

# Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat

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**ABSTRACT:** Nursery habitat use and growth rates of juvenile scalloped hammerhead sharks *Sphyrna lewini* were measured in a Hawai'i nursery (Kāne'ohe Bay, Ō'ahu) using a 28 mo tag-and-recapture study augmented by experimental determination of the relative age of neonate sharks. An estimated 7700 ( $\pm 2240$  SD) hammerhead sharks are born in Kāne'ohe Bay each year. Neonates are born in the summer between May and September and had low retention (from 0.07 to 0.15, as a fraction of neonate population size) within the bay from Age 0 to Age 1. A primary cause of low retention appears to be mortality from starvation. Most juvenile sharks recaptured after short periods of time at liberty (<60 d) showed weight loss. There was also a significant negative relationship between shark weight and umbilical wound condition. Sharks with healed wounds had lower average body weights than sharks with open wounds, indicating that many sharks lose weight in the first few weeks after birth. Shark condition factor ( $\text{body weight} \times \text{length}^{-3}$ ) was also significantly lower during late summer and early fall. Despite this apparent lack of foraging success, growth rates and size distribution of recaptured sharks indicated that juvenile *S. lewini* utilize Kāne'ohe Bay for up to 1 yr. During their residency, sharks move throughout the nursery and there is no discernible ontogenetic shift in habitat use. These findings confirmed recent hypotheses that Kāne'ohe Bay may be more important in providing protection from predators than in providing a plentiful source of food for juvenile *S. lewini*.

**KEY WORDS:** Tag-recapture · Mark-recapture · Umbilical wound · Philopatry · Growth rate

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## INTRODUCTION

Nursery habitats are usually shallow, coastal areas that are geographically separated from adult feeding grounds (Springer 1967). They have been an important component in the reproductive strategy of chondrichthyans for at least 350 million years (Lund 1990). Adult sharks typically migrate to nurseries for birthing (and possibly mating), but are not thought to stay long in protected nursery habitats (Branstetter 1990). In contrast, neonates and juveniles spend the first part of their life within the nursery (Branstetter 1990, Castro 1993). Hypothesized benefits of nurseries include accessibility of food items (i.e. catchable prey), increased prey abundance (i.e. nutrient rich habitat), and

decreased predation risk (Simpfendorfer & Milward 1993, Morrissey & Gruber 1993a).

Scalloped hammerhead sharks *Sphyrna lewini* are large, semi-coastal, viviparous sharks that utilize near-shore nurseries throughout their circumtropical range (Clarke 1971, Snelson & Williams 1981, Compagno 1984, Branstetter 1990, Castro 1993, Simpfendorfer & Milward 1993). Kāne'ohe Bay (Ō'ahu, Hawai'i) is an example of an estuarine bay used as a birthing ground by *S. lewini* (Fig. 1). It is the largest embayment in the Hawai'ian Islands (61 km<sup>2</sup>, Holthus 1986), and is separated from offshore adult hammerhead habitat by barrier reef flats and shallow sand channels. Kāne'ohe Bay is also the location of the University of Hawai'i's Institute of Marine Biology (HIMB), and several previ-

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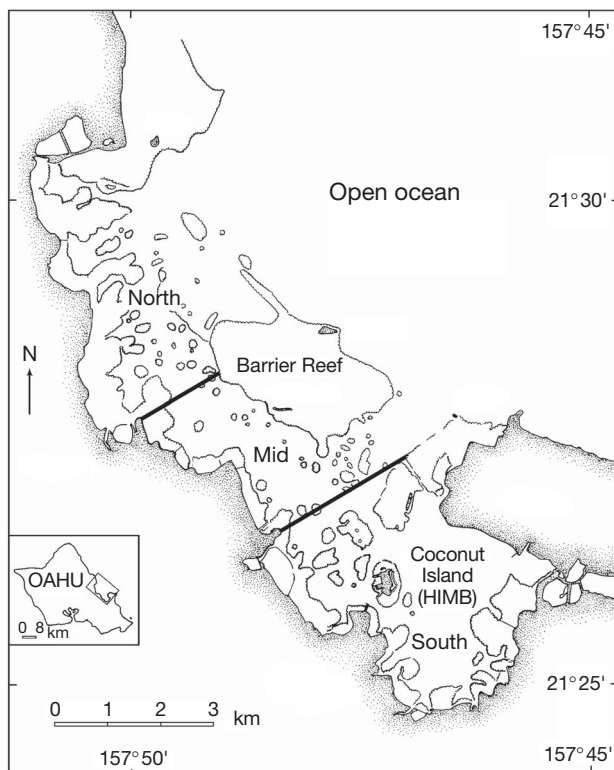


Fig. 1. Kāne'ōhe Bay. Outline of patch reefs and shallow sand flats, location of HIMB research facility at Coconut Island, and designated bay zones (North, Mid, and South) are indicated. Inset: location of Kāne'ōhe Bay on island of O'ahu, Hawai'i

ous studies have focused on (1) the physiology and behavior of *S. lewini* within the bay (Lowe 2001, 2002, Holland et al. 1993), (2) the population dynamics of the bay's juvenile hammerhead population (Clarke 1971, Bush & Holland 2002, Bush 2003, H. Harkins et al. unpubl. data), and (3) the impact of that population on the ecology of the bay (Bush & Holland 2002, Lowe 2002). Results of the more recent studies have suggested that Kāne'ōhe Bay may not provide sufficient prey resources for *S. lewini*, which lends greater weight to the predator avoidance hypothesis.

Different methodologies have yielded a range of census size estimates for the juvenile hammerhead population within Kāne'ōhe Bay. H. Harkins et al. (unpubl. data) estimated 2300 individuals, whereas Clarke (1971) estimated a summertime peak as high as 10 000 sharks. These 2 estimates were based on studies conducted many years apart, each restricted to a short period of time (<1 yr). Thus, the difference in population size estimates could be due to differences in methodology or to biologically meaningful inter-annual variation, making it difficult to assess the impact of juvenile populations on the ecology of the bay, or to evaluate the amount of intra-specific com-

petition for food (which could impact survivorship). Juvenile hammerhead sharks have relatively high metabolic rates and commensurately high daily food requirements (Lowe 2001, 2002). If the population is as large as Clarke's estimate, high juvenile shark densities could result in food becoming a limiting resource, especially in mid-summer when the population is largest (Clarke 1971, Bush & Holland 2002, Lowe 2002), and newborn sharks may be compromised by naïve foraging abilities (Lowe 2002).

Since nurseries are usually presumed to be places of ample forage, Clarke (1971) suggested that the winter decline in juvenile hammerhead population size results from emigration out of Kāne'ōhe Bay, and that juvenile hammerheads reside in the nursery for only ~3 to 4 mo. Emigration would explain the observed drop in population size in winter without contradicting the hypothesis that nursery habitats offer abundant prey. An alternative explanation for juvenile hammerhead population decline in the winter months is starvation-induced mortality; this is supported by the fact that, in Kāne'ōhe Bay, juvenile hammerheads consume on average less food than that needed for daily maintenance: 2.7% of body weight  $d^{-1}$  is actually consumed (Bush & Holland 2002) whereas 3.7% of body weight  $d^{-1}$  is required as a minimum maintenance ration (Lowe 2002).

Clarke (1971) further hypothesized that hammerhead sharks are born in the southern (most turbid) portion of Kāne'ōhe Bay and migrate north, exiting the bay a few months after birth. Acoustic tracking studies have since been used to follow the movements of juvenile hammerhead sharks in real time. The data indicate that juveniles utilize muddy benthic habitat in the deeper portions of the bay and, although this type of habitat is continuous from the south bay to the north bay, the tracking studies showed that juvenile hammerheads move over relatively small areas. Sharks tracked in the south bay showed no evidence of directional patterns or dispersal toward the north bay (Holland et al. 1993, Lowe 2002). These results did not support Clarke's (1971) concept that individual juvenile sharks migrate north prior to emigration. However, each individual track spanned a period of only a few days, which may not have been long enough to observe northerly migration.

To elucidate the role of nursery areas in the life-history strategy of hammerhead sharks, tag-and-recapture techniques were used to make a more accurate estimate of juvenile hammerhead shark abundance, distribution throughout the bay, and duration of residency within the nursery. The study was conducted over a time period sufficient to capture 3 cohorts. Based on the previously described winter decrease in hammerhead population size, a

lower catch per unit effort (CPUE) and a decrease in the number of recaptured sharks was expected in winter. If starvation is an ultimate cause of population decline, evidence of weight loss was also expected.

## MATERIALS AND METHODS

**Fishing and tagging.** Juvenile scalloped hammerhead sharks were tagged throughout Kāne'ohe Bay over a period of 28 mo, from July 2000 to October 2002. Kāne'ohe Bay is the largest enclosed body of water in the Hawai'ian archipelago and covers 61 km<sup>2</sup> (Holthus 1986); to ensure adequate spatial sampling, the bay was divided into 3 zones: North, Mid, and South (Fig. 1, divisions based on Bathen 1968, Cox et al. 1973, Smith 1981). Fishing was conducted once per week in a randomly selected zone by groups of community volunteers supervised by trained biologists. Additionally, fishing was conducted simultaneously in all zones twice per month. Within each zone, fishing occurred at 2 randomly selected locations (located at least 5 m away from patch reefs to avoid bycatch of reef fish). Each fishing session lasted 3 h regardless of fishing success.

Fishing and handling techniques were designed to minimize trauma to sharks. Sharks were caught using 2 mm diameter braided hand-lines affixed with a weight, monofilament, swivel, and barbless J hook (size 4/0). Each hook was baited with a small piece of squid, fished just above the bay floor, and monitored constantly. Successfully landed sharks were unhooked, measured, tagged, weighed, sexed, and released. A small tissue sample was clipped from a pectoral fin to serve as a secondary indication of capture and to provide tissue for genetic studies (Duncan et al. 2006). The entire process took less than 2 min per shark. CPUE was calculated as the number of sharks caught per hook h<sup>-1</sup>.

Prior to field tagging, a short trial was conducted on captive sharks to determine the best type of tag for the task. It was determined that small Peterson disc tags caused very little trauma and were highly visible (K. Duncan unpubl. data). For this study, two 1.2 cm Peterson Disc tags that sandwiched the dorsal fin were secured by a stainless steel pin through the center of the discs. Tags were individually numbered and imprinted with a telephone number to facilitate reporting of recaptures by the public.

**Population parameters.** CPUE was used to estimate the relative abundance of juvenile hammerheads by month in each bay zone. Recapture rate was evaluated by plotting the total number of sharks tagged against the total number of sharks recaptured. A general linear

model (GLM) was used to determine which factors might influence CPUE. Factors included in the model were bay zone, month, tidal change, water depth, sediment composition, and weather. Tidal change was calculated as the difference between tide height at the beginning and end of each fishing session. Tide height was obtained from the weather station of HIMB. Water depth at fishing sites was determined using hand-held depth meters. Sediment composition at each site was determined by overlaying fishing sites with a 206-site sediment composition grid (J. Stimson unpubl. data). Weather conditions were categorized based on indices of sky (Sunny, Partly Cloudy, Overcast, or Rainy) and wind (0 to 10 knots = Light, 10 to 15 knots = Medium, 15 to 25 knots = High). The best GLM for CPUE was determined by looking for the combined highest adjusted R<sup>2</sup> and lowest Mallows' C<sub>p</sub> value of all variables and first-order interactions. The C<sub>p</sub> statistic is analogous to the Akaike Information Criterion:

$$C_p = \frac{SSE}{MSE} - (n - 2p)$$

where  $p$  is the number of parameters including the intercept,  $n$  is the number of observations, SSE is the sum of squares error, and MSE is the mean square error (Mallows 1973; SAS v8.2).

The population of juvenile scalloped hammerheads in Kāne'ohe Bay is constantly in flux due to new births, deaths, and emigration. Therefore, an open Jolly-Seber population model was used to estimate population size for each month of the study (Jolly 1965, Seber 1965). It was not possible to distinguish natural mortality, fishing mortality or emigration. These were combined into a single term, attrition, which was estimated as the fraction lost:

$$\text{attrition} = 1 - S$$

where the  $S$  is the fraction of sharks retained within Kāne'ohe Bay. Because the population of *Sphyrna lewini* in the bay increases quickly during the summer (Clarke 1971) (Fig. 3), the months of most rapid increase (May and June) were excluded from the retention analyses. Retention parameters were calculated from July through April by 3 methods: (1) the estimated average population size during spring (i.e. the surviving bay population in March and April) was divided by the average population size in July and August (i.e. the best estimate of recruitment size); (2) using the methods of Jolly (1965) and Seber (1965), the fraction retained was estimated as:

$$S = \frac{\text{size of marked population at time } t+1}{\text{size of marked population at time } t} \\ = \frac{M_{t+1}}{M_t + (s_t - m_t)}$$

where  $M_{t+1}$  is the estimated size of marked population just before time  $(t + 1)$  (i.e. March and April),  $M_t$  is the estimated size of marked population just before time  $t$  (i.e. July and August),  $m_t$  is the number of marked animals caught in sample  $t$ , and  $s_t$  is the total number of animals released after sample  $t$ ; and (3) the instantaneous coefficient of total attrition ( $Z$ ) was estimated using CPUE from July through April for 2000 to 2001 and for 2001 to 2002. Assuming that:

$$C = fqN$$

where  $C$  = Catch,  $f$  = effort,  $q$  = catchability (which is assumed constant) and  $N$  = population size, the natural log of CPUE was regressed against time in months to generate a linear equation with slope =  $Z$  (Beverton & Holt 1956, Pauly 1980). Retention was then estimated as:

$$\frac{N_2}{N_1} = e^{-Zt}$$

where  $N_2$  is population size in April,  $N_1$  is population size the previous July,  $Z$  is the instantaneous coefficient of total attrition, and  $t$  is time in months.

**Movement and dispersal.** Dispersal of individuals was assessed by calculating the distance and direction of movement between capture and recapture points in ArcView (ESRI 1996) and correlating the distance traveled with time at liberty. Statistics were calculated using MINITAB 14.0. Residence time of juveniles within the nursery was estimated in 2 ways: (1) directly from the number of days that recaptured sharks were at liberty, and (2) by comparing the size of the sharks caught in this study with the estimated size of a shark at liberty for 1 yr. An estimate of growth rate was obtained by regressing change in pre-caudal length (PCL) against time at liberty. This growth rate was then extrapolated to estimate the size of a shark at liberty for 1 yr. An ANOVA was used to evaluate the size distribution of juveniles with respect to bay zone.

The sharks' umbilical wound status was used to provide insight into the foraging success of neonate hammerhead sharks in the first few weeks after parturition. Scalloped hammerheads have placental viviparity; they are born live and have an umbilical connection to the mother. Immediately after parturition, the neonate sharks' umbilical wounds are open. The wound gradually heals, closes, and becomes barely visible. Captive sharks were used to quantify the rate of healing of the umbilical wound. Wild sharks with open wounds were collected and held in an indoor tank at near ambient water conditions (flow through system). The sharks were fed to satiation 3 times  $wk^{-1}$  with a diet of squid, herring, fish scraps, and miscellaneous crustaceans. This diet represented approximately 4% of their body weight  $d^{-1}$ . Photographs of their umbilical wounds were taken 3 times  $wk^{-1}$  for 2 mo. Wound condition

was categorized as: Open, Partly healed, Healed, or Well healed (Fig. 2). This healing index was subsequently used to evaluate the age of wild sharks and to assess whether or not starvation was occurring in neonatal sharks. ANOVA and pairwise comparisons ( $\alpha = 0.05$ ) were used to examine differences in shark weight relative to umbilical wound condition. To assess whether the average condition of the shark population declined in the months following peak birthing activity, a condition factor for all sharks was calculated by month:

$$\text{condition factor} = \text{weight (g)} \times \text{length (cm)}^{-3}$$

## RESULTS

### Fishing and tagging

Total fishing effort was 3562 hook hours (578 boat hours,  $4.2 \pm 1.07$  SD lines per boat). Tags were placed on 4120 juvenile hammerhead sharks and 151 were recaptured. Cooperating fishers returned 67 tagged sharks, and 84 sharks were recaptured by project personnel during fishing sessions. This resulted in an overall recapture rate of 3.7%. All recaptures were within Kāne'ohe Bay.

### Population parameters

Juvenile scalloped hammerhead sharks were caught throughout the year. Highest catch rates occurred during July in the Mid and South zones of the bay. Catch rates in all zones were lowest during winter (Fig. 3). Similarly, the ratio of tagged sharks to recaptured sharks was higher in summer and lower in winter (Fig. 4). The best predictive model of CPUE had an adjusted  $R^2$  value of 47.0% with a  $C_p$  value of 4.8, and included zone, month, zone  $\times$  month, water depth, weather, and tidal change (Table 1). Time of day, number of other fish caught (primarily the stingray *Dasyatis lata*), and percent organic material in the bottom sediment were not significant at  $\alpha = 0.05$ , nor were they important in terms of  $R^2$  and  $C_p$  criteria. There was a significant zone effect (ANOVA,  $p < 0.001$ ) and significant interaction of zone  $\times$  month ( $p = 0.0113$ ); however, there was no evidence of a sequential shift from one zone of the bay to another (Fig. 3). Catch rate was higher in the deeper portions of the bay. Although weather and tidal change were not statistically significant at  $\alpha = 0.05$ , they were included in the model because they contributed to a lower  $C_p$  statistic.

Sharks with open umbilical wounds, indicating recent birth, were caught from late May through early



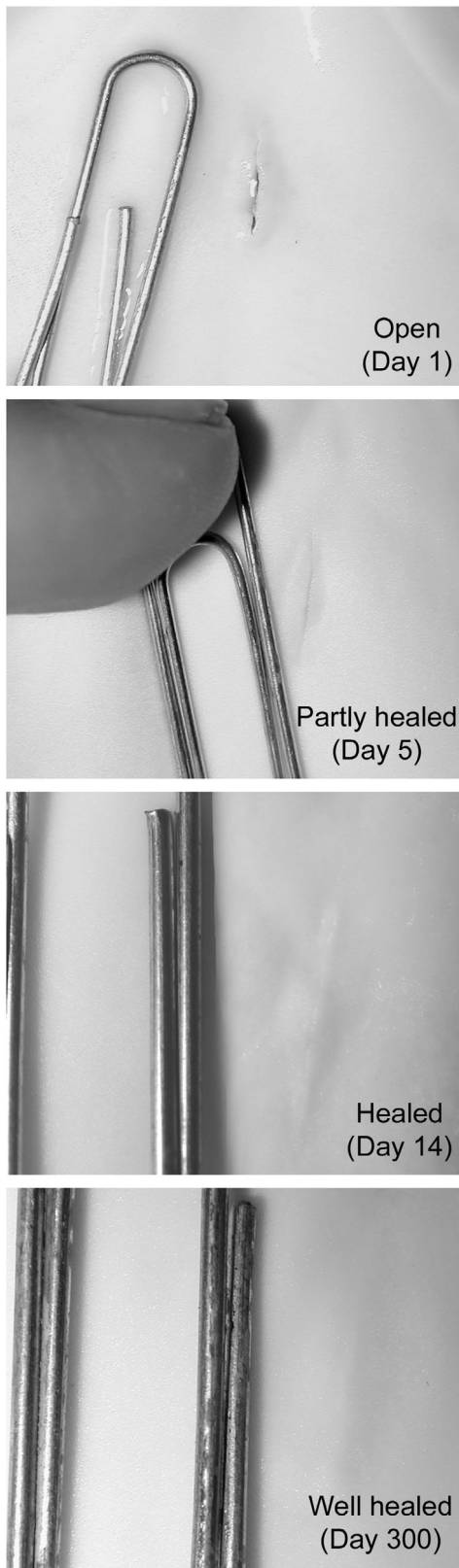


Fig. 2. *Sphyrna lewini*. Umbilical wounds at 4 stages of healing: Open, Partly healed, Healed, and Well healed. Photos of captive sharks taken on days indicated

September. Jolly-Seber population size estimates over the 3 summers (6 total estimates) ranged from 4300 to 9800 sharks for July to August (mean  $7700 \pm 2240$  SD sharks, Table 2). The retention ratio of population size in the spring (mean 1150 sharks) to population size in the previous summer (mean 7700 sharks) was 0.15, with corresponding attrition of 0.85. For the 2 years that sharks were tagged from summer (July and August) through spring (March and April), mean retention was  $0.08 \pm 0.036$  SD with a corresponding attrition of 0.92. The regression equation of  $\ln(\text{CPUE})$  against time (where month was numerical: July = 3, April = 12) was:

$$\ln(\text{CPUE}) = 3.48 - 0.294 (\text{month})$$

adjusted  $R^2 = 72.8\%$ ,  $p < 0.0001$ . The instantaneous coefficient of total attrition  $Z$  was  $0.29 \text{ mo}^{-1}$  (see Fig. 3). Based on this estimate of  $Z$ , retention was 0.07 with a corresponding attrition of 0.93.

Time at liberty for recaptured sharks ranged from 14 min to 324 d, with mean  $38 \pm 47.7$  SD d at liberty (median = 25 d). There was no significant correlation between distance traveled and time at liberty ( $r = 0.042$ ,  $p = 0.612$ ), nor was there a significant difference in distance traveled during different months (ANOVA,  $p = 0.756$ ). Sharks traversing between zones traveled both north (10 ind.) and south (14 ind., Fig. 5). The shark that was at liberty for the longest period of time (324 d) was caught in the same location as it was initially tagged, without being encountered in the interim. Sharks dispersed as much as 5.1 km within the same day, but the mean distance between capture points was 1.6 km (median = 0.86 km, Fig. 6).

Data from recaptured sharks at liberty for less than 60 d ( $n = 61$ ) showed a negative correlation between time at liberty and absolute growth (in g) ( $r = -0.56$ ,  $p < 0.001$ ). These sharks lost a mean  $2.4 \pm 3.25$  SD  $\text{g d}^{-1}$ . In contrast, recaptured sharks at liberty for more than

Table 1. General linear model for predicting catch per unit effort of sharks per line  $\text{h}^{-1}$

Source	df	SS	MS	F	p > F
ANOVA					
Model	40	531.949	13.2987	9.81	<0.0001
Error	443	600.610	1.3558		
C Total	483	1132.560			
Type III tests					
Month	11	287.901	26.1728	19.30	<0.0001
Zone	2	21.424	10.7122	7.90	0.0004
Depth	1	9.189	9.1889	6.78	0.0095
Zone $\times$ Month	22	55.237	2.5108	1.85	0.0113
Weather	3	7.143	2.3810	1.76	0.1548
Tide	1	0.084	0.0836	0.06	0.8040

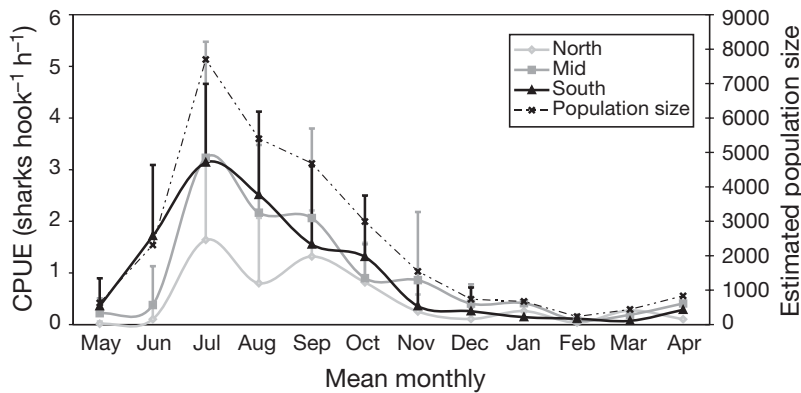


Fig. 3. *Sphyrna lewini*. Catch per unit effort (CPUE) of sharks per hook h<sup>-1</sup> for each bay zone and estimated bay-wide population size (based on Jolly-Seber population model). Values are 28 mo means (Jul 2000 – Oct 2002). Error bars = 1 SD

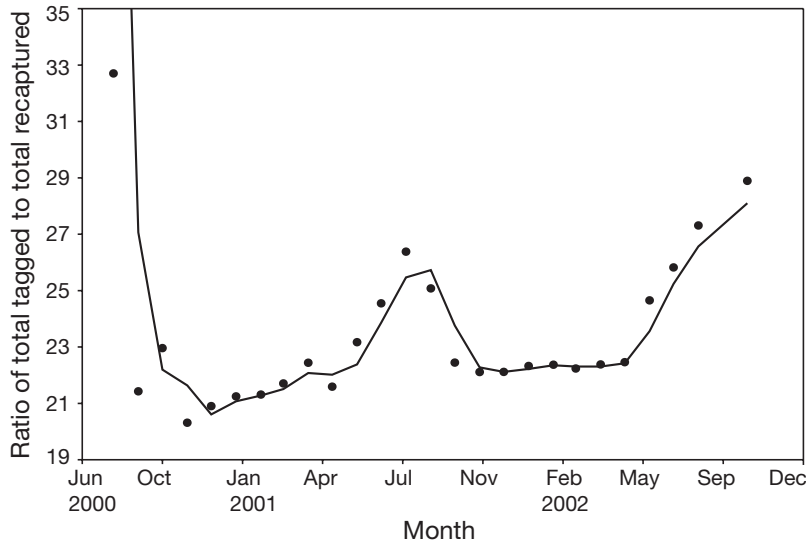


Fig. 4. *Sphyrna lewini*. Cumulative tag recapture ratio. Solid line indicates moving average

60 d (n = 40) exhibited positive growth. (Sharks recaptured by members of the general public were not included in this analysis due to lack of information on shark weight.) Growth for all recaptured sharks, measured as cm PCL, was expressed as:

$$PCL = 0.05 + 0.0263 (d)$$

adjusted R<sup>2</sup> = 58.7%, p < 0.0001. This was equivalent to a growth rate of 9.6 cm yr<sup>-1</sup>. Based on this rate of growth, and assuming that sharks with open wounds represented size at birth (32.0 to 41.0 cm PCL), juvenile hammerheads would reach 41.6 to 51.2 cm PCL in 1 yr. Of the 4120 sharks caught, 251 were within this size range. There was no significant difference in the size of sharks captured in different zones of the bay (ANOVA, p = 0.610).

During the captive study, umbilical wounds changed from Open to Partly healed in mean 4 ± 2.3 SD d and were Healed after mean 10 ± 3.6 SD d (n = 7). None of the wounds progressed from Healed to Well healed during the 2 mo study period. However, in the pre-trial tagging method evaluation in which sharks were maintained in outdoor ponds and fed a similar diet to sharks in the captive umbilical wound study, umbilical wounds progressed to a Well healed condition within 1 yr (K.Duncan unpubl. data) (n = 4, Fig. 2). When wild caught sharks were analyzed based on the condition of their umbilical wound,

Table 2. *Sphyrna lewini*. Population size estimates during peak population density (summer) for 3 tagging studies in Kāne’ohe Bay. Days indicate time over which population size was estimated rather than length of study. Data from Harkins et al. (unpubl. data) were analyzed with Schnabel & Petersen closed population models because their study violated Jolly-Seber assumption that sampling time is negligible in relation to intervals between samples. For Harkins et al. (unpubl. data) days were grouped so that number of recaptures during a given period was ≥ 3 (Ricker 1975). N/A: not applicable

Study	Method	Date	Location	Tagged/Recaptured	N <sub>max</sub>	Mean N	SD N
Clarke (1971)	Jolly-Seber (open population)	Aug 1969 (22 d)	Primarily south bay, some bay-wide fishing	214/7	8400	5500	3270
Harkins et al. (unpubl. data)	Petersen & Schnabel (closed) (multiple tag-and-recapture for closed)	Jul to Aug 1996 (40 d)	South bay	314/41	4400 (Petersen) N/A (Schnabel)	2500 (Petersen) 2300 (Schnabel)	776 (Petersen) N/A (Schnabel)
This study	Jolly-Seber (open population)	Jul & Aug 2000–2002 (six 31 d estimates)	Throughout bay	Average: 281/9	9800	7700	2240

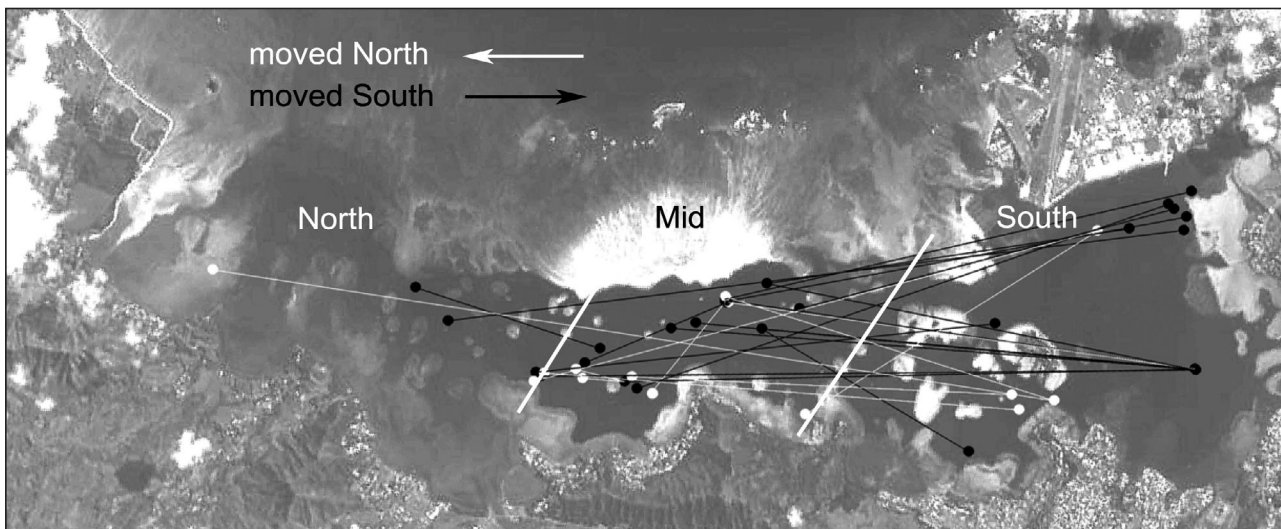


Fig. 5. Aerial photograph of Kāne'ohe Bay showing movement of sharks that traveled between bay zones (North, Mid, South). Minimum distance between tag and recapture points for sharks traveling north shown in white ( $n = 10$ ). Sharks traveling south shown in black ( $n = 14$ )

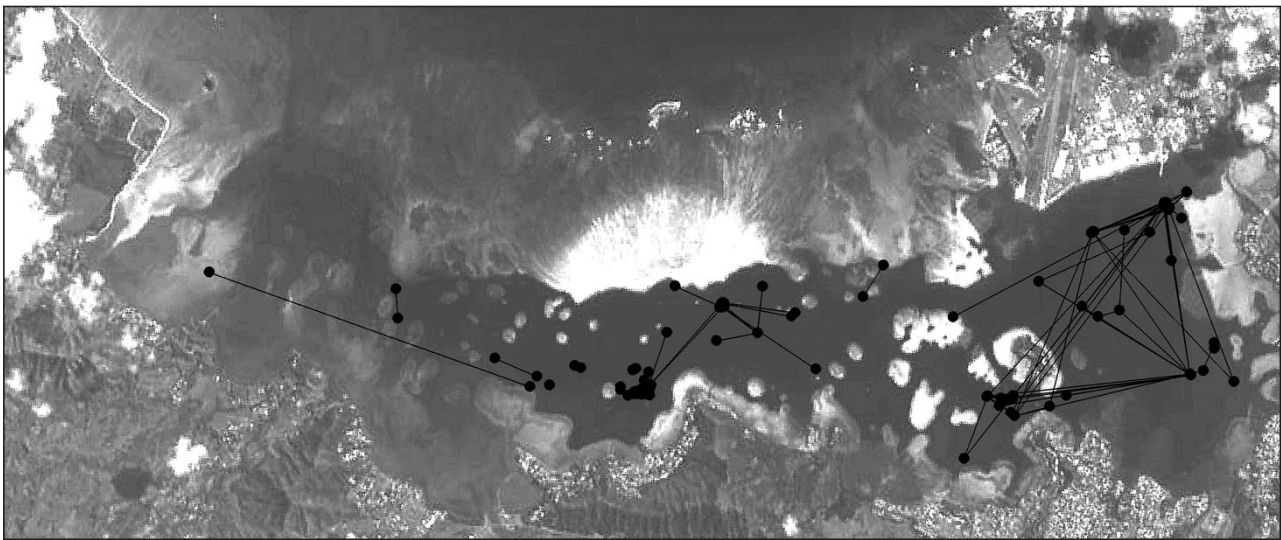


Fig. 6. Aerial photograph of Kāne'ohe Bay showing sharks that were tagged and recaptured within the same zone (North,  $n = 5$ ; Mid,  $n = 28$ ; South,  $n = 89$ )

the sharks with Healed wounds weighed significantly less than sharks with Open wounds (ANOVA,  $p < 0.001$ , Tukey's pairwise comparison  $\alpha = 0.05$ , Fig. 7). Similarly, the overall monthly condition factor of wild caught juveniles was lower in the late summer and fall, which corresponded to the period immediately following the peak in birthing activity (adjusted  $R^2 = 9.0\%$ ,  $p < 0.001$ , Fig. 8). Condition factor data were fitted to the quadratic expression:

$$\text{condition factor} = 1.47^{-2} - 9.43^{-4} (\text{mo}) + 7.74^{-5} (\text{mo})^2$$

where month was numerical beginning with May = 1 and ending with April = 12 (Fig. 8).

## DISCUSSION

Patterns in CPUE indicated that juvenile scalloped hammerheads show a daytime preference for deeper water, where habitat is characterized by mud and silt. These results were in agreement with movement patterns observed during active tracking (Holland et al. 1993, Lowe 2002). Locations of higher juvenile



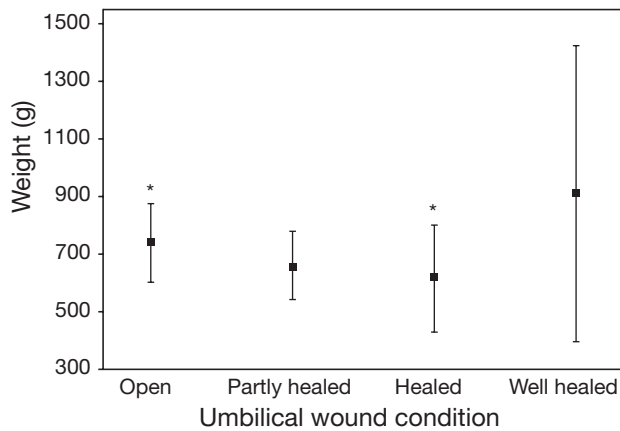


Fig. 7. *Sphyrna lewini*. Mean weight  $\pm$  SD of juvenile sharks by umbilical wound condition. \*Significant difference between Open and Healed categories

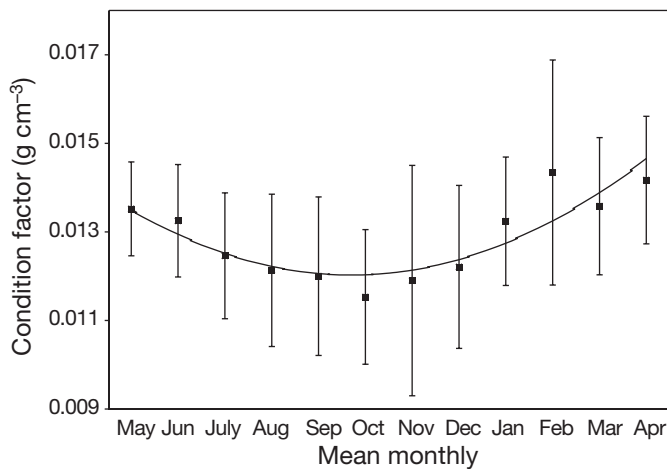


Fig. 8. *Sphyrna lewini*. Mean condition factor  $\pm$  SD by month for juvenile sharks. Values are 28 mo means (Jul 2000–Oct 2002)  $\pm$  1SD

shark abundance also corresponded to areas of higher sedimentation and nutrient flow (Cox et al. 1973).

#### Sharks use core areas but also make long swims

Most recaptures occurred close to points of initial capture and within the range of daily movements estimated by active tracking (mean  $1.26 \pm 1.12$  SD km<sup>2</sup>, Holland et al. 1993; mean  $1.41 \pm 0.41$  SD km<sup>2</sup>, Lowe 2002). The hammerhead's apparent localized distribution was similar to juvenile lemon sharks *Negaprion brevirostris* and neonate blacktip sharks *Carcharhinus limbatus*, which use relatively small, core areas of their nurseries (Morrissey & Gruber 1993b, Heupel et al. 2004). However, some hammerhead sharks in this study covered relatively large distances (as much as 5.1 km within a single day). Therefore, it appears that

juvenile hammerhead sharks may make long distance excursions, but tend to reuse core areas. This behavior is similar to that of sandbar sharks *Carcharhinus plumbeus* in Delaware Bay; individuals travel great distances but tend to return to the same general area (Rechisky & Wetherbee 2003).

There was no evidence to support Clarke's (1971) hypothesis of sequential shark movement from the south bay to the north bay; recapture data showed that sharks moved both north and south, and there was no significant difference in size of sharks captured in different bay zones. Sharks appeared to move throughout the bay during their residence in the nursery without an ontogenetic shift in nursery habitat use. This contrasts with the behavior of juvenile blacktip sharks *Carcharhinus limbatus*, which progressively expand their range within the nursery area (Heupel et al. 2004).

#### Concordance between population size estimates

There was good agreement between our population size estimates and Clarke's (1971) initial estimate. Based on the current estimate of a mean  $7700 \pm 2240$  SD sharks born yr<sup>-1</sup> and a litter size of 15 to 30 (Compagno 1984), approximately 180 to 660 adult female sharks use Kāne'ohe Bay as a birthing area each year. Differences between the current population estimate and those of Harkins et al. (unpubl. data) may result from differences in study design (Table 2). In the present study and Clarke's (1971) study, large numbers of sharks were tagged during each fishing session, but the sessions were several days apart. In the work of Harkins et al. (unpubl. data), sharks were tagged in a restricted area and a small number of sharks were tagged on many successive days. Because sharks tend to remain close to their capture point in the short term (Holland et al. 1993, Lowe 2002), and because fishing over consecutive days reduces mortality between fishing events from other causes, Harkins et al. (unpubl. data) tagged fewer sharks but recaptured more (13.1%). Their estimate of population size (mean = 2300 to 2500, Table 2) was probably a good estimate of the number of sharks in south Kāne'ohe Bay during summer months. Indeed, if this value were extrapolated to an area equivalent to the entire Kāne'ohe Bay, it would be close to the estimate from the present study of the population in the bay during July and August.

#### Weight loss contributes to high mortality

In our study, juvenile hammerhead attrition (as a fraction of neonate population size) was estimated to be 0.85 to 0.93 for the first year of life. This was higher



than the 0.56 mortality used by Lui & Chen (1999) in life table calculations for *Sphyrna lewini*, but closer to empirically-derived mortality estimates of Age 0 lemon sharks *Negaprion brevirostris* (0.64, Manire & Gruber 1993; 0.38 to 0.65, Gruber et al. 2001), and within the range of 0.61 to 0.92 determined for blacktip sharks *Carcharhinus limbatus* (Heupel & Simpfendorfer 2002). The high attrition rate estimate in Kāne'ohe Bay included both natural and fishing mortality, as well as any emigration that may have occurred. Although fishing mortality is probably high within the bay, weight loss data from sharks at liberty for less than 60 d suggested that there may also be a large natural mortality component to the overall attrition estimate. The lower condition factor of sharks in the months following the birthing peak supported this interpretation. Weight loss can be associated with poor nutritional condition, and mortality may be due to poorly developed foraging ability, reduced food availability, or both (see Lowe 2002, Bush 2003).

Further evidence for weight loss among newborn sharks came from the analysis of shark weights corresponding to various umbilical wound conditions. Although it is possible (but unlikely) that the short wound healing times observed in the captive study (Healed condition within 2 wk, Fig. 2) may be accelerated due to captive conditions, healing time does provide a useful gauge for estimating the relative age of neonate and juvenile sharks. Sharks held in captivity were fed slightly above maintenance ration (fed 4.0% rather than the 3.7% body weight  $d^{-1}$  required for maintenance, Lowe 2002), which may have accelerated the healing rate; conversely, the stress of captivity may have slowed the healing rate. Moreover, even if natural healing time was twice that estimated by the captive studies, sharks would still achieve a healed umbilical wound condition within 1 mo post-parturition. Thus, we have confidence in our conclusion that weight loss was a significant factor contributing to high natural mortality of shark pups in the first few months after birth.

### Long residence within the nursery

The sizes of sharks captured in the fishing sessions and the time-at-liberty for recaptured sharks indicated that most hammerhead juveniles are resident within the bay for more than a few months. Although only 1 recaptured tagged juvenile had a time-at-liberty that indicated it could have resided in Kāne'ohe Bay for 1 yr, 251 (6.1%) of the 4120 sharks captured in this study were Age 1 sharks (based on growth estimates from recaptured sharks). This value was close to that of estimated retention (0.07 to 0.15, as a fraction of neo-

nate population size), and the existing difference may have been due to gear selectivity. Light line and small hooks were purposely used to prevent damage to neonate sharks, and this probably reduced the catch of larger juvenile sharks. Notably, 89% of sharks recaptured after being at liberty for over 90 d were caught in gill nets by cooperating fishermen.

### CONCLUSIONS

Data from this study indicated that a significant number of juvenile hammerhead sharks remain in Kāne'ohe Bay for up to (or more than) 1 yr, and that they aggregate in the deep, turbid areas. There appears to be high mortality following the peak summer birthing period, and early weight loss indicated that malnutrition and starvation make a major contribution to this mortality. Sharks that survive this period eventually begin to grow, probably from combined effects of reduced intraspecific competition for food and improved hunting skills. These results did not support the hypothesis that nursery grounds provide enhanced prey availability, but instead suggested that elasmobranch nurseries are a valuable refuge from predators. Although predation by adult male hammerhead sharks is probably high immediately after parturition (Clarke 1971, Branstetter 1990), over the long term, Kāne'ohe Bay contains fewer large sharks and other top level predators than surrounding open waters (Crow et al. 1996). A similar scenario was recently proposed for the Florida blacktip shark nursery (Heupel & Hueter 2002). The shelter provided by Kāne'ohe Bay may explain why it is a prominent nursery despite limited prey availability.

Relative age estimates based on umbilical wound status contributed significant insight into the growth and survival dynamics of juvenile hammerhead sharks in Kāne'ohe Bay. This technique could be used in other nursery areas and with other species to determine whether high mortality due to starvation is unique to the hammerheads of Kāne'ohe Bay, or is ubiquitous in the youngest age class of sharks.

The overall energetic budget of the nursery is also affected by hammerhead mortality. High mortality of neonate scalloped hammerhead sharks will reduce the total energetic demand on the bay ecosystem. Previous work by Bush & Holland (2002) and Lowe (2002) estimated that a population of 5000 juvenile sharks (with an average individual weight of 700 g) would require 15 750 kg of food over a 5 mo period, assuming a constant size population of constant weight sharks consuming at the observed intake ration of 3% of their body weight  $d^{-1}$  (Bush & Holland 2002). This is equivalent to consumption of 5.5% of the yearly prey pro-

ductivity in Kāne'ohe Bay (Bush & Holland 2002). However, even with the larger estimated starting population from this study (7700 individuals) and accounting for growth, the inclusion of a mortality estimate reduces expected prey intake. Using the growth estimate of 9.6 cm PCL yr<sup>-1</sup>, an average Age 1 shark would be 50.3 cm PCL and weigh 2000 g. Given the estimated population size during each month, and assuming that sharks grow linearly over 12 mo, juvenile sharks in Kāne'ohe Bay would consume 4658 kg yr<sup>-1</sup>. This amounts to only 1.6% of the bay's yearly prey productivity. Although there is a large amount of uncertainty associated with this estimate, it demonstrates that high mortality within the first few months can offset the energetic draw associated with extended residence times of surviving pups.

It is also possible that the relative paucity of juvenile shark prey within Kāne'ohe Bay is a recent phenomenon resulting from anthropogenic alterations to the bay's ecology (Bush 2003). Original estimates of prey density within Kāne'ohe Bay (Harrison 1981) suggested a prey base adequate to sustain a relatively large population of juvenile scalloped hammerheads. However, a subsequent survey (Bush 2003) indicated that present-day prey levels had dropped, concurrent with changing water quality in the bay (see Smith et al. 1981, Laws & Allen 1996). Kāne'ohe Bay is proceeding through a well-documented ecological transition, after experiencing sewage outflow from the early 1900s until 1977, followed by gradual recovery of reefs (Hunter & Evans 1995, Stimson et al. 2001). The continued selection of Kāne'ohe Bay as nursery area by adult sharks may be the result of philopatric behavior where, even in the face of environmental uncertainty, the animal returns to a place that has proved successful in the past (Cury 1994). In other words, like sea turtles (Bowen & Karl 1996), scalloped hammerheads may return to the same nursery even after it has become less than optimal for its original intended use.

### Ecological implications

Nurseries such as Kāne'ohe Bay may provide young sharks protection against large marine predators, but also make young sharks more vulnerable to anthropogenic disturbance. In the case of juvenile scalloped hammerheads, expanded head shape and obligate ram ventilation make them particularly vulnerable to common nearshore activities such as gill netting. Moreover, gill net fishing does not discriminate between a neonate hammerhead and an Age 1 hammerhead. Although high mortality of neonates within the first few months may be natural, the survival of sharks to Age 1 and Age 2 is crucial for the maintenance of viable adult

populations (Congdon et al. 1993, Liu & Chen 1999). Fishing in the nursery can have direct negative effects on the biomass of hammerhead populations, as well as indirect negative effects on genetic diversity if populations of hammerheads are indeed philopatric. These types of fishing activities are not restricted to hammerhead sharks or to Kāne'ohe Bay. Many species of sharks that use nurseries as juvenile habitat may be similarly vulnerable.

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