM*) of the total prey, and the percentage frequency of occurrence (*F*) were determined. An index of relative importance (IRI) was calculated for each prey taxon as $IRI_i = F_i \times (N_i + WM_i)$ (Pinkas et al., 1971), where *i* denotes the taxon. The *IRI* for each major group of prey taxa was then standardized to *%IRI* (Cortés, 1997):

$$\%IRI_i = 100 \times IRI_i / \sum_i^n IRI_i ,$$

where *n* is the total number of groups collected.

Copepod mandible size is directly related to the carapace length of several calanoid copepods in the North Atlantic (Karlson and Båmstedt, 1994); therefore mandible width was used as an indicator of relative prey size to compare copepod prey size with squid mantle size. A total of 87 mandibles were measured from the stomachs of 10 squid measuring 29–102 mm ML.

Results

Of the 338 stomachs examined, 267 (79%) contained prey, and 220 (65%) contained identifiable prey (Table 1). Individual SCI values ranged from 0% to 8.0% (station mean=1.0%). SCI values varied significantly among sampling times (Kruskal-Wallis test, $P<0.001$), and the two highest SCI values occurred in the afternoon and just after sunset (Fig. 3).

The diet of *B. anonychus* comprised seven major prey groups and was dominated by copepods (*N*=70%, *WM*=85%, *F*=74%, *%IRI*=87%) and chaetognaths (*N*=24%, *WM*=11%, *F*=48%, *%IRI*=12%) (Table 2). The five other prey groups (amphipods, euphausiids, ostracods, unidentified fish, and unidentified gelatinous prey) each had a *%IRI* value ≤1%.

Copepod prey comprised four genera, and 86% by number of the copepods were from the genus *Neocalanus*. *Neocalanus cristatus* was the most abundant prey taxa, composing 50% by mass and 35% by number of the total diet. The three *Neocalanus* taxa (*Neocalanus* spp., *N. plumchrus+flemingeri,* and *N. cristatus*) composed 85% by mass and 68% by number of the diet. *Neocalanus cristatus* was identified based on the presence of the head crest, which develops at the C5 copepodite stage (Brodsky, 1950). Thus, this taxon comprises only the C5 and C6 stages, and possible members of the *Neocalanus* spp. taxon include *N. plumchrus*, *N. flemingeri,* and earlier stages (C1–C4) of *N. cristatus*. Squid ≥60 mm ML fed mainly on *Neocalanus cristatus* (*N*=39%, *WM*=53%, *F*=50%) and *Neocalanus* spp. (*N*=29%, *WM*=31%, *F*=40%), whereas those <60 mm ML fed mainly on *Neocalanus* spp. (*N*=43%, *WM*=53%, *F*=29%) and *Neocalanus plumchrus+flemingeri* (*N*=8%, *WM*=10%, *F*=14%), and consumed few C5–C6 *Neocalanus cristatus* (*N*=4%, *WM*=4%, F=6%). The mandible size of copepod prey showed a clear positive relationship with ML (Fig. 4), indicating that the squid fed on larger copepods as the squid grew. Taxa from other copepod genera (i.e., *Candacia, Metridia,* and *Pleuromamma*) composed 0.5% of the total prey number and 0.1% of the total wet mass (Table 2).

Parasagitta elegans, the only identified chaetognath, occurred in more stomachs (47%) than any other prey taxon and in 58% of the stomachs from squid ≥60 mm

Table 2

Prey items identified from stomach contents of *Berryteuthis anonychus* collected in the northeast Pacific during May 1999. %IRI: standardized index of relative importance. *%IRI* values in parentheses are those for <60 mm ML and ≥60 mm ML squid. Frequency of occurrence was calculated from the number of stomachs containing food. "—" means prey taxon was not present in stomachs.

Taxon	Number (%)	Wet mass (%)	Frequency of occurrence (%)	*%IRI* (<60 mm ML, ≥60 mm ML)
Copepoda	70.2	85.3	74.2	86.5 (80.9, 84.8)
Candacia columbiae	0.2	0.1	1.9	
Candacia sp.	<0.1	<0.1	0.4	
Metridia pacifica	0.2	<0.1	2.2	
Neocalanus cristatus	35.0	50.4	23.2	
Neocalanus plumchrus+flemingeri	3.1	1.8	12.4	
Neocalanus spp.	30.0	32.3	33.3	
Pleuromamma spp.	0.1	<0.1	1.9	
Calanoida (generalized form)	0.5	0.3	4.9	
Calanoida (specialized form)	0.1	0.1	0.4	
Unidentified Calanoida	0.9	0.3	14.2	
Unidentified Copepoda	0.1	0.1	2.6	
Chaetognatha	23.9	10.8	47.6	12.4 (18.1, 13.9)
Parasagitta elegens	23.8	10.7	47.2	
Unidentified Chaetognatha	0.1	0.1	1.1	
Amphipoda	4.6	2.5	19.1	1.0 (1.0, 1.3)
Hyperia medusarum	0.8	0.9	2.2	
Themisto pacifica	2.5	0.9	7.5	
Unidentified Hyperiidae	0.4	0.5	0.7	
Unidentified Physocephalata	<0.1	<0.1	0.4	
Unidentified Hyperiidea	0.7	0.2	7.5	
Unidentified Amphipoda	0.1	<0.1	1.9	
Euphausiacea	0.5	0.9	4.5	<0.1 (<0.1, 0.1)
Euphausia pacifica	<0.1	0.4	0.5	
Thysanoessa sp.	<0.1	<0.1	0.4	
Unidentified Euphausiacea	0.5	0.5	3.7	
Ostracoda	<0.1	<0.1	1.1	<0.1 (<0.1, —)
Unidentified fish	<0.1	0.8	0.4	<0.1 (—, <0.1)
Unidentified gelatinous prey	<0.1	<0.1	0.4	<0.1 (<0.1, —)
Unidentified crustacea	0.1	<0.1	1.1	
Unidentified material	0.6	0.1	18.7	

Neocalanus plumchrus and *N. flemingeri* were grouped as a single taxon (*N. plumchrus+flemingeri*) because of difficulty in distinguishing these species in partly digested materials.

Neocalanus cristatus comprises stages C5 and C6 only.

Neocalanus spp. = *N. cristatus* (stages C1–C4), *N. plumchrus,* and *N. flemingeri.*

Calanoida (specialized form) = unidentified individuals with markedly enlarged appendages, strongly developed chelae, a spine on the posterior corner of the terminal thoracic segment, or asymmetrically swollen genital segments.

Calanoida (generalized form) = unidentified *Calanus*-type individuals that share none of the characters of the specialized form.

ML. *P. elegans* was the third most abundant prey taxon, composing 24% by number and 11% by mass of the total diet (Table 2).

Amphipods (mainly *Themisto pacifica* and *Hyperia medusarum*) were consumed by 19% of the squid but composed only 5% by number and 3% by wet mass of the total prey consumed. The four other prey groups combined composed <2% by mass and <1% by number of the diet. There were no major changes in *%IRI* values through the size range of squid examined (Table 1) and no evidence of cannibalism or predation on other cephalopod species.

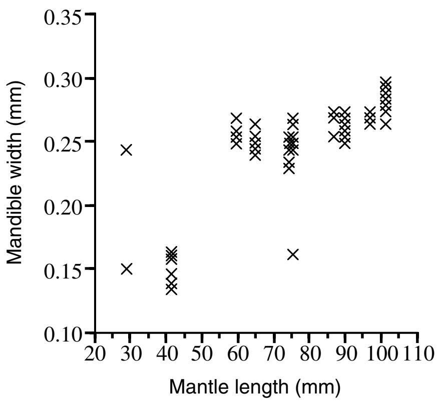

Figure 4

Relationship between mandible width of copepod prey and mantle length of *Berryteuthis anonychus*.

Discussion

The diet of *Berryteuthis anonychus* collected in the northeast Pacific during May was dominated by calanoid copepods and chaetognaths. During early July in this area, *B. anonychus* larger than those examined in the present study (ML: 75–127 mm vs. 10–102 mm) fed on a wider variety of prey, including primarily calanoid copepods, hyperiid amphipods, pteropods, and euphausiids (Lapshina, 1988). Possible causes for this change in diet include seasonal change in prey availability and an ontogenetic change in the squid's ability to capture prey.

The zooplankton composition in the upper 150 m of the subarctic North Pacific is highly seasonal. *Neocalanus* copepods, the major prey of *B. anonychus*, dominate the epipelagic zooplankton community during spring and early summer (Mackas and Tsuda, 1999). They then descend from the upper layer to spend the late summer, autumn, and early winter at 400–2000 m, well below the depth range of *B. anonychus* (0–200 m; Nesis, 1997). As a result of this ontogenetic descent, the upper ocean zooplankton biomass decreases greatly, and the community is then dominated by a different group of species. This group includes euphausiids (Mackas and Tsuda, 1999), which are consumed by more *B. anonychus* in July (28%; Lapshina, 1988) than in May (5%; present study). Other prey that show a large increase in frequency of occurrence between May and July are amphipods (19% in May, 52% in July) and pteropods (0% in May, 40% in July).

Oceanic squids such as *B. anonychus* generally feed on small crustaceans as juveniles and then shift their diet to larger fish and other cephalopods as they grow (Rodhouse and Nigmatullin, 1996). We observed no such ontogenetic shift within the size range examined, but copepod prey size was found to increase with growth. These data are consistent with those for other squids in that prey size increases during development (Nixon, 1987; Hanlon and Messenger, 1996). Most gonatids undergo ontogenetic vertical descent (Roper and Young, 1975; Nesis, 1997), and a clear shift in the diet can accompany this habitat shift (e.g., as seen in *Berryteuthis magister*; Nesis, 1997). Nesis (1997), however, suggested that *B. anonychus* does not undergo ontogenetic descent; therefore no such habitat-change–related shift in diet would be expected to occur in this species.

Highest feeding intensities were recorded in the afternoon and just after sunset, which would indicate that *B. anonychus* feeds both day and night. Such a feeding scenario is supported by the high overlap in depth distributions of *B. anonychus* (day: 50–200 m, night: 0–150 m; Nesis, 1997) and its main prey, *Neocalanus cristatus*; during spring, *N. cristatus* occurs mainly at 50–150 m, and like the other *Neocalanus* species, shows no evidence of diel vertical migration (Mackas et al., 1993). Therefore *B. anonychus* and *N. cristatus* occupy nearly the same depth range both day and night.

The chaetognath *Parasagitta elegans* was the third most abundant prey taxon and was consumed by more squid than any other taxon. *Parasagitta elegans* forms an important fraction of the springtime macrozooplankton community in the North Pacific (Brodeur and Terazaki, 1999) and inhabits mainly the epipelagic layer (0–200 m) (Kotori, 1976; Terazaki and Miller, 1986); therefore predation on *P. elegans* could also occur both day and night. Another gonatid squid, *Gonatus madokai*, has also been found to prey on *Parasagitta* sp. (Kubodera and Okutani, 1977).

There was no evidence of cannibalism, which commonly occurs in many gonatids, particularly *Berryteuthis magister* and *Gonatopsis borealis* (Lapko, 1996; Nesis, 1997). Cannibalism in squids appears to occur less frequently when prey are abundant (Shchetinnikov, 1992; Santos and Haimovici, 1997), as is the case in the North Pacific during spring. In addition, at nearly every station sampled, squid of a small size range were collected (Bower et al., 2002); therefore it seems that opportunities for intercohort cannibalism were limited.

The large stock size of *B. anonychus* in the North Pacific (Nesis, 1997) and its importance in the diet of higher predators may indicate that the food chain from copepods through squids and these higher predators is an important trophic pathway in the pelagic food web of the Subarctic Pacific during spring. The large seasonality in zooplankton composition in the upper 150 m may indicate that these trophic pathways will show similar seasonal variations.

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