

Feeding ecology of the swordfish *Xiphias gladius* in the subtropical region and transition zone of the western North Pacific

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ABSTRACT: This is the first time a quantitative analysis has been carried out on feeding habits of swordfish *Xiphias gladius* ($n = 455$), mainly ranging from 1200 to 2100 mm in eye–fork length, in the western North Pacific. Based on these data, we examined the feeding ecology of this species in relation to its seasonal south–north migration between subtropical and transition waters. The main *X. gladius* prey size was 80 to 500 mm, and the size spectrum of the prey shifted to a smaller range from spring to summer. In winter and spring, *X. gladius* was distributed in the subtropical region and fed mainly on the winter–spring cohort of neon flying squid *Ommastrephes bartramii*, followed by Pacific pomfret *Brama japonica*. In summer and autumn, *X. gladius* migrated to the transition zone between the Kuroshio front and subarctic boundary and fed mainly on the winter–spring cohort of *O. bartramii*, which also migrates into the transition zone from the subtropical region in summer. Other common prey species in summer and autumn were the gonatid squid *Gonatopsis borealis* and the myctophid fish *Diaphus gigas*, which are endemic to transition and/or subarctic regions. *B. japonica* almost disappeared from the stomachs of *X. gladius* during these seasons because this species migrates in summer into the subarctic region, north of the range of *X. gladius*. Therefore, seasonal changes in stomach contents of *X. gladius* could be explained by the difference in seasonal south–north migration patterns between predator and prey. The seasonal south–north migration of *X. gladius* seems to be a feeding migration, following the migration of the winter–spring cohort of *O. bartramii*.

KEY WORDS: *Xiphias gladius* · Feeding habits · *Ommastrephes bartramii* · Seasonal migration · Subtropical and transition waters · Western North Pacific

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INTRODUCTION

The swordfish *Xiphias gladius* is among the largest pelagic fish, reaching 2500 to 3000 mm in eye–fork length (EFL). The species occurs worldwide from tropical to transition waters (Sakagawa & Bell 1980, Nakamura 1985). The main habitat of this fish in the western North Pacific is the subtropical region, which consists of the subtropical frontal zone north of the subtropical front, the subtropical domain to the south, and the transition zone between the Kuroshio front and the subarctic boundary (Favorite et al. 1976, Pearcy 1991, Roden 1991; Fig. 1). *X. gladius* migrates northward from the subtropical region to the transition zone dur-

ing spring and summer, and southward during autumn and winter for reproduction (Polovina et al. 2000, Seki et al. 2002, Takahashi et al. 2003). Previous studies have indicated that *X. gladius* feeds mainly on large squid and finned fish, suggesting that this species plays an important role as a top predator in high-sea ecosystems (Scott & Tibbo 1968, Stillwell & Kohler 1985, Pearcy 1991, Hernandez-Garcia 1995). Although considerable knowledge has been accumulated pertaining to the feeding habits of *X. gladius* in the North Atlantic and the eastern North Pacific (Scott & Tibbo 1968, Toll & Hess 1981, Stillwell & Kohler 1985, Moreira 1990, Markaida & Sosa-Nishizaki 1998), such information is extremely restricted in the western

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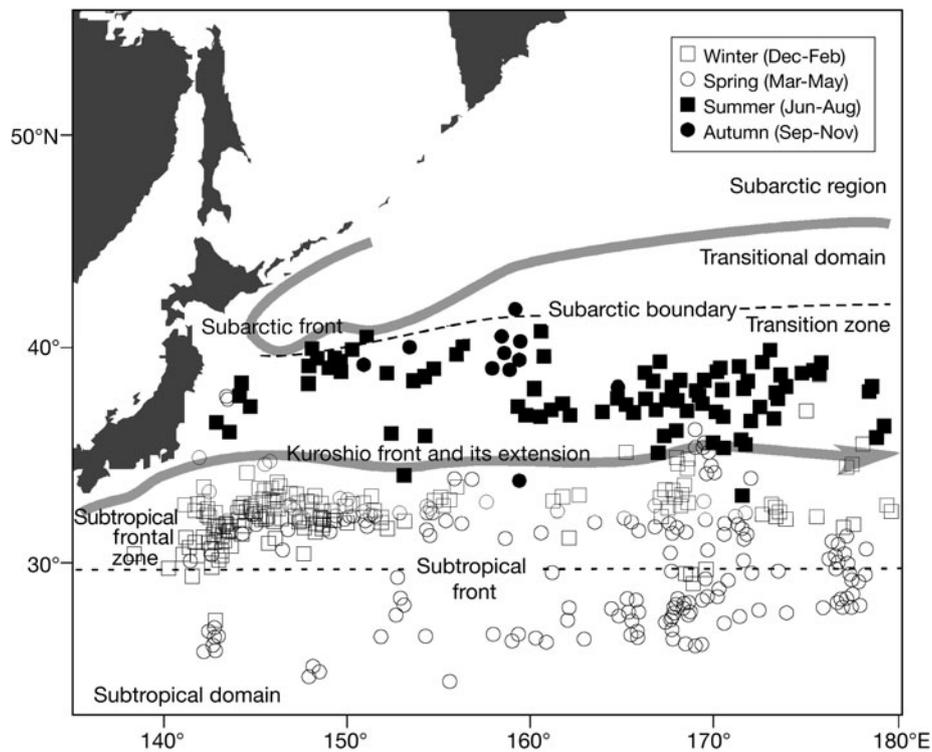


Fig. 1. Sampling localities in each season in the western North Pacific

North Pacific, especially in the subtropical and transition regions (Moteki et al. 2001). These data are essential not only for estimating the feeding strategy of swordfish in this region, but also for establishing new methods for the sustainable exploitation of this important fisheries resource based on ecosystemic information, which is recognized worldwide as an important management approach for future fisheries (World Summit on Sustainable Development 2002, Garcia & Zerbi 2003). Several projects under the North Pacific Marine Science Organization (PICES) and Global Ocean Ecosystem Dynamics (GLOBEC) are ongoing in the North Pacific in relation to the development of such ecosystem approaches to fisheries.

We aimed to quantitatively examine the feeding habits of *Xiphias gladius* in the subtropical and transition waters of the western North Pacific during each season, and to determine their feeding strategies in relation to their south–north migrations and diel vertical migrations.

MATERIALS AND METHODS

Samples were taken from both the subtropical region and transition zone during June 1996, March–July 2000, March–December 2001, February–July and December 2002, and January–April 2003 in the west-

ern North Pacific (Table 1). Sampling localities corresponded well with the distribution centers of *Xiphias gladius* in each season (see 'Discussion'), and generally shifted northward in summer and autumn due to summertime migrations of the fish (Fig. 1). All *X. gladius* were collected by commercial swordfish fishing vessels using long lines in the 0–100 m layer, which corresponds with the main habitat depth of *X. gladius* at night. Long lines were deployed at dusk and

Table 1. *Xiphias gladius*. Numbers of swordfish collected in each year and month

Month	Year					Total
	1996	2000	2001	2002	2003	
1	0	0	0	0	59	59
2	0	0	0	4	46	50
3	0	12	5	17	52	86
4	0	35	6	14	15	70
5	0	17	20	16	0	53
6	6	2	31	5	0	44
7	0	1	48	2	0	51
8	0	0	11	0	0	11
9	0	0	8	0	0	8
10	0	0	1	0	0	1
11	0	0	3	0	0	3
12	0	0	7	12	0	19
Total	6	67	140	70	172	455

retrieved before dawn on the following day. During each sampling period, sea surface temperature (SST) was measured. Aboard the ship, swordfish wet body weights (BW) were measured and stomachs were removed. Stomachs were frozen at -30°C for further analysis in the laboratory ashore. We estimated EFL (cm) of each individual from the BW (kg) values using the following equations obtained in this study area in each season (K. Yokawa unpubl. data):

$$\text{Winter (Dec to Feb): BW} = e^{-12.1389} \times \text{EFL}^{3.2231} \quad (1)$$

$$\text{Spring (Mar to May): BW} = e^{-12.4565} \times \text{EFL}^{3.2915} \quad (2)$$

$$\text{Summer (Jun to Aug): BW} = e^{-11.6042} \times \text{EFL}^{3.1003} \quad (3)$$

$$\text{Autumn (Sep to Nov): BW} = e^{-10.7864} \times \text{EFL}^{2.9558} \quad (4)$$

In total, 455 individuals were examined for stomach content analysis. We excluded all fresh and minimally digested Japanese common squid *Todarodes pacificus*, mackerel *Scomber* spp., and Jack mackerel *Trachurus japonicus* from the stomach content analysis to avoid contamination of the samples with long line bait. Zooplankton prey items were counted and identified to the lowest taxonomic level possible, and wet weights of each taxon were measured. All fresh and minimally digested cephalopod and fish prey were identified to the lowest taxonomic level possible, and their body length (dorsal mantle length, DML, for cephalopods and standard length, SL, for fish) and wet wt were recorded. Heavily digested cephalopod and fish prey items were identified based on the morphology of their lower beaks and sagittal otoliths, respectively. For these items, the rostral lengths of the lower beaks of cephalopods and the maximum diameters of sagittal fish otoliths were also measured to estimate the original body sizes and wet weights of the prey, using relationships generated from intact specimens of the main prey species (Kubodera 1982, Clarke 1986, Kubodera & Furuhashi 1987, Kubodera & Shimazaki 1989, Smale et al. 1995, Ohizumi et al. 2001, T. Kubodera & H. Watanabe unpubl. data). These relationships could not be obtained for some minor prey species, such as the octopus *Japetella diaphana* and gonostomatid fishes like *Gonostoma elongatum*. For these species, the original wet weights were estimated based on values for similar-sized individuals or values for only slightly digested specimens of each species. The number of eaten fish was estimated as the maximum number of right or left fish otoliths.

The stomach content index (SCI) was calculated as:

$$\text{SCI (\%)} = (\text{wet wt of stomach contents including both fresh and digested items/BW excluding wet wt of stomach contents}) \times 100 \quad (5)$$

We calculated the proportion of each prey item among the total number of food items identified (N), the wet wt contribution of each food item to the total wet wt of the stomach contents (W), and the frequency of the occurrence (F) of each food item in the total number of stomachs examined. Using these 3 indices, an index of the relative importance (IRI; Pinkas et al. 1971) of each food item i was calculated using the equation:

$$\text{IRI}_i = (N_i + W_i) \times F_i \quad (6)$$

This index is represented by the size of the rectangle resolved by plotting the 3 values on a 3-way graph. To readily allow comparison among prey items, the IRI was standardized to %IRI for each prey item (Cortes 1997).

RESULTS

Habitat, SST, and size composition

Sea surface water temperatures in which *Xiphias gladius* were generally captured were $17\text{--}20^{\circ}\text{C}$ in winter, spring, and autumn, and $17\text{--}21^{\circ}\text{C}$ in summer, suggesting that *X. gladius* were distributed mainly in areas with similar SSTs in all seasons (Fig. 2a). EFL size-frequency distributions showed a clear mode between 1200 and 2000 mm from winter to summer, representing 4 to 7 year old individuals (Sun et al. 2002; Fig. 2b). In autumn, these modes were not found due to the small sample size, but the size range of captured individuals was 1200 to 2100 mm EFL, which was similar to the main size range of the fish collected in other seasons. Therefore, the age composition of the present *X. gladius* sample may have been similar throughout the seasons.

Diet composition

We identified 70 prey species belonging to 57 genera in the 455 examined stomachs (Table 2). Of these stomachs, 21 (4.6%) were empty. The following results indicate that *Ommastrephes bartramii* was one of the most common prey species regardless of season (Table 3).

Subtropical region in winter

The most common prey species was *Ommastrephes bartramii*, with N , W , and F values of 28.0, 61.8, and 57.8%, respectively, followed by Pacific pomfret *Brama japonica* (9.7, 13.8, and 40.6%). In terms of W , *B. japonica* and diamondback squid *Thysanoteuthis*

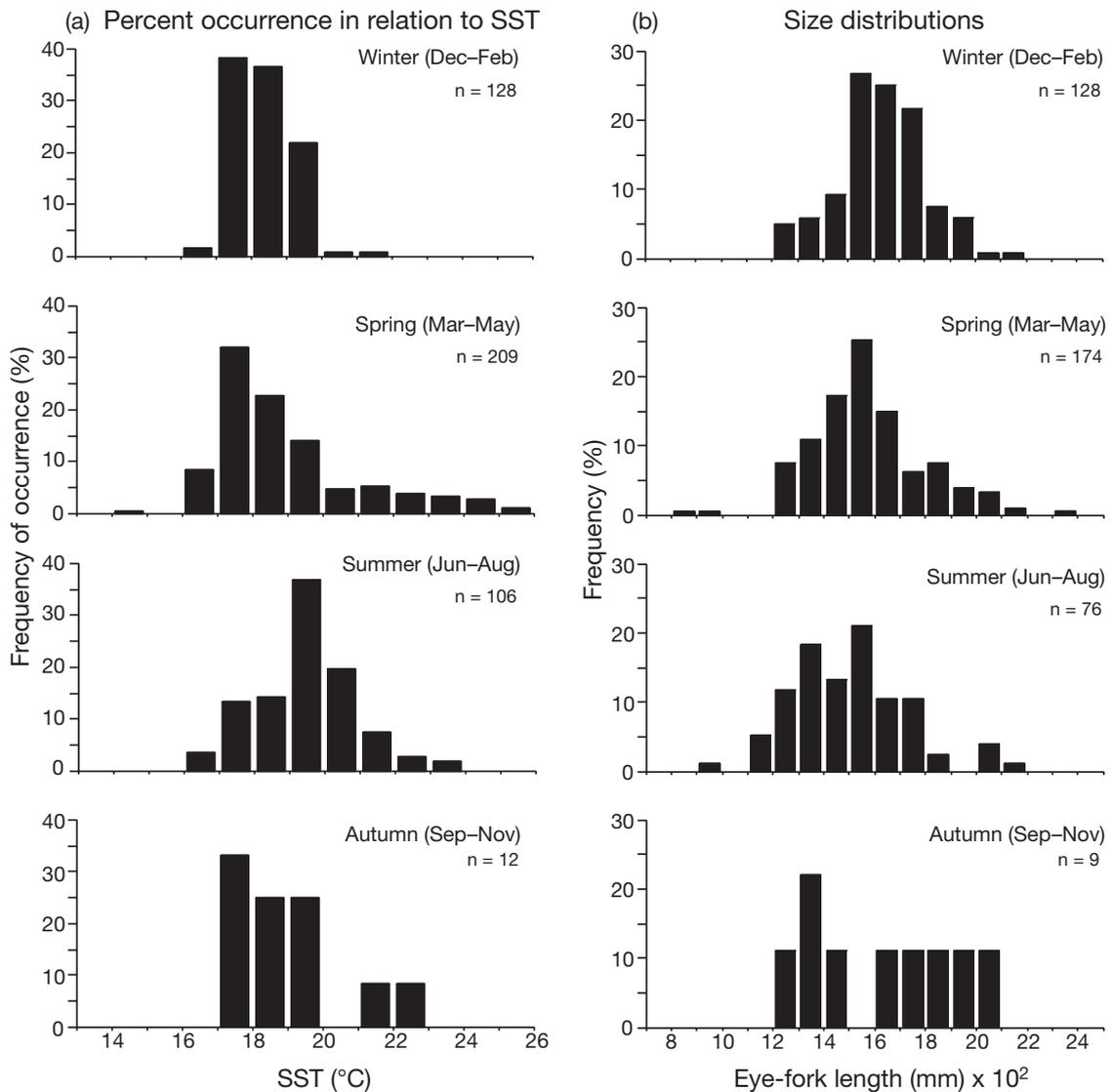


Fig. 2. *Xiphias gladius*. (a) Percent occurrence of the total number of samples in relation to sea surface water temperature (SST) in each season. (b) Size distributions in each season. n: number of individuals captured

rhombus (13.0%) were equally important. However, both *N* (1.6%) and *F* (7.0%) values of *T. rhombus* were much lower than those of *B. japonica*. As a result, the %IRI of *O. bartramii* (78.6%) was the highest, followed by *B. japonica* (14.5%), while values of other species were <2.0%. These results suggest that *Xiphias gladius* preyed mainly on *O. bartramii* and secondarily on *B. japonica*.

Subtropical region in spring

Ommastrephes bartramii was the most common species in the stomachs, with *N*, *W*, and *F* values of 30.1, 61.8, and 45.5%, respectively, followed by *Brama*

japonica (8.8, 18.2, and 22.5%). The %IRI values of *O. bartramii* and *B. japonica* were 84.4 and 12.3%, respectively, whereas those of other species were <1.0%. These results suggest that in the subtropical region, the main prey species were the same in winter and spring.

Transition zone in summer

The subarctic gonatid squid *Gonatopsis borealis* was the most common prey by *N* (13.5%), *W* (28.4%), *F* (46.4%), and %IRI (46.4%) values. In terms of *W* and *F* values, *Ommastrephes bartramii* ranked as the second (22.6%) and third (30.2%) most important prey,

Table 2. *Xiphias gladius*. Prey species list in the subtropical and transition regions of the western North Pacific

Family/group	Species/lowest taxon	Family/group	Species/lowest taxon	Family/group	Species/lowest taxon
Zooplankton		Histioteuthidae	<i>Histioteuthis</i> spp.	Emmelichthyidae	<i>Emmelichthys</i> sp.
Euphausiids	Unidentified	Chiroteuthidae	<i>Chiroteuthis picteti</i>	Caproidae	<i>Antigonia</i> spp.
Amphipods	<i>Platyscelus ovoides</i>	Chiroteuthidae	<i>Chiroteuthis calyx</i>	Apogonidae	<i>Epigonus pectinifer</i>
Platyscelidae	<i>Platyscelus</i> spp.	Chiroteuthidae	<i>Galiteuthis phyllura</i>	Moridae	Unidentified
Platyscelidae	Unidentified	Octopoteuthidae	<i>Octopoteuthis sicula</i>	Serranidae	Unidentified
Decapods	Unidentified	Octopoteuthidae	<i>Octopoteuthis megaptera</i>	Trichiuridae	Unidentified
Crustaceans	Unidentified	Octopoteuthidae	<i>Taningia danae</i>	Pentacerothidae	<i>Pentaceros richardsoni</i>
Pteropods	Unidentified	Cycloteuthidae	<i>Discoteuthis discus</i>	Berycidae	<i>Beryx splendens</i>
	Unidentified	Cycloteuthidae	<i>Discoteuthis</i> spp.	Zeidae	Unidentified
Cephalopods		Mastigoteuthidae	<i>Idioteuthis cordiformis</i>	Himantolophidae	Unidentified
Squids		Mastigoteuthidae	<i>Mastigoteuthis glaukopsis</i>	Alepisauridae	<i>Alepisaurus ferox</i>
Ommastrephidae	<i>Stenoteuthis oualaniensis</i>	Pholidoteuthidae	<i>Pholidoteuthis adami</i>	Myctophidae	<i>Ceratoscopelus warmingii</i>
Ommastrephidae	<i>Ornithoteuthis volatilis</i>	Pholidoteuthidae	<i>Pholidoteuthis boschmai</i>	Myctophidae	<i>Notoscopelus japonicus</i>
Ommastrephidae	<i>Ommastrephes bartramii</i>	Cranchiidae	<i>Megalocranchia maxima</i>	Myctophidae	<i>Diaphus perspicillatus</i>
Ommastrephidae	<i>Eucleoteuthis luminosa</i>	Cranchiidae	<i>Teuthowenia</i> sp.	Myctophidae	<i>Diaphus gigas</i>
Ommastrephidae	Unidentified	Octopods		Myctophidae	<i>Diaphus perspicillatus/gigas</i>
Thysanoteuthidae	<i>Thysanoteuthis rhombus</i>	Bolitaenidae	<i>Japetella diaphana</i>	Myctophidae	<i>Electrona</i> sp.
Onychoteuthidae	<i>Onychoteuthis borealijaponica</i>	Haliphronidae	<i>Haliphron atlanticus</i>	Myctophidae	<i>Protomyctophum crockeri</i>
Onychoteuthidae	<i>Onychoteuthis banksii</i>	Tremoctopodidae	<i>Tremoctopus violaceus gracialis</i>	Myctophidae	<i>Lampadena luminosa</i>
Onychoteuthidae	<i>Onykia</i> spp.	Ocythoidae	<i>Ocythoe tuberculata</i>	Myctophidae	<i>Diaphus</i> sp.
Onychoteuthidae	Unidentified	Argonautidae	<i>Argonauta argo</i>	Myctophidae	Myctophidae
Onychoteuthidae	<i>Onykia robusta</i>	Other		Scopelarchidae	<i>Scopelarchus analis</i>
Onychoteuthidae	<i>Onykia loennbergi</i>	Vampyroteuthidae	<i>Vampyroteuthis infernalis</i>	Paralepididae	<i>Lestidiops similis</i>
Architeuthidae	<i>Architeuthis martensi</i>			Paralepididae	Unidentified
Gonatidae	<i>Gonatus pyros</i>	Fish		Notosuidae	<i>Scopelosaurus</i> sp.
Gonatidae	<i>Gonatus berryi</i>	Teleost fish		Gonostomatidae	<i>Cyclothone</i> sp.
Gonatidae	<i>Gonatus middendorffi</i>	Bramidae	<i>Brama japonica</i>	Gonostomatidae	<i>Gonostoma elongatum</i>
Gonatidae	<i>Gonatus onyx</i>	Bramidae	<i>Brama</i> sp.	Phosichthyidae	<i>Woodsia nonsuchae</i>
Gonatidae	<i>Gonatus onyx</i>	Scombridae	<i>Scomber</i> spp.	Melanostomiidae	<i>Tactostoma macropus</i>
Gonatidae	<i>Berryteuthis anonychus</i>	Scombridae	<i>Katsuwonus pelamis</i>	Sternopychidae	Unidentified
Gonatidae	<i>Gonatopsis borealis</i>	Scombridae	<i>Auxis</i> sp.	Chauliodontidae	<i>Chauliodus sloani</i>
Enoploteuthidae	<i>Watasenia scintillans</i>	Scombridae	Unidentified	Gonostomatidae	<i>Ichthyococcus elongatus</i>
Enoploteuthidae	<i>Enoploteuthis chuni</i>	Tetragonuridae	<i>Hyperoglyphe</i> sp.	Bathylagidae	<i>Bathylagus ochotensis</i>
Enoploteuthidae	<i>Enoploteuthis</i> spp.	Tetragonuridae	<i>Tetragonurus atlanticus</i>	Microstomatidae	<i>Leuroglossus schmidti</i>
Enoploteuthidae	<i>Abraliopsis</i> spp.	Gempylidae	<i>Rexa prometheoides</i>	Argentinidae	Unidentified
Ancistroleptidae	<i>Ancistroleptus lesueurii</i>	Gempylidae	<i>Nealotus tripes</i>	Engraulidae	<i>Engraulis japonicus</i>
Taoninae	<i>Taonius pavo</i>	Gempylidae	Unidentified	Cartilaginous fish	
Histioteuthidae	<i>Histioteuthis dofleini</i>	Trachipteridae	<i>Desmodema</i> sp.	Squalidae	<i>Isistius brasiliensis</i>
Histioteuthidae	<i>Histioteuthis inermis</i>	Evermannellidae	<i>Coccorella atlantica</i>	Chimaeridae	Unidentified
Histioteuthidae	<i>Histioteuthis celestaria pacifica</i>	Argentinidae	<i>Nansenia</i> spp.		

Table 3. *Xiphias gladius*. The 15 most important prey species in terms of % index of relative importance (%IRI, see 'Materials and methods' for details) in each season. Prey species composition by abundance (*N*, %) and wet wt (*W*, %), and frequency of occurrence (*F*, %) of each prey in the total number of stomachs examined are also depicted. CR: crustacean zooplankton; SQ: squid; OC: octopus; TF: teleost fish

Rank of IRI	Prey category	Species	<i>N</i> (%)	<i>W</i> (%)	<i>F</i> (%)	IRI (%)	Rank of IRI	Prey category	Species	<i>N</i> (%)	<i>W</i> (%)	<i>F</i> (%)	IRI (%)
Winter (Dec–Feb)							Summer (Jun–Aug)						
1	SQ	<i>Ommastrephes bartramii</i>	28.0	61.8	57.8	78.6	1	SQ	<i>Gonatopsis borealis</i>	13.5	28.4	43.4	46.4
2	TF	<i>Brama japonica</i>	9.7	13.8	40.6	14.5	2	SQ	<i>Ommastrephes bartramii</i>	6.4	22.6	30.2	22.3
3	SQ	<i>Moroteuthis loennbergi</i>	5.1	1.9	17.2	1.8	3	TF	<i>Diaphus gigas</i>	11.9	2.7	36.8	13.7
4	SQ	<i>Thysanoteuthis rhombus</i>	1.6	13.0	7.0	1.6	4	SQ	<i>Onychoteuthis banksii</i>	7.5	2.3	11.3	2.8
5	SQ	<i>Stenoteuthis oualaniensis</i>	3.9	2.1	10.9	1.0	5	TF	<i>Brama japonica</i>	1.7	5.0	14.2	2.4
6	SQ	<i>Onychoteuthis borealijaponica</i>	3.7	0.2	14.1	0.8	6	TF	Paralepididae	5.9	0.2	14.2	2.2
7	TF	<i>Diaphus perspicillatus/gigas</i>	13.6	0.2	3.9	0.8	7	TF	<i>Alepisaurus ferox</i>	0.8	10.4	6.6	1.9
8	SQ	<i>Eucleoteuthis luminosa</i>	1.2	0.4	5.5	0.1	8	SQ	<i>Eucleoteuthis luminosa</i>	3.0	2.8	12.3	1.8
9	SQ	<i>Taningia danae</i>	0.4	2.8	2.3	0.1	9	SQ	<i>Gonatus</i> spp.	4.0	1.0	12.3	1.5
10	TF	<i>Alepisaurus ferox</i>	0.9	0.8	3.9	0.1	10	SQ	<i>Onykia loennbergi</i>	1.8	4.0	4.7	0.7
11	CR	Amphipods	2.4	0.0	2.3	0.1	11	SQ	<i>Gonatus berryi</i>	2.6	0.0	10.4	0.7
12	SQ	<i>Enoploteuthis</i> spp.	1.3	0.0	3.9	0.1	12	SQ	<i>Stenoteuthis oualaniensis</i>	0.3	7.1	2.8	0.5
13	TF	Paralepididae	1.0	0.0	3.9	0.1	13	SQ	<i>Onychoteuthis borealijaponica</i>	1.8	0.4	9.4	0.5
14	SQ	<i>Histioteuthis dofleini</i>	1.0	0.4	2.3	<0.1	14	SQ	<i>Gonatus pyros</i>	1.5	0.1	8.5	0.3
15	TF	Trichiuridae	0.7	1.0	1.6	<0.1	15	TF	<i>Nansenia</i> spp.	1.4	0.2	4.7	0.2
Total no. inds: 669							Total no. inds: 1426						
Total wet wt (g): 450628.5							Total wet wt (g): 138486.5						
Spring (Mar–May)							Autumn (Sep–Nov)						
1	SQ	<i>Ommastrephes bartramii</i>	30.1	61.8	45.5	84.4	1	SQ	<i>Ommastrephes bartramii</i>	20.4	38.0	33.3	42.0
2	TF	<i>Brama japonica</i>	8.8	18.2	22.5	12.3	2	SQ	<i>Gonatopsis borealis</i>	13.3	13.8	41.7	24.3
3	SQ	<i>Onychoteuthis borealijaponica</i>	3.8	0.6	10.0	0.9	3	TF	<i>Diaphus gigas</i>	9.2	1.1	50.0	11.1
4	SQ	<i>Thysanoteuthis rhombus</i>	0.8	9.3	3.3	0.7	4	SQ	<i>Eucleoteuthis luminosa</i>	7.1	4.9	16.7	4.3
5	SQ	<i>Moroteuthis loennbergi</i>	2.2	1.0	5.3	0.3	5	SQ	Paralepididae	7.1	0.1	25.0	3.9
6	SQ	<i>Enoploteuthis chuni</i>	1.7	0.1	7.2	0.3	6	TF	<i>Gonatus middendorffi</i>	7.1	1.5	16.7	3.1
7	TF	<i>Diaphus gigas</i>	4.3	0.2	2.4	0.2	7	SQ	<i>Onykia robusta</i>	1.0	13.6	8.3	2.6
8	TF	<i>Alepisaurus ferox</i>	0.8	0.7	2.4	0.1	8	TF	<i>Desmodema</i> sp.	1.0	13.1	8.3	2.5
9	SQ	<i>Histioteuthis inermis</i>	1.2	0.5	1.9	0.1	9	SQ	<i>Histioteuthis dofleini</i>	2.0	2.8	16.7	1.8
10	SQ	<i>Stenoteuthis oualaniensis</i>	0.8	0.3	2.9	0.1	10	TF	<i>Brama japonica</i>	1.0	6.3	8.3	1.3
11	TF	<i>Katsuwonus pelamis</i>	0.6	1.5	1.4	0.1	11	TF	<i>Nansenia</i> spp.	2.0	0.2	16.7	0.8
12	SQ	<i>Eucleoteuthis luminosa</i>	0.7	0.2	2.4	<0.1	12	SQ	<i>Gonatus onyx</i>	1.0	2.9	8.3	0.7
13	OC	<i>Haliphron atlanticus</i>	1.4	0.0	1.4	<0.1	13	SQ	<i>Chiroteuthis calyx</i>	1.0	1.0	8.3	0.4
14	TF	Paralepididae	0.8	0.0	2.4	<0.1	14	SQ	<i>Chiroteuthis imperator</i>	1.0	0.4	8.3	0.3
15	OC	<i>Japetella diaphana</i>	0.7	0.0	2.4	<0.1	15	TF	<i>Lampadena luminosa</i>	1.0	0.1	8.3	0.2
Total no. inds: 861							Total no. inds: 98						
Total wet wt (g): 478595.1							Total wet wt (g): 18228.8						

respectively. The transition water myctophid fish *Diaphus gigas* ranked second in both *N* (11.9%) and *F* (36.8%). As a result, %IRI values did not differ greatly between *O. bartramii* (22.3%) and *D. gigas* (13.7%), indicating that *O. bartramii* contributed more to prey composition by weight, whereas *D. gigas* contributed more in number and frequency of occurrence. Although Pacific lancetfish *Alepisaurus ferox* ranked second in *W* (10.4%), its *N* (0.8%) and *F* (6.6%) values were much lower than those of *G. borealis*, *O. bartramii*, and *D. gigas*. The %IRIs for *A. ferox* and other prey species were <3.0%. These results indicate that *B. japonica*, one of the main prey species during winter and spring, almost disappeared from the stomachs of *Xiphias gladius* in summer, and was replaced by *G. borealis* and *D. gigas*.

Transition zone in autumn

Ommastrephes bartramii was the most common species found in the autumn, with *N* and *W* values of 20.4 and 38.0%, respectively, followed by *Gonatopsis borealis* (13.3 and 13.8%). These 2 species and *Diaphus gigas* were commonly found in the stomachs of *Xiphias gladius* (*F*, 33.3–50.0%). *D. gigas* was the third most important prey in terms of *N* (9.2%), although *W* of this species (1.1%) was much lower than those of *O. bartramii* (38.0%), *G. borealis* (13.8%), giant squid *Onykia robusta* (13.6%), and ribbonfish *Desmodema* sp. (13.1%). As a result, the %IRIs were 42.0, 24.3, and 11.1% for *O. bartramii*, *G. borealis*, and *D. gigas*, respectively. The %IRIs for other species were <4.5%.

Prey size and seasonal changes in SCI

The size-frequency distribution of *Ommastrephes bartramii* found in the *Xiphias gladius* stomachs showed a clear mode between 300 and 450 mm DML in winter (Fig. 3). In spring, *O. bartramii* found in the fish stomachs ranged from 80 to 500 mm, and 2 modes were recognized, between 80 and 150 mm and between 300 and 500 mm. The first mode was between 100 and 300 mm in summer and between 150 and 350 mm in autumn. In both winter and spring, the other common prey species, *Brama japonica*, ranged in size from 300 to 400 mm SL (Fig. 3). In the transition zone in summer and/or autumn, sizes of *Gonatopsis borealis* and *Diaphus gigas*, which were frequently found in *X. gladius* stomachs in these seasons, were mainly 100–250 mm DML and 100–140 mm SL, respectively (Fig. 3). These results, and the aforementioned finding that *O. bartramii* >300 mm were rarely fed on by *X. gladius* during summer and autumn, indicate that the prey size spectrum of *X. gladius* shifts to a smaller range from

spring to summer (80–500 mm vs. 100–300 mm). These results also indicate that the main prey size of *X. gladius* was 80 to 500 mm in this study area.

The mean SCI was significantly larger in winter and spring than in summer and autumn (1.74 vs. 0.84–1.05%, Mann-Whitney *U*-test with Bonferroni correction factor: $p < 0.05$; Table 4), suggesting that feeding conditions for *Xiphias gladius* were better in the subtropical region in winter and spring than they were in the transition zone in summer and autumn.

DISCUSSION

Differences in feeding conditions between subtropical and transition regions

The main distribution area of *Xiphias gladius* in each season approximately corresponded to the 17–19°C SST isotherm line throughout the year (Polovina et al. 2000, Seki et al. 2002, Baker et al. 2007). This SST

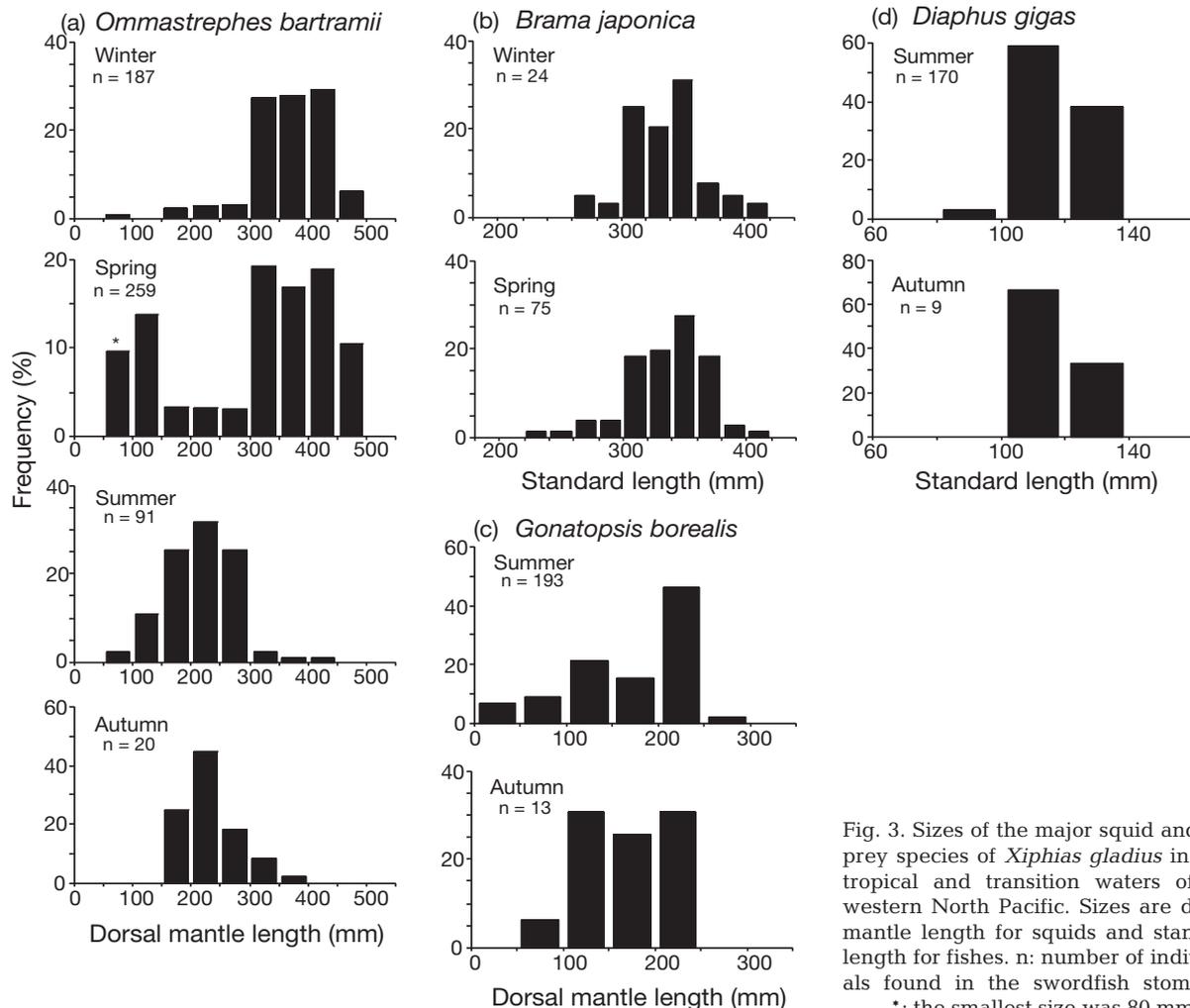


Fig. 3. Sizes of the major squid and fish prey species of *Xiphias gladius* in subtropical and transition waters of the western North Pacific. Sizes are dorsal mantle length for squids and standard length for fishes. n: number of individuals found in the swordfish stomachs; *: the smallest size was 80 mm

Table 4. *Xiphias gladius*. Seasonal changes in the stomach content index (SCI, %) in the western North Pacific

Season	Average	SD	Range	
			Minimum	Maximum
Winter	1.74	1.50	0.01	7.13
Spring	1.74	1.75	0	10.80
Summer	1.05	1.02	0	5.14
Autumn	0.84	0.86	0.05	0.12

range corresponded well with the SST range of *X. gladius* captured in this study. Furthermore, the sampling positions in each season well corresponded to the habitat of *X. gladius* estimated from archival tag data (Takahashi et al. 2003). These facts suggest that the present samples were taken in the main habitat of *X. gladius* during each season. During winter and spring, these SST areas are mainly located in the subtropical frontal zone (Seki et al. 2002), which, due to its high productivity, is a foraging region for major large pelagic nekton including *Brama japonica* and the winter–spring cohort of *Ommastrephes bartramii* before reproduction (Seki & Bigelow 1993, Seki et al. 2002, Young & Hirota available at: www.soest.hawaii.edu/PFRP/pdf/young99.pdf). Therefore, the main distribution area of *X. gladius* in winter may be associated with a food-rich habitat (Fig. 4).

In contrast, the prey environment for *Xiphias gladius* could be poor in summer and autumn in their main habitat because average SCI values of this species were significantly lower in these seasons than in winter and spring. Previous data indicating that the average BW excluding internal organs of *X. gladius* of 1500 and 2000 mm EFL collected in this study area is 1.18 to 1.27 times heavier in winter and spring than in summer and autumn (K. Yokawa unpubl. data) might support this view. However, the main habitat of *X. gladius* in each season also corresponds with the transition zone chlorophyll front (TZCF), which migrates into the transition region close to the subarctic boundary from the subtropical frontal zone during spring and summer (Polovina et al. 2000, 2001, Bograd et al. 2004, Baker et al. 2007; Fig. 4). The TZCF is a zone of surface convergence where cool surface waters from the north, containing high levels of chlorophyll *a*, sink beneath warm, oligotrophic waters to the south; this indicates that the region to the north of the TZCF is a productive area (Polovina et al. 2000, 2001, Baker et al. 2007). According to Polovina et al. (2001), albacore tuna *Thunnus alalunga* also exploit the TZCF as a migration route and as a forage habitat from spring to summer. In the western North Pacific during spring and summer, *T. alalunga* measuring 489 to 762 mm in fork length predated heavily on juvenile Japanese anchovy *Engraulis*

japonicus (20 to 80 mm SL), which were mainly distributed around the TZCF area, suggesting an enhanced feeding regime for this predator (Watanabe et al. 2004, H. Watanabe unpubl. data). This information and our results might indicate that in terms of summer prey availability, the productive TZCF region is favorable for albacore, which mainly consume small prey (<80 mm), but unfavorable for *X. gladius*, which seem to prefer larger prey (>80 mm). It appears that *X. gladius* could not adequately utilize the productivity of the TZCF in summer, because many large-sized epipelagic nekton, including the autumn cohorts of *Ommastrephes bartramii* and *Brama japonica*, forage in the subarctic region and/or transitional domain north of the subarctic boundary during this time of the year. This probably causes a shift in the size spectrum of prey in the TZCF to a smaller range from spring to summer (Pearcy et al. 1993, 1996, Ichii et al. 2004; Fig. 3). Therefore, the decline in the feeding regime of *X. gladius* from spring to summer is not caused by seasonal changes in productivity in their main habitat, but may be explained by the difference in the size spectrum of potential prey species between these seasons. However, from a trophic standpoint, in summer and autumn the transition zone may be favorable over the subtropical region for *X. gladius*, because the latter area is an oligotrophic region where the flux of nutrients into the euphotic zone is among the lowest of any oceanic environment in these seasons, whereas the former area is more productive (Gjøsaeter & Kawaguchi 1980, Cullen 1982, Sassa et al. 2002, Ichii et al. 2009).

Although the prey environment is more favorable in the subarctic region than it is in the transition zone in summer (Gjøsaeter & Kawaguchi 1980, Sassa et al. 2002, Ichii et al. 2004), *Xiphias gladius* rarely migrate into the subarctic region (Polovina et al. 2000, Takahashi et al. 2003). This is probably due to the low temperature field in the subarctic region, because *X. gladius* are mainly distributed in the mesopelagic zone at 3–6°C in the daytime and migrate up to the epipelagic zone at 17–27°C at night (Matsumoto et al. 2003, Takahashi et al. 2003, Yokawa 2004), and the water temperatures of the subarctic region, in the both meso- and epipelagic zones, are generally lower than they are in the transition region (approximately less than 4°C and 15°C, respectively; Kawai 1972). Therefore, the summertime northward migration of *X. gladius* is believed to be a feeding migration within their optimal habitat temperature range.

Feeding habits related to northward migration

Ommastrephes bartramii is among the dominant large pelagic squid in the subtropical and temperate

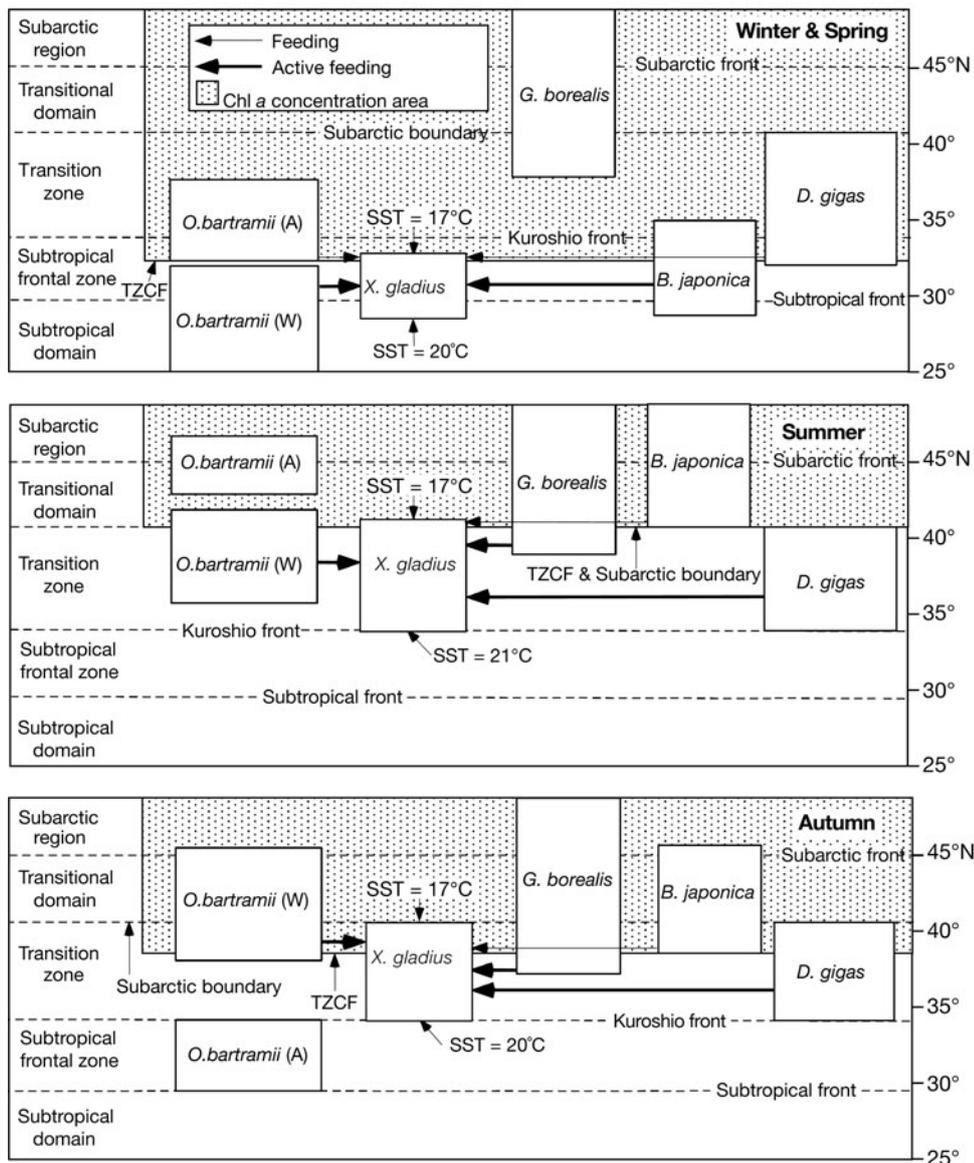


Fig. 4. Predator–prey relationships and seasonal south–north migration patterns of *Xiphias gladius* and its prey species in sub-tropical and transition waters of the western North Pacific. Full species names of prey are given in Table 2. A: autumn cohort; W: winter–spring cohort; TZCF: transition zone chlorophyll front

waters of the North Pacific, and its population is composed of the autumn and winter–spring cohorts (Roper et al. 1984, Murata 1990, Murata & Hayase 1993, Seki 1993, Yatsu et al. 1997). Previous reports on the size-frequency distribution of *O. bartramii* in each season (Murata & Hayase 1993, Chen & Chiu 2003) suggest that most of the individuals found in *Xiphias gladius* stomachs came from the winter–spring cohort; i.e. *X. gladius* fed on the spawning population of the cohort during winter and spring (>300 mm DML) and on newly recruited individuals of the cohort from spring to autumn (<200 mm DML in spring, <350 mm DML in

summer, and 150–400 mm DML in autumn). The squid found in the stomachs of *X. gladius*, measuring approximately 200–300 mm DML in spring and >350 mm DML in summer and autumn, were possibly members of the autumn cohort (Murata & Hayase 1993). However, their abundance was much lower than that of the winter–spring cohort (see Fig. 3). Previous information of seasonal south–north migration patterns of the 2 cohorts strongly suggests that the predator–prey relationship between *X. gladius* and the winter–spring cohort of *O. bartramii* is maintained almost throughout the year, because their seasonal

south–north migration patterns are spatiotemporally similar to each other (Fig. 4, Ichii et al. 2009, Young & Hirota available at: www.soest.hawaii.edu/PFRP/pdf/young99.pdf). Conversely, *X. gladius* rarely fed on the autumn *O. bartramii* cohort, because their distributions are almost separate in each season (Yatsu et al. 1997, Ichii et al. 2009, Fig. 4).

Brama japonica was frequently predated upon by *Xiphias gladius* in the subtropical frontal zone during winter and spring, but almost disappeared from *X. gladius* stomachs in summer and autumn. This corresponds well with the fact that *B. japonica* migrates into the transitional domain and subarctic region in summer (Shimazaki & Nakamura 1981, Pearcy et al. 1993, Ichii et al. 2004; Fig. 4). *Diaphus gigas* and *Gonatopsis borealis* are typical subarctic or transition water species and rarely occur in subtropical waters (Wisner 1976, Naito et al. 1977, Kawaguchi & Shimizu 1978, Kubodera et al. 1983, Kubodera & Jefferts 1984). Our results showed that *X. gladius* frequently fed on these species only in the transition zone during summer and/or autumn, reflecting the zoogeographical distribution patterns of these prey species (Fig. 4).

Feeding habits related to diel vertical migrations

Fig. 5 shows the diel vertical migration patterns of *Xiphias gladius* and their prey, as well as possible predator–prey relationships estimated from stomach content analyses. Generally, *X. gladius* are distributed in the 300–600 m layer during the day and migrate to the 0–100 m layer at night (Carey & Robinson 1981, Matsumoto et al. 2003, Takahashi et al. 2003, Yokawa 2004). Among the main *X. gladius* prey in each season, *Brama japonica* is frequently captured in the epipelagic zone at depths shallower than 100 m during both day and night (Shimazaki & Nakamura 1981, Ichii et al. 2004, H. Watanabe unpubl. data). The distribution depth of *B. japonica* overlaps with that of *X. gladius* during the night in the epipelagic zone (Fig. 5). In the continental shelf region, *X. gladius* is distributed near the bottom and frequently feeds on demersal fish during the day (Carey & Robinson 1981, Hernandez-Garcia 1995). In the present study, the Histioteuthidae and Chiroteuthidae squid fed on by *X. gladius* are non-migratory, and throughout the day are mainly distributed in the mesopelagic zone (Watanabe et al. 2006; see Table 2). These results might indicate that *X. gladius*

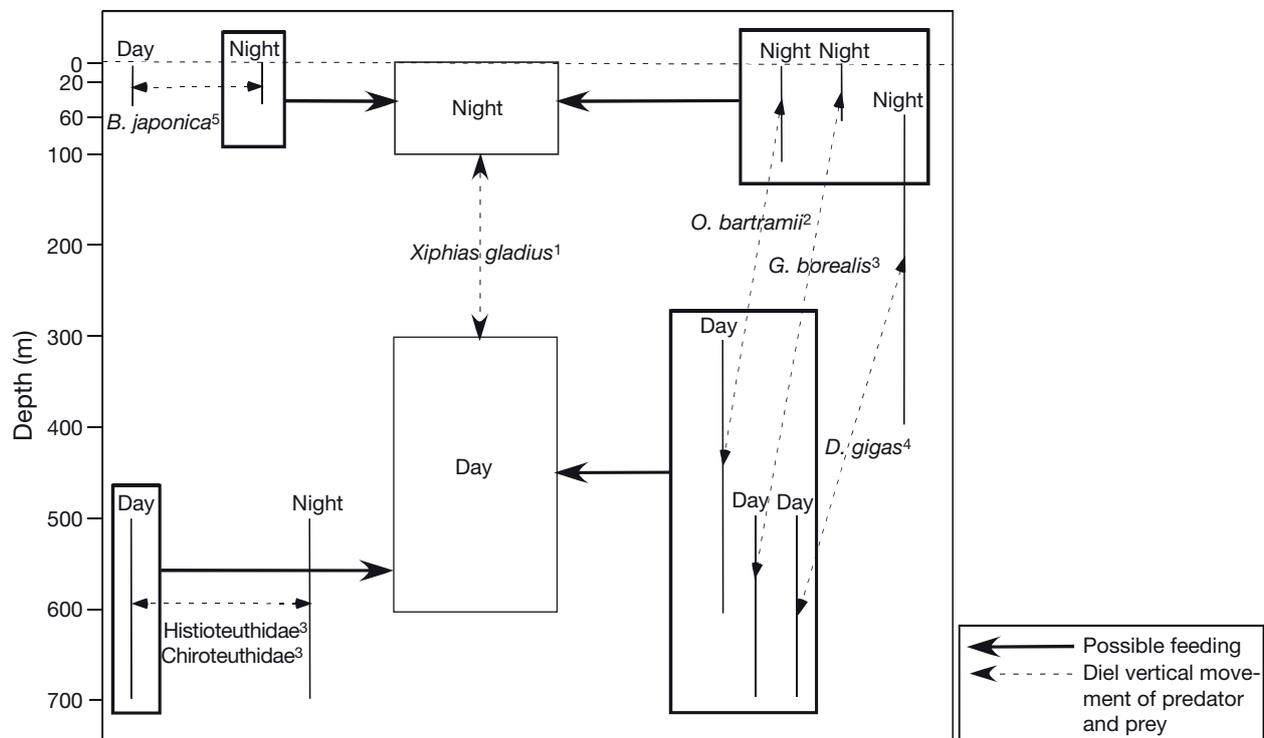


Fig. 5. Predator–prey relationships and diel vertical migration patterns of *Xiphias gladius*, major prey species, and 2 typical mesopelagic squid prey (Histioteuthidae and Chiroteuthidae) in subtropical and transition waters of the western North Pacific. Full species names of prey are given in Table 2. Data of day–night vertical distribution of each species are cited from ¹Takahashi et al. (2003), ²Tanaka (2001) and Nakamura (1993), ³Watanabe et al. (2006), ⁴Watanabe et al. (1999), and ⁵H. Watanabe (unpubl. data)

ius possibly feeds in the mesopelagic zone during the day in this study area. Therefore, it is possible that *X. gladius* feeds on prey that migrate vertically, such as *Ommastrephes bartramii*, *Gonatopsis borealis*, and *Diaphus gigas*, during both day and night, because their diel vertical migration patterns overlap each other (Nakamura 1993, Watanabe et al. 1999, 2006, Tanaka 2001; Fig. 5). Since these vertical migratory species are abundant in the transition waters of the western North Pacific (Kubodera et al. 1983, Watanabe et al. 1999, 2006, Ichii et al. 2004), their continuous availability would be beneficial to *X. gladius*.

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