

## The Role of the Neon Flying Squid, *Ommastrephes bartrami*, in the North Pacific Pelagic Food Web

by

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### I. ABSTRACT

Trophic relationships of neon flying squid, *Ommastrephes bartrami*, are examined during their summer occupation of waters within the Subarctic Frontal Zone and after their spawning migration south to subtropical waters. An examination of 174 stomachs from driftnet-caught *O. bartrami* near the Subarctic Boundary revealed many squid with empty stomachs and a high incidence of cannibalism. Squid with stomach contents fed exclusively on fishes (mainly micronektonic mesopelagic myctophids and stomiiformes) and other cephalopods. No significant difference was found between the diets (nor the degree of cannibalism) of *O. bartrami* when the stomach contents of squid taken near the Subarctic Boundary were compared with those of mature females collected during the winter in the subtropics.

Stomach contents are also described for blue sharks, *Prionace glauca*, captured by surface longlines in the North Pacific Transition Zone. Their most important diet items were myctophids, small gonatid squids, and *O. bartrami*. *Ommastrephes bartrami*, however, appeared important only among the larger sharks caught.

Results of these diet studies are discussed together with a review of pertinent literature to clarify the role of *O. bartrami* in the North Pacific pelagic food web.

### II. INTRODUCTION

Pelagic cephalopods are important both to commercial fisheries (Roper *et al.* 1984) and for their role within oceanic ecosystems. Epipelagic squids in particular are major components of oceanic food webs (Hedgepeth 1983). Considerable interest has been focused on the flying squid, *Ommastrephes bartrami*, an oceanic species found throughout temperate and subtropical regions worldwide and now the target of international driftnet fishing fleets (Roper *et al.* 1984; Murata 1990). Presently, little is known regarding the

role of *O. bartrami* in the North Pacific pelagic food chain; such information, however, is an important consideration in any evaluation of the fishery's effects on the ecosystem.

The diets of *O. bartrami* and various fish species are being studied to understand trophic relationships in the central North Pacific ecosystem. Preliminary results of *O. bartrami* feeding habits during winter occupation of subtropical waters and their trophic relationship with swordfish, *Xiphias gladius*, were presented in Seki (in press). The intent of the present paper is threefold: to provide comparative information on the diet of *O. bartrami* taken near the Subarctic Boundary in the Subarctic Frontal Zone (SAFZ) during the summer fishing season; to present results on the feeding habits of a major predator, the blue shark (*Prionace glauca*), in the SAFZ; and to discuss these results, together with a review of pertinent literature, to clarify the role of *O. bartrami* in the North Pacific pelagic food web.

### III. MATERIALS AND METHODS

A total of 174 *O. bartrami* were collected from 18 sets of research gillnet during July-August 1990 aboard the research vessel *Shōyō maru* in waters of the SAFZ (Fig. 1). The gillnet was typically set around dusk and retrieved the ensuing morning. Although the gillnet was composed of varying mesh sizes (range = 48 to 157 mm stretch mesh), most of the flying squid were captured in 115 mm netting. Specifications of the fishing gear were described in Seki (1990). Squid ranging in dorsal mantle length from 163 to 490 mm ( $\bar{L}$  = 322 mm, SD = 98.1) were frozen upon capture and returned to the laboratory for analysis. All of the squid were reproductively immature; 122 were females, 49 were males, and 3 were unsexed.

In the laboratory, frozen squid were thawed; stomachs were extracted and examined for the presence of food items. Empty stomachs were noted and discarded.

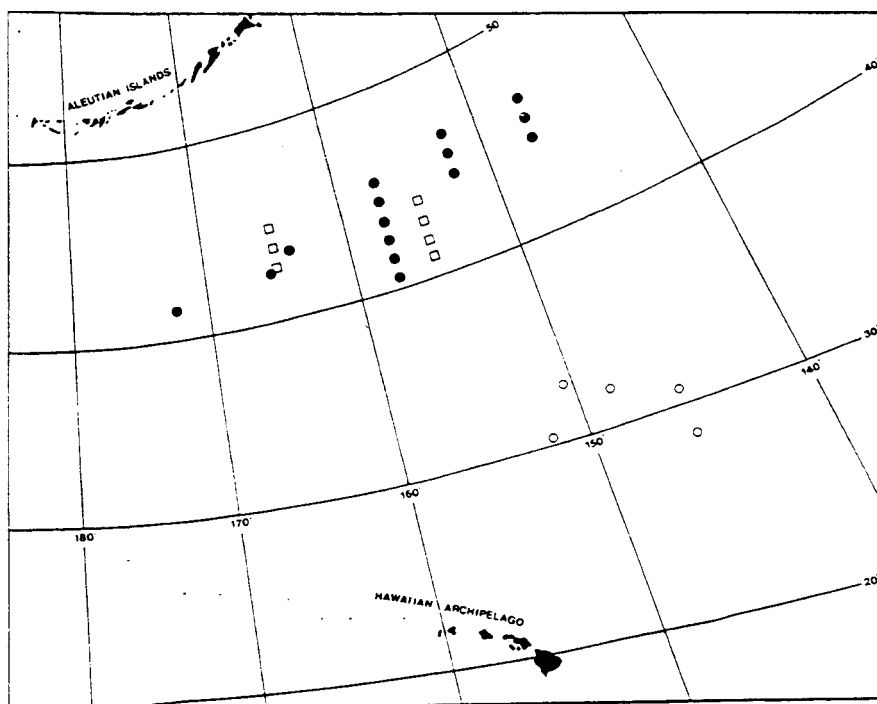


Fig. 1. Capture locations of *Ommastrephes bartramii* and *Prionace glauca* examined for analysis of stomach contents. Filled circles are summer *O. bartramii* collected by the research vessel *Shōyō maru*, open circles are winter *O. bartramii* collected by the research vessel *Shinriasu maru* (from Seki in press), and open squares are *P. glauca* collected via surface longlines by the NOAA ship *Townsend Cromwell*.

Stomachs with food items were fixed in a 10% phosphate-buffered formalin solution (Hunter 1985) and then transferred within 24 h to 50% isopropanol for preservation and storage. During processing, stomach contents were emptied into a 0.333 mm Nitex strainer, rinsed under running water, and sorted into identifiable groups. Sorted food items were blotted dry, and wet weights were measured to the nearest 0.1 g. Prey were identified to the lowest possible taxon; however, since stomach contents of cephalopods are normally minced into small fragments and are often well digested (Boucher-Rodoni *et al.* 1987), most of the food items were only classifiable into broad taxonomic categories. Cephalopod prey were identified primarily from suckers, hooks, beaks, and gladii; and fishes from vertebrae, teeth, epidermis, and otoliths. These stomach contents from squid captured in the SAFZ during summer were compared with similar feeding data from squid taken during the winter in subtropical

waters (Fig. 1) (Seki in press), using the approach developed by Somerton (1991) to statistically detect seasonal differences in diets. Briefly, this approach (named DIETTEST) calculates variance and covariance of the gravimetric proportions for each prey group within each sample and subsequently measures between-sample differences utilizing Hotelling's  $T^2$  statistic. For this test, *O. bartramii* stomach contents data were classified into three broad prey groups: fishes, squid, and cannibalized *O. bartramii*. The statistical significance of the measure was then determined from an empirical probability distribution of  $T^2$  computed through randomization (Somerton 1991). Two thousand iterations of randomization were used on the present data set.

To provide additional information on the ecosystem dynamics of the region, food habit studies were also initiated on some fish species that are incidentally caught in the high seas driftnet fisheries targeting *O.*

*bartrami*. Included among these fishes is the blue shark, *Prionace glauca*. A total of 72 blue sharks 42.9-154.5 cm precaudal length (PCL),  $\bar{L} = 73.6$  cm PCL,  $SD = 32.9$ ) were collected via surface longlines by the NOAA ship *Townsend Cromwell* within waters of the SAFZ during October 1989 (Fig. 1). Longlines were normally set just prior to sunrise and hauled about an hour after dawn. Upon capture, sharks were measured and stomachs extracted and examined for food items. Empty stomachs were noted and discarded; stomachs with food items were preserved in 10% formalin and returned to the laboratory for analysis. Laboratory procedures for the stomach analysis were similar to those described above for *O. bartrami*.

The index of relative importance (IRI) modified from Pinkas *et al.* (1971) was employed to assess the relative value of prey items. The IRI incorporates percentage by number (N), weight (W), and frequency of occurrence (F):  $IRI = \%F(\%N + \%W)$ .

#### IV. RESULTS

Thirty-seven of the 174 *O. bartrami* stomachs examined contained prey. By weight, stomach contents ranged from 0.1 to 40.4 g ( $\bar{W} = 15.7$  g;  $SD = 12.1$ ) and were composed entirely of cephalopods (51.8%) and fishes (48.2%) (Table 1).

Cephalopods occurred in 67.6% of the stomach samples. Although much of the cephalopod material was not identified, at least 56.9% by weight can be attri-

buted to cannibalized *O. bartrami*. This cannibalism was found in 29.7% of the squid examined (i.e., those with some stomach contents) and represented 29.5% of the total aggregate weight of prey. Some teuthoid prey possessed several varieties of arm and tentacular hooks (probably from the families Gonatidae, Enoploteuthidae, and Onychoteuthidae) and were grouped together since they could be distinguished from the cannibalized material. These squid, normally well digested, made up 8.7% of the cephalopod food items by weight.

Fish remains were found in 62.2% of the stomachs and were typically in an advanced state of digestion. The identified fishes were composed of micronektonic myctophid and stomiiform fishes and the Pacific saury, *Cololabis saira*. As many as eight pairs of myctophid otoliths were recovered from a single stomach.

In the two-tailed probability tabulation, no significant difference was found between the summer and winter diets of *O. bartrami* ( $T^2 = 0.7775$ ; 3 tests;  $\alpha = 0.05$ ). Comparative proportions of the major prey classes for the two seasons and localities are presented in Figure 2.

Thirty-two of the 72 blue shark stomachs examined contained some prey; stomach contents averaged 2.7 prey items ( $SD = 1.8$ ) weighing 109.0 g ( $SD = 249.2$ ) (Table 2). Fishes and cephalopods composed nearly all of the diet. Lanternfishes of the family Myctophidae (%IRI = 46.1), *O. bartrami* (%IRI = 29.3), and gonatid squids (%IRI = 14.8) were the most important dietary components based upon percent of IRI.

Table 1. Diet composition of 37 *Ommastrephes bartrami* captured in gillnets near the North Pacific Subarctic Boundary, July-August 1990.

PREY SPECIES	WEIGHT (G)	PERCENT WEIGHT	FREQUENCY	PERCENT FREQUENCY
<b>Cephalopods</b>				
<i>Ommastrephes bartrami</i>	170.5	29.5	11	29.7
Unidentified teuthoids (with hooks)	26.0	4.5	4	10.8
Unidentified Cephalopoda	103.2	17.8	15	40.5
Total	299.7	51.8	25	67.6
<b>Fishes</b>				
Myctophidae	47.5	8.2	8	21.6
Stomiiformes	13.3	2.3	2	5.4
<i>Cololabis saira</i>	33.7	5.8	1	2.7
Unidentified fishes	184.6	31.9	12	32.4
Total	279.1	48.2	23	62.2

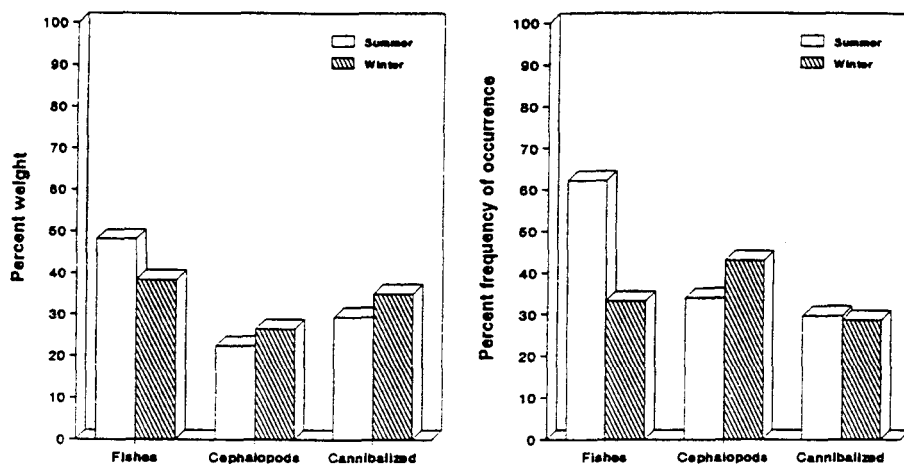


Fig. 2. Comparative proportions, by weight and by frequency of occurrence, of major prey classes in diets of *Ommastrephes bartrami* captured during summer in the Subarctic Frontal Zone ( $n = 37$ ) and during winter in the subtropics ( $n = 42$ ).

Table 2. Stomach contents of blue shark, *Prionace glauca* ( $n = 32$ ), captured by surface longlines in the Subarctic Frontal Zone (IRI = index of relative importance).

PREY ITEMS	NO.	%	WEIGHT	%	FREQUENCY	%	IRI	%
<b>Fishes</b>								
Sternoptychidae								
<i>Argyroleucosp.</i>	1	1.15	2.9	0.08	1	3.13	3.85	0.1
Myctophidae	34	39.08	60.0	1.73	17	53.13	2167.93	46.1
Alepisauridae								
<i>Alepisaurus ferox</i>	1	1.15	240.3	6.92	1	3.13	25.22	0.5
Bramidae								
<i>Brama japonica</i>	2	2.30	418.4	2.05	2	6.25	89.67	1.9
Pentaceroptidae								
<i>Pseudopentaceros wheeleri</i>	1	1.15	226.4	6.52	1	3.13	23.96	0.5
Gempylidae	1	1.15	106.4	3.06	1	3.13	13.17	0.3
Unidentified fishes	6	6.90	283.2	8.15	4	12.50	188.14	4.0
<b>Cephalopods</b>								
Ommastrephidae								
<i>Ommastrephes bartrami</i>	8	9.20	1865.8	53.73	7	21.88	1376.41	29.3
Onychoteuthidae	3	3.45	37.3	1.07	3	9.38	42.40	0.9
Gonatidae	24	27.59	6.1	0.18	8	25.00	694.05	14.8
Ocythoidae								
<i>Ocythoe tuberculata</i>	1	1.15	209.4	6.03	1	3.13	22.43	0.5
Unidentified squid	3	3.45	14.3	0.41	3	9.38	36.19	0.8
<b>Others</b>								
Lophogastridae								
<i>Gnathophausia</i> sp.	2	2.30	2.3	0.07	2	6.25	14.81	0.3
<b>Total</b>	<b>87</b>	<b>100.00</b>	<b>3472.8</b>	<b>100.00</b>	<b>—</b>	<b>—</b>	<b>4698.23</b>	<b>100.0</b>

Figure 3 presents the diet composition of blue sharks when grouped into two size modes:  $\leq 65$  cm and  $> 65$  cm PCL. Twelve of the 25 stomachs from sharks  $> 65$  cm PCL contained food, including all of the *O. bartrami* recorded as prey in this study. Forty-seven of the sharks were  $\leq 65$  cm PCL; 27 had empty stomachs. Micronektonic myctophids and small gonatids dominated prey consumed by the smaller sharks.

## V. DISCUSSION

In the North Pacific Ocean, *O. bartrami* are generally distributed between  $25^{\circ}$  and  $50^{\circ}$ N latitude (Roper *et al.* 1984), and exhibit extensive seasonal horizontal and diel vertical migrations. During late spring, *O. bartrami* migrate from presumed winter

spawning grounds in the Subtropical Domain northward to feeding grounds near the Subarctic Boundary in the SAFZ. Reverse migration occurs during autumn through early winter (Araya 1983; Gong 1985; Murata *et al.* 1988; Murata 1990). Recent studies employing ultrasonic telemetry have revealed that *O. bartrami* occupy waters within 100 m of the surface at night, vertically migrating to waters below 400 m (often to depths of  $> 700$  m) where they remain during the day (Nakamura *in press*). The wide-ranging habitat of the species would seem to make *O. bartrami* highly susceptible to numerous predators, and consequently, their trophic relationships are quite complex. Nevertheless, understanding the role of *O. bartrami* in the North Pacific pelagic food web is critical in the evaluation of the ecosystem effects of the high seas driftnet fishery.

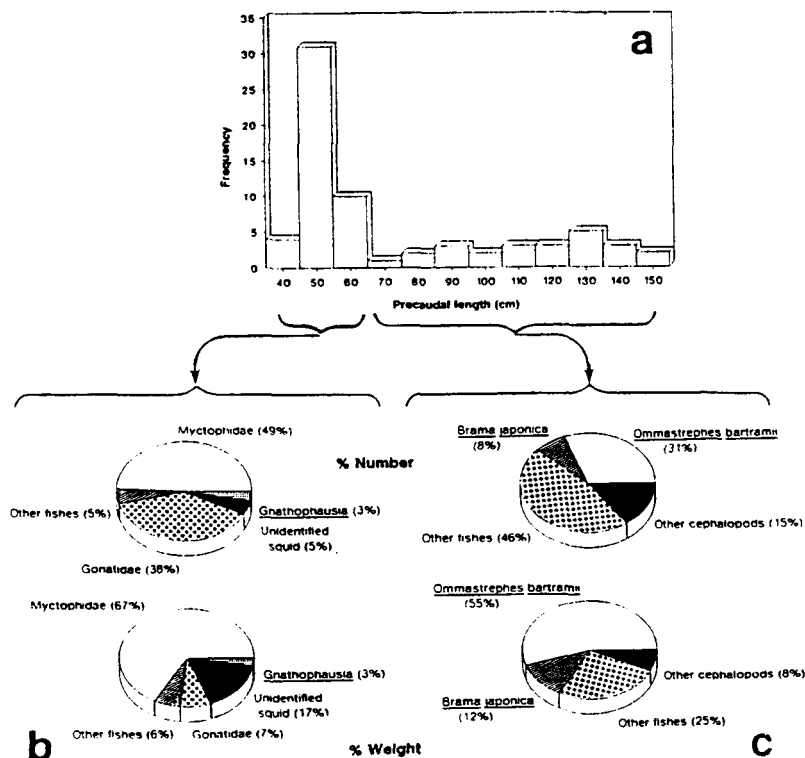


Fig. 3. Length frequency (a) and comparison of diet composition in blue sharks, *Prionace glauca*,  $\leq 65$  cm precaudal length (b) and  $> 65$  cm PCL (c) taken by surface longlines near the Subarctic Boundary.

*Ommastrephes bartrami*, like most teuthoids in general, are nonselective, active carnivores (Boucher-Rodoni *et al.* 1987) and, in the present study, fed totally on fishes and squid. Jig-caught *O. bartrami* in the western North Pacific also fed primarily on fishes and secondarily on squid (Naito *et al.* 1977; Araya 1983). Fishes included lanternfishes and small pelagics (e.g., sardines, juvenile mackerel, and saury); identified squids were the euploteuthin *Watasenia scintillans*; boreal clubhook squid, *Onychoteuthis borealijaponica*; and cannibalized *O. bartrami*. Crustaceans, such as euphausiids and hyperiid amphipods, were found occasionally among flying squid stomach contents in these temperate studies, but this result was attributed to the inclusion of smaller, immature squid that tend to feed more readily on plankton (Murata 1990). Fishes and cephalopods were the predominant prey of large female *O. bartrami* taken in subtropical central North Pacific waters (Seki 1991). Most of the cephalopod prey were attributed to cannibalism; however, the possibility that the cannibalism was an artifact induced by sampling techniques was suggested. In the present study, no significant difference was found between the diets (nor the degree of cannibalism) of squid taken in the summer in the SAFZ and mature female squid taken during winter in the subtropics. The inability to distinguish more of the prey into lower taxonomic levels limits the testing of qualitative differences in diet.

The limited information presented here on blue shark diets in the central North Pacific corroborates the results of prior diet studies. Blue sharks are known to feed indiscriminately on numerous species of small pelagic fishes and cephalopods (Strasburg 1958; Tricas 1979; Compagno 1984b). Overall, blue sharks in the present study also fed almost totally on small fishes and cephalopods. However, forage composition differed markedly for sharks  $\leq 65$  cm PCL as compared to those  $> 65$  cm PCL. Certain species were eaten by only larger sharks: *O. bartrami* and species such as Pacific pomfret, *Brama japonica*; pelagic armorhead, *Pseudopentaceros wheeleri*; and the pelagic octopus, *Ocythoe tuberculata*, which frequents surface waters. By comparison, small micronektonic lanternfishes and gonatid squids dominated the diet in sharks  $\leq 65$  cm PCL. Most of the prey species undergo diel vertical migrations, occupying surface waters at night. As nocturnally active predators (Tricas 1979), the blue sharks likely fed on most of the prey species during this time.

Few other fishes have been identified as predators of *O. bartrami* and none while the squid occupy SAFZ waters. Brodeur (1988) reviewed available trophic information for the dominant epipelagic fishes of the North Pacific Subarctic and Transition Zones. Abun-

dant species such as *B. japonica* and albacore, *Thunnus alalunga*, were intermediate level predators feeding on micronektonic epi- and mesopelagic fishes, crustaceans, and cephalopods. Apex predatory fishes in the SAFZ were primarily sharks, including the blue shark; salmon shark, *Lamna ditropis*; and mako shark, *Isurus oxyrinchus*. Salmon sharks are not known to feed on cephalopods (Brodeur 1988); mako sharks feed opportunistically on available nekton (Compagno 1984a).

It is worth noting that, although diets of many of the pertinent species encountered in and potentially affected by the squid driftnet fishery have been studied, results are often not directly applicable to current assessments of *O. bartrami* trophic interactions. Nearly all of these past studies were conducted in geographical areas where *O. bartrami* are not common. Nevertheless, likely predators of *O. bartrami* are inferred on the basis of similar prey preferences and current knowledge of the species' distribution.

In subtropical waters, predators of *O. bartrami* include tunas, billfishes, and resident shark species. Perhaps the most notable of these predators is *X. gladius*, the target of a recently developed surface longline fishery. Ommastrephids, including large, mature *O. bartrami*, comprised most of the squid sampled from stomachs of *X. gladius* captured in large mesh driftnets (Seki in press). Predator-prey relationships between aggregations of winter-migrating *O. bartrami* and the seasonally abundant *X. gladius* have been suggested as possible impetuses for the fishery. Other billfishes—including blue marlin, *Makaira mazara*; striped marlin, *Tetrapturus audax*; and shortnose spearfish, *T. angustirostris*—reportedly feed commonly on ommastrephid squid (Nakamura 1985). Similarly, tuna species such as yellowfin tuna, *Thunnus albacares*; bigeye tuna, *T. obesus*; bluefin tuna, *T. thynnus*; and skipjack tuna, *Katsuwonus pelamis*, are also known to feed heavily on squid (Reintjes and King 1953; King and Ikehara 1956; Pinkas *et al.* 1971; Matsumoto 1984) and are likely predators of particularly the young *O. bartrami*.

Most information available on the interrelationships of *O. bartrami* and marine mammals can be found in an extensive review of the role of marine mammals in the oceanic food web of the eastern subarctic Pacific by Kajimura and Loughlin (1988). Basically, 11 marine mammal species (9 toothed cetaceans and 2 pinnipeds) have been identified to feed in oceanic areas near the Subarctic Boundary where encounters with *O. bartrami* are likely. Cetaceans include the sperm whale, *Physeter macrocephalus*; the short-finned pilot whale, *Globicephala macrorhynchus*; Dall's porpoise, *Phocoenoides dalli*; the Pacific whitesided dolphin, *Lagen-*

*orkynchus obliquidens*; Risso's dolphin, *Grampus griseus*; the northern right whale dolphin, *Lissodelphis borealis*; Baird's beaked whale, *Berardius bairdii*; Cuvier's beaked whale, *Ziphius cavirostris*; and the Stejneger's beaked whale, *Mesoplodon stejnegeri*. In warmer waters of the SAFZ and subtropics, other cetaceans that potentially feed on *O. bartramii* include the pygmy sperm whale, *Kogia breviceps*; dwarf sperm whale, *K. simus*; common dolphin, *Delphinus delphis*; and striped dolphin, *Stenella coeruleoalba*. Although the above-mentioned toothed cetaceans appear to favor oceanic squid as prey, only sperm whales reportedly have specifically fed on *O. bartramii* (Okutani *et al.* 1976; Okutani and Satake 1978; Kawakami 1980; Fiscus 1982). Among pinnipeds, remains of *O. bartramii* have been found in lavage studies of the northern elephant seal, *Mirounga angustirostris* (Antonelis *et al.* in press). Northern fur seals, *Callorhinus ursinus*, studied in neritic environments are also known to favor oceanic squid (Kajimura 1984).

The distribution and feeding ecology of pelagic seabirds in the subarctic Pacific have been summarized

in Sanger and Ainley (1988). Forty species reportedly occur in the region (21 commonly); most of them are small Procellariiformes (i.e., shearwaters and petrels). Not surprisingly (since adult squid outweigh the birds), none of the bird species has been found to prey on *O. bartramii*. In the subtropics, however, juvenile *O. bartramii* are seasonally eaten by red-footed boobies, *Sula sula* (Seki and Harrison 1989), and many of the unidentified young ommastrephids found in winter-collected regurgitations from other seabird species in the Northwestern Hawaiian Islands also were very likely *O. bartramii* (Harrison *et al.* 1983).

A schematic representation of direct predator-prey relationships involving *O. bartramii*, based upon information summarized in the present paper, is illustrated in Figure 4. Relationships between individual prey and predator groups were not considered, and no attempt was made at estimating annual biomass, production, or consumption rates for the components. Estimation of these input parameters in future studies is critical for the development of an ecosystem model.

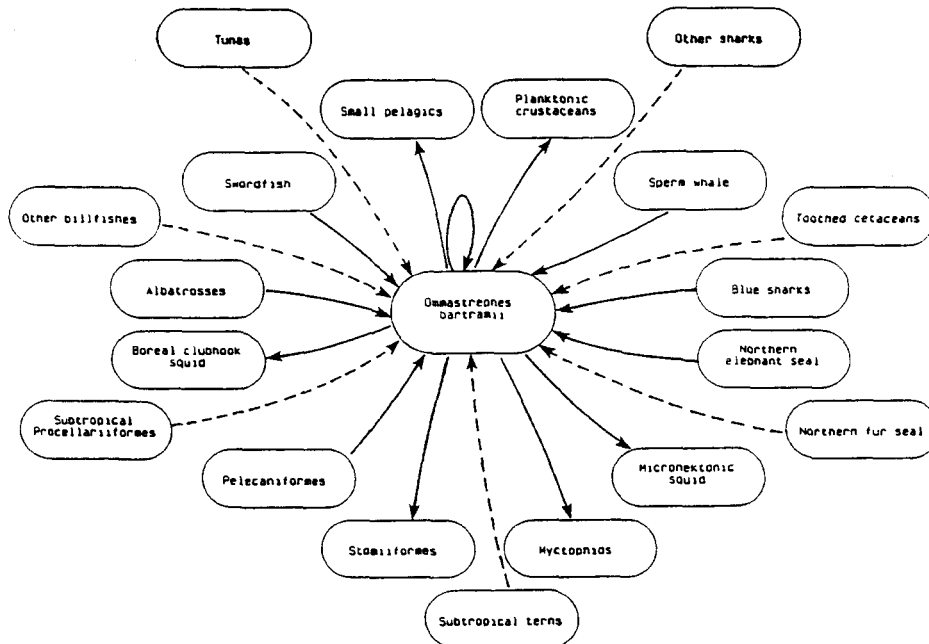


Fig. 4. Simplified schematic representation of *Ommastrephes bartramii* predator-prey relationships in the central North Pacific Ocean. Solid lines indicate known relationships; dashed lines are likely predators.

## VI. ACKNOWLEDGEMENTS

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