Cephalopods in the Diet of Swordfish (*Xiphias gladius*) Caught off the West Coast of Baja California, Mexico[1]

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Abstract: The lower beaks of 1,318 cephalopods from the stomach contents of 175 swordfish, *Xiphias gladius*, caught off the west coast of Baja California, Mexico, between 1988 and 1996 were analyzed. In total, 20 species of teuthoids, 4 octopods, and one vampyromorph were identified. Weights and lengths of cephalopods were estimated from the lower rostral lengths. Ommastrephid squids, primarily jumbo squid *Dosidicus gigas* of different maturing sizes, composed 60% by number and 82% by estimated weight. Three species of gonatids were identified and represented 22% by number. An unidentified species of *Argonauta* was the most abundant octopod, with 5.8% of the beak total. *Ancistrocheirus lesueurii* is recorded for the first time in the California Current. Distribution of cephalopods in the California Current and their size in the diet of other marine predators are discussed. The diet of swordfish was dominated by medium to large muscular squid species that probably are eaten in surface waters at night.

CLARKE (1966) NOTED that marine predators prey on species of cephalopods that often are poorly known. In fact, the study of cephalopod remains in the stomach contents of marine predators has contributed greatly to our knowledge of the distribution and ecology of these mollusks. Information on oceanic cephalopods in the diet of marine predators in the California Current and northeastern Pacific Ocean has come principally from studies on marine mammals, mainly odontocetes or toothed whales and pinnipeds.

Squids recovered from the stomach contents of sperm whales, *Physeter macrocephalus* Linnaeus, 1758, from the Bering Sea and Gulf of Alaska were documented by Okutani and Nemoto (1964). Clarke and MacLeod (1980) identified cephalopod remains from 20 sperm whales caught off western Canada, and Fiscus et al. (1989) reported on beaks found in 175 specimens of the same predator off California. Mead et al. (1982) analyzed beaks from several Hubbs' beaked whales, *Mesoplodon carlhubbsi* Moore, 1963, stranded in California and provided drawings of a pair of *Gonatus* sp. beaks. Cephalopods found in a short-finned pilot whales, *Globicephala macrorhynchus* Gray, 1846, salvaged off California were listed by Seagars and Henderson (1985) and Hacker (1992). The beaks of an unidentified gonatid squid collected from pilot whales are illustrated in Hacker (1992).

Fiscus (1982) examined cephalopod remains recovered from the northern fur seal, *Callorhinus ursinus* (Linnaeus, 1758), and other marine mammals taken from California to the

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Bering Sea. Cephalopods in the diets of the California sea lion, *Zalophus californianus* (Lesson, 1828), and the northern elephant seal, *Mirounga angustirostris* (Gill, 1866), off southern California were discussed in reports by Lowry and coworkers (1990, 1999), Hacker (1986), and Antonelis et al. (1994). Other works on the diet of marine predators have only listed cephalopod prey. For teleosts Galván-Magaña et al. (1985) treated in detail the cephalopods found in yellowfin tuna, *Thunnus albacares* (Bonnaterre, 1788), from the California Current.

Several guides are available that provide illustrations useful for identification of the beaks of cephalopods found in predator stomachs in the northeastern Pacific Ocean; see especially Iverson and Pinkas (1971), Wolff (1984), and Fiscus (1991).

The swordfish, *Xiphias gladius* Linnaeus, 1758, is one of the largest teleost predators that is distributed, and commercially fished, worldwide in temperate and tropical seas (Nakamura 1974). Swordfish also undertake daily vertical migrations (Carey and Robinson 1981). These characteristics, coupled with the fact that cephalopods account for a large percentage of the diet of this predator, have encouraged studies on cephalopods from the stomach contents of swordfish in various regions of the world: northwestern Atlantic Ocean (Florida Straits: Hess and Toll 1981, Toll and Hess 1981), eastern Mediterranean Sea (Bello 1991), northeastern Atlantic Ocean (Guerra et al. 1993, Clarke et al. 1995, Hernández-García 1995), and North-central Pacific Ocean (Hawai'i: Seki 1993). In this study we examined the cephalopod remains collected from the stomach contents of swordfish from the southern portion of the California Current, in the northeastern Pacific Ocean.

MATERIALS AND METHODS

The stomach contents of 173 swordfish caught off the west coast of Baja California, Mexico, during 1992 and January 1993 were analyzed in a swordfish food and feeding habits study (Markaida and Sosa-Nishizaki 1998). The lower beaks of cephalopods found in 138 of those stomachs are treated here. An additional collection of 37 swordfish stomachs irregularly collected in the same area by commercial fishermen from 1988 to 1996 also was analyzed. Prey quantification in these stomach contents was made as previously described (Markaida and Sosa-Nishizaki 1998). Both collections of cephalopod lower beaks were examined together in the study described here.

Cephalopod beaks were identified utilizing keys in Iverson and Pinkas (1971), Wolff (1984), Clarke (1986), and Fiscus (1991). Identifications were checked against identified voucher samples in the collection of the Department of Invertebrate Zoology, Santa Barbara Museum of Natural History (SBMNH), Santa Barbara, California. Vouchers of almost every cephalopod species identified in the fauna of the eastern Pacific Ocean are present in the collections of SBMNH. Two beak samples were identified by Malcolm Clarke (pers. comm., January 1995). Rostral lengths (LRL) or hood lengths (LHL) of lower beaks were measured with a vernier caliper or micrometer to 0.05 mm. Frequency histograms for the most numerous species were constructed from these measurements. Darkening of the wings of lower beaks was analyzed because it indicates the maturity process in cephalopods (Mangold and Fioroni 1966). In ommastrephids the presence of completely pigmented beak wings indicates sexual maturity (Hernández-García et al. 1998). Equations were available for certain cephalopod species that were used to estimate weights and mantle lengths (ML), based on measurements of LRLs or LHLs (Wolff 1984, Clarke 1986, Kubodera 1986, Smale et al. 1993).

RESULTS

Cephalopods dominated the diet of the swordfish in the 37 samples collected between 1988 and 1996. They occurred in all stomachs and represented 92% by number and 76% by weight of all prey (Table 1). In total, 1,318 lower beaks belonging to at least 25 cephalopod species (Table 2) were identified pooling these and previous samples (Mar-

TABLE 1

Prey Species by Number, Weight, and Frequency of Occurrence in the Stomach Contents of 37 Swordfish Caught off the West Coast of Baja California during 1988–1996

Taxon	Number	%	Weight (g)	%	Frequency	%
CEPHALOPODA	384	92.53	14,618	76.24	37	100.00
Dosidicus gigas (jumbo squid)	197	47.35	12,481	65.09	33	89.18
Sthenoteuthis oualaniensis (flying squid)	11	2.64	—	—	7	18.91
Gonatus berryi	109	26.20	—	—	23	62.16
"*Gonatus californiensis*"	3	0.72	112	0.58	2	5.40
Gonatopsis borealis	4	0.96	—	—	3	8.10
Onychoteuthis cf. *banksii*	7	1.68	—	—	6	16.21
Onychoteuthis borealijaponicus	2	0.48	—	—	2	5.40
Unidentified onychoteuthid	30	7.21	—	—	4	10.81
Ancistrocheirus lesueurii	6	1.44	520	2.71	4	10.81
Histioteuthis heteropsis	3	0.72	—	—	3	8.10
Mastigoteuthis sp.	2	0.48	—	—	2	5.40
Loligo opalescens (market squid)	2	0.48	—	—	1	2.70
Thysanoteuthis rhombus	1	0.24	—	—	1	2.70
Unidentified teuthoids	2	0.48	—	—	2	5.40
Octopus rubescens	3	0.72	—	—	1	2.70
Argonauta spp. (papershell)	2	0.48	—	—	2	5.40
Cephalopoda remains	—	—	1,505	7.84	17	45.94
TELEOSTEI	31	7.45	4,554	23.75	15	40.54
Sardinops sagax (Pacific sardine)	9	2.16	396	2.06	4	10.81
Auxis spp. (frigate or bullet tuna)	8	1.92	2,731	14.24	6	16.21
Trachurus symmetricus (jack mackerel)	4	0.96	241	1.25	3	8.10
Scomber japonicus (Pacific mackerel)	3	0.72	106	0.55	2	5.40
Alepisaurus ferox (longnose lancetfish)	1	0.24	64	0.33	1	2.70
Unidentified scopelarchid	1	0.24	8	0.04	1	2.70
Merluccius productus (Pacific hake)	1	0.24	—	—	1	2.70
Unidentified teleosts	5	1.20	1,006	5.24	5	13.51
Total	416	100.00	19,174	100.00	37	100.00

kaida and Sosa-Nishizaki 1998). The most important cephalopod families found in the swordfish diet are treated here.

Order Teuthoidea (Squids)
Family Ommastrephidae

This family dominated the squid remains found in the diet of the swordfish studied. In total, 802 ommastrephid lower beaks were identified. This accounts for 60% of all beaks found and represents 82% of the estimated weight of all cephalopods consumed (Table 2). *Sthenoteuthis oualaniensis* (Lesson, 1830) and *Dosidicus gigas* (Orbigny, 1835) commonly inhabit waters off western Baja California (Sato 1975, Wormuth 1976, Voss 1979, Roper et al. 1995, Klett-Traulsen 1996). Separation between beaks of these species was made on the basis of the intrafamilial differences in size and darkening of the beaks (Perrin et al. 1973, Clarke et al. 1976, Markaida and Sosa-Nishizaki 1998). However, intraspecific population structure of both ommastrephid species is complex, involving several size-at-maturity groups, which makes beak identification difficult. According to Nesis (1993) only the medium size-at-maturity group (12–25 cm ML) of *S. oualaniensis* occurs in the California Current, although individuals of 20–30 cm ML are known from the eastern Pacific, including western Baja (Wormuth 1976, Wolff 1984).

Previous researchers largely believed that in the Northern Hemisphere *Dosidicus gigas* matures at smaller sizes and assumed that its beak wings darken faster (Clarke 1986).

TABLE 2

Lower Beak Numbers and Estimated Weights and Mantle Lengths (ML) of Cephalopods Found in Stomach Contents of 175 Swordfish Caught off Western Baja California (Species for Which Equations Were Not Available Are Not Included in Total Weight Estimates)

		Lower Beaks		Estimated Weight			Estimated ML (cm)	
Family	Species	No.	%	Mean (g)	Total (kg)	%	Mean	Range
TEUTHOIDEA								
Ommastrephidae	*Sthenoteuthis* or *Dosidicus*	665	50.4	452	300.57	44.5	23.3	7–30
	Dosidicus gigas	137	10.3	1,851	253.63	37.6	41.3	30–65
Gonatidae	*Gonatus berryi*[a]	233	17.6	28	6.60	0.9	8.8	1–19
	"Gonatus californiensis"[a]	45	3.4	667	30.05	4.4	32.3	25–35
	Gonatopsis borealis	16	1.2	370	5.91	0.8	19.5	7–42
Onychoteuthidae	*Onychoteuthis* cf. *banksii*	11	0.8	39	0.43	<0.1	10.9	9–14
	Onychoteuthis borealijaponica[b]	25	1.8	334	8.37	1.2	21.8	16–27
	Unidentified onychoteuthid[b]	13	0.9	<1	0.01	<0.1	2.1	1–3
Ancistrocheiridae	*Ancistrocheirus lesueurii*	18	1.3	408	7.34	1.0	18.6	11–23
Mastigoteuthidae	*Mastigoteuthis dentata*[a]	2	0.1	17	0.03	<0.1	7	6–7
	Mastigoteuthis spp.[a]	4	0.3	74	0.30	<0.1	11.7	10–14
Thysanoteuthidae	*Thysanoteuthis rhombus*	24	1.8	2,383	57.21	8.4	38.0	13–61
Histioteuthidae	*Histioteuthis heteropsis*	19	1.4	100	1.90	0.2	6.9	4–9
	Histioteuthis hoylei	2	0.1	433	0.86	0.1	10.8	—
Enoploteuthidae	*Abraliopsis* sp.	3	0.2	2	<0.01		4.0	3–4
Grimalditeuthidae	*Grimalditeuthis bonplandi*	3	0.2					
Octopoteuthidae	*Octopotheutis deletron*[a]	2	0.1	66	0.01	<0.1	9.8	9–10
Pholidoteuthidae	*Pholidoteuthis boschmai*	1	<0.1	77	0.07	<0.1	14.6	—
Loliginidae teuthoids	*Loligo opalescens*	1	<0.1	19	0.01	<0.1	11.3	—
Unidentified		5	0.3					
OCTOPODA								
Argonautidae	*Argonauta* spp.[a]	77	5.8	8	0.61	<0.1	3.6	2–8
Octopodidae	*Octopus rubescens*?[a]	6	0.4	7	0.04	<0.1	3.1	2–3
Alloposidae	*Haliphron atlanticus*	3	0.2					
Bolitaenidae	*Japetella diaphana*	1	<0.1					
VAMPYROMORPHA								
Vampyroteuthidae	*Vampyroteuthis infernalis*	1	<0.1	111	0.11	<0.1	6.4	—
Total		1,318	100.0	524	674.09	100.00	20.4	1–62

[a] Estimates from genus equations.
[b] Estimates from family equations.

However, all three maturing size groups described by Nigmatullin et al. (2001) have been observed off western Baja. Wormuth (1976) described small mature females (23 cm ML), and Sato (1975) studied mature males (14–29 cm ML) and mated females (16–29 cm ML). Sato (1975) noted mature medium-sized squid in the 30- to 40-cm ML range, and large *Dosidicus* (>50 cm ML) were reported by Klett-Traulsen (1996). Other ommastrephids found in the area include *Ommastrephes bartramii* (Lesueur, 1821) (up to 30 cm ML), *Eucleoteuthis luminosa* (Sasaki, 1915), and *Hyaloteuthis pelagica* (Bosc, 1802) (Young 1972, Wormuth 1976, Fiscus 1982, Roper et al. 1995).

Only 10% of the beaks were greater than 7.5 mm LRL (Figure 1), indicating that squid over 30 cm ML could reliably be assigned to *Dosidicus gigas* on the basis of size. These ac-

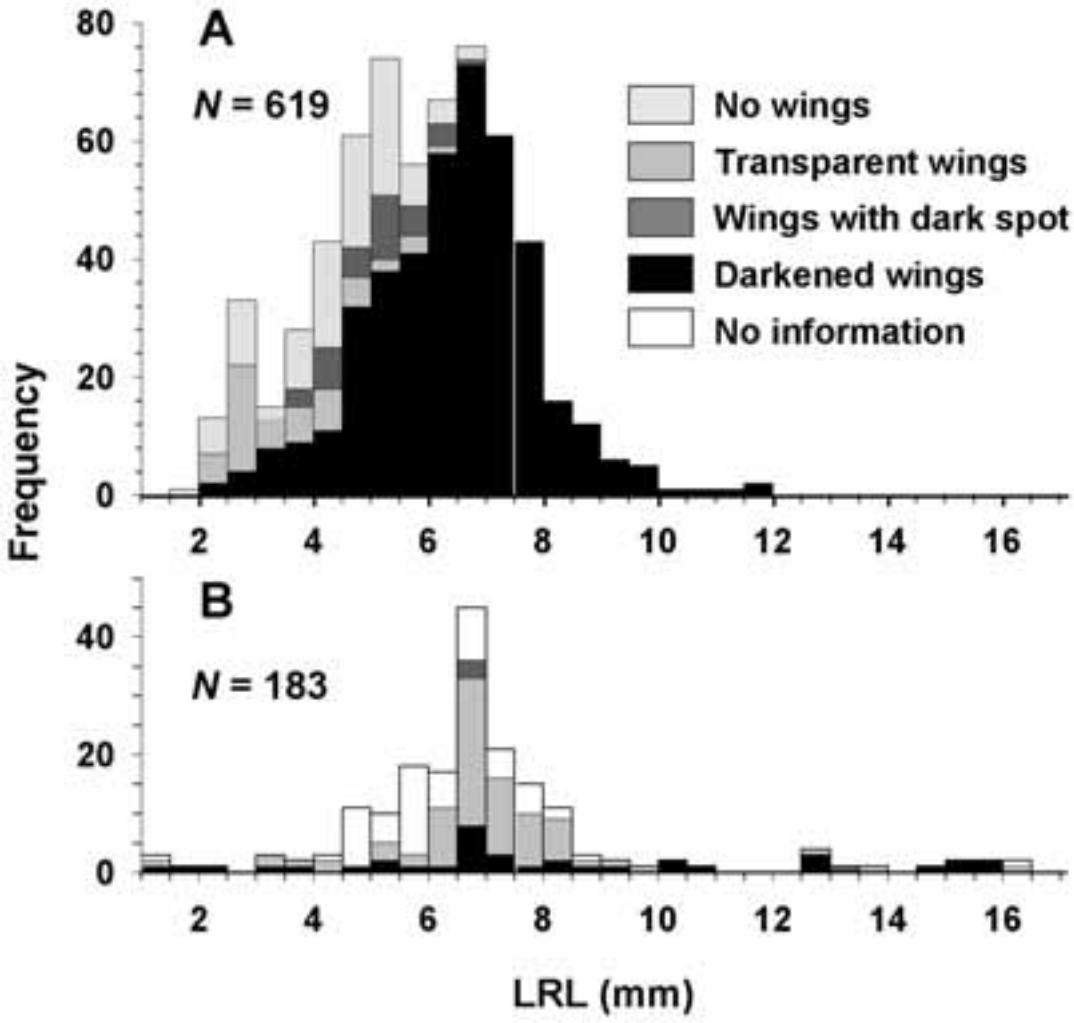

FIGURE 1. Lower rostral length (LRL) distributions of ommastrephid beaks found in swordfish stomachs. *A*, Beaks from 138 swordfish caught in 1992 and January 1993 (Markaida and Sosa-Nishizaki 1998); *B*, Beaks from 37 swordfish caught between 1988 and 1996. The white line at 7.5 mm LRL indicates positive identification of *Dosidicus gigas* beaks at right.

counted for 37% of the estimated weight of all cephalopods (Table 2). In the majority of all beaks (90%), the LRL measured $\leq$7.5 mm ($\leq$30 cm ML), which meant that the species could not be identified (Figure 1). However, considering that *Dosidicus* was fished by Japanese vessels during October 1989 to June 1992 off western Baja (Klett-Traulsen 1996), we believe that these smaller beaks also probably represent *D. gigas*.

Temporal variation in size structure is evident in the ommastrephids found in the diet of swordfish off Baja California. Of all beaks sampled in 1992–1993, 418 were completely pigmented. In these the LRL ranged between 2.2 and 11.6 mm (median 6.65 and mode 6.9 mm), suggesting squid maturing at MLs of 27–28 cm (Figure 1*A*). The LRLs of nearly 20% of these beaks were larger than 7.5 mm and thus they could be identified as *Dosidicus*.

Larger beaks among these with transparent or clear patches in the wings were 6.5 mm LRL. Those from 1988 to 1996 showed a wider distribution of beak size, with a mode of mostly unpigmented beaks at 7 mm, suggesting much larger maturing size squid (Figure 1*B*). The LRLs of almost half of the pigmented beaks were larger than 7.5 mm, and 13 beaks were larger than 12 mm. This yielded estimated MLs of 53–65 cm. Thus, almost all these beaks correspond to both the medium and large maturing size groups of *D. gigas*.

Ommastrephid beaks found in this study are smaller than *Dosidicus* beaks found in sperm whales but larger than those found in the stomach contents of striped marlin, *Tetrapturus audax* (Philippi, 1887), and blue marlin, *Makaira nigricans* Lacepède, 1802. The beaks are also larger than *Sthenoteuthis oualaniensis* beaks recorded from tuna and lancetfish (*Alepisaurus*) stomach contents (Table 3). In spite of difficulties in separating the beaks of the two dominant ommastrephids, they are known to co-occur in the stomachs of several predators from the tropical eastern Pacific (Perrin et al. 1973, Clarke et al. 1976, Abitia-Cárdenas 1992). Both squid species are common in the eastern Pacific from California to Chile (Wormuth 1976, Voss 1979, Roper et al. 1995). Ommastrephid squids typically congregate in schools of 30 or more individuals and are distributed vertically from 1,500 m to the surface, where they usually are observed at night (Wormuth 1976, Roper and Young 1975).

Family Gonatidae

This family, particularly diverse and abundant in the subarctic Pacific Ocean, composed 22% by number and 6% by weight among cephalopods in the diet of swordfish. Gonatid species consumed by swordfish are characterized as being large and muscular and they are epipelagic to mesopelagic or eurybathic in distribution (Okutani et al. 1988).

Gonatus berryi Naef, 1923

The LRL of 233 beaks of *G. berryi* ranged from 1.3 to 5.5 mm ($\bar{x} = 3$ mm) (Figure 2). The beaks are smaller than those found in sperm and toothed whales but larger than those from Pacific pomfret, *Brama japonica* Hilgendorf, 1878 (Table 3). Most beaks examined had no wings and in the rest the wings were transparent. The estimated MLs (range 1–19 cm, Table 2) probably are from immature specimens (Table 3). Imber (1978) considered that the beaks illustrated and identified by Iverson and Pinkas (1971) as from *Gonatus* sp. actually represent *G. berryi*. This species is reported to range in distribution from the Bering Sea to Mexico, north of Guadalupe Island (30° N) (Young 1972, Okutani et al. 1988). In this study, beaks of *G. berryi* were found in swordfish caught off the western coast of Baja California as far south as Magdalena Bay (25° N), which suggests a more southern distribution limit. This species lives mainly between 400 and 800 m and does not appear to migrate vertically (Roper and Young 1975).

"*Gonatus californiensis*" Young, 1972

A distinct and characteristic beak type found in this study is tentatively identified as from "*G. californiensis*" following Clarke (1986). Currently *G. californiensis* is known only from juvenile and immature specimens collected in the California Current between 28 and 44° N, with one record as far south as 7° N (Young 1972, Roper and Young 1975, Jefferts 1983). The LRL distribution of 45 beaks, all with well-pigmented wings, ranged from 6.8 to 9.1 mm ($\bar{x} = 8.6$ mm) (Figure 2). These measurements coincide with or are greater than those observed in the beaks of other *Gonatus* species found in the stomach contents of large marine predators (Table 3). Based on available regressions for *Gonatus* (Clarke 1986), data from this study suggest squids of much greater body size than specimens of *G. californiensis* examined by Young (1972). MLs that are estimated to range from 25 to 35 cm probably represent adult individuals (Table 2). All beaks of this type were collected from swordfish caught off southern Baja California (27 to 23° N); however, similar beaks are common in the diet of blue sharks (*Prionace glauca*) caught off Todos Santos Bay, northern Baja California (32° N) (U.M., pers. obs.).

TABLE 3

Most Numerous Cephalopods Found in This Study (Maximum Recorded Mantle Lengths [ML] in the Literature, and Lower Rostral Lengths [LRL] and Mantle Lengths [ML] Recorded from Stomach Contents of Selected Other Marine Predators)

Species	ML (cm) [Source][a]	LRL (mm) predator[b] [Source][a]	ML (cm) predator[b] [Source][a]
Sthenoteuthis oualaniensis	25–35 [20, 29, 34]	—	23.5 SHS [9]; 3.2–8.6 L, T [23]; 6.2 L [26]; 18.7–33.4 SF [30][c]
Dosidicus gigas	13–120 [21]	1.8–3.7 M [1]; 10–30 SW [7]; 2.7–5.5 SW [10]	—
Gonatus berryi	20 [25]	5–5.8 SW [10]; 0.8–2.8 P [16]; 3.5–6.6 SBW [32]; 2.4–7.5 BW [33]	—
(= *Gonatus* sp.) *Gonatus californiensis* (= *Galiteuthis* sp. A)	12.2 [35]	7–9 SW [10]; 3.2–6.5 HW [18]; 5.0–10.2 SB [31]; 2.4–10.2 BW [33]	—
Gonatus fabricii	35 [19]	3.5–7.2 NBW [4]; 4.8–6.0 SW [5]	30 SW [22]
Gonatus antarcticus	35 [19]	4.0–9.0 SW [7]; 5.0–8.9 SB [14]; 8 TS [26]	—
Gonatopsis borealis	33–50 [19, 25]	7–9 SW [10]; 4–8.5 PW [15]; 3.5–4.2 SBW [32]; 2.2–8.3 BW [33]	13.6–28 ES [2]; 20–32 SW [10]; 4.4–40.5 DP [17]; 30–35 SW [22]
Onychoteuthis borealijaponica	30–37 [19, 29]	3, 5.5, 6 SW [10]; 5.1–7 HW [18]; 1.5–3.2 BW [33]	30.3–32 SW [10]; 0.9–12.1 DP [17]
Onychoteuthis banksii	30 [29]	0.8–2.6 FS [6]	9.7 SF [3]; 1.3–3.7 L, T [23]
Thysanoteuthis rhombus	100 [19, 29]	3.3–7.6 SF [12]	40 SF [13]; 25.2–72.7 SF [12][c]; 9.5, 9.7 T [23]; 17 L [26]; 33 SF [30]
Histioteuthis heteropsis	13 [19]	—	—
Histioteuthis hoylei	12 [28]	3–7 SW [10]; 6.3–8.2 SF [11]; 5.4–7 SF [12]; 4–7.5 PW [15]; 3.7–4.2 HW [18]; 2.3–8.2 BW [33]	8.1–12.7 SF [11][c]; 9.5–12.8 SF [12][c]
Ancistrocheirus lesueurii	39 [28]	6.1 SF [3]; 4.0–9.0 SW [7]; 5.5–7.1 BW [33]	20.7 SF [3][c]; 19.1 SHS, 13.8 SCHS, 14–36 BS, 19.3 SM [9][c]; 17, 18.6 SF [12][c]; 1.5–2.9 L [23]; 11 SW [24]
Argonauta spp.	10 females, 1.1 males [19]	2.2–5.9 SF [3][d]; 3.8–7.2 SF [12]	3.5–8.8 SF [3][c]; 1.6–5.8 SF [8][c]; 0.7–8 L [26]

[a] References: [1] Abitia-Cárdenas 1992; [2] Antonelis et al. 1994; [3] Bello 1991; [4] Clarke and Kristensen 1980; [5] Clarke and MacLeod 1980; [6] Clarke and Trillmich 1980; [7] Clarke et al. 1976; [8] Clarke et al. 1995; [9] Dunning et al. 1993; [10] Fiscus et al. 1989; [11] Guerra et al. 1993; [12] Hernández-García 1995; [13] Hess and Toll 1981; [14] Imber 1978; [15] Kubodera and Miyazaki 1993; [16] Kubodera and Shimazaki 1989; [17] Kuramochi et al. 1993; [18] Mead et al. 1982; [19] Nesis 1987; [20] Nesis 1993; [21] Nigmatullin et al. 2001; [22] Okutani and Nemoto 1964; [23] Okutani and Tsukada 1988; [24] Okutani et al. 1976; [25] Okutani et al. 1988; [26] Rancurel 1970; [27] Rancurel 1973; [28] Roper et al. 1984; [29] Roper et al. 1995; [30] Seki 1993; [31] W. A. Walker, pers. com.; [32] Walker and Hanson 1999; [33] Walker et al. 2002; [34] Wormuth 1976; [35] Young 1972.

[b] Predators: (BS) blue shark, *Prionace glauca;* (BW) Baird's beaked whale, *Berardius bairdii;* (DP) Dall's porpoise, *Phocoenoides dalli;* (ES) northern elephant seal, *Mirounga angustirostris;* (FS) Galápagos fur seal, *Arctocephalus galapagoensis;* (HW) Hubbs' beaked whale, *Mesoplodon carlhubbsi;* (L) lancetfish, *Alepisaurus* sp.; (M) striped marlin, *Tetrapturus audax* and blue marlin, *Makaira nigricans;* (NBW) northern bottlenose whale, *Hyperoodon ampullatus;* (P) pomfret, *Brama japonica;* (PW) shortfin pilot whale, *Globicephala macrorhynchus;* (SB) sea birds; (SBW) Stejneger's beaked whale, *Mesoplodon stejnegeri;* (SCHS) scalloped hammerhead shark, *Sphyrna lewini;* (SF) swordfish, *Xiphias gladius;* (SHS) smooth hammerhead shark, *Sphyrna zygaena;* (SM) shortfin mako, *Isurus oxyrinchus;* (SW) sperm whale, *Physeter macrocephalus;* (T) tunas; (TS) tiger shark, *Galeocerdo cuvieri*.

[c] Estimated mantle length.

[d] Lower hood length.

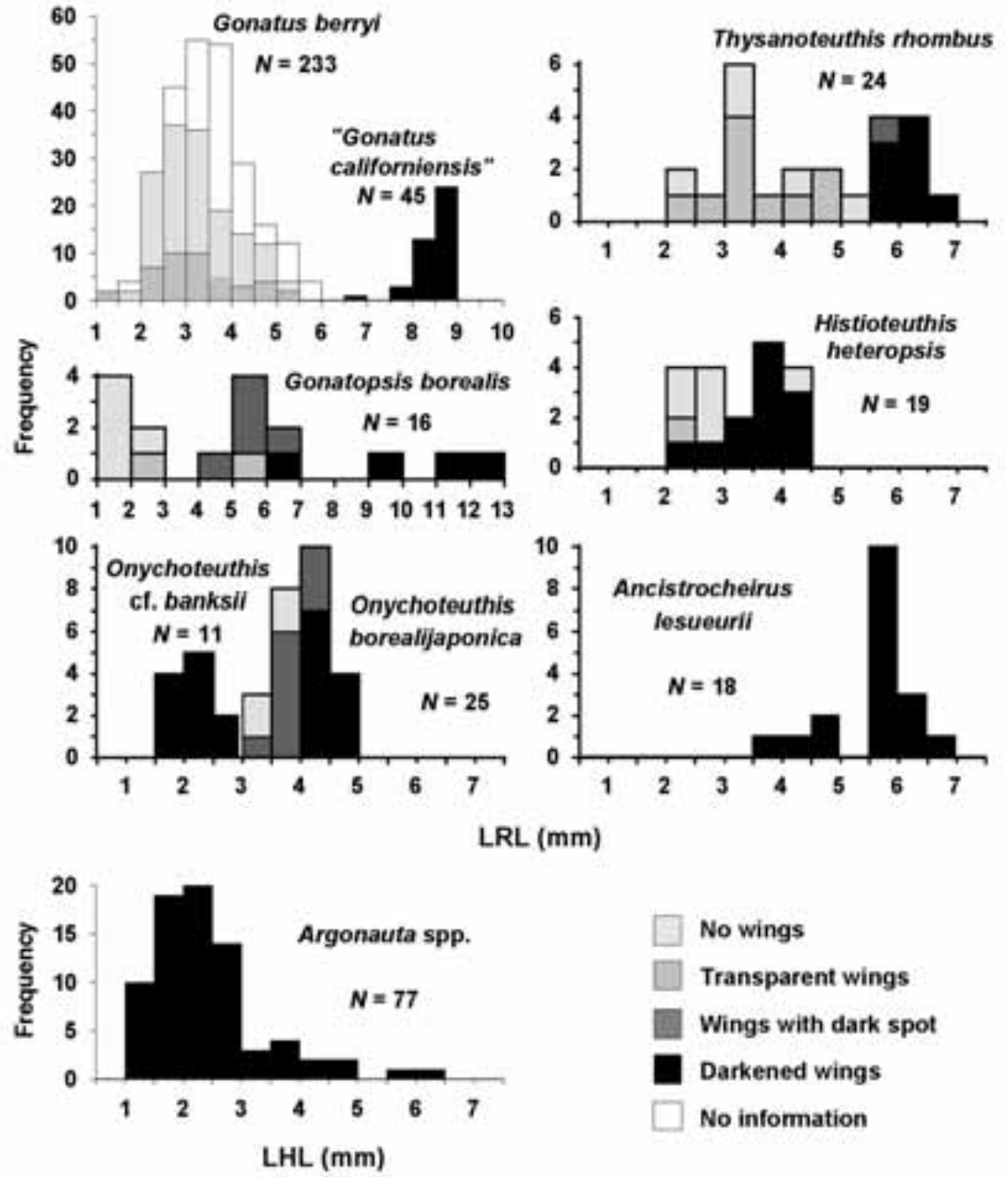

FIGURE 2. Lower rostral length (LRL) distributions of beaks from *Gonatus berryi*, "*G. californiensis*," *Gonatopsis borealis*, *Onychoteuthis* cf. *banksii*, *O. borealijaponica*, *Thysanoteuthis rhombus*, *Histioteuthis heteropsis*, and *Ancistrocheirus lesueurii*. Lower hood length (LHL) distributions of *Argonauta* spp.

Although beaks with configuration similar to the ones encountered in swordfish repeatedly have been recorded from the stomach contents of marine predators in the California Current, there is considerable disagreement as to taxonomic placement. In earlier publications this beak type was identified as from various species in the genus *Gonatus* (Table 3; see Clarke 1986, Fiscus et al. 1989). In more recent publications, especially the reports on the stomach contents of albatrosses from the North Pacific (Gould et al. 1997) and beaked whales from Japan (Walker et al. 2002), similar beaks provisionally were assigned to the squid genus *Galiteuthis*, a member of the family Cranchiidae. Because both genus and species identifications remain in question we have chosen to enclose the name in quotation marks.

Resolving problems relating to the generic and specific identification of this beak type is beyond the scope of this paper. Positive identification can only be confirmed when beaks from large, adult specimens of the various species of *Gonatus* and *Galiteuthis* are available for examination and side-by-side comparison.

Gonatopsis borealis Sasaki, 1923

The lower beaks of 16 *G. borealis* ranged in size from 1.4 to 12.5 mm LRL (Figure 2), corresponding with estimated MLs of 7–42 cm (Table 2). Beaks with LRLs of 5.3–6.2 mm had isolated patches on the wings, which was at larger beak sizes than reported by Clarke (1986) and Fiscus (1991). Only the three largest beaks appeared to represent adult specimens; mean LRLs and estimated ML distribution were smaller than those found in beaks in sperm whales, but their ranges overlapped the sizes recorded from short-finned pilot whales; Dall's porpoise, *Phocoenoides dalli* (True, 1885); and northern elephant seals (Table 3).

In the Northeast Pacific *G. borealis* ranges in distribution from subarctic waters to Guadalupe Island, Mexico, and it is also present in the western Pacific (Young 1972, Okutani et al. 1988, Fiscus et al. 1989). The beaks identified as from *G. borealis* in this study were found in the waters off northern Baja California (30° N). There is only a single species of *Gonatopsis* in these waters. The species is considered to be meso- and epipelagic (Fiscus et al. 1989). During the day juveniles live at depths ranging from 400 to 700 m, whereas at night they migrate to 0–400 m (Roper and Young 1975). Fiscus et al. (1989), Fiscus (1991), and Hacker (1992) discussed the difficulty involved in separating beaks of this species from those of *Berryteuthis*. North-central California is the southern limit of *Berryteuthis* (Okutani et al. 1988, Fiscus et al. 1989).

Family Onychoteuthidae

Onychoteuthis borealijaponica Okada, 1927

Because this is the largest species of *Onychoteuthis*, a large size class of onychoteuthid beaks was attributed to this species. A total of 25 lower beaks of this species ranged in LRL from 3.1 to 4.9 mm ($\bar{x} = 4$ mm) (Figure 2) and their estimated MLs from 16 to 27 cm (Table 2). These specimens appear to be nearly mature, smaller than those from sperm whales and Hubbs' beaked whales, but larger than those reported for Dall's porpoises (Table 3). An isolated pigmented patch or spot is present in the wings at LRLs between 3.8 and 4.3 mm. *Onychoteuthis borealijaponica* is a meso- to epipelagic species distributed, in the northeastern Pacific, from subarctic waters to northern Baja California (29° N) (Young 1972, Jefferts 1983). In agreement with this distribution data, beaks of this species were found in the diet of swordfish caught off northern Baja California (south to 29° N).

Onychoteuthis cf. *banksii* (Leach, 1817)

Eleven beaks, tentatively identified as from *O. banksii*, were found along the coast of western Baja California (Figure 2). The LRLs ranged from 2.0 to 2.8 mm and had darkened wings. This species is cosmopolitan in subtropical and tropical waters, replaced by *O. borealijaponica* in colder waters of the North Pacific (Young 1972). Although the species is reported to be epipelagic, it is probably not restricted to surface waters (Roper and Young 1975). Because the species *O. banksii* likely

represents a species complex (Young 1972), the identification of species should wait until a set of beaks can be assembled from properly identified specimens of species in this squid complex. Similar rostral lengths have been reported from beaks in the diet of the Galápagos fur seal, *Arctocephalus galapagoensis* Heller, 1904, whereas MLs found in beaks from tuna and lancetfish are smaller than those estimated to be present in the stomach contents of swordfish (9–13 cm ML) (Tables 2, 3).

In addition, 13 beaks of a small unidentified onychoteuthid also were found. The LRL of these samples measured 0.7–1 mm, suggesting that the animals were small, in the size range of 1–3 cm ML.

Family Thysanoteuthidae

Thysanoteuthis rhombus Troschel, 1857

The LRLs of 24 *T. rhombus* beaks had a distribution of 2.3–6.7 mm ($\bar{x} = 4.5$) (Figure 2). These measurements correspond to estimated MLs of 13–61 cm, which represent juvenile and immature specimens of this large squid species. The beaks found in swordfish are larger than those collected from tuna and lancetfish (Table 3). Wing darkening occurs at LRLs of 4.6–5.7 mm, approximately the size indicated by Clarke (1986). One beak with an LRL of 5.8 mm had an isolated dark patch or spot on the wings. This species had the largest estimated mean weight, over 2 kg, and its low presence (1.8% of all cephalopods) contrasts with its relatively high occurrence (8.4%) in swordfish diet (Table 2). The largest specimen had an estimated ML of 61 cm and weight of over 6 kg. They were found mainly in the stomach of swordfish caught off the southern coast of Baja California in 1992, although beaks and large flesh remains were found in a swordfish caught as far north as 30° N. This species appears to replace large jumbo squid in the swordfish diet when large *Dosidicus* are not present. Fishermen have reported incidental catches of *T. rhombus* while fishing for jumbo squid in recent years. This large squid is a vertical migrator and has a cosmopolitan distribution in tropical and subtropical waters (Nesis 1992, Nigmatullin and Arkhipkin 1998). There are only a few records of its presence in the California Current. Off southern Baja California, Galván-Magaña et al. (1985) identified its presence in the diet of yellowfin tuna, and off California it has been reported in the pygmy sperm whale, *Kogia brevicepes* (Blainville, 1838) (see Morejohn et al. 1978) and blue shark (Tricas 1979).

Family Histioteuthidae

Histioteuthis heteropsis (Berry, 1913)

In total, 19 beaks were identified as from *H. heteropsis* (M. R. Clarke, pers. comm., January 1995). They ranged in LRLs from 2.1 to 4.3 mm ($\bar{x} = 3.2$) (Figure 2). In almost all cases the wings were either completely dark or missing. MLs estimated from these beak measurements ranged from 4 to 9 cm (Table 2), suggesting that all squid were immature individuals. This species has an antitropical distribution in the eastern Pacific. In the Californian Current it has been reported to occur as far south as central Baja California (27° N [Voss 1969 *in* Young 1972]). In our study most beaks were collected from swordfish caught off northern Baja California. However, Galván-Magaña et al. (1989) found it in the diet of hammerhead sharks (*Sphyrna* spp.) caught in the southern part of the Gulf of California (24° N). *Histioteuthis heteropsis* is a mesopelagic species that during the day lives at depths of 500–700 m and at night migrates vertically to 300–400 m (Roper and Young 1975).

Histioteuthis hoylei (Goodrich, 1896)

Two lower beaks of *H. hoylei* with LRLs of 6.9 and 7.0 mm were found in this study. These beak sizes suggest mature specimens, similar or slightly smaller than those recorded from sperm and short-finned pilot whales, and larger than beaks from the Hubbs' beaked whale (Tables 2, 3). *Histiotheuthis hoylei* is a mesopelagic species widely distributed in tropical to subtropical waters (Young 1972, Nesis 1987). In older literature (i.e., Young 1972) this species was identified as *H. dofleini*.

Family Ancistrocheiridae

Ancistrocheirus lesueurii Orbigny, 1842

Ancistrocheirus lesueurii was represented by 18 beaks ranging in LRL from 3.8 to 6.6 mm ($\bar{x} = 5.6$ mm) (Figure 2). The beaks in swordfish are smaller than those found in the stomach contents of sperm whales (Table 3). Estimated MLs (Table 2) indicate immature individuals, similar to those reported in the diet of sharks, such as hammerhead, blue shark, and the shortfin mako shark, *Isurus oxyrinchus* Rafinesque, 1810, but larger than those found in lancetfish (Table 3). All beaks had darkly pigmented wings, although Clarke (1986) mentioned that darkening occurs at LRLs of 4–6 mm. Beaks of this species were found in the stomach contents of swordfish caught off southern Baja California, but they also have been found in the diet of blue sharks caught off Todos Santos Bay, northern Baja California (U.M., pers. obs.). Although a mesopelagic species with a cosmopolitan distribution in tropical and subtropical waters (Nesis 1987), *A. lesueurii* rarely has been recorded in the Pacific Ocean (Clarke et al. 1976, Okutani et al. 1976) and has not been reported previously from the California Current.

Miscellaneous Squids

The LRLs of other teuthoid beaks identified in this study include two *Mastigoteuthis dentata* Hoyle, 1904 (2.3 and 2.7 mm); four *Mastigoteuthis* sp. (3.4 to 4.8 mm); three *Grimalditeuthis bonplandi* (Verany, 1839) (1.3, 1.4, and 2.6 mm); three *Abraliopsis* sp. (1.0–1.1 mm); one *Pholidoteuthis boschmai* Adam, 1950 (3.3 mm); one *Loligo opalescens* Berry, 1911 (1.3 mm); and three unidentified beaks, probably from cranchiids (1.15, 1.65, and 1.75 mm).

Order Octopoda
Family Argonautidae

Argonauta spp.

Probably more than one species of *Argonauta* was represented by 77 lower beaks found along all the western coast of Baja California. The LHLs ranged in size from 1.5 to 6.5 mm ($\bar{x} = 2.8$ mm) (Figure 2), suggesting a ML range of 2–8 cm (Table 2), similar to that found in the lancetfish diet (Table 3). Despite a relatively high abundance (5.8% by number), the contribution of *Argonauta* to the swordfish diet by weight was minimal (<0.1%) (Table 2).

Several species of this strictly epipelagic genus live off the coast of western Baja California: the cosmopolitan tropical and subtropical *Argonauta argo* Linnaeus, 1758; *A. hians* Lightfoot, 1786; and the eastern Pacific species *A. cornuta* Conrad, 1854, and *A. nouryi* Lorois, 1852 (Nesis 1987). *Argonauta pacifica* Dall, 1871, may represent an eastern Pacific form of *A. argo* (Young 1972, Nesis 1987). Although a regional effort was made to identify the beaks of *Argonauta* (Smale et al. 1993), the lack of keys for this family prevented specific identification of the beaks determined to belong to this genus.

Miscellaneous Octopods

Other octopodid beaks included one from *Japetella diaphana* Hoyle, 1885 (0.18 mm LHL), three from *Haliphron atlanticus* Steenstrup, 1861 (7.2, 6.45, and 3.8 mm LHL), and six from *Octopus rubescens* Berry, 1953 (1.5–2.3 mm LHL). A single lower beak of *Vampyroteuthis infernalis* Chun, 1903 (7.7 mm LRL) also was found.

Cephalopod Prey Size

Swordfish feed on cephalopods of a wide range of target sizes (Figure 3), of which the majority (77%) are between 10 and 35 cm ML. The diet consists principally of ommastrephids and secondarily of gonatids, onychoteuthids, and *Ancistrocheirus*. A small number of squid (6%) are larger, mainly *Dosidicus gigas* and half of the *Thysanoteuthis rhombus* samples, with maximum sizes of 60–65 cm ML. Cephalopods smaller than 10 cm ML accounted for 16% by number and are composed primarily of *Gonatus berryi*, *Argonauta* spp., and *Histioteuthis heteropsis*.

Discussion

Our results confirm the preference of swordfish for muscular, active squids that form

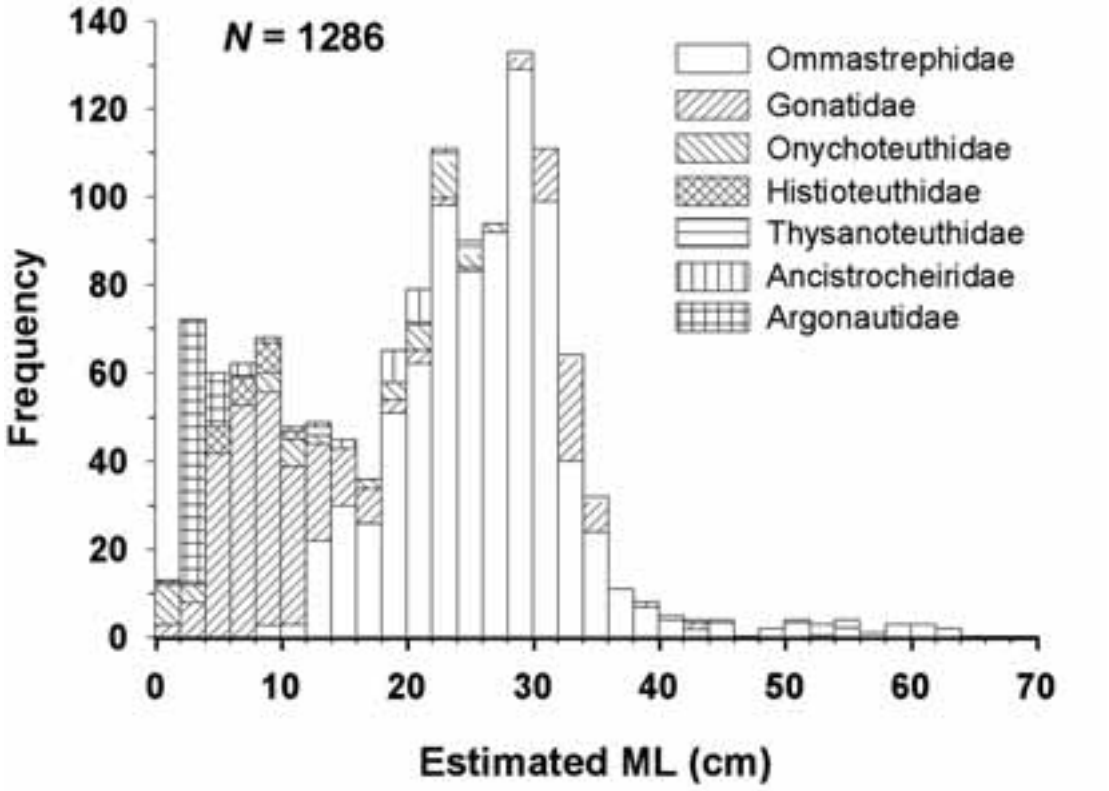

FIGURE 3. Estimated mantle length (ML) distributions of the most important cephalopod families found in the diet of swordfish.

schools (Toll and Hess 1981) at the surface. Ommastrephids, muscular gonatids, onychoteuthids, *Thysanoteuthis*, and *Ancistrocheirus* are mainly epipelagic (and some also mesopelagic), powerful swimmers, whereas the histioteuthids are predominantly mesopelagic drifters. Swordfish detect their prey visually (Carey and Robinson 1981), hence, fast-swimming medium to large cephalopods would be more attractive to swordfish than small slow-moving or planktonic forms.

Swordfish undertake daily vertical migrations that allow them to exploit mesopelagic waters. Most likely, feeding occurs near the surface at night, as suggested in previous studies (De Sylva 1962). Both predator and prey concentrate in surface waters at night, where chances for feeding interactions increase. Ommastrephid squids dominate the teuthofauna in swordfish diet, as previously documented (Tibbo et al. 1961, De Sylva 1962, Toll and Hess 1981, Stillwell and Kohler 1985, Moreira 1990, Bello 1991, Guerra et al. 1993, Seki 1993, Clarke et al. 1995, Hernández-García 1995). This can be explained by the fact that squid in this family are common in surface waters at night throughout the world (Roper and Young 1975).

Despite the bias that predator migration has on studies of cephalopod prey distribution, swordfish stomach contents reflect the relative abundance of its cephalopod prey. *Sthenoteuthis oualaniensis* and *Dosidicus gigas* are the dominant ommastrephids in subtropical to equatorial waters of the eastern Pacific.

Results of samples from different years suggest that ommastrephid size composition in swordfish diet varies dramatically off the coast of Baja California where *D. gigas* sustains swordfish feeding.

The importance of gonatid squids in the diet of swordfish from the California Current is not surprising given the abundance of species in that family in the North Pacific (Okutani et al. 1988). In contrast, only a very low percentage of gonatids has been reported in the diet of swordfish from the Atlantic Ocean (Stillwell and Kohler 1985, Hernández-García 1995). Our study confirms the southern limit of *Gonatopsis borealis* at 30° N but extends the distribution of *Gonatus berryi* to the west coast of Baja California. Both species are abundant (Young 1972, Jefferts 1983) and have been found in the diets of other predators (see Markaida and Sosa-Nishizaki 1998). *Gonatus californiensis* appears to be the lesser abundant species in the genus (Young 1972, Roper and Young 1975, Jefferts 1983). Distribution limits of this species in the North Pacific and proper identification of the beaks from predator stomach contents that we tentatively referred to this species need further study. It is curious that the other two species of gonatids reported to live in the California Current, namely *G. pyros* and *G. onyx*, considered abundant off California (Young 1972, Roper and Young 1975, Jefferts 1983), have only rarely been reported in the diets of predators in the California Current (Fiscus et al. 1989, Antonelis et al. 1994).

The occurrence of two species of tropical cosmopolitan squids, *Thysanoteuthis rhombus* and *Ancistrocheirus lesueurii*, in the stomach contents of swordfish caught off western Baja California suggests that this area represents the northern limit of their distribution. The presence of these two species in the eastern tropical Pacific is poorly known. The occurrence of rare or uncommon cephalopods in swordfish diets has been documented previously in other areas (Hess and Toll 1981, Toll and Hess 1981, Bello 1991).

The beaks of two *Octopoteuthis deletron* Young, 1972 (6.15 and 5.25 mm LRL), found during a previous study of swordfish feeding by Markaida and Sosa-Nishizaki (1998), were thought to represent secondary prey elements in the diet (Perrin et al. 1973). Small beaks found in this study, such as those of *Onychoteuthis* cf. *banksii* and the unidentified onychoteuthid, also probably represent secondary prey. Their importance by number and weight in the swordfish diet is negligible.

The results of this study agree with ommastrephid sizes reported in other swordfish diet studies (measured or estimated MLs, in cm): 15–35 (Hess and Toll 1981), 6–33 (Bello 1991), 14–43 (Guerra et al. 1993), 18–49 (Seki 1993), 14–53 (Hernández-García 1995), and 13–37 (Clarke et al. 1995). Similar agreements are found in the sizes of other cephalopod species (*Histioteuthis hoylei*, *Thysanoteuthis rhombus*, *Ancistrocheirus lesueurii*, and *Argonauta* spp.) reported here and in other studies (Hess and Toll 1981, Bello 1991, Guerra et al. 1993, Clarke et al. 1995, Hernández-García 1995) (see Tables 2 and 3). The estimated sizes of cephalopods found in the swordfish diet suggest that swordfish prey upon individuals that are larger than those found in other teleost predators (tuna, lancetfish, and marlin), similar in size to the prey of some odontocetes (e.g., Dall's porpoise, short-finned pilot whale, and Hubbs' beaked whale), and smaller than those found in sperm whales.

Considerable variation was found in pigmentation patterns with beak size in the species examined in this study. The ecological ramifications of this may be extensive; however, more data are needed on the relationships between beak pigmentation and sexual maturity before we can be confident of the interpretation. Nevertheless pigmentation patterns can be a great help in resolving beak identifications.

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