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## Trophic Relationships of *Ommastrephes bartramii* During Winter Migrations to Subtropical Waters North of the Hawaiian Islands

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**Abstract:** *Ommastrephes bartramii*, occupy waters in the North Pacific near the Subarctic Boundary during summer and fall where they are targeted by international driftnet fishing fleets. During the winter, *O. bartramii* migrate south to spawn in subtropical waters probably between 25° and 35°N latitude. Diet and trophic relationships were examined for *O. bartramii* during the winter occupation of these subtropical waters. Food composition was determined for stomachs from 42 large (48–57 cm mantle length), mature female *O. bartramii* captured by large (180 mm) mesh driftnet (ōme ami) during 12–19 February 1991. The bulk of the diet was composed of cephalopods (60.5%) and micronektonic fishes (37.7%); cannibalism was common. The relationship between winter-migrating *O. bartramii* and the recently developed swordfish, *Xiphias gladius*, longline fishery is also discussed. Squids found among swordfish stomach contents included adult *O. bartramii*, *Thysanoteuthis rhombus*, and *Sphenoteuthis oualaniensis*.

### Introduction

*Ommastrephes bartramii*, are broadly distributed in temperate and subtropical regions worldwide (Roper *et al.*, 1984). In the North Pacific, *O. bartramii* generally are known to occur between 25° and 50°N latitude. During summer and fall, *O. bartramii* occupy waters near the Subarctic Boundary (primarily between 36° and 46°N latitude), where they are targeted by international driftnet fishing fleets. With the onset of winter, these squid are thought to undergo extensive seasonal migration from these "feeding" grounds to the subtropics (ca. 25° and 35°N latitude) where presumed spawning occurs from late January through May (Araya, 1983; Gong, 1985; Murata *et al.*, 1988; Murata, 1990). Apparently, within a few months of hatching, juvenile *O. bartramii* begin a spring-summer migration northward to the region of the Subarctic Boundary, where they rapidly grow and remain until late fall when the return southern migration begins (Murata, 1990).

Information on the distribution of mature females (Nakamura, 1988) and the capture of the species' rhynchoteuthion paralarvae (Okutani, 1968) indicate that spawning grounds for *O. bartramii* exist west of 165°E longitude between 26° and 35°N latitude. Similarly, Young and Hirota (1990) and Hayase (1990) have reported captures of *O. bartramii* paralarvae along the Hawaiian Ridge during February–May. Little else, however, is known about the distribution, ecology, and life history of these squid during their winter and spring occupation of subtropical waters.

As a surface longline fishery targeting swordfish, *Xiphias gladius*, developed in the waters north of the Hawaiian Archipelago, swordfish landings in Hawaii increased from just 23,000 kg in 1988 to approximately 300,000 kg in 1989 and exceeded 1,000 metric tons in 1990. The fishery normally operates in the waters north of the Hawaiian Archipelago between 25° and 40°N latitude; peak effort and catches occur during March through May (NMFS, unpubl. data). Interestingly, the timing of the fishery coincides with the winter migration of *O. bartramii* to the subtropics. Since swordfish are recognized as major predators of squid (and ommastrephids in particular), possible predator-prey interrelationships exist between the aggregations of winter-migrating *O. bartramii* and the abundant swordfish. Swordfish stomach contents were investigated to examine these relationships.

In this paper, trophic relationships of winter-migrating adult *O. bartramii* are examined. Information is presented on the diet of these subtropical resident squid and their predator-prey relationship with swordfish.

#### Materials and Methods

Stomachs from 42 large (48–57 cm mantle length (ML)), mature female *O. bartramii* captured by 180 mm stretched mesh surface gillnet (ōme ami) were extracted and frozen aboard the research vessel *Shin-Riasu maru* on 12–19 February 1991 in the general vicinity of 30°N latitude, 150°W longitude (Fig. 1). Squid were sampled from five gillnet sets which were deployed during 1500–1600h and normally retrieved during 0000–0300h. One gillnet set was retrieved at 0700–1035h the ensuing morning.

In the laboratory, the frozen stomachs were thawed and the contents removed for quick fixing in a 10% phosphate buffered formalin solution (Hunter, 1985). After 24h, stomach contents were transferred to 50% isopropanol for preservation and storage. During processing, stomach contents were emptied into a 333  $\mu$ m 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 0.1g. 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 systematic categories. Cephalopod prey were identified primarily from suckers, hooks, beaks, and gladii; and fishes from vertebrae, teeth, epidermis, and otoliths.

To examine the predator-prey relationship between adult *O. bartramii* and *X. gladius*, squid from the stomachs of 22 swordfish caught in subtropical waters in the vicinity and north of the Hawaiian Archipelago were opportunistically collected and frozen during 1989 through 1991. Nineteen of the swordfish were captured by surface longline aboard the NOAA ship *Townsend Cromwell* or on commercial fishing vessels; the remaining three swordfish were caught in ōme ami driftnet operations aboard the *Shin-Riasu Maru* (Fig. 1).

In the laboratory, individual squid from swordfish stomachs were thawed and identified to the

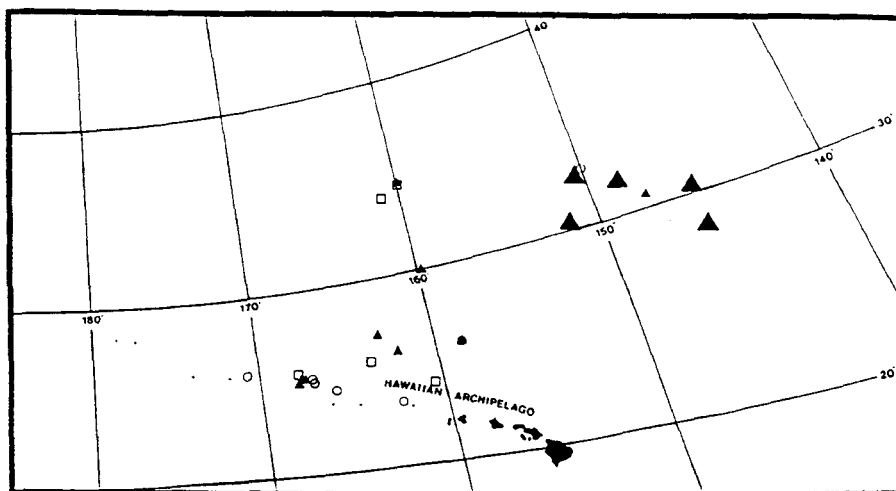


Fig. 1. Capture locations of 42 *Ommastrephes bartramii* and 22 *Xiphias gladius* in waters north of the Hawaiian Archipelago.

- ▲: *O. bartramii* collected from the stomachs of *X. gladius*
- : *Thysanoteuthis rhombus* collected from the stomachs of *X. gladius*
- : *Sthenoteuthis oualaniensis* collected from the stomachs of *X. gladius*
- ▲: *O. bartramii* collected from ōme ami gillnet operations aboard the *Shin-Riasu Maru*

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lowest possible taxon using the methodology similar to that described by Hess and Toll (1981). Briefly, squid identifications were based on a composite of characters such as mantle musculature, shape of mantle locking mechanism, gladius and beak morphology, statoliths, and light organs. All of the long-lines from which samples were obtained were baited with *Illex* sp. (all examined were *I. argentinus*), which were excluded from the analysis when found among the stomach contents.

The MLs were obtained for squid that had undergone minimal digestion; gladius length was interpreted as ML for others. The ML estimations for squid digested beyond reliable length measurements (particularly *Sthenoteuthis oualaniensis*) were based upon the relationship between rostral length of the lower beak (LRL) and ML (Wolfe, 1982).

Results

All 42 of the examined *O. bartramii* stomachs contained prey; some samples (13), however, contained < 1.0g total prey weight and could be considered empty. By weight, stomach contents ranged from 0.1 to 220.0g ( $\bar{x}$  = 16.3g; SD = 34.4) and were composed primarily of cephalopods (60.5%) and fishes (37.7%) (Table 1).

Cephalopods occurred in 71.4% of the stomach samples. Thus far, only squid of the family Ommastrephidae have been positively identified—a reflection of the unusually fresh condition of the prey which facilitated identification. Cannibalized *O. bartramii* were determined to be present in at least 14.3% of the stomachs and by weight represented 77.0% of the ommastrephid and 32.9% of the overall cephalopod material consumed. Non-ommastrephid squid normally were well digested and possessed several varieties of arm and tentacular hooks. These were probably from the families Gonatidae, Onychoteuthidae, and Enoploteuthidae.

Fish remains were found in 33.3% of the stomachs and were typically in advanced stages of digestion. Vertebrae morphology and pieces of epidermis suggested that most of the fishes were either micronektonic myctophids or stomiiforms. A single pair of otoliths was identified as belonging to *Myctophum* sp.

Miscellaneous prey such as pyrosomes, crustaceans, barnacles (suborder Lepadomorpha), undigestible plastics (monofilament), and general unidentifiable remains also were found among the stomach contents. These items together made up only 1.8% of the total aggregate weight.

Large teuthoids of the families Ommastrephidae (*O. bartramii* and *S. oualaniensis*) and Thysanoteuthidae (*Thysanoteuthis rhombus*) composed the cephalopod fauna collected from sword-

Table 1. Diet composition of 42 mature female *Ommastrephes bartramii* from the subtropical central North Pacific Ocean, 12–19 February 1991.

Prey species	Weight (g)	Percent weight	Frequency	Percent frequency
Cephalopods				
<i>Ommastrephes bartramii</i>	136.3	19.9	6	14.3
Unidentified Ommastrephidae	67.2	9.8	4	9.5
Non-Ommastrephidae (i.e. teuthoids with hooks)	58.0	8.5	7	16.7
Unidentified Cephalopoda	152.9	22.3	13	30.9
Total Cephalopoda	414.4	60.5	30	71.4
Fishes				
<i>Myctophum</i> sp.	17.9	2.6	1	2.4
Unidentified fishes	240.0	35.1	13	30.9
Total fishes	257.9	37.7	14	33.3
Others				
Barnacles (Suborder Lepadomorpha)	3.2	0.5	1	2.4
Crustacea	0.8	0.1	2	4.8
Pyrosomatidae	0.3	<0.1	1	2.4
Unidentified remains	6.7	1.0	11	26.1
Plastic (monofilament)	1.1	0.2	2	4.8
Total others	12.1	1.8	17	40.5
Totals	684.5	100.0	122	—

**Table 2.** Number, percent frequency of occurrence, estimated range of mantle lengths (ML), and months of capture of squids collected from the stomachs of 22 swordfish, *Xiphias gladius*, in the subtropical central North Pacific Ocean, 1989–1991.

Species	No.	Percent frequency	ML (mm)	Months of capture
<i>Ommastrephes bartramii</i>	9	40.9	357–495	Jan, Feb, June, Sept, Oct
<i>Sthenoteuthis oualaniensis</i>	5	18.3	187–334	Jan, July, Aug, Sept
<i>Thysanoteuthis rhombus</i>	7	31.8	330*	Jan, Feb, June, Nov, Dec
Unidentified ommastrephid	3	13.6	210	Jan, Feb, Aug

\* Most specimens too digested to obtain reasonable ML estimations; good relationship between beak length and ML for *Thysanoteuthis rhombus* not available.

fish stomachs in the subtropical central North Pacific Ocean (Table 2). Nine *O. bartramii* ranged in estimated ML from 357 to 495 mm ( $\bar{x} = 437.7$ ,  $SD = 49.6$ ); five were females possessing mature eggs in the oviducts. Only one of the *T. rhombus* was sufficiently intact to obtain an ML measurement (330 mm). Although both upper and lower beaks were recovered from all of the *T. rhombus* individuals, a good relationship between beak morphometrics and ML does not exist at the present time.

One specimen of *O. bartramii* taken from the swordfish stomachs possessed an intact stomach which unfortunately was empty.

### Discussion

In this study, cephalopods and fishes dominated the prey composition in diets of the large adult female *O. bartramii* examined while crustaceans were virtually nonexistent. These results suggest that the winter diet of *O. bartramii* in the subtropics is similar to that reported for the species in more temperate regions. Naito *et al.* (1977) and Araya (1983) examined the stomach contents of jig-caught *O. bartramii* in North Pacific waters adjacent to Japan and described the species as primarily piscivorous (myctophids composed the bulk of fishes eaten) and cannibalistic. In addition to its own species, cephalopod prey included the enoploteuthid *Watasenia scintillans*. Crustaceans were more prevalent among the stomach contents of *O. bartramii* in these temperate studies, but this was attributed to the inclusion of smaller immature squid that tend to feed more readily on plankton (Murata, 1990).

The natural feeding habits of *O. bartramii*, however, are difficult to assess because existing methods of squid fishing are inadequate for obtaining unbiased samples for diet studies. Most feeding studies of oceanic squid historically have obtained samples through the use of jigs after attraction of the animals with high-intensity lamps. Because fishing with lights also attracts and aggregates smaller, photopositive, vertically migrating micronekton, an artificially rich feeding environment with abnormal illumination is created. Naturally, feeding activity is increased, and ultimately stomach content analysis is affected by artifacts of the sampling. To circumvent potential biases that may have been created from the use of lights and jigs in sampling, the present study used only squid sampled with drift gillnets. Off Australia, Dunning and Brandt (1985) conducted the only published feeding study on *O. bartramii* captured with gillnets. In an examination of 138 individuals, 67% of the stomachs were found empty. Fishes and cephalopods composed most of diet, although pteropods also were common. Moreover, no evidence of cannibalism was presented.

Cannibalism is a commonly reported phenomenon among some schooling squid species and especially so among ommastrephids (Nixon, 1987) and appeared to be common among *O. bartramii* in the present study. Some authors (Maurer and Bowman, 1985) have suggested that cannibalism indicates a lack of other suitable prey in the area. Field observations, however, support the notion that much of the reported cannibalism may be induced by the sampling technique (Breiby and Jobling, 1985). *Sthenoteuthis oualaniensis* has been observed in Hawaiian waters to prey upon its own species when injured animals were being retrieved during jigging operations (R.E. Young, pers. commun., June 1991). Not surprisingly, freshly cannibalized squid could often be found in stomachs of those captured and examined (R.F. Harman, pers. commun., June 1991). Undoubtedly, this is a common behavior among ommastrephids around fishing lights. Cannibalism was also unexpectedly observed for *O. bartramii* during high seas squid driftnet fishing operations conducted aboard the research vessel *Shōyō-Maru*

operating in the vicinity of the Subarctic Boundary in July 1990. Remains of partially cannibalized *O. bartramii* commonly were entangled in retrieved nets and also were identified in stomachs casually examined during shipboard processing. Apparently, squid were attacking others that had been caught by the nets during fishing. The fresh condition of cannibalized squid found in the stomachs during the present study suggests that this too may be an induced artifact of sampling rather than a natural feeding behavior.

Cephalopods comprised all of the fresh material in the stomachs; the majority were ommastrephids and specifically *O. bartramii*. Normally these items included only portions of an individual, such as a fraction of an arm with suckers or minced mantle often with the epidermis intact. Breiby and Jobling (1985) suggested using only the most digested stomachs in squid feeding studies that employ gravimetric analysis. Dietary analysis using gravimetric (or volumetric) methods was found to treat recently consumed prey as the most important components (i.e., emphasized the importance of cannibalism). If fresh material were to be excluded from this analysis, fishes and cephalopods would still dominate the food composition; however, the diet would appear to be considerably more piscivorous (Fig. 2). Ommastrephids would still represent 38.0% of the cephalopods eaten, but none of the remaining material has been verified as *O. bartramii*. The average weight of stomach contents would fall to 10.6g (SD = 21.2), and 16.7% of the individuals would now be classified as empty. Further study is required to determine whether the cannibalism exhibited among *O. bartramii* is induced by sampling techniques or is, in part, a function of natural feeding behavior and survival.

The limited results presented here for the central North Pacific corroborate the findings of prior swordfish feeding studies conducted in other areas. Swordfish appear to demonstrate a clear predilection for teuthoids as prey (Toll and Hess, 1981), and among squid species, ommastrephids in particular are preferred. This is exemplified by the predation on species of *Illex* in the North Atlantic (Scott and Tibbo, 1968; Stillwell and Kohler, 1985) and off Portugal (Moreira, 1990), on *Illex* and *Ommastrephes* off South Florida (Toll and Hess, 1981), and on *Dosidicus gigas* in the eastern Pacific (DeSylva, 1962). Similarly, *O. bartramii* and *S. oualaniensis*, the most abundant, large ommastrephid species in the central Pacific, were among common prey.

Swordfish undergo diel vertical migrations, swimming deep during the day (to about 100m) (Carey and Robison, 1981) and occupying near-surface epipelagic waters at night where they feed (Palko et al., 1981; Toll and Hess, 1981). Similarly, *O. bartramii* inhabit near-surface waters at night, as evidenced by their susceptibility to surface gillnets, and diurnally occupy depths greater than 400m (Nakamura, this volume). In addition, swordfish are thought to exploit schools of prey as opposed to individuals (Scott and Tibbo, 1968). *Ommastrephes bartramii*, like many teuthoids, commonly aggregate for feeding (Clarke, 1966). With these convergent behaviors, swordfish predation on *O. bartramii* (or any ommastrephid species) would seem likely.

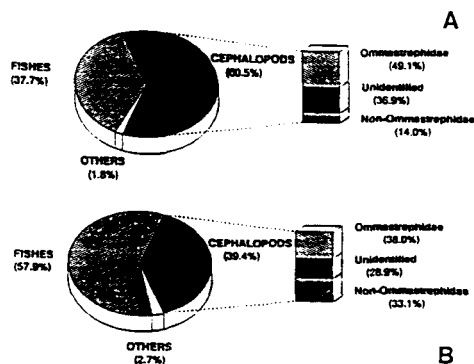


Fig. 2. Comparative proportions by weight of major prey classes in diets of *Ommastrephes bartramii* with fresh (recently consumed) material (A) included in and (B) excluded from the analysis.

Many of the squids sampled from swordfish stomachs were mature, suggesting that swordfish may indeed be feeding on concentrations of spawning *O. bartramii*. Additional data of this type may aid in delineating spawning grounds and season in the central North Pacific for this species. Further study is needed to understand the role of *O. bartramii* both as predator and prey in the ecosystem of the subtropical North Pacific. Sampling constraints that result in cannibalism will continue to hinder qualitative as well as quantitative assessments of diet until new capture methodologies are developed.

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