

## PREY COMPOSITION OF THE MARKET SQUID, *LOLIGO OPALESCENS* BERRY, IN RELATION TO DEPTH AND LOCATION OF CAPTURE, SIZE OF SQUID, AND SEX OF SPAWNING SQUID.

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### ABSTRACT

Squid feeding was investigated for Monterey Bay and adjacent areas. Squid were found to feed mostly on crustacea and to a much lesser degree on fish, cephalopods, gastropods, and polychaetes. Animals from deeper offshore waters fed more on euphausiids and copepods. Inshore, off the spawning ground, euphausiid feeding still dominated, although to a lesser degree. Mysids, megalops larvae, cephalopods, and fish were more important in these waters. On the spawning ground, feeding habits changed a great deal. Here crustacean feeding still dominated, although euphausiids were lacking from the diet. Demersal feeding became most important, with such items as megalops larvae, egg-like spheres, juvenile gastropods, and nereid polychaetes comprising the diet. Little difference in prey composition was found between sexes on the spawning grounds. Male squid tended toward larger meals (in terms of number of megalops larvae), and there was a more frequent occurrence of cephalopod fragments. A comparison of large and small squid from non-spawning ground areas revealed little difference in prey composition. Larger animals (101- to 180-mm mantle length) fed slightly more on euphausiids, cephalopods, and fish than smaller squid (21- to 100-mm mantle length).

### INTRODUCTION

This study involves an analysis of the prey composition of the common Pacific market squid, *Loligo opalescens* Berry. Recent works by Fields (1965) and Loukashkin (1977) have determined the gross composition of this squid's diet but failed to resolve specific problems such as how this diet is affected by the habitat and biological state of the animal. Fields (1965) examined 106 squid stomachs with contents, obtained from subsampling commercial fish seiners and squid lampara boats in the Monterey Bay area. Most of these samples were taken from night catches and only from nearshore areas. Loukashkin (1977) examined 331 *L. opalescens* with contents. These samples were collected throughout the California coast but again from predominantly night catches. Loukashkin (1977) made no attempt to distinguish the samples caught on the spawning grounds from those caught in other nearshore and offshore areas. The purpose of our study is to evaluate the effect of depth and location of capture, size of squid, and sex of spawners on the prey composition of *L. opalescens*.

### MATERIALS AND METHODS

Prey were identified from samples of *Loligo opalescens* taken from a variety of sources. Sampling was limited to Monterey Bay and its adjacent areas from Point Sur to Pigeon Point, California (Figures 1-3).

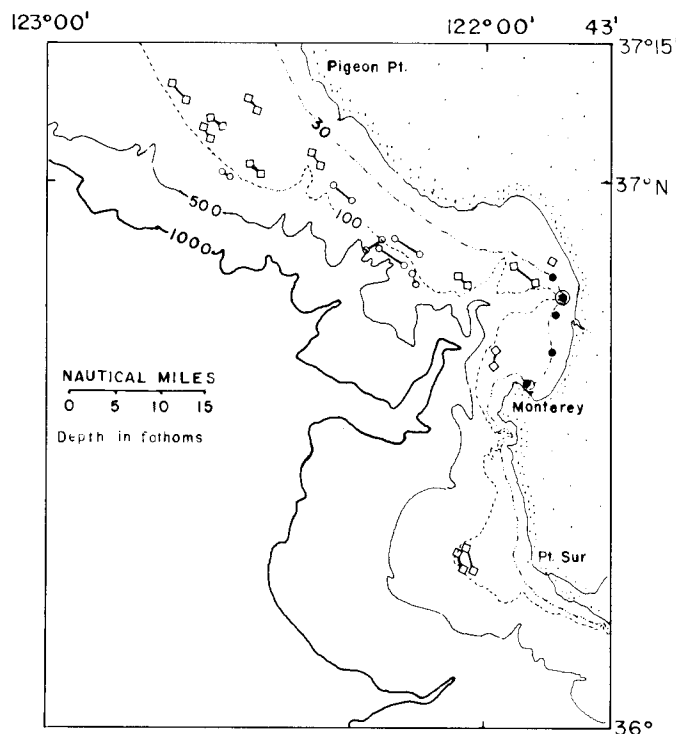


Figure 1. Locations of midwater and bottom trawls; Point Sur to Pigeon Point:  $\diamond$  = Bottom trawls day;  $\circ$  = Midwater trawls day;  $\bullet$  = Midwater trawls night.

These were obtained from directed bottom and midwater trawls aboard three research vessels: The California Department of Fish and Game R/V *Alaska*, the National Marine Fisheries Service R/V *Cobb*, and the R/V *Pacific Raider*, leased by the National Marine Fisheries Service. Samples were also taken from commercial squid, anchovy, and bottom-trawl catches.

The R/V *Alaska* used a large midwater trawl, as described by Ally and Mais (1975), with a ½-inch (1.27-cm) stretch mesh cod end netting, during June 1976. A total of seven samples taken in the Monterey Bay area were used in this study, with only two of these taken during daylight hours. All samples were taken at depths less than 40 fathoms (73.2 m; Figures 1 and 2). The R/V *Pacific Raider* used a large 60 by 60-foot (18.3 x 18.3-m) Herman Engel midwater trawl, with a 1½-inch (3.8-cm)

mesh cod end net. The R/V *Cobb* used an Eastern bottom trawl, having a 94-foot (28.7 m) lead rope, equipped with roller gear and a 71-foot (21.6 m) lead rope. The cod end had a liner with 1¼-inch (3.2-cm) stretch mesh. A total of 14 samples were taken by both these vessels between Moss Landing Harbor and Pigeon Point, California, during August 1976. Samples were taken during daylight hours, at depths greater than 40 fathoms (73.2 m; Figures 1 and 2).

Squid taken on the spawning grounds in Monterey Bay included two samples from the R/V *Alaska* and subsamples of commercial squid catches. All samples were taken within a few miles of Monterey harbor at depths less than 20 fathoms (36.6 m; Figure 2). The commercial catches were subsampled while unloading between 24 September and 28 October 1975. During this period ten different samples were taken from seven different vessels. The squid were landed using lampara nets as described by Fields (1965). All catches were made between 2300 and 0800 hours.

The commercial anchovy fishery at Moss Landing, California, was also subsampled. *L. opalescens* can be taken directly from the conveyor belt while these boats are unloaded (Cailliet et al. 1976). Anchovies are fished in Monterey Bay using purse seine (Messersmith 1969), and these nets had a maximal depth penetration of 35 fathoms (64 m). Twenty samples were collected between 5 September 1975 and 10 March 1976. The hauls sampled were all taken during night hours with none of these taken near the spawning grounds (Figure 3).

Subsampling commercial bottom trawlers yielded three samples of squid from two separate vessels. These were taken on 24 September and 19 December 1975 and 9 January 1976. Depths of sampling were between 47 (86 m) and 80 (146 m) fathoms. Two of the samples were taken off Point Sur, and one was taken off Point Pinos, Monterey (Figure 1). Both vessels used large trawls with a 4½-inch (11.4-cm) stretch mesh cod-end net.

In addition, an incidental sample of *L. opalescens* was collected by the R/V *Tage* of Hopkins Marine Station, using a small otter trawl with a 24-foot (7.3-m) head rope and a ¼-inch (0.6-cm) stretch mesh cod-end liner. This sample was taken north of Moss Landing Harbor (Figure 2) at a depth between 10 and 20 fathoms (18.3 to 36.6 m) on 9 March 1976.

A maximum of ten squid with contents were analyzed in detail for prey composition from any one sample. These animals were first sexed, and their dorsal mantle lengths were recorded. Then, the stomachs were removed, and the contents were sorted, identified, and enumerated. Prey were identified to the lowest possible taxa. Rarely were whole organisms encountered in the stomachs examined, and for this reason key fragments had to play the major role in the identification process. Identification to the species level could not often be accomplished. Some

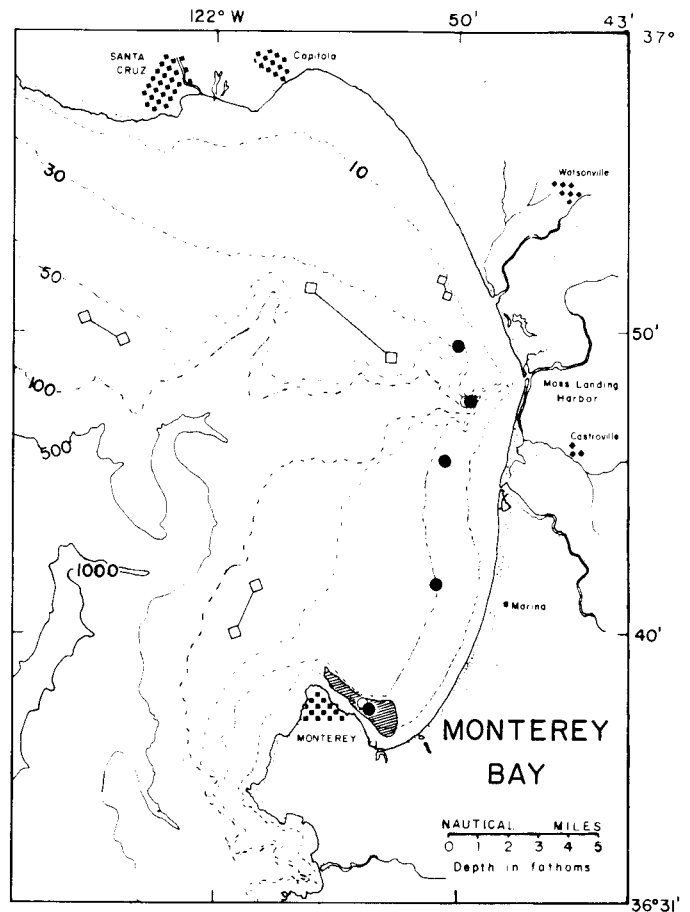


Figure 2. Locations of midwater and bottom trawls in Monterey Bay: ◇ = Bottom trawls day; ○ = Midwater trawls day; ● = Midwater trawls night; ■ = Squid spawning grounds.

species of crustacea were identified from a reference collection in the museum at Moss Landing Marine Laboratories. Squid could be individually recognized by using their beaks as a taxonomic tool. Recognition to the family level was possible using the key developed by Clark (1962), and some species could be identified by using the beak drawings furnished by Pinkas et al. (1971).

Most other identifications were more generalized. Crustaceans such as mysids, euphausiids, megalops larvae, amphipods, and shrimp possess distinctive eyes, mandibles, statoliths, and other parts that when taken together offer distinctive recognition. A collection of detailed drawings of such parts was assembled to aid prey recognition.

To assess the number of stomachs needed to adequately reflect feeding habits of the squid population, plots of cumulative numbers of taxa encountered per stomach were constructed for squid captured away from the spawning ground (Figure 4, upper) and from the spawning ground (Figure 4, lower) using 50 randomly selected squid stomachs for each category. Both plots leveled off at about 20 squid, indicating that this number

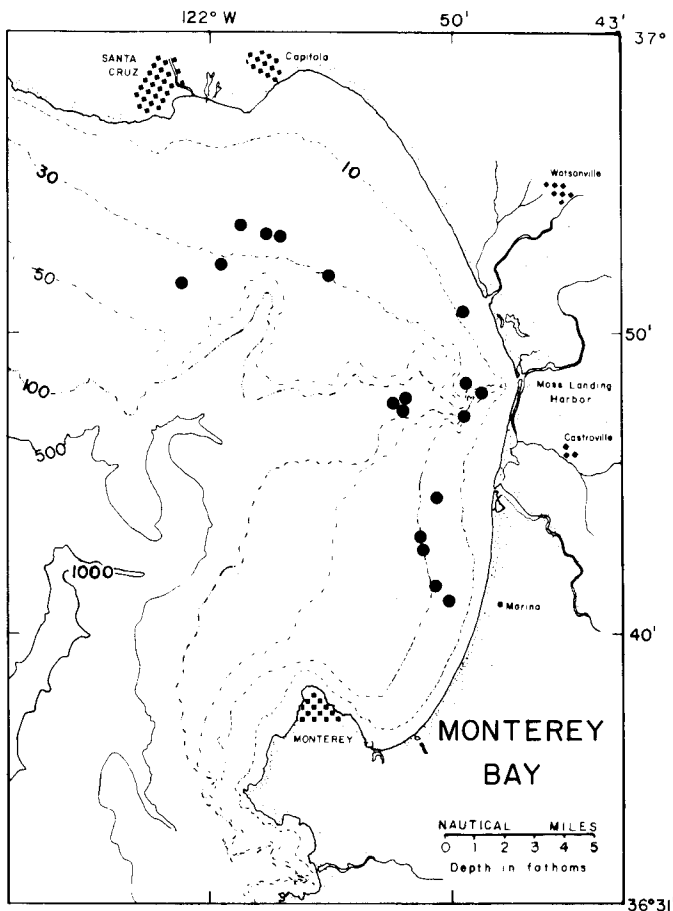


Figure 3. Locations of commercial anchovy seine sets in Monterey Bay.

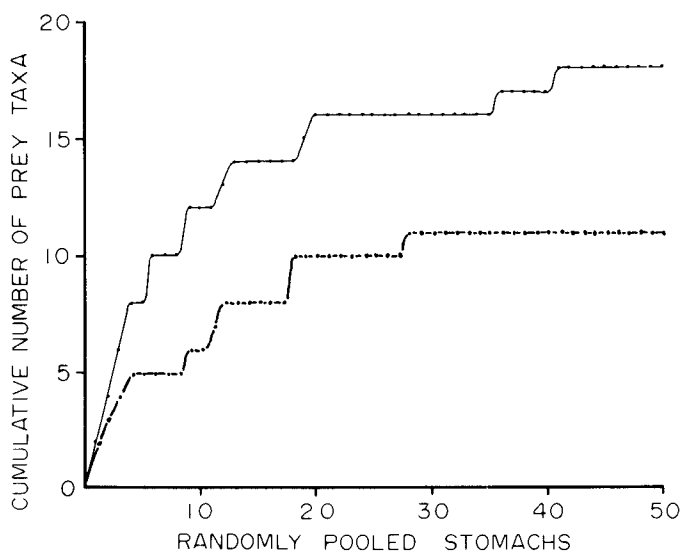


Figure 4. Cumulative sum of new taxa identified from the stomachs of 50 randomly selected *Loligo opalescens*. Upper curve is for non-spawning-ground samples, and lower curve is for spawning-ground samples.

of stomachs is sufficient to represent a valid comparison in any category. The smallest set of categories compared was between sexes on the spawning grounds, with 24 females and 27 males sampled.

The fragmented and often well-digested state of the stomach contents made counts of individual prey difficult and relative volume determinations impossible. Therefore, counts were based on pairs of eye lenses, mandibles, statoliths, otoliths, or polychaete jaws. Counts were not based on paired soft parts, such as decapod eyes, which were subject to digestion. Occasionally, stomachs were largely distended and filled with numerous euphausiid mandible pairs. These stomachs were divided into approximate halves; one portion was enumerated and the other portion was qualitatively examined. In such cases, counts were doubled.

A modified form of the Pinkas et al. (1971) "index of relative importance" was calculated in each comparison of depth, location, and size of squid for the major prey types eaten. The index was modified by using only numerical importance and frequency of occurrence. The numerical importance of a particular item was the percentage ratio of its abundance to the total abundance of all items in the contents. Its percent frequency of occurrence was the percentage of squid examined that contained at least one individual. The product in percents [(number) x (frequency)] is the index of relative importance, which ranges from zero, when both values are zero, to 10,000 when both indices are 100% (a monodiet).

Percent frequency and number histograms were constructed for comparison of squid sizes, depths of capture, location on or off the spawning grounds, and the sexes of spawning-ground squid. Non-spawning squid were grouped into two size categories for comparison. Animals with 21- to 100-mm mantle lengths were compared to those with 101- to 180-mm mantle lengths. These two categories equally divided the number of animals yet retained a significant number of shallow-water and deep-water animals in each category.

Deep-water samples were defined as those taken from depths of at least 40 fathoms (73.2 m). These categories were somewhat arbitrary since the gear used did not sample at discrete depths. These trawls included most of the day midwater and bottom-trawled samples. Samples were considered shallow regardless of bottom depth when they were taken from water depths of less than 40 fathoms. These included all anchovy hauls, R/V *Alaska*, and R/V *Tage* samples. No samples taken near the spawning grounds were included in either category.

Rank correlation coefficients and indices of species similarity were calculated for these comparisons. The Spearman rank correlation test (Fritz 1974) was used to compare ranks of prey items, and the "percent similarity index" was used to examine the degrees of similarity

for comparisons of percent by number (Silver 1975). This index has no significance levels but serves to illustrate relative similarities between comparisons.

**RESULTS**

**Prey Determination—Large versus Small Squid**

In general, squid fed mostly on crustacea and to a much lesser degree on fish, cephalopods, gastropods, and polychaetes (Table 1). In most categories, euphausiids and copepods dominated the diet, but other crustaceans such as mysids, megalops larvae, cumaceans, and amphipods were important food items.

TABLE 1  
 Index of Relative Importance in Prey Composition

Number of Squid	Squid Size		Sample Location		
	Small 123	Large 103	Deep Water 134	Shallow Water 94	Spawning Grounds 52
Crustacea unknown	73.3	17.5	23.8	135.2	95.4
Euphausiacea	3988.0	5400.0	6552.2	1553.4	0.0
Copepoda	97.5	37.5	103.8	1.0	0.0
Mysidacea	7.4	10.6	6.3	28.2	54.7
Megalops	4.9	0.0	0.1	23.3	1088.0
Natantia	0.2	0.6	0.0	1.9	0.0
Cumacea	12.2	0.0	2.6	1.0	0.0
Amphipoda	0.0	0.1	0.1	0.0	11.3
Ostracoda	0.0	0.1	0.1	0.0	0.0
Cephalopoda (whole)	16.2	9.7	2.6	187.6	0.0
Gastropoda	5.0	1.2	1.9	5.7	295.8
Radiolaria	0.0	0.4	0.1	1.0	0.0
Polychaeta	0.0	0.0	0.0	0.0	24.9
Fish	2.0	8.8	1.3	44.8	11.3
Miscellaneous	-	-	-	-	197.2

A comparison of prey composition of large (101- to 180-mm mantle length) versus small (21- to 100-mm mantle length) *Loligo opalescens* from off the spawning grounds revealed few major differences (Figure 5, Table 1). Both size categories fed mostly on crustaceans, primarily the euphausiids, *Euphausia pacifica* and *Thysanoessa spinifera*. Other crustaceans taken included calanoid copepods; cumaceans; mysids; and the shrimp, *Sergestes* sp.

In both size categories, cephalopods and other non-crustaceans played a small role in the diet. Whole cephalopods eaten included *Gonatus* sp. and other *L. opalescens* individuals (cannibalism). Fragments of *L. opalescens* were also ingested and were most often identifiable as tentacle tips. Fish eaten were either unidentifiable species or *Engraulis mordax*. Gastropods and bottom debris were also ingested.

Histograms of percent frequency and percent by number of prey species indicated that large squid fed more frequently on euphausiids, cephalopods (whole and fragments), and fish (Figure 5). Rare taxa encountered only in the large squid feeding were the amphipod, *Jassa*

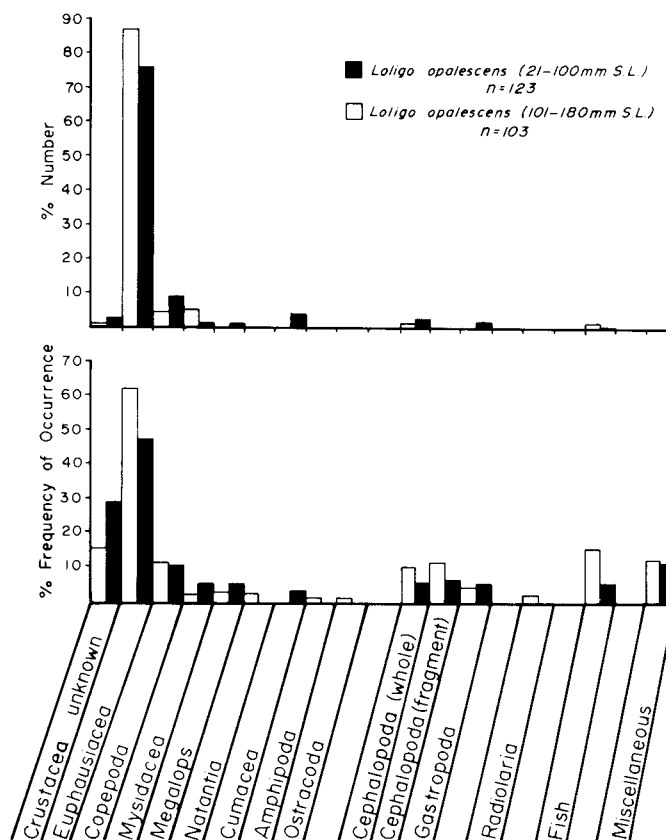


Figure 5. Comparison of prey frequency and number by size for non-spawning squid.

sp., ostracods, and radiolarians. Small squid fed more frequently on other crustaceans such as megalops larvae and cumaceans. Few inferences can be drawn from percent by number of prey species since both size classes were overwhelmed by the number of euphausiids eaten (Figure 5). The percent similarity index between the two size groups was high (84.9%), and the Spearman rank correlation test showed these two groups to have similar proportions of food items in percent frequency of occurrence ( $P \leq 0.025$ ), but not in percent by number (Table 2).

**Prey Determination—Deep versus Shallow Water**

Comparison of prey composition by depth of capture revealed major differences (Figure 6, Table 1). Squid captured in deeper water fed more frequently on euphausiids and copepods. Squid taken nearer the surface fed far less frequently, although still predominantly, on euphausiids, whereas fish, whole cephalopods, mysids, and megalops larvae were more important to these squid. Despite a relatively high similarity index (71.8%), no significant correlation of prey item ranks was found in either percent frequency or occurrence or percent by number of prey species between deep and shallow water (Table 2).

TABLE 2  
 Comparison between Sizes and Locations  
 Using Percent Similarity Index (P.S.I.)  
 and Spearman Rank Correlation Coefficient ( $r_s$ )

	Percent Frequency of Occurrence		Percent by Number	
	$r_s$	P.S.I.	$r_s$	
Large squid versus small squid (101-180 DML vs. 20-100 mm DML)	0.699*	84.9	0.506	n.s.
Deep samples vs. shallow (0-40 fathoms = shallow)	0.549 n.s.	71.8	-0.230	n.s.
Shallow samples vs. spawning-ground samples	-0.272 n.s.	16.8	-0.350	n.s.
Spawning-ground samples Male vs. female	0.852*	60.8	0.697	n.s.

\* = significant at  $P = 0.025$   
 n.s. = not significant  
 DML = dorsal mantle length

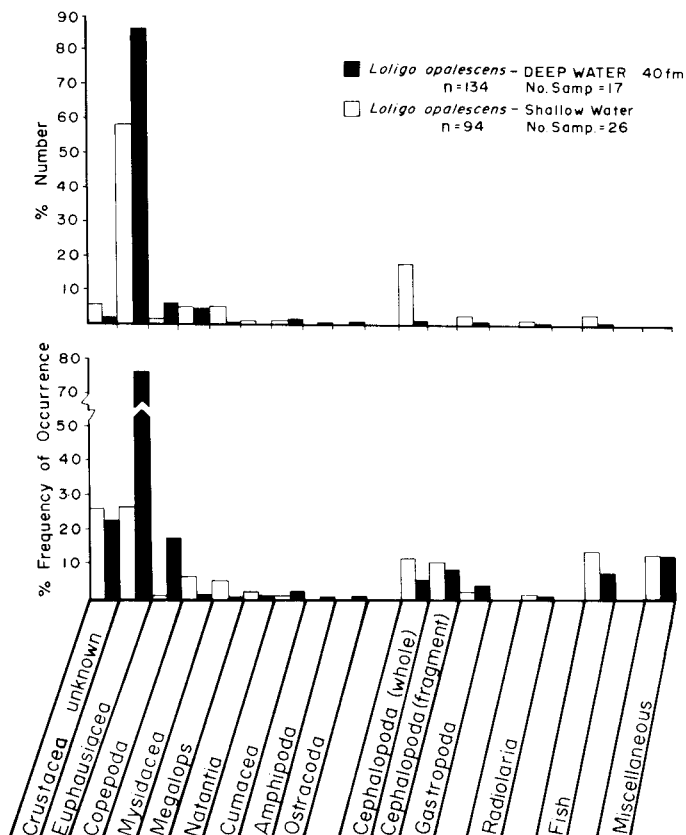


Figure 6. Comparison of prey frequency and number by depth of capture for non-spawning squid.

**Prey Determination—Spawning Ground Males versus Females**

Little difference was found between the feeding habits of male and female *L. opalescens* from the spawning

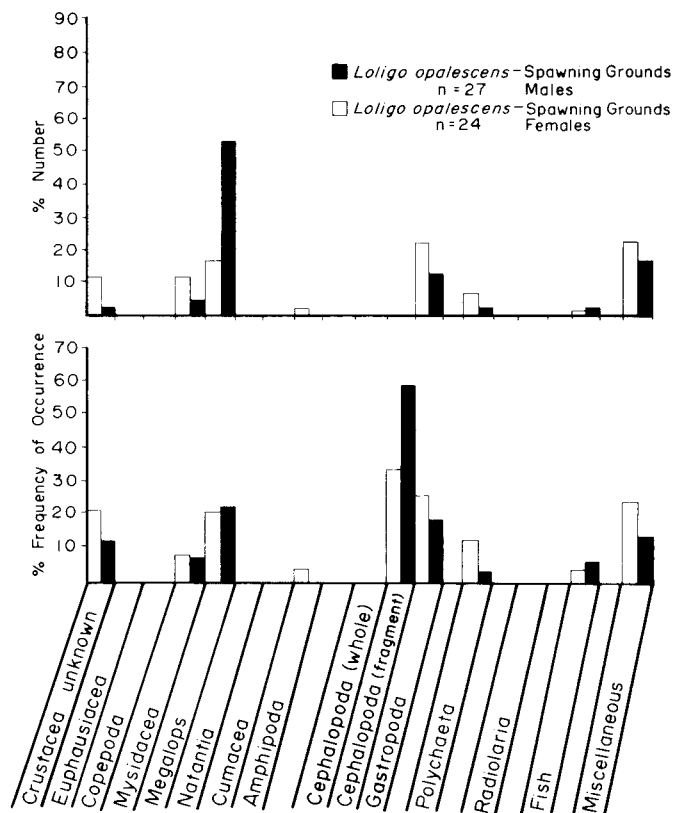


Figure 7. Comparison of prey frequency and number by sex of spawning-ground captured squid.

grounds (Figure 7, Table 1). In both sexes crustacean feeding predominated, with mysids and megalops larvae being the primary foods. Juvenile gastropods also were important, with nereid polychaetes, and fish (juvenile *Sebastes* sp. and pleuronectiforms) playing lesser roles (Table 1). No whole-cephalopod feeding was found, although cephalopod fragments were ingested more often than off the spawning grounds. The miscellaneous category was dominated by egg-like spheres, but sand particles were also found.

The only major differences between sexes were in megalops larvae and cephalopod fragments (Figure 7). Male squid took cephalopod fragments more frequently and ate more megalops per meal than females. Females fed more on polychaetes, egg-like spheres, and cumaceans. A significant association between prey ranks was found in percent frequency of occurrence but not in percent by number of prey species, although the similarity index was relatively high (60.8%; Table 2).

**Prey Determination—Spawning Grounds versus Shallow Water**

A marked contrast was found in food items eaten by squid taken from spawning grounds compared to squid

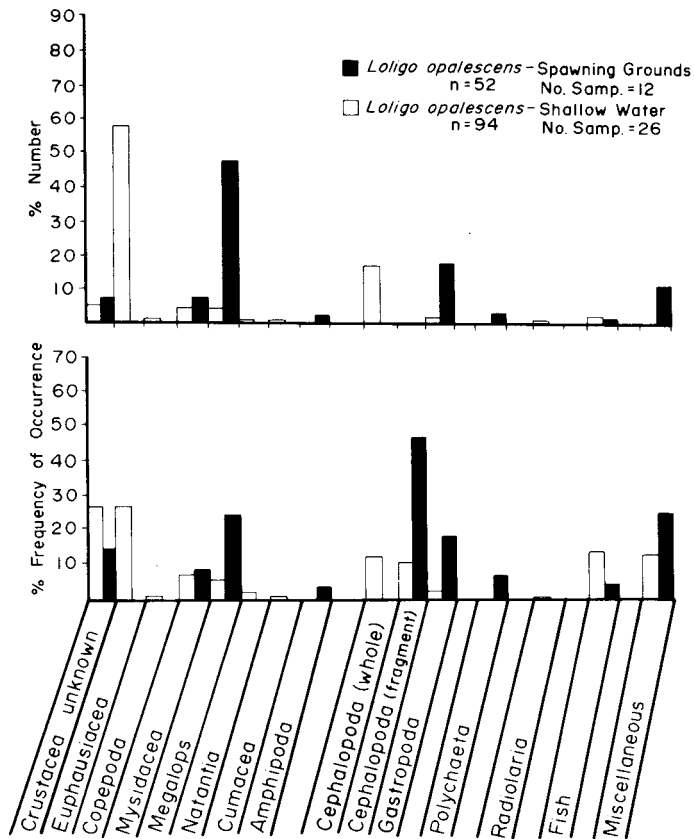


Figure 8. Comparison of prey frequency and number by location and depth of capture.

taken in near-surface waters (Figure 8, Table 1). On the spawning grounds, crustacean feeding still dominated, although of a different kind, with megalops larvae replacing euphausiids. Polychaetes, juvenile gastropods, and egg-like spheres also became more common, replacing fish and whole cephalopods. Cephalopod fragments played a much larger role on the spawning grounds. A very low similarity index (16.8%) agreed well with the finding that no significant association occurred between prey ranks of spawning ground and shallow-water squid in either percent frequency of occurrence or percent by number of prey species. (Table 2).

### DISCUSSION

Squid have been reported to change their feeding habits with growth in size. Squires (1957) described for the Newfoundland squid *Illex illecebrosus* a diet of mostly euphausiids in small animals (100- to 200-mm mantle length), with fish in only 12% of the food-containing stomachs. In larger squid, the occurrence of crustacea declined to insignificance, with fish increasing in importance until they became the major component of the diet. Cannibalism increased among the largest animals

(250- to 300-mm mantle length).

Vovk (1972) reported a similar trend in the East Coast squid, *Loligo pealei*. Planktonic feeding was dominant in the smallest squid (75-mm mantle length). Euphausiid feeding became increasingly important to larger squid (125-mm mantle length). Cannibalism and fish feeding dominated in sizes larger than the 160-mm mantle length.

Kore and Joshi (1975), working with the Indian squid, *Loligo duvauceli*, reported a similar increase in cannibalism and decrease in crustacean feeding for larger squid. These were the only authors that distinguished true cannibalism from the ingestion of cephalopod fragments such as skin and tentacle fragments.

Fields (1965) also reported a similar trend for *L. opalescens* captured in Monterey Bay. His study was based on a sample of 75 animals subsampled from commercial fish seiners and 31 male squid from the spawning grounds. Only those squid whose stomachs appeared from external examination to have contents were used in his study. He reported a trend of crustacean to fish feeding of 3:1 in small squid, 1:1 for young squid, and 1:3 for adult squid (males from the spawning grounds). Fields stated that feeding on the spawning grounds was probably atypical because of the ground's localized nature and the increased crowding that the animals experienced. These spawning adults were reported to show 75% cannibalism in frequency of stomachs with contents. No distinction was made between true cannibalism and cephalopod fragments. In our study no spawning-ground animals were included in the comparison between sizes in order to avoid the localized nature of feeding on these grounds.

We found a closer correlation in feeding habits between different sizes of *L. opalescens* than was reported by Fields (1965). Certainly, there was a trend for larger animals to feed more on cephalopods and fish than the smaller sizes of squid, but significance of association by frequency of occurrence and a high percent similarity index does not support this trend. The possibility that other squid do show major differences in feeding habits between size categories can still be explained. Both *L. pealei* and *I. illecebrosus* are larger animals than *L. opalescens*. If feeding habits of sizes similar to *L. opalescens* are examined for these two species, crustacean feeding dominates. Another possible explanation is that, unlike our study, these authors did not separate location of capture from size of squid captured. Squires (1957) pointed out that *Illex* captured on the outer edge of the Grand Banks were also the smaller squid and were found to feed more on euphausiids than larger squid taken on the Grand Banks.

Our comparison by depth of capture could not clearly be separated from a comparison of location since the shallow water (less than 40 fathoms [73.2 mm]) was also

from the more inshore areas. It is, therefore, not clear if the greater amount of euphausiid and copepod feeding in deep-water samples resulted from increased availability in deeper waters, or offshore waters, or both. It does appear, however, that as reported by Squires (1957) for *Illex*, *L. opalescens* taken inshore had a different diet from those taken offshore.

Fields (1965) suggested that female *L. opalescens* do not actively feed on the spawning grounds. Our results indicate that females do feed on the spawning grounds, although perhaps less intensively than males. Only percent frequency of occurrence of prey items between spawning ground males and females was significantly associated, while percent by number was not. Males ate larger meals by number than females. Perhaps, as suggested by Fields (1965), female squid do have digestive tracts in less active condition than do males.

It became clear that spawning-ground feeding was indeed atypical, as suggested by Fields (1965), when these samples were compared to other areas at similar depths. The percent similarity index was lowest in this comparison, and no correlation was found in either percent by number or frequency of occurrence.

Demersal feeding was more important on the spawning grounds, with bottom-associated organisms such as megalops larvae, polychaetes, gastropods, and eggs being more common in the diet. Crustacean feeding still dominated, with euphausiids being replaced by the more seasonal, and perhaps more localized, megalops larvae. Cephalopod fragments occurred most frequently in spawning-ground samples. True cannibalism, however, did not occur on these grounds. Cephalopod fragments probably do not reflect true feeding, but some form of behavior associated with crowding. This could explain the higher incidence of cephalopod fragments on the spawning grounds where animals tend to be more crowded.

Overall, it appears that *Loligo opalescens* is an important predator in the pelagic ecosystem of Monterey Bay, and presumably elsewhere in the California coastal waters. It feeds primarily on smaller crustaceans such as euphausiids, copepods, megalops larvae, mysids, and amphipods but also utilizes larger prey items such as fish and other cephalopods. The diet of *L. opalescens* changes markedly with depth of water and location but does not differ much between size categories or sexes. This appears to indicate that market squid tend to utilize similar prey items regardless of sex or size, but that differences in prey utilization may result from changes in patches of available prey or different behavior of this predator at different locations.

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