RELATIONSHIPS OF THE BLUE SHARK, *PRIONACE GLAUCA*, AND ITS PREY SPECIES NEAR SANTA CATALINA ISLAND, CALIFORNIA[1]

TIMOTHY C. TRICAS[2]

ABSTRACT

Small fishes and cephalopods associated with both pelagic and inshore habitats composed the major prey for the blue shark, *Prionace glauca*, near Santa Catalina Island, Calif. The northern anchovy, *Engraulis mordax*, was the predominant prey for sharks in the immediate study area while at least 13 species of pelagic cephalopods constituted major prey for sharks in more distant oceanic waters. Inshore species taken by sharks included pipefish, *Syngnathus californiensis*; jack mackerel, *Trachurus symmetricus*; and blacksmith, *Chromis punctipinnis*. In addition, sharks moved inshore to feed on winter spawning schools of market squid, *Loligo opalescens*. Digestive rate studies and telemetric monitoring of activity patterns indicate that sharks forage in waters near the surface from around midnight through dawn. Diel activities of prey species were examined and show that most prey dispersed in the upper water column at night and refuged during the day either by schooling (anchovies and jack mackerel) or by retreating to deeper waters (pelagic cephalopods). Field observations of shark feeding behavior indicate that predatory modes vary in response to prey behavior.

The blue shark, *Prionace glauca* (Carcharhinidae) (Figure 1), is a pelagic carnivore cosmopolitan in tropical and warm temperate seas. Because of its pelagic habits, the majority of ecological studies on this species have been predicated on data from sharks captured by sport and commercial fisheries. As a result data has been largely qualitative, and the shark's role as a predator in the epipelagic habitat has remained unclear.

The importance of small fish as prey items for blue sharks has been described by Couch (1862), Lo Bianco (1909), Bigelow and Schroeder (1948), Strasburg (1958), LeBrasseur (1964), Bane (1968), Stevens (1973), and others. These prey generally are schooling species common in productive coastal waters. Cephalopods were also reported as major prey but little information is available on specific identifications (see Stevens 1973; Clarke and Stevens 1974).

Although blue sharks have been observed feeding on dead or wounded cetaceans (Bigelow and Schroeder 1948; Cousteau and Cousteau 1970) there is little indication that they habitually prey on live, healthy marine mammals. The occurrence of mammalian tissue in the diet of blue sharks is rare (Strasburg 1958; Stevens 1973), and such feeding is most likely directed to dead mammals or those in poor health. Air/sea disasters have resulted in attacks on humans by blue sharks (see Schultz and Malin 1963; Fitch[3]) but these cases usually involved injured persons or corpses.

Standard tagging programs (Weeks 1974; Casey 1976; Stevens 1976) and telemetric trackings (Sciarrotta and Nelson 1977) have provided some information on large-scale movements of blue sharks but relatively little is known of their orientation mechanisms and predatory behavior.

Despite the profusion of descriptive reports, there still exists a great need for quantitative data on ecological relationships between the blue shark and its prey species. With these ideas in mind, I undertook this study within a limited geographic area to 1) provide a quantitative assessment of the diet of blue sharks near Catalina Island, 2) establish temporal and/or geographical shifts in food habits, and 3) describe behavioral interactions between the blue shark and its prey species.

METHODS

The study area was located north of the Isthmus, Santa Catalina Island, Calif. (Figure 2). Beds of

[3]J. E. Fitch, California Department of Fish and Game, Operations Research Branch, 350 Golden Shore, Long Beach, CA 90802, pers. commun. May 1976.
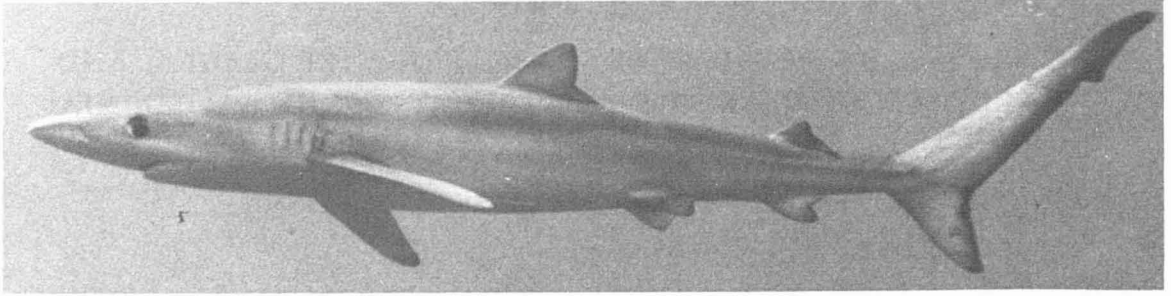
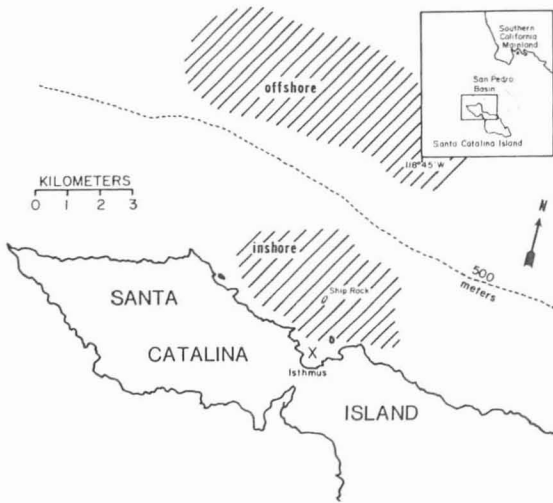FIGURE 1.—Female blue shark near the ocean surface.

FIGURE 2.—Study area at Catalina Island, Calif. Hatching indicates sampling regions. Sharks feeding among squid schools were observed at ×.

giant kelp, *Macrocystis pyrifera*, composed the major habitat along the island shore. A submarine shelf, averaging 150 m deep, extends approximately 2 km seaward then slopes to depths near 900 m and forms the floor of the San Pedro Basin. "Inshore" sampling stations were located above the shelf within 3 km of the island, and "offshore" stations centered approximately 6 km north of the Isthmus, over deeper basin waters.

Sharks were collected monthly between March 1975 and March 1976. Samples were taken during morning and afternoon hours at both inshore and offshore areas with an attempt to maintain a consistent area-time sampling schedule. 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 sur-

face. 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 then measured, sexed, and inspected for mating scars and general health. Contents of esophagi and stomachs were filtered through 1-mm mesh netting and preserved. Recognizable prey items and their digestive states were recorded on site. Intestinal tracts were occasionally examined but contributed little information on the diet because of the small pylorus which restricted passage of identifiable prey fragments.

Except for the market squid, cephalopods in the diet were represented exclusively by beaks. Beaks were paired into sets of upper and lower halves, and identified when possible according to Clarke (1962) and Pinkas et al. (1971). Specific identifications were verified by comparisons with beaks from collections of local species. Whole volumes of squid were estimated from beak-size/body-weight regressions for the major cephalopod families given by Clarke (1962). For calculations, the density of cephalopod flesh was assumed to be 1 g/cm³. A regression for the family Ocythoidae (not given by Clarke) was generated by plotting beak measurements and body weights from local specimens on Clarke's Octopodidae and Argonautidae regressions and constructing a parallel relationship curve. Beak-size/body-weight regressions for *Vampyroteuthis infernalis* were obtained from specimens of local collections. Unidentified cephalopods were omitted from the quantification as they represented only a minor portion of the diet (four small, infrequent species in eight stomachs).

In order to approximate normal shark feeding times, digestive rates for captive sharks were determined and then compared with field data on the

digestive states of anchovies recovered from wild sharks. Three healthy, active sharks were acclimated for 24 h in large seawater holding tanks (14°-16°C) at Marineland of the Pacific, and then fed marked anchovies and market squid. Stomach contents were examined at 6, 12, and 24 h after feeding and the digestion rates recorded.

Short-term movements of sharks were monitored in the fall and winter seasons by telemetric instrumentation similar to those of Ferrel et al. (1974) and Nelson (1974). Transmitters were applied externally to free-swimming sharks with stainless-steel darts. Effective transmission range was approximately 2 km under good conditions but depended largely upon ambient noise from waves, wind, and biological sources. Some transmitters included a depth sensor for a record of vertical movements. Signals were tracked using a tuneable ultrasonic receiver and a staff-mounted directional hydrophone. These trackings supplement the spring through fall trackings of Sciarrotta and Nelson (1977).

The feeding behavior of blue sharks among spawning squid was studied in January 1976. Just before sunset, squid schools were detected near the bottom (30-40 m deep) using a recording Fathometer[4] and the work boat anchored directly above. A 1,500-W light was then suspended over the water. Squid typically converged beneath the light and formed a large surface school at which sharks usually appeared and began to feed.

Orientation and feeding responses of sharks to moving prey were documented during baiting sessions at offshore stations. In these tests, a dead anchovy, attached to a light fishing line was cast beyond the bait-attracted sharks and then retrieved back towards the boat. All field observations of shark and prey activities were made from the boat, using scuba and/or by snorkeling.

RESULTS

Sharks were captured during all months of the 1-yr study. Of the 81 sharks sampled, 94% had recognizable food items in their stomachs. The northern anchovy, *Engraulis mordax*, was the predominant prey item for sharks in the study area while other small fishes occurred at much lower frequencies (Figure 3).

Although sharks fed on a wide variety of cephalopods, an analysis of relative importance (Table 1) showed *L. opalescens* and squid of the genus *Histioteuthis* as the most common and substantial cephalopod prey. Monthly analysis revealed important shifts between these prey items
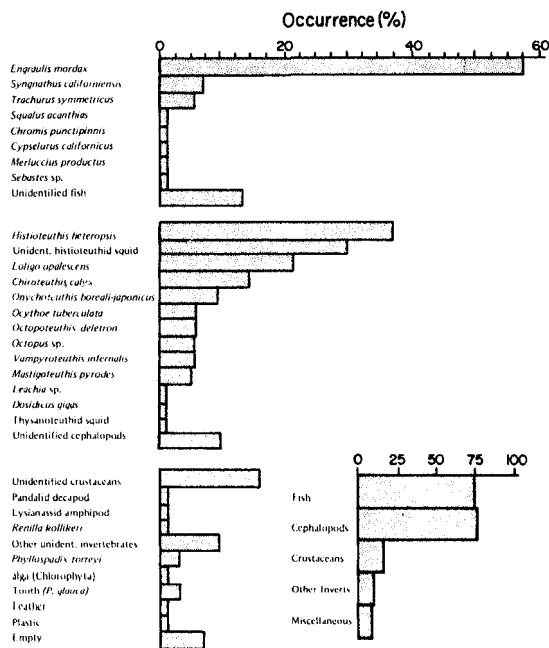

FIGURE 3.—Stomach contents of 81 blue sharks sampled during the year. Occurrence = percent of the 81 individuals containing that prey species. Inset gives a summary by broader food categories.

TABLE 1.—Annual relative importance of identified cephalopod prey in the diet of blue sharks near Santa Catalina Island, Calif. Importance was estimated as an index of relative importance (IRI) in accord with Pinkas et al. (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 species of all cephalopods recovered; and F (frequency) is the percent of individual shark stomachs containing that prey species.

Rank	Species	F	N	V	IRI
1	*Loligo opalescens*	21.0	70.6	31.9	2,152.5
2	*Histioteuthis heteropsis*	37.0	11.4	10.4	806.6
3	*Histioteuthis* sp.	23.5	5.0	.3	124.6
4	*Chiroteuthis calyx*	14.8	5.3	1.4	99.2
5	Thysanoteuthid squid	1.2	.2	43.3	52.2
6	*Onychoteuthis boreali-japonicus*	8.6	2.4	3.6	51.6
7	*Vampyroteuthis infernalis*	4.9	.8	2.2	14.7
8	*Octopoteuthis deletron*	6.2	1.0	.8	11.2
9	*Dosidicus gigas*	1.2	.2	5.1	6.4
10	*Ocythoe tuberculata*	4.9	.8	.4	5.9
11	*Mastigoteuthis pyrodes*	3.7	.6	.3	3.3
12	*Octopus* sp.	4.9	1.4	.2	7.8
13	*Leachia* sp.	1.2	.2	.004	.3

---

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

(Table 2). The high index for *L. opalescens* in January 1976 reflected the squid's extensive winter spawning assemblages in the study area, and similarly is the reason for its high annual rank (Table 1). Histioteuthid squid were probably the most significant cephalopod prey for sharks in more oceanic waters away from inshore spawning aggregations of *L. opalescens*. The low average number of anchovies and histioteuthid squid per stomach and the relatively small coefficients of dispersion for these two prey indicate that sharks obtained them somewhat regularly over a wide area (Table 3). Conversely, the large coefficient for market squid during its spawning season concurs with observations that this prey was taken from large schools during its spawning runs at inshore areas.

Digestive rate tests for healthy, captive sharks were in order with digestive states of prey recovered from wild sharks. Anchovies removed from captive sharks at 6 h after feeding were easily identified, and showed only preliminary digestion of fins and margins of the opercula. Likewise, whole squid were easily recognized and had only slight signs of external surface decomposition. At 12 h after feeding, digestion of anchovies was characterized by decomposed abdominal walls, moderate scale loss, and some skin deterioration. Digestion of squid was still negligible. At 24 h, anchovies were well digested with only vertebrae, otoliths, and small sections of muscle present. Squid heads were separated from the body and lenses had detached from the optic cups, but beaks were still implanted within the buccal mass. In general, digestive rates were at least twice as fast for anchovies than for squid.

Times of normal feeding activity were estimated by comparing the digestive rate data obtained from captive sharks with recognizable anchovies recovered from wild sharks. Anchovies that were

TABLE 3.—Dispersion of the three major prey species in blue shark stomachs off Santa Catalina Island, Calif. Means for market squid were computed for squid spawning season (Mar. 1975, Dec.-Jan. 1976) and nonspawning season (Apr.-Nov. 1975, Feb. 1976). Coefficients of dispersion (ratio of variance to mean) indicate grouping of prey among stomachs. A coefficient of 1 describes a random distribution. Larger coefficients describe increasingly contagious (clumped) distributions of prey among shark stomachs (Sokal and Rohlf 1969).

Prey item	No. of sharks sampled	Mean no. prey per stomach	Coefficient of dispersion
Anchovies	81	1.06	1.92
Histioteuthid squid	81	1.52	2.68
Market squid:			
Spawning season	29	11.52	162.57
Nonspawning season	52	0.423	6.81

freshly ingested predominated in sharks captured in early morning hours (Figure 4) and corresponded to a duration of approximately 0-8 h after ingestion. Moderately digested anchovies were prevalent in sharks sampled in the afternoon and represent anchovies held about 9-20 h after consumption.

Tooth marks on anchovies recovered from wild sharks indicate that prey were almost exclusively captured from behind. When present, tooth marks were usually located on the posterior lateral one-third of the anchovy, and in many cases impressions penetrated only the skin and not the myotome.

The movements of four sharks were monitored using ultrasonic telemetry in the winter (October-February) and supplement the spring, summer, and fall trackings of a previous study in the same area (Sciarrotta and Nelson 1977). Sharks ranged over wide areas (e.g., approximately 50 km² in 18 h: Tracking 2) and did not exhibit movements oriented towards the island shore. Vertical movements, except for the initial plunge immediately following tag application, were confined to the upper 15-m depth range.

TABLE 2.—Monthly index of relative importance (*IRI*) of identified cephalopod prey in stomachs of blue sharks near Santa Catalina Island, Calif. See caption of Table 1 for calculation of *IRI*.

| Species	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Loligo opalescens	1,596	—	—	392	21	378	1,597	9,571	—	1,098	11,564	—
Histioteuthis heteropsis	780	17,369	3,917	6,454	166	9,406	2,298	254	—	1,376	370	—
Histioteuthis sp.	21	440	1,596	—	234	275	1,800	102	1,625	388	—	4,000
Chiroteuthis calyx	—	429	—	—	67	1,318	783	1,259	6,395	1,174	—	—
Thysanoteuthid squid	—	—	—	—	—	—	—	—	—	1,561	—	—
Onychoteuthis boreali-japonicus	68	—	—	—	169	—	—	—	—	1,188	23	—
Vampyroteuthis infernalis	—	—	—	—	130	—	521	—	—	136	—	—
Octopoteuthis deletron	40	—	1,373	—	19	—	—	—	—	55	—	—
Dosidicus gigas	—	—	—	—	216	—	—	—	—	—	—	—
Ocythoe tuberculata	14	—	—	—	23	—	138	—	—	47	—	—
Mastigoteuthis pyrodes	—	—	—	—	—	—	—	—	1,825	189	—	—
Octopus sp.	—	—	—	—	142	—	—	102	—	50	—	—
Leachia sp.	—	—	—	—	14	—	—	—	—	—	—	—
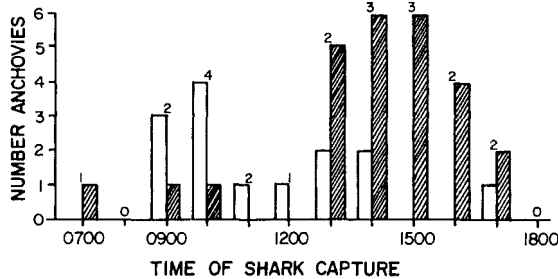
FIGURE 4.—Frequency of digestive states of anchovies in relation to time recovered from wild blue shark stomachs. Freshly ingested (light bars): anchovy body, scales, skin, and fins intact; represent anchovies about 0-8 h after ingestion. Moderate digestion (hatched bars): anchovy with head detached, open body cavity, and exposed myotome; represents anchovies about 9-20 h after ingestion. Advanced digestion (identification of anchovy possible only by vertebrae or otoliths) not included in distribution because of broad time span represented by this state (about 20 h or longer). Numbers indicate sharks sampled that contained anchovies in freshly ingested or moderately digested states. Water temperatures in the field ranged from 13° to 19°C.

Free-swimming sharks responded to moving prey (bait on slowly retrieved light fishing line) with a consistent posterior orientation, as illustrated in my field notes: "As I retrieved the bait towards the boat, a 1.5-m male shark sighted the anchovy and then swam in a wide arc so as to approach the bait from behind. He then made a rapid posterior-oriented dash up to the anchovy, bit the bait once at mid body, and swallowed it whole." Replicate tests using Pacific mackerel elicited similar posterior attacks; in these cases, the shark rolled partially on its side to take the larger fish prey. Tooth marks on bait in these test situations were similar to those on anchovies recovered from stomachs of wild sharks.

Sharks also showed several distinct patterns of predatory behavior while feeding on schools of spawning squid. Each feeding pattern appeared to be correlated with the size and level of activity of each shark as well as the physical configuration and alertness of the squid within the school. Surface and underwater observations of sharks feeding on night-light attracted squid revealed four feeding responses:

1) SLOW HEAD SWAYING: This feeding behavior was most common among larger sharks moving either through the center of moderately dense squid schools, or at the periphery of large, more diffuse aggregations. Sharks swam among the squid at a relatively slow speed, with pro-

nounced lateral head movements and corresponding broad tail sweeps. Squid were generally captured in the corners of the mouth and swallowed whole. In this behavior, sharks did not show rapid head shaking (as often occurs when sharks bite on relatively large prey) although lateral head jerks to position prey for swallowing were common. Sharks moved in a relatively straight path, and created minimal disturbance to the school.

2) TURNING: Turning behavior was most frequent among sharks feeding at the surface when squid were in an alert state or not in tight schools. As the shark approached the school, the squid (which swam backwards and could view the predator's approach) began to turn in tight arcs away from the shark's path. The shark would respond by turning in an accelerated pursuit, but was most often eluded by the squid. Sharks that were successful quickly whipped their heads to one side and captured squid in the corner of their mouths.

3) CHARGING: This behavior can best be described as a straight accelerated rush through a dense school of squid. Charging was most prevalent among the more active sharks that had just arrived at a squid congregation. Typically, the shark showed no orientation to specific individuals, and indiscriminately engulfed large numbers of prey.

4) TAIL STANDING: Sharks also fed on the lower portions of squid schools. As previously described, squid would often be concentrated directly beneath the light source so as to form a dense school. In this feeding behavior, the shark first circled the lower portion of the school and then moved up to the squid and assumed a near vertical attitude, using broad tail sweeps to maintain position. Then the shark lunged its head into the bottom of the school and engulfed many individual squid. The longest duration of a tail-standing posture was 20 s in which approximately 30 squid were consumed by one individual. This behavior was observed only when squid schools were most dense and was not as common as other feeding modes.

DISCUSSION

Blue sharks fed on a variety of small fishes and cephalopods associated with both pelagic and inshore habitats. Northern anchovies were the major prey for sharks in this investigation, and off Newport Beach, Calif. (Bane 1968), while small schooling fishes composed a major portion of blue

shark diets in other coastal areas of the world (Bigelow and Schroeder 1948; LeBrasseur 1964; Stevens 1973). Major concentrations of anchovies in the California Current system were centered in the semiprotected waters of the Southern California Bight (Mais 1974) which lies between Point Conception and Point Descanso, Mexico (approximately from lat. 32.0°N to 34.5°N, area of about 50,000 km²). The main portion of the southern California anchovy population was reported by Mais to be distributed within 37 km of the mainland over deep water (228.6-731.5 m) which includes the study area at Catalina.

The most prevalent schooling behavior for anchovies in deep open waters (bottom depth >183 m) was the formation of small (4-15 m thick), near-surface daytime schools (0-54.9 m deep) that dispersed at night into a thin surface scattering layer (Mais 1974). Field observations from the present study indicate a similar behavior for anchovies near Catalina. In offshore waters during the day, anchovies occurred in large, dense, polarized schools near the surface. In the early evening, schools dispersed horizontally into less dense feeding assemblages with individuals spaced approximately 0.5 m apart. Later at night (0100-0400 h) more dispersed groups and solitary individuals were observed on several occasions, indicating a more complete nocturnal dissolution.

In spite of the abundance of this prey no sharks examined near Catalina had stomachs distended with anchovies; usually only one or two had been taken per day. Data from the digestion studies indicate that most predation on anchovies occurred in predawn hours which correlates with the increased nocturnal activity of telemetered sharks reported by Sciarrotta and Nelson (1977). It seems probable then, that the few anchovies taken by each shark was at least partially due to the nocturnal dispersion of schools in offshore waters, whereby assemblage densities were reduced and anchovies taken individually.

The localized variability of anchovy abundance and schooling behavior that existed between areas and seasons presented different feeding opportunities for sharks. For example, blue sharks captured during the day off Newport Beach, Calif., and in commercial anchovy fishing grounds near Los Angeles Harbor (author unpubl. data) contained many more anchovies (approximately 10-20/individual) than did sharks sampled in the Catalina study area. The two former areas feature nearshore submarine escarpments where the size

and concentrations of anchovy schools were among the greatest anywhere in southern California (Mais 1974).

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 Scomber japonicus and Pacific sardine, Sardinops sagax, populations (MacCall et al. 1976), both natural prey for blue sharks (author unpubl. data). Although such declines in major forage species may have resulted in increased predation on anchovies, the southern California population is apparently in little danger of overexploitation by commercial fisheries or pelagic fish predators (Pinkas et al. 1971; Mais 1974; MacCall et al. 1976).

Fishes associated with inshore habitats were also taken by sharks. Jack mackerel, Trachurus symmetricus, are widely distributed throughout the Gulf of Alaska (Miller and Lea 1972), and inhabit both inshore and pelagic habitats (Feder et al. 1974). In southern California waters, adults of this species generally aggregate near the bottom or under kelp forests at rocky banks and shallow coastal areas during daylight and venture into deeper waters at night. Only rarely do jack mackerel form sizeable surface schools in the open sea (Mais 1974). Similarly, smaller jack mackerel (e.g., near 25 cm TL), common at inshore areas of Catalina, swam along the outer edges of kelp beds during the day in closely spaced schools and sometimes aggregated within the kelp forest proper. At night jack mackerel occurred in open waters (away from kelp) often interspersed with Scomber japonicus. Larger pelagic individuals might represent a schooling prey source for blue sharks in open waters, but stomach content data indicate this was not the case near Catalina. Neave and Hanavan (1960) described concurrent expansion of blue shark and jack mackerel ranges in the Gulf of Alaska during the summer, although no data was presented on possible predator-prey interactions.

Pipefish were the second most frequent fish prey for sharks in this study and a principal prey for blue sharks off Newport Beach (Bane 1968), but because of their small biomass must be regarded as a prey species of minor importance. Free-swimming pipefish were observed at the surface in open water (far from surfgrass or kelp beds) at night, among flotsam kelp during daylight, and during daytime scuba dives in kelp forest and

surfgrass, *Phyllospadix torreyi*, habitats along the shore of the island. The occurrence of pipefish at the surface in the San Pedro Channel at night and the fact that sharks containing freshly ingested pipefish were captured 2-5 km from the island imply that this prey was most likely taken in waters away from inshore kelp and surfgrass habitats.

Freshly ingested blacksmith, *Chromis punctipinnis*, were recovered from a shark captured near Ship Rock at noon. At Catalina, this planktivorous damselfish formed midwater feeding aggregations at the outer edges of the kelp forest during the day, and at times ranged seaward up to 100 m from the nearest kelp. At dusk, blacksmith retreated to the protection of rocks and crevices (see Quast 1968; Hobson 1976). Blue sharks frequented waters near exposed kelp stands at Ship Rock and have been reported chasing and feeding on blacksmith during the day (Sciarrotta and Nelson 1977; Given[5]).

With the exception of *Mastigoteuthis pyrodes*, *Vampyroteuthis infernalis*, and nonspawning *Loligo opalescens*, all of the cephalopod prey species (or their congeners for which data are available) occur near the surface at night through vertical ascent from greater depths or by normal epipelagic distribution (Roper and Young 1975; Tricas 1977). *Mastigoteuthis pyrodes* (mesopelagic) and *V. infernalis* (bathypelagic) occasionally migrate to the lower limits of the epipelagic zone at night (Roper and Young 1975).

In their study of blue shark movements near Catalina, Sciarrotta and Nelson (1977) described evening-twilight shoreward movements of sharks from late March through early June and suggested the change in movement patterns as a response to seasonal increases of inshore spawning squid and decreases in availability of pelagic fishes offshore. Such movements, however, may not be strictly food related. For example, daily inshore-offshore migrations of sharks (late March through early June) would not be synchronous with the cold-water winter peak (December through February) of inshore squid spawning activity near the Isthmus. Also, some sharks observed during this study fed among spawning squid schools throughout the day and therefore did not exhibit the diel inshore-offshore movement

pattern. Furthermore, sharks fed upon anchovies in offshore waters throughout the year and there is no indication that the availability of anchovies or jack mackerel to blue sharks significantly changed over the course of this study.

Detection of prey by sharks is often dependent on the reception of abnormal or unusual stimuli such as low-frequency vibrations of struggling or fleeing fishes (Nelson and Gruber 1963; Nelson and Johnson 1972). In addition, olfaction plays a well-documented role in location of injured, stressed, or bleeding prey (Tester 1963; Hobson 1963). Ultimately, however, vision (Gilbert 1963) and possibly electroreception (Kalmijn 1971) are the principal senses used immediately prior to attack. For blue sharks in a normal nocturnal feeding mode, it is probable that search images are formed for a general size rather than for a particular species. Pipefish, for example, were relatively small in biomass, but represented a length characteristic of other prey species. Similarly, most cephalopods in the diet fell within the common prey size range (e.g., 5-25 cm TL). Bioluminescent trails of darting anchovies and other small fish and squid were frequently seen while snorkeling at night in offshore waters and likewise would be readily visible to sharks. Also, the majority of cephalopod species taken by sharks possessed photophores. Bioluminescence associated with prey movements and light organs may represent significant predatory cues for sharks at night.

ACKNOWLEDGMENTS

LITERATURE CITED

BANE, G. W.
1968. The great blue shark. Calif. Curr. 1(1):3-4.
BIGELOW, H. B., AND W. C. SCHROEDER.
1948. Sharks. *In* J. Tee-Van, C. M. Breder, S. F. Hilde-
brand, A. E. Parr, and W. C. Schroeder (editors), Fishes of
the western North Atlantic, Part one, p. 59-546. Mem.
Sears Found. Mar. Res., Yale Univ. 1.
CASEY, J. G.
1976. Migrations and abundance of sharks along the At-
lantic coast. *In* W. Seaman, Jr. (editor), Sharks and
man—a perspective, p. 13-14. Fla. Sea Grant Program,
Rep. 10.
CLARKE, M. R.
1962. The identification of cephalod "beaks" and the rela-
tionship between beak size and total body weight. Bull.
Br. Mus. (Nat. Hist.), Zool. 8:419-480.
CLARKE, M. R., AND J. D. STEVENS.
1974. Cephalods, blue sharks and migration. J. Mar.
Biol. Assoc. U.K. 54:949-957.
COUCH, J.
1862. A history of the fishes of the British Islands. Vol. 1, p.
26-36, 41-44. Groombridge and Sons, Lond.
COUSTEAU, J.-Y., AND P. COUSTEAU.
1970. The shark: splendid savage of the sea. Doubleday
and Co., Garden City, N.Y., 277 p.
FEDER, H. M., C. H. TURNER, AND C. LIMBAUGH.
1974. Observations on fishes associated with kelp beds in
southern California. Calif. Dep. Fish Game, Fish Bull.
160, 144 p.
FERREL, D. W., D. R. NELSON, T. C. SCIARROTTA, E. A. STAN-
DORA, AND H. C. CARTER.
1974. A multichannel ultrasonic biotelemetry system for
monitoring marine animal behavior at sea. ISA (In-
strum. Soc. Am.) Trans. 13:120-131.
GILBERT, P. W.
1963. The visual apparatus of sharks. *In* P. W. Gilbert
(editor), Sharks and survival, p. 283-326. D. C. Heath
and Co., Boston.
HOBSON, E. S.
1963. Feeding behavior in three species of sharks. Pac.
Sci. 17:171-194.
HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters
near shore at Santa Catalina Island, California. Fish.
Bull., U.S. 74:567-598.
KALMIJN, A. J.
1971. The electric sense of sharks and rays. J. Exp. Biol.
55:371-383.
LEBRASSEUR, R. J.
1964. Stomach contents of blue shark (*Prionace glauca* L.)
taken in the Gulf of Alaska. J. Fish. Res. Board Can.
21:861-862.
LO BIANCO, S.
1909. Notizie biologiche riguardanti specialmente il
periodo di maturità sessuale degli animali del golfo di
Napoli. Mitt. Zool. Stn. Neapel 19:666-667.
MACCALL, A. D., G. D. STAUFFER, AND J.-P. TROADEC.
1976. Southern California recreational and commercial
marine fisheries. Mar. Fish. Rev. 38(1):1-32.

MAIS, K. F.
1974. Pelagic fish surveys in the California cur-
rent. Calif. Dep. Fish Game, Fish Bull. 162, 79 p.
MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California.
Calif. Dep. Fish Game, Fish Bull. 157, 235 p.
NEAVE, F., AND M. G. HANAVAN.
1960. Seasonal distribution of some epipelagic fishes in the
Gulf of Alaska region. J. Fish. Res. Board Can. 17:221-
233.
NELSON, D. R.
1974. Ultrasonic telemetry of shark behavior. Nav. Res.
Rev. 27(12):1-21.
NELSON, D. R., AND S. H. GRUBER.
1963. Sharks: Attraction by low-frequency sounds. Sci-
ence (Wash., D.C.) 142:975-977.
NELSON, D. R., AND R. H. JOHNSON.
1972. Acoustic attraction of Pacific reef sharks: Effect of
pulse intermittency and variability. Comp. Biochem.
Physiol. 42A:85-96.
PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSON.
1971. Food habits of albacore, bluefin tuna, and bonito in
California waters. Calif. Dep. Fish Game, Fish Bull.
152, 105 p.
QUAST, J. C.
1968. Observations on the food of the kelp-bed fishes. *In*
W. J. North and C. L. Hubbs (editors), Utilization of kelp-
bed resources in southern California, p. 109-142. Calif.
Dep. Fish Game, Fish Bull. 139.
ROPER, C. F. E., AND R. E. YOUNG.
1975. Vertical distribution of pelagic cephalo-
pods. Smithson. Contrib. Zool. 209, 51 p.
SCHULTZ, L. P., AND M. H. MALIN.
1963. A list of shark attacks for the world. *In* P. W. Gil-
bert (editor), Sharks and survival, p. 509-567. D. C. Heath
and Co., Boston.
SCIARROTTA, T. C., AND D. R. NELSON.
1977. Diel behavior of the blue shark, *Prionace glauca*,
near Santa Catalina Island, California. Fish. Bull., U.S.
75:519-528.
SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. W. H. Freeman and Co., San Franc., 776
p.
STEVENS, J. D.
1973. Stomach contents of the blue shark (*Prionace glauca*
L.) off south-west England. J. Mar. Biol. Assoc. U.K.
53:357-361.
1976. First results of shark tagging in the North-east At-
lantic, 1972-1975. J. Mar. Biol. Assoc. U.K. 56:929-937.
STRASBURG, D. W.
1958. Distribution, abundance, and habits of pelagic
sharks in the central Pacific Ocean. U.S. Fish Wildl.
Serv., Fish. Bull. 58:335-361.
TESTER, A. L.
1963. The role of olfaction in shark predation. Pac. Sci.
17:145-170.
TRICAS, T. C.
1977. Food habits, movements, and seasonal abundance of
the blue shark, *Prionace glauca* (Carcharhinidae), in
southern California water. M.S. Thesis, California State
Univ., Long Beach, 79 p.
WEEKS, A.
1974. Shark! NOAA 4(1):8-13.