The Ecology of the Scalloped Hammerhead Shark, *Sphyrna lewini,* in Hawaii[1]

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ABSTRACT: Kaneohe Bay, Oahu, is a pupping ground for the scalloped hammerhead shark, *Sphyrna lewini,* the pups being most abundant between April and October. While in the bay, the pups stay in the most turbid areas by day and move out at night to reef areas where they feed on reef fishes and crustaceans. The pups spend a maximum of three to four months in the bay and then apparently leave nearshore areas. The total number of pups passing through Kaneohe Bay may be as high as 10,000 per year.

Adult hammerheads are present inshore also between April and October. They apparently move in for delivery and breeding. Squid beaks in their stomachs indicate that the adults are pelagic the rest of the year—possibly living below the surface layers.

SHARKS ARE COMPONENTS of most marine ecosystems and are usually the top carnivores in the community. As with large carnivores in most communities, data on food habits, reproduction, migrations, and so forth are mostly scattered and based on few specimens. This is probably a result of the difficulty in capturing and handling sufficient numbers to draw valid conclusions. The more comprehensive studies of sharks, e.g., Springer (1960), Olsen (1954), Ripley (1946), have utilized data from shark fisheries. Unfortunately, fishery data are not always collected with ecologists in mind and are limited to a few species in a few regions. Consequently, the ecology of most sharks, particularly the larger species, is poorly known. This paper presents results of a study on one such species, the scalloped hammerhead shark, *Sphyrna lewini.*

The hammerhead sharks (family Sphyrnidae) are found in all tropical and warm-temperate oceans. Although the family is easily identified, the different species are not and until recently were poorly described. Gilbert (1967) has recently reviewed the family and relegated many previously recognized species to synonymy. Unfortunately much of the literature previous to this revision is of negligible specific value.

Sphyrna lewini is one of the wider-ranging hammerheads. It occurs in all oceans and shares much of its range with a similar species, *S. zygaena.* These two species are the only hammerheads recorded from Hawaii. They are easily separated by the conspicuous medial indentation on the head of *S. lewini,* which is absent in *S. zygaena.* In spring and summer, adults and pups of *S. lewini* are found in shallow estuarine or protected areas throughout the islands. Neither species appears to be abundant elsewhere or during other seasons.

The large numbers of *S. lewini* pups found in Kaneohe Bay, Oahu, suggest that the bay is one of the principal pupping grounds for this species. During an exploratory survey in the spring of 1968, the pups were collected frequently with gill nets and appeared to be the most abundant large predator in the bay. Because the University of Hawaii's marine laboratory is located in this bay, a large population of sharks could be conveniently studied and the results correlated with a considerable amount of ecological and physical background data from other studies in the area. A concentrated study of *S. lewini* was carried out from the spring of 1968 to the fall of 1969. The results provide a picture of the ecology of *S. lewini* in the bay, its role in the bay community, and some indications of its habits elsewhere.

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STUDY AREA

Kaneohe Bay (Fig. 1) is the largest enclosed body of water in the Hawaiian Islands. It is surrounded on three sides by land and protected on the fourth, offshore side by a large shallow reef 0 to 3 m deep. There are two channels across the reef—one at the north end about 10 m deep and a shallower (3 m) one, the Sampan Channel, at the south end. Patch reefs and a few small islands are found throughout the bay, but are more numerous and smaller in the north and middle sections. Aside from these patch reefs, most of the bay is about 14 m deep, with the deepest spots being 19 m. The bottom sediment is soft coral mud. Surface water temperatures taken daily at the marine laboratory on Coconut Island during the study ranged from 20.3° C in February 1969 to 29.2° C in August 1968.

The south section of the bay, where most of the study was conducted, is partially cut off from the rest of the bay by patch reefs and is completely closed from the open ocean by Mokapu Peninsula. Owing to restricted circulation and large amounts of runoff, this section is considerably more estuarine than the remainder of the bay. Going from the southeast to the northwest ends of the bay, salinity generally increases, and turbidity, nutrient content, and productivity decrease. (For details, see Bathen, 1968.)

MATERIALS AND METHODS

Most of the sharks collected for this study were caught in gill nets. Because the sides of their heads become entangled in the mesh, hammerheads are particularly susceptible to gill nets. Almost any size mesh smaller than the head width is effective. Mesh sizes of 1″, 1 1/2″, 3″, and 5″ stretch were tested initially. The 5″ mesh (no. 415 nylon thread) was used almost exclusively during the remainder of the study because it caught pups as effectively as smaller meshes and also held large sharks, which could escape from and considerably damage the lighter nets.

Each link of net was 30 m long and either 3 or 6 m high. With few exceptions the nets were set on the bottom 12 to 15 m deep with the ends anchored by concrete blocks. Usually only one link was set at each site. Most of the sets were made near a reef and perpendicular to the reef's edge. This type of set consistently collected more sharks than sets parallel to the reef's edge or on the open bottom of the bay. Usually the nets were set in the late afternoon and retrieved the following morning. (Six daytime sets collected no sharks.)

The number caught per set did not necessarily give an estimate of the number of sharks passing an area during the night, since an unknown fraction may have avoided the net before hitting it. However, since the same type of net and set was used, the numbers caught probably gave reliable estimates of relative abundance. Given the depth and general turbidity of Kaneohe Bay waters, the differences in turbidity, and moonlight probably did not change the effectiveness of the nets on different nights.

Except in a very few extreme cases, the worst being 52 pups in a 30×6 m^2 net, it is also unlikely that the effectiveness of the nets was impaired by small sharks already captured. Large sharks, however, usually fouled the net, and, if they were caught early in the night, certainly decreased its effectiveness for pups.

Since the gill nets worked only at night and all sharks captured were dead, daytime distribution was studied and live sharks collected by longline. The main line with 25 to 50 hooks was set slowly in a straight line and checked, rebaited, and reset every 20 to 30 minutes; longer delays resulted in dead sharks. For each set, the number of sharks and number of missing hooks were recorded. The catch per hook per minute was calculated for different areas and used to estimate relative abundance. Because of the short time between sets, gear saturation and lost baits were ignored. The sharks captured were either tagged and released or returned to the laboratory.

Pups were tagged with numbered plastic dart tags which were inserted just behind and below the first dorsal fin (Fig. 2). Sex, total length to the nearest millimeter, and side tagged were recorded for each pup. Once the pup was brought to the edge of the skiff, the entire tagging operation took only about 30 seconds. Occasionally pups were very weak or dead from having been on the line too long; this was recorded as was excessive bleeding from the hook

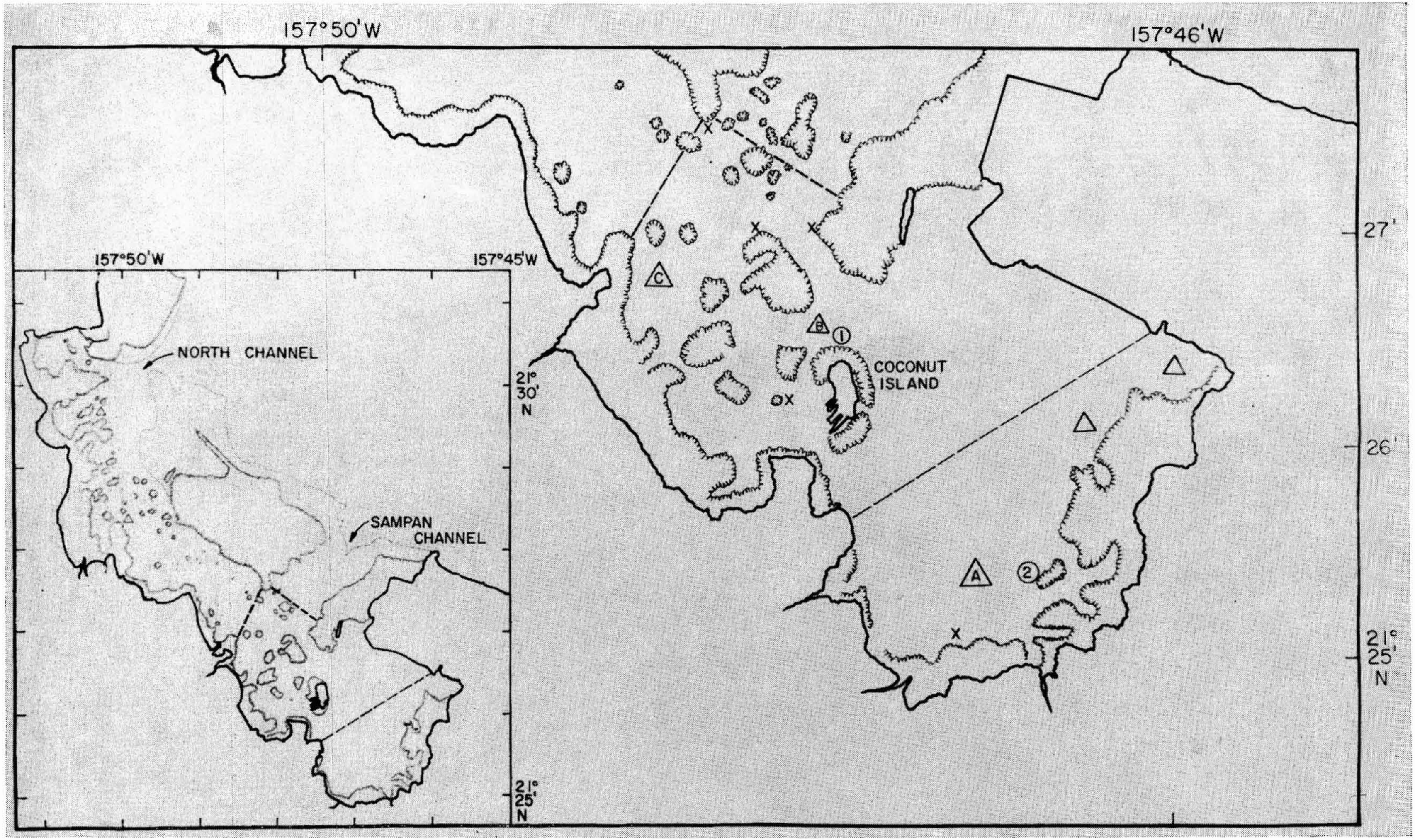

FIG. 1. Map of Kaneohe Bay (inset) and of southern section of the bay. Shoreline and islands are outlined in solid lines; reefs with lighter, stippled lines. The southern section, bounded by heavier dashed lines, is separated into the outer and far southern ends by a lighter dashed line. Gill-net stations 1 and 2 are shown as circles; other frequently used gill-net stations are indicated with an *x*. Longline stations are shown as triangles.

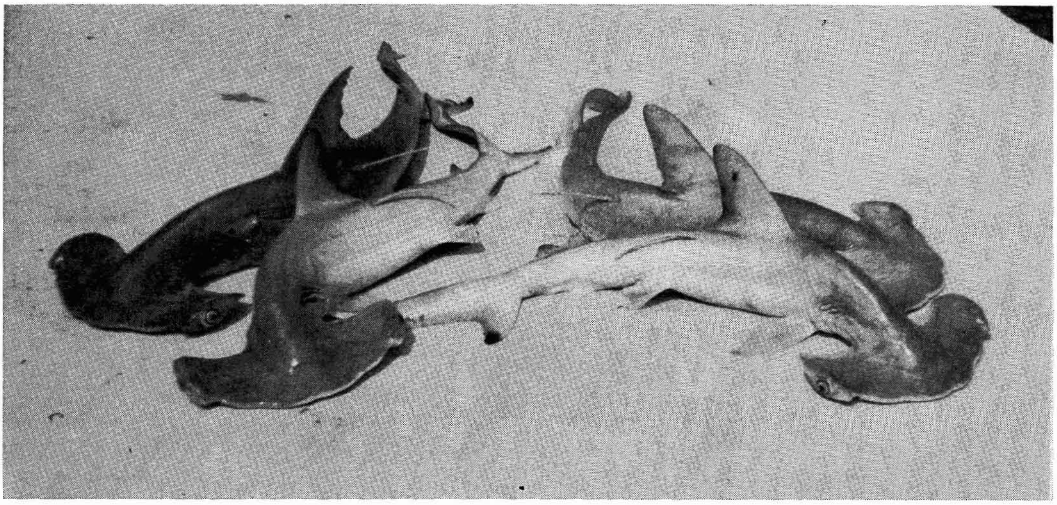

FIG. 2. Photograph of four *Sphyrna lewini* pups with dart tags inserted below the first dorsal.

wound. With the exception of those recorded as nearly dead, the weak or bleeding sharks were recaptured as frequently (relatively) as those released in good condition. Thus all tagged pups except those recorded as nearly dead were counted as successful releases.

Among sharks tagged in the laboratory, there were no deaths directly attributable to tagging. As these sharks had been handled more and had been held in a small container en route to the lab, it seems unlikely that there was significant tagging mortality among those released immediately after capture in the field. Occasionally tags dropped off sharks kept in the laboratory. However, a tag scar was clearly visible for at least 1 month afterwards and still discernible after 3 months. All pups collected in the field were examined for tag scars. Out of a total of 76 recoveries, the tag had dropped off in only three cases.

For laboratory growth studies, live sharks were kept in shallow outdoor holding ponds. They were fed smelt and squid and probably supplemented their diet with other fish and with crustaceans. The captive sharks were tagged for identification, and total length and weight recorded periodically.

Several methods were used to identify stomach contents of collected sharks. Crustacea could usually be identified to major taxa and often to species since the exoskeleton was usually digested last. Fishes were identified mostly by scales. Because a complete study of scales of fishes from Kaneohe Bay was not made, most identifications are reliable only to family or genus. On some small species, especially gobioids, the scales were digested rapidly or lost, and identification had to be made from body form. The cephalopod beaks were identified and size of individuals estimated by Richard E. Young.

Total length, measured to the nearest millimeter was used throughout this study. For 87 pups (470 to 840 mm long) weighed to the nearest gram, the relationship between weight and total length was: $W = L^{3.07} \times 2.76 \times 10^{-6}$. Adult sharks were measured only to the nearest centimeter and were not weighed.

RESULTS

Distribution of Pups in the Bay

It is well known locally that hammerhead pups are most abundant in Kaneohe Bay during the summer months. Fig. 3 shows catch per unit effort at two stations frequently fished with gill nets in the south section of the bay. These show that the pups were present all year round, but in consistently larger numbers from about May to October. (Actually, numbers may start to increase in April but no sets were made in that month.)

Within the bay, the pups appeared to be generally more abundant in the south section. Six

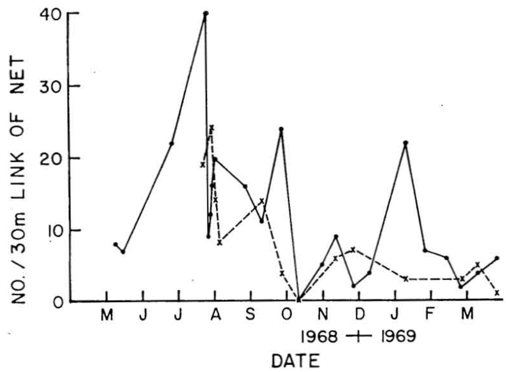

FIG. 3. Catch per unit effort (link of gill net) from May 1968 through March 1969 at station 1 located off the reef at Coconut Island (dots, solid line) and station 2 located along the perimeter of the far southern end (x's, dashed line).

gill-net sets were made north of the Sampan Channel August 6–8, 1968. The median catch was 8.5 pups per set (range: 2–20) as opposed to a median of 16 pups per set (range: 8–24) in 11 sets in the south section made just before and just after the north section series. (The difference is significant, $p \leqslant .05$, rank-sum test.)

Daytime longline sets were made at eight locations in the bay (Fig. 1), usually three sets at each in the forenoon. Catches were consistently higher at the far south end of the bay (*A* in Fig. 1) where the water was extremely turbid. The catch per 100 hooks per minute in this area ranged between .26 and .82 ($\bar{x} = .422$) for 6 mornings' fishing. At station *C*, the catches were .31 and .05 per 100 hook-minutes for 2 mornings; at the other stations, catches ranged between 0 and 0.07 ($\bar{x} = 0.032$).

Even in the far south end, the catch dropped off in the late morning hours and, in the afternoon, became as low as elsewhere. There was no concomitant increase in afternoon catches in other areas. When the longline was used at night near a site that regularly yielded high gill-net catches (*B* in Fig. 1), catches were high —0.70 and 0.65 pups per 100 hook-minutes in 2 nights' fishing. Catches in the same area were practically nil during the day.

Together the longline and gill-net data indicate that the pups concentrated at the far south end of the bay during the day and dispersed at night, most of them remaining in the south section. Possibly the longline data reflects inclination to feed rather than relative abundance. It seems highly unlikely, however, that only the sharks in the far south end were hungry during the daytime. Tag-return data also substantiated such movements (see below).

Gill-net catches were usually higher off the patch reefs near Coconut Island than along the perimeter of the far south end (see Fig. 3). Sets away from the edges of the reefs caught few sharks. Three sets with a small gill net on the reef flat near Coconut Island yielded no pups. However, pups were frequently seen and caught by fishermen over shallow mud flats in the far south end.

The pups apparently stay close to the bottom. In May 1968 the approximate position of each shark was noted for 18 sets of nets 6 m high. Out of 131 pups, only 12 were in the top 1/3 and 18 in the middle 1/3. A 6-m-high floating gill-net set near the reef collected only zero to four sharks per set, while bottom nets nearby collected 10 to 20 and more per set. Thus the pups appear to move along the edge of the base of the reef instead of the open bottom, and rarely rise to the surface except in the muddy flats at the far south end of the bay.

Although no quantitative records were kept, the longline catches, both day and night, suggest that the pups school or aggregate to some degree. Frequently there were sections of the line with sharks on every hook followed by the sections with no sharks.

Food

A total of 143 pup stomachs with food remains was examined. With the exception of a green bean, the prey were all fish or crustaceans (Table 1). It is unlikely that the data were biased by different rates of digestion for different foods; because many pups were available, only stomachs with relatively fresh food were saved for analyses.

Fish—principally scarids and various gobioids —were the most frequent items in pups collected near Coconut Island. The scarids and most of the other species recorded are reef fish not normally found over the open bottom or in midwater. Most of the prey species are active during the day and seek shelter at night. Since

TABLE 1

PREY FOUND IN STOMACHS OF PUPS OF THE SCALLOPED HAMMERHEAD SHARK, *Sphyrna lewini*, IN TWO SECTIONS OF KANEOHE BAY, OAHU, HAWAII

	NUMBER OF STOMACHS IN WHICH PREY FOUND		ESTIMATED LENGTHS OF PREY (cm)
	NEAR COCONUT ISLAND	FAR SOUTH END OF BAY	
Total Number of Stomachs Examined	108	33	
Fish: Total	73	12	
Scarids	23	2	5–15
Gobioids	22	0	3–5
Labrids	9	0	8–12
Pomacentrids	6	1	6–8
Apogonids	5	0	5–10
Mullids	4	0	12–15
Synodontids	2	0	—
Chaetodontids	1	0	6
Congrids	1	0	10
Bothids	1	0	8
Hemiphamphids	1	0	—
Engraulids	0	2	3–5
Atherinids	0	1	4–5
Unidentified	15	6	—
Crustacea: Total	58	29	
Alpheid Shrimps	47	25	2–4
Other Shrimps	7	12	1–3
Stomatopods	8	0	4–7
Crabs	4	8	1–3
Isopoda	2	0	1

the hammerheads apparently were present and fed around the reefs at night, it is difficult to conjecture how they captured these species. The gobioids were difficult to identify principally because their scales were small and easily lost or digested; many of the unidentified fishes were probably gobioids. The principal species were *Bathygobius fuscus* and *Opua nephodes*. These are rather ubiquitous species found in a variety of habitats in the bay. They are abundant on both the reef and the rubble slope below it. It is not known if they are active at night.

The crustaceans were mostly alpheid shrimps (principally *Alpheus malabaricus*). These and most of the remaining crustaceans almost certainly came from the reef rather than the open bottom or mid-water.

In pups from the far south end of the bay, crustaceans—principally alpheids—were found more frequently than fishes. This probably reflected both a relative lack of fish in this area and a change in feeding habits. The reefs in this area are dead and heavily silted. Organisms of all kinds are generally more abundant on the reef flats and mud flats. The sharks probably spent more time in this area foraging over the flats. This is also indicated by the type of fishes recorded. The engraulid *Stolephorus purpureus* and the atherinid *Pranesus insularum*, which were not recorded from pups taken around Coconut Island, are species which school in shallow muddy water over the reef and mud flats.

Growth

The size range of 1,566 pups caught in gill nets was 395 to 895 mm. (The smallest adult was 217 cm; no intermediates were taken.) The average size of all pups was 557.5 mm. There was no apparent size difference with sex: 769 males ranged from 430 to 840 mm ($\bar{x} =$ 559.1 mm); 797 females ranged from 395 to 895 mm ($\bar{x} =$ 556.00). Data to be presented subsequently predicted that, on the average, the youngest pups were those from gill-net collections from the far south end of the bay. The average size of 150 pups collected there in 1969 was 432 mm; the range, 395 to 693 mm.

There was no regular change in average size with season; the larger pups were not caught in any one season. Thus the average residence time of the pups in the bay was short relative to the growth rate.

Because tagged sharks were usually recovered rather soon after release and also because they were usually dead and had shrunk, the "growth" of tagged sharks was usually negligible or negative. Three tagged pups out for 33, 56, and 78 days showed growths of 11, 37, and 60 mm, respectively. These are minimum estimates of growth in the field.

Table 2 shows the growth of 10 pups kept in ponds at the laboratory. Those from 1968 were fed twice daily—usually all they would eat. Thus their growth rate was probably higher than that in the field. Those from 1969 were fed only once daily and not to satiation. (Their ration was about 5 percent of body weight per

TABLE 2

GROWTH OF 10 PUPS OF *Sphyrna lewini* RETAINED IN LABORATORY PONDS AT COCONUT ISLAND, KANEOHE BAY, OAHU, HAWAII

YEAR	INITIAL LENGTH (mm)	INITIAL WEIGHT (gm)	FINAL LENGTH (mm)	FINAL WEIGHT (gm)	TIME (days)	GROWTH LENGTH (mm)	GROWTH WEIGHT (gm)
	485	—	610	—	60	125	—
	537	590	597	1100	30	60	510
1968	539	617	790	1710	60	151	1093
	550	590	615	1120	30	65	530
	567	700	710	1870	60	143	1170
	547	—	606	—	92	59	—
	552	—	683	—	92	131	—
1969	556	—	733	—	100	177	—
	566	—	683	—	92	117	—
	572	—	637	—	92	65	—

day.) Thus their growth was probably closer to that realized in the field. The final lengths were greater than those of most pups caught in the bay; of 808 pups caught during 1969, 11.1 percent were over 600 mm and only 3.7 percent were over 700 mm. The experimental pups averaged slightly larger than the youngest pups, but were probably less than a month old when caught. This suggests that most pups have left the bay by the time they are about 3 to 4 months old. The longest time between tagging and recapture, 95 days, is close to this estimate.

Tag Recaptures

A total of 410 pups were tagged and released during the study—106 during the summer of 1968, and 304 during the summer of 1969. Of these, 319 were tagged at area *A* in the daytime, 70 at area *B* at night, and the remainder at various locations during the daytime. Seventy-six tagged sharks were recovered, but full recapture data were available for only 68—seven in 1968, and 61 in 1969. All but three of these were recovered from the south section of the bay. Eight tags were recovered by longline, 25 by gill net, and 35 were turned in by fishermen. Table 3 summarizes the tag return data.

Daytime recaptures were, with one exception, inshore of Coconut Island; most were at the far south end of the bay where longline catches indicated sharks were concentrated during the day. This result was not entirely an artifact

TABLE 3

TAGGING AND RECOVERY DATA OF PUPS OF *Sphyrna lewini* IN KANEOHE BAY, OAHU, HAWAII DURING SUMMER, 1968 AND 1969

TAGS OUT		RECOVERIES: DAY				RECOVERIES: NIGHT						TOTAL TAGS RECOVERED/ TOTAL RELEASED = % RECOVERY
AREA TAGGED	NUMBER TAGGED	FS NO.	FS MEDIAN	OTHER NO.	OTHER MEDIAN	FS NO.	FS MEDIAN	CI NO.	CI MEDIAN	OTHER NO.	OTHER MEDIAN	
Station *A*	319	19	17 (0–50)	1	28	24	15 (3–95)	17	28 (6–80)	1	78	62/319 = 19.5%
Station *B*	76*	1	13	—	—	2	46.5 (28–64)	2	36 (15–56)	—	—	5/76 = 6.6%
Other	15	—	—	—	—	—	—	—	—	1	23	1/15 = 6.7%
Totals	410	20		1		26		19		2		68/410 = 16.6%

NOTE: FS, far southern end of bay; CI, near Coconut Island; Other, other areas outside the southern section. Median time at liberty given in days (ranges are in parentheses) for each set of recaptures.

* All but six tagged at night.

from our fishing principally in the far south end during the day. Fishermen, who returned over one-half of the tags, fished generally all over the bay.

The nighttime recaptures were about evenly divided between the far south end and the patch reefs outside Coconut Island. For those originally tagged in area *A*, the ranges of the time at liberty overlapped for the two groups, but the medians were different ($p = 0.04$, one-tailed rank-sum test), that for the far south end being about 2 weeks less than that for the areas outside Coconut Island. This would result if the younger pups tended to stay in the far south end at night as well as during the day. The older pups (at time of tagging) would be recaptured at various sites and after various times at liberty, thus accounting for the overlap of the ranges. The younger pups would be at first recaptured more frequently in the far south end and later in the other areas, accounting for the difference in median time at liberty between the two sections of the bay.

The gill-net results substantiated this idea. The average size of 150 pups caught in the far south end during 1969 was 532 mm. The average size of 658 caught during the same period in the outer reef areas was 563 mm. The size frequency curves from the samples differed significantly ($p < 0.01$, Kolmogorov-Smirnov test), the curve from the far south end being displaced toward smaller sizes. Thus the pups caught in the far south end at night tended to be smaller and presumably younger than those caught outside.

Of the pups tagged at locations other than station *A*, i.e., outside the far south end, only about 7 percent were recovered as compared to 18 percent of the ones tagged near station *A*. Most of these pups (70 ex 91) were tagged near Coconut Island (station *B*) at night. This suggests that, once the pups began ranging far at night, they were more likely to leave the southern part of the bay permanently. Only three tags were recovered outside the south section of the bay, one of them in an area about 12 km north. Although we exerted little fishing effort in the northern sections, the local fishermen worked these areas often. The few tag returns from these areas indicate that some pups worked their way up the bay and eventually out the deep channel but that most probably left directly from the south end via the Sampan Channel or over the reef. Unfortunately, the nets could not be set in the latter channel. (The depth of water and height of the nets were nearly optimum for catching one of the fishing vessels for which the channel is named.)

The rather low rate of recapture indicates that the total population of pups was large. A total of 1,669 pups was either gillnetted or long-lined during or immediately after the two periods of tag releases, and only 36 tags were collected. Fishermen caught nearly the same number of tagged sharks, indicating that they caught a similar total number during the same periods. (This is plausible since 50 to 100 pups are often taken in a single night's commercial gill-net operation.) In spite of this mortality, the population appeared to remain high throughout the summer, suggesting that it was considerably larger than the above numbers or that the birth of new pups matched the mortality.

Since most tagging was done in the far south end during the daytime and there was probably no selection for younger or older pups, the tags were probably distributed at random in the population in spite of differences in the nighttime habits of younger and older pups. Using the methods of Jolly (1965), it is possible to estimate population size during August of 1969. Between August 11 and 26, 214 pups were tagged. Seven were recaptured in the course of tagging; 20 were recaptured by gill nets (out of a total catch of 741 pups) between August 18 and October 9; and 28 were turned in by fishermen between August 26 and November 14. Because the calculations require capture of old tags and release of new ones on the same day, population size could be estimated for only 4 days (Table 4).

The method uses all subsequent tag returns to estimate the number of tags out at time i ($= M_i$ of Jolly). In three of the four cases, M_i exceeded the actual number released. For these it seemed appropriate to use the smaller value to estimate population size.

Since the estimates were based on only one return for each day, the variances due to errors of estimation for the values of N_i in Table 4 were expectedly very large. Thus the estimates

TABLE 4

ESTIMATES OF POPULATION SIZE OF *Sphyrna lewini* IN KANEOHE BAY, OAHU, HAWAII, DURING AUGUST 1969

DATE	M_i	S_i	N_i
August 13	41	14	476
August 19	61	83	8425
August 21	111	103	1958
August 25	265	140	6021

NOTE: M_i, estimated number of tags out; S_i, actual number released previous to collecting date; N_i, population size at time i (notation from Jolly, 1965).

only generally indicate population size. The value for August 13 is almost certainly too low and due to a "lucky" recapture; almost as many sharks as estimated were collected within about 2 weeks of that date. The other estimates indicate that the number of pups present was of the order of several thousand. Gill-net catches (Fig. 3) indicate that comparable numbers were present from May to October. Since the average residence time appears to be 3 months or less, the total number of pups passing through the bay during the summer may be as high as 10,000.

Adults

I caught 35 adult hammerheads in Kaneohe Bay and examined two others during this study. In addition, A. L. Tester kindly loaned unpublished data on all *Sphyrna lewini*, including 11 adults, caught by the Hawaii Cooperative Shark Research and Control Program between July 1967 and June 1969 (Tester, 1969).

All of the adults caught in Kaneohe Bay (43) were males. Their lengths ranged between 195 and 272 cm (median = 248 cm). All but one, caught in January 1968, were caught between March and September. All had swollen claspers and all examined (9) carried ripe sperm.

All but two of the adult males were captured outside Coconut Island and most of these near the Sampan Channel. The two exceptions were, however, captured at station 2, at the far south end. Also, adults were not infrequently seen coming through the Sampan Channel or in the bay during the day. During long-lining at station *A* in the daytime, particularly in 1968, large numbers of hooks were frequently lost. This was quite likely due to adult hammerheads eating hooked pups. One adult caught near Coconut Island had a longline hook in his throat and tags in the gut from two pups caught 3 days earlier and recorded as "nearly dead" when released. Thus the adults caught near the Sampan Channel were probably intercepted on their way into the bay. The males apparently spend at least several days in the bay and move over all areas.

In 1969 there was almost no "unexplained" loss of hooks while long-lining, and catch rates for pups were distinctly higher. Possibly a large percentage of adult males were caught in the gill nets that year and did not reach the far south end of the bay. Twenty-three males were caught during 1969 as opposed to 14 in 1968. This may have been a sizeable fraction of the total number entering the bay. Furthermore, the effect of both years' fishing would be cumulative if the same males tended to return each year.

Adult males were not restricted to eating hooked or recently tagged pups. Five of the 35 gill-netted adults had remains of one to three pups in the stomachs and no tags or longline hooks. Pup remains were also found in the stomach of one small blacktip shark, *Carcharinus limbatus,* out of the 10 blacktips caught during the study (74 to 210 cm long). The sandbar shark, *Carcharinus milberti,* and the tiger shark, *Galeocerdo cuvieri,* may also prey on the pups but these species are found in the bay relatively infrequently. Adult males are probably the major source of mortality for pups while the latter are in the bay.

Three other males had eaten a surgeon fish, *Naso brevirostris,* about 30 cm long; a milkfish, *Chanos chanos,* about 1 m long; and an octopus about 70 cm radius, respectively. Nineteen stomachs contained cephalopod beaks, up to six pairs. Those from 15 were examined by Richard E. Young. All were from pelagic species, principally oegopsid squid. *Histioteuthis* sp. occurred most frequently; two species of Ommastrephids, six other oegopsids, and one species of pelagic octopod were also found. Estimated mantle lengths ranged from 50 to 200 mm. Some of the beaks had flesh on them, indicating that they had been eaten recently. The pups, fishes, and the large octopus were almost certainly eaten in the bay, but the other cephalopods were almost as certainly taken in mid-water well away from shore and over quite deep water.

Adult females have been collected in the bay in previous years. The reports, though anecdotal, agree that all females were about 1 meter (3 or 4 feet) longer than the males and that they usually were carrying well-developed embryos. Such distinctly larger sharks were sighted in the bay during this study. Quite likely these were mature females, which are known to be larger than mature males (Springer, 1960).

Subsequent to this study, I examined two females caught on the shallow reef southeast of the Sampan Channel—just outside the bay. One, caught May 26, 1970, was 304 cm long and carried seven pups. One of these pups was partially extruded, and eight others with very fresh umbilical scars were caught in the same net. Some pups were evidentaly released while she struggled in the net. The average length of all the pups collected was 530.5 mm (range: 429 to 562 mm). These figures agree well with those for the youngest pups in the bay. The other female, 294 cm long and caught June 9, 1970, had recently given birth, judging from the condition of the uterus. She had also recently mated; fresh, superficial mating wounds were found on the left side between the dorsal fins, and live sperm were present in the uterus. The stomach of the first female contained pelagic squid beaks, that of the second was empty.

All but one record of *Sphyrna lewini* from outside Kaneohe Bay were from the Shark Program. The program caught 1,727 sharks, principally with night sets of hooks on the bottom between 30 and 60 m. Only 22 *S. lewini* were caught; 11 of these, five pups and six adult males, were caught in Kaneohe Bay.

The *S. lewini* from outside the bay were caught between 33 and 140 m at locations off Oahu, Kauai, Molokai, and Niihau. All were caught between March and September. Size and sex were available for only eight. Three were males 210 to 260 cm long—similar to those caught in Kaneohe Bay. One female, 214 cm, was immature; another, 309 cm, carried 31 embryos. The average length of these was 447 mm, smaller than the average of the youngest pups in Kaneohe Bay, 532 mm.

Three individuals 82, 108, and 138 cm long were taken by the program at depths of 46, 140, and 60 m, respectively. The first is the only known record of a pup taken outside a nursery ground. (I have also questioned several local fishermen about this.) During an exploratory fishing project, I collected an individual 129 cm long in a gill net set at 275 m. These were the only individuals of intermediate size collected. The collection depths and the infrequent occurrence of juveniles nearshore suggest that, once the pups leave the nursery area, they move to fairly deep and possibly oceanic water. The stomach contents of the 129-cm individual—about 200 beaks of an enoploteuthid squid species—also suggest this strongly.

DISCUSSION

The pups apparently prefer more dimly lighted areas. While in Kaneohe Bay, they stayed in the most turbid section both day and night for a few weeks and later ranged to other areas only at night. Perhaps the "stimulus" to leave the bay comes when a pup swims too far from the turbid south end to return by dawn. He would then continue to wander, perhaps spending days in smaller turbid areas farther up the bay, until he eventually left the bay. Once outside the pups could seek darkness by swimming deeper.

If this hypothesis is true, the low number of pups in the bay during winter time may not be entirely due to few females' pupping during that season (although the latter appears true from records of adult sharks). From about March to October is "trade-wind" season in Hawaii; trade-wind chop keeps the bay waters stirred and turbid nearly constantly. During the remainder of the year, the trade winds alternate with spells of south or "kona" winds, frequently of lower velocity. Quite frequently during the latter periods the bay is flat calm, and water clarity increases markedly even in the far south end. The higher illumination would likely act as a stimulus for the pups to begin wandering and leave the bay sooner, thus decreasing their residence time. In fact, marked decreases in gill-net catches in the fall of both 1968 and 1969 closely coincided with the first spell of "kona" weather.

In spite of the fact that no adult females were caught inside the bay during the study, it seems likely that they come into the bay to deliver their pups and also to mate with the males there. It is doubtful that the females deliver on the reef flats where two were caught. Pups were taken very rarely in this area, and the two adults were probably caught in transit. Females may be less likely to be caught in the bay because of their behavior. Female sharks apparently do not feed just prior to delivery (Springer, 1960). The female hammerheads then would not be expected to patrol the edge of the reefs for food and consequently would not be taken by the gill nets. Also, their residence time in the bay may be very short relative to that of the males. Pupping and mating could be accomplished in a matter of a day or even a few hours. This would also decrease the chance of catching females.

The apparent relative rareness of adult hammerheads except in Kaneohe Bay and other breeding areas and their near absence except during the principal pupping season suggest that they move inshore only for reproductive purposes. The presence of pelagic squid beaks in their stomachs indicate that the adults spend the remainder of the year at sea.

These results agree with a suggestion by Gilbert (1967) that *S. lewini* and *S. zygaena* are more oceanic than other hammerheads because they are the only species occurring in Hawaii. Hammerheads, *S. zygaena* and *S. lewini,* have been recorded far at sea (Bigelow and Schroeder, 1948; Strasburg, 1958); but rather infrequently. Strasburg recorded only four hammerheads, one definitely *S. lewini,* out of a total of over 6,000 sharks collected by pelagic longline in the Central Pacific. The longlines fished mainly in the upper 100 m and not below 200 m. *S. lewini*'s black, rather than blue, dorsal color, large eyes, and the preference of its young for dimly lighted areas suggest that this species may inhabit greater depths and thus is not susceptible to conventional fishing methods.

Inshore-offshore migration could explain apparent north-south migration along larger land masses. Bigelow and Schroeder (1948) infer from seasonal changes in abundance that hammerheads (probably *S. zygaena*) migrate along the east coast of the United States. Judging from the habits of *S. lewini* in Hawaii, it is possible that such changes could be, at least in part, due to onshore-offshore migration combined with latitudinal difference in the seasons.

If *S. lewini* is normally dispersed at sea, the inshore breeding migration increases the chance of contact between the sexes and probably increases survival among the newly born pups. Food for the pups is probably more abundant in the inshore areas and predation likely less. The bay and other inshore areas where pups are found are generally very productive compared to the deeper offshore areas where adults apparently feed. Although adult hammerheads may be a significant source of mortality in the pupping grounds, there are few sharks of other species, particularly in the far south end of Kaneohe Bay. The lower visibility of inshore areas may also reduce predation. Given these advantages and the seasonal weather pattern, the principal pupping season is well timed. By being born during the trade-wind season, the pups are almost assured a longer residence time in the bay, a consequently larger size upon leaving, and therefore, an increased chance for survival.

The large number of pups must have a major effect on the energy budget of Kaneohe Bay. Particularly around the reefs, pups appear to be the most abundant large carnivore. The nets used during most of the study tended to overestimate the relative abundance of pups since they were selected for catching the latter. However, when lighter, smaller mesh gill nets, which tended to be more effective for teleosts, were set near the reefs, about 75 percent of the predatory fishes caught and a larger fraction of the biomass were still hammerhead pups. Among the resident reef predators, only the moray eels and octopi are possibly comparable in abundance. The sharks and other nonresident predators must consume a significant portion of the reef's resources.

The importance of nonresident predators has been neglected in studies of reef ecology. Both in Kaneohe Bay (Wass, 1967) and elsewhere (e.g., Odum and Odum, 1955; Bardach, 1959), abundances of fishes were estimated and trophic pyramids produced based on visual censuses or poisoning collections. These methods are adequate for resident species and allow consideration of input to the reef community through resident fishes' feeding on nonresident prey. Neither method, however, is likely to record any but a small fraction of nonresident fishes—carangids, elopids, and so forth, as well as sharks—that may constitute an important output in the reef's economy. Future studies should make some effort to include estimates of the abundance of such species before considering trophic structure of reef communities.

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