RANGE EXPANSION AND TROPHIC INTERACTIONS OF THE JUMBO SQUID, *DOSIDICUS GIGAS*, IN THE CALIFORNIA CURRENT

JOHN C. FIELD AND KEN BALTZ
NOAA Fisheries Southwest Fishery Science Center
110 Shaffer Road
Santa Cruz, California 95060
John.Field@noaa.gov

A. JASON PHILLIPS
Cooperative Institute for Marine Resources Studies
Oregon State University
Hatfield Marine Science Center
2030 Marine Science Drive
Newport, Oregon 97365

WILLIAM A. WALKER
NOAA Fisheries National Marine Mammal Laboratory
Alaska Fisheries Science Center
7600 Sand Point Way N.E., Building 4
Seattle, Washington 98115

ABSTRACT

Although jumbo squid (*Dosidicus gigas*) have been occasional visitors to the California Current over the last century, their abundance and distribution increased between 2002 and 2006. We report several time series of jumbo squid relative abundance from commercial and recreational fisheries as well as resource surveys and food habits studies. To evaluate the trophic relationships of jumbo squid, we report the results of 428 stomach samples collected between 2005 and 2006 at various locations and seasons along the U.S. West Coast. Prey were identified using hard parts, primarily squid beaks and otoliths, and prey sizes were estimated where possible. While jumbo squid forage primarily on small midwater and forage fishes, they also prey on adult groundfish such as Pacific hake (*Merluccius productus*), shortbelly rockfish (*Sebastes jordani*), and other species with semi-pelagic life histories. As their ability to prey on larger items suggests potential impacts on ecosystems, we also consider the role of jumbo squid in a food web model of the northern California Current.

INTRODUCTION

The jumbo squid (*Dosidicus gigas*) is one of the largest and most abundant nektonic squid in the epipelagic zone throughout the Eastern Tropical Pacific (ETP). As such, jumbo squid are an important component of subtropical food webs, representing a conduit of energy transfer from the mesopelagic food web to higher trophic level tunas, billfish, sharks, and marine mammals (Nesis 1983; Nigmatullin et al. 2001; Olson and Watters 2003). Jumbo squid also support major fisheries in the Gulf of California, the ETP, and the coastal waters of Peru and Chile, although catches are highly variable in space and time. Like most cephalopods, jumbo squid are characterized by rapid growth and short life spans. In the Gulf of California, growth rates of 1 to 1.5 mm dorsal mantle length (DML) per day were estimated for squid in 50 to 70 cm size classes, consistent with lifespans of 1.5 to 2 years (Markaida et al. 2005). There is general consensus that females are more abundant and grow larger than males, with DMLs as large as 100 to 120 cm, corresponding to weights of 30 to 50 kg (Nigmatullin et al. 2001). Nigmatullin et al. (2001) described some apparent population structure of jumbo squid, with individuals growing to a smaller size and maturing earlier in the core of their range in the ETP, and growing (and maturing) larger at the poleward fringes of their range, consistent with the observation by O'dor (1992) that squid tend to grow larger and reproduce later in cooler waters.

Gilly et al. (2006) found that while squid spent most daylight hours at depths greater than 250 m and foraged in near-surface waters at night, they often made short-term vertical migrations from surface waters to depth throughout the night. Their results demonstrated a greater appreciation for the extent of diel movement and the tolerance of jumbo squid for a wide range of both temperature and oxygen levels over short time periods. Tagging results also demonstrate that jumbo squid are capable of migrating up to 30 miles a day for several days in a row (Markaida et al. 2005; Gilly et al. 2006). The usual range of jumbo squid extends from central Chile through the coastal and pelagic waters of the ETP, and into the Gulf of California. However, the distribution and density of jumbo squid throughout their range are characterized by irregular migratory incursions of large numbers of squid at the fringes of their habitat in both hemispheres (Nesis 1983; Ehrhardt 1991; Nigmatullin et al. 2001; Ibáñanez and Cubillos 2007).

Jumbo squid were described as "not uncommon" to the waters of southern and central California by Berry (1912) and Phillips (1933), and were particularly abundant for several years in the mid 1930s, when they were described as a nuisance to salmon, tuna, rockfish, and recreational charter boat fishermen (Clark and Phillips 1936; Croker 1937). There are few records of their presence in California waters between the late 1930s and 1950s (Phillips 1961), although episodic strandings and fisheries occurred sporadically throughout the 1960s and 1970s (Fitch 1974; Anderson 1978; Nesis 1983; Mearns 1988), and their presence in the Southern California

Bight was episodic throughout most of the 1980s and 1990s. During the 1997–98 El Niño event, jumbo squid were observed in substantial numbers off California, as well as in coastal waters off of Oregon and Washington states (Pearcy 2002). In situ video observations taken from remotely operated vehicle (ROV) surveys from the Monterey Bay region show that jumbo squid continue to be present and sporadically abundant since the 1997–98 El Niño, particularly between 2003 and 2006. Their presence in the surveys has been associated with declines in observations of Pacific hake (*Merluccius productus*) (Robison and Zeidberg[1]). Since 2003, jumbo squid have been frequently reported in beach strandings, commercial and recreational fisheries, and resource surveys along the West Coast and through southeast Alaska (Cosgrove 2005; Brodeur et al. 2006; Wing 2006).

In this study, we report several time series of jumbo squid relative abundance from commercial and recreational fisheries as well as resource surveys and food habits studies in order to evaluate the trophic relationships of jumbo squid along the U.S. West Coast.

METHODS

To consider trends in jumbo squid abundance throughout the California Current, we evaluated several sources of landings and trend information for jumbo squid from commercial and recreational fisheries, resource surveys, and food habits studies. We evaluated catch records from Commercial Passenger Fishing Vessel (CPFV) records north and south of Point Conception from 1980 through 2006.[2] We also discussed the spatial and temporal distribution of squid with a large number of commercial and recreational fishermen. Jumbo squid have also been noted in food habits studies of predators in the California Current; Antonelis and Fiscus (1980) described them as common in the diets of northern fur seal (*Callorhinus ursinus*) off of California, and both Tricas (1979) and Harvey (1989) noted their presence (albeit rare) in the diets of blue sharks (*Prionace glauca*) collected off of the Channel Islands and Monterey Bay respectively in the mid 1970s. Consequently, we considered the frequency of occurrence of jumbo squid in the diets of California sea lions (*Zalophus californianus*) on San Clemente and San Nicolas Islands, based from quarterly monitoring from 1981 to the present (as described in Lowry and Carretta 1999), as well as in the food habits of shortfin mako shark (*Isurus oxyrinchus*) collected from gillnet fisheries off of southern California from 2002–05

(A. Preti, NOAA/NMFS/SWFSC, La Jolla, California, pers. comm.).

Fisheries resource surveys have provided both quantitative and qualitative estimates of abundance for many commercially and ecologically important species relevant to this study. We compiled data from pelagic midwater trawl surveys for juvenile groundfish conducted in May and June off of the central California coast by the NOAA Fisheries Southwest Fisheries Science Center (SWFSC) since 1983 (Sakuma et al. 2006), and a comparable midwater trawl survey conducted by the NOAA Fisheries Northwest Fisheries Science Center (NWFSC) off of Oregon and Southwest Washington between May and November from 2004–06 (Brodeur et al. 2006). Finally, bycatch monitoring data by fisheries observers on commercial at-sea catcher-processors targeting Pacific hake off of Oregon and Washington, including average weights per haul, are available from 1991 to the present, although jumbo squid were only routinely identified to species in 2006. In recent years, catches of squid have increased substantially, with hauls of 25 to 75 tons of squid not uncommon, and most large squid hauls were composed primarily of jumbo squid (V. Wespestad, At-Sea Processors Assn., pers. comm.). Consequently, we evaluated a range of factors including the relative catches of squid to hake, the frequency of occurrence of hauls with large volumes of squid, and the size composition of the squid catch during years for which no reliable taxonomic identity of squid bycatch are available (V. Tuttle, At-Sea Hake Observer Program NOAA/NMFS/ NWFSC, pers. comm.).

To evaluate food habits, stomach samples were collected from jig-caught jumbo squid in CPFV and commercial fisheries off of southern and central California, as well as from jig, midwater, and bottom trawl gear aboard the resource surveys described above. The locations, dates, depths (including a range where appropriate), number of specimens collected, and size information for collected specimens are provided in Table 1 and Figure 1. Although size (DML, in cm) was recorded for all specimens, weight (kg) and sex were recorded only for a subset of specimens due to the opportunistic nature of most collections. Weights were estimated with the standard weight (w) to length (l) relationship based on 85 specimens ranging from 35 to 82 cm mantle length, where:

$$w = al^b \tag{1}$$

Whole squid or stomachs alone were frozen at capture, although in many instances stomach removal was delayed by 1 to 2 hours. Upon thawing and weighing, stomach contents were washed through a 0.45 mm mesh sieve. Identification of prey items was made from otoliths, squid beaks, scales, bones, and other hard parts based on

TABLE 1
**Sampling locations, dates, collection gear, number of animals sampled, and average mantle length of animals
for samples in which animals were collected. For gear type, jig represents sport or commercial line jigging,
MT represents midwater (survey) trawls, BT represents bottom (survey) trawls.**

Location	Month/year	Depth (m)	gear	number	length mean	length range
Nine mile bank	2/2005	200	jig	27	60	50–69
Carmel Canyon	2/2006	250	jig	21	69	65–75
Pioneer Canyon 1	1/2005	200–300	jig	46	65	56–75
Pioneer Canyon 2	2/2005	200–300	jig	33	66	59–74
Pioneer Canyon 3	6/2005	200	MT	20	54	46–63
Pioneer Canyon 4	2/2006	200–300	jig	19	68	50–78
Pioneer Canyon 5	3/2006	200–300	jig	12	63	57–70
Pioneer Canyon 6	9/2006	200–300	jig	9	66	61–70
Pioneer Canyon 7	12/2006	200–300	jig	11	72	66–76
Cordell Bank 1	2/2005	200–300	jig	9	66	57–70
Cordell Bank 2	1/2006	200–300	jig	16	71	63–81
Cordell Bank 3	2/2006	200–300	jig	20	66	56–80
Cordell Bank 4	3/2006	200–300	jig	34	66	57–79
Cordell Bank 5	6/2006	1200	MT, jig	37	57	35–65
Cordell Bank 6	11/2006	200–300	jig	21	70	62–82
Arena Canyon, offshore	5/2006	3000	MT, jig	18	51	46–59
Arena Canyon, nearshore	9/2006	400	jig	41	54	38–68
Cape Mendocino	6/2006	60	MT, jig	30	54	49–61
Heceta Bank	8–9/2006	950	MT	29	54	45–64
Astoria Canyon	8–9/2006	900	MT	21	58	51–68
Coastwide	6–10/2005–2006	100–600	BT	29	61	55–68

published guides to fish otoliths (Fitch 1964, 1969; Harvey et al. 2000), squid beaks (Pinkas et al. 1971; Wolff 1982; Clarke 1986), and other sources (McGowan 1968), as well as reference collections. The number of individuals consumed was reported based on the maximum number of upper or lower beaks for cephalopods, and the maximum number of left or right sagittal otoliths for fishes. Only the presence or absence was recorded for euphausiids or small unidentifiable crustaceans, as digestion typically made meaningful enumeration impossible. The frequency of occurrence and the number of prey items was enumerated for all other prey. We also report the percentage of stomach contents weight to the estimated predator size, where empty or trace contents were those with less than 0.001% of body weight, and very full stomachs were those in which stomach weight was greater than 1% of total body weight. Finally, we recorded qualitative estimates of prey digestion state for most samples, in which the degree of digestion was ranked from 1 for recently ingested prey to 5 for trace prey material.

As larger prey items are typically bitten into smaller pieces when consumed, and squid tend to have extremely rapid digestion rates, weighing of prey items is impractical, and was not attempted in this study. Consequently, commonly reported indices, such as the index of relative importance (Pinkas et al. 1971), are not available. However, an alternative index, the geometric index of importance (Assis 1996; Preti et al. 2004), was used, in which

$$GII_j = \frac{\left[\sum_{i=1}^{n} V_i\right]_j}{\sqrt{n}} \qquad (2)$$

where GII_j represents the geometric index of importance for the jth prey category, V_i represents the vectors for the relative measures of prey quantity (here % frequency occurrence and % of total number), and n is the number of relative measures of prey quantity used (in this case, 2). Additionally, standard lengths (for fishes), DML (for cephalopods), and prey weights were reconstructed based on fitted regressions against otolith lengths and beak rostral lengths where measurements could be taken (to the nearest 0.1 mm), and for which regression information was available (Wolff 1982; Wyllie-Echeverria 1987; Harvey et al. 2000; W. Walker unpubl. data; J. Field unpubl. data; M. Lowry, NOAA/NMFS/SWFSC, La Jolla, California, pers. comm.). Finally, the resulting information was integrated into an existing food web model of the shelf and slope ecosystem of the northern California Current (Field et al. 2006b), and trophic relationships were compared to those in a food web model of the ETP (Olson and Watters 2003).

RESULTS

Trends in jumbo squid abundance include the number of jumbo squid landed by recreational fishers in CPFV fisheries north and south of Point Conception,
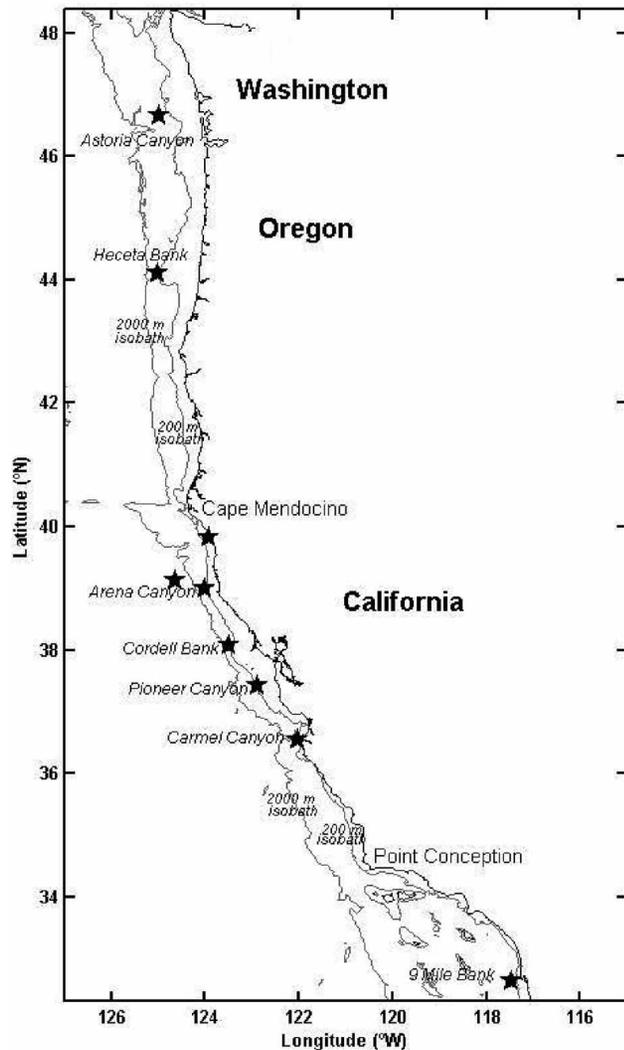
Figure 1. Collection locations of jumbo squid (*Dosidicus gigas*) for food habits studies in 2005 and 2006.

California (fig. 2A). Anecdotal information suggests that the high numbers of squid landed south of Point Conception in 2002 were smaller animals caught primarily in summer months, while catches from 2005–06 were caught almost exclusively in winter months and tended to be large (50–82 cm DML). Information from food habits studies off of southern California are consistent with these trends (fig. 2B), including data from California sea lion foods (1981–2003) and mako sharks (2002–05). Jumbo squid first appeared in the diets of California sea lions in 1995, increased in 1997–98, and increased again from 2002–03. Although the data for mako sharks extends only from 2002 through 2005, jumbo squid were among the most frequently encountered prey item for each of these years, indicating a sustained presence of squid in the offshore waters of southern California throughout this period.

Jumbo squid have also been increasingly encountered in resource surveys along the West Coast, and data from two pelagic midwater trawl surveys are shown (fig. 2C). In the SWFSC survey, jumbo squid were encountered for the first time in 2005, and frequently in 2006, while in the NWFSC midwater survey they were encountered frequently from 2004–06. Although the NWFSC survey shown here began in 2004, comparable midwater trawl surveys in this region prior to 2003 did not encounter jumbo squid (Brodeur et al. 2006). The discrepancy between the northern and southern surveys can be explained largely by their seasonality; although the SWFSC survey occurs in a continuous 45-day period during May and June (between San Diego and Cape Mendocino), the NWFSC survey occurs monthly from May through November (from central Oregon to southwest Washington). In the NWFSC survey, squid were encountered in only 2% of hauls made from May through August, but 14% of hauls made between September and November.

These trends in the seasonality of jumbo squid catches were consistent with those observed from monitoring data from the at-sea fishery for Pacific hake, in which catch rates of all squids in all years are an average of twenty times greater from September through November relative to April through August. Figure 2D shows the total catch of all squid as a percentage of the total catch of hake (to control for changes in year-to-year catches and monitoring coverage), as well as the frequency of occurrence of large catches of squid, defined as tows in which squid represented 10% or more of the total catch of hake by weight. Although jumbo squid were only identified to species in 2006, when they accounted for over 90% of all squid caught, the distribution of average sizes (collected in bycatch monitoring programs) of squid caught in the hake fishery between 2002–05 is much more consistent with the size of jumbo squid relative to the (larger) robust clubhook squid (*Moroteuthis robusta*) or the smaller species seen through most of the 1990s.

A total of 503 stomach samples were collected for food habits studies from 2005–06. From the 85 samples in which weight and length were recorded, the weight-length relationship was estimated ($a = 7.83 * 10^{-6}$, $b = 3.33$, $R^2 = 0.94$). Digestion state and stomach fullness relative to the inferred body weight of samples by gear type are shown in Figure 3. Although only a modest number of stomachs (29) were collected with bottom trawls, over 60% of these stomachs contained recently ingested prey (digestion state of 1), and another 16% had relatively recently ingested prey (digestion state of 2). Along with obvious incidents of cannibalism, this suggests that most prey items from samples collected in bottom trawls represented opportunistic net feeding. Net feeding was also inferred in many of the midwater trawl
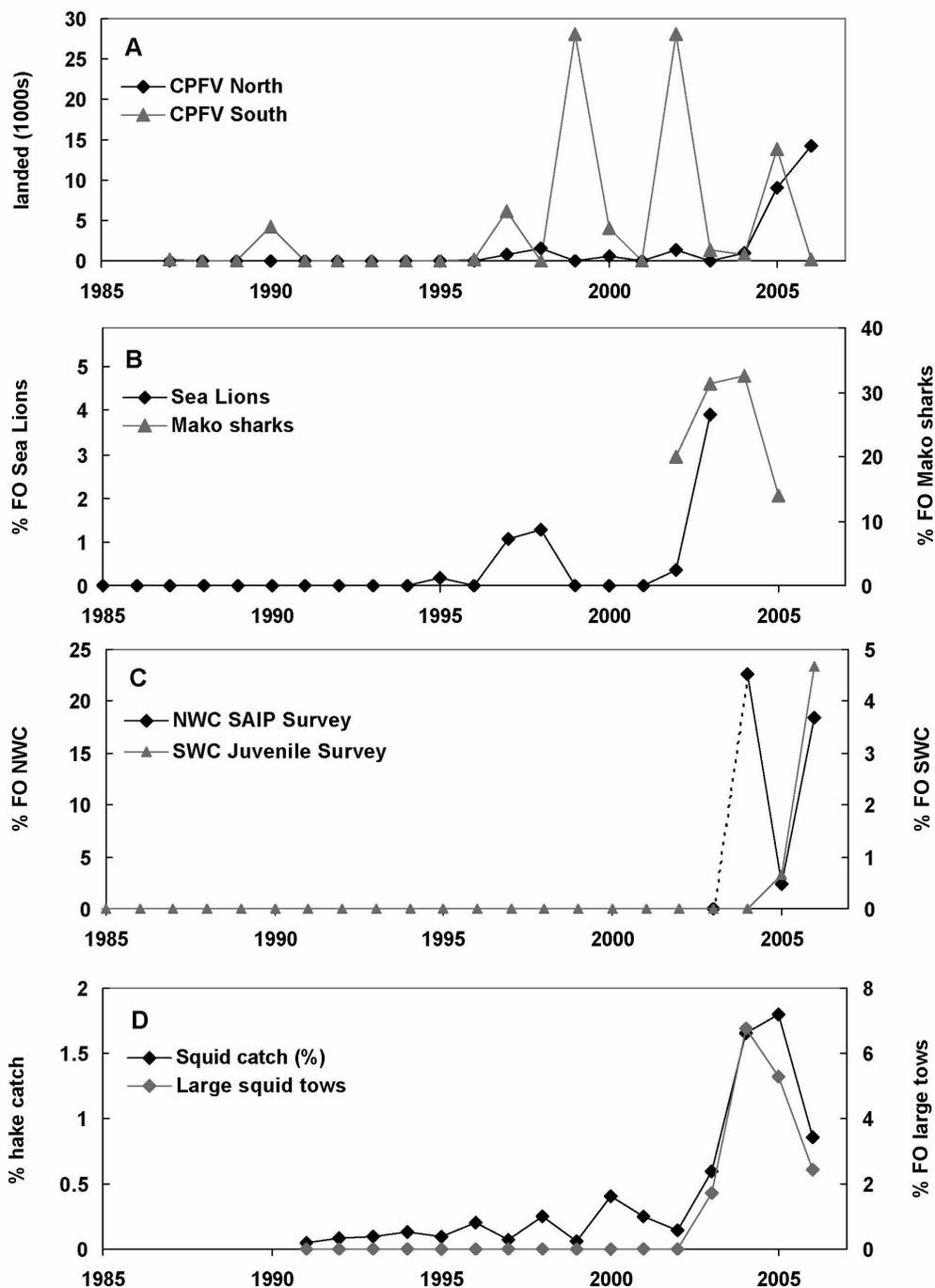
Figure 2.   Indices of relative jumbo squid (*Dosidicus gigas*) abundance from (A) California commercial passenger fishing vessels (CPFV) north and south of Point Conception (note that 1999 and 2002 CPFV landings south of Conception were approximately 50,000 and 200,000 squid respectively), (B) frequency of occurrence of jumbo squid in sea lion (*Zalophus californianus*) and shortfin mako shark (*Isurus oxyrinchus*) food habits studies, (C) SWFSC and NWFSC pelagic midwater trawl surveys, and (D) catch statistics from the observer program for the at-sea processing sector of the Pacific hake (*Merluccius productus*) fishery.

collected species, with 28% of stomachs including very recently ingested prey, and 18% including relatively recently ingested prey. By contrast, recently ingested prey items were infrequent (5%) in jig-caught specimens, and in many cases represented cannibalism. Although factors such as seasonality, time of day, and behavior are also rel-

evant, we excluded all samples collected with bottom trawl ($n = 29$) as well as samples collected with midwater trawl with digestion state codes of 1 or 2 ($n = 46$) from further analysis.

The resulting prey composition from 428 samples (375 jig-caught and 53 midwater trawl) are consistent
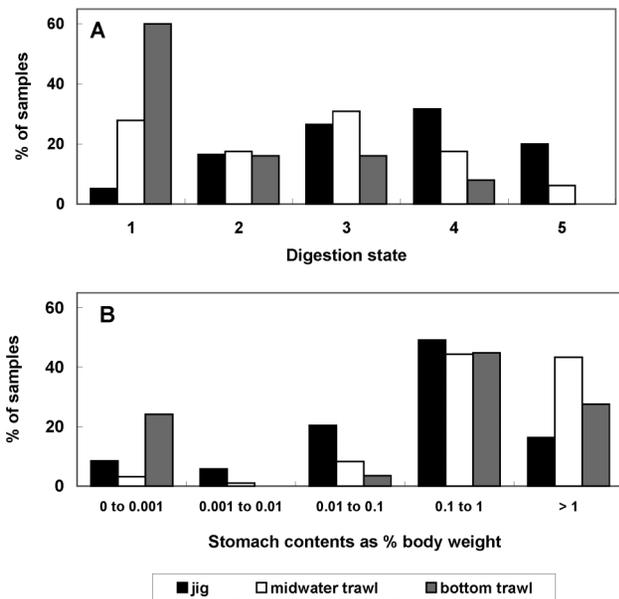
Figure 3. Qualitative estimate of digestion state for all three gear types used to collect jumbo squid (*Dosidicus gigas*), (A) where 1 represents recently ingested prey and 5 represents well digested or trace fragments of prey, and (B) stomach contents as a percentage of predator body weight.

copsarus), northern anchovy (*Engraulis mordax*), blue lanternfish (*Tarletonbeania crenularis*), and Pacific sardine (*Sardinops sagax*). Although other jumbo squid were present in 11% of samples, cannibalism may be overestimated from many jig-caught cephalopods (Nesis 1983; Dawe et al. 1997; Markaida and Sosa-Nishizaki 2003), and all instances were of bite-size pieces of other large squid, rather than predation on smaller jumbo squid of the size ranges encountered for other cephalopods. Pteropods, euphausiids, and other unidentified crustaceans were all important prey items that could rarely be identified to species or accurately enumerated due to digestion. Additionally, many rockfish could not be identified to the species level, as otoliths of larger individuals were rarely recovered. Given the well armored nature of most rockfish heads, and the tendency of many cephalopods to discard the heads of larger prey items (Dawe et al. 1997), this result is not surprising. Finally, among the more unique remains were bird feathers, which were present in two samples. Observations from commercial fishermen confirm that jumbo squid will attack seabirds (F. Bertroni, F/V *Santina*, Fort Bragg, California, pers. comm.), although the observation of feathers alone in stomachs may suggest unsuccessful attempts.

Some insights with respect to the patchiness of food habits over space and time can be inferred from Table 3, which lists the frequency of occurrence for the eight most frequently encountered prey items, and aggregations of remaining prey items as delineated in Appendix A, for each of the major collection sites described in Table 1. These results show that Pacific hake tended to be important prey across all space and time, as only two location/time combinations did not include their presence. Mesopelagics tended to be ubiquitous, while northern anchovy tended to be more frequently encountered

with the expectation that jumbo squid are opportunistic predators, capable of feeding on a wide range of prey items throughout the waters of the California Current. The fifteen most frequently encountered prey items (excluding cannibalism) are presented as Table 2, and a complete taxonomic breakdown of over 60 prey items identified to the genus or species level, with corresponding general prey category groupings and size (length, weight) information is included as Appendix A. Pacific hake was the most numerically important prey item, followed by northern lampfish (*Stenobrachius leu-*

TABLE 2

The percent frequency of occurrence (FO) and total number (N) of the fifteen most important prey items of jumbo squid (*Dosidicus gigas*) based on a geometric index of importance. A complete taxonomic summary of all prey items, including length and weight information, is provided in Appendix A.

Species or taxonomic group	GII	%FO	%N	FO	N
Pacific hake (*Merluccius productus*)	30.9	22.7	20.9	96	305
Northern lampfish (*Stenobrachius leucopsarus*)	21.5	20.1	10.3	85	150
Northern anchovy (*Engraulis mordax*)	19.9	16.3	11.9	69	173
Blue lanternfish (*Tarletonbeania crenularis*)	15.3	13.5	8.2	57	119
Pacific sardine (*Sardinops sagax*)	9.2	9.7	3.4	41	49
Euphausiids (Euphausidae)	N/A	9.0	N/A	38	N/A
Shortbelly rockfish (*Sebastes jordani*)	8.6	8.7	3.4	37	50
California headlightfish (*Diaphus theta*)	8.3	6.9	4.9	29	71
Pteropods (*Clio* spp.)	7.5	7.8	2.8	33	41
Broadfin lampfish (*Nannobrachium ritteri*)	6.3	5.7	3.3	24	48
Rockfish spp. (*Sebastes* spp.)	5.4	5.9	1.7	25	25
Pelagic shrimp (Decapoda)	4.4	4.5	1.8	19	26
Clubhook squid (*Onychoteuthis borealijaponicus*)	3.9	2.6	2.9	11	42
California lanternfish (*Symbolophorus californiensis*)	3.6	3.8	1.4	16	20
California market squid (*Loligo opalescens*)	3.2	3.1	1.5	13	22

TABLE 3

Prey frequency of occurrence (%) by sampling site and number of samples. Differences between this table and Table 1 reflect exclusion of net feeding samples from midwater trawl collections. The top eight most frequently encountered prey from Table 2 are provided, with aggregated groups of remaining prey items.

	Nine Mile Bank	Carmel Canyon	Pioneer Canyon 1	Pioneer Canyon 2	Pioneer Canyon 3	Pioneer Canyon 4	Pioneer Canyon 5	Pioneer Canyon 6	Pioneer Canyon 7	Cordell Bank 1	Cordell Bank 2	Cordell Bank 3	Cordell Bank 4	Cordell Bank 5	Cordell Bank 6	Arena Canyon offshore	Arena Canyon nearshore	Cape Mendocino	Heceta Bank	Astoria Canyon
# samp	27	21	46	33	11	19	12	9	11	9	16	20	37	23	21	18	41	30	11	13
gear	jig	jig	jig	jig	MT	jig	jig	jig	jig	jig	jig	jig	jig	MT	jig	MT	jig	jig	MT	MT
Merluccius productus	8	10	17	16		47	42	67	36	22	6	20	33	4	32		5	47	45	62
Stenobrachius leucopsarus	8	10	26	38	27	6	33	11	55	11	6	20	11	22	32		27	20	27	8
Engraulis mordax	36	38	26	25	73		8	22	55		6						26	20	3	
Tarletonbeania crenularis			9	22	36	6			18	22	6		8		42	6	29	7	36	46
Sardinops sagax	4								9		6	45	50	26			6	7	9	8
Euphausidae			4	6		6	17								5	6	39	3	9	8
Sebastes jordani		24	7	13			25	56	27			5				6	17	7	9	
Diaphus theta	4		28	28		18	17		36	11	6	5			11					
other crustaceans			7						0							4	11	2	9	15
pteropods	12								9		15	19				11	37		9	38
cephalopods	16	62	28	28	73	12	33	22	36	22	25	20	22	30	42	17	44	13	27	46
other coastal pelagics	4		2	3		18			18		6			4			5	18		
other mesopelagics	12	14	4	16	18	53		67	9		6	30		9	5	22	37	10	136	15
other rockfish		5	13	19	9	6		44	55		19	10	6		5		6	3		
flatfish			4	16					9		6		6		5					8
other or unidentified	8	14	39	22	9	6	25	11	18	33	25	10	17	9	21	6	10	13	18	38

in nearshore and canyon areas (Carmel Canyon, Nine Mile Bank, and Pioneer Canyon) and Pacific sardine were more frequently encountered in offshore areas (particularly Cordell Bank). Shortbelly rockfish were most frequently encountered in Pioneer Canyon, long known to be a region of high abundance for that species (Chess et al. 1988), while other rockfish and small flatfish were most frequently seen at both Pioneer Canyon and Cordell Bank, generally in winter months.

Of the 1,293 fish and cephalopod prey items that could be identified to a species or genus level, 1,122 (87%) could be associated with length and weight information. The resulting length frequencies for several of the more frequently encountered species of commercial importance are shown in Figure 4. Most Pacific hake were less than 15 cm standard length, primarily young-of-year and age-1 fishes, although hake as large as 42 cm were observed. While most of the rockfish are shortbelly rockfish, an unfished species, other rockfish species were present, and many of the unidentified rockfish are unlikely to be shortbelly due to the large size inferred by vertebral remains. Pacific sardine were observed primarily in the 15 to 21 cm size classes, corresponding to age 1–3 sardines, which are age classes commonly targeted in commercial fisheries.

As Pacific hake and other groundfish for which lengths and weights could be reconstructed tended to be con-siderably larger than those for mesopelagic fishes, coastal pelagics, and cephalopods, a comparison of the relative importance of prey by weight is insightful. Figure 5 shows binned length classes of all prey items that could be associated with a length and weight by their general taxonomic groups described in Appendix A (where groundfish includes rockfish and flatfish). While small mesopelagics were numerically the most important prey item (accounting for 34% of all measured prey items), their estimated mass represented less than 5% of the mass of all measured prey. By contrast, groundfish other than Pacific hake represented only 9% by number, but 41% by mass. Similarly, smaller (0–20 cm) hake represented 22% of measured prey by number but only 9% by mass, while larger (>20 cm) hake represented only 4% by number but 21% by mass. Other cephalopods represented 13% of prey by number and 7% by mass, while coastal pelagics represented 20% by number and 17% by mass. Although clearance rates for larger prey items could be extended relative to smaller prey, these results indicate that larger prey items are likely to make a greater contribution to squid diets than might be expected by the frequency-of-occurrence information alone. The relationships between the mantle length of jumbo squid and standard length (for fish) or mantle length (for cephalopods) of prey are shown in Figure 6, along with smoothed 10th, 50th, and 90th percentiles of prey size by preda-
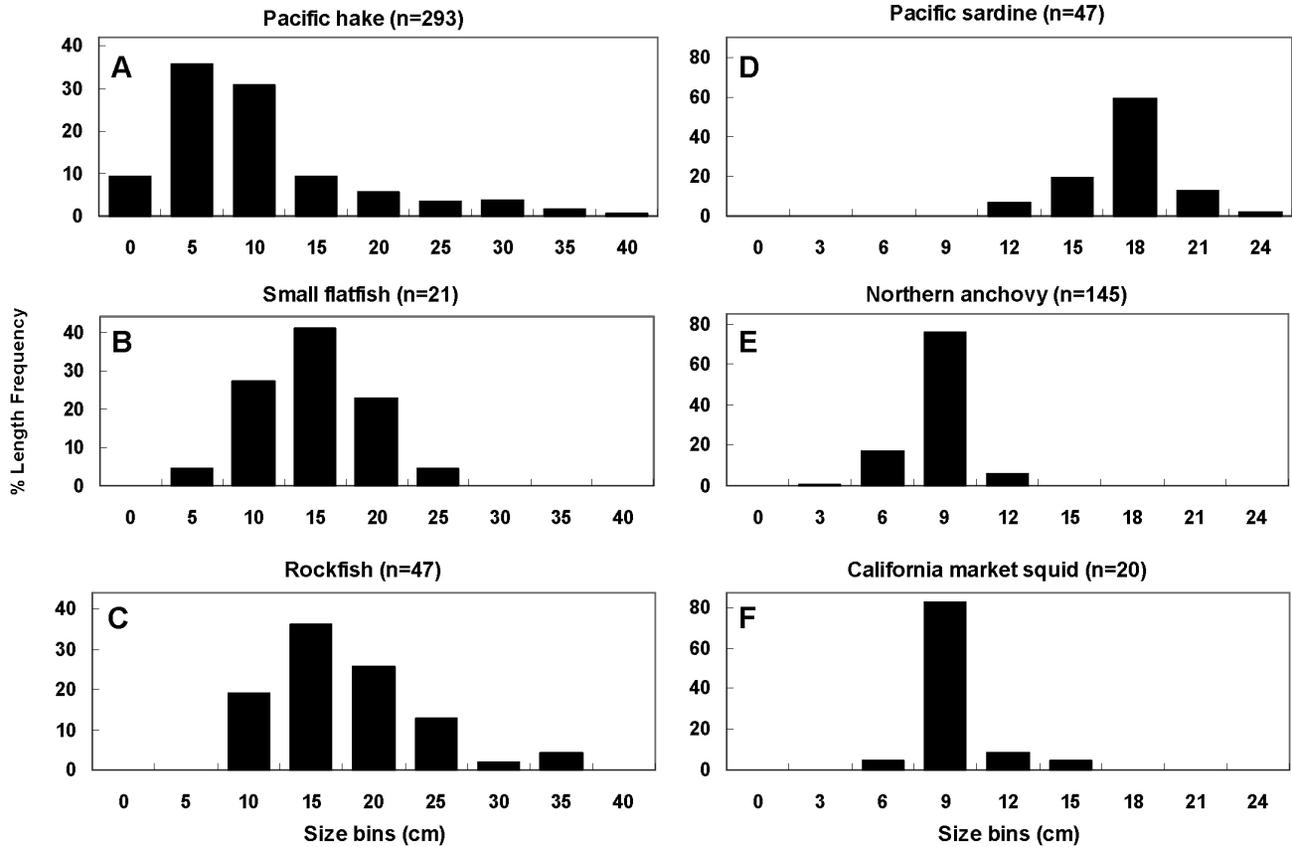
Figure 4.   Size composition of most frequently consumed species of commercial interests, including, (A) Pacific hake (*Merluccius productus*), (B) small flatfish, (C) rockfish, (D) Pacific sardine (*Sardinops sagax*), (E) Northern anchovy (*Engraulis mordax*), and (F) California market squid (*Loligo opalescens*). Sizes are based on otolith length/standard length regressions for fishes, and rostrum length/mantle length regressions for market squid. Length bins are labeled by the lower end of the bin, such that 5 represents fish from 5 to 9.9 cm.
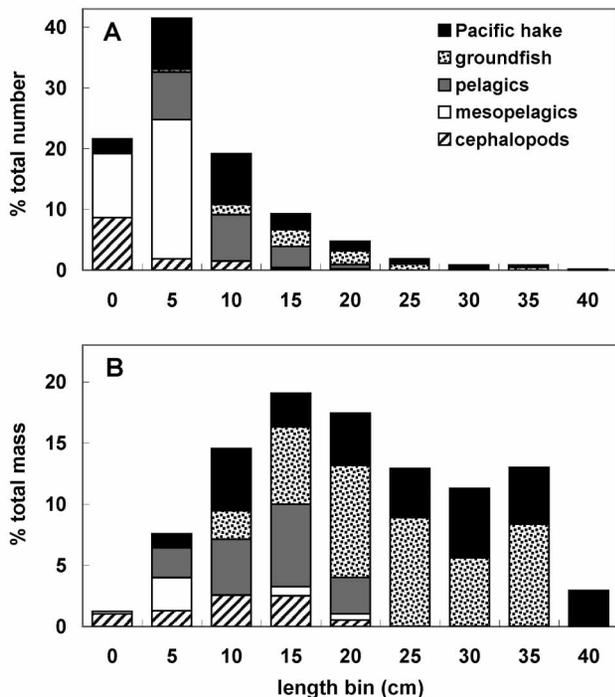
tor size (in 5 cm bins). The relationship suggests a log-normal distribution across the prey spectrum, such that the size classes of the vast majority of prey items changes little with size, while the distribution of the prey spectrum extends towards larger prey items with size.

The role of jumbo squid in the ecosystem, including an estimate of trophic level, was evaluated by adding jumbo squid to a food web model of the northern California Current (Field et al. 2006b). To arrive at an estimate of prey composition we made the following assumptions. First, as the rapid digestion rates of soft-bodied prey complicate enumeration or weighing of those prey items, we assumed that the frequency of occurrence represented a plausible composition for euphausiids (9%), macrozooplankton (5%), and gelatinous zooplankton (8%). For the remaining prey items, we scaled the product of the frequency of occurrence and the percentage of total number by the average weight of all prey items

Figure 5.   Size composition of all measured jumbo squid (*Dosidicus gigas*) prey items in aggregated groups, (A) by the percentage of the total number of measured prey, and (B) with respect to the reconstructed total mass of prey.
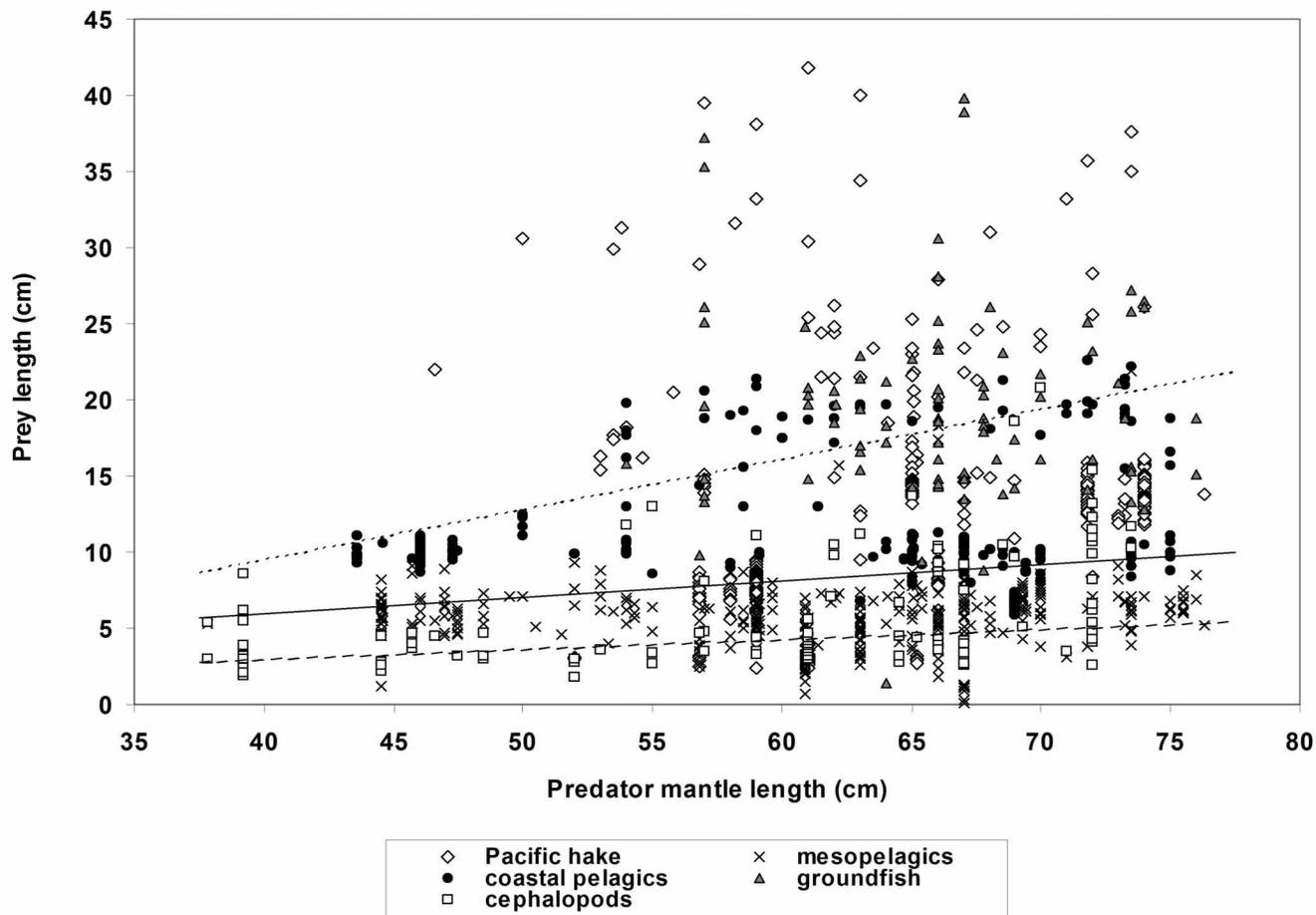
Figure 6. Jumbo squid (*Dosidicus gigas*) dorsal mantle length plotted against the standard length (for fish) and dorsal mantle length (for cephalopods) of 992 different prey items. Lines represent smoothed estimates of the 10th (dotted), 50th (solid line), and 90th (dashed) percentiles for predator length groups when dorsal mantle length was aggregated into 5 cm bins.

in that assemblage. This resulted in a diet composition (by mass) of 28% Pacific hake, 17% rockfish, 13% cephalopods, 7% mesopelagics, 6% anchovy and other forage fishes, 5% sardine, 1% mackerel, and 1% small flatfish (cannibalism was excluded from this model). Predators include the fisheries and pinnipeds discussed earlier, toothed whales[3], coastal sharks, and albacore (Pinkas et al. 1971). The abundance, consumption, and production parameters were based on Olson and Watters (2003), but do not affect the static model result.

The resulting food web model (fig. 7A) represents a plausible means of visualizing the role of adult jumbo squid in the California Current ecosystem. A compara-ble model of the ETP (Olson and Watters 2003), in which only predators with significant amounts of jumbo squid in their diets are highlighted, is also presented (fig. 7B). Although jumbo squid were not modeled inde-pendently of other cephalopods in the ETP, they do rep-resent a major fraction of the cephalopod biomass in that ecosystem, and parameters for cephalopods in the ETP model were based on data for jumbo squid (Nesis 1983; Ehrhardt 1991). Finally, Figure 8 presents the resulting model estimates of trophic levels (excluding producers and lower trophic level consumers) increasing from left to right along the *x*-axis, with estimates of production to biomass (PB) ratios on the *y*-axis. To some extent, PB ratios integrate life history characteristics of growth and mortality, and it is rapidly apparent that the relative PB ratio of cephalopods in the ETP is within the dis-tribution of PB values for many populations at compa-rable trophic levels, while in the California Current model the PB ratio of jumbo squid is considerably higher than populations at comparable trophic levels.

---

[3]Sperm whales (*Physeter catodon*) are key predators of jumbo squid throughout their usual range (Ruiz-Cooley et al. 2006 and references therein). Rissos dolphin (*Grampus griseus*) were observed in high numbers along the central California coast in 2005, particularly by CPFV vessels targeting squid, and the stomachs of several stranded animals contained very high numbers of jumbo squid beaks (J. Harvey, Moss Landing Marine Laboratory, Moss Landing, California, pers. comm.)

Figure 7. Food web models of the (A) Northern California Current and, (B) Eastern Tropical Pacific (ETP), with estimated trophic level along the y-axis. Jumbo squid (*Dosidicus gigas*) are in white and central (including other cephalopods in the ETP), known predators are in black, and prey items are in grey. The relative sizes of boxes are proportional to the log of their standing biomass, and the width of the lines represent relative energy flow, after Aydin et al. (2003).
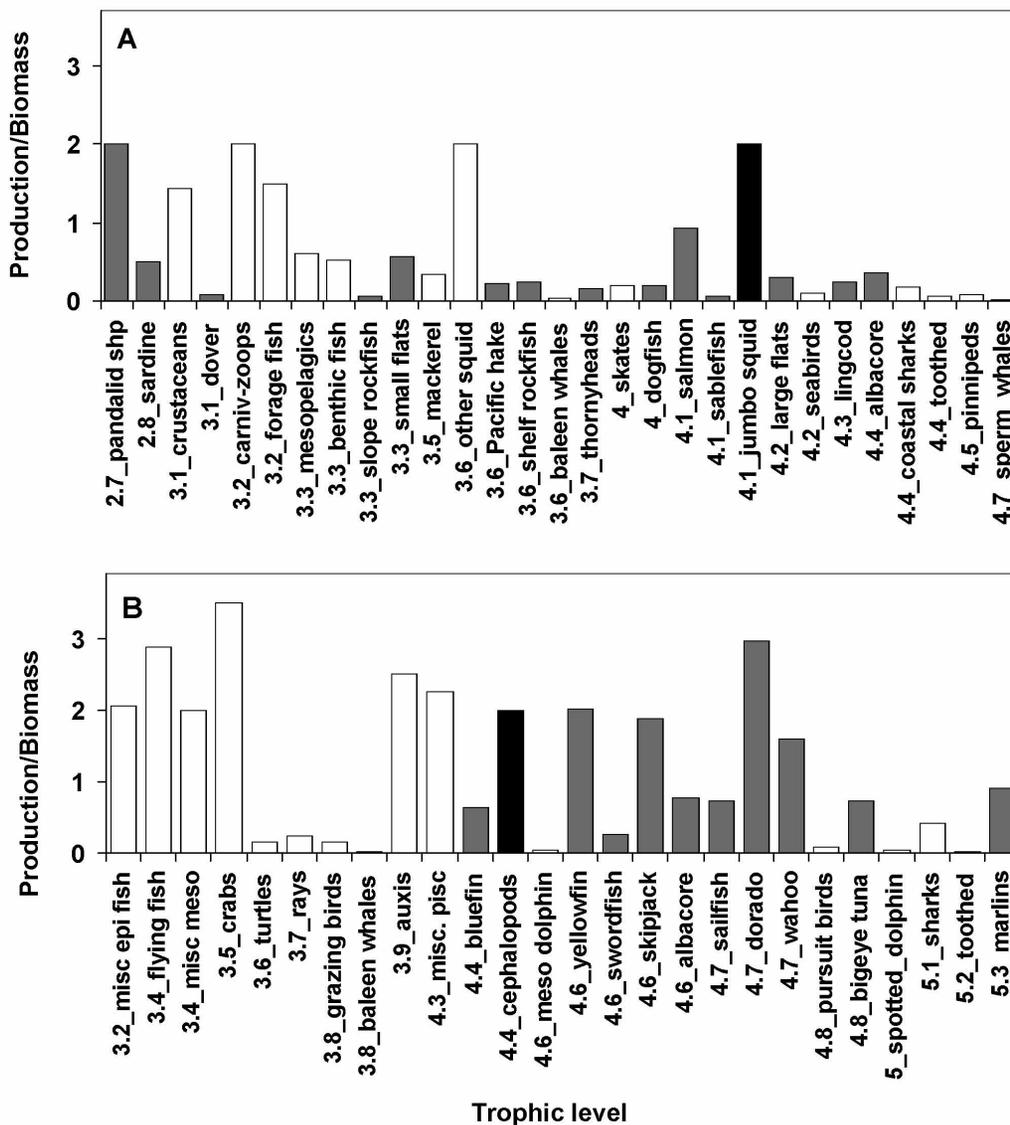
Figure 8.   Production to Biomass (PB) ratio plotted against trophic level for two Pacific Ocean ecosystem models, (A) the Eastern Tropical Pacific (ETP), and (B) the Northern California Current (NCC). Jumbo squid (*Dosidicus gigas*) (modeled with other squids in the ETP, but as a single component in the NCC) are designated in black, and grey boxes symbolize ecosystem components with the significant commercial or recreational fisheries landings.

DISCUSSION

Several studies have noted the rapid spread in the distribution and abundance of jumbo squid throughout the California Current over the past decade (Cosgrove 2005; Brodeur et al. 2006; Wing 2006), and the results shown here from recreational catches, food habits, resource surveys, and bycatch monitoring programs are highly consistent with these findings. Fishers targeting albacore (*Thunnus alalunga*) in offshore waters during late summer and fall have also reported that jumbo squid have been abundant in the tuna fishing grounds off of Washington and Oregon since at least the mid- to late-1990s. Off of central California there are similarities be-

tween the events in the mid 1930s and the 2002–06 period, with animals first showing up for several years in summer and fall months in the south, and later becoming more frequently encountered in fall and winter months over shelf break and slope habitats, particularly near canyons and offshore banks (Croker 1937). However, the extent of the northerly range expansion appears unprecedented, and raises questions about the abundance and distribution of this population in the future.

Food habits studies in general, and those for cephalopods in particular, suffer from a broad array of potential shortcomings and biases. The method of collection is clearly among these; for example, trawl gear

141

is generally a poor method for collecting specimens, as larger squids in particular tend to attack and ingest potentially atypical prey items while trapped within the codend of the trawl (Breiby and Jobling 1985). Such behavior has also been observed in jumbo squid caught in purse seine fishing operations, with squid attacking small tunas not otherwise known to be squid prey (Olson et al. 2006). Other biases may include changes in stomach fullness associated with both the time of day and the gear used in capture, as digestion and elimination of food is rapid and hungry squid may be more likely to attack jigs than satiated animals (Markaida and Sosa-Nishizaki 2003), as well as a potential to overestimate cannibalism as described earlier. Bias may also result when heads are not consumed in larger prey, and the size and shape of otoliths may also lead to variable retention rates (Dawe et al. 1997). Perhaps more significantly, the likelihood of underestimating the importance of soft-bodied organisms relative to organisms that leave hard remains can be a major source of bias (Tanasichuk 1999; Arai et al. 2003). For example, the frequent presence of pteropod shells suggests that other gelatinous zooplankton could also be important prey items, as has been observed (albeit infrequently) for other cephalopods (Heeger et al. 1992). Despite such shortcomings, the results presented here are unique relative to food habits studies from most other areas of the range of this animal.

Previous studies have shown that while jumbo squid are opportunistic predators, the primary prey of adults are smaller pelagic and mesopelagic fishes, other cephalopods (including other jumbo squid), and pelagic crustaceans (Wormuth 1976; Nesis 1983; Ehrhardt 1991; Nigmatullin et al. 2001; Markaida and Sosa-Nishizaki 2003; Markaida 2006). Our results are limited to a relatively narrow spatial and temporal window, yet they demonstrate that jumbo squid also prey quite heavily on moderately-sized (15–45 cm) groundfish. Submersible observations of squid predation on adult Pacific hake and sablefish (*Anoplopoma fimbria*) in the waters off of Cordell Bank in September 2005 also confirm this (R. Starr, California Sea Grant, Moss Landing, California and D. Howard, Cordell Bank National Marine Sanctuary, Point Reyes, California, pers. comm.). Consequently, these results diverge from those observed throughout most of the range of this animal, where consumption of large fish is minimal, and reflect the widely held perception of jumbo squid being a highly flexible predator with the ability to rapidly adapt to new environmental conditions during range expansions (Nesis 1983; Ehrhardt 1991; Nigmatullin 2001).

Although technically considered groundfish; Pacific hake, shortbelly rockfish, Pacific sanddab (*Citharichthys sordidus*), and slender sole (*Lyopsetta exilis*) are well known to have semi-pelagic life histories (Pearcy and Hancock

1978; Bailey et al. 1982; Chess et al. 1988), indicating that even in mid-latitude coastal waters jumbo squid may retain a foraging strategy focused on pelagic prey. However, the presence of more benthic-oriented animals, such as English sole (*Parophrys vetulus*), eelpouts (*Zoarcidae* spp.), and spotted ratfish (*Hydrolagus colliei*) in squid diets does indicate some predation on bottom-oriented prey, as did the submersible observations described above. Results also suggest that larger hake and rockfish may be more frequently consumed during winter months off of central California, consistent with the migratory pattern of Pacific hake, the observation that squid caught in winter months tend to be larger, and the suggestion that larger squid have a greater tendency to feed at higher trophic levels (Ruiz-Cooley et al. 2006).

Wilhelm (1954) noted that during range expansions in the southern hemisphere in the early part of the 20th century, jumbo squid off of the central portion of the Chilean coast (a latitudinal range similar to that of California) fed on Chilean hake (*Merluccius gayi gayi*) and ling (*Genypterus* spp.), among other prey. More recently, jumbo squid have again been observed in large numbers off of the central portion of the Chilean coast, along a latitudinal range similar to that of California (Ibáñanez and Cubillos 2007). As a consequence, predation on Chilean hake by jumbo squid has been described as potentially contributing to a decline in the hake resource in that region.[4] Rodhouse and Nigmatullin (1996) suggest that cephalopod predation is an important variable affecting natural mortality and recruitment success of many fish stocks, particularly clupeids, scombrids, and gadoids in continental shelf ecosystems, and this may be particularly true where there is a strong mismatch between subtropical and temperate life history strategies (e.g., growth rate, metabolism, swimming speed). Such impacts are also subject to high interannual variation due to the short lifespans and widely variable cohort strength that characterize most large oceanic squid populations.

Although the reorganization of energy pathways in coastal ecosystems as a result of fishing has been postulated as leading to increases in high turnover of cephalopod populations (Caddy and Rodhouse 1998), the coincidence of poleward range expansions of jumbo squid in both hemispheres suggests a physically-induced forcing mechanism. Climate change has already been shown to force the range expansions of many marine species towards the poles, with animals with the greatest turnover rates showing the most rapid distributional responses to warming (Perry et al. 2005). Observed

[4]Paya, I. Chilean Hake Stock Assessment. Institute for Fisheries Development (IFOP), 2005. Chile; H. Arancibia, Universidad de Concepción, Chile, pers. comm.

warming trends in the California Current (Mendelssohn et al. 2003; Field et al. 2006a), and the likelihood of continued warming in the future, may have facilitated the ongoing range expansion and could lead to the establishment of a permanent population or increased frequency of future incursions. However, the broad thermal tolerance of adult squid in the Gulf of California (Gilly et al. 2006) suggests that the mechanism responsible for the ongoing range expansion may not be as simplistic as changes in mean temperature alone.

Consideration of the role of jumbo squid in food web models suggests that while they tend to be predators of commercially important species in the California Current, they are principally prey to commercially important species in the ETP (figs. 7 and 8). Furthermore, the PB ratio of squid in the ETP is consistent with the distribution of PB values for many other model components in that subtropical ecosystem. By contrast, the PB ratio of jumbo squid in the California Current is anomalously high in an ecosystem that tends to be dominated by long-lived and slow-growing species at higher trophic levels. Currently there is insufficient information to estimate plausible or possible impacts on California Current food webs, due to a lack of abundance information and incomplete knowledge of how movement and food habits may differ across seasons and between inshore and offshore waters. However, that jumbo squid are opportunistic predators with high turnover rates and high consumption rates, and that among their important prey are several of the current (and historically) largest fisheries by volume along the U.S. West Coast, suggest that impacts are plausible. Such impacts could drive changes at both higher and lower trophic levels; for example Barlow and Forney (in press) show that the abundance of sperm whales (*Physeter macrocephalus*) in the California Current roughly doubled in 2001 and 2005 survey estimates, relative to those conducted in the 1990s. Future management approaches should recognize that fundamental changes in ecosystem structure and dynamics are likely to occur, particularly in the face of future global change. Quantifying trophic relationships represents an important contribution in understanding such interactions, and facilitating a rational response by managers and stakeholders.

ACKNOWLEDGEMENTS

REFERENCES

Anderson, M. E. 1978. Notes on the cephalopods of Monterey Bay, California with new records for the area. Veliger. 21:255–262.

Antonelis, G. A., and C. H. Fiscus. 1980. The Pinnipeds of the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 21:68–78.

Arai, M. N., D. W. Welch, A. L. Dunsmuir, M. C. Jacobs, and A. R. Ladouceur. 2003. Digestion of pelagic Ctenophora and Cnidaria by fish. Can. J. Fish. Aq. Sci. 60:825–829.

Assis, C. A. 1996. A generalized index for stomach contents analysis in fish. Scientia Marina 60:385-389.

Aydin, K. Y., G. A. McFarlane, J. R. King, and B. A. Megrey. 2003. The BASS/MODEL Report on trophic models of the subarctic Pacific basin ecosystems. N. Pac. Mar. Sci. Org. Rep 25. Sydney, CA. 97 pp.

Bailey, K. M., R. C. Francis, and P. R. Stevens. 1982. The life history and fishery of Pacific whiting, *Merluccius productus*. Calif. Coop. Oceanic Fish. Invest. Rep. 23:81–98.

Barlow, J., and K. A. Forney. In press. Abundance and density of cetaceans in the California Current ecosystem. U.S. Fish. Bull.

Berry, S. S. 1912. A review of the cephalopods of Western North America. Bull. Bur. Fish. Wash. 30:269–336.

Breiby, A., and M. Jobling. 1985. Predatory role of the flying squid (*Todarodes sagittatus*) in north Norwegian waters. NAFO Sci. Coun. Stud. 9:125–132.

Brodeur, R. D., S. Ralston, R. L. Emmett, M. Trudel, T. D. Auth, and A. J. Phillips. 2006. Anomalous pelagic nekton abundance, distribution, and apparent recruitment in the northern California Current in 2004 and 2005. Geophysical Research Letters 33 doi:10.1029/2006GL026614.

Caddy, J. F., and P. G. Rodhouse. 1998. Cephalopod and groundfish landings: evidence for ecological change in global fisheries? Rev. Fish Bio. Fish. 8:431–444.

Chess, J. R., S. E. Smith, and P. C. Fischer. 1988. Trophic relationships of the shortbelly rockfish, *Sebastes jordani*, off central California. Calif. Coop. Oceanic Fish. Invest. Rep. 29:129–136.

Clarke, M. R. 1986. A handbook for the identification of cephalopod beaks. Clarendon Press: Oxford. 273 p.

Clark, F. N., and J. B. Phillips. 1936. Commercial use of the jumbo squid, *Dosidicus gigas*. Cal. Dep. Fish Game Fish Bull. 22:143–144.

Cosgrove, J. A. 2005. The first specimens of Humboldt squid in British Columbia. PICES Press 13:2:30–31.

Croker, R. S. 1937. Further notes on the jumbo squid, *Dosidicus gigas*. Cal. Dep. Fish Game Fish Bull. 23:246–247.

Dawe, E. G., E. L. Dallet, and W. W. Lidster. 1997. Fish prey spectrum of short-finned squid (*Illes illecebrosus*) at Newfoundland. Can. J. Fish. Aq. Sci. 54 (Suppl. 1):200–208.

Ehrhardt, N. M. 1991. Potential impact of a seasonal migratory jumbo squid (*Dosidicus gigas*) stock on a gulf of California sardine (*Sardinops sagax caerulea*) population. Bull. Mar. Sci. 49:325–332.

Field, D. B., T. R. Baumgartner, C. D. Charles, V. Ferreira-Bartrina, and M. D. Ohman. 2006a. Planktonic foraminifera of the California Current reflect 20th-century warming. Science 311:63–66.

Field, J. C., R. C. Francis, and K. Aydin. 2006b. Top-down modeling and bottom–up dynamics: linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. Prog. Oceanogr. 68:238–270.

Fitch, J. E. 1964. The fish fauna of the Playa del Rey locality, a southern California marine Pleistocene deposit. Los Angeles County Mus. Nat. Hist., Contribs. in Sci. 82:1–35.

Fitch, J. E. 1969. Fossil lanternfish otoliths of California, with notes on fossil Myctophidae of North America. Los Angeles County Museum of Nat. Hist., Contribs. in Sci. 173. 20 pp.

Fitch, J. 1974. California coast squid invasion. Smithsonian Institute Center Shortlived Phenomena Event Notification Report 99–74: Card No. 1900–1901.

Gilly, W. F., U. Markaida, C. H. Baxter, B. A. Block, A. Boustany, L. Zeidberg, K. Reisenbichler, B. Robison, G. Bazzino, and C. Salinas. 2006. Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. Mar. Eco. Prog. Ser. 324:1–17.

Harvey, J. T. 1989. Food habits, seasonal abundance, size, and sex of the blue shark, *Prionace glauca*, in Monterey Bay, California. Cal. Dep. Fish Game Fish Bull. 75:33–44.

Harvey, J. T., T. R. Loughlin, M. A. Perez, D. S. Oxman. 2000. Relationship between fish size and otolith length for 63 species of fishes from the Eastern North Pacific Ocean. NOAA Tech. Rep. NMFS 150. 36 pp.

Heeger, T., U. Piatkowski, and H. Möller. 1992. Predation on jellyfish by the cephalopod *Argonauta argo*. Mar. Eco. Prog. Ser. 88:293–296.

Ibáñanez, C. M., and L. A. Cubillos. 2007. Seasonal variation in the length structure and reproductive condition of the jumbo squid *Dosidicus gigas* (d'Orbigny, 1835) off central-south Chile. Sci. Mar. 71:123–128.

Lowry, M. S., and J. V. Carretta. 1999. Market squid (*Loligo opalescens*) in the diet of California Sea Lions (*Zalophus californianus*) in southern California (1981–1995). Calif. Coop. Oceanic Fish. Invest. Rep. 40:196–207.

Markaida, U. 2006. Food and feeding of jumbo squid *Dosidicus gigas* in the Gulf of California and adjacent waters after the 1997–98 El Niño event. Fish. Res. 79:16–27.

Markaida, U., and O. Sosa-Nishizaki. 2003. Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephihdae) from the Gulf of California, Mexico. J. Mar. Bio. Assn. U.K. 83:507–522.

Markaida, U., J. J. C. Rosenthal, and W. F. Gilly. 2005. Tagging studies on the jumbo squid (*Dosidicus gigas*) in the Gulf of California, Mexico. U.S. Fish. Bull. 103:219–226.

McGowan, J. A. 1968. Thecosomata and Gymnosomata. Veliger 3 (supp2):103–135.

Mearns, A. J. 1988. The "odd fish": unusual occurrences of marine life as indicators of changing ocean conditions. *In* Marine Organisms as Indicators, D. F. Soule and G. S. Kleppel, eds. New York: Springer-Verlag, pp. 137–176.

Mendelssohn, R., F. B. Schwing, S. J. Bograd. 2003. Spatial structure of subsurface temperature variability in the California Current, 1950–1993. J. Geophys. Res. 108:3093.

Nesis, K. N. 1983. *Dosidicus gigas*. *In* Cephalopod life styles, Vol. 1. Species Accounts. P. R. Boyle, ed. London: Academic Press, pp. 216–231.

Nigmatullin, Ch. M., K. N. Nesis, and A. I. Arkhipkin. 2001. A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae). Fish. Res. 54:9–19.

O'dor, R. K. 1992. Big squid in big currents. S. Afr. J. Mar. Sci. 12:225–235.

Olson, R. J., and G. M. Watters. 2003. A model of the pelagic ecosystem in the Eastern Tropical Pacific Ocean. Inter-Amer. Trop. Tuna Com. Bull. 22:3:135–218.

Olson, R. J., M. H. Roman-Verdesoto, G. L. Macias-Pita. 2006. Bycatch of jumbo squid *Dosidicus gigas* in the tuna purse-seine fishery of the eastern Pacific Ocean and predatory behavior during capture. Fish. Res. 79:48–55.

Pearcy, W. G. 2002. Marine nekton off Oregon and the 1997-98 El Niño. Prog. Oceanogr. 54:399–403.

Pearcy, W. G., and D. Hancock. 1978. Feeding habits of Dover Sole, (*Microstomus pacificus*), Rex sole (*Glyptocephalus zachirus*); slender sole (*Lyopsetta exilis*); and Pacific sanddab (*Citharichthys sordidus*), in a region of diverse sediments and bathymetry off Oregon. U.S. Fish. Bull. 76:641–662.

Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. Science 308:1912–1915.

Phillips, J. B. 1933. Description of a giant squid taken at Monterey, with notes on other squid taken off the California coast. Cal. Dep. Fish Game Fish Bull. 19:129–136.

Phillips, J. B. 1961. Two unusual cephalopods taken near Monterey. Cal. Fish. Game 47:416–418.

Pinkas, L., M. S. Oliphant, and I. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Cal. Dep. Fish Game Fish Bull. 152. 105 pp.

Preti, A., S. E. Smith, and D. A. Ramon. 2004. Diet differences in the thresher shark (*Alopias vulpinus*) during transition from a warm-water regime to a cool-water regime off California-Oregon, 1998-2000. Calif. Coop. Oceanic Fish. Invest. Rep. 45:118–125.

Rodhouse, P. G., and Ch. M. Nigmatullin. 1996. Role as consumers. Philosophical Transactions of the Royal Society London 351:1003–1022.

Ruiz-Cooley, R. I., U. Markaida, D. Gendron, and S. Aguiniga. 2006. Stable isotopes in jumbo squid (*Dosidicus gigas*) beaks to estimate its trophic position: comparison between stomach contents and stable isotopes. J. Mar. Biol. Assn. U.K. 86:437–445.

Sakuma, K. M., S. Ralston, and V. G. Wespestad. 2006. Interannual and spatial variation in the distribution of young-of-the-year rockfish (*Sebastes* spp.): expanding and coordinating a survey sampling frame. Calif. Coop. Oceanic Fish. Invest. Rep. 47:199–126.

Tanasichuk, R. W. 1999. Interannual variation in the availability and utilization of euphausiids as prey for Pacific hake (*Merluccius productus*) along the southwest coast of Vancouver Island. Fish. Oceanogr. 8:150–156.

Tricas, T. C. 1979. Relationships of the blue shark, *Prionace glauca*, and its prey species near Santa Catalina Island, California. U.S. Fish. Bull. 77:175–182.

Wilhelm, O. 1954. Algunas observaciones acerca de las mortandades de jibias (*Dosidicus gigas* D'Orb.), en el litoral de Concepción. Rev. Biol. Mar., 4:196–201.

Wing, B. L. 2006. Unusual invertebrates and fish observed in the Gulf of Alaska, 2004–2005. PICES Press 14:2:26–28.

Wolff, G. A. 1984. Identification and estimation of size from the beaks of 18 species of cephalopods from the Pacific Ocean. NOAA Tech. Rep. NMFS 17.

Wormuth, J. H. 1976. The biogeography and numerical taxonomy of the oegopsid squid family Ommastrephidae in the Pacific Ocean. Bull. Scripps. Inst. Oceanogr. 23. 90 pp.

Wyllie Echeverria, T. 1987. Relationship of otolith length to total length in rockfishes from Northern and Central California. U.S. Fish. Bull. 85:383–387.

APPENDIX A

Taxonomic summary of prey, with the frequency of occurrence (FO), total number, and size (average length in cm, weight in gm, range of length and weight) where available. Broad groupings include mesopelagics (MS), coastal pelagics (CP), crustaceans (CR), rockfish (RK), pteropods (PT), cephalopods (CE), flatfish (FL), and other (OT).

Taxa	group	GII	%FO	%N	FO	N	length mean	range	weight mean	range
Arthropoda										
Crustacea										
Decapoda	CR	4.4	4.5	1.8	19	26	–	–	–	–
Euphausidae	CR	N/A	9.0	N/A	38	N/A	–	–	–	–
Mollusca										
Pteropoda										
Clio sp. cf *C. pyrimida*	PT	7.5	7.8	2.8	33	41	–	–	–	–
Cresis sp.	PT	1.1	1.2	0.4	5	6	–	–	–	–
Limacina sp.	PT	0.4	0.5	0.1	2	2	–	–	–	–
Cephalopoda										
Enoploteuthidae										
Abraliopsis felis	CE	2.4	2.4	1.0	10	14	4	2–8	3	<1–15
Ommastrephidae										
Dosidicus gigas	CE	N/A	11.4	N/A	49	N/A	–	–	–	–
Onchyoteuthidae										
Onychoteuthis borealijaponicus	CE	3.9	2.6	2.9	11	42	4	3–13	11	2–136
Loliginidae										
Loligo opalescens	CE	3.2	3.1	1.5	13	22	11	9–15	23	14–42
Gonatidae										
Gonatus onyx	CE	1.8	0.9	1.6	4	23	4	2–9	2	<1–19
Gonatus berryi	CE	1.1	0.9	0.6	4	9	5	6	10	40
Gonatopsis borealis	CE	0.9	0.9	0.3	4	5	–	–	–	–
Gonatus spp.	CE	2.3	1.9	1.3	8	19	–	–	–	–
Histioteuthidae										
Histioteuthis hoylei	CE	0.4	0.5	0.1	2	2	14	7–21	91	8–173
Cranchidae										
Cranchia scabra	CE	0.3	0.2	0.1	1	2	–	–	–	–
Galiteuthis sp. cf *G. phyllura*	CE	0.2	0.2	0.1	1	1	–	–	–	–
Chiroteuthidae										
Chiroteuthis calyx	CE	0.2	0.2	0.1	1	1	3	–	20	–
Octopoteuthidae										
Octopoteuthis deletron	CE	2.4	2.6	0.8	11	11	10	4–19	269	24–792
Argonautidae										
Argonauta sp.	CE	0.4	0.5	0.1	2	2	–	–	–	–
Cephalopoda unidentified	CE	5.9	6.4	2.0	27	29	–	–	–	–
Chordata										
Chondrichthyes										
Chima eridae										
Hydrolagus colliei	OT	0.2	0.2	0.1	1	1	31	–	1873	–
Osteichthyes										
Clupeidae										
Clupea pallasii	CP	1.3	1.4	0.4	6	6	18	16–19	84	51–106
Sardinops sagax	CP	9.2	9.7	3.4	41	49	19	13–23	54	16–97
Engraulidae										
Engraulis mordax	CP	19.9	16.3	11.9	69	173	10	6–13	12	4–23
Argentinidae										
Nansenia sp. cf. *N. crassa*	MS	0.3	0.2	0.1	1	2	–	–	–	–
Bathylagidae	MS	2.5	2.6	1.0	11	14	–	–	–	–
Bathylagus wesethi	MS	0.4	0.5	0.1	2	2	–	–	–	–
Bathylagus pacificus	MS	0.2	0.2	0.1	1	1	–	–	–	–
Leuroglossus stilbius	MS	0.6	0.7	0.2	3	3	–	–	–	–
Lipolagus ochotensis	MS	0.2	0.2	0.1	1	1	–	–	–	–
Stomiidae										
cf. *Tactostoma macropus*	MS	1.0	0.9	0.4	4	6	–	–	–	–
Scopelarchidae										
Benthalbella dentata	MS	0.2	0.2	0.1	1	1	–	–	–	–
Paralepididae	MS	1.9	2.1	0.6	9	9	–	–	–	–
Arctozenus risso	MS	1.5	1.2	0.9	5	13	–	–	–	–
Lestidiops ringens	MS	0.9	0.9	0.3	4	4	–	–	–	–
Magnisudis sp. cf. *M. atlantica*	MS	0.2	0.2	0.1	1	1	–	–	–	–
Myctophidae										
Ceratoscopelus townsendi	MS	2.2	2.4	0.8	10	11	3	2–6	4	<1–9
Diaphus theta	MS	8.3	6.9	4.9	29	71	4	<1–9	2	<1–11
Nannobrachium ritteri	MS	6.3	5.7	3.3	24	48	4	1–8	2	<1–15

APPENDIX A (continued)

Taxonomic summary of prey, with the frequency of occurrence (FO), total number, and size (average length in cm, weight in gm, range of length and weight) where available. Broad groupings include mesopelagics (MS), coastal pelagics (CP), crustaceans (CR), rockfish (RK), pteropods (PT), cephalopods (CE), flatfish (FL), and other (OT).

Taxa	group	GII	%FO	%N	FO	N	length mean	range	weight mean	range
Protomyctophum crockeri	MS	1.0	0.9	0.4	4	6	–	–	–	–
Symbolophorus californiensis	MS	3.6	3.8	1.4	16	20	8	7–9	7	4–11
Stenobrachius leucopsarus	MS	21.5	20.1	10.3	85	150	6	2–9	2	<1–5
Tarletonbeania crenularis	MS	15.3	13.5	8.2	57	119	6	2–8	4	<1–9
Merlucciidae										
Merluccius productus	PH	30.9	22.7	20.9	96	305	13	2–42	39	<1–520
Ophidiidae										
Chilara taylori	OT	0.2	0.2	0.1	1	1	–	–	–	–
Zoarcidae										
Bothrocara brunneum	OT	0.2	0.2	0.1	1	1	–	–	–	–
Lycodes sp. cf *L. pacificus*	OT	0.2	0.2	0.1	1	1	–	–	–	–
Batrachoididae										
Porichthys notatus	MS	1.0	0.9	0.4	4	6	15	9–22	74	14–168
Scomberesocidae										
Cololabis saira	CP	0.7	0.7	0.3	3	5	–	–	–	–
Melamphaidae										
Melamphaes lugubris	MS	0.2	0.2	0.1	1	1	9	–	3	–
Melamphaes sp. cf. *M. lugubris*	MS	0.6	0.7	0.2	3	3	–	–	–	–
Scopelogadus mizolepis bispinosus	MS	0.2	0.2	0.1	1	1	–	–	–	–
Scorpaenidae										
Sebastes aurora	RK	0.9	0.9	0.3	4	4	21	13–27	285	69–471
S. jordani	RK	8.6	8.7	3.4	37	50	20	14–28	109	32–289
S. paucispinis	RK	0.2	0.2	0.1	1	1	13		79	
S. rufus	RK	0.3	0.2	0.1	1	2	36	35–37	968	904–1032
S. zacentrus	RK	0.3	0.2	0.1	1	2	–	–	–	–
Sebastes spp.	RK	5.4	5.9	1.7	25	25	–	–	–	–
Carangidae										
Trachurus symmetricus	CP	0.2	0.2	0.1	1	1	22	–	198	–
Embiotocidae										
Zalembius rosaceus	OT	0.5	0.5	0.2	2	3	10	10–11	147	143–151
Gempylidae										
Gempylus sp. cf *G. serpens*	MS	0.2	0.2	0.1	1	1	–	–	–	–
Scombridae										
Scomber japonicus	CP	0.6	0.7	0.2	3	3	19		223	
Bothidae										
Citharichthys sordidus	FL	1.9	1.7	1.0	7	14	17	13–21	85	39–133
Pleuronectidae										
Lyopsetta exilis	FL	1.3	1.4	0.5	6	7	15	18	45	77
Glyptocephalus zachirus	FL	0.2	0.2	0.1	1	1	25	–	139	–
Parophrys vetulus	FL	0.2	0.2	0.1	1	1	14	–	43	–
Unidentified Osteichthyes	OT	8.1	8.5	2.9	36	42	–	–	–	–
Aves (bird feathers)	OT	0.4	0.5	0.1	2	2	–	–	–	–