Feeding habits of neon flying squid *Ommastrephes bartramii* in the transitional region of the central North Pacific

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ABSTRACT: We examined the feeding habits of the neon flying squid *Ommastrephes bartramii* from late spring to mid-summer in relation to its northward migration in the transitional waters of the central North Pacific. The winter–spring cohort (ca. 15 to 25 cm in May and 20 to 35 cm in July) and the autumn cohort (ca. 30 to 45 cm in May and 35 to 50 cm in July) were identified by their dorsal mantle lengths. In May and July, the winter–spring cohort was distributed only in the transition zone (TZ) south of the subarctic boundary. This cohort preyed primarily on crustaceans such as euphausiids and amphipods in May, but in July, their primary prey shifted to the sternoptychid fish *Maurolicus imperatorius*. In May, the larger-sized autumn cohort was also distributed only in the TZ, but in July, these individuals migrated to the transitional domain (TD) north of the subarctic boundary. The main prey of the autumn cohort were micronektonic animals that dominated the TZ in May: the transitional-water myctophid *Symbolophorus californiensis*, and 2 subtropical myctophids, *Ceratoscopelus warmingi* and *Electrona risso*. Secondary important prey items included the transitional-water squid *Onychoteuthis borealijaponica* and subarctic gonatid squids such as *Gonatus berryi* and *Berryteuthis anonychus*. In July, the main prey species in the TD were *S. californiensis* and *O. borealijaponica*, both of which also migrated from the TZ into the TD, crossing the subarctic boundary in summer. We estimated the feeding impact of the autumn squid cohort on myctophids in the TD during summer.

KEY WORDS: Neon flying squid · Feeding habits · Myctophid fishes · Seasonal migration · Transitional waters · Central North Pacific

INTRODUCTION

The neon flying squid *Ommastrephes bartramii* is an oceanic squid occurring worldwide in subtropical and temperate waters (Roper et al. 1984). It is one of the dominant large pelagic nekton in the North Pacific (Roper et al. 1984, Murata 1990, Murata & Hayase 1993, Seki 1993a). The main habitat of this squid is the so-called transitional region of the North Pacific (Pearcy 1991), which consists of the transitional domain north of the subarctic boundary and the transition zone to the south (Favorite et al. 1976; Fig. 1). This species migrates south–north to feed between the subtropical region and the transitional domain, since the latter area is highly productive in summer (Taniguchi 1981, Murata 1990, Murata & Hayase 1993).

Previous studies have indicated that in the transitional region of the North Pacific, neon flying squid feed mainly on micronektonic and small pelagic fishes such as myctophids, Japanese sardine, and saury, as well as on small pelagic cephalopods such as *Berryteuthis anonychus* (Shevstov 1972, Filippova 1974, Naito et al. 1977a, Tung 1981, Pearcy 1991, Seki 1993a,b, Arimoto & Kawamura 1998). Neon flying squid are also important prey of larger fishes, such as swordfish and blue sharks, and marine mammals such as fur seals and sperm whales (Okutani et al. 1976, Okutani & Satake 1978, Pearcy 1991, Seki 1993a, Mori et al. 2001). There-

fore, *Ommastrephes bartramii* has been thought to play an important role in connecting animals of the tertiary trophic level with apex predators in oceanic food webs, although quantitative data on the feeding habits of this species are extremely limited.

From spring to summer, neon flying squid are found as a large-sized autumn cohort and a small-sized winter–spring cohort (Yatsu et al. 1998). We aimed to quantitatively examine the feeding habits of each cohort in the transitional waters of the central North Pacific from late spring to mid-summer and determine their feeding strategies in relation to their seasonal south–north migrations and diel vertical migrations. We also estimated the impact of feeding by the autumn cohort on the biomass of myctophids in the transitional domain during the summer.

Fig. 1. Sampling localities (O) of *Ommastrephes bartramii* and CTD cast stations (•) in central North Pacific in May and July 2001. SA: subarctic domain; SB: subarctic boundary; SF: subarctic front; TD: transitional domain; TZ: transition zone

MATERIALS AND METHODS

Samples were collected in the transition zone (TZ) of the central North Pacific from May 4 to 26, 1999 and May 6 to 16, 2001, and in both the TZ and the transitional domain (TD) from July 7 to 25, 2001. The sampling localities in May and July 2001 are shown in Fig. 1. In this sampling area, the Emperor seamounts are located along ca. 170° E. We used 2 sets of surface gillnets; one was a non-size-selective net, which comprised 30 units (1 unit = 7 m high × 50 m wide) with mesh sizes of 48, 55, 63, 72, 82, 93, 106, 121, 138, and 157 mm and the other was a commercial net, which comprised 20 units with a mesh size of 115 mm. Gillnets were deployed at dusk and retrieved at dawn on the following day. We sampled the 0 to 7 m layer, which corresponds to the main habitat depth of neon flying squid at night. Samples were frozen at −30°C for further analysis in the laboratory. A CTD (conductivity, salinity, depth profiler) cast was made down to 500 m at each sampling station and between sampling stations to determine the position of the subarctic boundary and the subarctic front (Fig. 1).

Dorsal mantle length (DML), body wet weight, and wet weight of stomach contents were measured. We used the samples collected by the non-size-selective gillnet to evaluate the DML composition. Zooplankton prey were counted and identified to species or genus, depending on their state of digestion. Total body length (TL) and wet weight (WW) were measured for each taxon. All cephalopod and fish prey were identified to the lowest taxonomic level possible based on the morphology of their lower beaks and sagittal otoliths, respectively, since these prey items were highly masticated. Sagittal fish otoliths were sorted into left and right otoliths, and basically the left otoliths were counted. When the numbers of left and right otoliths differed, the larger number was taken to represent the number of fish prey. Their rostral length of the lower beak of cephalopods and the maximum diameter of sagittal fish otoliths were also measured to estimate wet weights and body sizes (DML for cephalopods and standard length [SL] for fishes), using relationships generated from intact specimens of the main prey items (Kubodera 1982, Clarke 1986, Kubodera & Furuhashi 1987, Kubodera & Shimazaki 1989, Smale et al. 1995, Ohizumi et al. 2001, T. Kubodera unpubl. data, H. Watanabe & H. Ohizumi unpubl. data).

The stomach content index (SCI) was calculated as

$$\text{SCI(\%)} = \frac{\text{wet weight of stomach contents}}{\text{body wet weight}} \times 100$$

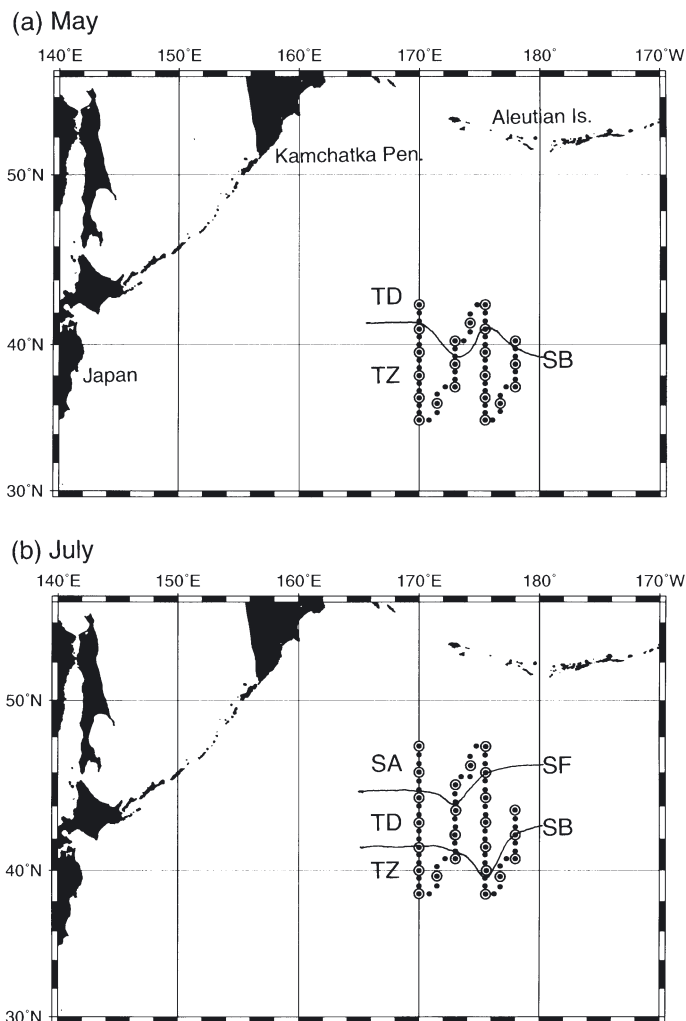The frequency of occurrence (*F*) of each food item in the total number of stomachs examined, the ratio of

each food item to the total number of food items identified (Cn), and the ratio of the wet weight of each food item to the total wet weight of the stomach contents were calculated for Species i as follows:

$$Fi(\%) = \frac{\text{no. of stomachs including food item } i}{\text{total no. of stomachs}} \times 100$$

$$Cni(\%) = \frac{\text{total no. of food item } i}{\text{total no. of food items identidied in stomachs}} \times 100$$

$$WWi(\%) = \frac{\text{total wet weight of food item } i}{\text{total wet weight of stomach contents}} \times 100$$

Using these 3 indices, an index of relative importance (IRI; Pinkas et al. 1971) of food item i was calculated using the equation: $IRIi = (Cni + WWi) \times Fi$
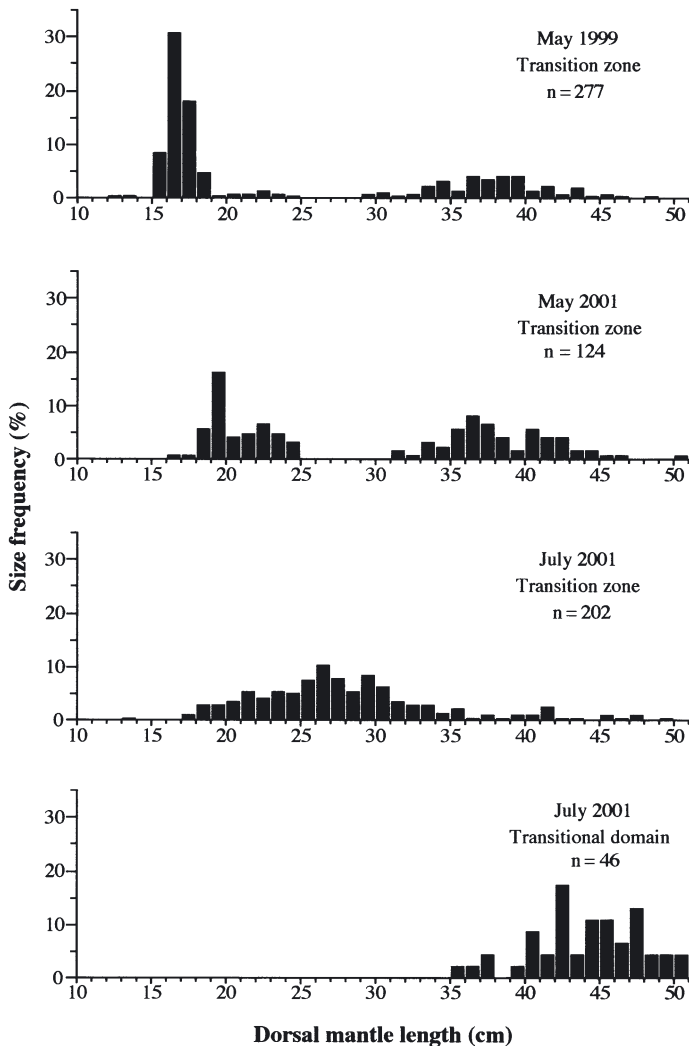

Fig. 2. *Ommastrephes bartramii*. Size distributions in May 1999 and 2001, and in July 2001

This index is represented by the size of a rectangle resolved by plotting the 3 values on a 3-way graph.

We were unable to estimate the body wet weight of 2 cephalopod species, *Japetella diaphana* and *Ancistrocheirus lesueuri*, and 3 micronektonic fish species, *Diaphus kuroshio*, *Ichtyococcus elongatus*, and *Argyropelecus sladeni*. However, because these were minor prey items with very low Cn and F values (see Tables 1 & 2), they did not significantly affect the wet weight composition of prey species.

RESULTS

Size composition

The frequency distribution of DML showed a clear first mode between 15 and 25 cm in May, representing the winter–spring cohort; this mode shifted to between 20 and 35 cm in July (Fig. 2), indicating a growth of 5 to 10 cm DML over 2 mo. Individuals that formed the first mode were distributed only in the TZ in both May and July (Fig. 2) and showed no seasonal migrations into the TD. The second mode, representing the autumn cohort, measured between 30 and 45 cm DML in the TZ in May, and between 35 and 50 cm in the TD in July, indicating a growth of 5 to 10 cm over 2 mo. In July, the distribution center of the larger-sized autumn cohort shifted northward into the TD, although a small part of this cohort still remained in the TZ (Fig. 2), suggesting a general northward summertime migration from the TZ to the TD.

Diet composition

We identified 32 prey species belonging to 27 genera in 397 examined stomachs (see Tables 1 & 2). Of these stomachs, 48 (12.1%) were empty. Most of the fish remains such as vertebrate and jaws found in the stomachs were identified as parts of micronektonic fishes. These fish remains did not occur in the stomachs of the winter–spring cohort in May.

Winter–spring cohort (juveniles)

The winter–spring cohort was at a juvenile stage from May to July and remained in the TZ.

May. Most prey items in the stomachs of this cohort were planktonic crustaceans, such as euphausiids and amphipods, in both 1999 and 2001 (Table 1). In 1999, euphausiids ranked first, with Cn and WW values of 57.1 and 51.4%, respectively, followed by amphipods (Cn, 28.6%; WW, 22.8%). In 2001, they also mainly

Table 1. Prey–species composition of winter–spring cohort (juveniles) of *Ommastrephes bartramii* in transition zone (TZ) of central North Pacific by abundance (*Cn*, %), wet weight (WW, %), and frequency of occurrence (*F*, %) in total number of stomachs examined. DML: dorsal mantle length; IRI: index of relative importance (see 'Materials and methods' for details); n: no. of stomachs examined (no. of empty stomachs); –: no data

Prey species	May 1999: 15.8–24.9 cm DML n (n) = 4 (1)				May 2001: 15.0–24.9 cm DML n (n) = 50 (7)				July 2001: 13.0–34.9 cm DML n (n) = 136 (21)			
	Cn	WW	*F*	IRI	*Cn*	WW	*F*	IRI	*Cn*	WW	*F*	IRI
Zooplankton	85.7	87.3	50.0	8651	100	100	42.0	8400	4.2	0.2	10.3	44
Euphausiids (unidentified)	57.1	51.4	25.0	2714	61.7	22.7	16.0	1350	1.7	<0.1	3.7	6
Amphipods	28.6	22.8	25.0	1284	38.3	35.8	12.0	889	2.6	0.1	5.1	13
Phronima sedentaria	0	0	0	0	0	0	0	0	0.3	<0.1	0.7	0
Phronima spp.	0	0	0	0	0	0	0	0	0.3	<0.1	0.7	0
Unidentified	28.6	22.8	25.0	1284	38.3	35.8	12.0	889	2.0	0.2	4.4	9
Crustaceans (unidentified)	–	13.1	50.0	–	–	41.5	36.0	–	–	<0.1	10.3	–
Cephalopods	14.3	12.7	25.0	675	0	0	0	0	7.9	11.5	6.6	128
Gonatids												
Gonatopsis borealis	0	0	0	0	0	0	0	0	2.3	2.1	2.2	10
Gonatus spp.	0	0	0	0	0	0	0	0	0.6	1.2	1.5	3
Berryteuthis anonychus	0	0	0	0	0	0	0	0	0.3	0.1	0.7	<0.1
Others												
Onychoteuthis borealijaponica	0	0	0	0	0	0	0	0	0.3	5.8	0.7	4
Japetella diaphana	0	0	0	0	0	0	0	0	0.3	–	0.7	–
Abraliopsis spp.	0	0	0	0	0	0	0	0	2.6	2.3	3.7	18
Unidentified	14.3	12.7	25.0	675	0	0	0	0	1.3	–	1.5	–
Fishes	0	0	0	0	0	0	0	0	87.8	87.9	29.4	5166
Myctophids												
Ceratoscopelus warmingi	0	0	0	0	0	0	0	0	1.7	3.0	1.5	7
Symbolophorus californiensis	0	0	0	0	0	0	0	0	0.3	1.0	0.7	1
Electrona risso	0	0	0	0	0	0	0	0	0.3	0.8	1.5	2
Unidentified	0	0	0	0	0	0	0	0	0.3	–	1.5	–
Others												
Engraulis japonicus	0	0	0	0	0	0	0	0	1.0	1.2	2.2	5
Maurolicus imperatorius	0	0	0	0	0	0	0	0	75.6	81.9	16.9	2663
Ichthyococcus elongatus	0	0	0	0	0	0	0	0	0.3	–	0.7	–
Unidentified	0	0	0	0	0	0	0	0	8.3	–	14.7	–

fed on euphausiids and amphipods, with euphausiids showing higher *Cn* (61.7 vs 38.3%) and *F* (16.0 vs 12.0%) values, while amphipods had higher WW values than euphausiids (35.8 vs 22.7%). The IRIs of euphausiids and amphipods were 2714 and 1284, respectively, in 1999 and 1350 and 889, respectively in 2001 (Table 1), indicating that juvenile squids fed primarily on euphausiids and secondarily on amphipods.

July. Fishes were the most common prey, as indicated by high *Cn* (87.8%), WW (87.9%), and *F* (29.4%) values (Table 1). The IRI of fishes was 5166, while IRI values of other taxa were <130, indicating that the diet shifted from crustacean zooplankton to fishes in midsummer in the TZ. Most of the fish prey was composed of the sternoptychid *Maurolicus imperatorius*, which had very high *Cn* (75.6%), WW (81.9%), *F* (16.9%), and IRI (2663) values (Table 1). The smallest individuals that fed on cephalopods and fishes were 18 and 21 cm DML, respectively, suggesting a shift in prey items from crustacean zooplankton to micronektonic fishes upon reaching a DML of around 20 cm.

Autumn cohort (adults)

Individuals of the autumn cohort were at an adult stage in summer, and most of the population moved north and crossed the subarctic boundary during the summer feeding migration from the TZ into the TD.

Transition zone in May. The most common prey item was fishes both in 1999 and 2001, with *Cn* values of 74.7 and 64.0% and *F* values of 63.8 and 70.7%, followed by cephalopods (*Cn*, 15.7 and 28.0%; *F*, 53.2 and 31.7%; Table 2). In terms of wet weight of prey (WW), however, fishes and cephalopods were equally important, since the WW of fish was 55.7 and 42.0% in 1999 and 2001, respectively, while the values for cephalopods were 44.1 and 57.9%. In both 1999 and 2001, the IRIs were highest for fishes (8320 and 7492), followed by cephalopods (3181 and 2723; Table 2). The IRIs of other taxa such as euphausiids and amphipods were <40 in 1999 and <80 in 2001 (Table 2), suggesting that adult neon flying squid mainly prey on fishes and secondarily on cephalopods.

Among the fish prey, this cohort mainly fed on the transitional-water myctophid *Symbolophorus cali-*

Table 2. Prey–species composition of autumn cohort (adults) of *Ommastrephes bartramii* in transition zone (TZ) and transitional domain (TD) of central North Pacific by abundance (*Cn*, %), wet wt (WW, %), and frequency of occurrence (*F*, %) in all stomachs examined. Further details given in Table 1

Prey species	May 1999, TZ 29.0–45.9 cm DML n (n) = 47 (3)				May 2001, TZ 31.0–50.9 cm DML n (n) = 41 (4)				July 2001, TZ 35.0–49.9 cm DML n (n) = 49 (6)				July 2001, TD 35.0–50.9 cm DML n (n) = 70 (6)			
	Cn	WW	*F*	IRI	*Cn*	WW	*F*	IRI	*Cn*	WW	*F*	IRI	*Cn*	WW	*F*	IRI
Zooplankton	18.6	0.2	10.6	200	16.0	0.1	14.6	236	0.4	0.1	12.2	6	0	<0.1	14.3	1
Euphausiids	8.9	<0.1	4.3	38	8.0	<0.1	9.8	79	0	0	0	0	0	0	0	0
Euphausia spp.	0.4	<0.1	2.1	1	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified	8.5	<0.1	4.3	37	8.0	<0.1	9.8	79	0	0	0	0	0	0	0	0
Amphipods (unidentified)	0.8	<0.1	4.3	3	0	0	0	0	0.4	<0.1	2.0	<0.1	0	0	0	0
Crustaceans (unidentified)	–	<0.1	8.5	–	–	<0.1	9.8	–	–	<0.1	12.2	–	–	<0.1	14.3	
Pteropods (unidentified)	0	0	0	0	–	<0.1	2.4	–	0	0	0	0	0	0	0	0
Cephalopods	15.7	44.1	53.2	3181	28.0	57.9	31.7	2723	6.8	32.2	16.3	636	37.8	64.7	44.3	4542
Gonatids																
Gonatus berryi	4.2	9.7	10.6	148	0	0	0	0	0.4	0.9	2.0	3	0	0	0	0
Gonatus onyx	2.0	5.1	6.4	45	0	0	0	0	0	0	0	0	1.3	4.0	4.3	23
Gonatus pyros	0.8	4.3	4.3	22	1.0	2.4	4.9	17	0.4	4.2	2.0	9	1.3	5.2	4.3	28
Gonatus middendorffi	0	0	0	0	5.5	7.6	17.1	224	0	0	0	0	3.0	3.9	5.7	39
Gonatus spp.	0	0	0	0	5.5	10.1	19.5	304	0.4	2.5	2.0	6	1.3	1.5	4.3	12
Berryteuthis anonychus	0	0	0	0	12.0	23.3	22.0	776	0	0	0	0	0	0	0	0
Gonatopsis borealis	0.8	2.1	2.1	6	0.5	1.5	2.4	5	0.9	0.5	4.1	6	0.4	0.7	1.4	2
Others																
Onychoteuthis borealijaponica	2.7	6.2	8.5	76	2.5	12.8	7.3	112	0.9	1.1	4.1	8	9.0	29.1	17.1	654
Histioteuthis inermis	0.4	6.5	2.1	15	0	0	0	0	0	0	0	0	0	0	0	0
Histioteuthis dofleini	0	0	0	0	0	0	0	0	0.4	12.5	2.0	26	0	0	0	0
Ommastrephes bartramii	0.4	7.2	2.1	16	0	0	0	0	0.4	3.8	2.0	9	0	0	0	0
Galiteuthis phyllura	0.4	1.4	2.1	4	0	0	0	0	0	0	0	0	0	0	0	0
Taonius pavo	0	0	0	0	0.5	0.1	2.4	1	0.4	0.5	2.0	2	1.3	4.1	5.7	31
Chiroteuthis imperator	0	0	0	0	0.5	–	2.4	–	0.4	5.8	2.0	13	0	0	0	0
Japetella diaphana	0.8	–	4.3	–	0	0	0	0	0	0	0	0	0	0	0	0
Ancistrocheirus lesueuri	0.8	–	2.1	–	0	0	0	0	0	0	0	0	0	0	0	0
Abraliopsis spp.	0.4	1.6	2.1	4	0	0	0	0	0.9	0.4	4.1	5	18.9	16.2	14.3	501
Unidentified	2.0	–	10.6	–	0	0	0	0	1.3	–	2.0	–	1.3	–	2.9	–
Fishes	74.7	55.7	63.8	8320	64.0	42.0	70.7	7492	92.7	67.7	57.1	9163	62.2	35.2	48.6	4735
Myctophids																
Symbolophorus californiensis	19.9	32.2	23.4	1219	8.5	9.9	14.6	269	0	0	0	0	8.6	15.9	12.9	315
Ceratoscopelus warmingi	12.5	16.1	21.3	609	6.0	9.5	9.8	152	0	0	0	0	0.9	1.4	2.9	6
Electrona risso	2.3	2.7	6.4	32	11.0	14.3	22.0	556	2.6	2.9	4.1	22	4.3	3.8	4.3	35
Protomyctophum thompsoni	7.8	1.9	4.3	41	0	0	0	0	0	0	0	0	0	0	0	0
Lampanyctus jordani	1.6	1.6	2.1	7	0	0	0	0	0	0	0	0	0	0	0	0
Notoscopelus resplendens	0.4	0.4	2.1	2	0	0	0	0	0	0	0	0	0	0	0	0
Notoscopelus japonicus	0	0	0	0	0	0	0	0	1.3	6.3	2.0	15	0	0	0	0
Diaphus theta	0	0	0	0	0.5	0.8	2.4	3	0	0	0	0	2.6	4.2	5.7	39
Diaphus gigas	0	0	0	0	0	0	0	0	0.4	2.3	2.0	6	0	0	0	0
Diaphus kuroshio	0	0	0	0	3.5	–	7.3	–	0.9	–	4.1	–	0	0	0	0
Myctophum asperum	0	0	0	0	0.5	0.6	2.4	3	0	0	0	0	0	0	0	0
Unidentified	0	0	0	0	2.0	–	7.3	–	0.4	–	2.0	–	8.6	–	7.1	–
Others																
Engraulis japonicus	1.2	0.8	2.1	4	0	0	0	0	8.1	6.7	6.1	91	0	0	0	0
Bathylagus ochotensis	0	0	0	0	1.0	6.5	2.4	18	0	0	0	0	5.6	9.9	7.1	111
Maurolicus imperatorius	0	0	0	0	0.5	0.4	2.4	2	71.1	49.5	20.4	2460	0	0	0	0
Ichthyococcus elongatus	2.3	–	6.4	–	1.5	–	7.3	–	0	0	0	0	0	0	0	0
Argyropelecus sladeni	0.4	–	2.1	–	0	0	0	0	0	0	0	0	0	0	0	0
Argyropelecus spp.	0.8	–	2.1	–	0	0	0	0	0.4	–	2.0	–	0	0	0	0
Gempylidae	0.4	–	2.1	–	0	0	0	0	0	0	0	0	0	0	0	0
Carangidae	0.4	–	2.1	–	0	0	0	0	0	0	0	0	0	0	0	0
Paralepididae	0.4	–	2.1	–	4.5	–	9.8	–	0.4	–	2.0	–	0.9	–	2.9	–
Bathylagidae	0	0	0	0	1.0	–	4.9	–	0	–	0	–	0.4	–	1.4	–
Scopelarchidae	0	0	0	0	0.5	–	2.4	–	0	0	0	0	0	0	0	0
Unidentified	24.3	–	27.7	–	23.0	–	41.5	–	7.2	–	57.1	–	30.4	–	40.0	–

forniensis and subtropical water myctophids such as *Ceratoscopelus warmingi*. In 1999, *S. californiensis* was the most common species in the stomachs, with *Cn*, WW, and *F* values of 19.9, 32.2 and 23.4%, respectively, followed by *C. warmingi* (12.5, 16.1 and 21.3%; Table 2). The IRI values of *S. californiensis* and *C. warmingi* were 1219 and 609, while the IRIs of other fish species were <45. In 2001, the subtropical water myctophid *Electrona risso* was the most common fish prey, with *Cn*, WW, and *F* values of 11.0, 14.3 and 22.0%, followed by *S. californiensis* (8.5, 9.9 and 14.6%) and *C. warmingi* (6.0, 9.5 and 9.8%; Table 2). The IRI of *E. risso* (556) was also the highest, followed by *S. californiensis* (269) and *C. warmingi* (152), while values of other fish species were <20.

Among the cephalopod prey, the subarctic gonatids such as *Gonatus berryi* and *Berryteuthis anonychus* and the transitional-water species *Onychoteuthis borealijaponica* were commonly found in the stomachs of adult squid. In 1999, *G. berryi* was the most common cephalopod, with *Cn* and *F* values of 4.2 and 10.6%, respectively, followed by *O. borealijaponica* (2.7 and 8.5%) and *G. onyx* (2.0 and 6.4%; Table 2). In terms of WW, these species were also the most common cephalopods (5.1 to 9.7%). The IRIs of *G. berryi*, *O. borealijaponica*, and *G. onyx* were as low as 148, 76, and 45, respectively, while those of other cephalopod species were <25 (Table 2). In 2001, *B. anonychus* was the most common cephalopod by *Cn* (12.0%), WW (23.3%), and *F* (22.0%) values, followed by *Gonatus* spp., or *G. middendorffi* or *O. borealijaponica* (Table 2). The IRIs of these species (112 to 776) were significantly higher than those of other cephalopod species (<20).

Transition zone in July. A small part of the adult population remained in the TZ in July. These individuals exclusively fed on fishes, with *Cn*, WW, and *F* values of 92.7, 67.7, and 57.1%, respectively (Table 2). Of these fishes, *Maurolicus imperatorius* was the most common, with very high *Cn* (71.1%), WW (49.5%), *F* (20.4%), and IRI (2460) values (as also observed in the spatio-temporally coexisting juveniles), i.e. the main fish and cephalopod prey in May (e.g. *Symbolophorus californiensis* and *Onychoteuthis borealijaponica*) disappeared from the TZ in July due to their northward migrations, and were replaced by *M. imperatorius*.

Transitional domain in July. In terms of *Cn*, fishes were the most common prey (62.2%), followed by cephalopods (37.8%; Table 2). In terms of weight (WW), however, cephalopods were more important than fishes (64.7 vs 35.2%), while the *F* values of fishes and cephalopods were similar (48.6 vs 44.3%). As a result, the IRI values were not very different between fishes (4735) and cephalopods (4542), indicating that fishes contribute mostly to prey composition in numbers, and cephalopods in weight (Table 2).

The transitional-water species *Symbolophorus californiensis* and *Onychoteuthis borealijaponica* were 2 of the most common prey items, as observed in the TZ in May. Among the fish prey, *S. californiensis* was the most common, with *Cn*, WW, and *F* values of 8.6, 15.9, and 12.9%, respectively, followed by the subarctic bathylagid *Bathylagus ochotensis* (5.6, 9.9 and 7.1%; Table 2). The IRIs of *S. californiensis* and *B. ochotensis* were 315 and 111, respectively, while those of other fish species were <40.

Among the cephalopod prey, *Onychoteuthis borealijaponica* was the most common in terms of both WW and *F* (29.1 and 17.1%, respectively), followed by *Abraliopsis* spp. (16.2 and 14.3%; Table 2). *Abraliopsis* spp. were more abundant than *O. borealijaponica* (*Cn* = 18.9 vs 9.0%), but the IRI values did not differ much between these 2 categories (501 vs 654). This indicates that *Abraliopsis* spp. contributed mostly to prey composition in numbers and *O. borealijaponica* in weight. The IRIs for other cephalopods were all <40.

Prey size

Winter–spring cohort (juveniles)

Euphausiids, the main prey of squids in May, ranged from 1.3 to 1.5 cm TL (n = 3). In July, the most common fish prey, *Maurolicus imperatorius*, was estimated to be 2.0 to 5.2 cm SL (mean ± SD = 3.8 ± 1.4); this was generally smaller than other fish prey, such as *Ceratoscopelus warmingi*, *Engraulis japonicus* and *Symbolophorus californiensis* (4.8 to 7.7 cm SL; Table 3). Sizes of cephalopod prey in July ranged from 1.4 to 7.0 (4.4 ± 2.6) cm DML, similar to the size range of the fish prey.

Autumn cohort (adults)

Among the common fish prey in the TZ in May, *Symbolophorus californiensis*, *Ceratoscopelus warmingi* and *Electrona risso* ranged in size from 9.2 to 10.2 cm (9.8 ± 0.7), 6.0 to 8.8 cm (7.6 ± 1.1), and 6.0 to 11.4 cm (8.6 ± 1.7) standard length, respectively, indicating that adult squid fed mainly on myctophids of 6 to 11 cm SL (Table 3). In the TZ in July, *Maurolicus imperatorius* found in squid stomachs were 2.0 to 5.2 cm SL (3.9 ± 1.0); i.e. of similar size to those consumed by spatio-temporally coexisting juveniles (Mann-Whitney *U*-test, p > 0.05). This indicates that in the TZ, the prey-size spectrum of adult squid shifts to a smaller range from May to July in accordance with the northward migration of the prey species into the TD (see 'Discussion'). In the TD in July, the size ranges of *S. cali-*

Table 3. Estimated size (cm) of cephalopod and fish prey-species of *Ommastrephes bartramii* in transition zone (TZ) and transitional domain (TD) of central North Pacific. Sizes are dorsal mantle length for cephalopods and standard length for fishes

Species	Winter–spring cohort (juveniles) July 2001 (TZ)			Autumn cohort (adults) May 1999 (TZ)			May 2001 (TZ)			July 2001 (TZ)			July 2001 (TD)		
	n	avg.	range (cm)	n	avg.	range (cm)	n	avg.	range (cm)	n	avg.	range (cm)	n	avg.	range (cm)
Cephalopods															
Onychoteuthis borealijaponica	1	1.4	–	7	7.1	4.1–13.5	3	15.9	12.5–22.7	2	8.5	4.4–12.5	16	10.8	5.0–13.8
Gonatus berryi	0	–	–	10	6.5	6.2–7.5	0	–	–	1	7.2	–	0	–	–
Gonatus onyx	0	–	–	5	5.3	3.2–9.4	0	–	–	0	–	–	4	5.0	4.1–6.0
Gonatus pyros	0	–	–	2	9.4	–	2	6.8	4.9–8.7	1	14.3	–	2	8.4	5.7–11.1
Gonatus middendorffi	0	–	–	0	–	–	13	6.1	3.6–11.3	0	–	–	7	6.6	5.5–8.0
Gonatus spp.	2	3.8	2.3–5.3	0	–	–	13	3.5	2.3–4.2	1	4.2	–	1	10.9	–
Berryteuthis anonychus	1	3.1	–	0	–	–	25	6.3	1.7–8.2	0	–	–	0	–	–
Abraliopsis spp.	8	4.7	3.6–7.0	1	3.8	–	0	–	–	2	5.4	3.8–7.0	47	4.6	2.8–6.4
Gonatopsis borealis	7	4.9	3.9–5.6	2	5.7	5.2–6.2	2	6.3	6.0–6.5	2	4.8	4.4–5.3	1	6.2	–
Galiteuthis phyllura	0	–	–	1	6.9	–	0	–	–	0	–	–	0	–	–
Ommastrephes bartramii	0	–	–	1	8.8	–	0	–	–	1	8.2	–	0	–	–
Histioteuthis inermis	0	–	–	1	6.0	–	0	–	–	0	–	–	0	–	–
Histioteuthis dofleini	0	–	–	0	–	–	0	–	–	1	7.9	–	0	–	–
Chiroteuthis imperator	0	–	–	0	–	–	1	1.6	–	1	8.7	–	0	–	–
Taonius pavo	0	–	–	0	–	–	1	1.8	–	1	3.3	–	4	8.3	4.9–10.4
Cephalopod total	19	4.4	1.4–7.0	30	6.6	3.2–13.5	60	6.2	1.6–22.7	13	7.0	3.3–14.3	82	6.4	2.8–13.8
Fishes															
Maurolicus imperatorius	229	3.8	2.0–5.2	0	–	–	1	3.8	–	167	3.9	2.0–5.2	0	–	–
Symbolophorus californiensis	1	7.7	–	51	9.8	9.2–10.2	17	9.6	9.4–10.2	0	–	–	16	10.4	9.5–11.3
Ceratoscopelus warmingi	5	4.8	–	32	7.5	6.0–8.8	12	7.7	6.7–8.4	0	–	–	2	8.3	–
Electrona risso	2	6.0	–	6	8.8	6.0–11.4	22	8.6	6.2–11.1	6	9.0	6.2–12.4	10	8.8	7.7–11.1
Protomyctophum thompsoni	0	–	–	20	4.1	3.9–5.0	0	–	–	0	–	–	0	–	–
Lampanyctus jordani	0	–	–	4	11.4	11.0–11.8	0	–	–	0	–	–	0	–	–
Notoscopelus resplendens	0	–	–	1	6.2	–	0	–	–	0	–	–	0	–	–
Notoscopelus japonicus	0	–	–	0	–	–	0	–	–	3	12.9	12.7–13.2	0	–	–
Diaphus theta	0	–	–	0	–	–	1	6.7	–	0	–	–	6	8.0	7.6–8.2
Diaphus gigas	0	–	–	0	–	–	0	–	–	1	13.6	–	0	–	–
Myctophum asperum	0	–	–	0	–	–	1	7.3	–	0	–	–	0	–	–
Bathylagus ochotensis	0	–	–	0	–	–	2	10.8	8.6–12.9	0	–	–	13	11.9	10.2–13.1
Engraulis japonicus	3	5.4	5.0–6.0	2	5.5	–	0	–	–	19	5.6	4.7–6.0	0	–	–
Fish total	240	4.0	2.0–7.7	116	8.0	3.9–11.8	56	8.6	3.8–12.9	196	4.4	2.0–13.6	47	10.6	7.6–13.1

forniensis and *Bathylagus ochotensis* were 9.5 to
11.3 cm SL (10.4 ± 0.8) and 10.2 to 13.1 cm SL (11.9 ±
1.1), respectively (Table 3).

Among the main cephalopod prey in the TZ in May,
the size range of *Onychoteuthis borealijaponica* was
4.1 to 13.5 cm DML (7.1 ± 2.8) in 1999 and 12.5 to 22.7
(15.9 ± 5.4) in 2001 (Table 3). In this month, other com-
mon cephalopod prey such as *Gonatus berryi* and
Berryteuthis anonychus (3.2 to 9.4 cm DML [6.4 ± 3.3]
in 1999 and 1.7 to 11.3 [5.5 ± 4.1] in 2001) were gener-
ally smaller than *O. borealijaponica*. In the TD in July,
the estimated size range of *O. borealijaponica* was 5.0
to 13.8 cm DML (10.8 ± 2.6). The second most common
cephalopod, *Abraliopsis* spp., was estimated to be 2.8
to 6.4 cm DML (4.6 ± 1.5).

Seasonal changes in average SCI of the 2 cohorts

In the TZ in May, the mean SCI of juveniles (0.13 ±
0.14 % in 1999 and 0.18 ± 0.22 % in 2001) was signifi-
cantly smaller than that of adults in both 1999 and 2001
(0.55 ± 0.83 % in 1999 and 0.67 ± 1.11 % in 2001; Mann-
Whitney *U*-test, p < 0.05). In July, however, these val-
ues did not differ between the 2 cohorts due to an
increase in the SCI of juveniles (0.39 ± 0.53 and 0.61 ±
1.16 %, Mann-Whitney *U*-test, p > 0.05). This suggests
that the prey environment of juveniles improved in
July, when they shifted their prey from zooplankton to
micronekton. In the TD in July, the mean SCI of adults
was 0.57 ± 0.74 %, similar to that in the TZ in both May
and July (ANOVA, p > 0.05).

DISCUSSION

Possible biases in diet composition analysis

Generally, ommastrephid squids are known to dis-
card the heads of fish prey when fish exceed 50 to 60 %
of the DML of the squid (Froerman 1984, Kitagawa et
al. 1992). In this study, the main fish prey, myctophids
and *Maurolicus imperatorius*, were generally less than
30 % of the DML of the predator, suggesting that neon
flying squid is able to feed on these micronektonic ani-
mals in their entirety. Therefore, our diet analysis may
not have been heavily biased by eventual rejection of
fish heads by the predator.

Diet shifts in TZ from May to July

Maurolicus imperatorius, which is endemic to the
insular slope and seamount waters, is one of the domi-
nant micronektonic fish species in the TZ around the

Emperor seamounts and the Shatsky Rise area (Parin &
Kobyliansky 1996, Sassa et al. 2002). Its biomass is very
large in summer, and it occurs exclusively in the areas
between 30 and 40° N and 160 and 180° E, which
include the TZ of our study area (Boehlert et al. 1994,
Sassa et al. 2002). Its abundance probably explains
why adult neon flying squid mainly depended on this
sternoptychid species in the TZ in July. Juvenile squid
changed their prey from crustacean zooplankton to *M.
imperatorius* in July. This diet shift in summer is not
only due to the high abundance of *M. imperatorius*, but
also to the increasing ability of growing squids to catch
micronektonic prey. *M. imperatorius* was the smallest
fish species found in the stomachs of neon flying
squid; this means that it was also available to juveniles
as a main prey. Similar size-related diet shifts from
crustacean zooplankton to micronekton have been
reported for other ommastrephid squids such as *Illex
argentinus*, *I. illecebrosus*, *Nototodarus gouldi*, and
Todarodes sagittatus (Vinogradov & Noskov 1979,
O'Sullivan & Cullen 1983, Froerman 1984, Breiby &
Jobling 1985, Maurer & Bowman 1985, Ivanovic &
Brunetti 1994, Quetglas et al. 1999). The increase in
SCI of the juveniles from May to July suggests that
their food environment improves in July due to their
expanding prey size range and also as a result of
increased *M. imperatorius* biomass in summer.

Feeding habits related to northward migration

Fig. 3 shows the predator–prey relationship between
juvenile and adult neon flying squid and their main
prey in relation to the northward migration of the
squid. *Symbolophorus californiensis* and *Onychoteuthis
borealijaponica* are so-called transitional-water spe-
cies that undertake extensive northward feeding
migrations from the TZ to the TD between spring and
summer (Ogawa 1961, Naito et al. 1977b, Mishima
1981, Kubodera et al. 1983, Willis et al. 1988). These
species were the top 2 prey items of adult squid in both
the TZ in May and the TD in July. This predator–prey
relationship is maintained from May to July since
their seasonal migration patterns are spatio-temporally
similar to each other (Fig. 3).

Gonatid squids such as *Gonatus berryi*, *G. midden-
dorffi* and *Berryteuthis anonychus* are typical sub-
arctic species and rarely occur in transitional waters
(TZ and TD) in the summer (Kubodera et al. 1983,
Kubodera & Jefferts 1984, Kubodera & Shimazaki
1989). Our results showed that adult neon flying squid
frequently fed on these species in the TZ only in May,
reflecting their distribution in the TZ in winter and
spring and their northward migration to subarctic
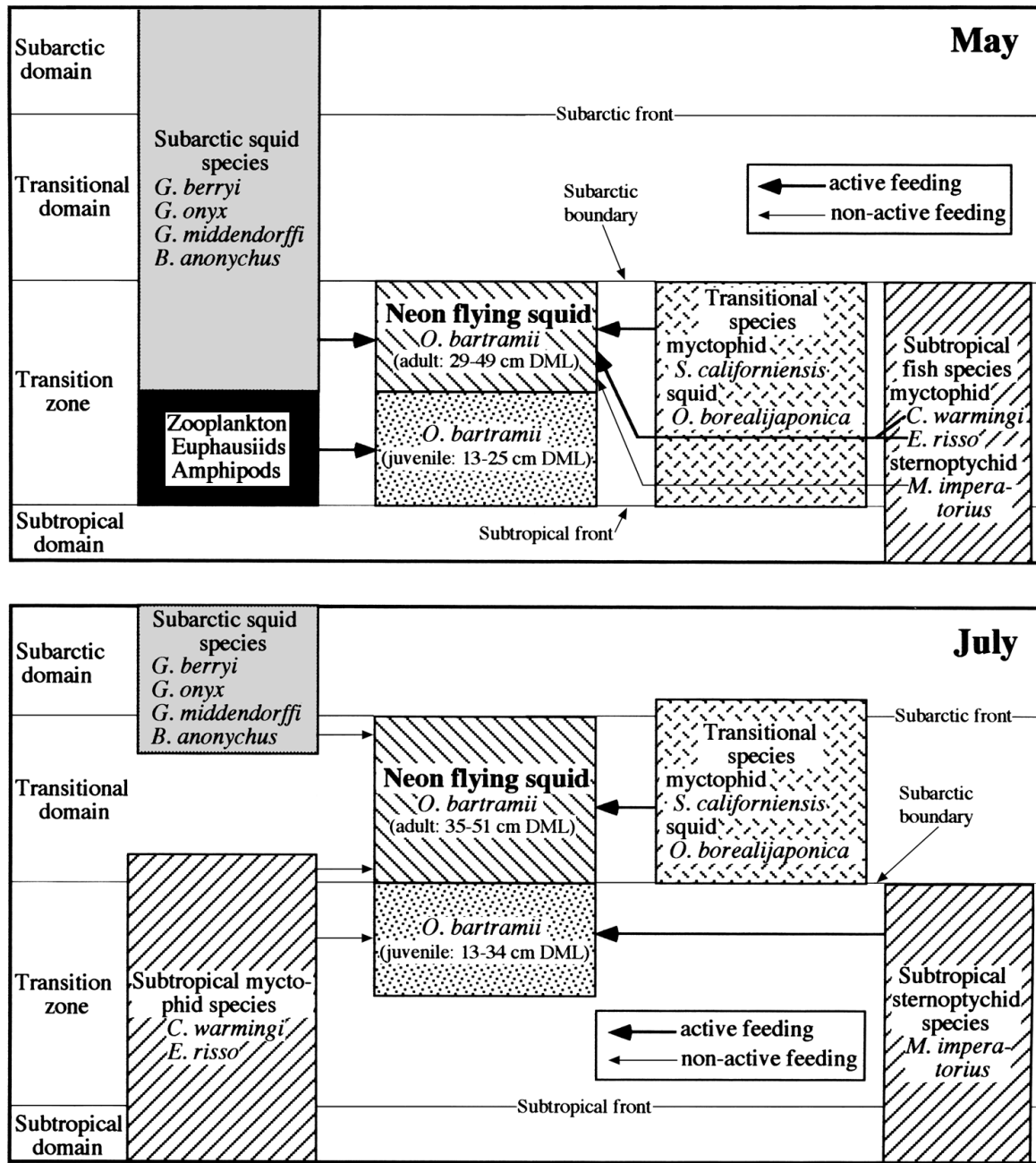waters in summer (Fig. 3).

Fig. 3. Predator–prey relationship and seasonal northward migration patterns of *Ommastrephes bartramii* and their prey in transitional waters of central North Pacific in May and July. Full specific names of prey are given in Table 2

Although juvenile neon flying squid have been reported to undertake northward migrations into the TD in autumn (Murata & Hayase 1993), they remained in the TZ in July during this study, and mainly fed on *Maurolicus imperatorius*. The biomass of *M. imperatorius* is very high (ca. 14 g m^{-2}) at night in the 0 to 20 m layer near the Shatsky Rise area (Sassa et al. 2002), which would support the flying squid population in the TZ in summer.

Feeding habits related to diel vertical migration patterns

Diel vertical migration patterns of adult neon flying squid and their prey, as well as possible predator–prey relationships estimated from stomach-content analyses are shown in Fig. 4. Adult neon flying squid larger than ca. 30 cm DML (mostly the autumn cohort in this study) are mainly distributed in the 300 to 600 m layer during
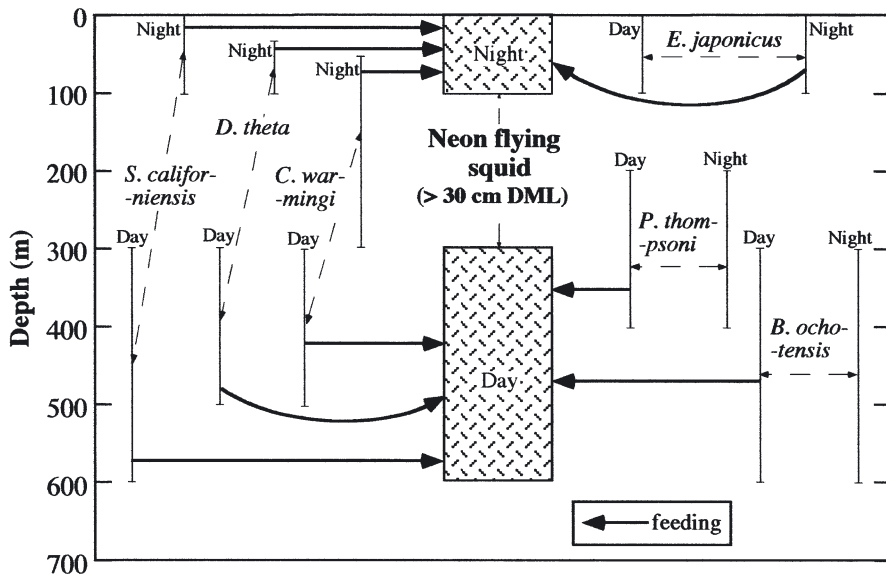
Fig. 4. Predator–prey relationship and diel vertical migration patterns of adult *Ommastrephes bartramii* >30 cm in dorsal mantle length (DML) and fish prey in transitional waters of central North Pacific. Full specific names of prey are given in Table 2

the daytime and migrate to the 0 to 100 m layer at night in transitional waters of the central North Pacific (Nakamura 1991, 1993, Tanaka 2001). Among the fish prey of the adults, *Protomyctophum thompsoni* and *Bathylagus ochotensis* are non-migratory, and throughout the day are mainly distributed in the 200 to 400 m layer and the 300 to 600 m layer, respectively (Miya 1995, Watanabe et al. 1999). The distribution depth of these fishes overlaps with that of adult squid only during the daytime in the upper mesopelagic zone (Fig. 4). In contrast, Japanese anchovy *Engraulis japonicus* is mainly distributed in the epipelagic zone shallower than 100 m during both day and night, and is expected to be available to adult squid only at night (Fig. 4). Adult neon flying squid fed on all these non-migratory fishes, suggesting they feed both during the day in the mesopelagic zone and at night in the epipelagic. It is possible that they feed on migratory myctophids such as *Symbolophorus californiensis* and *Ceratoscopelus warmingi* during both day and night, since their diel vertical migration patterns overlap each another (Fig. 4). Since *S. californiensis* and *C. warmingi* are abundant in the transitional waters of the western and central North Pacific (Wisner 1976, Willis et al. 1988, Watanabe et al. 1999), their 24 h availability would be beneficial to adult neon flying squid.

In contrast to adults, early juveniles of <20 cm DML have been observed in the upper 10 m during both day and night (Murata 1988, H. Watanabe unpubl. data). This may indicate that they occur in the zooplankton-

rich epipelagic zone throughout the whole 24 h. This distribution pattern would be favorable for early juveniles (which were found mainly in May in the TZ), since they exclusively feed on crustacean zooplankton. These juveniles are thought to begin active diel vertical migrations upon reaching 20 to 30 cm DML, corresponding to the size at which their feeding habits switch from crustacean zooplankton to micronekton.

Predation impact of adult neon flying squid on myctophids

Results of CTD casts together with data on the diel vertical migration pattern of adult squids indicate that their day and night habitat-temperatures ranged from 5 to 8°C at depths of 300 to 600 m in the day and 10 to 16°C at depths of 0 to 100 m in the night in the TD in July (Tanaka 2001, T. Ichii unpubl. data). For another ommastrephid species, *Illex illecebrosus*, of >20 cm DML, daily rations were estimated to be 5.2% of body wet weight at 7°C and 6.7% at 16°C (O'Dor et al. 1980). Since 7 and 16°C are similar to the habitat-temperature ranges of adult neon flying squid during the daytime and nighttime, respectively, and the feeding habits of *I. illecebrosus* of >20 cm DML are also similar to those of adult neon flying squid (Froerman 1984, Maurer & Bowman 1985), we adopted these daily rations to represent those of adult neon flying squid. Hence, we adopted a daily ration of 6.0% of body wet weight (i.e. the average of 5.2% for the day and 6.7% for the night). The biomass of adult neon flying squids is estimated to have been 240 to 610 mg wet weight m^{-2} in the study area in July over the past 10 yr (Ichii 2002, and unpubl. data). Furthermore, myctophids, most of which were composed of *Symbolophorus californiensis*, accounted for 25.3% of the total stomach contents (WW) of adult squid in in the TD in July (Table 2). Based on these data and the estimated daily ration, an adult neon flying squid is believed to consume 3.6 to 9.3 mg wet weight myctophids m^{-2} every day. The biomass of vertical migratory trans-Pacific myctophid fishes (mainly *S. californiensis*) is estimated to be 5.2 g wet weight m^{-2} in the Oyashio–Kuroshio transitional waters of the western North Pacific in summer (H. Watanabe unpubl. data). Since their abundance in this region and the TD in the central North Pacific (Sassa et al. 2002) is similar, we adopted this value for the biomass of vertical migratory myctophids

in the TD of the study area. According to Murata & Hayase (1993), adult neon flying squid are mainly distributed in the TD for ca. 70 d, from early July to mid-September. Therefore, the amount of myctophid prey consumed by adult squid during the summer (70 d) is estimated as 273.2 to 694.5 mg wet weight m^{-2}, which is equivalent to 4.9 to 12.4% of the total estimated biomass of vertically migrating myctophids. These estimates are probably conservative, because myctophids that we could not identify to species (and hence for which we could not estimate body wet weight) due to digestion of sagittal otoliths accounted for 27.0% of the total number of fish prey identified in the TD in July.

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