ABSTRACT

FOOD HABITS, MOVEMENTS, AND SEASONAL ABUNDANCE OF THE BLUE SHARK, *PRIONACE GLAUCA* (CARCHARHINIDAE), IN SOUTHERN CALIFORNIA WATERS

By

Timothy C. Tricas

January 1977

Eighty-one blue sharks were collected near Santa Catalina Island, California from March 1975 to March 1976. Sharks were sexed, measured and examined for stomach contents. The northern anchovy, *Engraulis mordax*, represented the major teleost prey item. *Histioteuthis heteropsis* was the predominant pelagic cephalopod in the diet, while the market squid, *Loligo opalescens*, represented the major inshore squid prey. Findings from telemetric trackings, digestion-rate experiments, and observations on local anchovy activity suggest that blue sharks feed primarily on dispersed near-surface schools of anchovies at night.

Male blue sharks of all sizes predominated during warmer months, while female sharks predominated in cooler months. Results of conventional taggings suggest that sharks do not maintain local home ranges and that immature

sharks exhibit an annual migration to coastal waters. Observations of blue sharks feeding on squid schools attracted to a night light revealed four general types of feeding behavior.

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By Timothy C. Tricas

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WE, THE UNDERSIGNED MEMBERS OF THE COMMITTEE

HAVE READ AND APPROVED THIS THESIS

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INTRODUCTION

The significance of top predators in a marine environment and their effects on trophic dynamics rests largely on their success as a predator on available prey species and subsequent competition with other predators. Sharks are among the top predators in nearly all oceans of the world, yet quantitative assessments of their roles in marine ecosystems have been severely neglected. The low status of sharks as an economic resource has in turn overshadowed their importance as predators and competitors with sport and commercial fisheries. The blue shark, Prionace glauca Linnaeus, fits well into this scheme both as a top marine predator and because of its widespread distribution in all warm temperate oceans of the world.

Descriptive accounts of the abundance and habits of the blue shark were provided in early investigations of oceanic shark distributions. In his classic paper on the sharks of the central Pacific, Strasburg (1958) established that the blue shark is the most widely distributed shark in the Pacific and that a northward expansion of its range occurs in the warmer summer and fall months. Neave and Hanavan (1960) reported a middle and late summer range extension for the blue shark into the Gulf of Alaska. In Atlantic waters, Bigelow and Schroeder (1948) have described a similar widespread abundance of blue sharks, and a corresponding range expansion in warmer months off the coast of the northeastern United States and Canada. Templeman (1963) reported the blue shark range in the northeast Atlantic to be bounded by the Gulf Stream south of the Grand Banks, with summer movements of sharks northward into the Gulf of St. Lawrence. The blue shark was recorded as a summer visitor to the North Sea and Baltic Sea (Aasen, 1966) with a northernmost record near Finnmark, Norway at $69^{o}45'$ N (Pethon, 1970). South Atlantic ranges include the west coast of South Africa (Bigelow and Schroeder, 1948) and the waters near Uraguay (McKenzie and Tibbo, 1964). Blue sharks also occur in the Mediterranean Sea (Bigelow and Schroeder, 1948; Lo Bianco, 1909) and the Indian Ocean (Smit, 1895). Longitudinal distributions of blue sharks in the western Pacific were reported by Suda (1953) and suggested the influence of oceanic currents on blue shark distributions and movements.

Information on the vertical distributions of blue sharks was given by Strasburg (1958), who provided evidence that blue sharks are broadly euythermal, frequenting water temperatures from 7.2 to $20.6^{o}C$. Other authors gave temperatures ranging from 8.5 to $22^{o}C$ (Johnson, 1974; McKenzie and Tibbo, 1964; Neave and Hanavan, 1960; Sciarrotta, 1974; Templeman, 1963). Strasburg (1958) also described greater blue shark abundance in the upper levels of northern waters and a "tropical submergence" in southern equatorial waters. Firsthand accounts were given by Davies and Bradley (1969) who observed blue sharks from a submersible at a depth of 275 m. The deepest record was given by Pethon (1970) who reported a blue shark captured at a depth of 370 m in Norwegian waters.

The predominance of small fish in the diet of blue sharks has been established by a number of authors. Bigelow and Schroeder (1948) reported that in northern Atlantic waters small fishes such as herring, _Clupea harengus_, and mackerel, _Scomber scombrus_, predominated in the blue shark diet, while spiny dogfish, _Squalus acanthias_, and sardine were prevalent in the diet in European waters. They also stated that blue sharks consumed large quantities of cod, haddock, and pollock commonly found on fishing banks. Stevens (1973) reported a major diet of clupeids; mackerel, _S. scombrus_; garfish, _Belone belone_; and jack mackerel, _Trachurus trachurus_, in sharks sampled from the southwest of England. Strasburg (1958) found that blue sharks from the central Pacific contained a mixed diet of fish, cephalopods and crustaceans. LeBrasseur (1964) noted that blue sharks from the northeast Pacific ocean fed on pomfret, _Brama raii_, lanternfish (Myctophidae), daggertooth, _Anotopterus pharao_, salmon, _Oncorhynchus_ sp., squid, shrimp, and salps.

Bane (1968) found that blue sharks from southern California waters fed principally on small fish like anchovies, *Engraulis mordax*, and pipefish, but that squid and pelagic crabs (Galatheidae) were also included in the diet. Blue sharks examined from Cornish waters by Couch (1862) revealed herring, garfish, dogfish, and eel, *Conger conger*. Lo Bianco (1909) reported finding anchovies, cephalopods, and flying fish eggs, *Exocoetus* sp., in blue sharks collected from the Bay of Naples.

Cephalopods have been described as a major component in the diet of blue sharks by Bigelow and Schroeder (1948), LeBrasseur (1964) and Strasburg (1958), but little information was given on specific identity. Stevens (1973) found several deep-water species of squid in sharks captured over the continental shelf off southwest England. Further investigation by Clarke and Stevens (1974) revealed at least nine different families of cephalopods occurring in the blue shark diet, many normally found in deep-basin waters indicating recent onshore movements of sharks from deeper waters.

In spite of accounts of sharks feeding on dead or wounded cetaceans, there is little evidence that blue sharks habitually prey on live, healthy marine mammals. Evidence of opportunistic feeding is presented by Bigelow and Schroeder (1948) in their accounts of blue sharks feeding on harpooned whale carcasses, and by Cousteau and

Cousteau (1970) of blue sharks feeding on an injured baby sperm whale. Stevens (1973) and Strasburg (1958) reported the presence of mammalian tissue in the stomachs of blue sharks, but it is most likely that predation is largely directed to dead mammals or those in poor health. Air/sea disasters have resulted in blue shark attacks on humans (Fitch, personal communication; Schultz and Malin, 1963), but these were generally directed to injured (e.g., bleeding or limp) persons or corpses, and most likely represents an unusual opportunistic feeding situation.

Relatively little is known of the general behavior of large, pelagic sharks due primarily to (1) problems encountered with keeping pelagic sharks alive in captivity, and (2) problems associated with extended field studies and observations in an aquatic environment (e.g., weather, limited time under water, locating and maintaining contact with sharks in the open ocean, etc.). Because of such logistical problems, many population and food habit studies on blue sharks have been based on data from sharks captured by sport and commercial fisheries during favorable seasons. As a result of uncontrolled sampling, quantitative ecological data are scarce, and little information exists in regard to seasonal shifts in food habits and size frequencies. Telemetric trackings have provided information on the diel movements of blue sharks (Sciarrotta, 1974), but relatively little is known of their orientation mechanisms and general behavior.

Early papers on the blue shark have established its widespread abundance and circumglobal distribution, and that it is a predator on and competitor with both commercial and sport fish resources. With these ideas in mind, I undertook a study in a fixed sampling area to provide a quantitative assessment of the diet of blue sharks in southern California waters, and to establish any seasonal variation in food habits, abundance, and related movements.

METHODS

Study Area

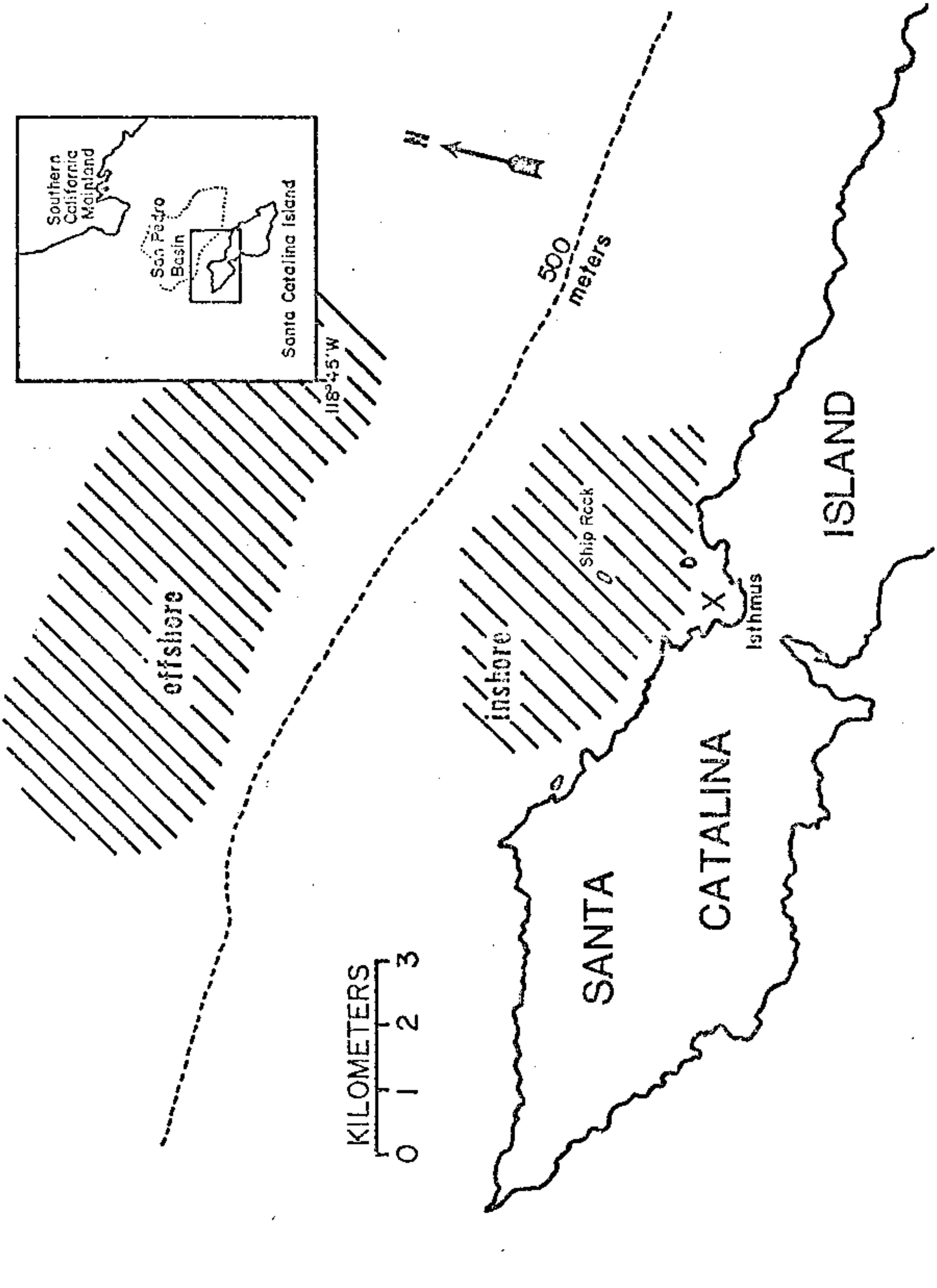
The study area included the waters north of the Isthmus, Santa Catalina Island, California (Figure 1). The northern coastline of the island is located 37 km south of Los Angeles Harbor and is separated from the mainland by the San Pedro Channel. Here the island is characterized by intermittent broad canyons and steep cliffs dropping to a narrow rock-sand shoreline. Beds of giant kelp, *Macrocystis pyrifera*, form the major inshore habitat along the island shore. A submarine shelf, averaging 150 m deep, extends about 2 km seaward where it slopes to a depth of 900 m, forming the floor of the San Pedro Basin.

Fishing stations were categorized as either inshore or offshore, relative to the island and submarine topography. Inshore stations were those above the shelf lying within 2 km of the island. Offshore stations were those beyond 2 km, lying above deeper basin waters, and were centered approximately 6 km north of the Isthmus.

Shark Collection

Sharks were collected between March 1975 and March 1976 on a monthly basis at sampling locations near

Figure 1. The study area off Santa Catalina Island, California. Sampling sites were located within the shaded areas. Site of observations of sharks feeding on spawning squid indicated by (x).


Southern California Mainland
San Pedro Basin
Santa Catalina Island
118°45'W
N
500 meters
offshore
inshore
Ship Rock
X
Isthmus
SANTA
CATALINA
ISLAND
KILOMETERS
0 1 2 3

the Isthmus area of Santa Catalina Island, California. (Sharks sampled in April 1976 were sexed, measured, tagged, and released. These sharks did not contribute to the gut analyses.) Shark sampling was arranged into morning (a.m.) and afternoon (p.m.) fishing sessions at inshore and offshore areas (Figure 1). The sampling schedule was arranged so that equivalent monthly fishing times were spent for the inshore-offshore/a.m.-p.m. combinations whenever possible.

Sharks were attracted to a drifting 7-m work-boat by baiting with slashed pacific mackerel, Scomber japonicus, suspended in a wire basket 5 m beneath the surface. Once attracted, sharks were captured by hook and hand line using mackerel or market squid, Loligo opalescens, as bait. Sharks were landed as quickly as possible to minimize regurgitation and were measured, sexed, and inspected for mating scars and general health. Esophagi and stomachs were removed and contents strained through a 1-mm mesh netting and preserved in 15 percent formalin. Recognizable items were identified on site and their states of digestion recorded. Intestinal tracts were occasionally examined but contributed little information on shark feeding because of the small pylorus which apparently restricts passage of identifiable prey fragments. Each shark was inspected internally for signs of sexual maturity. The arrival of all sharks near the bait was recorded, whether they were captured, tagged, or only observed. Temperature/depth profiles to 120 m were recorded with a bathythermograph.

Stomach Content Analysis

Cephalopod beaks. Except for the market squid, *Loligo opalescens*, cephalopods in the diet were represented exclusively by beaks. All beaks were matched into sets of upper and lower halves, and identified according to Clarke (1962) and Pinkas et al. (1971). Identifications were verified by comparisons with beaks from collections of local species.

Although cephalopod beaks constituted positive evidence of the feeding of blue sharks, some basic assumptions had to be made before quantification of their importance could be established. In this analysis I assumed that all beaks found within a particular stomach (1) were obtained by the shark during a relatively short time (e.g., a few days), and (2) had not been retained for extended periods (e.g., weeks or months). These assumptions are supported by the relatively few beaks found per stomach and by the similar decomposition state of beaks that were present in each stomach. It is most probable that beaks were regurgitated by the sharks at frequent intervals, thus voiding the stomachs of hard-to-digest material. Even the smallest beaks were apparently rejected since those examined were rarely fragmented, suggesting they had not been in the stomach for great lengths of time.

Digestion rates. Digestive rates were determined for captive blue sharks. Three healthy, active sharks were acclimated for 24-48 h in holding tanks at Marineland of the Pacific and then fed marked anchovies and market squid. Stomach contents of these sharks were examined at 6, 12 and 24 h after feeding. These digestion rates were applied to the digestive states of prey recovered from wild sharks from which times of ingestion (feeding) were estimated.

Distribution of prey among stomachs. Relative distributions of major prey species among shark stomachs were expressed as a simple coefficient of dispersion (COD):

COD = sample variance/sample mean.

Sample mean was computed as the average number of prey per shark stomach. Sample variance was calculated from the frequency distribution of the numbers of prey per stomach for sharks. Theoretically, a coefficient of 1 describes a random distribution, a coefficient >1 describes a contagious distribution, and a coefficient <1 describes a uniform (evenly spaced) distribution. A large coefficient would indicate that prey are clumped among stomachs, i.e., many being empty and few having high numbers of prey. A low coefficient would suggest a more dispersed distribution of prey among stomachs.

Quantifying Cephalopod Prey

Quantification of cephalopods was expressed as an "Index of Relative Importance" (IRI) as described by Pinkas (1971):

$$IRI = (N+V)F,$$

where N (numerical percent) is the percent of individuals of that species among all individual cephalopods recovered; V (volumetric percent) is the percent volume represented by that particular species of all cephalopods recovered; and F (frequency) the percent of individual shark stomachs containing that prey species. Whole volumes were estimated from beak-size/body-weight regressions for the major cephalopod families as provided by Clarke (1962). Density of cephalopod flesh was assumed to be 1 gm/cm^3. A regression line for the family Ocythoidae was estimated by plotting beak measurements and body weights on Clarke's Octopodidae and Argonautidae regressions and constructing a parallel growth rate. Beak-length/body-weight regressions for *Vampyroteuthis infernalis* were obtained from Binder (unpublished). Personal examination of the squid, *Loligo opalescens*, revealed some variation in beak-size/body-weight characteristics, but these were consistent enough to fit in with Clarke's regression for the Loliginidae. Unidentified cephalopods were omitted from the quantification as they represented only a minor portion of the diet (four species in eight stomachs).

Movement Studies

Two types of tagging were employed in this study. Conventional tagging used Floy FH9 stainless steel dart tags with plastic spaghetti streamers which were addressed and color coded for day and station. Tags were applied to bait-attracted sharks from the boat with an applicator pole as they swam near the surface. When possible, the animals' sex was observed and its length estimated.

Short-term movements of sharks were monitored by ultrasonic telemetry using instrumentation and techniques similar to that described by Ferrel et al. (1974) and Nelson (1974). The transmitters operated at fixed frequencies near 40 Khz. Transmitters were applied to free-swimming sharks via FH69 stainless steel darts. Range of the units was approximately 2 km under good conditions, but useable transmission distance was highly dependent upon physical factors such as ambient noise from waves, wind, and biological sources. When possible, transmitters were equipped with a depth sensor which allowed monitoring of vertical movements. Transmitter signals were tracked with a DuKane N15A235 tuneable ultrasonic receiver with a staff-mounted directional hydrophone.

Field Observations

In an effort to obtain insight on prey availability in areas frequented by sharks, habits and ranges of actual and potential prey species were observed using scuba and by snorkeling. By observing selected inshore fishes, general abundance of prey could be established and thus contribute understanding to the overall inshore prey potential. Open water diving provided a means for gathering information on the occurrence and activity of prey species in offshore areas.

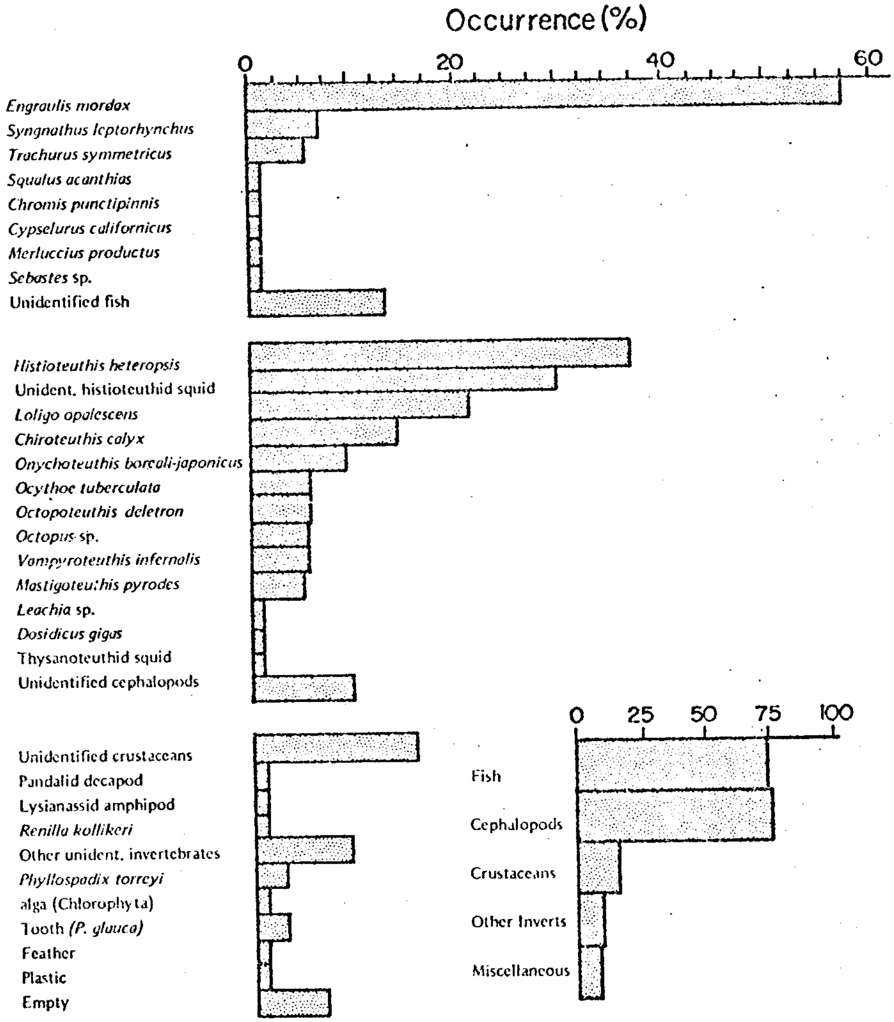
Night-lighting in offshore and inshore waters was used to attract potential blue shark prey. The Isthmus spawning run of market squid, _Loligo opalescens_, occurred in January 1976. At dusk, large schools of squid were located near the bottom (30-40 m deep) with a Gemtronics GT-1056 recording fathometer. The boat was then anchored directly above the school, and a 1500-watt light suspended over the water. Squid schools would normally rise towards the light, concentrate at the surface and begin mating. Feeding behavior of blue sharks among these spawning squid schools was observed and recorded.

RESULTS AND DISCUSSION

Prey Species

Sharks were captured in all months of the study. Of the 81 sharks sampled, 96 percent had recognizable food items in their stomachs (Figure 2). Fish remains occurred in 72 percent, with the northern anchovy, *Engraulis mordax*, present in 57 percent. Other fish occurred at relatively low frequencies in the diet. Cephalopod remnants occurred in 74 percent of the stomachs, with the pelagic squid, *Histioteuthis heteropsis*, present in 38 percent. Other cephalopods included numerous other pelagic species as well as inshore spawning market squid, *Loligo opalescens*. Crustaceans were found in 18 percent of sharks sampled and generally appeared as single unidentifiable individuals in an advanced digestive state. Benthic forms in the diet included the sea pansy, *Renilla kollikeri*, surfgrass, *Phyllospadix torreyi*, and a portion of flat green alga (Chlorophyta). Flotsam such as plastic and feathers was occasionally found, as were gelatinous planktonic invertebrates. On two occasions, blue shark teeth were recovered from stomachs. There were most likely swallowed after being dislodged by new replacement teeth or during the capture of prey.

Figure 2. Total stomach contents from the 81 blue sharks sampled during the year. Offshore and onshore data combined. Frequency = percent of the 81 individuals containing that prey species.

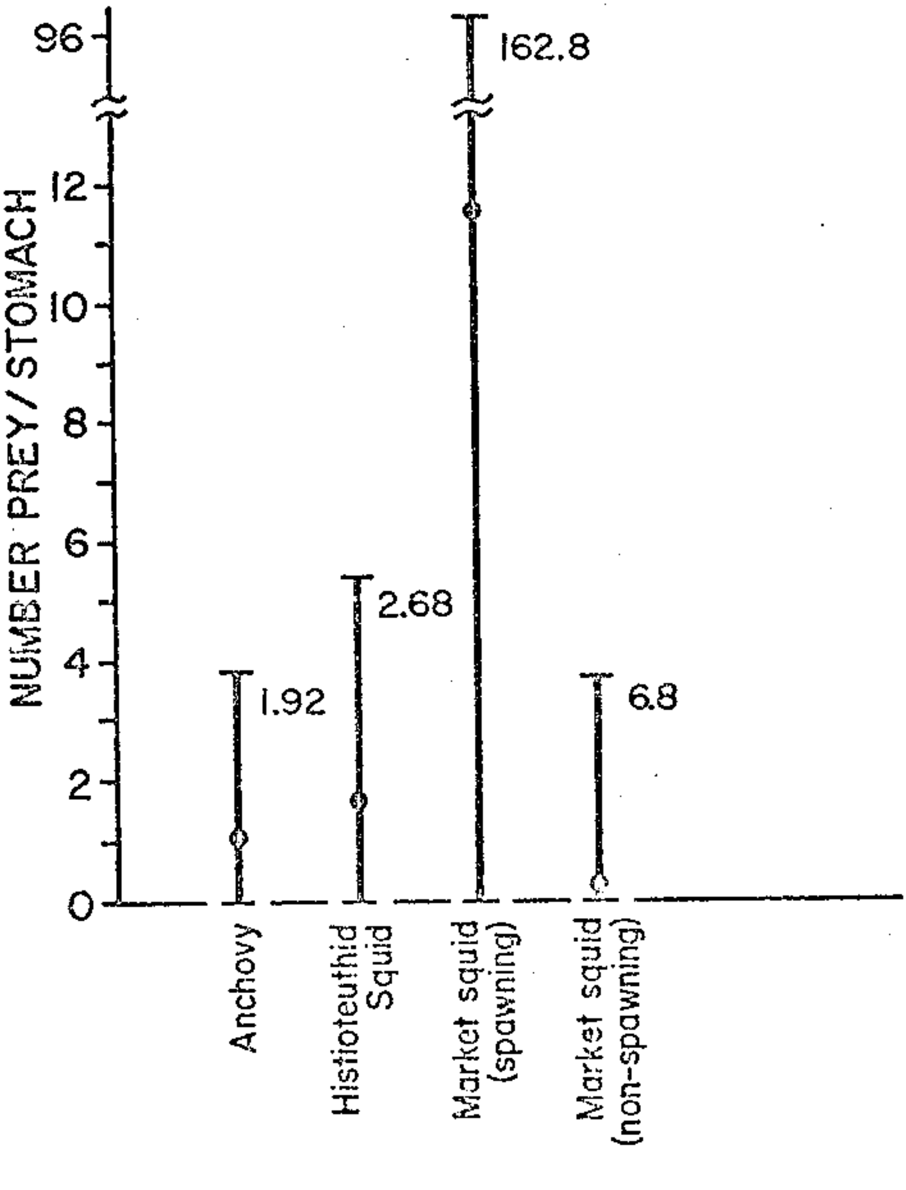

Occurrence (%)
0
20
40
60
Engraulis mordax
Syngnathus leptorhynchus
Trachurus symmetricus
Squalus acanthias
Chromis punctipinnis
Cypselurus californicus
Merluccius productus
Sebastes sp.
Unidentified fish
Histioteuthis heteropsis
Unident. histioteuthid squid
Loligo opalescens
Chiroteuthis calyx
Onychoteuthis boreali-japonicus
Ocythoe tuberculata
Octopoteuthis deletron
Octopus sp.
Vampyroteuthis infernalis
Mastigoteuthis pyrodes
Leachia sp.
Dosidicus gigas
Thysanoteuthid squid
Unidentified cephalopods
Unidentified crustaceans
Pandalid decapod
Lysianassid amphipod
Renilla kollikeri
Other unident. invertebrates
Phyllospadix torreyi
alga (Chlorophyta)
Tooth (P. glauca)
Feather
Plastic
Empty
0
25
50
75
100
Fish
Cephalopods
Crustaceans
Other Inverts
Miscellaneous

Distribution of Prey Among Stomachs

Mean number of prey per shark for the three most frequent food items are given in Figure 3. Anchovies and histioteuthid squid were consistently found in relatively low numbers, averaging about one per stomach. Overall, market squid, Loligo opalescens, averaged four individual prey per shark stomach. However, the seasonal spawning of L. opalescens created a special condition under which prey availability varied from the non-spawning season. In winter months, large spawning schools of squid were found close inshore and presented a more grouped (clumped) prey to the sharks. At these times market squid were usually found in either great numbers within a stomach, or not at all. In non-spawning months, market squid did not form inshore schools and were found only infrequently in the stomachs.

Coefficients of dispersion show the relative distributions of these prey items among shark stomachs. The consistent occurrence of few anchovies and histioteuthid squid per shark stomach created relatively small coefficients, and suggests that sharks are most likely obtaining these prey species somewhat regularly over a large area. The large coefficient of dispersion in the case of spawning market squid strongly supports the feeding of sharks on "clumped" (schooling) prey.

Figure 3. Distribution of the three major prey items found in blue shark stomachs. Horizontal bars = 95 percent confidence limits. Mean number of anchovy and histioteuthid squid are for the 81 sharks sampled. Means for market squid were computed for squid spawning season (March 1975, December-January 1976: 21 sharks) and non-spawning season (April-November 1975, February 1976: 60 sharks). Coefficients of dispersion (numbers shown) indicate relative dispersion of prey among stomachs (see text for explanation).


NUMBER PREY / STOMACH
96
12
10
8
6
4
2
0
162.8
2.68
1.92
6.8
Anchovy
Histioteuthid Squid
Market squid (spawning)
Market squid (non-spawning)

Relative Importance of Cephalopod Prey

On an annual basis, *L. opalescens* constituted the overall major cephalopod food item in the blue shark diet as listed in Table 1. *H. heteropsis* represents the major offshore cephalopod prey item for blue sharks with other pelagic and open-water species complimenting the diet. Monthly analysis revealed a shift in index of relative importance (IRI) between *L. opalescens* and *H. heteropsis*, as well as other deepwater cephalopod species. Seasonal shifts of IRI's, on a monthly basis, are listed in Table 2.

Digestive States of Prey

The digestive states of bony fish recovered from blue shark stomachs were classified into three stages:

Stage 1: included freshly ingested fish with scales, skin and fins intact; some preliminary digestion may have occurred, especially around the operculum and eye, but the whole animal was easily recognized.

Stage 2: was characterized by exposed myotome, an open body cavity, viscera at least partially intact, head usually separated from main body by digestion, and some bone exposure.

Stage 3: was the advance digestive state where identification of the prey could be made only by vertebral or otolith characteristics.

Table 1. Annual relative importance of cephalopod prey[a]

Rank	Species	Percent sharks with this item (F)	Percent of all cephalopod species (N)	Percent of diet volume (V)	Index of relative importance (IRI)
1	Loligo opalescens	21.0	70.70	31.9	2155.0
2	Histioteuthis heteropsis	37.0	11.50	10.4	813.0
3	Histioteuthis sp.	23.5	4.98	0.31	124.0
4	Chiroteuthis calyx	14.8	5.38	1.45	101.0
5	Thysanoteuthid squid	1.23	0.20	43.3	53.5
6	Onychoteuthis boreali-japonicus	8.64	2.40	3.63	52.1
7	Vampyroteuthis infernalis	4.94	0.80	2.21	14.9
8	Octopoteuthis deletron	6.17	1.00	0.82	11.2
9	Dosidicus gigas	1.23	0.20	5.05	6.46
10	Ocythoe tuberculata	4.94	0.80	0.38	5.83

Table 1 (continued)

Rank	Species	Percent sharks with this item (F)	Percent of all cephalopod species (N)	Percent of diet volume (V)	Index of relative importance (IRI)
11	*Mastigoteuthis pyrodes*	3.70	0.60	0.30	3.33
12	*Octopus* sp.	4.94	1.39	0.21	7.90
13	*Leachia* sp.	1.23	0.20	0.0042	0.251

[a]Four small unidentified species (in eight stomachs) were omitted from the ranking analysis.

Table 2. Monthly index of relative importance (IRI) of cephalopod prey[a]

Species	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb
Loligo opalescens	1596	-	-	392	21	378	1597	9571	-	1098	11564	-
Histioteuthis heteropsis	780	17369	3917	6454	166	9406	2298	254	-	1376	370	-
Histioteuthis sp.	21	440	1596	-	234	275	1800	102	1625	388	-	4000
Chiroteuthis calyx	-	429	-	-	67	1318	783	1259	6395	1174	-	-
Thysanoteuthid squid	-	-	-	-	-	-	-	-	-	1561	-	-
Onychoteuthis boreali-japonicus	68	-	-	-	169	-	-	-	-	1188	23	-
Vampyroteuthis infernalis	-	-	-	-	130	-	521	-	-	136	-	-
Octopoteuthis deletron	40	-	1373	-	19	-	-	-	-	55	-	-
Dosidicus gigas	-	-	-	-	216	-	-	-	-	-	-	-
Ocythoe tuberculata	14	-	-	-	23	-	138	-	-	47	-	-

Table 2 (continued)

Species	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb
Mastigoteuthis pyrodes	-	-	-	-	-	-	-	-	1825	189	-	-
Octopus sp.	-	-	-	-	142	-	-	102	-	50	-	-
Leachia sp.	-	-	-	-	14	-	-	-	-	-	-	-

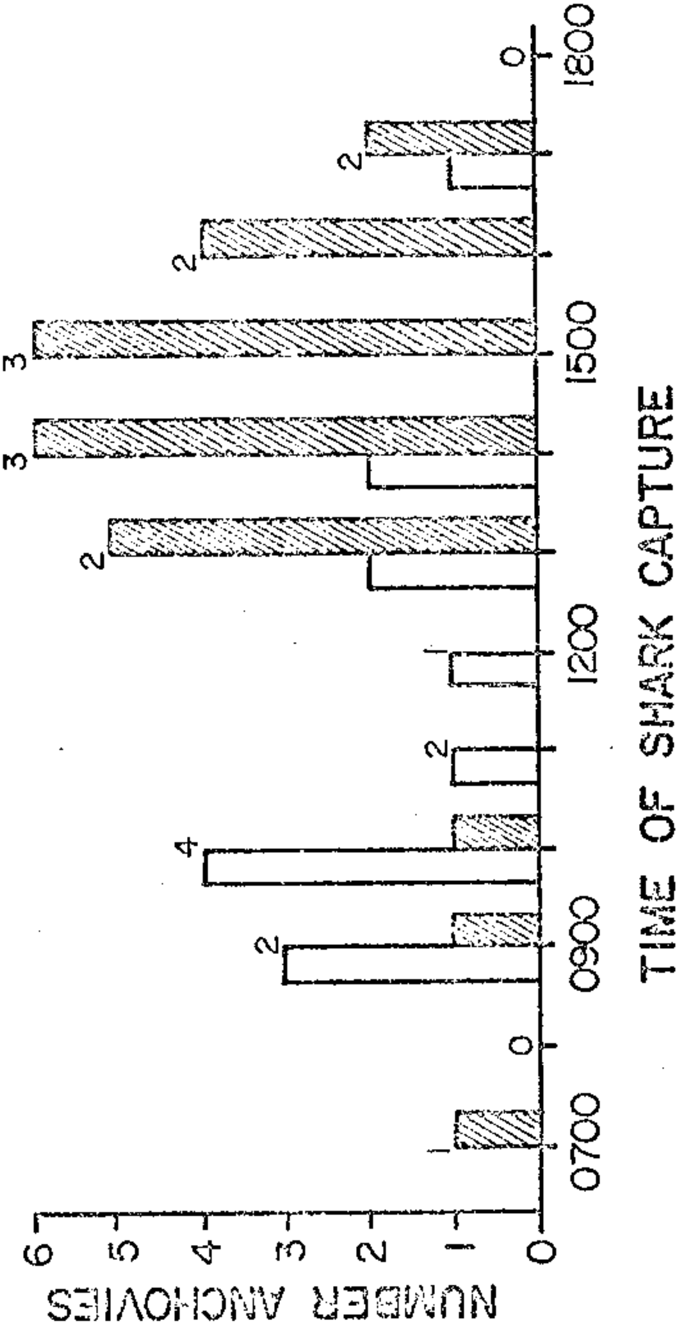
[a]Four unidentified species (in eight stomachs) were omitted from the ranking analysis.

Digestion rates were determined for healthy, active blue sharks held in tanks at Marineland of the Pacific. Anchovies removed from shark stomachs at 6 h were easily recognizable and showed only preliminary digestion of fins and the edge of the operculum. At 12 h the ventral abdominal wall of the anchovy had been digested, exposing the viscera. The head was usually attached, but only by the vertebral column and dorsal flesh. Scales had begun to separate from the skin and some myotome was exposed on smaller anchovies. At 24 h, anchovies were well digested with only small portions of myotome and digested vertebrae present. Some otoliths were recovered and appeared to be somewhat decomposed. Digestive rates were generally faster for smaller anchovies.

Times of ingestion for the digestive stages of anchovies recovered from wild sharks were estimated by applying data from the above digestive rate test. Stage 1 (slight digestion) corresponded to a duration of up to 6-8 h from time of ingestion. Stage 2 (moderate digestion) occurred at about 15 h after consumption of the anchovies, and Stage 3 (advanced digestion) represented food held approximately 24 h or longer.

The digestive states of all Stage 1 and 2 anchovies recovered from the stomachs of blue sharks are given in Figure 4. Anchovies that were freshly ingested (Stage 1)

Figure 4. Time frequency distribution of digestive Stage 1 and Stage 2 anchovies recovered from shark stomachs. Stage 1 = light bars; Stage 2 = shaded bars. Numbers at top of bars indicate quantity of sharks sampled containing anchovies in Stage 1 and/or Stage 2 of digestion.


NUMBER ANCHOVIES
0
1
2
3
4
5
6
0700
0900
1200
1500
1800
TIME OF SHARK CAPTURE

predominated in sharks captured in early morning hours, while partially digested anchovies (Stage 2) were more common in sharks sampled in the afternoon. Anchovies in advanced digestive stages (Stage 3) were not included because of the overlapping time span of that stage, i.e., more than 24 h.

Market squid, Loligo opalescens, generally showed slower digestion than anchovy. At 6 h after ingestion, whole squid were easily recognizable, showing only slight decomposition of chromatophores and skin. At 12 h after ingestion, digestion was still negligible. At 24 h, the squid head had detached from the body and lenses had separated from the optic cups. The squid pens (dorsal cartilage) were intact, but had lost their rigidity. Beaks were still implanted within the buccal mass. Digestion appeared to be faster for smaller squid.

Teleost Prey

Engraulis mordax (Engraulidae), northern anchovy. Anchovies represented both the highest numerical count of any prey species and the most frequent food item occurring in the blue shark diet. The prevalence of fresh anchovies recovered from shark stomachs indicated this prey species to be the main forage item for sharks in the study area. Sharks of all size ranges (81-207 cm total length) were found to feed on anchovies in all months of the year, further emphasizing the significance of this prey.

Pelagic fish surveys indicate a great abundance of anchovies in southern California waters. Mais (1974) reported that major anchovy concentrations in the California Current System were centered within the Southern California Bight. These semi-protected waters lie between Point Conception and Point Descanso, Mexico, with a seaward boundary extending from San Miguel Island to the Sixty Mile Bank (approximately 50,000 km^2). Outside of this area anchovy population densities were reported to be significantly lower. Concentrations of anchovy schools were greatest within 37 km of the mainland over deep water (228.6-731.5 m). More distant deep waters (37-111 km from the mainland) collectively contained the largest portion of the population. Anchovy populations in southern California waters were reported to have a central stock spawning biomass of 3.5 million tons (MacCall et al., 1976), the largest of any local wet fish stock.

Schooling characteristics of the anchovy have been shown to be dependent on submarine topographies, underlying bottom depths, and season (Mais, 1974). Anchovies in waters over bottom depths of more than 183 m most commonly exhibited schooling in small, low density, near-surface schools during daylight hours. These schools occurred at depths between 5 and 30 m from the surface and ranged from 4-15 m thick. Schools typically dispersed at night into a thin surface scattering layer and reassembled at daylight. Another frequent schooling behavior reported by Mais was the formation of large, deep, dense schools (about 100-200 m from the surface) during the day, which dispersed into a coarse scattering surface layer at night. Similar types of schooling behavior were reported with apparent seasonal variations.

Such nocturnal dispersion of anchovy schools appeared to be the case in this study area. Loose, non-polarized aggregations of anchovies were observed while snorkeling in offshore waters during post-twilight hours. At these times, anchovies were observed to be dispersed a minimum of 0.5 m apart, engaged in apparent feeding behavior. Stationary individuals exhibited a "sigmoid" lateral flexing and then lunged forward with mouths open in what appeared to be an attempt to capture individual zooplankters. Low-density aggregations such as these may represent an early stage of school dispersion. Later at night (0100-0400) lone individual anchovies were observed on several occasions, suggesting more complete nocturnal dissolution of anchovy schools.

The low numerical average of anchovies per shark stomach suggests that anchovies were not taken in large numbers by sharks in the study area. Sharks captured were never gorged with anchovies; commonly, they contained one or two freshly ingested fish. It seems probable that the low anchovy count per stomach is at least partially due to the nocturnal dispersion of anchovies at night, whereby school densities are reduced and individual anchovies are taken by the nocturnally active sharks.

Anchovy populations in other areas may exhibit different schooling behaviors and abundance, and might therefore present completely different feeding conditions for blue sharks. It would seem likely to find large numbers of anchovies in shark stomachs from an area where anchovy schools are more abundant and show less dispersion. Variability of blue shark feeding would also influence consumption rates as would chance encounters with anchovy schools during the day. In addition, sharks might pick up large numbers of anchovies as a result of dives to deeper daytime schools. Blue sharks previously captured off Newport Beach, California were found to contain large numbers (approximately 12-15) of freshly eaten anchovies (Tricas, unpublished), indicating that blue sharks do consume large quantities of anchovies, and that predator-prey relationships may vary with area.

The location of toothmarks on recently ingested anchovies suggest that prey were almost exclusively captured from behind and that they were swallowed whole, and were rarely found to be bitten in half. When present, tooth marks were usually located on the posterior lateral third of the anchovy, in many cases only deep enough to penetrate the skin and not the myotome. Often tooth marks were totally absent indicating that prey had been engulfed whole, without any use of the teeth for capture.

Reactions of blue sharks to moving prey were observed during tests with excited sharks attracted to the work-boat. "Prey" consisted of a dead anchovy attached to a light fishing line which was cast beyond the circling sharks and then retrieved towards the boat. Numerous trials revealed a consistent approach of the sharks to the prey from behind, as described in my field notes: "As I retrieved the 'prey' towards the boat, a 1.5-m male [shark] sighted the anchovy and seemed to intentionally make a wide circle so as to come up from behind. He then made a rapid rush up to the anchovy and bit the bait at mid body and swallowed it whole." The same tests using Pacific mackerel as "prey" revealed similar posterior attacks--in these cases, the shark partly turning on its side to take the "prey." Tooth marks on these artificial prey items were similar to those observed on anchovies recovered from blue shark stomachs.

The present status of the blue shark-anchovy association may be the aftermath of a previously more complex predator-prey web. Southern California commercial fisheries have severely depleted Pacific mackerel (Scomber japonicus) and Pacific sardine (Sardinops caeruleus) populations (MacCall et al., 1976), both natural prey species for the blue shark. The disappearance of sardines as a food source for larger predatory game fish has affected other commercial and sport fisheries and certainly has similar implications on predator-prey relationships for local blue shark populations. Although such declines in forage species may have significantly increased predation on local anchovy populations in recent years, the anchovy population in southern California waters is in an apparently thriving state. Pinkas (Pinkas et al., 1971) reported an apparent increase in anchovy abundance in recent years. Furthermore, with present commercial fishing techniques, it appears that the northern anchovy is in little danger of commercial over-exploitation (MacCall, 1976; Mais, 1974); and the role of the northern anchovy as a prime forage species of the blue shark is likely to remain constant in the near future.

Syngnathus leptorynchus (Syngnathidae), kelp pipefish. The kelp pipefish was the second most frequent teleost food item in the blue shark diet. The pipefish, however, was found in only 6 percent of the stomachs, and because of its small size, must be regarded as of minor importance. The average size recovered was 15.7 cm (total length), corresponding to less than a 2 gm body weight.

Pipefish normally occur in shallow inshore areas among kelp canopy habitats and in shallow beds of surfgrass, Phyllospadix torreyi. Blue sharks containing freshly ingested pipefish were captured 2-5 km offshore, well away from kelp and surfgrass communities. It cannot be ruled out that pipefish might have been taken by blue sharks from inshore surfgrass beds, but it seems more probable that these were picked up near floating vegetation in open waters. Pipefish were observed swimming at the surface in open water (away from surfgrass or kelp) at night and among flotsam kelp during daylight. It has also been reported (Galt, personal communication) that pipefish normally are found at the surface at night in the San Pedro Channel, possibly suggesting a more common occurrence in open water than previously thought.

Trachurus symmetricus (Carangidae), jack mackerel. Although only 5 percent of sharks examined contained evidence of jack mackerel, abundance of this prey was at times enormous, especially in inshore areas. Throughout the study, vast schools of T. symmetricus were observed near kelp beds during daylight hours. Jack mackerel were commonly seen swimming in tight schools along the outer edges of kelp beds, or sometimes aggregated within the kelp itself. At night, jack mackerel were often observed apparently feeding in open inshore waters (away from kelp) often interspersed with Pacific mackerel, Scomber japonicus. During squid spawning season, both Pacific and jack mackerel were often found directly beneath squid schools, but blue sharks were never observed attempting to capture either fish, squid apparently being preferred.

The jack mackerel is widely distributed throughout the eastern Pacific from southern Baja California to the Gulf of Alaska (Miller and Lea, 1972), and is found from inshore waters to hundreds of miles offshore (Feder et al., 1974). Knaggs (1973) estimated a large standing biomass of 0.7 to 1.5 x 10^6 tons (in 1972) for the jack mackerel population in southern California waters.

On a basis of distribution, T. symmetricus presents at least two prey opportunities for blue sharks. Smaller jack mackerel, common in inshore areas, apparently undergo a nocturnal movement away from kelp beds to feed, and thus become a potential prey to sharks in the area at night, later returning to the protection of kelp beds during the day. Larger pelagic jack mackerel represent a schooling prey source for blue sharks in open waters. Neave and Hanavan (1960) reported expansion of both blue shark and jack mackerel ranges in the Gulf of Alaska during the summer which might suggest feeding motivated blue shark movements.

Chromis punctipinnis (Pomacentridae), blacksmith. Three blacksmith were recovered from a large male blue shark captured inshore (near Ship Rock) at noon. Digestive states suggested that they were recently ingested, probably near dawn. No tooth marks were found on any of the blacksmith, indicating that they had been engulfed whole without being bitten. Blacksmith of the size recovered were commonly observed in mid-water feeding aggregations and comprised a major portion of local symbiotic cleaning stations (Limbaugh, 1961). At times, *C. punctipinnis* were observed 200 m from the nearest surface kelp over 75 m of water. Should a shark enter the area, such exposed blacksmith would have no immediately available shelter and would make an easy prey target.

Many pomacentrids form mid-water feeding aggregations in daylight hours and retreat to the shelter of rocks and crevices during darkness (Hobson, 1968, 1974) and the blacksmith behaves similarly. The presence of these diurnal planktivores in the water column during the day presents a potential food source to those sharks near kelp beds. It has also been suggested that blacksmith are vulnerable to some predation, e.g., from swell sharks, *Cephaloscyllium ventriosum*, while in their inactive nocturnal phase near bottom shelter (Johnson, 1974).

During breeding in late spring, adult blacksmith were observed in widespread concentrations over the rocky substrate. During courtship, spawning and subsequent guarding of the nest, large numbers of blacksmith developed external infections, skin loss, and necrotic tissue, soon after which a "die off" occurred, similar to that described by Turner and Ebert (1962). This event created an opportunistic feeding situation for large predator fish. White sea bass, Synocion nobilis, kelp rockfish, Sebastes atrovirens, and swell sharks, Cephaloscyllium ventriosum, were observed feeding on dying or injured blacksmith. Standora (1972) found blacksmith in the stomachs of angel sharks, Squatina californica, captured at Ship Rock. Blue sharks have been observed chasing blacksmith at the edge of beds of giant kelp, Macrocystis pyrifera, by Nelson (personal communication) and Given (personal communication).

Cephalopod Prey

The high occurrence and advanced digestive state of pelagic cephalopod remnants suggests that cephalopods are a major component in the diet of blue sharks while in relatively distant offshore waters. Examination of known diel migrations and other behavioral movements of these positively identified prey species can be useful in establishing feeding movements and vertical ranges of the blue sharks.

Histioteuthis heteropsis (Histioteuthidae). This pelagic squid was the most frequent and numerically abundant cephalopod prey item. Beaks occurred in 39 percent of stomachs examined and were recovered from sharks in almost every month of the study. A smaller Histioteuthid beak form was also commonly found. This squid may be a juvenile or subadult *H. heteropsis*, or another genus. Nonetheless, histioteuthid squid were present in 43 percent of sharks collected in this study. The lack of any whole or partially digested squid bodies suggests that these were probably in the stomach for a number of days and were most likely taken over deep outer basin waters.

Roper and Young (1975) reported that *H. heteropsis* populations are concentrated between 500 and 800 m during daylight hours and undergo a vertical migration to the surface at night. The relatively high percentage of individual sharks possessing *H. heteropsis* suggests that blue sharks are obtaining them regularly, most likely near the surface at night in waters farther out to sea.

Loligo opalescens (Loliginidae), market squid. This species is a seasonal food source utilized primarily by female blue sharks during the winter spawning of the squid near the island (refer to section on blue sharks and spawning squid, page 53). Individual beaks of *L. opalescens* were recovered on occasion from sharks taken in summer (non-squid spawning) months. Leatherwood (personal communication) of the Naval Undersea Center, San Diego, California, noted evidence that pilot whales make deep dives into submarine canyons and ledges to feed on schools of L. opalescens in non-spawning months. Blue sharks may make similar dives or may pick up squid on the upper limits of these deep schools. Individual market squid were observed and captured in surface waters during daylight hours 2 months before squid spawning activity began at the Isthmus. Sharks may have obtained solitary market squid that were in pre-spawning upward movements from deeper waters.

Mastigoteuthis pyrodes (Mastigoteuthidae). The occurrence of M. pyrodes beaks was rare (4 percent of sharks examined) and represented those of juvenile squid.

This species is commonly found in deep sea waters. Roper and Young (1975) have described upper diurnal limits at about 600 m with a slightly higher occurrence of 300-400 m at night. Clarke and Lu (1974) reported capturing a juvenile Mastigoteuthis during the day at 0-200 m in Atlantic waters, one of the shallowest captures of any Mastigoteuthis, which might indicate juveniles in upper water levels and adults in deeper regions (ontogenic descent). The rare occurrence of M. pyrodes suggests that blue sharks are probably feeding in waters above the normal adult distribution of this squid.

Octopoteuthis deletron (Octopoteuthidae). This pelagic squid was found in 6 percent of blue shark stomachs sampled. The upper daytime limit of this species is about 200 m (Roper and Young, 1975), and is reported as not exhibiting a "typical" diel vertical migration, rather a nocturnal expansion over a greater range of depths. This expansion includes concentrations of *O. deletron* in near-surface waters at night.

Vampyroteuthis infernalis (Vampyroteuthidae). This bathypelagic squid occurred infrequently (5 percent) in the blue shark diet. It is a deep water non-migrating species which appears to be restricted by a number of physical factors such as temperature, salinity, and dissolved oxygen. The normal upper limit has been given by Roper and Young (1975) to be around 600 m. Clarke and Lu (1975) reported 610 m to be the shallowest depth that *V. infernalis* was found in north Atlantic waters. A few scattered instances of captures between 100 and 400 m were reported by Roper and Young (1975), but such finds were rare. Its occurrence in the blue shark diet may be a result of sharks picking up stragglers on the upper fringes of the main population as in the case of *Mastigoteuthis*, or as a result of occasional deep dives by blues.

Chiroteuthis calyx (Chiroteuthidae). This species was found in 15 percent of shark stomachs examined. Beaks recovered were from larval or subadult squid.

Members of this family have large larval stages which are commonly found in southern California waters. Vertical distribution of C. calyx include a characteristic ontogenic descent with smaller larvae in upper water levels and larger subadults deeper. Roper and Young (1975) reported an indication of some larval vertical migration at night to the upper 100 m waters. Vertical movement data for subadults is scarce, but there may be some degree of nocturnal ascent from daytime ranges of 500-800 m.

Movements

Conventional tagging. One hundred, twenty blue sharks were tagged with conventional plastic dart tags from August to February in the general area 5 km north of the Isthmus (Table 3). (In addition, three mako sharks, Isurus oxyrinchus, were tagged, of which one was recovered approximately 160 km southwest of the Isthmus 3 days later.) As of 1 September 1976, three of these sharks have been recovered. One shark, tagged in mid September 1975, was recovered on the south side of Santa Cruz Island, 105 km northwest of the tagging site, 39 days later. Another shark, tagged in May 1976, was

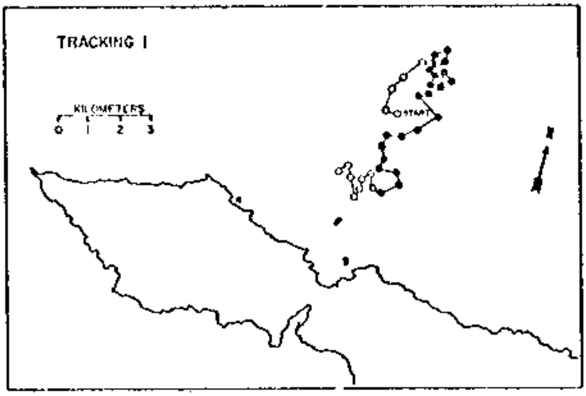
Table 3. Unpublished blue shark data from sharks captured by other investigators in the general vicinity of the study area

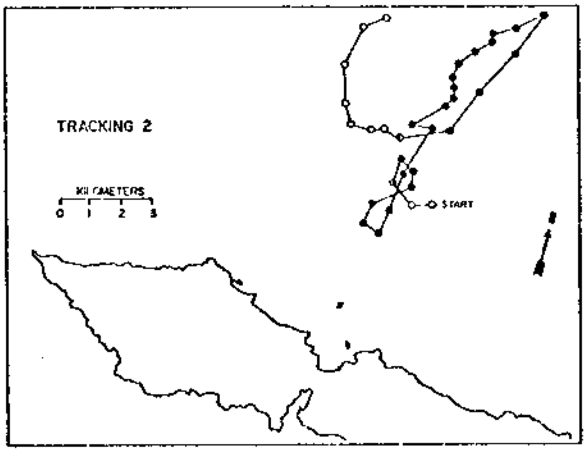
Date	Male:female	Total length male $\overline{X}$	Total length female $\overline{X}$	Locality	Principle investigator
June 1964	5:1	167.4	170.2	Harrison Reef, Magu Canyon	S. Applegate
Aug. 1966	4:2	148.44	129.25	West end of Catalina Island	D. Nelson
Sept. 1966	7:1	167.1	223.52	San Pedro Channel	D. Nelson
Oct. 1966	23:2	160.52	145.1	San Pedro Channel	D. Nelson
Nov. 1966	1:2	153.67	164.47	San Pedro Channel	D. Nelson
April 1967	3:6	160.02	149.0	San Pedro Channel	D. Nelson
July 1967	7:0	173.45	-	San Pedro Channel	S. Applegate
July 1967	6:0	174.03	-	San Pedro Channel	D. Nelson

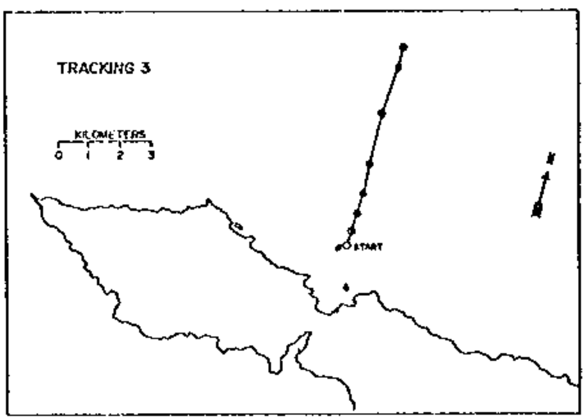
recovered 10 km west of Point Loma, 145 km southeast of the Isthmus, 241 days later. A third shark, tagged in August 1975, was recaptured on the south side of Santa Cruz Island, 120 km from the Isthmus, 346 days later. No tagged sharks were reobserved in the study area after the original tagging session, even after considerable baiting for sharks in the same general area on successive days. This suggests that the blue shark population is either large or does not normally remain within a limited offshore area.

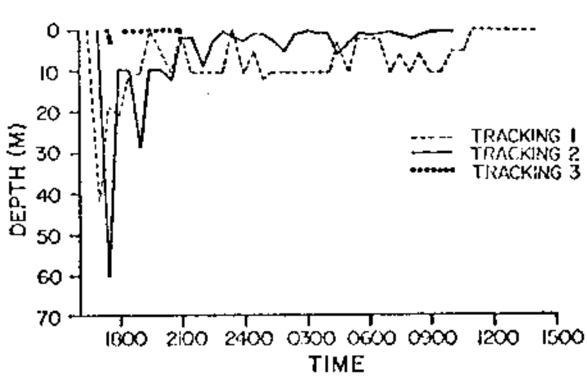
Ultrasonic telemetry. Four successful telemetry trackings were accomplished, which revealed blue shark movements in near-surface waters with increased activity (movements) at night (Figure 5). The sharks with depth sensors showed the characteristic initial "plunge" to depths of at least 50 m, as described by Sciarrotta (1974), as well as the subsequent return to the surface and apparent normal behavior. Tag no. 4 was not equipped with a depth sensor, but the shark was visually observed to disappear into deeper waters after application of the transmitter. This shark soon returned to the surface, and its brightly painted transmitter float was in view for most of the tracking.

Figure 5. Movements of three telemetered blue sharks. Tracking 1, 9/20/75; tracking 2, 10/11/75; tracking 3, 2/17/76. Dots represent day (○), dusk (◑), night (●), and dawn (◐) estimated shark positions taken at half-hour intervals. Bottom graph shows vertical movements of sharks during trackings.


TRACKING 1
KILOMETERS
0 1 2 3
START


TRACKING 2
KILOMETERS
0 1 2 3
START


TRACKING 3
KILOMETERS
0 1 2 3
START


DEPTH (M)
0
10
20
30
40
50
60
70
1800 2100 2400 0300 0600 0900 1200 1500
TIME
TRACKING 1
TRACKING 2
TRACKING 3

Seasonal Abundance, Sex and Size Variations

Although sharks occurred in the study area at all times of the year, seasonal shifts in abundance were characteristic of populations frequenting the study area. Abundance was estimated as a function of the numbers of sharks attracted to the bait by the standardized fishing method over a 1-year period. Sharks that contributed to the counts included those that were captured for gut analysis and those observed near the bait while fishing. Special care was made not to include duplicate counts of a shark observed near the bait which was then captured shortly thereafter.

Seasonal shifts of male/female shark ratios were observed (Figure 5). Male frequency increased in early summer, and males were the predominant sex during the warmer later summer and fall months. Female blue sharks predominated in the cooler months.

The seasonality of size classes for each sex is given in Figure 7. Male blue sharks ranged from a total length of 205 to 85.9 cm, both captured in July. The largest female (199.8 cm total length) was captured in January, and the smallest (81.2 cm total length) in July. Unlike males, female blue sharks revealed a marked decrease in average size as water temperature increased, and a subsequent increase in mean total length as waters

Figure 6. Seasonal sex ratios of all blue sharks positively sexed during the study. Includes sharks seen or captured during standard baitings, those observed under water, and those sexed during tagging operations.

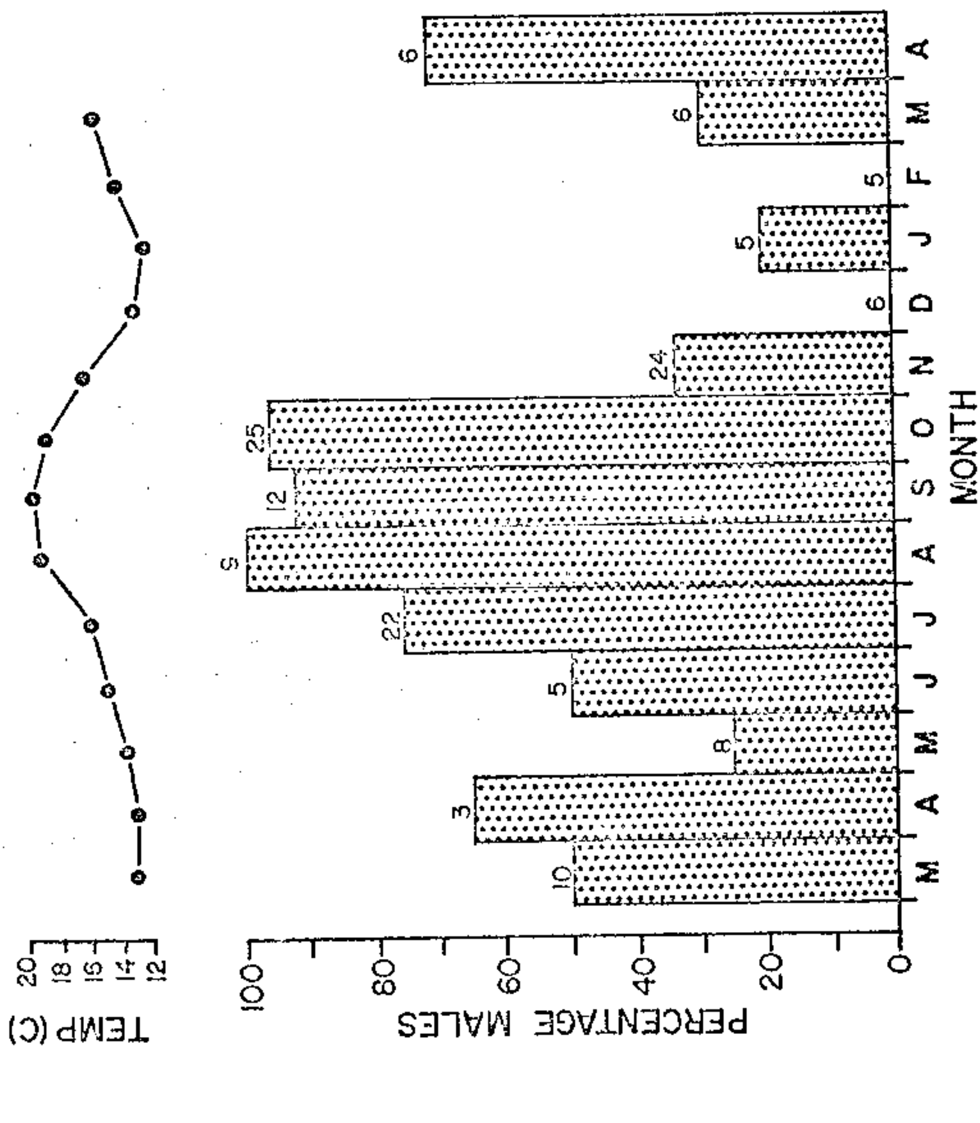
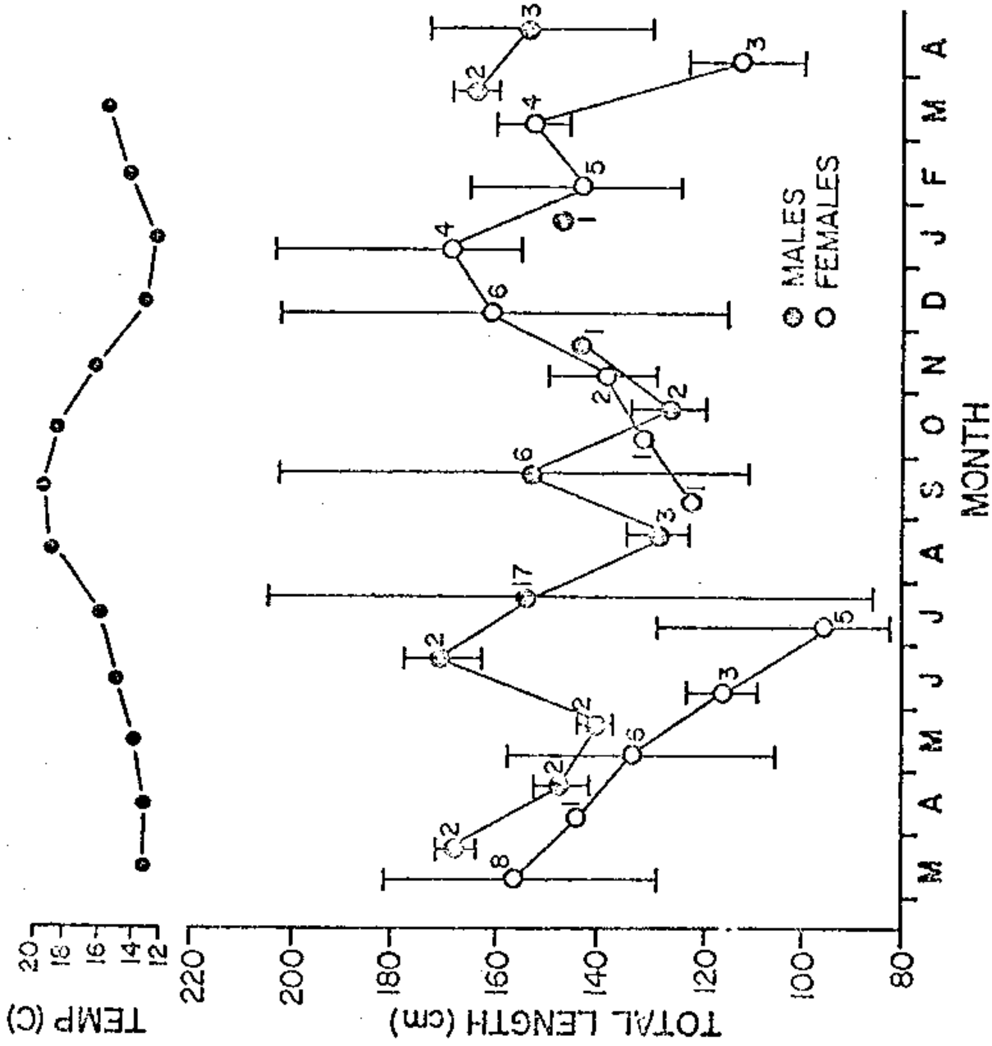

TEMP (C)
20
18
16
14
12
PERCENTAGE MALES
100
80
60
40
20
0
MONTH
M
A
M
J
J
A
S
O
N
D
J
F
M
A
10
3
8
5
22
5
12
25
24
6
5
5
6
6

Figure 7. Seasonal mean sizes of all male and female sharks captured after standard bait attraction. Horizontal bars = ranges. Numbers near mean indicate quantity of sharks sampled per month.


TEMP (C)
20
18
16
14
12
TOTAL LENGTH (cm)
220
200
180
160
140
120
100
80
M A M J J A S O N D J F M A
MONTH
MALES
FEMALES

cooled in fall and winter months. No females were captured in August where water temperatures were near maximum. No males were captured in December and in February, when water temperatures were near minimum.

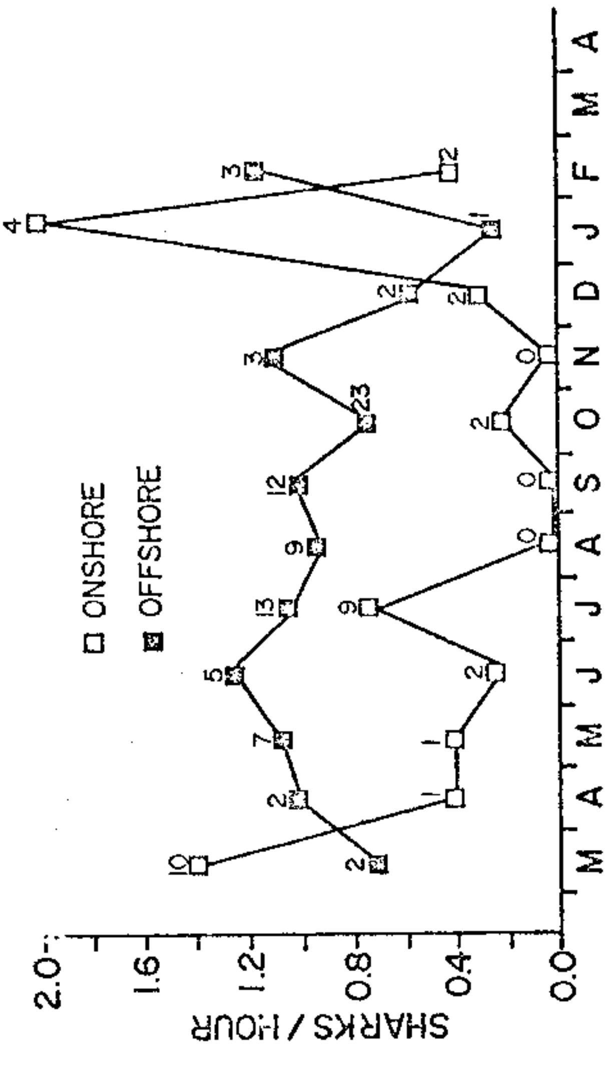
"Catches" per unit baiting effort for onshore and offshore sampling stations are given in Figure 8. Those areas near shore generally revealed high levels of shark abundance during the squid spawning season (March 1975 and December through February 1976). The intervening months of April through November showed relatively few individuals at inshore sampling sites, sharks being concentrated in offshore areas at these times.

Blue Sharks and Spawning Squid

During winter months, when water temperatures were minimal (12°C), large spawning schools of Loligo opalescens appeared in shallow (35 m) onshore waters. These schools generally remained at depths near the bottom during daylight hours, and moved towards the surface at night. Artificial lighting at night has been used by commercial fishermen to attract spawning schools of squid for harvest. This technique also provided a good opportunity for observing shark feeding behavior among schooling prey.

Mating behavior of Loligo opalescens, in Monterey, California, has been described in detail by Fields (1965).

Figure 8. Relative seasonal abundance of blue sharks at onshore and offshore stations. Based on recorded arrival times of all sharks to boat during standard baitings.



SHARKS / HOUR
2.0
1.6
1.2
0.8
0.4
0.0
M A M J J A S O N D J F M A
MONTH
ONSHORE
OFFSHORE

I will very briefly summarize the mating behavior of *L. opalescens*, as observed in this study during night-lighting operations at the Isthmus (see Figure 1). Males usually rose to the lighted area first, spaced somewhat randomly apart, where they moved about the area either in short rapid spurts or very slowly. A short time later, schools of female squid would move rapidly through the area, dispersing to individuals as they approached the surface. As individual females dashed through the area, they were quickly and vigorously grabbed by male squid. If the female was receptive and did not resist, the actual mating event began. Two or three males would often grasp a single female and compete for the primary mating position. Soon after this male-female contact began, the entire school would begin to tighten up, with inter-individual space reduced to a minimum. The squid soon became unwary of their surroundings and swam either in tight circles beneath the light, or remained stationary in a single mass if sufficient head current was present. Some mating still occurred, but a majority of the school was swimming in an unguarded state. The school was 0.5 to 2 m thick, and concentrated close to the light source.

It was when these large, dense schools of squid were formed that the blue sharks generally appeared. Feeding behavior appeared to be dependent on size and motivation of the shark, as well as the physical characteristics and alertness of the squid school. Surface and underwater observations of blue sharks feeding on squid attracted to the night-light revealed at least four feeding responses to a schooling prey.

Slow head-swaying: This feeding behavior was most commonly observed among larger blue sharks moving either through the center of moderately dense squid schools, or at the periphery of sizeable schools. The shark would swim through the school at a moderately slow velocity, with pronounced lateral head movements and corresponding broad tail sweeps. Squid were generally captured in the corners of the mouth and swallowed whole. No rapid head-shaking was observed (as often occurs when sharks bite on relatively large prey), although single lateral head jerks to position prey for swallowing were sometimes seen. The shark moved in a relatively straight path, and created minimal disturbance to the squid school.

Charging: This movement can best be described as an accelerated rush through a dense school of squid. The mouth was generally open and there seemed to be no orientation to specific individuals, rather a sightless attempt to engulf large numbers of squid. This behavior was observed repeatedly at the first sight of a shark among the squid and commonly occurred near the surface of the school. The pathway of the rushes were generally straight and often included a breaking of the surface by the shark, which in turn disturbed the squid.

Turning: This behavior was most frequently observed when squid were not in tight schools and were thus more wary of predators. As the shark approached the school, the squid (which swim backwards and could see the approach of the predator) began to turn tightly away from the shark's path. The shark responded and turned in pursuit, but was most often eluded by the squid.

Sharks were observed to capture squid in the corner of their mouths during these tight turning movements or by quickly whipping their head to one side and thus capturing squid. The shark would often break water in its attempt to seize the squid, which disturbed the squid school. This behavior was observed primarily in surface waters.

Tail-standing: Sharks also fed on squid schools from beneath. As previously described, the squid school would often be tightly packed directly beneath the light source so as to form an extremely dense mass. In this feeding behavior, the shark first circled the lower portion of the compact school and then moved up to the squid and assumed a near vertical attitude, using broad tail sweeps to keep from sinking. Then the shark began to feed on the lower portion of the squid school by lunging its head into the mass and engulfing many squid.

The longest duration that I observed a shark in the tail-stand posture was for 20 sec, after which the shark swam from view. I estimate that the shark consumed about 30 whole squid during the tail-stand. This behavior was observed when squid were in maximum densities and was not as common as other feeding modes.

GENERAL DISCUSSION

Feeding

Findings from investigations on blue shark food habits indicate that these sharks feed principally on small schooling fish while in coastal waters. Anchovies were the major prey item for blue sharks in Catalina waters, and those off Newport Beach, California (Bane, 1968). Small schooling fishes comprised a major portion of blue shark diets in other coastal areas as well (Bigelow and Schroeder, 1948; LeBrasseur, 1964; Stevens, 1973).

Predation on small fish is most likely due to high prey abundance rather than shark preference. Smaller schooling fish tend to be distributed within productive coastal waters where plankton is abundant, and are bounded by less productive oceanic waters. Anchovies in southern California waters, for example, show greatest concentrations within 37 km of the mainland, their range reportedly extending a maximum of 157.4 km seaward (Mais, 1974). Once sharks enter these coastal waters, anchovy schools become widespread and present an expansive prey potential.

While in oceanic seas, far from productive coastal waters, blue sharks rely heavily on pelagic cephalopods as major prey. Strasburg (1958) found cephalopods to be a significant component of the blue shark diet in the central Pacific waters. The fact that only beaks were found in stomachs examined in this study strongly suggests that sharks had recently moved in from deeper, more distant waters and recently shifted to anchovies as the major prey item. Clarke and Stevens (1974) reported similar findings of cephalopod beaks from sharks captured in English coastal waters which indicated recent inshore migrations from deeper waters.

Morphologically, the blue shark is not designed for a high speed pelagic lifestyle as, for example, are some sharks of the family Lamnidae, which also occur in southern California waters. The long, thin body and heterocercal tail is not well-adapted for the pursuit of larger fast-swimming prey such as tuna, jacks, bonito, etc. The mouth and teeth are relatively small, being best suited for obtaining small prey, rather than larger, fast-swimming fishes, as in the case of the mako shark, *Isurus oxyrinchus*. Blue sharks often did not use their teeth for capturing prey, and almost always swallowed their prey in one piece.

Freshly ingested anchovies that prevailed in sharks captured during the morning hours represent food held for about 6-8 h. Anchovies recovered from sharks captured in the afternoon represent food which had been held approximately 15-18 h. These findings suggest that blue shark predation on anchovies is primarily nocturnal, from around midnight through dawn. Sciarrotta (1974) reported a generally elevated nocturnal activity for his telemetered blue sharks and also suggested this as being food related.

Predator success in these waters is at least partially dependent on the dispersion characteristics of anchovy schools. Diurnal schooling and nocturnal dispersion of many inshore fishes has been extensively described by Hobson (1968, 1974). Schooling in daylight can be thought of as a strategy for reducing prey availability over a given area (i.e., making it harder to locate) and, when located by a predator producing a "confusion effect" whereby the predator would have difficulty in singling out one individual due to the darting about of the school. Such prey evasion strategies are, however, complimented by the necessity to feed and many species have adapted to feeding under the cover of darkness as apparently is the case of the anchovy. This strategy appears to be relatively successful against blue shark predation, since anchovies occurred in relatively few numbers per shark.

Telemetric trackings from this study and that of Sciarrotta (1974) have provided data on the location of sharks during these nocturnal feeding times. Sciarrotta described shoreward movements of sharks at dusk from late March through early June and noted the possibility of these being related to feeding on inshore spawning market squid. He also found non-island oriented movements in offshore Catalina waters from late June through early October. In this study, sharks were tracked in the winter season (October, November, December, and February) and were found to exhibit non-island oriented behavior similar to that of sharks in the summer and fall season of Sciarrotta's study.

The non-island oriented movements of sharks observed in this study during the winter season (and island squid spawning) might suggest other motivating factors for inshore movements of sharks during the spring, in addition to those of a possible squid food source. During squid spawning at the Isthmus, sharks were commonly seen at the surface at all times of the day, indicating that some sharks do not return to offshore waters during the day in the presence of squid. During April (after squid spawning season) large surface "schools" of blue sharks were reported (by an apparently credible island resident) as showing daytime onshore-offshore movements during successive days. In addition, extremely large surface concentrations (greater than 100 sharks in 1 ha) were observed (by this author) close to the shoreline just east of the Isthmus in March. The large size of these congregations and close proximity of individuals within them implies some social interaction of the sharks. It is of interest to note that the spring season was found to be the time of a major size and sex ratio shift, and predominance of sexually mixed single size group schools.

Abundance

General abundance of sharks in the study area showed seasonal variation closely associated with water temperature. Late summer and winter abundance peaks coincided with maximum and minimum water temperatures respectively. Males predominated in the warm summer months with a very low number of female sharks present. At this time a majority of shark activity was in offshore waters (Figure 7), where anchovy schools were abundant. As male blue sharks began to leave the area in fall and winter, fishing success (number of sharks attracted to bait per hour) declined with females predominating in relatively low numbers. Similar findings by other investigators are summarized in Table 4.

Size/sex segregations observed in this study appear to be influenced by water temperature as well. Departure of larger females from warming waters (Figure 5) suggests a preference for low temperatures. By July, larger female sharks had left the study area where water

Table 4. Known recoveries of blue sharks tagged in California waters[a]

Sex	Date tagged	Date recovered	Days at liberty	Tagging location	Recovery location	Absolute distance traveled (km)	Investigator
M	10/29/66	10/21/69	1088	20 km west of San Diego, California	02 54 S 113 19 W	3589	Nelson (unpublished)
M	7/16/67	10/08/70	1180	mid San Pedro Channel, California	Todos Santos Island, Baja, California	387	Nelson (unpublished)
M	7/25/67	11/15/67	113	33 33 40 N 117 57 50 W	07-05 N 1117-50 W	2561	Bane (1968)
M	4/4/68	5/02/71	758	Laguna Beach, California	Coronado Island, California	97	Bane (unpublished)
?	4/16/69	7/19/70	455	Newport Beach, California	pier at Gaviota, California	455	Bane (unpublished)
M	8/13/75	7/25/76	346	6 km north of Isthmus, Santa Catalina Island, California	Gull Island, Santa Cruz Island, California	107	Tricas (this study)

Table 4 (continued)

Sex	Date tagged	Date recovered	Days at liberty	Tagging location	Recovery location	Absolute distance traveled (km)	Investigator
M	8/13/75	9/21/75	39	6 km north of Isthmus, Santa Catalina Island, California	5 km south of Santa Cruz Island, California	111	Tricas (this study)
M	10/11/75	5/08/76	241	6 km north of Isthmus, Santa Catalina Island, California	10 km west of Point Loma, California	119	Tricas (this study)

[a]Data from International Shark Tagging Program of the American Institute of Biological Science (courtesy of S. Spinger).

temperatures then averaged 16°C. In the same month, near Moss Landing in central California, a majority of blue sharks, sampled by Harvey (personal communication), Moss Landing Marine Laboratory, Moss Landing, California, were female where waters then averaged 11°C. The departure of large females from the Catalina study area occurred in late June when mean water temperature was about 15°C. Johnson (1974) reported that female blue sharks disappear from San Diego waters at about 60°F (15.5°C). Neave and Hanavan (1960) reported summer movements of blue sharks into the Gulf of Alaska where waters ranged from 11-17°C. Similar movements of large blue sharks into Newfoundland waters (15.3°C) were given by Templeman (1963), but little is provided on sex ratios. Pethon (1970) mentioned the movement of sharks into northeastern Atlantic waters and stated the probability of blue shark distributions in northern waters as being mainly temperature dependent. The northward movement of females up the California coast suggests a maximum temperature preference of about 15-16°C, which coincides with the northerly advance of warming waters in summer months.

Size schooling appears to be predominant among smaller, immature sharks, as evidenced by the capture of both the smallest male (86 cm total length) and female (81 cm total length) sharks during the same fishing session in July. Sexually mixed schools of subadult sharks were common during spring and fall. During months of unisexual predominance (winter and summer), larger, immature sharks were often observed to be in a single size group. Most notably, males were observed exhibiting this behavior in pre-dusk hours during late summer and fall. Fishing for sharks was very unproductive during a majority of the day in the fall season. However, "packs" of highly active males (approximately 1.2-1.6 m total length) would predictably appear at the bait in late afternoon. Sciarrotta (1974) observed similar "packs" of blue sharks, and reported free-roaming pairs of individuals apparently remaining together for 8 h. Such behavior might suggest a social aspect of male blue shark feeding, although data is too scarce to be conclusive.

The sharp increase in inshore fishing success between December and January occurred concurrently with the beginning of the onshore spawning run of *Loligo opalescens* at the Isthmus. A drop in water temperature and decrease in sharpness of the thermocline, along with local upwelling, all occurred just prior to increased shark activity in inshore waters. This localized inshore increase and concurrent offshore decrease in shark abundance in January appears to have been caused by inshore squid concentrations. In weeks prior to the Isthmus squid run, squid were active at other island locations

(Silver Canyon and Long Point), and large numbers of sharks were observed in these areas during the day and among squid schools at night. During this time no blue sharks were seen in the Isthmus area (9 km from Long Point), and they did not appear there until after squid spawning had begun. Stomachs from sharks then captured in the Isthmus area contained large numbers of freshly ingested squid most likely taken from these spawning schools. The sudden appearance of sharks in areas of spawning squid implies some attracting mechanism, possibly olfactory. Fields (1965) discusses the possible release of a diffusible substance by spawning female squid to attract males. A large scale diffusion of chemical pheromones or sexual by-products from these vast schools of squid could have provided a stimulus sufficient to attract and retain nearby sharks. It is interesting that although mackerel odor was used to attract sharks throughout this study, sharks usually did not take mackerel-baited hooks during the squid spawning season, but would readily take squid-baited hooks. The refusal of mackerel (normally taken during these opportunistic feeding situations) and the acceptance of squid suggest a preference and a possible associated search image (visual and/or olfactory) for squid during the squid spawning season.

Sexual Maturity and Reproduction

No sharks collected during the study contained embryos. However, in May 1976, a 2-m female captured near the study area by a commercial fisherman gave birth to 26 young while on deck. Average size of the pups was 33 cm total length, suggesting they were near term.

In late summer and fall months, fresh mating scars were observed on female (185 cm total length and larger) blue sharks. Minimum length at reproductive maturity has been suggested to be about 7-8 feet total length (239-269 cm) by Strasburg (1958) and 140 cm by Suda (1953). Stevens (1974) reported tooth cuts occurring on sharks greater than 180 cm total length. Based on these lengths and the infrequent occurrence of mating scars on sharks observed in this study, it is most probable that blue sharks in southern California waters are generally subadult and therefore do not represent a major center of blue shark reproduction. Larger mature sharks are most likely found farther out to sea, as suggested by Strasburg's (1958) oceanic study.

The mixing of both males and females in late summer and fall might suggest reproductively related movements for mature sharks. Suda (1953) noted the occurrence of a sex ratio near 1:1 in late spring and summer, and a simultaneous occurrence of gravid females, or those bearing tooth cuts. Females have been reported as dominating in northeast Atlantic waters (Pethon, 1970), while males comprised the majority of blue sharks in the northwest Atlantic (Bigelow and Schroeder, 1949). Aasen (1966) reported a sex ratio of about 1:1 in a trans-Atlantic cruise. Strasburg found near equal numbers of males and females in winter in the central Pacific and females predominant in spring months. He also reported the formation of unisexual schools in summer and autumn months, and their probable reassembling as mixed schools in winter.

The seasonal segregations of adult sharks are characteristic of blue shark populations throughout the Pacific and Atlantic and are probably reproductively oriented. Mating probably occurs during the mixing of mature populations in fall months in pelagic waters where adult sharks are more numerous. The capture, in May, of the pregnant blue shark with near term pups strongly supports fall mating since gestation is approximately 9 mo. Bane (1968) reported blue sharks from southern California waters carrying pups in August (1967) and September (1966), but did not provide size information on the embryos. This may indicate a relatively broad mating season for blue sharks, but more data is needed on this matter. Strasburg's note of a 1:1 sex ratio in the central Pacific in winter months may suggest far offshore waters as major breeding grounds for blue sharks.

The spring/summer northward shift of female predominance may be related to parturition in order to minimize predation on newborn sharks by males and other warm water predators, and to place the newborn sharks in a productive nearshore environment where smaller nektonic food prey items are abundant.

Movements

All known blue shark tag returns from the eastern Pacific are summarized in Table 4. Two returns from sharks tagged by Bane (unpublished) in 1968 and 1969, one by Nelson (unpublished) in 1967, and two from this study, provide indications that young immature sharks may exhibit some type of seasonal migration, returning to the same area (coast) yearly. Annual movements may be based on food availability, prevailing currents and temperatures, or could possibly be reproductively oriented. More distant movements are common among larger sharks, as shown with blue sharks tagged by Bane (1968) in 1967 and Nelson (unpublished) in 1966. These transmigrations of large blue sharks are at least partially due to stronger swimming capabilities and an ability to capture and consume larger and more varied food items. The shortest liberty (39 days) of any of these tagged blue sharks showed a northwest movement which corresponds to probable pathways of female sharks in their early summer northward movements.

SUMMARY

1. Of 81 shark stomachs sampled, fish remnants occurred in 72 percent, cephalopod beaks in 74 percent, and crustaceans in 18 percent.

2. The northern anchovy, *Engraulis mordax*, was the predominant prey item for blue sharks in Catalina waters. Deep water cephalopods appeared to be the major prey item for blue sharks while in outer offshore waters. *Histioteuthis heteropsis* was the predominant deep water cephalopod stomach content. Winter spawning schools of *Loligo opalescens* constituted the major inshore prey item for sharks in the study area.

3. Near complete digestion of an adult anchovy by a blue shark was found to occur at about 24 h after consumption. The digestion of squid was found to proceed at a much slower rate.

4. Evidence obtained from analysis of anchovy digestive states, observations on nocturnal anchovy activity, and telemetric monitoring of blue sharks indicate peak feeding on anchovies to occur between pre-midnight and dawn. Tooth marks on anchovies recovered from stomachs reveal that prey are often swallowed whole and are generally captured from behind.

5. Inshore abundance of blue sharks was greatest

during the time of inshore squid spawning.

6. Surface and underwater observations of sharks feeding on night-light-attracted schools of squid revealed four types of feeding behavior: slow head-swaying, charging, turn, and tail-standing.

7. Male blue sharks of all size ranges occurred in warm summer months. Large female sharks predominated in cooler months, showing a maximum temperature preference of about 15°C and a northward migration ahead of warming waters to the south. Smallest sharks of both sexes occurred in the warmest months. Small blue sharks were found to school by size. Subadults schooled by sex and size. Larger adults appeared to be more solitary.

8. The majority of blue sharks frequenting this are are subadult and do not represent a major center of blue shark reproduction.

9. Conventional tag returns suggest the lack of a local home range and an annual return of smaller sharks to the coast of California.

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