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Social Organization of Schools of the Scalloped Hammerhead Shark, *Sphyrna lewini* (Griffith and Smith), in the Gulf of California

A dissertation submitted in partial satisfaction of the
requirements for the degree of Doctor of Philosophy
in Marine Biology

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1983

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and it is acceptable in quality and
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Table of Contents

List of Figures

List of Tables

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ABSTRACT OF DISSERTATION

Social Organization of Schools of the Scalloped Hammerhead Shark, *Sphyrna lewini* (Griffith and Smith), in the Gulf of California

by

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Doctor of Philosophy in Marine Biology

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The social behavior of the scalloped hammerhead shark is described with an emphasis on determining the function of its polarized schooling. This shark possesses a refuging social system in which individuals remain in groups in a small core of their home range during the inactive phase of their diel cycle and disperse into the surrounding environment during the active phase. Scalloped hammerhead sharks, followed by ultrasonic telemetry, swam slowly back and forth during the day along the ridge of seamount, El Bajo Espiritu Santo. These sharks moved rapidly away from the seamount late during the day or at dusk. The rhythmical dispersal and return of the sharks to the seamount was indicated by the return of telemetered sharks followed away from the seamount and the repeated observation of marked sharks at the seamount over periods up to seven weeks. At the seamount during the day the sharks can interact socially while remaining centrally positioned within their feeding arena. They are then ensured of foraging success at night. The diet of hammerheads consisted of cephalopods, fishes, and crustaceans.

The large schools were formed of sharks spanning a size range of 88 to 371 cm. This permitted size segregation within the schools. Both the total lengths and distances to the nearest neighbors increased significently toward the bottoms of groups at the insular site, Las Arenitas. Total lengths increased in a direction into the groups at the seamount sites, EL Bajo Espiritu Santo and Gorda. The sizes and spatial relations of school members were measured from stereophotographs taken by free-diving to the edges of the schools. The presence of larger female sharks at the bottoms of groups at Las Arenitas is believed to be caused by aggressive interactions among the females of which the schools were primarily composed. The sharks within the schools were mostly immature. The onset of maturity in male hammerheads occurred at 163 cm, that of females at 217 cm.

CHAPTER 1: INTRODUCTION

In his classical review, the "Social organization of shark populations," published in 1967, Stewart Springer recognized that individuals of some species of sharks formed groups. He believed that these groups were not only aggregations, formed in response to transient environmental changes, but schools of individuals, mutually attracted to each other. He noted that the groups occurring around boats were aggregations, responding to the presence of offal cast overboard. On the other hand, he believed very large groups of elasmobranchs such as several thousand cownose rays, Aetobatis narineri, observed by E. Clark, approximately 200 large sharks seen by P. Gilbert, and large groups of several species of carcharhinid and sphyrnid sharks observed by himself could not have assembled from local populations in response to sudden increases in prey densities. He felt that sharks in these groups had gathered from large areas and were joining in migratory movements. Members of these groups were often of the same size or sex. He reasoned that such segregation reduced predation on juveniles by adults and was caused by differences in swimming speeds and dietary preferences of sharks of different sizes coupled with the absence of aggression between such sharks. Springer noted, however, that direct observations revealed little information about the social organization within the groups such as whether they were structured by dominance hierarchies.

Grouping has been noted for only a few of the ca. 350 species of sharks (Table 1). However, the grouping species are diverse both phylogenetically and ecologically. This diversity in the context of the paucity of ethological studies on species of sharks implies that grouping is a common form of spatial dispersion among sharks. Individuals of the bullhead shark, *Heterodontus portusjacksoni*, considered primitive due to its possession of characters of the fossil hybodont taxon (Schaeffer, 1967), remain together in small groups in caves during the day (McLaughlin and O'Gower, 1971). The Pacific angel shark, (*Squatina californica*), a galeoid shark derived from an hybodont ancestor, at times forms diffuse, small groups over a sandy bottom during the day (Standora and Nelson, 1977). In addition, grouping also occurs in the more advanced carcharhinid species such as the lemon (*Negaprion brevirostris*), tiger (*Galeocerdo cuvieri*), gray reef (*Carcharhinus amblyrhynchos*), reef blacktip (*C. limbatus*), spinner (*C. maculapinnis*=*brevipinnis*), dusky (*C. obscurus*), and sandbar sharks (*C. milberti*=*plumbeus*) (for references, see Table 1). Shark species living in different habitats also form groups. The bullhead shark forages along the bottom on benthic invertebrates. The Pacific angel shark remains on the bottom and ambushes benthopelagic prey. The reef sharks most often feed on midwater prey. The basking shark (*Cetorhinus maximus*) and the whale shark (*Rhincodon typus*) inhabit offshore surface waters and feed upon

Table 1. References to species whose members form social groups with their size maxima, habitats, and proposed functions.

Classification	Description	Maximum Size	Habitat	Proposed Function	Reference
Squalimorphii					
Squalidae					
Squalus acanthias	size, sex segregation		inshore, at surface	increase predatory efficiency	Ford, 1921
Etmopterus virens	dense schools		mesopelagic	cooperative predation	Springer, 1967
Galeomorphii					
Heterodontidae					
Heterodontus portusjacksoni	size, sex segregation	sixteen	benthic, in reef caves		McLaughlin and O'Gower
Scyliorhinidae					
Cephaloscyllium ventricosum	aggregate in specific areas		inshore, midwater		Limbaugh, 1963
Orectolobidae					
Ginglymostoma cirratum	motionless, close to one another	thirty-six	inshore, on sandy bottom		Bigelow and Schroeder, 1948
--------	line up side by side	three	inshore, in caves, and crevices		Limbaugh, 1963
Rhincodontidae					
Rhincodon typus	gather in schools		offshore banks, at surface		Bigelow and Schroeder, 1948
Lamnidae					
Carcharodon carcharias		several juveniles obs. per dive	near surf zone at surface, bottom		Limbaugh, 1963
Cetorhinidae					
Cetorhinus maximus	schools	one hundred	offshore banks, at surface		Bigelow and Schroeder, 1948
-------	tandem	several	offshore banks, at	courtship, copulation	Matthews, 1950
Odontaspidae					
Odontaspis taurus	concentrations of adults	thirty		migration, courtship, copulation	Bass *et al.*, 1975a
Sphyrnidae					
Sphyrna levini	schools of pups		bay		Clarke, 1971
------	size segregated packs	large numbers	inshore		Bass *et al.*, 1975b

Classification	Description	Maximum Size	Habitat	Proposed Function	Reference
Sphyrnidae (cont.)					
Sphyrna lewini	size, sex segregated schools	two-hundred and twenty-five	dropoffs at coast, islands, seamounts	refuging	Klimley and Nelson, 1981
tiburo	groups and schools	seventy-five	shallow bays		Clark, 1963
------	aggregations	abundant	shallow, at shore	environ. factors, prey availability	Parker and Bailey, 1979
zygaena	size segr. schools	thousands	inshore		Bass *et al.*, 1975b
sp.	schools	small	coastal dropoffs		Limbaugh, 1963
Triakidae					
Galeorhinus australis	schools		coastal dropoffs	courtship, copulation	Olson, 1954
Mustelus californicus	groups		inshore, shallow		Limbaugh, 1963
Triakis semifaciata	groups		inshore, shallow		Limbaugh, 1963
----------	circ., lin. formations	fifty	within surf zone		Klimley, pers. obs.
Scyllium	motionless, close to one another	fifty	inshore, in caves		Clark, 1981
Carcharhinidae					
Carcharhinus amblyrhynchos	size segregated schools	fifty	inshore	increased predatory efficiency	Nelson and Johnson, 1980
brevipinnis	loose aggregations		inshore	migration	Springer, 1967
limbatus	loose aggregation	large	inshore	migration	Springer, 1967
--------	loose groups	four	inshore		Clark, 1963
falciformis	loose aggregations		pelagic	migration	Springer, 1967
-----------	schools	twelve	seamount dropoff		Klimley, pers. comm
melanopterus	loose groups	four	inshore		Nelson and Johnson, 1980
obscurus	loose aggregations	eight	inshore		Clark, 1963
--------	occas. in groups		coastal dropoffs		Limbaugh, 1963
plumbeus	aggregations, schools	large	inshore		Springer, 1960
--------	loose aggregations		inshore	migration	Springer, 1967
Galeocerdo cuvieri	loose aggregations		inshore	migration	Springer, 1967
Negaprion brevirostris	sex. segregated loose aggregat.	twenty			Springer, 1950
Triaenodon obesus	together, on bottom of caves	five	inshore		Randall, 1977
------	together in caves	few	inshore		Nelson and Johnson, 1980
Squatinomorphi					
Squatinidae					
Squatina californiensis	clumped	twenty	benthic		Standora and Nelson, 1977

macroplankton and small fishes. Adult scalloped hammerhead sharks remain along the dropoff during the day, but during the night disperse to feed on either neritic or pelagic prey. Grouping has been reported in twelve of the eighteen shark families recognized by Bigelow and Schroeder (1948). Indeed, the absence of observations of grouping in the other families probably stems from the infrequency with which their members have been encountered. Some families in which grouping has not been observed, the Dalatiidae, Hexanchidae, Pseudotriakidae, and Scaphanorhynchidae are composed of deepsea species; others, the Alopiidae and Echinorhinidae, are composed of seldom encountered neritic species.

Segregation of sharks of different sizes or sex into different habitats is common. Such segregation, usually inferred from unequal sex ratios in catches, is called geographical segregation (Backus _et al_., 1956). It occurs in the white (_Carchardon carcharias_) (Bass _et al_., 1975a), sandbar (Springer, 1960), cat (_Galeus arae_) (Bullis, 1967), soupfin (_Galeorhinus zygopterus_) (Ripley, 1946), Australian school (_Galeorhinus australis_) (Olson, 1954), the lemon (_Negaprion brevirostris_) (Springer, 1950), and scalloped hammerhead sharks (Clarke, 1971). Evidence for segregation of sharks of similar size and sex into groups is referred to as behavioral segregation (Backus _et al_., 1956). It is less commonly reported because of the difficulty in inferring this form of segregation from catches. Ford (1921) found daily differences in the size and sex of sharks from landings of the spiny dogfish (<u>Squalus acanthias</u>). He described social groups of: 1) small immature males and females, 2) medium-sized sharks, predominantly immature females, 3) medium-sized mature males, and 4) large mature females, often pregnant. McLauglin and O'Gower (1971) found females outnumbered males greatly in small groups of a bullhead shark in caves on a rocky reef, and these investigators suggested on the basis of this unequal sex ratio and offshore catches of males that the males remained generally in deep water and visited this inshore habitat infrequently. Clarke (1971) suggested that scalloped hammerhead pups aggregate or school based upon observations that some sections of his long lines had sharks on all hooks with bordering sections without hooked sharks. Bass (1975b) reported large numbers of the scalloped hammerhead of intermediate size swimming along the coast and thousands of juvenile smooth hammerheads (<u>Sphyrna zygaena</u>) swimming in an undirected manner at the sea surface off Natal, South Africa.

As to the function of such groups, authors have disagreed as to whether the groups were formed by sharks attracted to environmental factors such as favorable currents, light levels, temperatures, or prey abundances (such groups are termed aggregations by Shaw, 1978) or were formed by a mutual attraction of sharks to each other (termed schools by Shaw). Limbaugh (1963) believed that groups of hammerhead sharks at Clipperton Island and leopard sharks (*Triakis semifasciata*) off the California coast were formed in response to environmental factors although he did not specify what these factors were. Springer (1967) noted aggregations of sharks were attracted to vessels because of the presence of food or, perhaps, the novelty of the boat. As an example of this, Springer mentioned the large aggregations of Galapagos sharks (*Carcharhinus galapagensis*) swimming in an uncoordinated manner around the skiff of Limbaugh (1963) at Clipperton Island. Parker and Bailey (1979) argued that large aggregations of elasmobranchs along the coast in the Gulf of Mexico were caused by changing environmental factors such as rising daytime temperatures, increasing light levels, less dissolved oxygen, algal blooms, and aggregation of prey in the surf zone. Although only the bonnethead shark was identified from aerial photographs, the presence of other species was inferred by their presence in the catches of fishermen concurrently fishing in the area. These species were the finetooth (*Aprionodon isodon*), bull (*Carcharhinus leucas*), blacktip, narrowtooth (*Carcharhinus porosus*), tiger (*Galeocerdo cuvieri*), lemon, ragged-tooth (*Odontaspis taurus*, Atlantic sharpnose (*Rhizoprionodon terraenovae*, scalloped hammerhead, great hammerhead (*Sphyrna mokarran*, and the smalleye hammerhead sharks (*Sphyrna tudes*).

Other explanations have been given for the function of these groups. One such explanation is reproduction.

Grouping may facilitate courtship or copulation, or perhaps birthing in the sense that the pups might be collectively deposited in a favorable environment. Olson (1954) believed that the school shark in southeastern Australia formed groups to mate. He based this belief on large catches in July of male sharks with distended seminal vessicles which readily discharged semen and claspers which were turgid and engorged with blood. Bass _et al_. (1975a) dismissed the opinion that the ragged-tooth shark congregated off Natal, South Africa to give birth because newborn and juvenile sharks were not caught locally. Furthermore, group sightings occurred during midsummer when the species was probably carrying on courtship and copulation. Birthing occurred in early spring. Another explanation for schooling is the assembly of large numbers of sharks to move over large distances in a migration. Springer (1967) noted a tendency of sharks to assemble into large, loose groups during migratory movements and not at the destinations of these movements. Supporting this explanation is the large number of sharks in a broad column swimming in the same direction along the coastline pictured in an aerial photograph of Laguna Ojo de Libre along the western coast of the Baja Peninsula (Kenney, 1968). Bass _et al_. (1975) mentioned that aggregations of near-term females might form during the winter to migrate southward to give birth. An additional explanation for grouping is to facilitate the capture of prey. Springer (1967) suggested that the small squalid shark, _Etmopterus virens_, hunted cooperatively while in dense groups, held together by visual attraction of their members by distinctive photophore patterns in their dark mesopelagic habitat. Finally, none of the observers of groups felt that they could be formed in response to the danger of predation. This was probably because they felt the sharks' large sizes reduced the number of potential predators.

In conclusion, what information we have on the social behavior of sharks comes from a few studies of an indirect and cursory nature. Descriptions of grouping are primarily based on inferences from fishery catches (see prior references) and incidental observations by airborn or shipboard investigators (Clark, 1963; Springer, 1967; Kenny, 1968; and Bass *et al.*, 1975b). The few underwater observations of social behavior have been incidental (Eibl-Eibesfeldt and Hass, 1959; Limbaugh, 1963; Standora and Nelson, 1977; and Nelson and Johnson, 1980), with only McLaughlan and O'Gower examining in detail both circadian and circannual changes in composition of small groups of benthic bullhead sharks between shelter caves on a small rocky reef along the coast of Australia.

It was my intent to follow the example of McLaughlan and O'Gower and enter the habitat of a species of shark and thoroughly describe the social organization of its behavior. I chose the scalloped hammerhead shark as a subject for three primary reasons: 1) it remained grouped for long periods of time at locations in a non-baited context, permitting prolonged observations, 2) sea conditions were benign and water clarity good at these locations, and 3) the sharks were neither frightened nor aggressive in response to my presence. A single difficulty demanded was the neccesity to observe the hammerhead sharks either from the surface or during free dives because they avoided the bubbles produced by scuba equipment.

In my dissertation I will describe the behavior of hammerheads within and nearby the schools with an emphasis on observations and tests which provide insight into the function of these schools. The second chapter consists of a description of a photographic technique to remotely determine the sizes and relative positions of the sharks within the schools. In the third chapter I describe, aided by these photogrammetric measurements, the composition, structure, and dynamics of the schools. In the fourth chapter I describe the diel movement patterns of sharks within schools in relation to an offshore seamount, El Bajo Espiritu Santo. In the fifth chapter I examine reproduction in the scalloped hammerhead. In the sixth chapter I describe its feeding habits. Finally, in the seventh chapter I discuss how the observations and tests described in detail in the earlier chapters lead to an understanding of the function of these schools. Although this is the last chapter in the dissertation (because it is composed of information given in more detail in the preceeding chapters), I strongly recommend that the reader look at it first because the chapter will provide a framework within which the detailed description throughout the thesis can better be appreciated.

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CHAPTER 2: STEREOPHOTOGRAPHY FOR THE FIELD BIOLOGIST: MEASUREMENT OF LENGTHS AND THREE-DIMENSIONAL POSITIONS OF FREE-SWIMMING SHARKS

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ABSTRACT

A stereophotographic technique for determining size and relative position of free-swimming sharks is described and illustrated for schooling scalloped hammerhead sharks (Sphyrna lewini). The method yields total length and nearest-neighbor, interindividual distance; and each of these dimensions is expressed as a function of the shark's distance into a school on the vertical and horizontal planes. Stereopairs of photographs were taken by an aligned, beam-mounted pair of cameras (Nikonos III). The scale to determine the length of a shark from the paired photographic images was obtained from the horizontal displacement between the images. Displacement was correlated with optical axis separation from photographs of a scaled staff at known distances from the camera. Image dimensions on the photographs were measured by projecting a scale onto the stage through a camera lucida. The precision of repeated measurements of a 50-cm section of a scaled staff at

increasing distances from the cameras of 2, 4, and 8 m was ≤±4.4 %. Lengths of the sharks ranged from 109 to 371 cm with a median of 178 cm for 3 offshore sites in the Gulf of California during July and August 1979. At one site, El Bajo Gorda, lengths increased with both distance from the camera and distance into the group; in contrast, the interindividual distances (head-to-head) did not vary with distance into the group and possessed a median of 232 cm.

INTRODUCTION

Marine scientists have long known that the dimensions of an undersea object can be determined from (1) the displacement of the object's image on a stereopair of photographs, (2) the relevant dimension on one of the photographs, and (3) the separation distance between the cameras (Boyce, 1964; Van Sciver, 1972). Moreover, the distance from the camera to the object can be calculated if one knows the distance between the second nodal point of the lens and the film plane of the cameras (Van Sciver, 1972). This technique has been used often by marine geologists to map the topography of the sea floor (Pollio, 1971). However, measurements of biological objects are rare: e.g., determination of the 3-dimensional structure of fish schools (Cullen _et al_., 1965 and Dill _et al_., 1981) and densities of benthic epifauna (Ohta, pers. comm.). Even so, the use of stereophotography offers several advantages, especially in the study of large midwater animals: (1) densities of species and individuals can be studied directly, (2) the spatial dispersion of individuals can be described, and (3) body sizes can be measured without distortions that often result when large animals are measured out of the water either on a flat surface or hanging from a gallows. With stereophotography the field biologist can determine the size, density, and spatial dispersion of individuals of a species without disturbing them or removing them from the study population (an especially important consideration when studying animals protected from capture, such as marine mammals and endangered species).

In the present paper we will describe how the stereophotographic method can be used to study whether scalloped hammerhead sharks (Sphyrna lewini) of different sizes remain in different positions within a school and space themselves at different distances from their nearest neighbors. Emphasis will be placed on explaining how the technique has been modified to provide an accurate length dimension and 3-dimensional position of an actively moving marine animal. A measure of the technique's accuracy will be given based upon repeated measurements of a section of a scaled staff. The accuracy of stereophotographically determined lengths will be corroborated from length determinations from streamer tags of a known length. Histograms will be given of lengths and nearest-neighbor interindividual distances, and these will be regressed upon distance into the schools.

MATERIALS AND METHODS

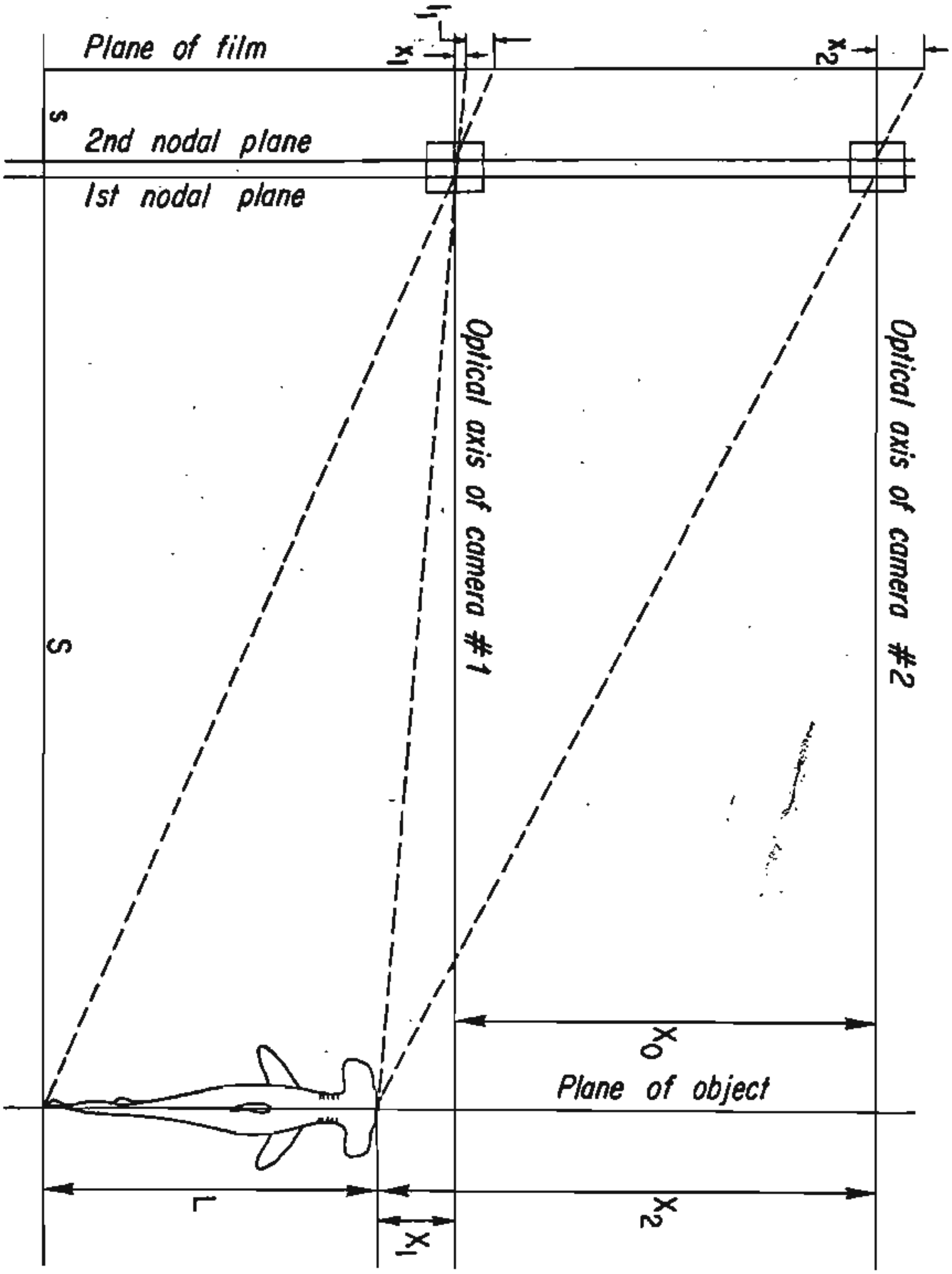
Description of Technique

The size of an unrecognized object and its 3-dimensional position in relation to a stereocamera system can be determined from a stereopair of photographs from parallel oriented cameras. The scale to measure a dimension of an image such as length of a shark comes from a knowledge of the camera separation and the width of the area of no overlap between the images on the 2 photographs. Van Sciver (1972) described the geometrical relationships on which the technique is based (Fig. 1). He derived the following equation for a dimension of an object (L) with its longitudinal axis parallel to that of the stereocamera (i.e., perpendicular to the optical axes of the cameras, which are presumed to be parallel):

$$L = l\,X / (x_2 - x_1)$$

where X is the separation between the optical axes of the cameras, l is the length dimension of the image on either photograph, and x_1 and x_2 are distances from an identical point on the images occurring on the 2 photographs to the

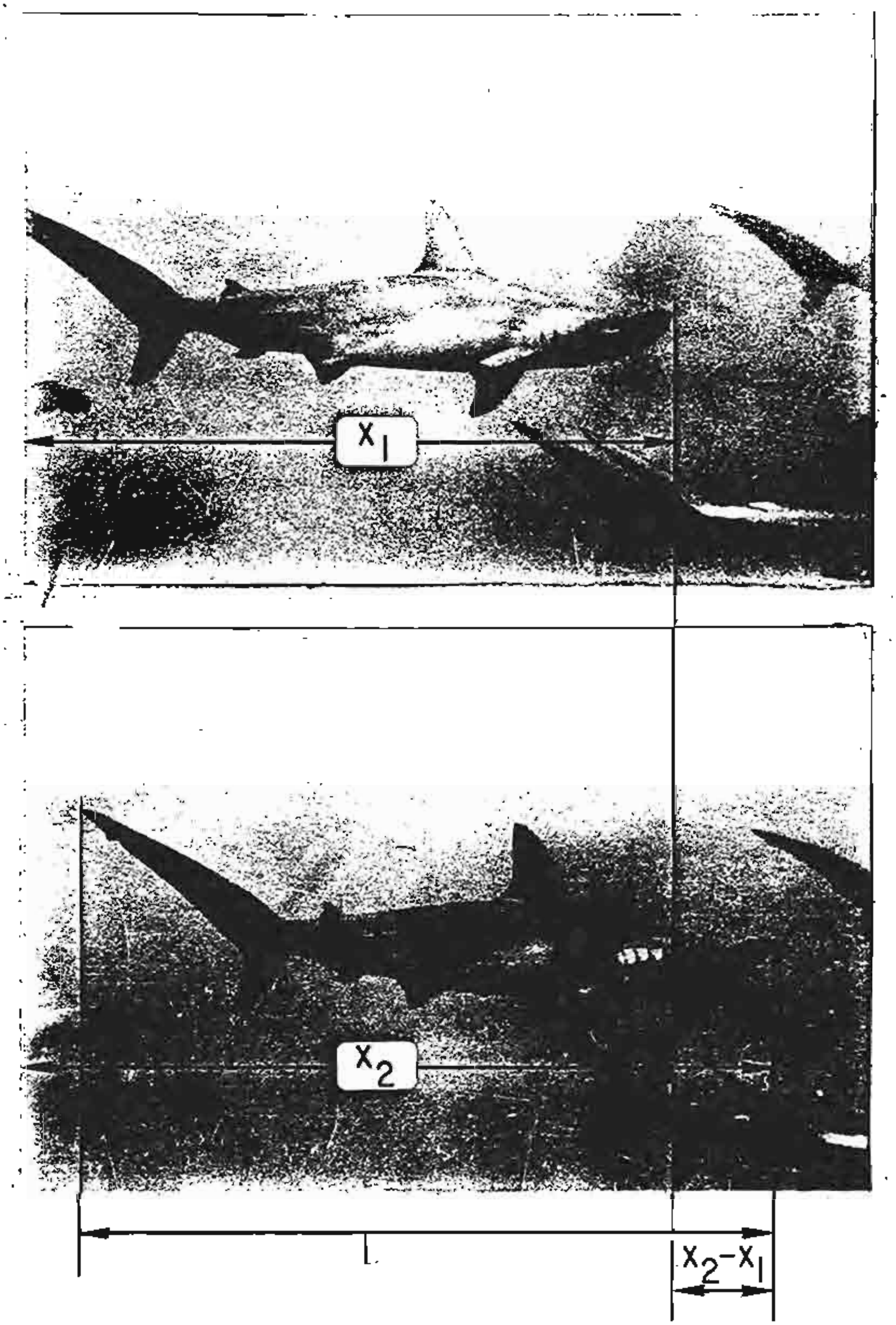
Fig. 1. Schematic of optical relationships between the stereocamera and the object photographed. Modified from Van Sciver, 1972.


Plane of film
x_1
l_1
x_2
s
2nd nodal plane
1st nodal plane
Optical axis of camera #1
Optical axis of camera #2
S
X_0
Plane of object
L
X_1
X_2

points on the film plane where the optical axis of the cameras intercept. These distances, however, can be obtained from any convenient reference point on the photographs such as the edge of the frame. We measured x_1 on the photograph taken by the righthand camera from the tip of shark's snout or caudal fin to the most proximate point along the lefthand edge of the photograph (Fig. 2). In a similar manner, we measured x_2 on the photograph taken by the lefthand camera from an identical point on the shark's image to the lefthand edge of the frame; this distance was parallel to the bottom edge of the frame. We measured l parallel to the longitudinal axis of the shark from the tip of its snout to the tip of its caudal fin. The value L then represented the total length (TL) of the shark. The values l, x_1, and x_2 were in mm when obtained from a contact print or transparency. Provided that l was in the same units of x_1 and x_2, L was given in units identical to X(cm).

Total length was measured from the image of the shark on both photographs in each stereopair. A mean was calculated from these TLs. A mean TL from a stereopair of the shark's lateral aspect would be spuriously short because the shark's longitudinal axis was bent into a sinusoidal configuration during swimming. This problem was solved by photographing some sharks dorsally. From these stereopairs we obtained a "linear" TL, the distance between perpendiculars drawn from the snout and the caudal tip to a

Fig. 2. Stereophotographic pair of free-swimming hammerhead shark. Upper photograph was taken by righthand camera; lower photograph was taken by lefthand camera. Measurements of x_1 and x_2 were made with respect to the lefthand edge of the frame. Measurement 1 was made from the tip of the snout to the tip of the caudal fin.


x1
x2
L
x2-x1

plane parallel to the longitudinal axis of the shark. We then obtained a "sinusoidal" length by aligning a flexible ruler with the bending body axis of the shark, marking the positions of the snout and caudal fin tips on the ruler, and noting the distance between the marks with the ruler extended. A ratio of "sinusoidal" to "linear" TL for each shark was then computed. A mean compensation factor, based on 31 dorsally photographed sharks, was 1.056 (S.D.=0.035). All TLs determined from lateral photographs were multiplied by this factor to produce a corrected TL. An alternative to using the flexible torso for length determinations would be to use an inflexible body part of the shark such as the pectoral fin length from dorsal photographs or dorsal height from lateral photographs. The shark's TL could then be determined from curves of TL as a function of these dimensions. Although such dimensions were available from a capture study (Bass *et al.*, 1975), we did not use this approach because pectoral length and dorsal height varied with the degree of the shark's rotation in respect to the photographer. Tilting, a motor pattern involving such rotation was common among schooling hammerheads.

In addition to a mean TL, mean values for x_1 and x_2 were measured both from the tip of the snout and from the caudal fin to the left edge of the frame. This minimized any error due to the one of these points (from which the scale to measure the shark was obtained) being at a different distance from the stereocamera than the rest of the shark's torso. In rare cases it was only possible to make a single TL determination because the entire image of the animal was not present on both photographs. TLs determined in this manner must be considered minimum TLs. If the longitudinal axis of the shark were not parallel to that of the stereocamera, the shark's image (l) would be smaller than if the shark were parallel. The displacement (x_2-x_1), however, would be the same in either orientation because it is the mean of displacements determined both for the tip of the snout and the tail. This potential error was minimized through positioning the stereocamera parallel to the body axes of the photographed sharks. Hammerheads swimming within the schools were very parallel in their orientation. The degree of parallelism was determined from dorsal photographs of sharks to be comparable to that of facultative schooling teleosts (Klimley, 1983). Also TLs were determined on stereopairs only for those sharks that appeared parallel to the stereocamera from the body parts visible and their relative proportions. An additional method of measuring TLs not prone error from lack of parallelism will later be mentioned.

To determine the distance of the object from the camera, one must either have knowledge of or determine the distance from the second nodal plane of the camera lens to the film plane (s). This distance is slightly longer than the focal length (f) of the camera used in air. It may be calculated from the optics formula:

$$1/f = 1/s + 1/S$$

When the camera is used underwater, the value s obtained from the above formula must be multiplied by the index of refraction of water. Following the suggestion of Van Sciver (1972), we empirically determined s from underwater photographs of a scaled staff at a distance (S) of 200 cm from the camera; on each photograph we measured an image dimension (l) equivalent to a marked 50-cm distance (L) along the staff and solved for s by substituting these values in the following geometrical formula:

$$s = S\ l\ /\ L$$

This distance was 48.4 mm (N=10). To determine an unknown distance from the camera to an object (S), this value of s was then inserted together with other image dimensions into the following equation:

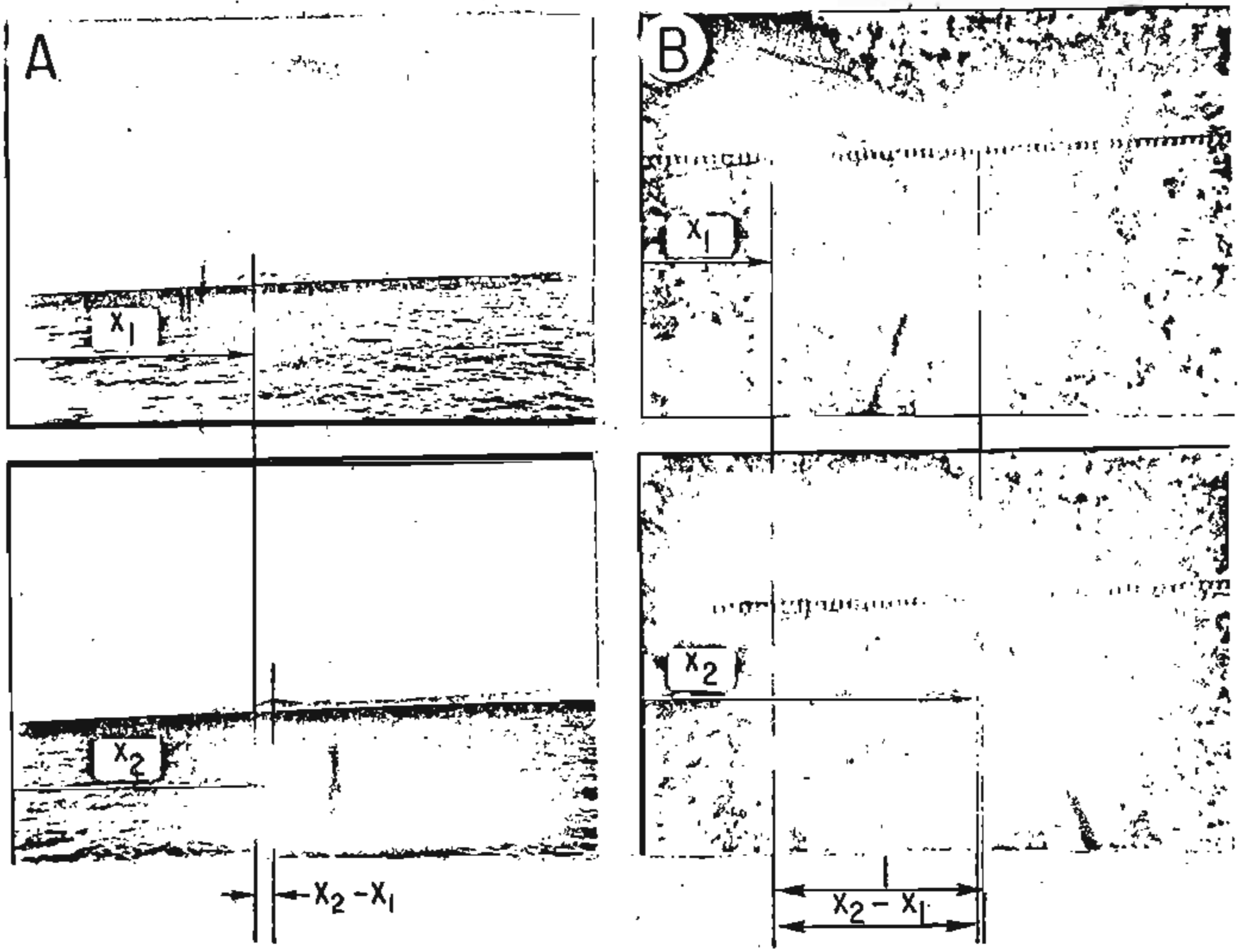
$$S = s\ X\ /\ (x_2 - x_1)$$

During the early part of the study, calibration stereopairs were taken at the beginning of each roll of film to determine the separation of the optical axes with distance from the cameras. A stereopair was taken of an object at a distance of several hundred meters or greater(Fig. 3A). Scrutiny of this stereopair quickly provided us with a check for a gross lack of optical parallax indicated by a large displacement between a landmark on the 2 photographs. This check enabled us to adjust the orientation of the cameras while at the study site. The choice of a sufficiently distant object was critical, since even if the camera axes converged, at greater distances they intersected and began to diverge. Another stereopair was taken of a scaled staff attached to the handles of the stereocamera and allowed to hang by stainless steel cables 2 m below the apparatus. The scale consisted of cm increments indicated by alternating black and white rings with 10-cm increments indicated by yellow rings(Fig. 3B). From later viewing and analysis of this stereopair the degree of convergence or divergence of the optical axes was quantified and included into the size and position determinations.

The compensation method is described below. It involved 2 functional relationships with distance from the stereocamera, the linear change in optical axis separation and the hyperbolic change in image dimension. The change in optical axis separation can be described by the following linear function:

$$X = mS + X_0$$

Fig. 3. Calibration stereopairs initially used to compensate for lack of parallax of the two cameras' optical axes. A. Stereopair of distant landmark. Note the displacement of the mountain peak (marked by arrows underneath the stereopair) indicative of lack of parallax. B. Stereopair of scaled staff with inequality between x_2-x_1, and l (equivalent to 50 cm) indicative of optical axis convergence.


A
x_1
x_2
$x_2 - x_1$
B
x_1
x_2
$x_2 - x_1$

The term X is the optical axis separation at distance S from the stereocamera, m the change in X over distance S from the first nodal points of the camera lenses, and X_0 the optical axis separation at the first nodal points of the cameras. The change in X over S (m) was determined by direct measurement of the separation between the first nodal points of the 2 lenses set at their smallest apertures (X_0) and by determinations of X from the stereopair at a distance of 2 m. Optical axis separation was determined from this calibration stereopair by dividing the average displacement for 2 bordering points and one central point on a 50-cm section of the calibration staff by the mean dimension of the staff section in photographs from the right and left cameras. The multiplication of the 50-cm length by the resulting dividend resulted in X. To obtain m, the value of X was subtracted from X_0, and the result expressed as the numerator with S (in cm) as the denominator. Later in the study after securing the cameras immovably to the beam, optical axis separations were determined for additional distances from the stereocamera in the University of California, San Diego swimming pool. The scaled staff was positioned parallel to the stereocamera on the same horizontal plane above the bottom of the pool. Mean optical axis separations were determined from 10 stereopairs of the staff at a distance of 2 m, 5 stereopairs at a distance of 4 m, and 3 stereopairs at a distance of 8 m. A line and slope were obtained from the regression of $\overline{X}$ on S (Fig. 4B). Correlation coefficients ranged from 0.986 to 0.960 indicating a strong linear relationship.

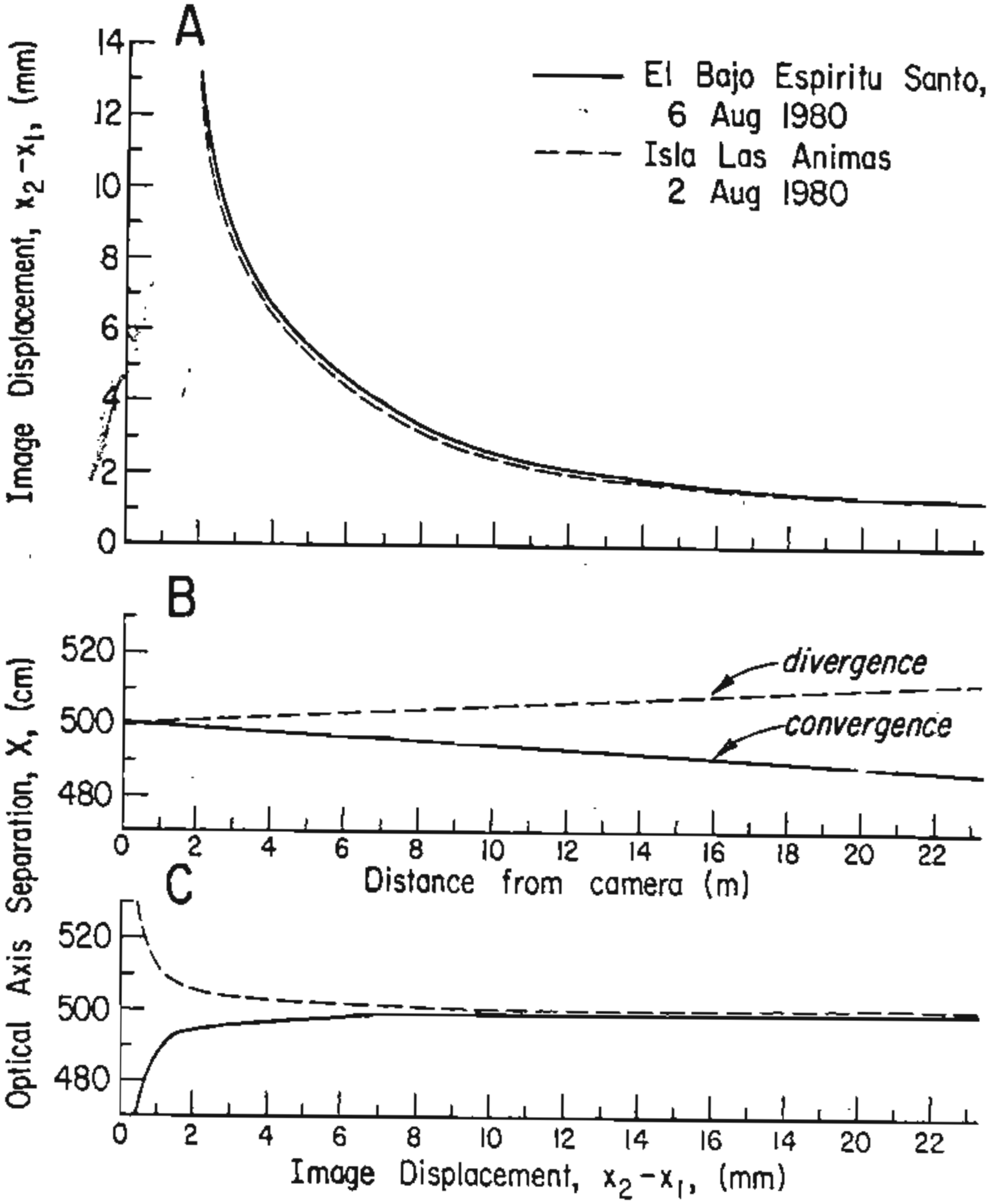
The change in image dimension on the photograph is described by the following hyperbolic function.

$$x_2-x_1 = (x_2'-x_1') / (S-200) \qquad S > 200$$

where $x_2'-x_1'$ is the displacement at the original calibration distance of 200 cm, and x_2-x_1 are displacements at successive distances from the stereocamera. The above optical relationship was originally proved trigonometrically and later demonstrated empirically from measurements of the staff section at different distances from the stereocamera. Mean displacements ($\overline{x_2-x_1}$) were determined for distances of 2, 4, and 8 m from the stereocamera. These means were based on 10, 5, and 3 determinations, respectively. A curve was fitted to these means (Fig. 4A). From the 2 functions described above, a plot of optical axis separation as a function of image displacement was constructed (Fig. 4C). Optical axis separations corresponding to the snout and caudal tip displacements were obtained using this curve, and entered into the total length and distance from the camera equations as term X.

To position the shark in the x-y-z Cartesian

Fig. 4 From a knowledge of the change in image dimension with distance (A) and optical axis separation with distance (B), optical axis separation was plotted as a function of image displacements (C). The different shapes of the curves depended upon whether the optical axis diverged (dashed line) or converged (solid line).

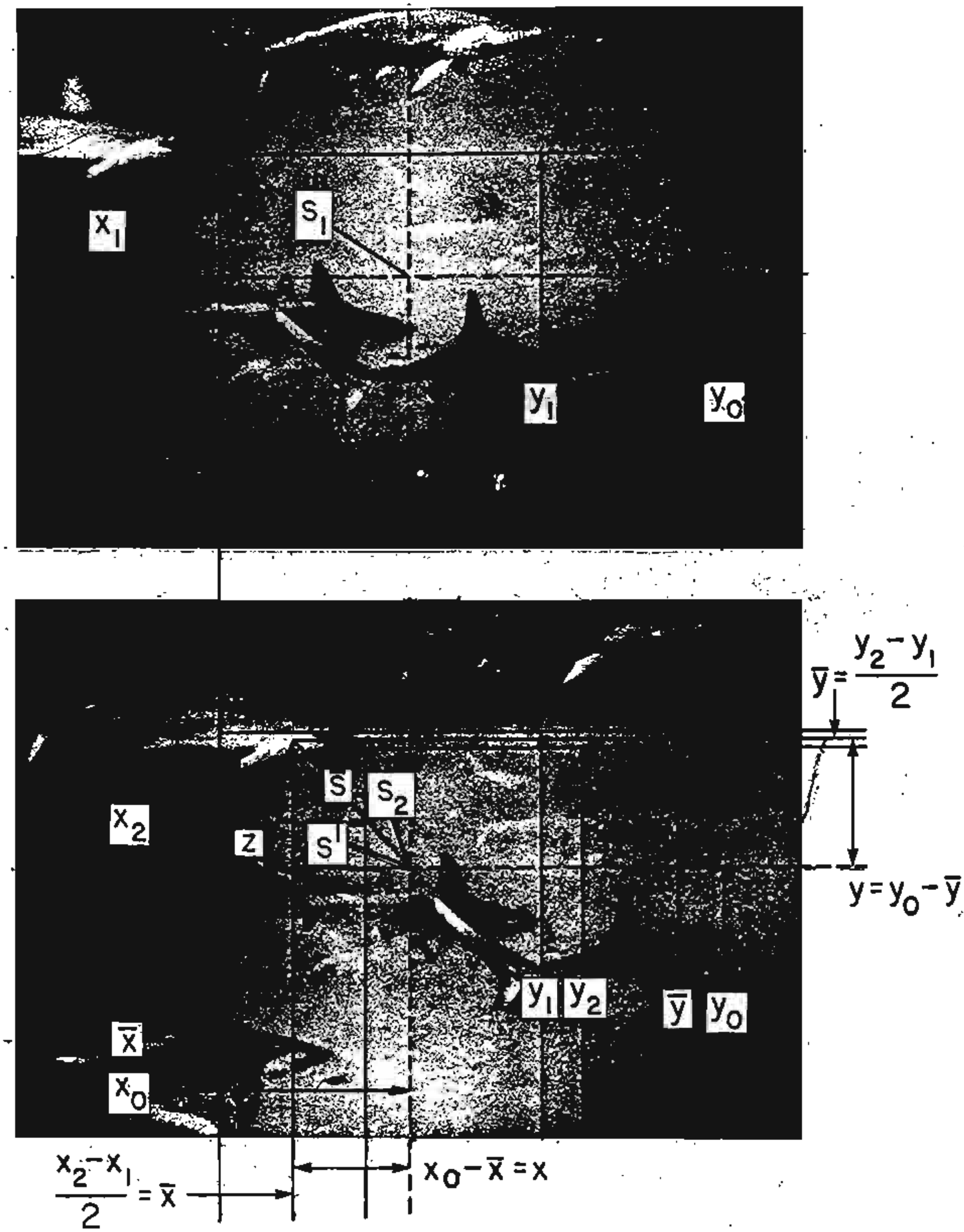

A
El Bajo Espiritu Santo, 6 Aug 1980
Isla Las Animas 2 Aug 1980
Image Displacement, x2-x1, (mm)
14
12
10
8
6
4
2
0
B
divergence
convergence
520
500
480
0
2
4
6
8
10
12
14
16
18
20
22
Distance from camera (m)
Optical Axis Separation, X, (cm)
C
520
500
480
0
2
4
6
8
10
12
14
16
14
20
22
Image Displacement, x2-x1, (mm)

coordinate system, we made several additional measurements on the photographs (Fig. 5). To obtain the x-coordinate, the mean ($\bar{x}$) of x_1 and x_2 was subtracted from the distance from the center of the side edge of the photographs (x_0). To obtain the y-coordinate, the mean ($\bar{y}$) of the distance from the tip of the snout of the shark to the bottom edge of the photographs taken by the righthand (y_1) and lefthand cameras (y_2) was subtracted from the distance from the center to the bottom edge of the photographs (y_0). The z-coordinate was determined by: (1) calculating the mean ($\bar{s}$) of the distance to the object from the righthand (s_1) and lefthand (s_2) cameras, (2) solving for s' with the Pythagorean theorem using $\bar{s}$ and y, and (3) solving for the z-coordinate using the Pythagorean theorem with values s' and x. Nearest-neighbor, interindividual distance (ID) in relation to the shark's snout was calculated using the distance formula.

$$ID = [(x_2-x_1)^2 + (y_2-y_1)^2 + (z_2-z_1)^2]^{1/2}$$

In addition to determining ID from the distance formula, TL could also be calculated using this formula. The distance between the x-y-z cordinate positions of the tip of the snout and tail represents the shark's TL. However, this would have to be multipled by the "sinusoidal" to "linear" ratio determined from the method described earlier to obtain a TL corrected for the shark's curving body axis. We did not

Fig. 5. Stereopair illustrating additional measurements necessary to determine position of hammerhead in x-y-z Cartesian coordinate system with stereocamera as the origin.

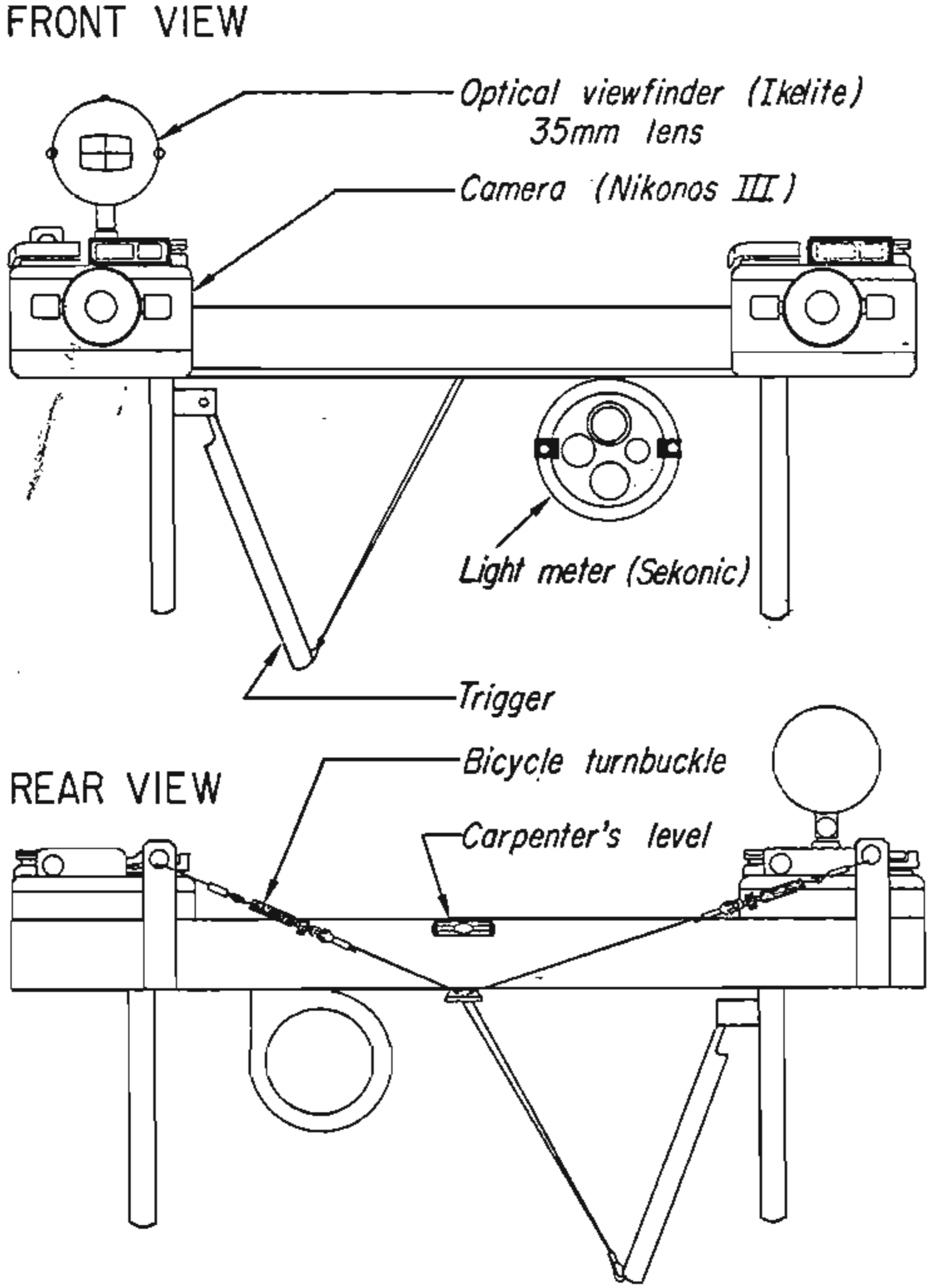

x_1
s_1
y_1
y_0
$\bar{y} = \frac{y_2 - y_1}{2}$
s
s_2
x_2
z
s^1
$y = y_0 - \bar{y}$
y_1
y_2
$\bar{y}$
y_0
$\bar{x}$
x_0
$\frac{x_2 - x_1}{2} = \bar{x}$
$x_0 - \bar{x} = x$

use this more complex method in our study because we delt only with animals which were essentially parallel to the stereocamera.

The values y_1 and y_2 were not always on the same plane (see Fig. 5). This was caused by slight bending of the stereocamera beam resulting in the individual camera being slightly out of parallel alignment on the y axis. The effect of this misalignment on the value y was minimized by calculating the mean of y_1 and y_2. This misalignment's effect on the determination of image dimensions was also negligible, since optical axis separation was determined empirically.

The stereophotographic apparatus consisted of 2 underwater cameras(Nikonos III, Nikon) with 35 mm f/2.5 or 80 mm f/4.0 lenses (Nikkor) mounted on both ends of a small section of aluminum angle (Fig. 6). The cameras were bolted to the angle using their single tripod mounts and were pivoted by the adjustment of 2 bolts passing through the backside of the angle in order that the optical axes of the cameras were relatively parallel. A parallax-correcting, optical viewfinder (5002, Ikelite) was mounted on the righthand camera to ensure that the shark's image was centered in one frame. The 2 cameras were fired simultaneously by plastic-coated, stainless-steel cables passing through 2 nylon-lined ferrules and attached to a

Fig. 6. Stereoscopic apparatus used to determine total lengths of free-swimming hammerhead sharks.


FRONT VIEW
Optical viewfinder (Ikelite)
35mm lens
Camera (Nikonos III)
Light meter (Sekonic)
Trigger
REAR VIEW
Bicycle turnbuckle
Carpenter's level

trigger beneath the righthand camera. The cables were connected to the camera triggers by plastic fittings secured with allen screws. Bicycle turnbuckles were used to adjust the relative lengths of the cables so that the cameras were triggered simultaneously. Shutter opening was synchronized by fitting reflective, polyethylene cards within the cameras behind the shutter mechanisms, slaving a strobe to one of the cameras, and adjusting the linkage so that reflection of light from the flash outward through the lenses appeared simultaneously at a shutter opening duration of 1/250 sec.

Of the 4 Nikkor lenses(15, 28, 35, and 80 mm) avalable for use with the Nikonos III, the 35 mm lens was utilized most often because in the past hammerheads of a mean TL of 175 cm were encountered at distances within a 2.1 to 8.1 m range. The resulting image lengths of such sharks varied from 25% to 100% the frame width, the range of acceptable length dimensions for stereophotographic analysis. Lens specifications and subject distances resulting in the range of useful image dimensions are given for the 4 Nikkor lenses in Table 1. The minimum distance of overlap and the distances at which image sizes were 25%, 75%, and 100% of the photographs' frame widths were calculated from the lenses' underwater angles of view, published in a brochure of technical specifications (available from Nikon, Inc., Garden City, USA). If image lengths were very small, the displacements were minute and difficult to measure. Later

Table 1. Lens specifications (angle of view, minimum distance of focus from film plane) and range of distances providing adequate image dimensions (100% frame, 75% frame, and 25% frame width) for stereophotographic analysis with four underwater lenses (Nikkor). The distances are based upon an estimated mean hammerhead total length of 175 cm (similar to the 178 cm median total length of hammerheads measured during study).

Lens Focal Leng.(mm)	Angle of View (deg.)	Min.Dist. of Focus (m)	Min.Dist. Overlap (m)	Image 100 % Frame (m)	Image 75 % Frame (m)	Image 25 % Frame (m)
15	94	0.3	0.2	0.8	1.1	3.3
28	59	0.6	0.4	1.6	2.1	6.2
35	46.5	0.8	0.6	2.0	2.7	8.1
80	22	1.0	1.3	4.5	6.0	18.0

during the study at El Bajo Espiritu Santo the sharks were more distant with a mean distance of 8.5 m and a range of from 4.6 to 17 m (N=46). For sharks at these distances the 80 mm lens was more effective than the 35 mm lens in providing useful stereophotographs. The 80 mm lens produced acceptable images with subject distances of from 4.5 to 18 m, and produced images closer to the optimal 75 frame width at the mean subject distance of 6 m. Pitted against the advantageously large image sizes of the 35 and 80 mm lenses was the greater distortion of images from these amphibious lenses than that from the 28 mm lens designed exclusively for underwater use(Jacobi, 1968).

A 50-cm separation between the cameras in the stereocamera was chosen because the relatively wide separation produced on the photographs larger displacements which could be more precisely measured on the photographs. This separation also produced adequate overlap in the nearfield since the fields of view of the 2 cameras with 35 mm lenses intersected at a distance of only 0.6 m from the photographer. Furthermore, a camera system with these dimensions was portable for the free-diving investigators. Free-diving was used instead of SCUBA diving because the sharks avoided divers with such equipment, which emitted sonically and visually conspicous bubbles.

Photographs were taken during free dives to the edge of the schools of sharks by the investigators who attempted to position the beam supporting the camera parallel to the free-swimming sharks' longitudinal axes. Stereopairs were taken both of the lateral and dorsal aspects of sharks. Usually we centered the closest shark in the viewfinder, but occasionally this was not possible because of the difficulty in remaining with the actively swimming sharks. At these times the stereocamera could only be pointed toward the center of the school with the beam axis held perpendicular to the direction in which the school was moving. Usually the cameraman could photograph only those sharks in the nearer half of a cross-section of the school.

Black and white film (Kodak Tri-X) was used early during the study. Because of the high ASA (400) of this film, photographs could be taken at the low light levels occurring underwater. Even at moderate light levels, the sensitivity of this film allowed photography with a smaller lens aperture. This resulted in a greater depth of field and more sharks in focus. Other reasons for favoring black and white film were its low cost and ease of processing, which was crucial because the film was processed aboard ship to ensure that an adequate sample was obtained before moving to the next study site. Contact prints were later made from the negative pairs for analysis. Such prints were dried on a water-absorbent surface and not ferrotyped because of the warning of Van Sciver (1972) that such drying might inhibit the paper from shrinking back to its original size. Later in the study, color film (Ektachrome 200, Kodak) was used to improve the contrast of the shark images against the background. This film was also processed aboard the ship by the Kodak E-6 developing process. Although this procedure was more difficult (30-min duration, 10 steps, steps temperature sensitive) in comparison to black-and-white processing(16.5-min duration, 8 steps, steps less temperature sensitive), color processing provided positives with a single session.

Measurements were made through a microscope (Wild, M5) with a camera lucida attachment on the resulting black and white contact prints or color transparencies. A scale placed under a camera lucida was projected onto the photograph on the stage of the microscope to measure dimensions on the images. Photographs could also be projected from an enlarger onto a digitizer board where the cursor could be used to record image dimensions.

Accuracy of Technique

Accuracy was not measured for a scaled staff in the field because environmental conditions (water clarity and light levels) varied so greatly throughout the day and between days; therefore, the maximal distance at which an observer could distinquish the scale would vary constantly.

Furthermore, the ability to distinguish the scale would also be influenced by the scale's position in relation to the photographer. This was particularly true with our ability to see sharks clearly: sharks were particularly visible against the background even at large distances when they were swimming above the photographer and off to his side. In this position reflected light from the shark's dorsum gave it a highly visible sheen. We chose to determine the precision of the technique under ideal water clarity and light levels. Rather than using a sharklike object with gray coloration, we used a staff with highly contrasting white and black bands. We believed an assessment of the precision of measurements on such an object would be of greater value to investigators working on a variety of marine animals with different color patterns. In our own length determinations, we attempted to reduce error by being very selective and measuring only those sharks clearly distinguishable from the background. Such sharks could be at greatly varying distances from the stereocamera depending on the water clarity, light level, and the shark's position relative to the photographer.

Stereopairs of color photographs taken of the calibration staff in the swimming pool at distances 2, 4, 8 m from the stereocamera were utilized to determine the accuracy with which image dimensions were recorded. Two sets of measurements of a 50-cm section of the staff for the 3 distances were made by one investigator (Table 2, measurer A)

Table 2. Repeated measurements with their means, standard errors, and ranges (also as ± percent mean) of 50-cm section of scaled staff from stereopairs taken at distances of 2, 4, and 8 m from stereocamera in swimming pool. Two sets of measurements by Measurer A and one set by Measurer B using color film.

50-cm Section of Staff

Iden. of Measurer	Dist. from Camera (m)	Stereo-pair N	Mean (cm)	Standard Dev. (cm)	Range Values (cm)	Range (±Perc. Mean)
A	2	10	51.4	0.3	51.0-51.7	0.7
A	4	5	53.8	2.0	52.1-56.7	4.3
A	8	3	55.5	1.0	54.3-56.2	1.7
A	2	10	51.4	0.3	50.6-51.7	1.0
A	4	5	53.8	2.0	52.1-56.7	4.2
A	8	3	56.2	0.3	56.0-56.3	0.3
B	2	10	51.9	0.6	50.2-52.9	2.6
B	4	5	54.4	2.0	51.3-56.7	5.0
B	8	3	56.4	2.1	53.5-58.5	4.4

and a single set by another (measurer B). The ranges of the measurements in the most accurate set was ±0.4 cm at a distance of 2 m, ±2.2 cm at 4 m, and ±0.9 cm at 8 m. The linear increase in the means of 51.4 cm at 2 m, 53.8 cm at 4 m, and 55.5 cm at 8 m was compensated for by the calibration technique described earlier. The primary source of error here we believe to be variability in reading the image dimensions determined from the stereopairs. The coefficients of variation for 1 and x_2-x_1 by investigator A were similar at 2 and 8 m but differed at 4 m. At 4 m the 0.034 of the image length was considerably less than the 0.370 of x_2-x_1. This difference probably resulted from the necessity of making 2 measurements in respect to the edge of the frame and subtracting one from the other to get the x_2-x_1 term. The variation in the measurements by investigator B increased between 2, 4, and 8 m, and these variances were heterogenous (Bartlett's Test, $P<0.001$). This increase in variability was mainly in the x_2-x_1 dimension.

Little variability appeared in repeated sets of measurements by a single investigator (see Table 2, measurer A). The means of these determinations were identical for camera-staff separations of 2 and 4 m and differed by only 0.7 cm at 8 m. There was more variability between determinations by different investigators(see Table 2, measurers A & B). The means of these measurements differed by 0.5 cm at 2 m, 0.6 cm at 4 m, and 0.9 and 0.2 cm at 8 m.

The sources of error discussed above appear to be independent of the size of the object measured, and for this reason were not expressed as % of the 50-cm section of scaled staff. While the precision of the measurements of the 50-cm staff section under an ideal light level over the distances measured was remarkably high, the precision of the TL determinations of free-swimming hammerhead sharks was undoubtably less at these distances because a shark's countershaded gray appearance blends into the blue background light conditions underwater. Accuracy of measurements would certainly be greater for non-countershaded marine animals such as delphinids and pinnipeds.

Spherical aberration in the camera lenses also reduced the precision of measurements. Dimensions of three 50-cm sections of the calibration staff lying horizontally across the entire frame were determined from 7 photographs both from the right and lefthand cameras. Sections were measured (in the center of the microscope's optical field) at both sides and the center of each photograph. The smaller mean of the center dimension differed from those at the right and left edges by ±0.9 and ±1.3 %, respectively for the lefthand camera. The smaller mean of the center dimension differed from both edge dimensions by ±1.7 % for the righthand camera. These errors were not corrected in different areas of the optical field because the images of the sharks usually occupied a large part of the frame (see measured sharks in Figs. 2 and 5). Some parts of the shark's image were increased and other parts decreased in size, in part cancelling out the effects of spherical aberration.

The accuracy of stereophotographically determined TLs was additionally corroborated with independent measurements of 4 sharks. These sharks were tagged with 21.5 cm, vinyl-streamer, dart-tags, which were applied underwater by spear to the shark's dorsum between the first and second dorsal fins. The vinyl tubing trailed backward parallel the torso of the swimming shark, and the tag's length could thus be used as a scale to measure the TL of the shark. The stereophotographically determined TLs differed from the tag-determined TLs of 145, 182, 202, 214 cm by 4.0, 0.6, 0.9, and 5.7%, respectively. The tag-determined TLs were probably less accurate because of changes in the tags' lengths caused by: (1) lack of parallelism of the tag's axis with the longitudinal axis of the shark, (2) partial insertion of the vinyl tubing into the epidermis of the shark, (3) curvature of the tag, and (4) the spreading apart of the separate, color-coded sections of the tag (and increasing its overall length).

RESULTS

Total lengths were determined for scalloped hammerheads schooling along an island (25°06'N, 110°31'W) and two seamounts (24°41'N, 110°16'W and 23°01'N, 109°28'W, respectively) in the Gulf of California (see Klimley, 1983 for maps). These TLs should be considered minimum TLs because they were determined using the first measuring technique described. TLs ranged from 109 to 371 cm with a median of 178 cm (Fig. 7). The sexual identity of the hammerheads could at times be determined from the presence or absence of claspers, the male intromittent organs, trailing from the inner margins of the pelvic fins. Females (stippled) greatly outnumbered males (solid). Females ranged in TL from 109 to 284 cm with a median of 171 cm. The 2 males were 154 and 171 cm.

Total lengths of sharks grouping at El Bajo Gorda, a seamount reaching to within 35 m of the surface ca. 5 naut. miles southwest of the southern end of the Baja Peninsula (23°01'N, 109°28'W), increased with distance from the camera (Fig. 8). TLs increased 9 cm for every 100 cm distant from the camera. If one plots TL in relation to distance into the school (actually distance from the camera on the z-axis), the increase is 12 cm. This reflects distance into the group since the photographer positioned the camera parallel to the longitudinal axes of the parallel swimming sharks in order that the z-axis of a camera-based coordinate system was directed into the group away from the photographer. The distance to the outermost shark in the group (nearest to the

Fig. 7. Frequency distribution of stereophotographically determined total lengths for free-swimming scalloped hammerheads. Superimposed upon the pooled frequency are those of unidentified (clear) and scarred (cross-hatched) individuals, males (solid), and females (stippled).

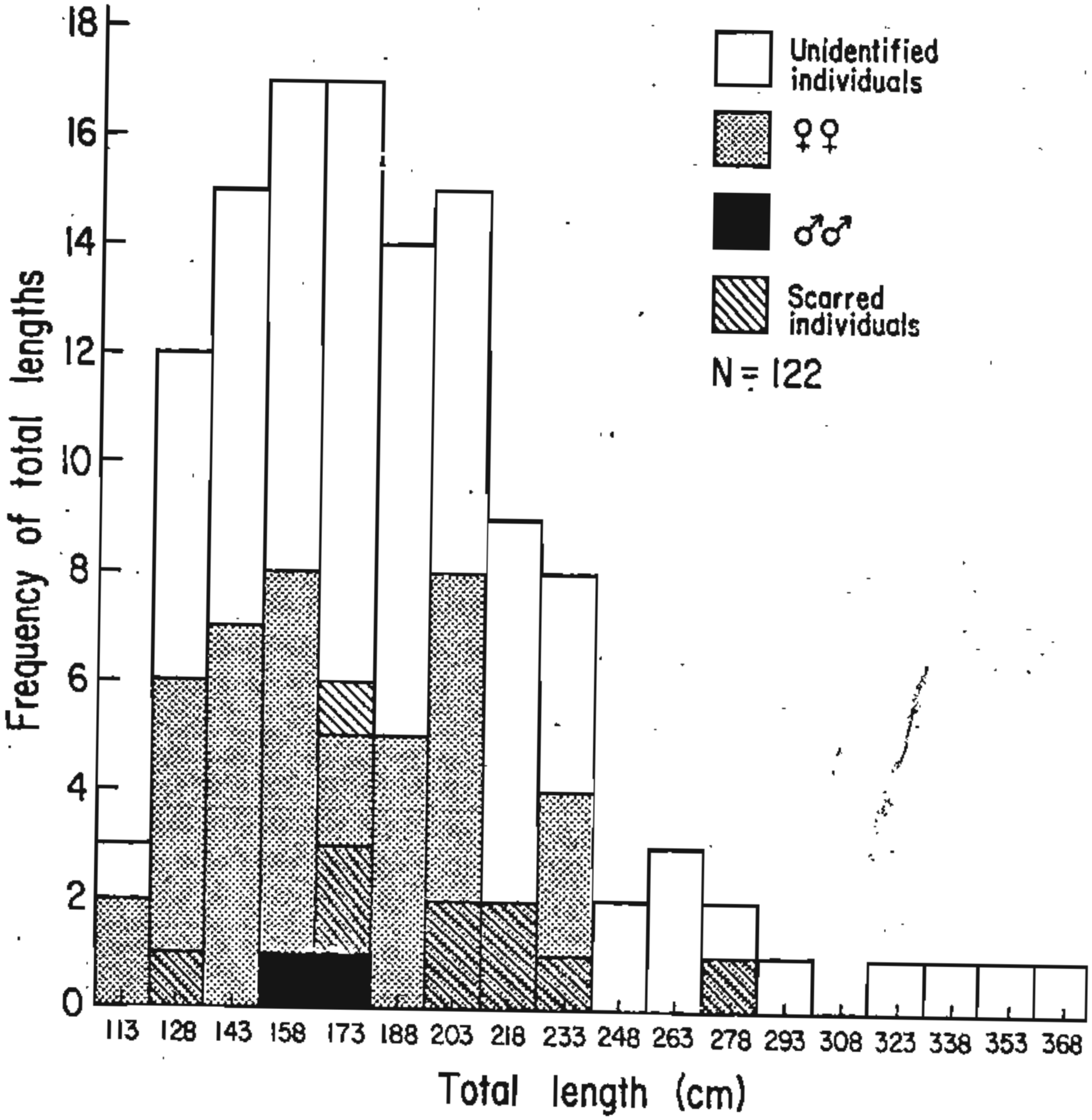
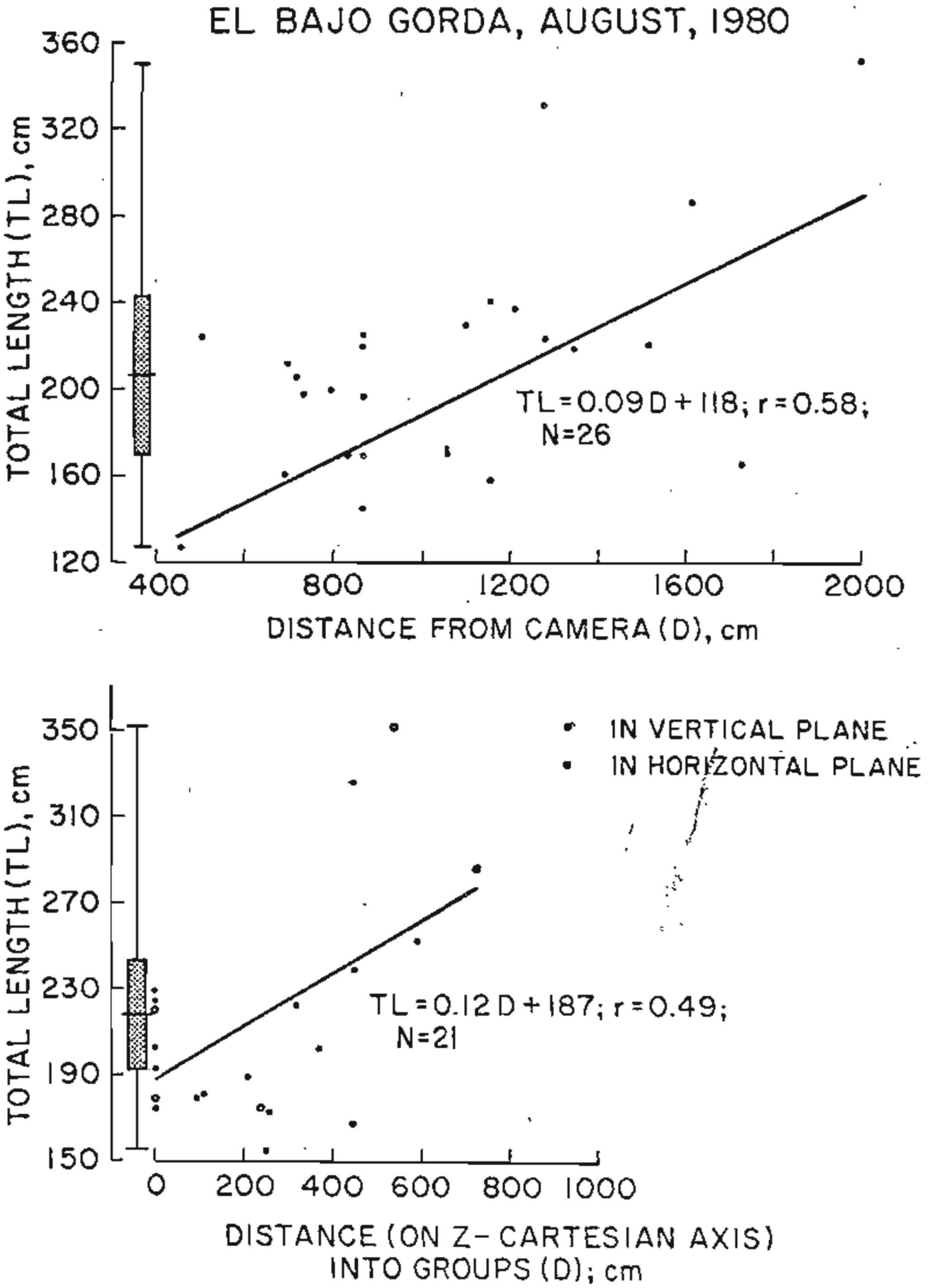

Unidentified individuals
♀♀
♂♂
Scarred individuals
N = 122
Frequency of total lengths
0
2
4
6
8
10
12
14
16
18
113
128
143
158
173
188
203
218
233
248
263
278
293
308
323
338
353
368
Total length (cm)

Fig. 8. Top. Total lengths (TL) of hammerheads at increasing distances from the camera (D). Bottom. Total lengths at increasing distances into the groups on the z-axis. Median, a quartile deviation to either side of the median and range indicated to left of abcissa. Regression line equation, correlation coefficient, and N noted.


EL BAJO GORDA, AUGUST, 1980
TOTAL LENGTH (TL), cm
360
320
280
240
200
160
120
400
800
1200
1600
2000
DISTANCE FROM CAMERA (D), cm
TL = 0.09 D + 118; r = 0.58;
N=26
TOTAL LENGTH (TL), cm
350
310
270
230
190
150
0
200
400
600
800
1000
○ IN VERTICAL PLANE
● IN HORIZONTAL PLANE
TL = 0.12 D + 187; r = 0.49;
N=21
DISTANCE (ON Z- CARTESIAN AXIS)
INTO GROUPS (D); cm

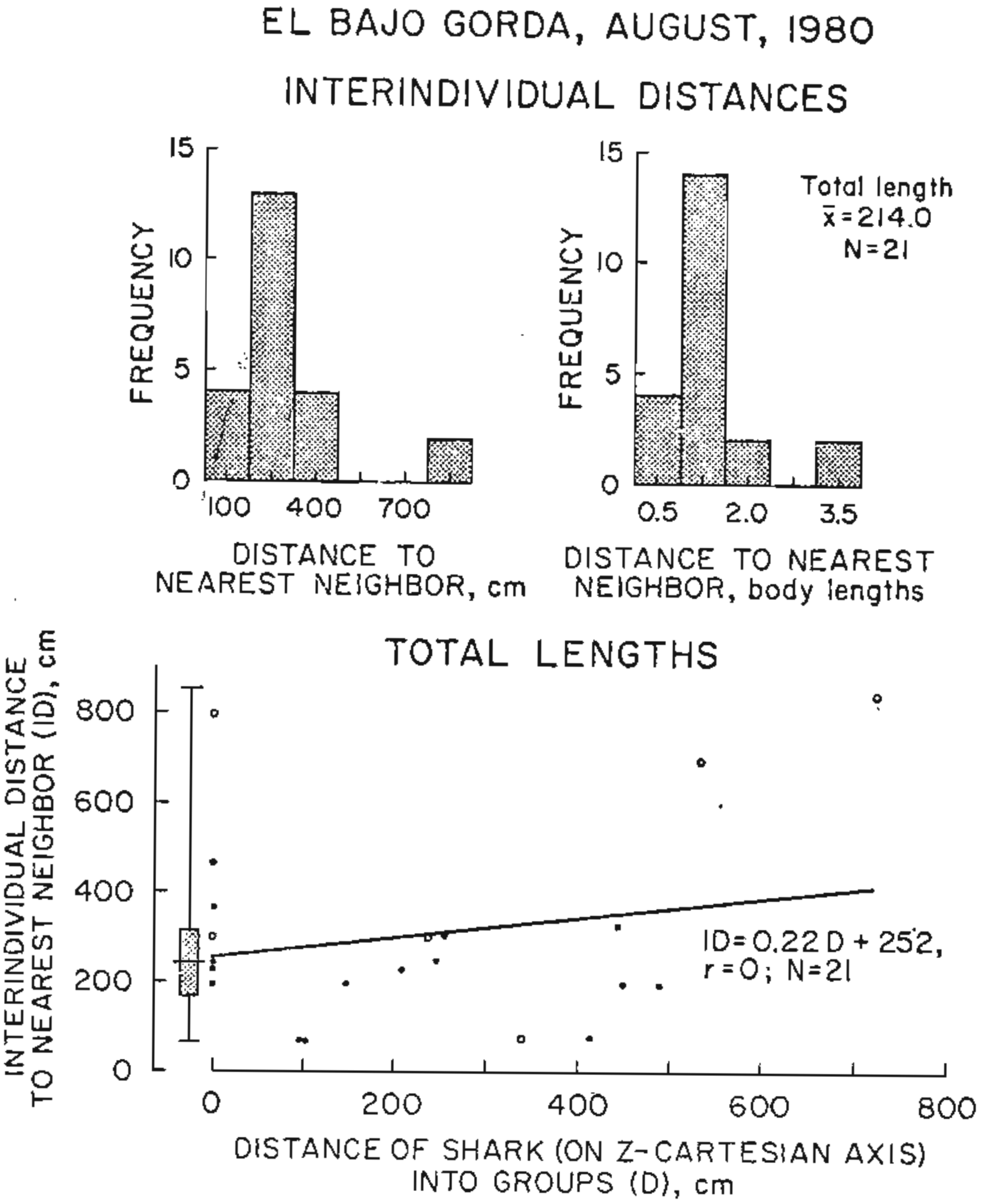
photographer) was subtracted from the distances to sharks more interior within the group (farther away from the photographer). TLs of sharks on the z-axis downward into the groups were indicated by solid circles and those laterally into the groups by clear circles. TLs of sharks outside the groups were eliminated in an arbitrary manner by determining IDs for the same sample and expressing them as body lengths. Sharks separated by the next most interior shark by more than 4 body lengths were considered outside the groups, and eliminated from the analysis. The sizes and spatial relationships of free-swimming sharks are examined in greater detail in the description of schools of scalloped hammerheads occurring at 4 locations in the Gulf of California (see Klimley, 1983).

Frequency distributions of IDs for sharks at El Bajo Gorda are shown both in cm and body lengths in Fig. 9. IDs are also plotted as a function of distance into the schools on the z-axis. Although a correlation does not exist between ID and distance into the group, this may be the result of the variation in the IDs at the edge of the groups. Some of these IDs are probably from either arriving or departing sharks which are not part of the school.

DISCUSSION

We will confine our discussion to a comparison of the

Fig. 9. Top. Histograms of nearest-neighbor, interindividual distances (ID) in both cm and body lengths. Bottom. These IDs plotted as a function of distance into the groups on the z-axis (D).


EL BAJO GORDA, AUGUST, 1980
INTERINDIVIDUAL DISTANCES
FREQUENCY
15
10
5
0
100
400
700
DISTANCE TO NEAREST NEIGHBOR, cm
FREQUENCY
15
10
5
0
0.5
2.0
3.5
Total length
x̄=214.0
N=21
DISTANCE TO NEAREST NEIGHBOR, body lengths
TOTAL LENGTHS
INTERINDIVIDUAL DISTANCE TO NEAREST NEIGHBOR (ID), cm
800
600
400
200
0
ID=0.22 D + 252,
r=0; N=21
0
200
400
600
800
DISTANCE OF SHARK (ON Z-CARTESIAN AXIS) INTO GROUPS (D), cm

stereophotographic measurement technique to other 3-dimensional measuring techniques. For field determinations of animal dimensions and positional relationships stereophotography is an alternative to the "shadow method" utilized in the laboratory by investigators (Dambach, 1963, Pitcher, 1973, Pitcher and Partridge, 1979a, 1979b, 1980; Partridge, 1980, 1982). This technique requires the arrangement of a light source a known distance from the bottom and a similarly positioned photographic or video monitor to record shadow positions on the bottom. In contrast, stereophotography requires only 2 cameras mounted on a beam and separated by a known distance. Unlike the shadow method, the stereophotographic system can easily be made portable. Furthermore, the latter is an improvment over a single camera system (e.g., Graves, 1977), which requires the assumption that the TLs are invariant so their image sizes can be used to measure spatial relationships. Although the single camera technique is useful for describing spatial relationships for _Engraulis mordax_ and other teleost species in which TL variations of school members may be small, it would not be useful for the scalloped hammerhead (see Klimley, 1983) and other species (see Muzinic, 1977) in which variation in TL of school members is relatively large.

The accuracy of stereophotographic systems varies substantially. The laboratory method used by Cullen _et al._(1965) to measure the height in the water column of members of small schools of Hepsetia sp. and Harengula sp. in the laboratory provided an accuracy of ±3.0% of the measured distances. Dill et al. (1981) in determining IDs between Onchorhynchus kisutch in a hatchery trough provided an accuracy of ±0.3%. Major and Dill (1978) in their field study of the 3-dimensional structure of flocks of the dunlin (Calidris alpina) and starling (Sturnus vulgarus) compared calculated and actual distances between the corners of a children's jungle gym. Mean calculated and measured distances between corners on the horizontal plane differed by ±3.5 % but no difference was detected on the vertical plane. We found a maximum error of ±4.3% from our repeated measurements of a scaled staff at distances of 2, 4, and 8 m from the camera. However, it is impossible to give an exact measure of error in length and positional determinations for the scalloped hammerhead sharks because of the reasons we have already mentioned.

CONCLUSIONS

We feel that the above-described technique is a powerful tool for remotely deterimining the sizes and relative positions of marine animals. Using this technique, the behavioral biologist can remotely determine the sizes of interacting subjects and their relative positions in the social group. Such a record could also be obtained of behavior patterns using a video camera with a stereoscopic lens attachment. The benthic ecologist can record densities of organisms along a transect, and with an knowledge of species size-mass relationships, determine biomass over an area. Furthermore, from determinations of IDs, the dispersion of the animals can be characterized as random, uniform, or clumped.

ACKNOWLEDGEMENTS

We would like to express our appreciation to those organizations who provided funding during the study. The National Geographic Society's Committee for Research and Exploration provided support(Contract-2204:senior author and D.R. Nelson, principal investigators) as well as the Foundation Ocean Research for for expedition costs. The Office of Naval Research provided salary support(Contract N00014-77-C-0113:D.R. Nelson, principal investigator) for the senior author and the Foundation for Ocean Research for the junior author during part of the study. We would like to thank D. Lluch, H. Nienhuis, and others from the Interdisciplinario de Ciencias Marinas, La Paz for providing their research vessel, the Juan de Dios Batiz, and participating in the joint SIO-CICIMAR cruises on which this research was carried out. D.R. Nelson of California State University, Long Beach and T. Rulison, MD, Sacramento helped greatly in the stereophotographic sampling. This report constitutes part of the doctoral dissertation of the senior

author at the University of California, San Diego under the guidance of R. H. Rosenblatt.

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CHAPTER 3: COMPOSITION, STRUCTURE, AND THE DYNAMICS OF SCHOOLS OF THE SCALLOPED HAMMERHEAD SHARK (SPHYRNA LEWINI) IN THE GULF OF CALIFORNIA

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ABSTRACT

Large schools of scalloped hammerhead sharks along the dropoffs into deep water in the Gulf of California are formed of individuals spanning a size range of from 88 cm to 371 cm in length with size coefficients of variation (CVs) at the sites ranging from 0.12 to 0.25. These polarized schools are composed primarily of females, outnumbering males in ratios from 1.6:1.0 to 34.0:1.0. It is suggested the preponderance of females at the dropoffs is due to the offshore movement of females at smaller sizes than males.

Although differences in the sizes of sharks in some schools indicated a tendency for the hammerheads to segregate by size, most groups consisted of individuals varying greatly in size (CVs ranged from 0.05 to 0.36 at El Bajo Gorda, 0.02 to 0.40 at Las Arenitas). This large size variation has permitted size segregation within schools. Both total shark length and distance to the nearest-neighbor increased toward the bottoms of schools at Las Arenitas. Total shark length

increased with distance into the schools at El Bajo Gorda and Espiritu Santo. The presence of larger sharks in only part of the schools is believed due to aggressive interactions primarily among females.

INTRODUCTION

Stewart Springer noted in his 1967 review, "Social organization of shark populations," that at times sharks were social animals forming groups. These groups could be not only aggregations formed in response to abundant prey, but also schools formed from a biosocial attraction possibly aiding in migration. As to the social organization of these schools, Springer noted that little was known other than the tendency for the schools to be composed of individuals of the same sex and size, and for larger-sized species to form smaller schools than smaller species. In species with the most complex social organization (the Carcharhinidae and Sphyrnidae), Springer believed the shark populations to be divided into social groups of sexually mature males, sexually mature females, and subadults of both sexes occupying different habitats at different times of the year. Although Springer suggested that such segregation might result from ontogenetic differences in swimming performance, dietary preferences, and the absence of aggression between similarly sized sharks, he admitted that little was known about the internal structure of these groups.

Grouping has been noted for only a few of the ca. 350 species of sharks. However, the grouping species are diverse both phylogenetically and ecologically, and this diversity in the context of the paucity of ethological studies on species of sharks implies that grouping is a common form of spatial dispersion among sharks. Bullhead sharks (Heterodontus portusjacksoni) considered evolutionarilly primitive due to their possession of characters of the fossil hybodont taxon (Schaeffer, 1967), remain together in small groups in caves during the day (McLaughlin and O'Gower, 1971). Pacific angel sharks (Squatina californica), galeoid sharks derived from hybodont ancestors form diffuse, small groups over a sandy bottom during the day (Standora and Nelson, 1967). In addition, grouping also occurs in the more advanced carcharhinid species such as the lemon (Negaprion brevirostris), tiger (Galeocerdo cuvieri), gray reef (Carcharhinus amblyrhynchos), reef blacktip (C. limbatus), spinner (C. maculapinnis=brevipinnis), dusky (C. obscurus), and sandbar shark (C. milberti=plumbeus) (Springer, 1950, 1967; Johnson, 1978; Nelson and Johnson, 1980). Shark species living in different habitats also form groups. The bullhead shark forages along the bottom on benthic invertebrates. The Pacific angel shark remains on the bottom and ambushes benthopelagic prey. The carcharhinid species most often feed on midwater prey. The basking shark (Cetorhinus maximus and the whale shark (Rhincodon typus) inhabit offshore surface waters and feed upon macroplankton and small fishes. Adult scalloped hammerhead sharks (*Sphyrna lewini*) remain along the dropoff during the day, but during the night disperse to feed on neritic and pelagic prey. Grouping has been reported in twelve of the eighteen shark families recognized by Bigelow and Schroeder (1948). Indeed, the absence of observations of grouping in the other families may stem from the infrequency with which their members have been studied. Some families in which grouping has not been observed, the Dalatiidae, Hexanchidae, Pseudotriakidae, and Scaphanorhynchidae are composed primarily of deepsea species; others, the Alopiidae and Echinorhinidae, are composed of seldom encountered neritic species.

Size or sexual segregation inferred from different size and sexual compositions of catches from different areas (termed "geographical" by Backus *et al.*, 1956) has often been noted for shark species. It occurs in the dogfish (*Squalus acanthias*) (Ford, 1921; Jensen, 1965), soupfin (*Galeorhinus zygopterus*) (Ripley, 1946), lemon (*Negaprion brevirostris*) (Springer, 1950), blue (*Prionace glauca*) (Suda, 1953), school (*Galeorhinus australis*) (Olson, 1954), oceanic whitetip (*Carcharhinus longimanus*) (Backus, *et al.*, 1956), sandbar (Springer, 1960), marbled cat (*Galeus arae*) (Bullis, 1967), scalloped hammerhead (Clarke, 1971), dusky, (Bass *et al.*, 1973), and white shark (*Carcharodon carcharias*) (Bass *et al.*, 1975a).

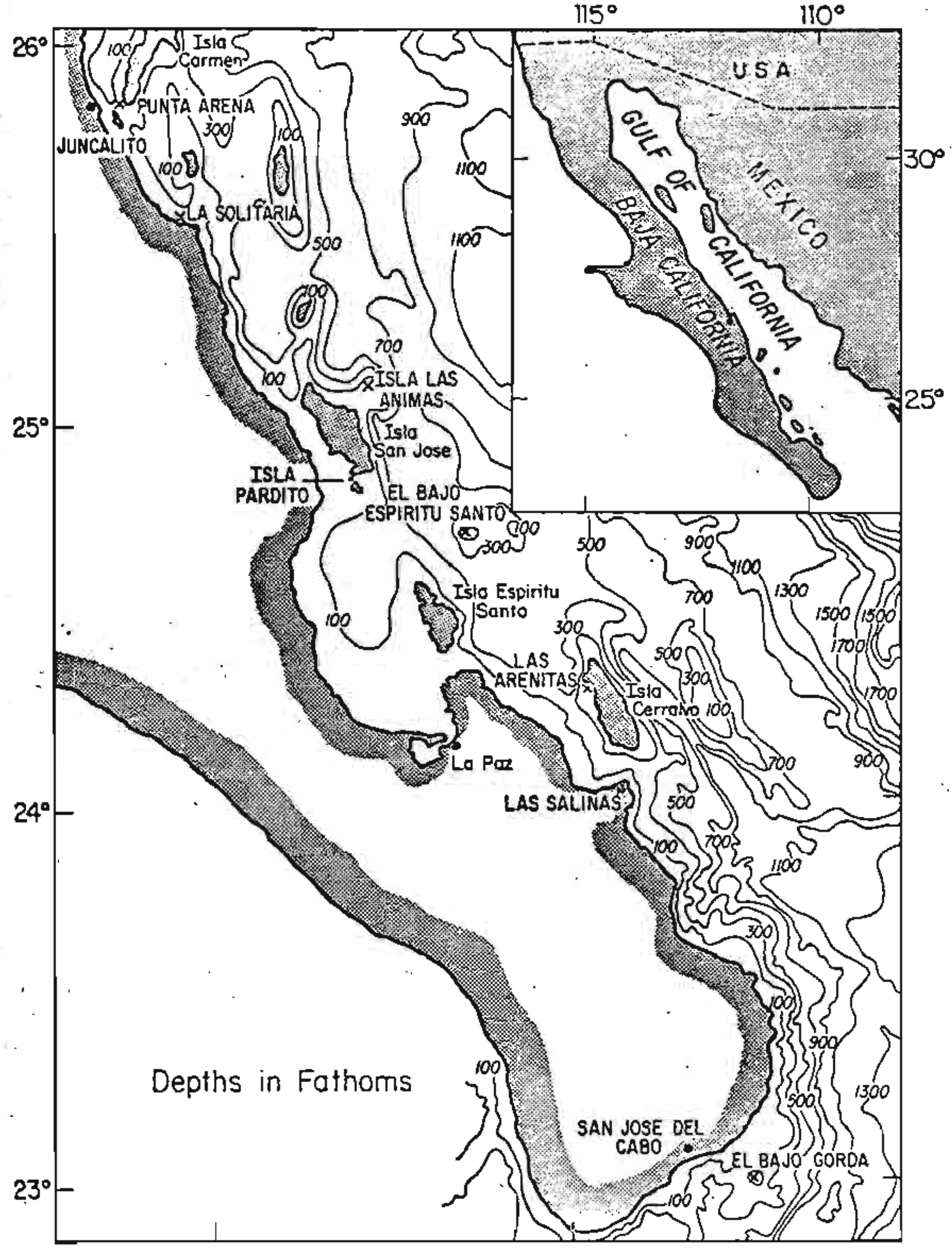
Evidence for size and sexual segregation among schools (termed "behavioral" by Backus _et al._, 1956) is less common for two reasons, firstly the difficulty in inferring segregation from catch records, and secondly the rarity of observational studies of sharks in their own habitat. Ford (1921) separated the spiny dogfish into four classes from catch records, and Clarke (1971) inferred that scalloped hammerhead pups group in either aggregations or schools from catch records. Bass _et al._ (1975b) noted that large numbers of scalloped hammerheads of from 80 to 120 cm in length were seen swimming in an undirected manner in the surface waters. Furthermore, aerial photographs have depicted schools composed of similarly sized, unidentified sharks (Kenny, 1968) and cownose rays, _Rhinoptera bonasus_ (Clark 1963). In their underwater studies McLaughlan and O'Gower (1971) observed a predominance of adult females in the inshore groups of the bullhead shark, and Nelson and Johnson (1980) noted separation of gray reef sharks into groups of first-year juveniles and adults.

In the following pages I will describe the composition, structure, and dynamics of schools of the scalloped hammerhead shark in the Gulf of California. The description will be based on stereophotographic measurements and repeated observations of marked sharks.

METHODS

Hammerhead groups were studied in the Gulf of California at four locations separated by a latitudinal distance of 232 km (125 naut. miles): 1) Isla Las Animas, 2) El Bajo Espiritu Santo, 3) Las Arenitas, and 4) El Bajo Gorda (Fig. 1). Isla Las Animas is a large rock jutting out of the water 13 km northeast of Isla San Jose at the edge of a broad shallow shelf with an average depth of 91 m. The depth drops off from the rock to 1134 m over a distance of 4.6 km in the northeasterly direction. El Bajo Espiritu Santo is a bank less than a km in diameter with a rocky ridge with pinnacles rising to within 14 m of the surface located 18 km from Isla Espiritu Santo. Surrounding waters reach depths of 585 m. Las Arenitas consists of an small rock 200 m offshore of the nothwestern coast of Isla Cerralvo and a nearby elevated reef. The bottom drops off rapidly on the seaward side of the reef and reaches a depth of 344 m within 1.9 km. El Bajo Gorda is an offshore bank with a ridge reaching to within 35 m from the surface 9.3 km southeast of the adjacent coastline. Surrounding waters reach depths of up to 604 m. All of the sites are characterized by rapid dropoffs with grades as high as 45 degrees such as at Las Arenitas where the depth dropped from 12 m at the top of the reef to 114 m over a distance offshore of only 150 m. The schools of hammerheads usually remained above these dropoffs with individuals visible at depths ranging from 0.6 to 22.7 m with a mean depth of 10.4 m (Klimley and Nelson, 1981).

Fig. 1. Locations (upper case letters) either where hammerhead grouping was studied underwater or where sharks from the catches of fishermen were examined.


Isla Carmen
PUNTA ARENA
JUNCALITO
LA SOLITARIA
ISLA LAS ANIMAS
Isla San Jose
ISLA PARDITO
EL BAJO ESPIRITU SANTO
Isla Espiritu Santo
LAS ARENITAS
Isla Cerralvo
La Paz
LAS SALINAS
SAN JOSE DEL CABO
EL BAJO GORDA
Depths in Fathoms
USA
MEXICO
GULF OF CALIFORNIA
BAJA CALIFORNIA
26°
25°
24°
23°
111°
110°
109°
115°
110°
30°
25°
100
300
500
700
900
1100
1300
1500
1700

Total lengths (TL) of free-swimming hammerheads, their position in three-dimensional space, and their individual distances (ID) were determined from measurements on stereophotographs. Although I have described this photogrammetric technique and its application to the study of the social organization of scalloped hammerhead schools elsewhere (chapter 2), I will briefly describe the technique here. Paired photographs were simultaneously taken of free-swimming sharks with two cameras mounted at the ends of a section of aluminum, carried on free dives to above or to the side of the schools. The camera was positioned parallel to the longitudinal axes of the sharks during picture taking. For this reason, size segregation of sharks within the schools could be examined both on the vertical (cameraman positioned above school) and horizontal (cameraman positioned to side of school) planes. A measurement of TL for each shark from the tip of its snout to the tip of its caudal fin was performed. The scale to convert this photographic length dimension to true length was obtained both from a knowledge of the separation between the optical axes of the cameras and the width of the area of no image overlap. Distance from the camera to the shark was calculated with the additional empirical measurement of the distance from the second nodal point of the camera lens to the film plane. The shark's position in an x-y-z cartesian coordinate system was further determined using additional measurements from the photographs on the x and y axes (x axis parallel to the longer edge of the frames). The z-coordinate distance was a measurement of the cross-sectional distance into the schools. The distances to sharks within a school were subtracted from the distance to the outermost shark, often nearest to the cameraman. This shark was given a distance of 0 m. Nearest-neighbor, individual distances (ID) between school members were calculated using the geometrical distance formula. A measure of the degree of structure of the schools was obtained from a ratio of the distances from the second to the first nearest-neighbors. If school members positioned themselves perfectly at the vertices of a cube, the ratio would be 1. If they positioned themselves randomly within a cube, the ratio would be 1.6 (Partridge, 1982). The commonness in direction of school members was determined from stereophotographs with the technique of Van Olst and Hunter (1970). Bearings of school members were measured in respect to the long axis of the photographs. A school bearing was calculated by vector addition, and angular deviations of individual sharks from this bearing were calculated together with a mean angular deviation.

Male sharks were distinguished from female sharks by their possession of ventral claspers along the inner margins of their pelvic fins. The presence or absence of claspers were determined either wholly by direct observation during free dives into the groups (sex ratios for Isla Las Animas, El Bajo Espiritu Santo, and El Bajo Gorda during July and

Aug. 1979) or by direct observations and viewing of video samples of hammerhead groups at the remaining locations. Although a conscious attempt was made to refrain from identifying a shark as a female unless its pelvic region was clearly seen, a potential for female bias did exist. Direct observations probably resulted in more accurate ratios than those determined from the video samples. However, the relative constancy between the sex ratios determined from direct observation at El Bajo Espiritu Santo, July and Aug., 1979 (male:female ratio 1.0:3.8, N=84) and those determined from video samples during the same months in 1980 (1.0:2.1, N=31) and 1981 (1.0:3.9, N=82) indicates that the bias may be relatively minor. Sexual identifications from the stereophotographic size samples were not pooled with identifications from direct observations and video samples because the former identifications were judged less accurate due to the poorer resolution especially on the black and white photographs.

School Dynamics

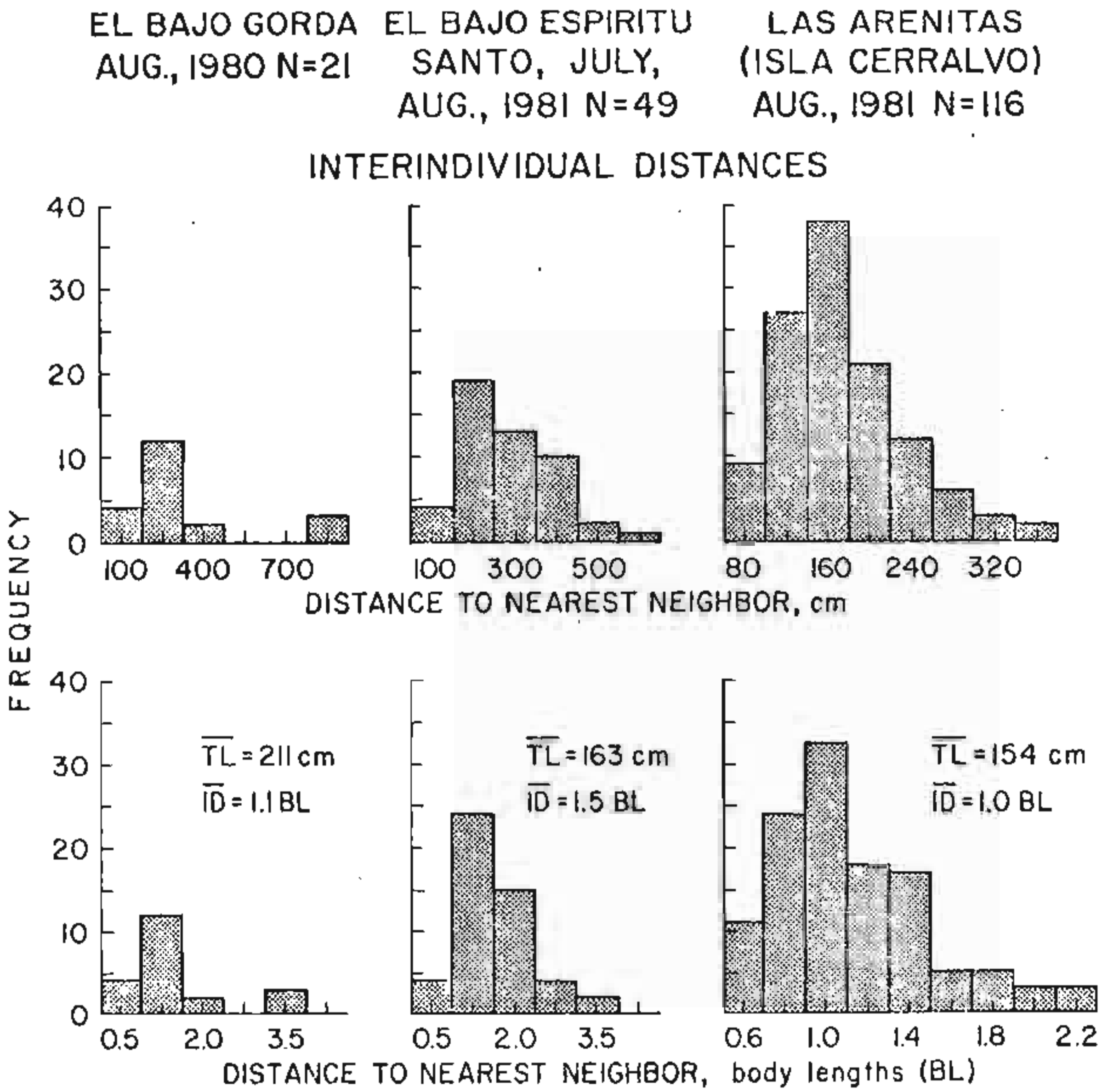
In order to determine just how stable the composition of the schools was, sharks were marked between the first and second dorsal fins with dart tags with color-coded, plastic streamers to facilitate individual recognition. The tags were applied underwater with a pole spear. Although tagged sharks momentarily accerated when tagged, they generally remained within the groups. When tagged sharks were later encountered, their location and time of reobservation as well as the number of accompanying tagged and untagged sharks were recorded on small plastic tablets. In this way the marked shark could be used to follow changes in group size and composition over a period of time.

RESULTS

School Polarity

The hammerhead schools were usually polarized in structure. Members moved together in a common direction, maintained a constant distance from their neighbors, and changed their directions synchronously (defin. of Shaw, 1970, 1978). To quantitatively substantiate the polarized nature of the schools, the commoness in direction of school members and the closeness between nearest-neighbors were measured. The mean angular deviation in the directions of individual sharks from the common direction of the schools at Isla Las Animas in August 1980 was 23.4 deg (SD=38.9 deg, N=57). IDs were measured at El Bajo Gorda during August 1980, El Bajo Espiritu Santo during July and August 1981, and Las Arenitas during August 1981 (Fig. 2). The ID medians ranged from 1.0 body length (154 cm) and 1.1 body lengths (211 cm) at Las Arenitas and El Bajo Gorda, respectively, to 1.5 body lengths (163 cm) at El Bajo Espiritu Santo. The second to first nearest-neighbor ratios varied from 1.4

Fig. 2. Frequencies of nearest-neighbor, interindividual distances (cm and body lengths) at El Bajo Gorda during August 1980, El Bajo Espiritu Santo during July and August, and Las Arenitas during August 1981. The median total length (TL) and individual distance (ID) of sharks included as well as the number of measurements (N) for each site.

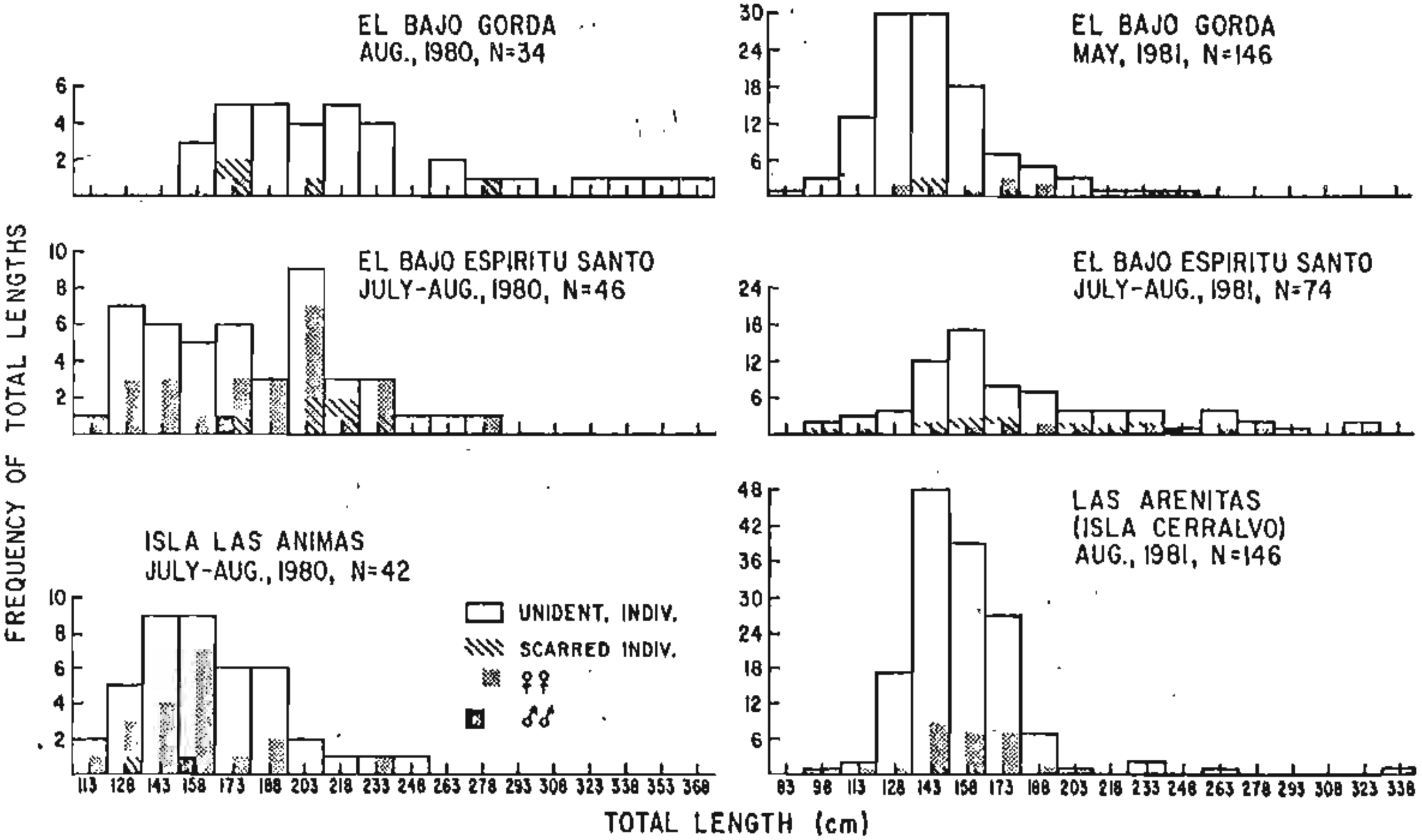

EL BAJO GORDA AUG., 1980 N=21
EL BAJO ESPIRITU SANTO, JULY, AUG., 1981 N=49
LAS ARENITAS (ISLA CERRALVO) AUG., 1981 N=116
INTERINDIVIDUAL DISTANCES
FREQUENCY
40
30
20
10
0
100
400
700
100
300
500
80
160
240
320
DISTANCE TO NEAREST NEIGHBOR, cm
TL=211 cm
ID=1.1 BL
TL=163 cm
ID=1.5 BL
TL=154 cm
ID=1.0 BL
0.5
2.0
3.5
0.5
2.0
3.5
0.6
1.0
1.4
1.8
2.2
DISTANCE TO NEAREST NEIGHBOR, body lengths (BL)

(indicative of moderate school structure) at El Bajo Espiritu Santo and Las Animas to >1.6 (indicative of random school structure) at El Bajo Gorda. The low ratio at the latter site may in part be due to the dynamic composition of schools there (see later discussion) with sharks constantly departing and entering the schools.

School Composition

The sizes of the sharks varied between locations. TLs of schooling hammerheads were measured at El Bajo Gorda, El Bajo Espiritu Santo, Isla Las Animas, and Las Arenitas during 1980 and 1981 (Fig. 3). The TL median (used in between-location comparisons due to to the non-normality of the El Bajo Gorda sample) of sharks occurring at El Bajo Gorda was 211 cm, significantly larger than the 162 and 168 cm medians occurring at Isla Las Animas and El Bajo Espiritu Santo, respectively (Kruskal Wallis Test, $P<0.05$; Nemenyi Multiple Comparison Test, $p<0.05$). The amount of size variation in sharks at each of the three sites was large. Coefficients of variation (CV) (ignoring the non-parametric nature of the El Bajo sample) ranged from 0.24 at El Bajo Espiritu Santo and El Bajo Gorda to 0.17 at Isla Las Animas. Wounds and and scarring indicative of aggression were often present on the measured hammerheads. The small oval areas where dermal denticles had been removed through a scraping contact with another shark varied in frequency at the three

Fig. 3. Frequencies of stereophotographically determined total lengths of scalloped hammerheads at four study sites in the Gulf of California during 1980 and 1981. Solid bars are for males, stippled bars for females, and clear bars for pooled frequencies. Cross-hatched bars are for wounded and scarred sharks.


EL BAJO GORDA
AUG., 1980, N=34
EL BAJO GORDA
MAY, 1981, N=146
EL BAJO ESPIRITU SANTO
JULY-AUG., 1980, N=46
EL BAJO ESPIRITU SANTO
JULY-AUG., 1981, N=74
ISLA LAS ANIMAS
JULY-AUG., 1980, N=42
LAS ARENITAS
(ISLA CERRALVO)
AUG., 1981, N=146
UNIDENT. INDIV.
SCARRED INDIV.
♀♀
♂♂
FREQUENCY OF TOTAL LENGTHS
TOTAL LENGTH (cm)
113 128 143 158 173 188 203 218 233 248 263 278 293 308 323 338 353 368
83 98 113 128 143 158 173 188 203 218 233 248 263 278 293 308 323 338
2 4 6
2 4 6 8 10
2 4 6 8 10
6 12 18 24 30
6 12 18 24
6 12 18 24 30 36 42 48

locations. The contusions were more common at El Bajo Espiritu Santo (13.0 percent of measured sharks) and El Bajo Gorda (8.8 percent) where greater variation in sizes existed than at Isla Las Animas (2.4 percent). The median TL of hammerheads measured at El Bajo Espiritu Santo during July and August 1981 of 163 cm differed significantly from the 152.5 cm length at Las Arenitas during August (Mann-Whitney Test, $p<0.01$). The CV of the TLs was higher at the former (CV=0.25) than at the latter study site (CV=0.13). The percentages of sharks scarred at the locations differed substantially. At El Bajo Espiritu Santo 22.1 percent of the sharks were scarred while at Las Arenitas only 2.1 percent of the sharks possessed scars.

The sizes of sharks at a site also varied between seasons. The median TL at El Bajo Gorda during August of 211 cm was much larger than the May median of only 141 cm. Variation in TLs was slightly larger in August (CV=0.24) than in May (CV=0.19). The frequency of scarring was suprisingly similar at both times. During the spring 6.3 and during the summer 8.8 percent of the sharks bore contusions.

Sizes of hammerheads varied little between years. The median TL of 168 cm at El Bajo Espiritu Santo during the 1980 summer did not differ significantly from that of 163 cm during the following summer (Mann-Whitney Test, $p<0.05$). The respective length CVs of 0.24 and 0.25 were almost identical.

The frequency of scarring, however, differed substantially as the percentages of scarred sharks nearly doubled from 13.0 percent in 1980 to 22.1 percent in 1981.

I felt that that the large variation in sizes of hammerheads at the different locations might not necessarily reflect size differences between members of different schools. For this reason, shark sizes and their variation for single schools were determined from individual stereophotographs. It was not possible to determine CVs for schools where the prior measured variation was greatest such as El Bajo Gorda during summer 1980 and El Bajo Espiritu Santo during 1980 and 1981 because of the small numbers of TL determinations from each stereophotograph at these locations. TLs and CVs only could be determined from stereophotographs taken at El Bajo Gorda during spring 1981 and at Las Arenitas during summer 1980(Figs.4 & 5). The mean TLs and CVs from stereopairs from these sites were similar to those for all sharks measured at the sites. Mean TLs for stereopairs from El Bajo Gorda varied from 108 to 167 cm with a pooled mean of 143 cm. The median TL for the site was 141 cm. The CVs for stereopairs varied from 0.05 to 0.36 with the pooled CV of 0.19 identical to the 0.19 CV for all sharks measured at the site. Mean TLs for stereopairs from Las Arenitas ranged from 150 to 183 cm with a pooled mean of 153 cm. This was similar to the TL median of 152.5 for the site. CVs ranged from 0.02 to 0.46 with a pooled CV of 0.17 slightly higher than the

Fig. 4. Mean (horizontal line), two standard errors (stippled bar), one standard deviation (clear bar) to either side of mean, and range (outer horizontal lines) of total lengths determined from different stereophotographs (reflecting different schools) at El Bajo Gorda during May 1981.

EL BAJO GORDA, MAY, 1981

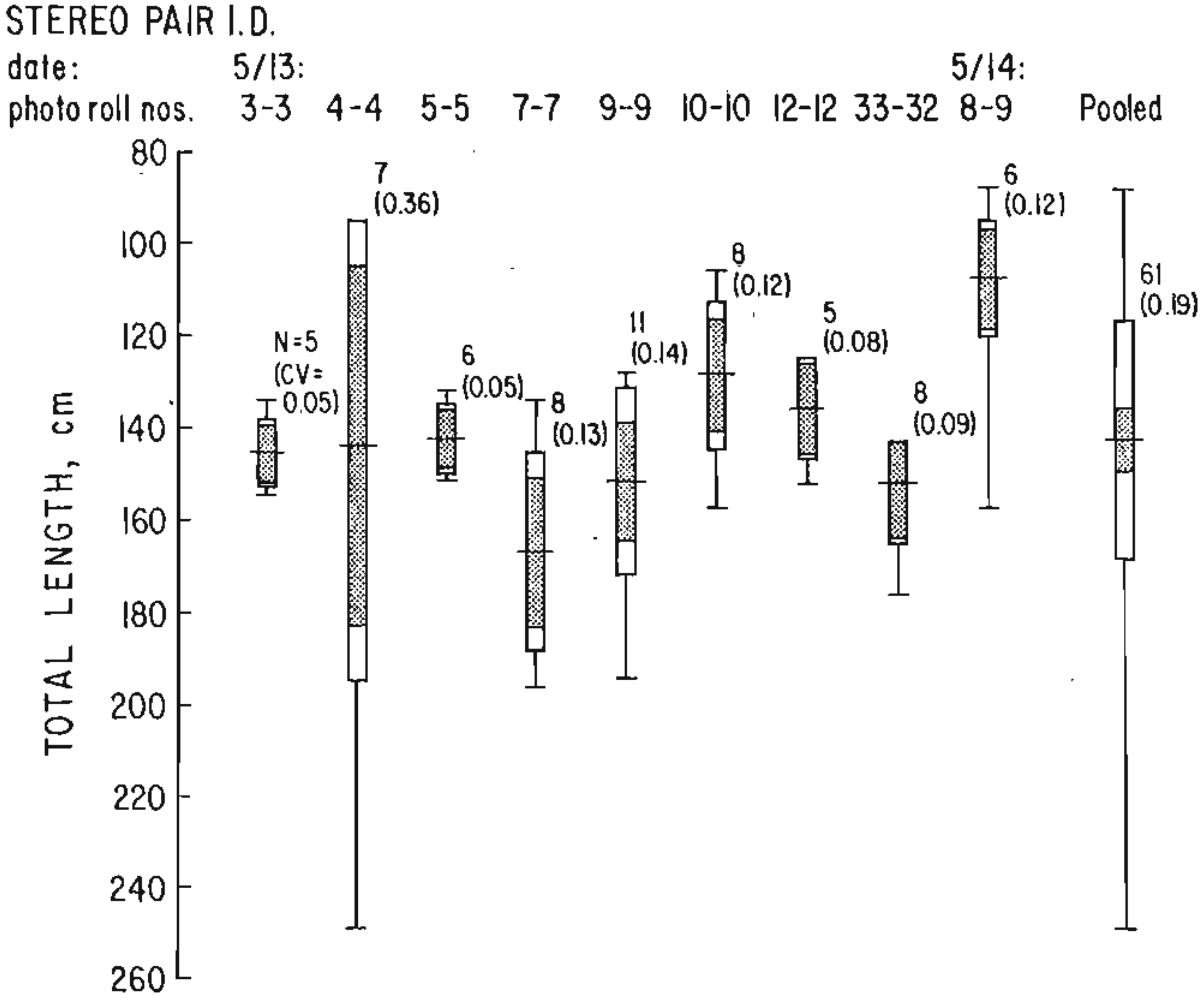
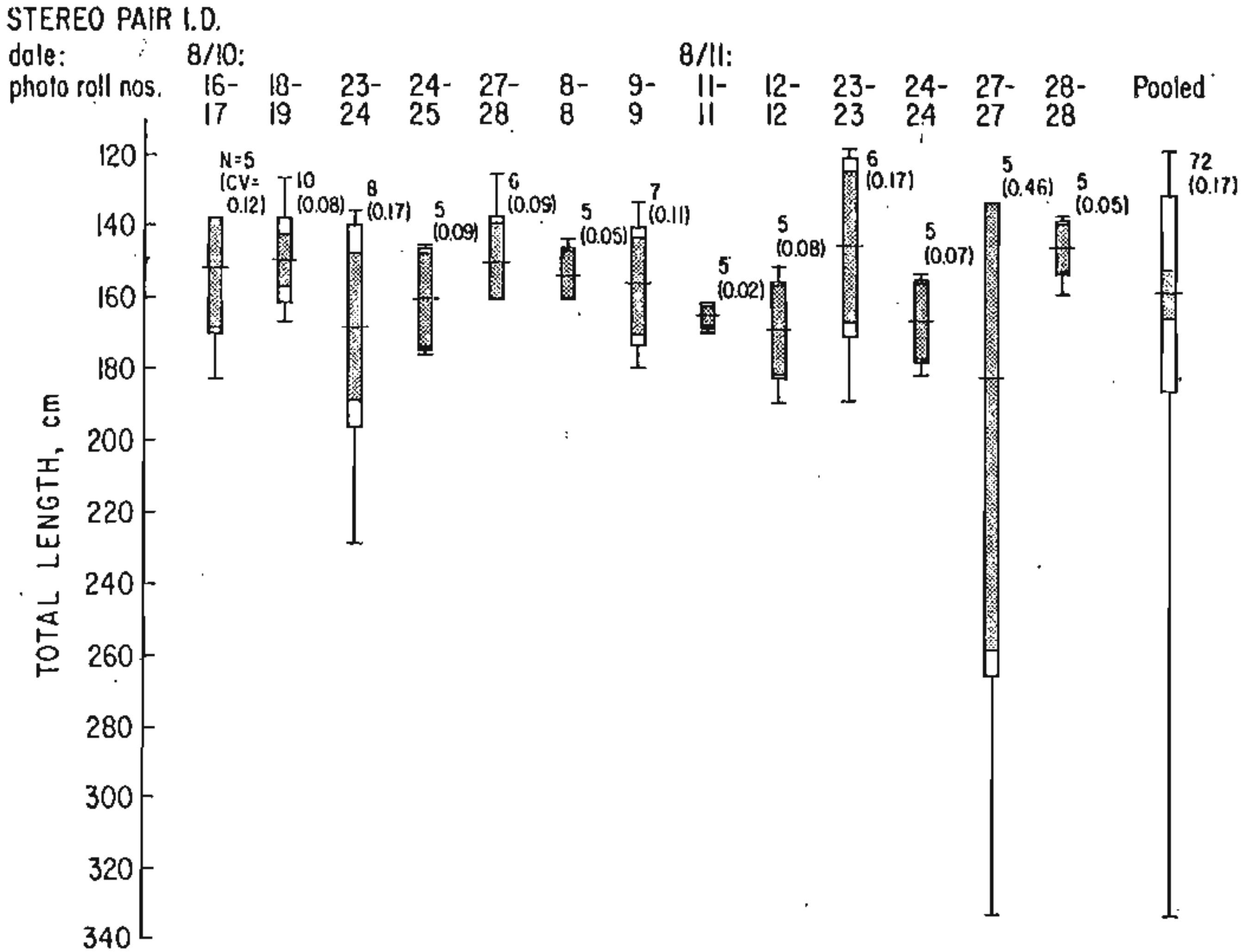


Fig. 5. Total lengths determined from different stereophotographs (reflecting different schools) at Las Arenitas during August 1981.



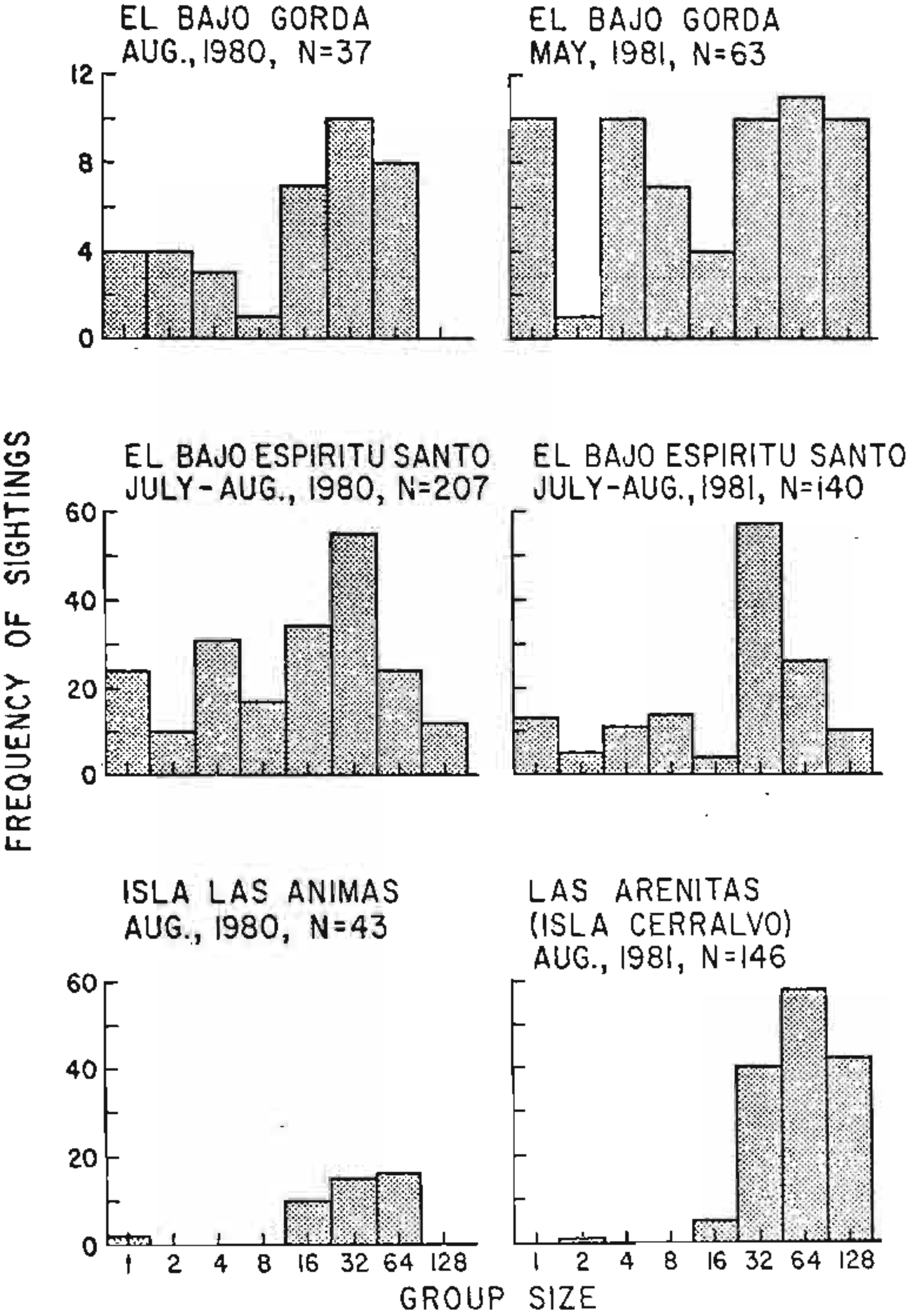
LAS ARENITAS, AUG., 1981

0.13 CV for all sharks measured at the site.

Some evidence indicates that those hammerheads of similar sizes remained together in groups. Hammerhead TLs were again compared from different stereophotographs with groups which had probably changed in composition. The sizes of sharks on these photographs were significantly different at El Bajo Gorda (Analysis of Variance, $p<0.01$), but were not different at Las Arenitas ($p>0.50$). The absence of size differences in photographs (and hence separate schools) at Las Arenitas was probably due to the smaller variation in sizes at Las Arenitas (CV=0.13) than El Bajo Gorda (CV=0.19). From the nine photographs from which five or more hammerheads were measured at El Bajo Gorda, the largest disparity in size existed between the mean of photograph 33/32 of 152.0 cm and those of photographs 10/10 and 8/9 with means of 128.8 and 107.8 cm, respectively.

The sizes of hammerhead groups varied between study sites in the Gulf of California. The frequencies of group sizes occurring at the four study sites during summer 1980 and spring and summer 1981 are shown in Fig. 6. A geometrical scale (modified by the inclusion of single sharks) was used to define the center marks of the size classes of hammerheads counted per observation. This was done to compensate for the tendency to recount sharks in the larger groups and to round the larger counts. Hammerheads

Fig. 6. Frequencies of hammerhead groups of different sizes at four study sites in the Gulf of California during 1980 and 1981. Note geometrical scale used to determine center marks in order to compensate for the declining accuracy of larger counts. N=sightings.

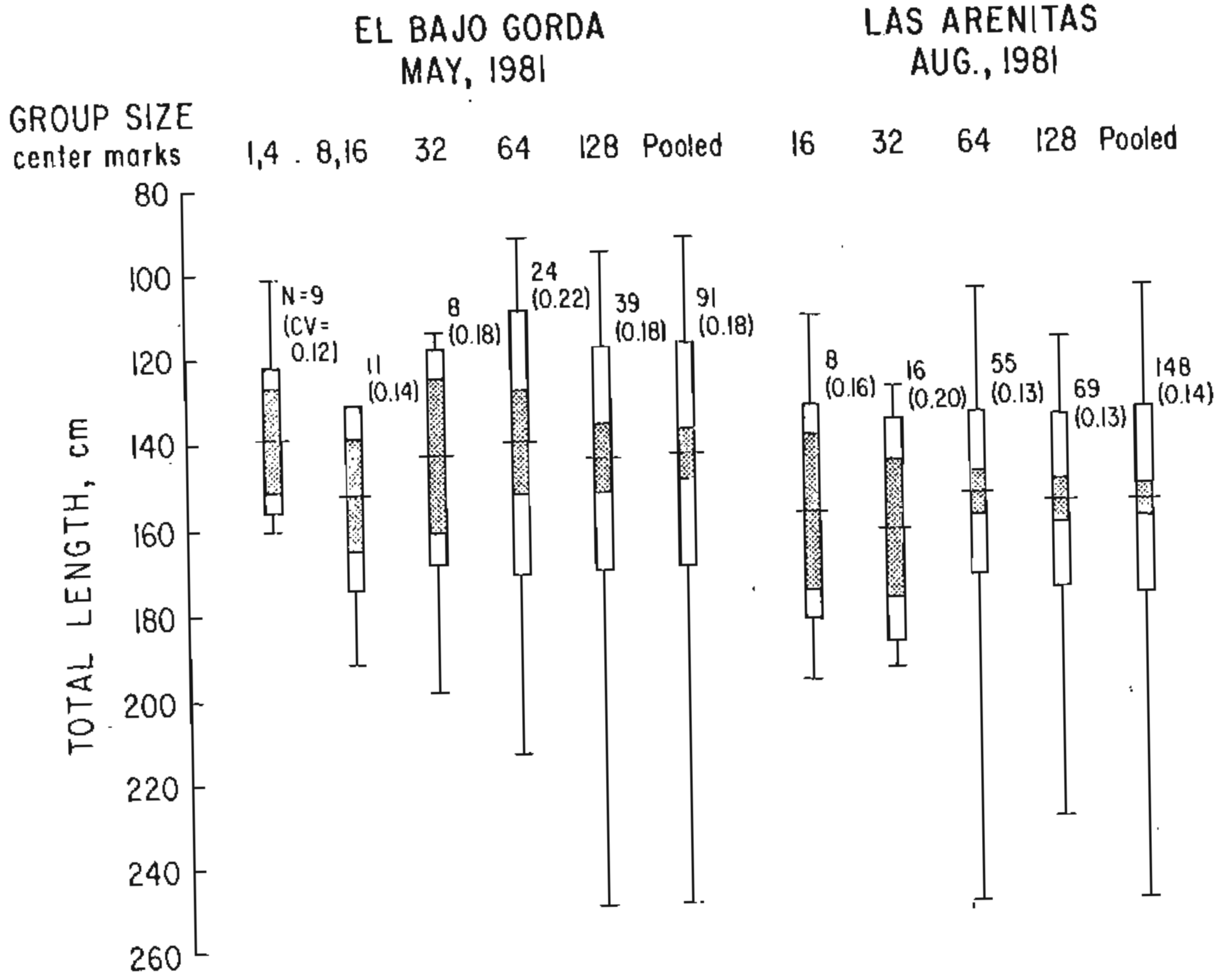

EL BAJO GORDA
AUG., 1980, N=37
EL BAJO GORDA
MAY, 1981, N=63
EL BAJO ESPIRITU SANTO
JULY-AUG., 1980, N=207
EL BAJO ESPIRITU SANTO
JULY-AUG., 1981, N=140
ISLA LAS ANIMAS
AUG., 1980, N=43
LAS ARENITAS
(ISLA CERRALVO)
AUG., 1981, N=146
FREQUENCY OF SIGHTINGS
GROUP SIZE
0
4
8
12
20
40
60
1
2
4
8
16
32
64
128

were seen as individuals, pairs, and groups ranging up to 150 members. Significent differences between groups sizes occurred between the three sites during summer 1980 (Chi-Square, $p0.001$, alternate classes pooled). The mode of the group-size classes at Isla Las Animas was 64, and this was larger than the 32 shark mode of El Bajo Gorda and El Bajo Espiritu Santo. Furthermore, groups were not present at Isla Las Animas in the smaller classes of 2, 4, and 8 sharks. They were present in these size classes at El Bajo Gorda and El Bajo Espiritu Santo. These differences in group size were not paralleled by differences in shark TL. Although group sizes were larger at Isla Las Animas than at El Bajo Espiritu Santo, the shark size medians at these locations of 162 and 168 cm differed very little. Significant differences also occurred between two sites during summer 1981 (Chi-Square, $p<0.001$, alternate classes pooled). The 64 shark mode at Las Arenitas was larger than the 32 shark mode at El Bajo Espiritu Santo. Groups were not present in the smaller size classes of 4 and 8 sharks at Las Arenitas unlike El Bajo Espiritu Santo. The difference between group sizes at one site between 1980 and 1981 was less. Although a comparison of the dispersion of the two frequency distributions indicated a barely statistically significant difference (Chi-Square, $p<0.05$), the central tendencies of the two distributions were very similar. During both years the group-size modes at El Bajo Espiritu Santo were the identical 32 sharks. Group size varied more on a seasonal basis

(Chi-Square, p<0.001, alternate classes pooled). A greater proportion of the groups seen were in the smaller classes during summer than during spring at El Bajo Gorda. This difference was correlated with a difference in the TLs of sharks in these groups. The sharks in the smaller groups were larger with a median TL of 211 cm than the sharks in the larger groups with a median length of 141 cm.

No correlation was found within sites between the sizes of the groups and lengths of their members. In this comparison group size could not be taken directly from a stereophotograph because this count of hammerheads did not always accurately reflect the field count of group size. This was because the investigator often photographed the sharks at such proximity that some sharks within the group were not detectable on the resulting photograph. Furthermore, sharks visible to the photographer making the field count often were not visible on the photograph (in particular on black and white photographs). This was indicated by the larger numbers of hammerheads counted on color transparencies than black and white contact prints for identical field counts. For these reasons, the field count was used as an indicator of group size. TLs for different group sizes were compared only at the locations with the two largest samples, El Bajo Gorda during May and Las Arenitas during August 1981 (Fig. 7). Due to the paucity of lengths for individual hammerheads and small groups at Las Arenitas,

Fig. 7. Mean (horizontal line), two standard errors (stippled bar), one standard deviation (clear bar) to either side of the mean, and range (outer horizontal lines) of total lengths for different group sizes at El Bajo Gorda, May 1981, and Las Arenitas, August 1981.

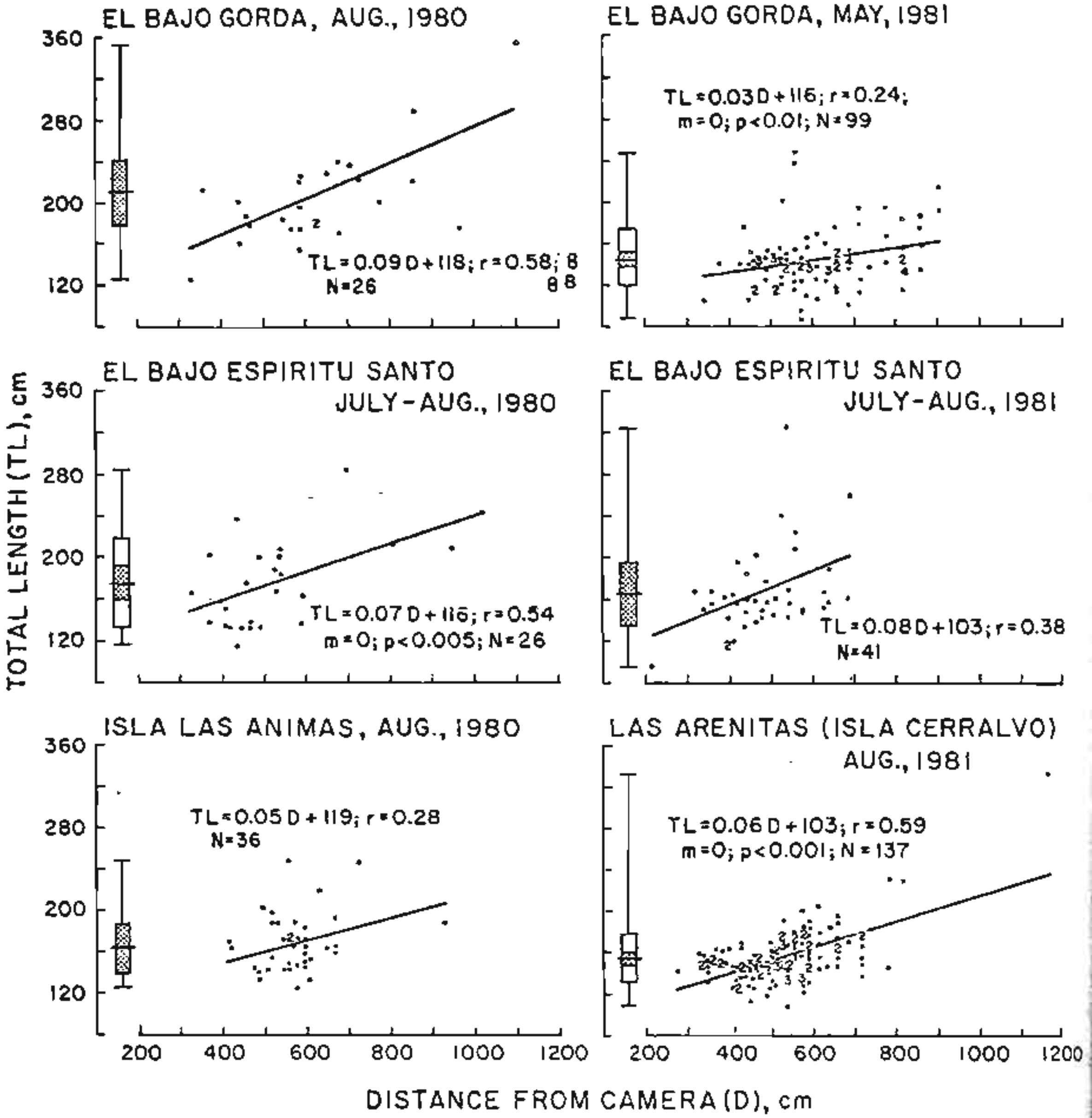

EL BAJO GORDA
MAY, 1981
LAS ARENITAS
AUG., 1981
GROUP SIZE
center marks
1,4 . 8,16
32
64
128
Pooled
16
32
64
128
Pooled
TOTAL LENGTH, cm
80
100
120
140
160
180
200
220
240
260
N=9
(CV=
0.12)
11
(0.14)
8
(0.18)
24
(0.22)
39
(0.18)
91
(0.18)
8
(0.16)
16
(0.20)
55
(0.13)
69
(0.13)
148
(0.14)

the lengths from the 1, 2, and 4 group-size classes as well as the 8 and 16 size classes were pooled. The mean TLs of hammerheads did not differ significantly between the five group size classes (Analysis of Variance, p>0.50). At El Bajo Gorda the mean TLs of hammerheads in five group-size classes also did not differ significantly(Analysis of Variance, p>0.50). The total length CVs did not change greatly with size of the groups, ranging from 0.12 to 0.22 at El Bajo Gorda and 0.13 to 0.20 at Las Arenitas.

School Structure

Differences in the lengths of sharks in the different parts of the schools were often reported (Klimley and Nelson, 1980), yet disagreement existed among observers as to whether larger sharks remained at the top or bottom of the groups. It was believed likely that this segregation was brought about by large or small sharks positioning themselves between the school and the observer. In order to determine if such segregation occurred, TLs of schooling hammerheads were plotted as a function of their distance from the cameraman positioned just outside of the schools (D) (Fig. 8). TL was regressed on D, and the regression equation is included on the plot together with a correlation coefficient (r). For those samples which were normally distributed, the probability that slope m=0 using the Student's t-test was given. Total length increases per 100-cm distances from the

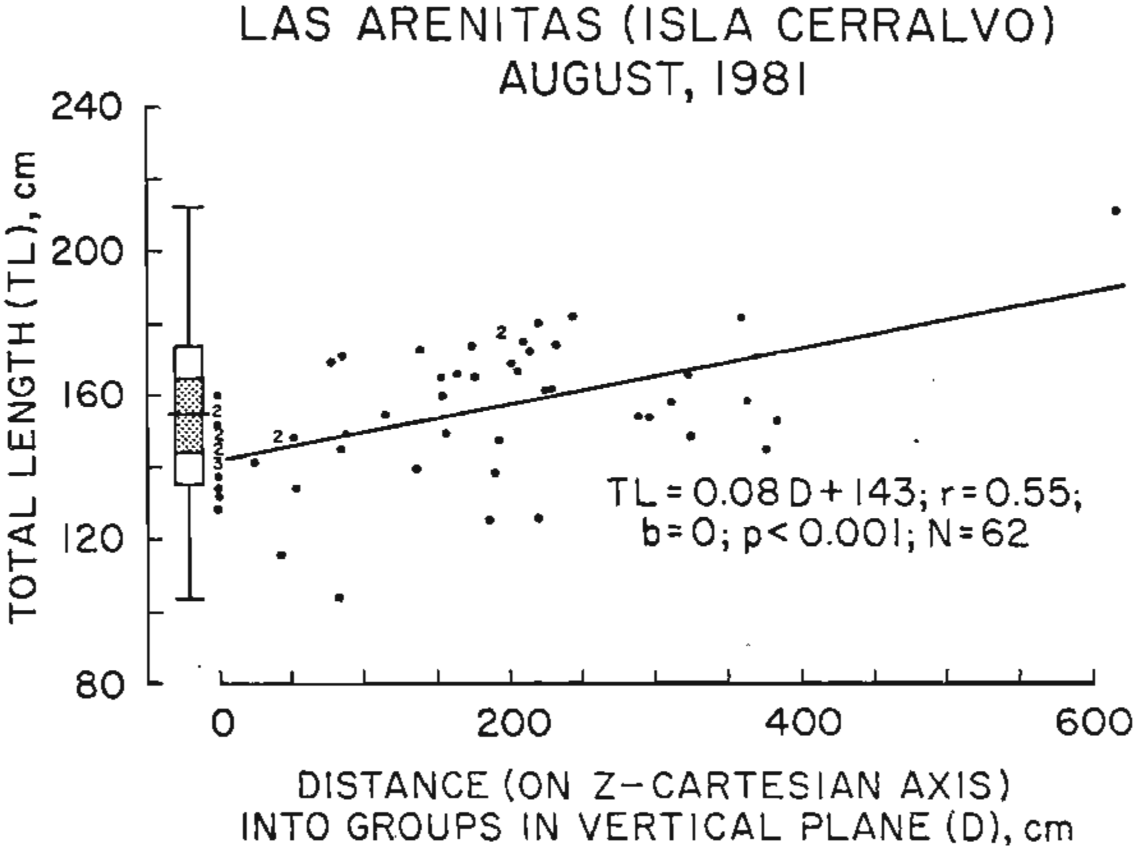
Fig. 8. Total lengths (TL) of schooling hammerheads at different distances from the camera (D) at four study sites in the Gulf of California. For normal distributions the horizontal line to the left of the abcissa indicates mean, stippled bar two standard errors, clear bar one standard deviation to either side of the mean, and the outer horizontal lines the range of the total lengths. For non-normal distributions the horizontal line to the left of the abcissa indicates median, the stippled bar one quartile deviation to either side of the median, and the outer horizontal lines the range of total lengths. Regression lines, equation, correlation coefficient, probability m=0, and N noted.

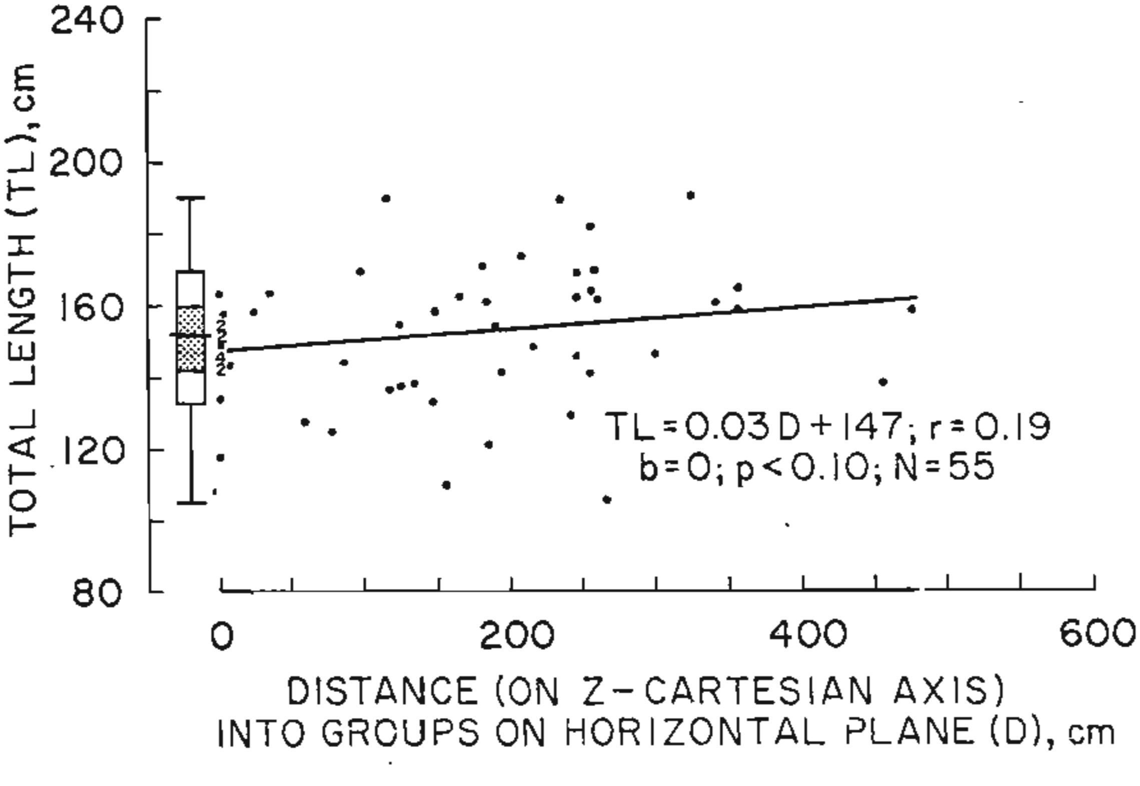

EL BAJO GORDA, AUG., 1980
TL=0.09D+118; r=0.58;
N=26
EL BAJO GORDA, MAY, 1981
TL=0.03D+116; r=0.24;
m=0; p<0.01; N=99
EL BAJO ESPIRITU SANTO
JULY-AUG., 1980
TL=0.07D+116; r=0.54
m=0; p<0.005; N=26
EL BAJO ESPIRITU SANTO
JULY-AUG., 1981
TL=0.08D+103; r=0.38
N=41
ISLA LAS ANIMAS, AUG., 1980
TL=0.05D+119; r=0.28
N=36
LAS ARENITAS (ISLA CERRALVO)
AUG., 1981
TL=0.06D+103; r=0.59
m=0; p<0.001; N=137
TOTAL LENGTH (TL), cm
360
280
200
120
DISTANCE FROM CAMERA (D), cm
200
400
600
800
1000
1200

cameraman ranged from 3 cm at El Bajo Gorda in May 1981 to 9 cm at El Bajo Gorda in August 1980. In all three sites with normally distributed TLs, m differed from 0 in a statistically significant manner. The degree of correlation (r) of TL with D ranged from 0.24 at El Bajo Gorda during May 1981 to 0.59 at Las Arenitas (Isla Cerralvo).

It was later believed possible that the increase in hammerhead sizes at increasing distances might not be only because larger sharks were avoiding the cameraman, but because they might be positioning themselves in the centers or bottoms of the groups through aggressive interactions with other school members. In order to test this possibility TLs were plotted as a function of the sharks' distances into the school in both the vertical and horizontal planes (on the z-axis of a coordinate system with the camera as origin), and these TLs were compared to TLs plotted similarly as a function of distance from the camera. The length sample from Las Arenitas was analyzed in this manner because its large size (N=137) allowed its separation into vertical and horizontal plane subsamples, and the length increase (6 cm per 100 cm from the camera) and degree of correlation (r=0.59) were relatively high (see Fig. 8). These results are plotted in Fig. 9. In the vertical plane (the cameraman photographed school members from above) lengths increased by 8 cm per 100 cm into the group (on the z-axis). This increase probably is based on increases in the size of sharks

Fig. 9. Total lengths (TL) of schooling hammerheads at increasing distances (on z-axis) from the camera (D) in vertical and horizontal planes at Las Arenitas, July and August 1981.


LAS ARENITAS (ISLA CERRALVO)
AUGUST, 1981
TOTAL LENGTH (TL), cm
240
200
160
120
80
0
200
400
600
DISTANCE (ON Z-CARTESIAN AXIS)
INTO GROUPS IN VERTICAL PLANE (D), cm
TL = 0.08 D + 143; r = 0.55;
b = 0; p < 0.001; N = 62


TOTAL LENGTH (TL), cm
240
200
160
120
80
0
200
400
600
DISTANCE (ON Z-CARTESIAN AXIS)
INTO GROUPS ON HORIZONTAL PLANE (D), cm
TL = 0.03 D + 147; r = 0.19
b = 0; p < 0.10; N = 55

in the half of the group's cross-section nearest to the photographer since the schools were so large. However, at times TLs may have been measured for sharks in the distal half of the group's cross-section or outside the group beyond its distant edge. In order to minimize the confounding effect of including these hammerheads in the analysis, those sharks separated from their nearest-neighbor by greater than four body lengths were excluded from the analysis. This necessitated the removal of two sharks of 144 and 333 cm at distances on the z-axis of 1358 and 2133 cm from the analysis on the vertical plane. The length increase was significant ($m=0$, Student's t-test, $p<0.001$) and the correlation was still relatively strong ($r=0.55$). However, in the horizontal plane (the cameraman photographed school members from the side) lengths increased only 3 cm per 100 into the group. Not only was this increase not significant ($m=0$, Student's t-test, $p<0.10$), but also TL was only weakly correlated with D ($r=0.19$). A single shark of 333 cm at a distance of 1340 cm on the z-axis was eliminated from the analysis on the horizontal plane. This indicated that at Las Arenitas the schools of hammerheads were stratified vertically with larger sharks toward the bottom.

When the same lengths were plotted as a function of distance from the camera in both the vertical and horizontal planes, the size increases were significant both in the vertical plane ($m=0$, Student's t-test, $p<0.001$) and in the horizontal plane (m=0, Student's t-test, $p<0.05$) (Fig. 10). However, the size increase with increasing distance from the camera on the vertical plane of 6 cm per 100 cm was less than that on the z-axis on the vertical plane of 8 cm per 100 cm (see Fig. 9). This indicates that the size segregation was not in response to the presence of the cameraman, but in response hammerheads within the school. The small increase in length with increasing distance from the camera of 3 cm per 100 cm was similar to that on the horizontal plane with increasing distance into the schools on the z-axis.

Not only were there larger sharks at the bottoms of groups at Las Arenitas, but these sharks were spaced farther apart than the smaller hammerheads at the tops. The distances of schooling hammerheads to their nearest-neighbors (ID) were plotted in relation to their distance into the schools (D) both on the vertical and horizontal planes (Fig. 11). As is the case with the lengths, the increase in nearest-neighbor, individual distances of 18 cm per 100 cm in the vertical plane was greater than that of 13 cm per 100 cm in the horizontal plane. The increase in individual distances would be higher in both planes if the school's outermost sharks, nearest to the camerman, were eliminated from the analysis. It is possible that many of these sharks were either arriving or departing, and for this reason apart from the groups. Thus, the large IDs at the distance of 0 m would not be representative of school spacing. This is the

Fig. 10. Total lengths (TL) of schooling hammerheads at increasing distances from the camera (D) in vertical and horizontal planes at Las Arenitas, July and August 1981.

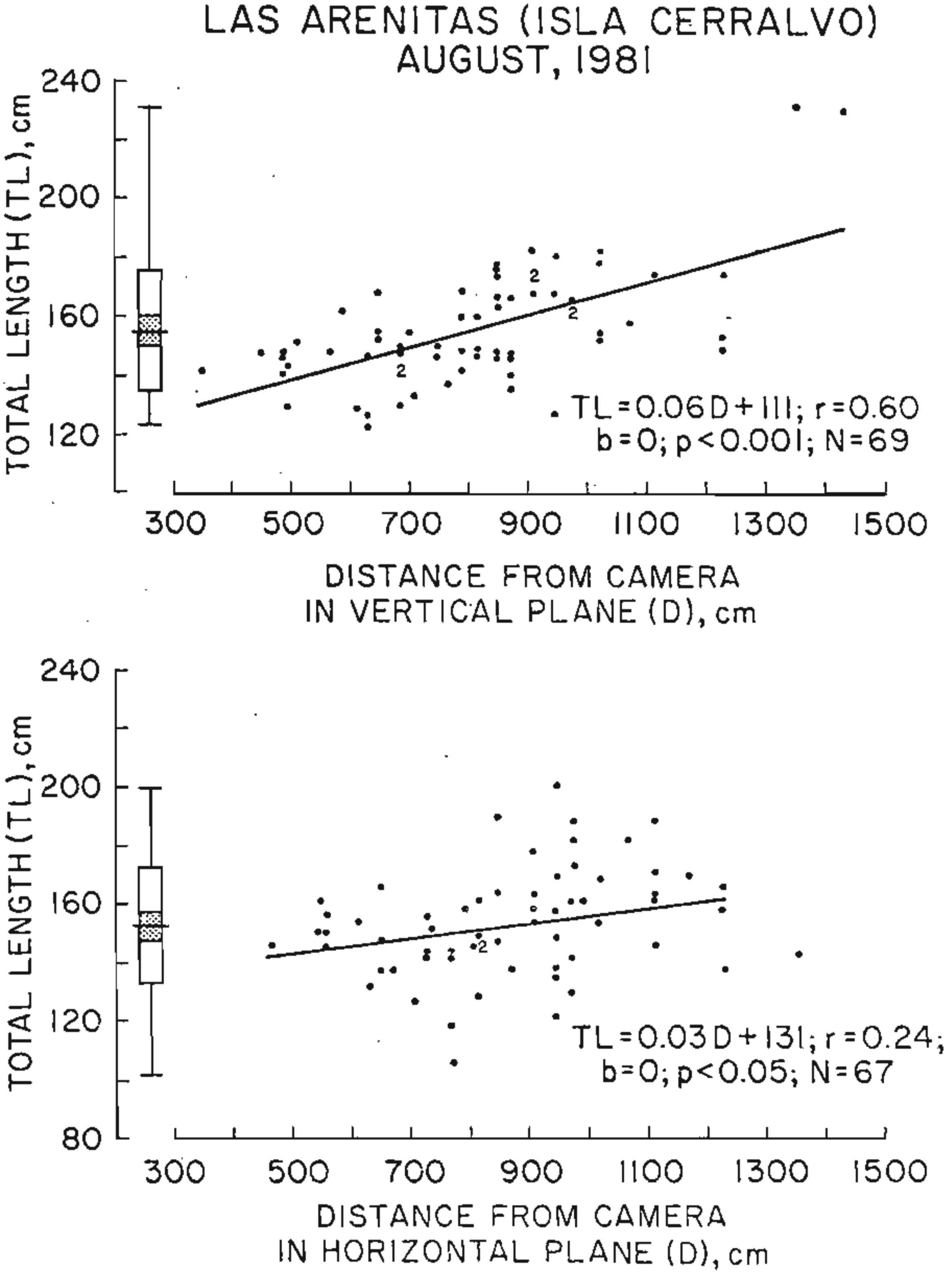
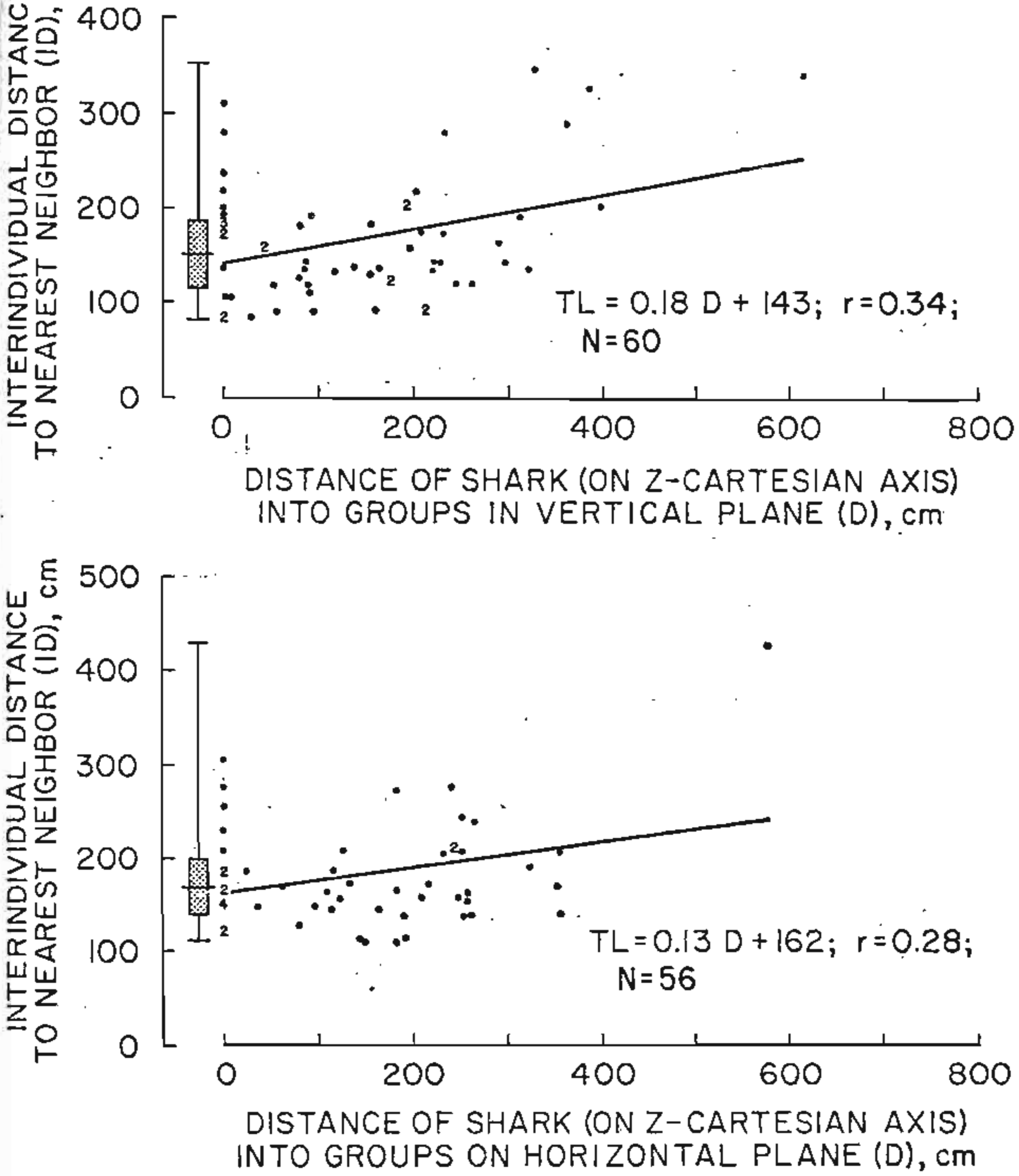

LAS ARENITAS (ISLA CERRALVO)
AUGUST, 1981
TOTAL LENGTH (TL), cm
240
200
160
120
300
500
700
900
1100
1300
1500
DISTANCE FROM CAMERA IN VERTICAL PLANE (D), cm
TL=0.06D+111; r=0.60
b=0; p<0.001; N=69
2
TOTAL LENGTH (TL), cm
240
200
160
120
80
300
500
700
900
1100
1300
1500
DISTANCE FROM CAMERA IN HORIZONTAL PLANE (D), cm
TL=0.03D+131; r=0.24;
b=0; p<0.05; N=67
2

Fig. 11. Interindividual distances to nearest-neighbors (ID) of schooling hammerheads at distances (on z-axis) into group (D) in vertical and horizontal planes at Las Arenitas, July and August 1981.


LAS ARENITAS (ISLA CERRALVO)
AUGUST, 1981

reason, I believe, for the relatively weak correlations both in the vertical (r=0.34) and the horizontal planes (r=0.28).

Total length and ID in relation to distance into the groups were also were also examined for the August 1980 sample at El Bajo Gorda (see Figs. 8 and 9 in chapter 2) and the July and August 1981 sample at El Bajo Espiritu Santo. These measures were determined for sharks at these study sites because their TLs increased relatively substantially with D for the former (m=9 cm) and latter location (m=8 cm) (see Fig. 8), but also the correlation of TL with D was strong at the former (r=0.58) and latter locations (r=0.38). The smallness of these samples precluded their division into separate vertical and horizontal plane subsamples. At El Bajo Gorda lengths increased by 12 cm per 100 cm into the schools. The correlation of length to distance on the z-axis was strong (r=0.49). Although the 22 cm increase in ID was large, a correlation between ID and D did not exist (r=0). At El Bajo Espiritu the TL increased 10 cm per 100 cm. However, the correlation between TL and D was relatively weak (r=0.40.2). The IDs, on the other hand, decreased by 3 cm per 100 cm into the schools, and this decrease was not statistically significant (m=0, Student's t-test, p<0.50). At El Bajo Gorda a correlation between ID and D did not exist.

The majority of hammerheads in the schools were females. Male to female ratios varied from 1:1.6 at Las Arenitas during July and August 1979 to greater than 1:34 at El Bajo Gorda during May 1981 (Table 1). Only at the former location did the sex ratio not differ significantly from a 1:1 ratio (Chi-square Test, p>0.05). The proportion of males to females varied between locations. The ratios at Isla Las Animas, El Bajo Espiritu Santo, and Las Arenitas during July and August 1979 differed significantly (Chi-square, p<0.05). The sex ratios at Isla Las Animas and El Bajo Espiritu Santo during July and and August also differed significantly (Chi-square Test, Yate's Correction, p<0.05). And finally, the sex ratio between El Bajo Espiritu Santo and Las Arenitas during July and August 1981 differed (Chi-square Test, p<0.001). It was not possible to determine whether these ratios changed seasonally. Although the sex ratio at El Bajo Gorda during May 1981 was dominated by females with less than one male to thirty-four males censused, the August 1980 sample was too small to make a useful comparison. The proportion of males to females differed significantly (Chi-square Test, p<0.025) at Las Arenitas between the 1979 and 1981, but did not differ at Las Animas (Chi-square Test, p<0.05) and El Bajo Espiritu Santo (Chi-square Test, p<0.05) between 1979, 1980, and 1981. A correlation of sex ratio and latitude as might have been expected if males joined with the females only when water temperatures increased (see Springer, 1960, for discussion of such thermally triggered movements). This was not seen during July and August 1979: the highest

Table 1. Sex ratios with number of sexual identifications (in parentheses) for study sites throughout the Gulf of California at different times of the year.

	Study Locations				
Year Season	Isla Las Animas	El Bajo Esp. Sto.	Las Arenitas	El Bajo Gorda	Pooled
1979** Jul.-Aug.	1:3.1(65)	1:3.8(84)	1:1.6(63)		1:2.7(212)*
1980 Jul.-Aug.	1:21.0(22)	1:4.3(58)			1:5.5(90)
1981					
May				<1:34(34)	<1:34(34)
Jul.-Aug.		1:3.9(82)	1:7.3(57)		1:6.1(139)

**sex ratios from Klimley and Nelson, 1981

*number of sexually identified scalloped hammerheads in parentheses sex ratio was at El Bajo Espiritu Santo midway between the more northerly Isla Las Animas and more southerly Las Arenitas.

It is possible that juvenile hammerheads form sexually segregated groups inshore. On three occasions inshore gill net sets captured numerous juvenile male hammerheads. On 11 November 1978 thirteen hammerheads ranging from 96 to 109 cm and a larger individual of 160 cm were caught. Eleven were males. On 7 February 1981 eight juvenile hammerheads ranging in length from 100 to 129 cm were caught close to shore at Isla Pardito in less than 20 m of water over a sandy bottom. Seven were males. On 8 May 1981 16 juvenile hammerheads ranging from 79 to 126 cm were caught close to shore at Punta Colorado in less than 3 m of water over a sandy bottom. Fifteen were males. Sharks within these groups varied little in length. Excluding the 160 cm hammerhead which probably was not caught in the net at the same time as the smaller hammerheads, the length CV of the November catch was 0.04. The CVs for the February and May 1981 catches were 0.09 and 0.11, respectively.

It was not possible to determine whether a relationship existed between the size and sex of sharks within the groups. Determining the sex of sharks from the stereophotographs was difficult because the claspers, used in sexual identification, were most often not visible. For this reason, it was not possible to determine whether sexual segregation occurred within the schools. Of particular interest was whether the observed size segregation could be brought about through aggressive encounters between members of one sex for access to members of the other sex. This question will be addressed in the future using videotapes of hammerhead behavior. On the other hand, it is possible here to consider the the relationship between the sizes of sharks and the sex ratios at different locations. This was done by considering the stereophotographically determined size medians with sex ratios determined from direct observations during free dives and later viewing of video samples. Those hammerhead schools most dominated by females such as at El Bajo Gorda during May 1981 (male:female, <1:34), Isla Las Animas during July and August 1980 (1:21.0), and Las Arenitas during July and August 1981 (1:7.3) were composed of smaller sharks with medians of 141, 162, and 153 cm, respectively. Schools of larger sharks with estimated means of 180 and 170 cm were characterized by lower ratios of females to males such as the ratios of 1:3.8 and 1:3.1 at El Bajo Espiritu Santo and Isla Las Animas during July and August 1979.

School Dynamics

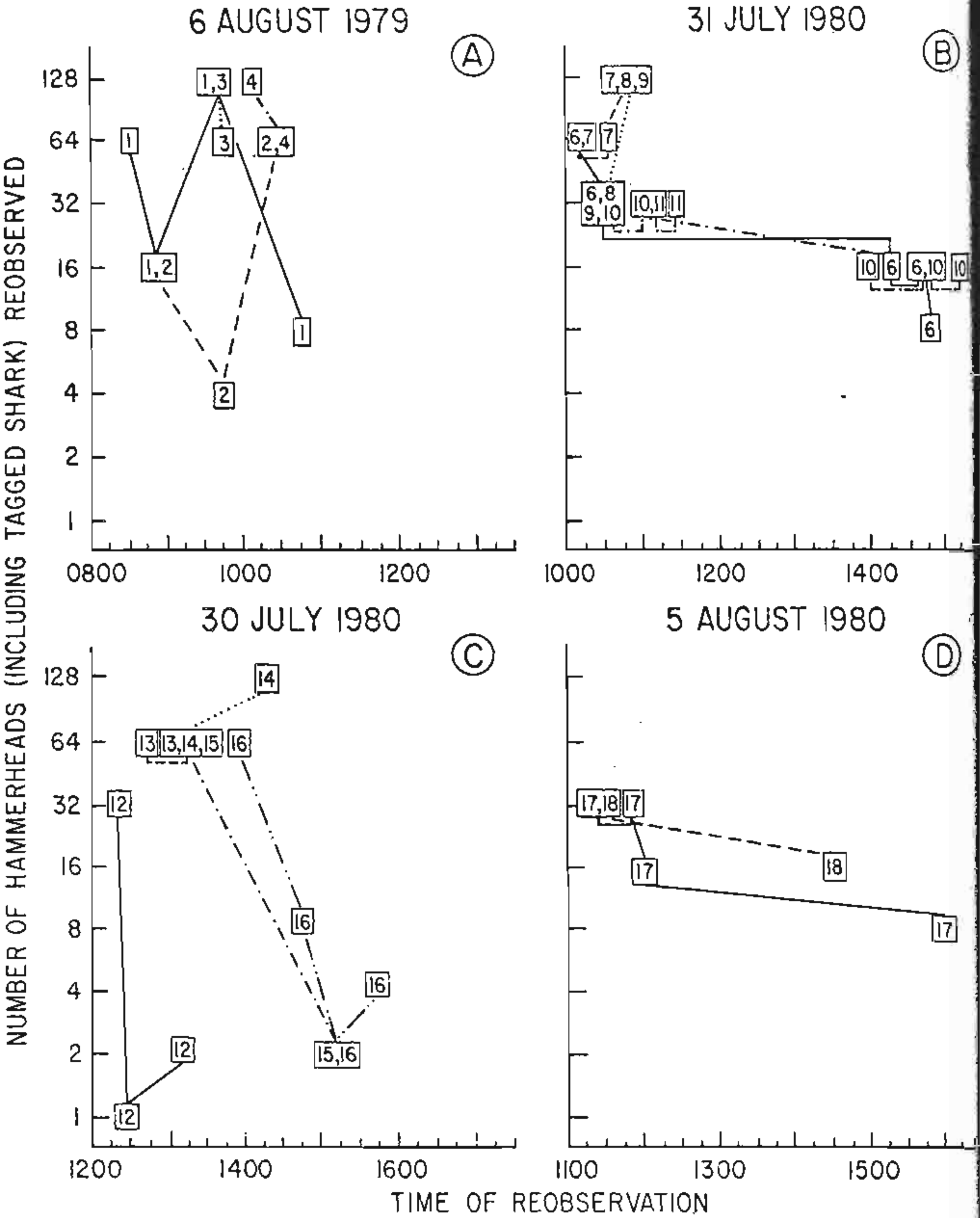
In order to test whether the groups were dynamic in their composition, sharks accompanying tagged sharks were recorded for a single day in Aug. 1979 (A), two days in July

(B and C), and one day in Aug. 1980 (D). The sizes of the groups in which the tagged sharks were swimming were plotted as a function of the time each tagged shark was reobserved (Fig. 12). If more than a single tagged shark was seen ✓ within a school at the same time, the tag numbers were combined within a single box on the figure. Changes in the numbers of sharks accompanying a specific tagged shark can be seen by following the lines (solid, dashed, dotted, etc.) connecting squares with reobservations of that tagged shark. Group sizes changed substantially over short periods of time in the former three days and remained relatively stable on the fourth day. For example, marked shark No. 1 was reobserved on four occasions during a period of 135 min on the morning of 6 Aug. 1979 with successive groups in size classes of 64, 16, 128, and 8 sharks. Such dynamics were also evident to an observer who remained for 120 min above one large group, which varied over that time period from 50 to 225 sharks (Klimley and Nelson, 1981). However, at other times group size could be relatively stable. For example, marked shark No. 17 was reobserved on four occasions during 365 min on 5 Aug. 1980 within groups of successive size classes of 32, 32, 16, and 16 sharks.

DISCUSSION

School Polarity

Fig. 12. Changes in the numbers of sharks accompanying 18 tagged sharks over short periods of time during 6 August 1979, 30 and 31 July, and 5 August 1980 at El Bajo Espiritu Santo in the Gulf of California. Numbers in boxes identify marked sharks. Reobservations of the same shark are connected by solid, dashed, and/or dotted lines.


6 AUGUST 1979
(A)
31 JULY 1980
(B)
30 JULY 1980
(C)
5 AUGUST 1980
(D)
NUMBER OF HAMMERHEADS (INCLUDING TAGGED SHARK) REOBSERVED
TIME OF REOBSERVATION
128
64
32
16
8
4
2
1
0800
1000
1200
1400
1100
1300
1500
1600
1,3
4
1
3
2,4
1,2
2
7,8,9
6,7
7
6,8
9,10
10,11
11
10
6
6,10
14
13
13,14,15
16
12
15,16
17,18
17
18

Polarized swimming characterized by common directional bearings, small and uniform interindividual distances, and simultaneous changes in direction has been described only qualitatively in a few other sharks. Matthews (1950) noted that small groups of basking sharks swam at times in tandem on the surface where individuals fed upon plankton. Approximately 450 individuals of an unidentified species of shark, pictured along ca. 300 m of coastline in Laguna Oja de Libre, were swimming in the same longshore direction (p. 254, Kenny, 1968). Schools of gray reef sharks are formed of as many as 50 parallel swimming members (Nelson and Johnson, 1980). Members of a large school of cownose rays in a photograph (Plate 1 and 2, Clarke, 1963) were parallel in their orientations. The greatest angle of deviation of a school member from the common school direction was 42 deg. The mean angular deviation of 23.4 of scalloped hammerhead school members is similar to those of the few bony fish species for which this measure has been calculated such as the 36 deg for the northern anchovy (*Engraulis mordax*), 33 deg for the topsmelt (*Atherinops affinis*), and 22 deg for the jack mackerel (*Trachurus symmetricus*) (Van Olst and Hunter, 1970).

There is little comparative information with which to compare the 1.0, 1.1, and 1.5 BL interindividual distances at El Bajo Gorda, El Bajo Espiritu Santo, and Las Arenitas except to the 1.0 to 3.0 BL distances between individuals of an unidentified species in Ojo de Libre (Kenny, 1968) and those of <0.5 to several BLs in the gray reef shark (Nelson and Johnson, 1980). The nearest-neighbor, interindividual distances between school members of cownose rays pictured in Clark (1963) ranged from 0.5 to 1.0 BL. These distance estimates were two-dimensional. The three-dimensional hammerhead individual distances lay between the two-dimensional individual distance range of 0.7 to 2.5 BLs of a silverside (Menidia sp.) (Shaw, 1960), 1.3 BLs for Tilapia (Dambach, 1963), larger than one BL for the Pacific bonito (Sarda chiliensis) (Magnuson and Prescott, 1966), one BL for the topsmelt (Atherinops affinis) (Van Olst and Hunter, 1970), 0.8 BL for the Pacific herring (Clupea harengus) and the pollock (Pollachius virens), and 0.6 BL for the Atlantic cod (Gadus morhua) (Pitcher and Partridge, 1979), and 0.7 BL for the coho salmon (Oncorhynchus kitsutch) (Dill et al., 1981). Pitcher and Partridge concluded from their three-dimensional analysis of the nearest-neighbor, interindividual distances of three species and the results of other investigators that one body length was a conservative upper limit of such distances although larger distances could occasionally be found in loosely organized schools. Graves (1977) measured the two-dimensional distances between school members of the northern anchovy from photographs taken in the field to be 1.2 BLs, and this was somewhat larger than those IDs reported in the laboratory. He suggested that the confinement of schooling fishes in laboratory tanks such as in the prior reported studies caused the fish to form more compact schools.

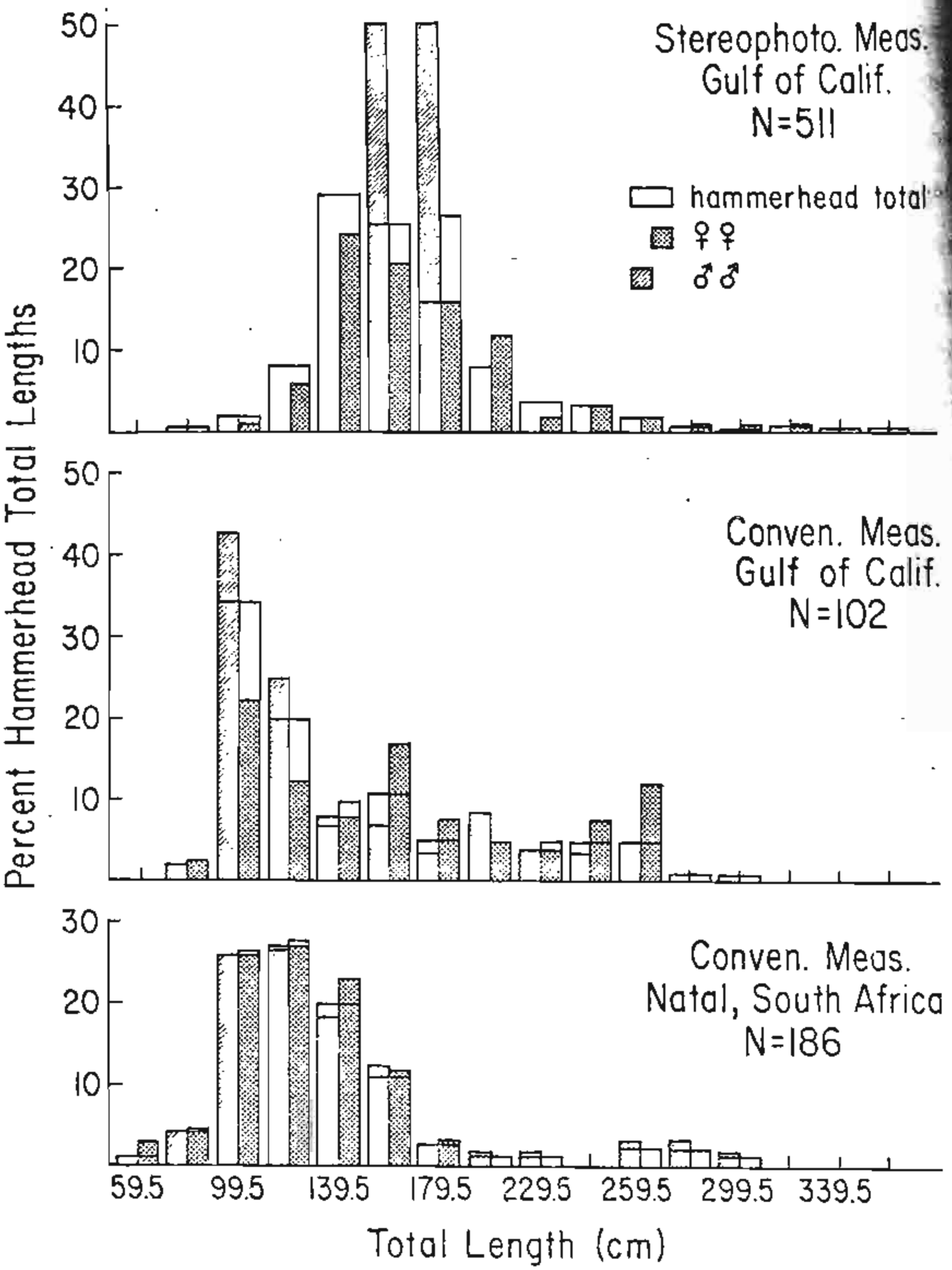
The degree of cubic structure has not been described for elasmobranch schools; and furthermore, it has been measured for only a few bony fishes. The mean ratios of the distance to the second nearest-neighbor to the distance to the first nearest-neighbor of 1.4 at El Bajo Espiritu Santo and Las Arenitas was intermediate between the 1.2 and 1.3 coefficients of the more orderly schooling Atlantic herring and the pollock, and the 1.5 coefficient of the less orderly schooling Atlantic cod reported by Partridge _et al._ (1980). The hammerheads at El Bajo Gorda were in a random configuration with a coefficient greater than 1.6.

School Composition

The sizes of free-swimming hammerhead sharks were very different from those caught by long line and gill net both in the Gulf of California and off the coast of South Africa. Stereophotographically determined lengths of free-swimming sharks from all study sites were pooled. The conventionally measured (by tape measure) sharks in the Gulf of California from several locations (see Juncalito, Isla Pardito, Las Salinas, and San Jose del Cabo in Fig. 2) adjacent to the offshore study sites. Fishing was carried out with either long lines or gill nets over primarily sandy bottoms in depths of from 4 to 320 m. Frequencies of lengths are expressed as percent of the total number of sharks in each sample to facilitate between sample comparisons (Fig. 13). Stereophotographically measured sharks were larger than those measured from catches. The 139.5 cm length mode of the stereophotographically measured sharks was higher than the 99.5 cm mode for those captured in the Gulf of California and the 119.5 cm mode of those captured off the coast of Durban, South Africa. Furthermore, the intermediate size classes of the stereophotographically measured sharks from 139.5 to 179.5 cm were larger than indicated by catches of fishermen and the smaller size classes of 79.5 to 119.5 cm were smaller. The presence of smaller sharks in the catches of fishermen than measured *in vivo* was probably due to differences in the sampling locations. The free-swimming sharks were measured adjacent to submarine pinnacles and offshore islands bordering the pelagic environment, and the sharks measured from fishermen's catches were caught both in bays and dropoffs into deep water.

The scalloped hammerheads appear to segregate by size with smaller individuals inshore and larger individuals offshore. In support of this conclusion, scalloped hammerheads caught in the Gulf of California in water less than 20 m in depth had a median length of 102.0 cm (N=26) while those caught in water deeper than 20 m had a median of 156.5 cm (N=75). When sharks reached the size classes of

Fig. 13. Percentages of lengths in different classes of scalloped hammerheads either measured stereophotographically (top) or conventionally (middle) from the Gulf of California and lengths measured conventionally from off the coast of Natal, South Africa (bottom). Cross-hatched bars are male, stippled bars female, and clear bars pooled frequencies.

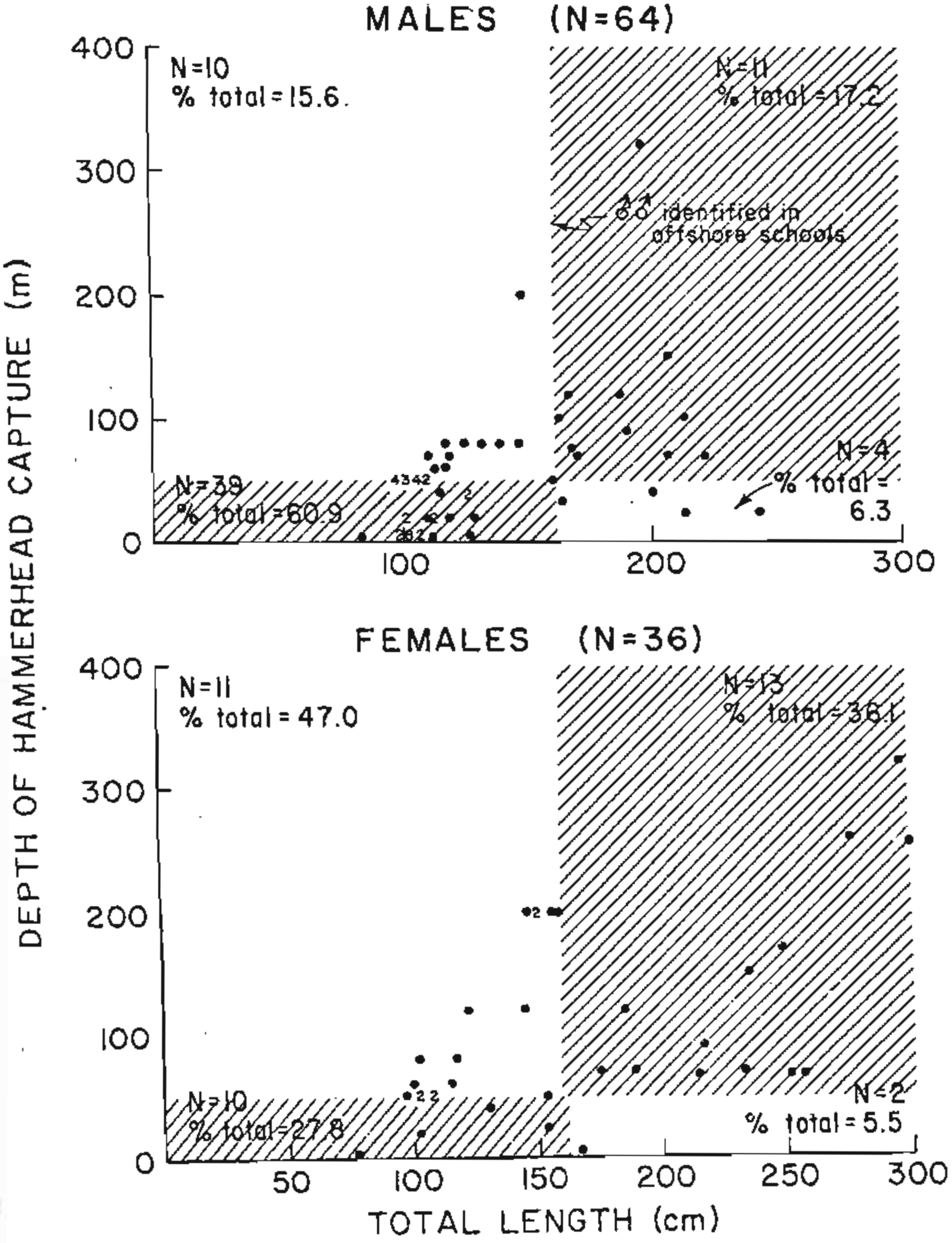

Stereophoto. Meas.
Gulf of Calif.
N=511
hammerhead total
♀♀
♂♂
Conven. Meas.
Gulf of Calif.
N=102
Conven. Meas.
Natal, South Africa
N=186
Percent Hammerhead Total Lengths
50
40
30
20
10
59.5
99.5
139.5
179.5
229.5
259.5
299.5
339.5
Total Length (cm)

from 99.5 to 139.5 cm, they appeared to move offshore and enter the schools at the dropoff into pelagic water. It is also possible that these differences were in part a result of the different sampling methods. Long line sets along the dropoffs might not capture sharks grouping there when not feeding during the day. Perhaps this explains the higher percentages of larger sharks in the sample of free-swimming hammerhead shark lengths.

Geographical segregation of the scalloped hammerhead by size was also found by Clarke (1971). He captured by long line and gill net 1566 pups ranging from 40 to 90 cm with a mean of 56 cm in Kaneohe Bay, Hawaii while at the same time capturing only 35 adult sharks ranging from 195 to 272 cm. Since the large males had swollen claspers and copious spermatazoa, and the females examined by him and others had mating scars or full-term pups, he concluded that the adults only temporarily moved into the bay to mate and give birth. Although schools of hammerheads have been encountered along the dropoff into deep water at Oahu by divers (Leighton, Taylor, Waikiki Aquarium, pers. comm.), few hammerheads have been caught there. Of the 1727 sharks caught at depths largely between 30 and 60 m on long line sets during the Hawaii Cooperative Shark Research and Control Program, only 11 scalloped hammerheads were captured (Clarke, 1971). Size and sex was obtained for only eight. They consisted of a 309 cm mature and 214 cm immature female and three 210-260 cm mature males and three 82 to 138 cm immature males. The three immature males and an additional 129 cm male caught 275 m during an exploratory fishing project were the only intermediate sized hammerheads taken. The depths of capture of these sharks, and their consequent absence from bay catches, led Clarke to conclude that scalloped hammerhead made an ontogenetic movement from the nearshore to the pelagic environment where they remained throughout their adulthood at depths below 200 m except for brief movements inshore to mate and give birth. This was based on the presence of beaks of mesopelagic cephalopods in the stomachs of adults. On the other hand, scalloped hammerheads are caught throughout the year on floating long lines at depths of 15 to 30 m in water less than 200 m deep in the southwestern waters off Japan (Taniuchi, 1974).

The disproportionate numbers of females to males in the schools along the dropoffs was probably because males left the inshore habitat prior to females. Hammerhead pups are often caught by fishermen in the shallow bay of La Paz. Both sexes are probably caught in equal numbers as is so in Kaneohe Bay, Hawaii (Clarke, 1971). The 1566 hammerhead pups ranging from 39.5 to 89.5 cm caught in Kaneohe Bay were divided relatively equally into 769 males and 797 females. In addition, approximately equal numbers of male and female hammerheads in the small 79.5 cm size class were caught by fishermen both in the Gulf of California and off Durban, South Africa (see Fig. 13). Correlated with the presence of females in the offshore schools in the Gulf of California in the size classes of 99.5 to 139.5 cm was the disapearance of females from the primarily inshore catches in the Gulf of California. It is probable that only females were moving offshore in this size range. The number of females equaled that of males only by the 159.5 cm size class for both catch samples while free-swimming males were first identified in the stereophotographic sample in this size class. Indicative of the presence of only larger males in the schools was the correlation of smaller length medians of 141.0 cm at El Bajo Gorda during spring 1981 and 152.5 cm at Las Arenitas during summer 1981 with female dominated sex ratios of <1:34.0 and 1:7.3, respectively. The temporal difference between females and males in their offshore migrations was further supported by plotting depth of capture as a function of hammerhead total length (Fig. 14). Smaller females than males were caught in deeper water. The scatterplot was divided into quadrats based on hammerhead size ($\leq$ and >160 cm: the size at which males first were observed free-swimming within schools) and depth ($\leq$ and > 50 m: an arbitrary inshore-offshore boundary). Only 15.6 percent of the small males were caught offshore in contrast to 47.0 percent of the small females. Only 27.8 percent of the small females were captured inshore in contrast to 60.9 percent of the small males. This difference in depth preference between females and males was statistically significant (Chi-Square, $p<0.01$).

Fig. 14. Capture depths of male (above) and female (below) hammerheads from the Gulf of California as a function of their total lengths. Plot arbitrarily divided into quadrats with the numbers and percentages included in the upper lefthand or righthand corners of the quadrats.


MALES (N=64)
N=10
% total=15.6
N=11
% total=17.2
♂♂ identified in offshore schools
N=39
% total=60.9
N=4
% total=
6.3
4342
2
2
302
400
300
200
100
0
100
200
300
FEMALES (N=36)
N=11
% total=47.0
N=13
% total=36.1
N=10
% total=27.8
N=2
% total=5.5
2
22
400
300
200
100
0
50
100
150
200
250
300
DEPTH OF HAMMERHEAD CAPTURE (m)
TOTAL LENGTH (cm)

Fewer large males (17.2 percent) than females (36.1 percent) were caught offshore, however, this was not reflected in a greater percentage of large males inshore. Clarke (1971) was not aware of the intermediate and large sized scalloped hammerheads which have since been observed to school along the Hawaiian dropoff (Taylor, pers. comm.). The reason why so few hammerheads were caught in from 30 to 90 m on long line sets reported in the Hawaiian Cooperative Research and Control Program is probably that the hammerheads foraged offshore on mesolpelagic cephalopods yet remained along the dropoff in schools in an inactive refuging state in the day (see Chapter 5).

Although there sometimes were statistically significent differences between mean sizes of sharks from different schools indicating a tendency toward segregation by size, the relatively high CVs for the schools was notable. These high CVs countered the usual scenario of size segregation described for sharks. Temporal differences in sizes and sex ratios were described for Squalus acanthias (Ford, 1921). Four distinct social groupings were evident: 1) small immature males and females, 2)medium-sized sharks, mostly immature females, 3) medium-sized mature males, and 4) large mature females, mostly in pregnant condition. McLaughlan and O'Gower (1971) noted a predominance of females in groups of bullhead sharks in rocky caves in a ratio of 5.7:1. They suggested on the basis of the difference between the group ratios and offshore catch ratios that males remained generally in deep water and visited inshore only infrequently. Nelson and Johnson (1980) noted that first-year juvenile gray reef sharks schooled in shallower water in Avatoru Lagoon than adults. The schooling juveniles could be seen from the surface in clear water while the adults remained farther back in the lagoon deeper in more turbid water. The juveniles (pictured on p. 493, Nelson and Johnson, 1980) were estimated to be a meter in length and were very uniform in size. The unidentified sharks photographed along the coast in Laguna Ojo de Libre (Kenny, 1968) also possessed remarkably similar sizes as well as the cownose rays photographed in Big Pass, Sarasota (Clark, 1963). Clarke (1971) suggested that pups of the scalloped hammerhead aggregate or school from his observations of sections of his long line. Schools of larger juveniles (80-120 cm) have been observed swimming in an undirected manner on the sea surface off Natal, South Africa (Bass _et al._, 1975b). Olson (1954) stated that the habit of the school shark to congregate offshore in schools of predominantly one sex with a relatively small range of sizes was responsible for its common name. Springer (1967) concluded in his review of the social organization of shark populations that many species of sharks formed groups made up of members of nearly the same size. Clark (1963) reported a fisherman caught ca. 700 similarly sized bonnethead sharks, _Sphyrna tiburo_ of from 2 to 3 feet in length off Sarasota, Florida.

The social organization of the scalloped hammerhead is more complex than the segregation into populations of subadults of both sexes, sexually mature males, and sexually mature females occupying different habitats at different times of the year as expoused for most sharks by Springer (1967). Springer (1960) based his belief that adult males remained offshore and only moved inshore to mate with females briefly on the prevalence of females in shark catches. McLaughlan and O'Gower (1971) also believed males remained offshore and moved inshore briefly to mate at certain times of the year. Neither authors provided evidence that males inhabited deeper water. The geographical distribution of the scalloped hammerhead may be more similar to that of the marbled catshark. From the length frequency distributions of male and female sharks of this species, a smaller number of females in relation to males at the shallower 200 fathom depths and conversely a larger number of females than males in the intermediate depths of 250 to 275 fathoms may reflect a movement of smaller females to these intermediate depths (p. 146, Bullis, 1967). For the scalloped hammerhead, I believe that neonate (<80 cm in length) probably school with equal numbers of males and females in bays and along shore in the Gulf of California. Schools may become composed primarily of males (80-110 cm) as females move offshore to join schools along the dropoffs. It is not known whether these females move as schools or singly. It is possible that the schools of hammerheads dominated by small females at El Bajo Gorda during May 1981 were comprised of females which recently had left their inshore habitat. However, offshore schools are generally not size segregated and consist of many smaller sized hammerheads and fewer larger individuals.

The high amount of size variation among individual scalloped hammerheads is unusual when compared to that within schools of bony fishes. Coefficients of variation from catch measurements are generally smaller such as 0.01 for the bigeye anchovy (Anchoa lamprotaenia) (calculated by author, p. 12, Breder, 1951), 0.04 for the chub mackerel (Scomber japonicus) (calc. by author, p. 76, Breder, 1951), 0.03 for the yellowfin tuna, and 0.02 for the skipjack tuna (Euthynnus pelamis) (calc. by author, p. 472, Broadhead and Orange, 1960), however, occasionally coefficients of variation can be as high as 0.26 for the yellowfin tuna, 0.09 for the skipjack tuna (calc. by author, p. 472, Broadhead and Orange, 1960), and 0.20 for Sardina pilchardus (Muzinic, 1977).

Several explanations have been given for the uniformity in the sizes of individuals. In elasmobranchs this has been attributed to lack of aggression between school members or disparities in swimming performance, and has been imputed to optimize foraging success and inhibit cannabalism (Springer, 1967). Breder (1951) also has noted the absence of aggression within stronger schooling bony fish species, and a more structured "peck order" in loosely schooling species.

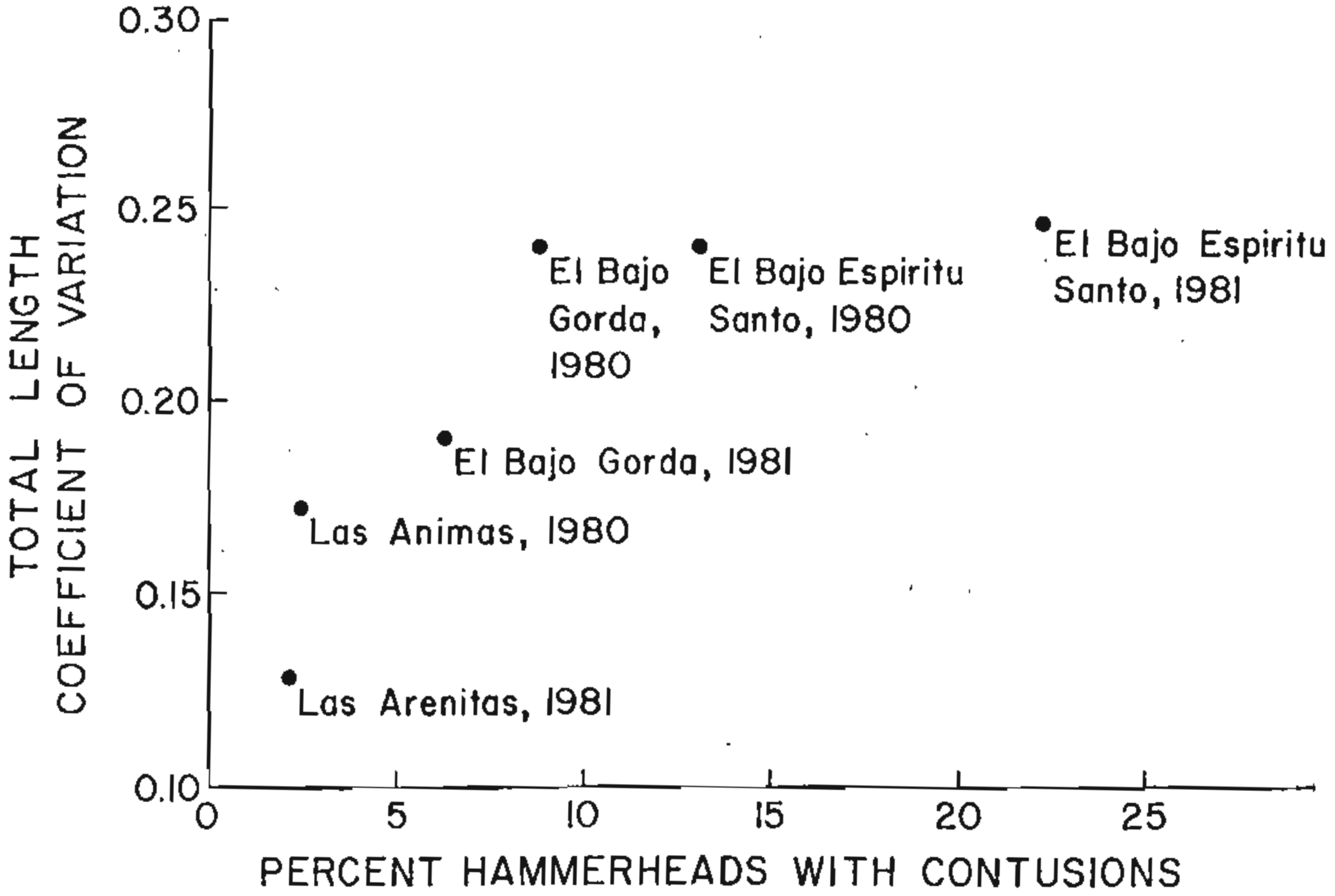
Possibly the large variation in size arises initially from a constant influx of sharks, some of which may be members of size-segregated schools. At El Bajo Espiritu Santo a substantial amount of emigration was recorded with population size remaining the same, implying considerable immigration (chapter 4). The possibility of migratory or dispersal movements was also supported by the occasional observation of hammerheads moving slowly at the surface over deep water between islands. Some of the individual schools photographed at Las Arenitas differed from each other statistically in their size composition, indicating a weak tendency toward segregation by size (see Fig. 4). Breder (1951) and Muzinic (1977) suggested that the mixing of schools of similarly sized individuals form schools with large size variation. It is probable that members of such schools would not forage as a group at night since the size disparities between individuals would be reflected in differences in swimming performance, preventing the optimal school cohesiveness when foraging. It is more likely that the sharks are remaining together only during the inactive phase of their diel activity cycle. At this time the smaller sharks could easily compensate for their poorer swimming abilities by swimming slightly more rapidly. If these sharks were to forage together, the groups would have to break up into smaller schools of more similarly sized individuals.

Positively correlated with the length variation among the schools was the frequency of abrasions, primarily on females (Fig. 15). These were small, recently inflicted, whitish patches (estimated diameter 4 to 8 cm) or partially healed black patches. These were generally located lateral or anterior to the first dorsal fin (see Fig. 5, p. 70, Klimley, 1981). Scarred individuals were predominantly females (23 out of 27 identified at El Bajo Espiritu Santo during the summer of 1979). These scars were believed to be inflicted by Hit, an aggressive behavior directed generally at other females. Captive small bonnetheads were observed to accelerate from a position just above and behind a large female and scrape her dorsum just between the first and second dorsal fins with their heads, leaving similar contusions (Myrberg and Gruber, 1974). The hits were generally directed by resident bonnetheads at newcomers to the relatively stable population. The positive correlation between length variation and frequency of scarring further suggested their infliction in female-female aggressive interactions.

School Structure

At Las Arenitas schools were stratified vertically

Fig. 15. Variation (CV) in total lengths of sharks at different study sites in the Gulf of California during 1980 and 1981 in relation to the frequency of contusions on the sharks.


0.30
0.25
0.20
0.15
0.10
0
5
10
15
20
25
TOTAL LENGTH
COEFFICIENT OF VARIATION
PERCENT HAMMERHEADS WITH CONTUSIONS
El Bajo Gorda, 1980
El Bajo Espiritu Santo, 1980
El Bajo Espiritu Santo, 1981
El Bajo Gorda, 1981
Las Animas, 1980
Las Arenitas, 1981

with larger sharks toward the bottom of the groups. Although such stratification has not been described for cartilaginous fishes, it has been described for two bony fishes, Engraulus japonicus (Kimura, 1934) and the Atlantic herring (Clupeia harengus) (Schafer 1955). Kimura towed a bait net with a 3.6 m opening height, separated into six 0.6 m horizontal compartments, through a school of E. japonicus and compared means of the resulting size frequency distributions and densities of the captured fish. He found that the smaller fish were distributed more densely in the upper layers, and the larger fish were conversely distributed less densely in the lower layers. Schafer found that in an aquarium young herring schooled at the surface above larger older herring.

Several possible mechanisms exist for stratification within a school. Differences in swimming performance between differently sized sharks is not favored. The hammerhead groups usually swam slowly while in the vicinity of the seamount. The smaller sharks could easily remain with the group. Additionally, smaller stragglers were not noted in the trailing sections of the groups. Furthermore, most often the size stratification was in the vertical plane and not the horizontal plane as one would expect if it resulted from differences in swimming performance. The stratification did not appear caused by dissimilarly sized sharks schooling less cohesively. If the size distributions of sharks were skewed, those sharks with sizes in the skewed tail of the distribution might remain at the periphery if a strong attraction by size existed among similarly sized sharks in the schools. If this were so, one would expect the more common, smaller sharks (near size-frequency's median) at the centers of the schools and the less common, larger sharks (at the size-frequency's skewed tail) at the edges. This distribution of large and small sharks did not exist. At Las Arenitas the larger sharks were at the bottom of the groups. Furthermore, although the size frequency distributions were skewed at El Bajo Gorda and Espiritu Santo, that at Las Arenitas was not skewed. Size segregation occurred within groups at all three locations. A more plausible model is that a motivation existed for all individuals to move inward or toward the school's bottom due to either reduced occurrence of predation (the "selfish herd" effect of Hamilton, 1971) or possibly greater probability of successful mating in these parts of the group. In order to produce such segregation, superimposed upon the centripetal or downward movements would be aggressive interactions in which larger, more dominant hammerheads forced smaller subordinate sharks upward to the top of the group. In a future study the causation of this segregation will be studied by examining the behavioral patterns occurring within the schools to see whether they are aggressive in nature possibly indirectly leading to reproductive success. They then could lead to the size distributions of sharks observed within the groups.

CONCLUSIONS

The scalloped hammerhead is a social species, spending much of its life in schools at dropoffs into deep water. Schools consist of both juveniles and adults. Females move offshore prior to males, and this movement results in inshore schools of intermediate-sized males. The influx of females to the offshore dropoff regions results in groups composed primarily of smaller females.

Schools are usually composed of sharks of a wide range of sizes although a small amount of size segregation exists among the schools. Owing to variability in sizes of sharks within schools, individuals within the school segregate by size. Larger sharks remain near the bottom of the groups at Las Arenitas and are separated from their nearest-neighbors by greater distances. The extent of size variation (and conversely segregation) within the schools is correlated with the frequency of wounds and scarring on school members. Size segregation within schools appears to result from aggressive interactions between females. The groups are dynamic in composition as marked individuals are seen in groups which change in size greatly over short time periods.

ACKNOWLEDGEMENTS

I would like to express my gratitute to those organizations who provided funding during the study. The Office of Naval Research provided salary support (Contract N00014-77-D-01131 to D.R. Nelson, Principal Investigator). The National Geographic Society's Committee for Research and Exploration provided funding for travel and ship rental (Grant 2204 to the author and D.R. Nelson), and the Foundation for Ocean Research funded the construction of the underwater video system (grant to author). I would also like to express my gratitude to Dr. Daniel Lluch, Henk Nienhuis, Felipe Galvan, and others from the Centro de Interdisciplinario de Ciencias Marinas, La Paz for allowing me to use their reseach vessel, the Juan de Dios Batiz, and joining myself on the seven joint SIO-CICIMAR cruises during 1979 through 1981. Dr. Donald R. Nelson, Ted Rulison, M.D., Felipe Galvan, and Scott Michael helped at times with the stereophotographic sampling. Steven Brown helped extensively not only with sampling but also with the arduous task of making the size and positional measurements of hammerhead school members. Tanya Tarshis helped with the directional measurements of school members. This report consititutes part of my doctoral dissertation at the University of California, San Diego under the guidance of Richard H. Rosenblatt.

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CHAPTER 4: DIEL MOVEMENT PATTERNS OF THE SCALLOPED HAMMERHEAD SHARK (SPHYRNA LEWINI) IN RELATION TO EL BAJO ESPIRITU SANTO: A REFUGING CENTRAL-POSITION SOCIAL SYSTEM

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ABSTRACT

Movement patterns of scalloped hammerhead sharks in the vicinity of El Bajo Espiritu Santo, a seamount in the Gulf of California, were determined by ultrasonic telemetry and marking. Hammerhead sharks swam back and forth along the seamount ridge throughout the day. They did not appear to position themselves differently when currents changed from a parallel to a perpendicular orientation to the ridge. For this reason, it is not believed that the sharks were seeking eddies characterized by reduced water velocities which might reduce swimming effort. Distances moved by sharks on the seamount were smaller than those moved after leaving the seamount (usually just prior or after sunset). Sharks tracked up to 8 km away in the pelagic environment soon returned to the seamount. From these trackings and repeated observations of marked sharks over periods of several weeks, it is believed that most sharks disperse and return to the seamount in a rythmical fashion. The separate departure of

individual hammerheads in five paired trackings indicated that the sharks left the seamount either in small groups or singly. For these reasons, we argue that the scalloped hammerhead shark possesses a refuging social system similar to that described by Hamilton and Watt (1970).

INTRODUCTION

Individuals of some shark species swim slowly or remain inactively on the bottom during the day at a single location. Often these sharks form groups. Bullhead sharks (Heterodontus portusjacksoni) repeatedly return to the same reef crevice in which they lie on the bottom often in small groups of up to sixteen members (McLaughlin and O'Gower, 1977). Whitetip reef sharks (Triaenodon obesus) also stay in "home" caves during the day (Randall, 1977). At times they form small groups of up to five members in these caves. Pacific angel sharks (Squatina californica) have been observed inactive during the day in small groups of up to twelve sharks at the sandy base of a large rock at Catalina Island (Standora and Nelson, 1977). Gray reef sharks (Carcharhinus amblyrhynchos) were observed to mill about in a group at a single location in Rangiroa Lagoon during the day. At dusk they moved considerable distances from this area presumably to forage individually (Johnson, 1978; Nelson and Johnson, 1980). This diel behavior pattern may indicate a common activity strategy for these predators to minimize activity when not foraging by remaining either on the bottom of a cave or swimming slowly at a single central location in their home range. Other species such as the bull shark (Carcharhinus leucas), reef (Carcharhinus springeri), and lemon (Negaprion brevirostris) brevirostris) have also been reported to remain at the bottom of caves in a torpor (Clark, 1975), but only as solitary individuals. Remaining at this time either in a cave or polarized school might offer an additional benefit such as protection from predation or facilitation of reproductive activies. Hamilton and Watt (1970) described this tendency to remain together in groups at a central place (or core) within an animal's home range during the inactive phase of the diel cycle as refuging.

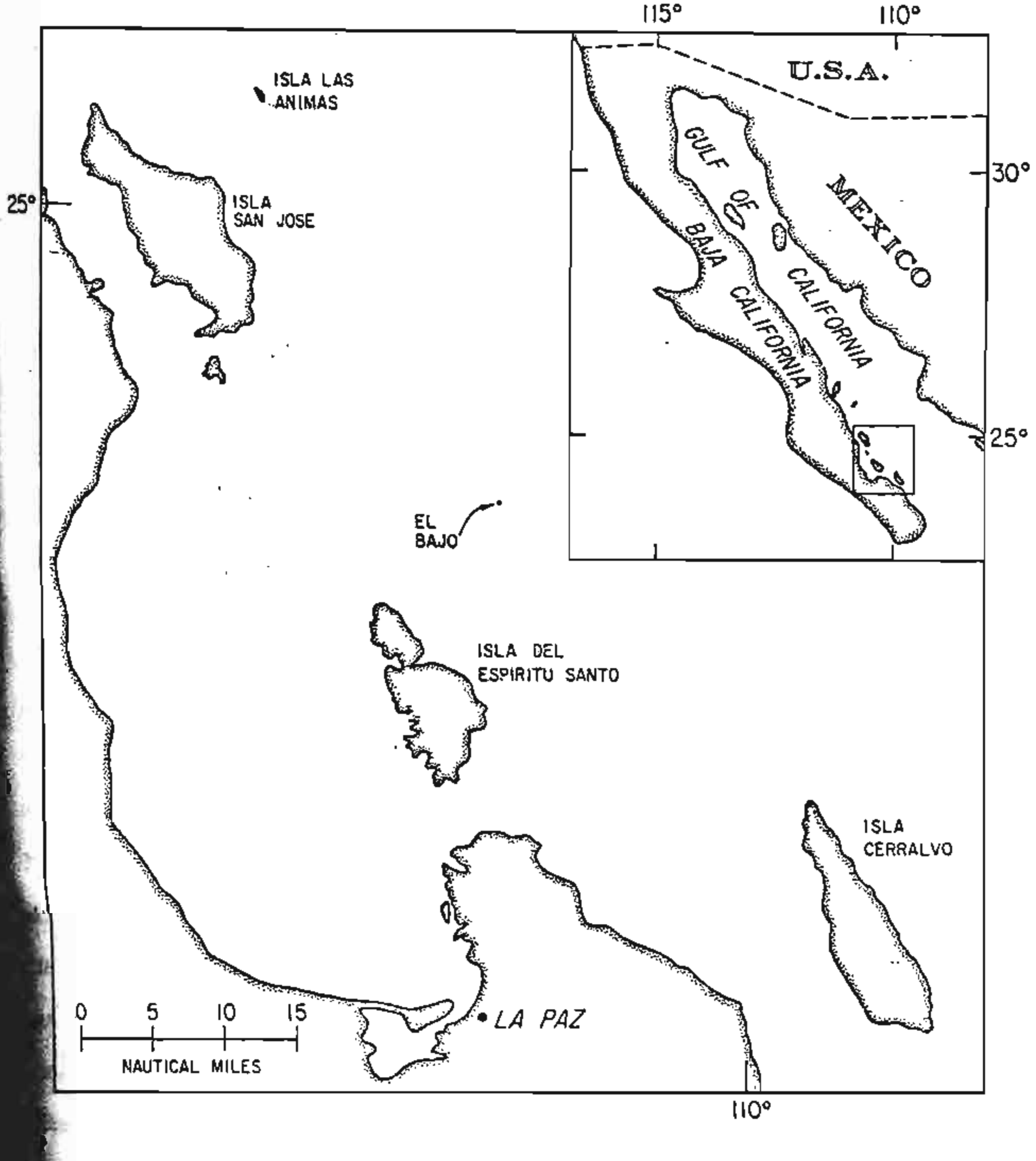
Adult scalloped hammerheads (Sphyrna lewini) are encountered swimming slowly during the day in large polarized schools along dropoffs into deep water in the Gulf of California. In this paper, we will describe the orientation of hammerhead sharks to a seamount, El Bajo Espiritu Santo (24 deg 41 min N., 110 deg 16 min W.) (Fig. 1), in the Gulf of California, and argue that this orientation pattern fits the refuging model of Hamilton and Watt (1970).

METHODS

Bathymetry of Study Site

It was our intent to examine hammerhead movements in

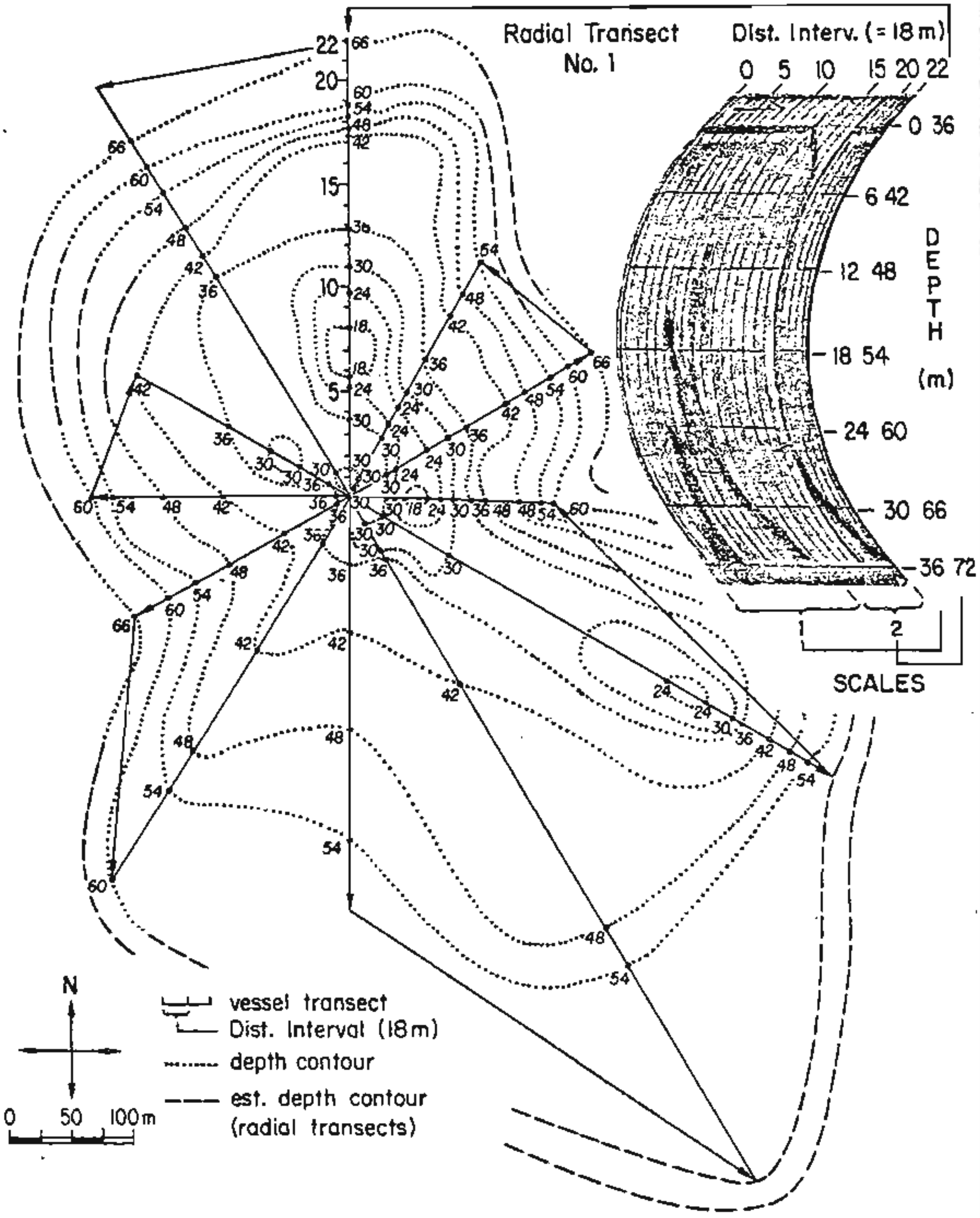
Fig. 1. El Bajo Espiritu Santo study site in the Gulf of California.


115°
110°
U.S.A.
30°
25°
GULF OF CALIFORNIA
BAJA CALIFORNIA
MEXICO
ISLA LAS ANIMAS
ISLA SAN JOSE
25°
EL BAJO
ISLA DEL ESPIRITU SANTO
ISLA CERRALVO
LA PAZ
0 5 10 15
NAUTICAL MILES
110°

relation to the bathymetry of El Bajo Espiritu Santo. For this reason, the bottom topography of the seamount was charted (Fig. 2). The research vessel was positioned above the highest point of the seamount, and radial transects were made in a small skiff equipped with a fathometer/odometer. This was done by moving outward until reaching the maximum depth resolved by the recorder, then moving circularly until a prechosen return bearing to the research vessel was reached (for the twelve transects, the return bearings were separated by 30 deg), and moving inward to the research vessel before starting outward again. Direction was determined by a hand-held compass (Davis Instruments). Bottom topography was recorded as an irregular trace on the chart paper together with concentric traces at distances through the water of 18 m. Depths and distances were then transcribed from the chart paper to produce a chart with depth contours in the following manner. The transects radiating from where the research vessel was stationed were drawn with 18 m distances indicated by tick marks. Depth changes of 6 m were then transferred to each transect line by measuring the distance in fractions of the 18 m distances on the chart between successive depth changes. The end of the fathometer record of the first transect (see righthand side, Fig. 2) is connected by an arrow to the end of the first transect on the chart (center of top, Fig. 2). Points on the transect lines (solid lines) were then connected with contour lines (dotted). These contour lines were drawn as curves rather than straight lines

Fig. 2. Illustration of method of charting bottom topography at El Bajo Espiritu Santo. Chart paper (upper righthand corner) from fathometer/odometer with irregular depth trace and concentric marks indicating 18 m distances moved through the water. Depth contours (dotted lines) indicating 6 m differences in depth are marked along radial transects (solid lines) by using the 18 m distance intervals (ticks) as a reference.

El Bajo Espiritu Santo (24° 41'N, 110°16'W)



to better reflect the intervening topographical changes. A few contours were drawn where measurements were lacking; these were are indicated by dashed lines. In this chart bottom resolution was greatest at the center of the transect pattern which was very close to the highest point on the ridge.

Ultrasonic Telemetry

Movements of sharks were most often determined by means of ultrasonic telemetry. Transmitters were designed and fabricated in the laboratory of the second author. Two transmitter types were used in the study. The first was a small, negatively buoyant cylindrical unit (3 cm dia., 8 cm length) with a small, cuboidal float attached to the unit. The second was a larger, neutrally buoyant unit (3.5 cm dia., 16 cm length) with a rounded anterior and conical posterior end with three fins for added hydrodynamic stability. The transmitters were identified either by their different frequencies (39.4, 40.0, or 40.9 kHz) or pulse interval durations. Signal transmission range was approximately two km. The maximization of transmission range was not considered of primary importance in transmitter design since the principle aim of the study was to examine the orientation of hammerheads to El Bajo Espiritu Santo with an area of less than a square km. Transmitter longlivity ranged from three days for the smaller units to a week for the larger units.

The transmitters are described in more detail in Nelson and McKibben (1981). The transmitters were attached underwater with a pole spear to the shark's dorsum by the insertion between the first and second dorsal fins of a subcutaneous dart with the transmitter attached to it by monofilament line. Due to the neutral buoyancy of the transmitters, they floated just above the dorsum of the shark except when the shark accelerated rapidly. Although the sharks momentarily accelerated upon application of the tag, they usually returned to a school and continued to swim within the school throughout the rest of the day indicating minimal stress. With the five paired trackings an attempt was made to relocate the tagged shark within a school and to tag a second member of the school. Usually we were only able to tag a second shark less than 100 m from the first shark. Either a single or two telemetry receivers (Dukane, N30A5B and Burnett, 522) were used to localize the source of the telemetry signals.

Due to the 17 km distance of the seamount from the coast of Isla Espiritu Santo and the even greater distance to the mainland, coastline bearings could not be used position the sharks accurately as they moved within the roughly square km area of the seamount. However, once the hammerheads left this area to move larger distances in the pelagic environment, it was possible to position them from bearings to landmarks along the coastline and the anchored research vessel. For this reason, movements away from the seamount were plotted on a nautical chart (U.S. Defense Mapping Agency, No. 21120), and movements nearby the seamount were plotted on the chart constructed by ourselves.

Positions on the seamount were determined in three manners. For the first four hammerhead sharks tagged a single tracking team anchored its boat on the highest pinnacle of the seamount and obtained directional bearings on the tagged sharks at 5-min intervals for the first two sharks and at 15-min intervals for the second two sharks. For these trackings only the presence or absence of the sharks near the seamount and their relative bearings were obtained. For the next three and last two hammerhead sharks the tracking team stationed its boat over the shark, and then positioned itself (and in most cases the hammerhead) from bearings to two spar buoys or vessels anchored at either end of the seamount ridge. The distance between these markers was determined with a rangefinder and corroborated by averaging distance measurements between the markers in opposite directions to eliminate the confounding effect of the current. The markers consisted of 6 m aluminum poles equipped with bouys for flotation and flags and strobe lights for positioning both during the day and night. These were attached with polypropylene line and a leader of steel cable to 5 gal buckets of concrete anchored on the surface of the seamount. This positioning technique was abandoned for three reasons. Firstly, large manta rays (Manta birostris) tangled themselves in the line leading to the spars and carried both the spars and concrete cannisters into the surrounding deeper water. One of the spars lost was found bent completely around the body of a large manta ray with the spar's two plastic buoys in a shattered condition caught between the ray's cephalic processes. A second reason for abandoning this positioning technique was the inherent error in the resulting positions due to the inability of the tracking team to position its boat directly above the shark. A third reason was the possibility that the noise of the engine and slapping of water against the hull of the continuously moving tracking boat might be frightening the sharks into leaving the seamount prematurely. Indeed, two of the three sharks followed in this manner left the seamount prior to dusk while most of the sharks positioned in other ways left at dusk. However, there were some advantages to this technique. Firstly, the tracking team could remain more easily with a hammerhead if it abruptly left the seamount. Secondly, the fathometer could be utilized to determine the bottom depth below the shark. With the next four telemetered sharks two tracking teams remained stationary in skiffs anchored at either end of the seamount ridge and simultaneously took bearings to the sharks. Bearings taken by the teams were transmitted by CB transceivers to the research vessel where the positions of the shark were immediately plotted. The advantage of such plotting was that incongruent lines of position could be detected and bearings immediately retaken. This technique was superior to the former because the position of the shark was directly triangulated. Furthermore, the shark was not frightened by a constantly moving small boat.

Lines of position were drawn on acetate sheets superimposed upon a large clipboard with a copy of the nautical chart laminated to its surface. The lines were drawn with a protracter plotter. Positions separated by 15 min were connected with straight lines to become track segments. Both the longest tracking and some of the paired trackings were presented in this manner.

It must be remembered that the track segments represent the result of swimming movements over a 15-min period with the hammerhead shark at any time during that period not necessarily along the track segment. The distances moved during these 15-min periods were often small, less than 100 m. Although instantaneous swimming velocities have not been measured for the sphyrnids, they have been for the related carcharhinids such as the bull (Carcharhinus leucas) and the sandbar shark (Carcharhinus plumbeus). These velocities were 0.67 and 0.64 m/sec, respectively (Weihs, et al., 1981). At this rate of swimming, it would take only 2.5 and 2.6 min to traverse this distance by straight-line swimming in the absence of currents. The balance between these times and 15-min could either be spent at one spot or moving considerable distances in several directions. For this reason, and to eliminate the confusion of many line segments, positions were in some cases represented by unconnected points, each of which represented a positional estimate over a 15-min period. The center of activity for such positions was determined using the technique of Hayne (1949). With this technique the mathematical center of the distribution of all positions was obtained by dividing a chart into a grid, weighting both rows and columns, multiplying these weightings by the numbers of positions in each row and column, summing these values, and dividing the row and column totals by the total number of positions. The center of activity was then located on the grid using the resulting row and column coordinates. The surrounding positions were then ranked in relation to their distances from this central point. Twenty-percent contours were then formed by connecting the outermost points with straight lines in a manner producing the minimum area such as recommended by Southwood (1966).

In order to compare and statistically evaluate directional movements in relation to the axis of the seamount ridge as well as different current directions and velocities, bearings from each position to its following position were totaled in 20 deg classes on polar plots. A depth contour of the seamount was superimposed on each polar plot. The circular distributions of bearings were tested as to whether they differed from a uniform distribution with either the Rayleigh or Chi-Square Tests (Batschelet, 1981). In one case, the distributions were bimodal. Since they were roughly centrally symmetrical, they were converted to unimodal distributions by the "doubling the angles" technique of Batschelet (1965) and tested using the F-Test.

Hourly measurements of surface current direction and velocity were made with a current meter and handheld compass.

Marking

In order to determine the degree of attachment of the hammerheads to the seamount, 100 sharks were marked between the first and second dorsal fins with dart-attached, color-coded, plastic streamers. These marks were also applied underwater with a pole spear. Forty tags were deployed during the summers of 1979 and 1980; twenty during the summer of 1981. During the summers of 1980 and 1981 the site was visited repeatedly over periods of a month and a month and a half, respectively. During these visits reobservations of tagged sharks were recorded.

RESULTS

Ultrasonic Telemetry

Thirteen trackings of scalloped hammerhead sharks (Table 1) were carried out during the summers of 1981 and 1982 at El Bajo Espiritu Santo. Transmitters were applied at times ranging from 0930 to 1700. Durations of the trackings ranged from 15 min to 14 hrs. Some durations of trackings were relatively short since we were interested primarily in orientations of the hammerheads to the seamount, and for this reason, did not often follow them once they left the vicinity of the seamount. In a few instances we did continue to track the sharks after they had left the seamount.

The scalloped hammerheads generally remained close to the seamount ridge. Their center of activity was just 25 m east of the 30 m depth contour of the ridge and rather equally spaced between two of the pinnacles rising to less than 18 m from the surface (Fig. 3). The activity contours (solid lines) roughly paralleled the depth contours (dotted lines), and this indicated a preference for the ridge. In fact, sixty percent of the positions occurred within the 48 m depth contour. The circular distribution of movements was non-uniform (Chi-Square Test, $p<0.02$). Directions were bimodally distributed with maxima corresponding to the seamount ridge's northwesterly-southeasterly orientation (see lower lefthand corner, Fig. 3). The longest tracking in the vicinity of the seamount (No. 9) further illustrates this daytime orientation to the seamount ridge (Fig. 4). Although the shark occasionally moved outside the 48 m depth

Table 1. Ultrasonic telemetry transmitter application date and time, duration of shark's stay on seamount, and duration of entire tracking. Dates of reobservations of sharks with transmitters at seamount also noted.

Track No.	Date of Track	Time(hrs)			Duration (hr:min)	Date of Reobs.*
		Begin.	Depart.	End		
1	4 Aug. 1980	1335	1940	1940	6:5	
2		1510	1855	1855	3:45	
3	11 July 1981	1150	1345	1345	1:55	14 July
4		1200	1900	1955	7:0	
5	12 July 1981	1400	1545	1700	2:40	14 July
6	13 July 1981	0930	1130	1600	6:30	
7		1025	1515	1920	8:55	
8	15 July 1981	0940	1043	1043	1:3	
9		1000	1930	0100	14:0	
10	16 July 1981	1030	1045	1045	:15	
11		1135	1545	1645	5:10	
12	17 July 1981	1354	1845	1845	5:9	
13	14 Sept. 1981	1215	1900	2100	8:45	15 Sept.
	15 Sept.	1030	1900	2215	11:45	

*Transmitter observed on 30 July 1981 but color-coded identification could not be seen.

Fig. 3. Positions determined every 15 min for 13 sharks in the vicinity of El Bajo Espiritu Santo. Center of activity and cumulatively increasing 20 percent activity contours (solid lines) are superimposed upon bathymetric contours (dotted lines). Frequency distribution of directions of movements between successive 15-min positions are on polar plot in the lower lefthand corner. Area of seamount above the 36 m depth contour indicated by stippling.

STUDY SITE: EL BAJO ESPIRITU SANTO

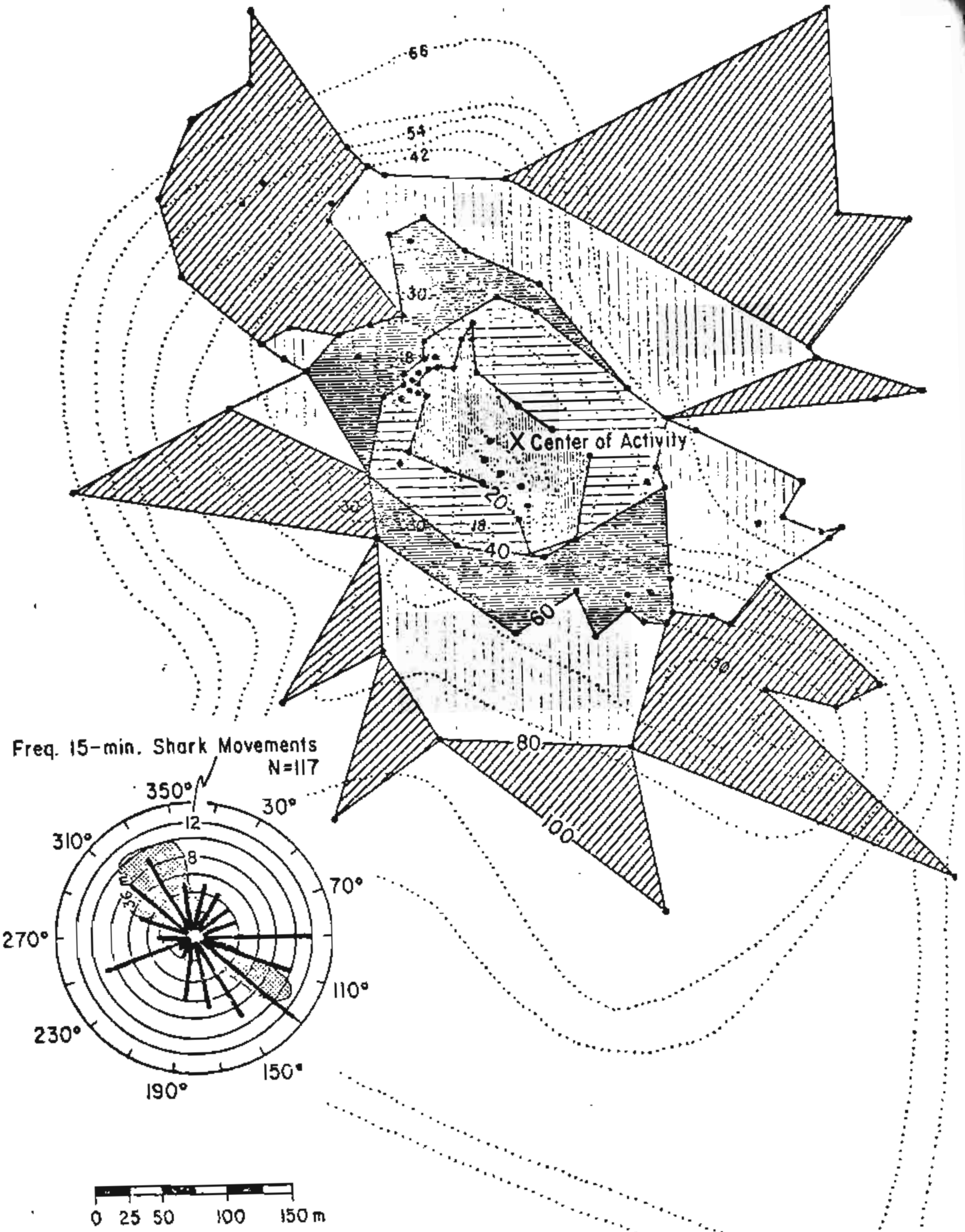
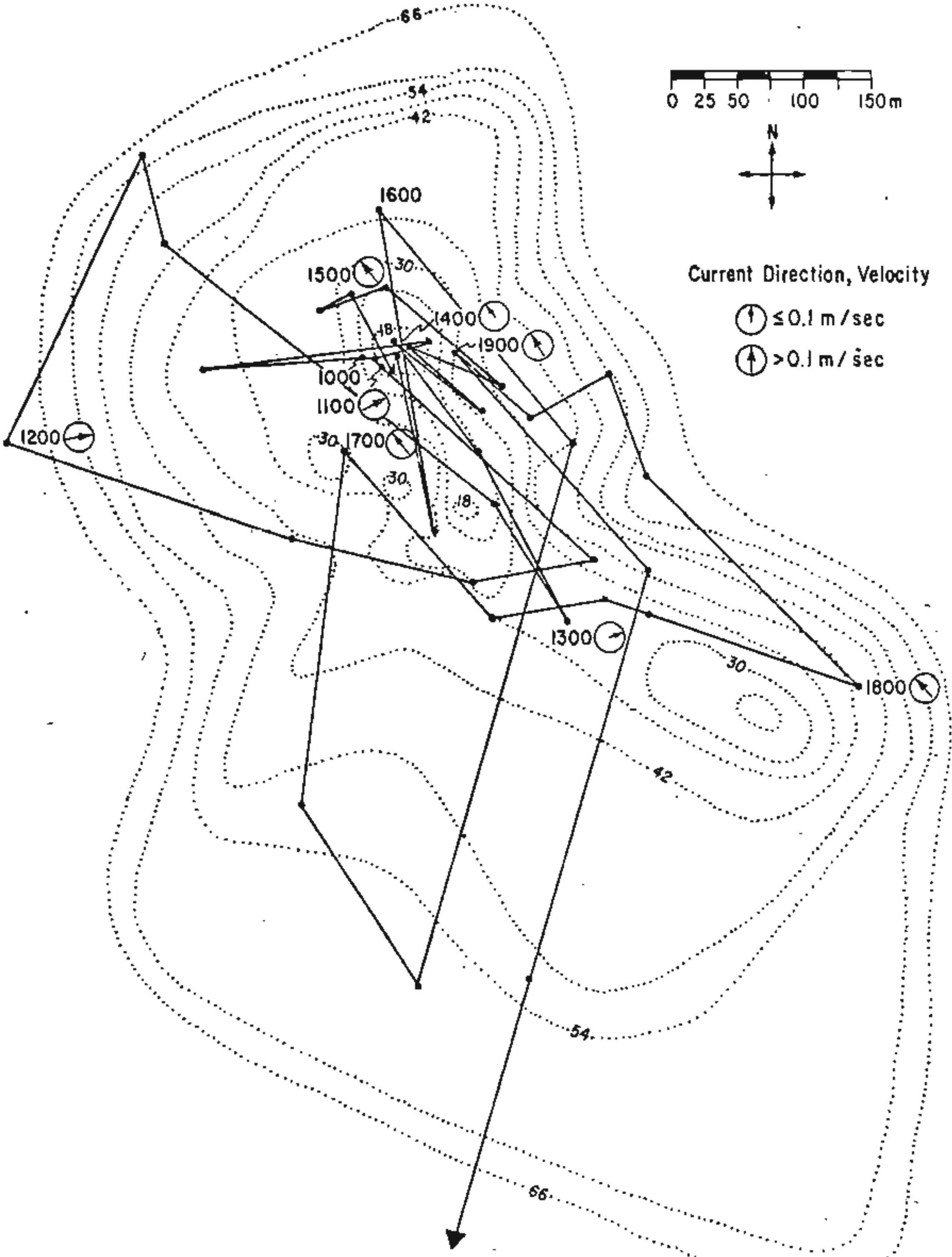


Fig. 4. Movements between positions determined every 15-min for hammerhead No. 9 at El Bajo Espiritu Santo. Hourly measurements of current direction and velocity indicated by arrows within circles. The direction of the current is indicated from the direction of the arrow, the velocity by its size.

STUDY SITE: EL BAJO ESPIRITU SANTO

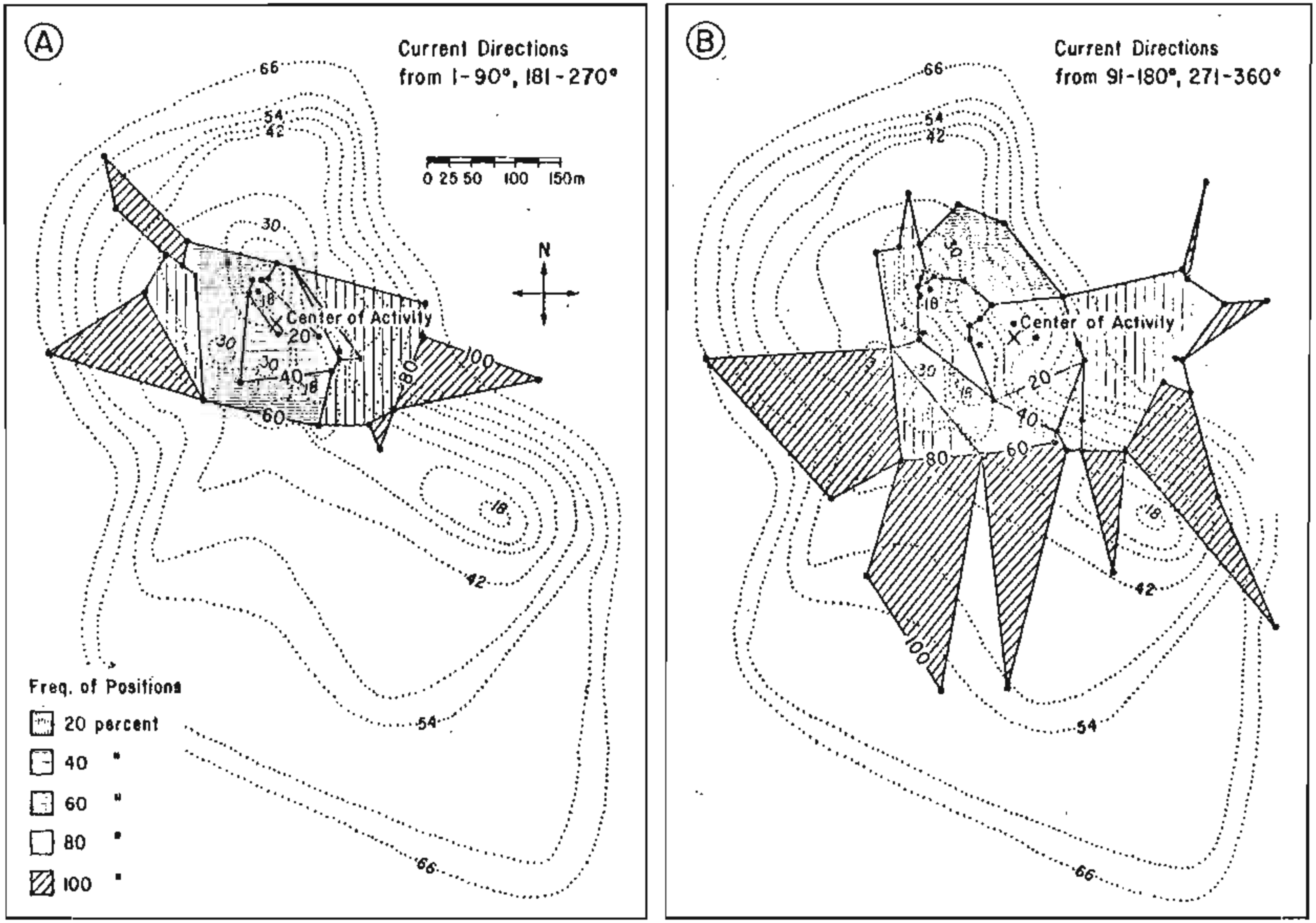


contour, it repeatedly returned to positions over the larger of the two pinnacles. Most of the movements were parallel to the direction of ridge.

The schooling hammerhead sharks might remain at the seamount to take advantage of reduced current velocities inside eddies downcurrent from the seamount ridge. If the sharks remained in such eddies, they might not have to swim as fast during the inactive phase of their diel cycle. This could be a reason for remaining at the seamount. Due to the presence of currents flowing roughly perpendicular to or parallel to the direction of the seamount ridge at different times, it was possible to test whether a change in the direction of the current affected the directions moved by the tagged sharks. Tracking positions, their centers of activity, and activity contours are shown both for currents flowing perpendicular to the seamount ridge (1-90 and 181-270 deg) (Fig. 5A) and in the same direction (91-180 and 271-360 deg) (B). Although the 60 percent activity contours' longitudinal axes under both current regimes paralleled the seamount ridge, the larger activity contours were different under the two current regimes. The contours were elongated in a westerly direction away from the seamount ridge when perpendicular currents were present. They were elongated in a southeasterly direction away from the ridge when parallel currents were present. These elongations of activity contours were in areas where eddies would be expected because

Fig. 5. Positions taken in 15-min intervals of 13 sharks in the vicinity of El Bajo Espiritu Santo when currents were perpendicular to the axis of the ridge (A) and parallel to the axis (B).

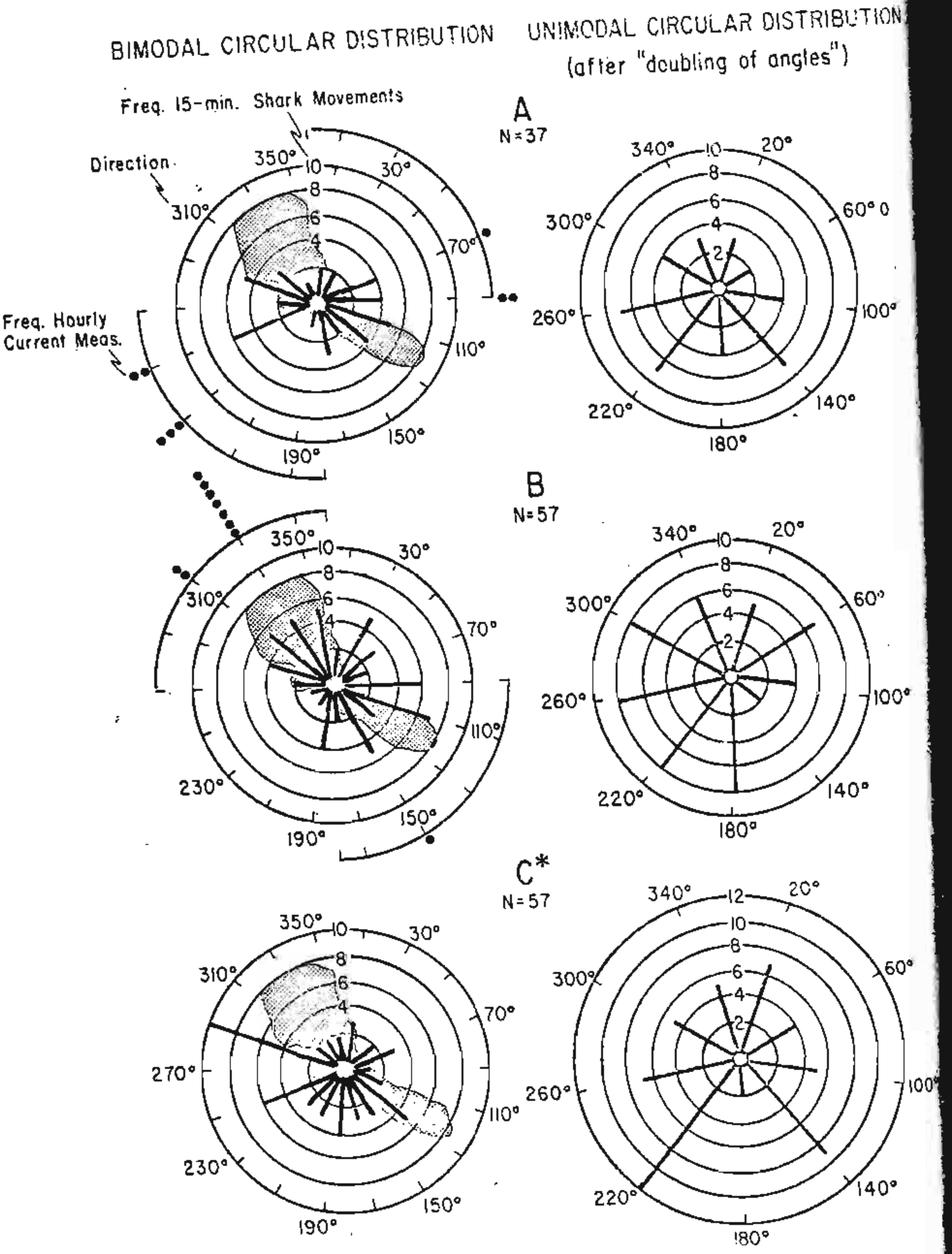
STUDY SITE: EL BAJO ESPIRITU SANTO



perpendicular currents flowed primarily from the southwest and parallel currents from the northwest.

Were the tagged scalloped hammerheads, presumably within the schools, changing their positions in response to changes in currents in a statistically significant manner? In order to test this, frequencies of directions moved were plotted on polar coordinates for both current regimes (Fig. 6). Superimposed upon the polar plots was the 36 m contour of the seamount. The frequency distributions were roughly bimodal with large frequencies of directional movements at 70 and 250 deg for currents perpendicular to the seamount ridge (see Fig. 6A), and 110 and 320 deg for currents parallel to the ridge (B). In order to test the two distributions, they were converted to unimodal distributions by the "doubling the angles" method. Since the directional size classes were doubled in width, and thus the mean angles of the slightly skewed distributions were changed, a correction was made (Batschelet, 1965). The distribution of directions of movements in the presence currents perpendicular to the seamounts did not differ statistically from that with currents parallel to the seamount (F-Test, p>0.05). It is possible that very different distributions could occur randomly. The distributions A and B under different current regimes did not differ significently (F-Test, p>0.05) from a control distribution C formed with the use of a random numbers table (Zar, 1974). Thus, the hammerheads did not

Fig. 6. Polar plots with bimodal (lefthand) and unimodal (righthand) frequency distributions of directions between 15-min positions and directions of hourly current measurements for currents flowing perpendicularly (A) and parallel (B) to the axis of the seamount. Also shown is a distribution of directional movements (C) created with random numbers table . Bimodal converted to unimodal distributions by "doubling the angles" technique of Batschelet.



*Control: movements from random numbers table (not bimodal dist.)

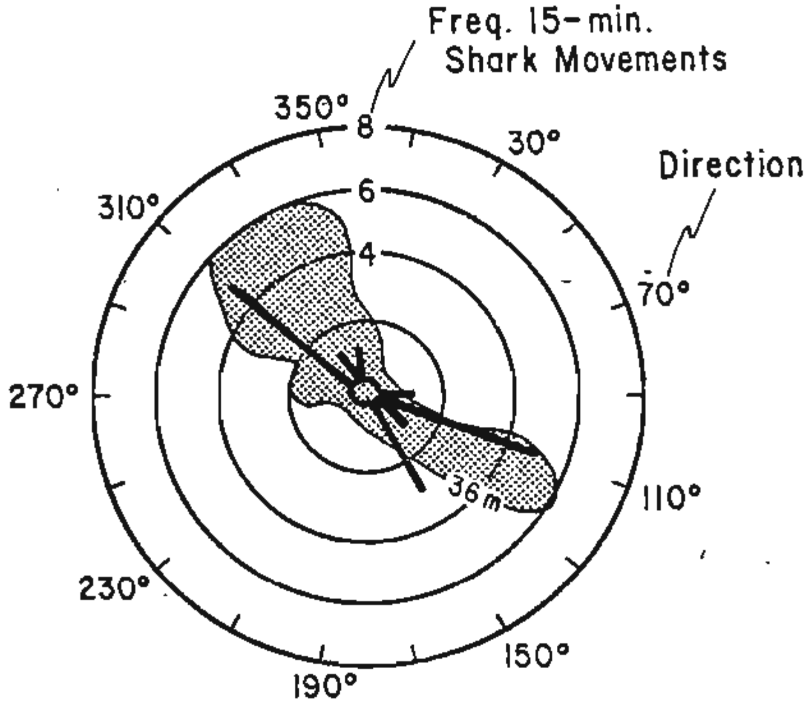
appear to change their positions in response to changes in current direction.

Supporting the conclusion that the sharks were not changing positions in response to changes in current direction was the lack of correlation between the movements of hammerhead No. 9 in the vicinity of the seamount with current directions (see Fig. 4). Current directions and velocities are included in this tracking. The measurements follow hourly positions in small circles with the direction of the inscribed arrow indicating the direction of the current and the length of the arrow indicating whether the currents were slow (≤0.1 m/sec, small arrow) or fast (>0.1 m/sec, large arrow). Although some of the movements preceeding or following the hourly current measurements were either in the same or opposite directions (see 1400, 1700-1900 hrs), others were in perpendicular directions (see 1100 and 1300 hrs).

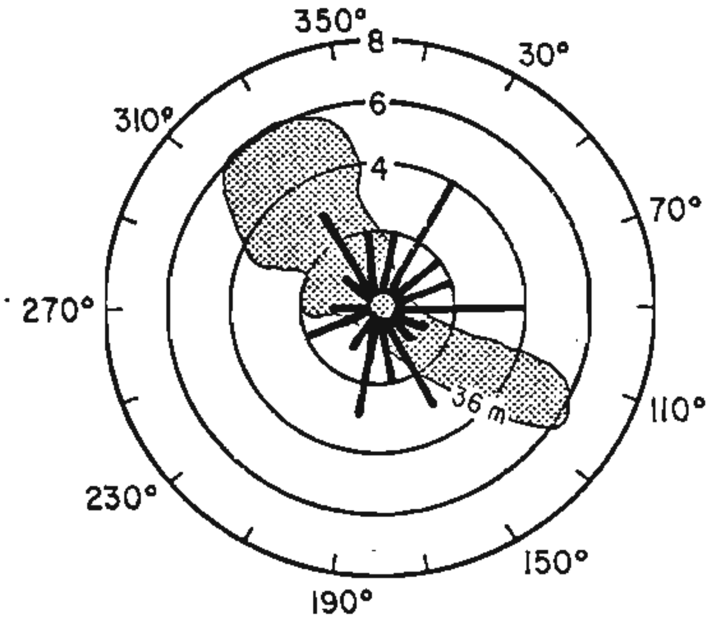
The movements of the scalloped hammerheads appeared governed by factors other than the current velocities at the seamount. The largest sample of movement directions (with currents flowing from the northwest in a direction parallel to the ridge) was divided into those movements occurring in currents of slow (≤0.1 m/sec) (Fig. 7) and fast velocities (>0.1 m/sec) . In the slow currents the directions of shark movements were almost all parallel to the direction of

Fig. 7. Polar plots of frequency distributions of movement directions between successive 15-min positions for current velocities ≤0.1 m/sec and >0.1 m/sec.

CURRENT VELOCITY ≤ 0.1 m/sec



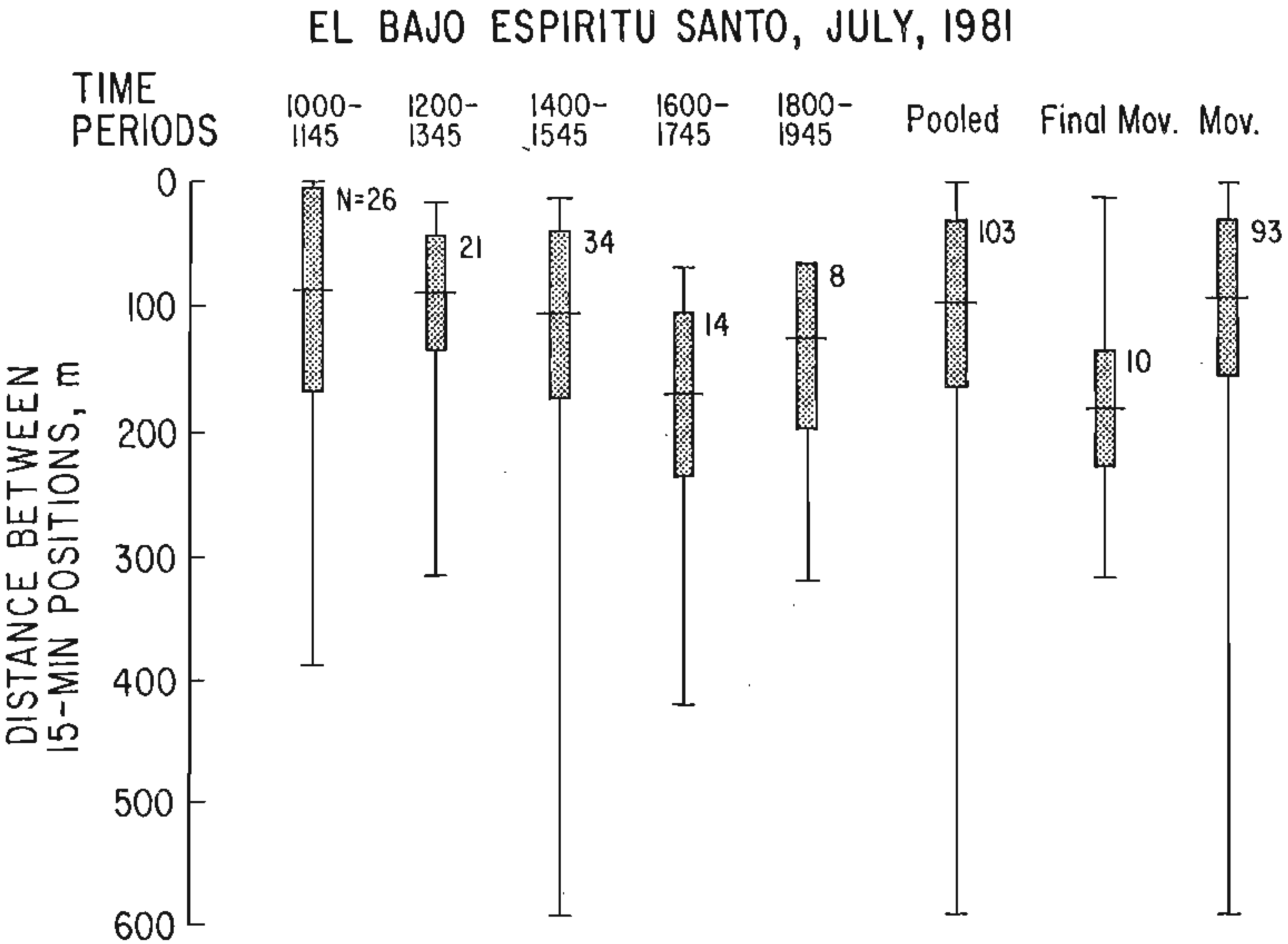
CURRENT VELOCITY > 0.1 m/sec



the current. However, when currents were fast, the directions of shark movements were in many directions, with some parallel but others perpendicular to the direction of the current. If the sharks were using current direction as a cue to remain at the seamount, their movements should have been in many directions when the currents were weak and parallel to the axis of the ridge when the currents were strong.

It appeared that the tagged hammerheads swam faster, and perhaps more erratically, during the late afternoon prior to their departure from the seamount than early during the day. To determine whether this was true, distances between subsequent positions were combined into five 2 hr time classes ranging from 1000-1145 hrs to 1800-1945 hrs (Fig. 8). Swimming activity was expressed indirectly on the ordinate as distance between 15-min positions rather than a rate of m/sec because, as argued before, the sharks certainly did not swim continuously in a straight line to where they were located after 15 min. We believe, however, that these distances do reflect to some degree swimming activity if a number of such movements for several sharks are considered. The median distance moved increased successively in the first four time periods from 87.5 to 171.0 m. The median distance moved in the last time period dropped unexpectedly to 126.5 m. The medians differed significantly between the 2 hr time intervals (Kruskal-Wallis Test, $p<0.05$ with the critical

Fig. 8. Distances between positions determined at 15-min intervals of 13 sharks for five time periods during the day at El Bajo Espiritu Santo. Also included are the distances moved immediately prior and those not prior to the sharks' departures from the seamount. The inner horizontal line on each bar indicates the median, the vertistippled bar one quartile deviation to either side of the median, and the outer horizontal lines the range of distances.


EL BAJO ESPIRITU SANTO, JULY, 1981
TIME PERIODS
1000-1145
1200-1345
1400-1545
1600-1745
1800-1945
Pooled
Final Mov.
Mov.
DISTANCE BETWEEN 15-MIN POSITIONS, m
0
100
200
300
400
500
600
N=26
21
34
14
8
103
10
93

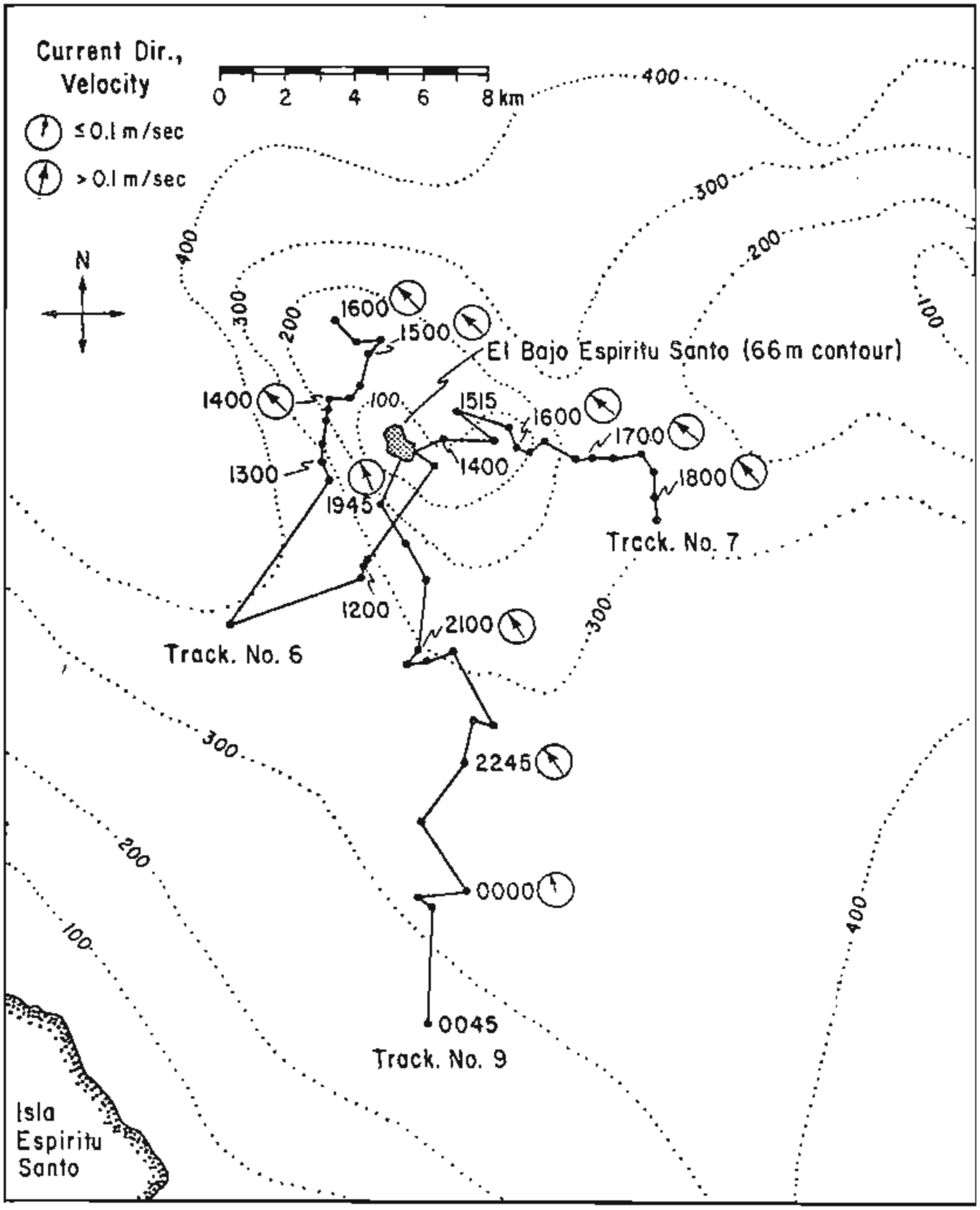
value for 4 deg of freedom of 9.5, only slightly less than the calculated value with a correction for ties of 9.6). However, comparisons between time classes differing the most such as 1000-1145 hrs and 1600-1745 hrs did not indicate significent differences (Neymenyi Multiple Comparisons Test, if critical value $\geq$ 1 difference detected with $p<0.05$, calculated value only 0.98). Possibly the conflicting results were due to the greater power of the Kruskal-Wallis than the Neymenyi Test. The reason for the unexpectedly smaller median for movements in the 1800-1945 hrs class may be that only one of the distances moved during this time period was immediately prior to the hammerhead's departure from El Bajo Espiritu Santo. Such movements might characteristically be longer than other movements. Indeed, the classes with larger medians contained at least two of these movements. However, when these movements were compared to all other movements regardless of time of day, no significent differences in the medians were found (Mann-Whitney Test, $p>0.05$, although $p<0.06$).

All tagged sharks departed from the vicinity of the seamount by night (see Table 1). On 4 Aug. 1980 the sun set at 1855 hrs. Civil twilight, the time period required for the upper circumference of the sun to follow an arc from the horizon to a point lying 6 deg below the horizon, ranged from 1855 to 1920 hrs. Nautical twilight, the time period required for the upper circumference to traverse an arc from the horizon to a point lying 12 deg below the horizon, ranged from 1855 to 1948. According to Beck (1980) changes of light intensity throughout both of these periods are of sufficient magnitude to trigger phototactic responses.

The hammerhead sharks did not leave the immediate vicinity of the seamount with preferred bearings. A uniform distribution of the 13 departure bearings could not be rejected statistically (Rayleigh Test, $p>0.05$). This may suggest another advantage to the hammerheads for remaining at the seamount. Due to its central position within the pelagic environment, abundant prey are present in all directions from the seamount.

After leaving El Bajo Espiritu Santo, the tagged scalloped hammerheads either swam in all directions uniformly (Tracking No. 6) or non-uniformly (No. 7 and 9). Trackings of these three sharks were plotted together with hourly current directions and velocities on a bathymetric chart (Fig. 9). Current directions and velocities on an hourly basis are indicated within small circles as in Fig. 4. Directions of successive movements between 15-min positions for the three sharks were tested against uniform distributions with the Rayleigh Test. Although tracking No. 6 did not differ significantly from a uniform distribution ($p>0.05$), trackings Nos. 7 and 9 differed significantly ($p<0.02$ and $p<0.01$, respectively). Hammerhead No. 7 swam

Fig. 9. Movements between 15-min positions for three scalloped hammerheads (Nos. 6,7, and 9) after they left El Bajo Espiritu Santo. Hourly measurements of directions and velocities of currents within the circles. The direction of the arrow denotes current direction, the size of the arrow its velocity.


Current Dir.,
Velocity
≤ 0.1 m/sec
> 0.1 m/sec
0
2
4
6
8 km
N
400
300
200
100
El Bajo Espiritu Santo (66 m contour)
1600
1500
1400
1300
1200
1945
Track. No. 6
1515
1400
1600
1700
1800
Track. No. 7
2100
2245
0000
0045
Track. No. 9
Isla
Espiritu
Santo

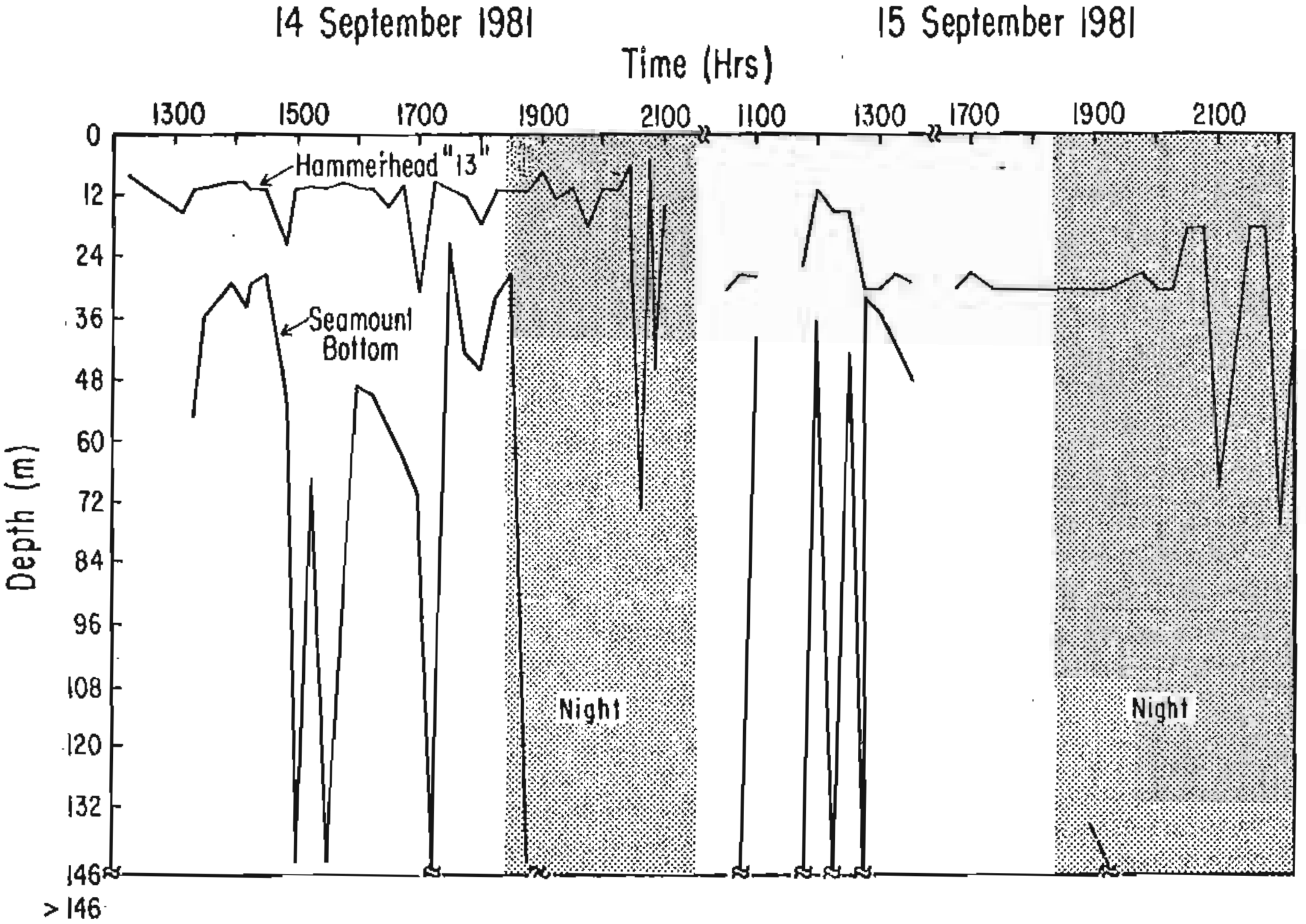
continuously southeastward over a distance of 8 km in 4 hrs, and No 9 swam southerly over a distance of 18 km in 5.5 hrs. The relatively straight-line movements of both sharks did not result from their being carried with the prevailing currents since these currents, usually greater than 0.1 m/sec, were flowing in directions opposite to those of the sharks' swimming paths. It is possible that the sharks were using as a directional cue the oppositely flowing currents to move over large distances in a straight-line manner. Unfortunately, current measurements were not available during the erratic movements of tracking No. 6 so that the importance of current direction to the orientation by these sharks could be be better evaluated. Further indicating an ability for the hammehead sharks to utilize directional cues in the open ocean was the prompt return of three (or possibly four) sharks to the seamount, one after an extensive movement away from the seamount. Hammerhead No. 13, which was tagged at 1215 hrs on 14 Sept. 1981, remained at the seamount during the daytime and moved away from the seamount in an northeasterly direction at 1900 hrs. In the following two hrs it swam ca. 8 km from the seamount in that direction (toward the center of the Gulf of California). The tracking was aborted at 2100 hrs due to inclement weather conditions. On the following day the same shark was located on the seamount at 1030 hrs. It remained at the seamount until 1900 hrs when it moved away in an easterly direction. Again it was followed ca. 8 km (toward the center of the Gulf of

California) before the tracking was aborted at 2215 hrs due to poor weather. This scalloped hammerhead was not found in the vicinity of the seamount on the following day, our last day at the seamount.

Distances moved between subsequent 15-min positions in the pelagic environment were significantly greater than those at El Bajo Espiritu Santo. In order to give a reference with which the movements in the pelagic environment could be compared, the 60 m depth contour of El Bajo Espritu Santo, within which daytime movements generally occurred, was added to Fig. 9. The median distance moved by hammerhead shark No. 6 at the seamount was 201 m compared to that away from the seamount of 464 m. This difference was significent (Mann-Whitney Test, $p<0.02$). The median distance of No. 7 nearby the seamount was 65 m and that away from the seamount was 741 m. The median distance of No. 9 at the seamount was 134 m and that away from the seamount was 1112 m. Both differences were significent ($p<0.001$). This conclusion, however, must be a guarded one since the distances moved over the seamount were much more accurately determined than those in the pelagic environment.

Both the depths at which hammerhead shark No. 12 swam and the bottom depths beneath it at the time of its positioning are shown in Fig. 10. During the first day the shark remained at a relatively constant depth of ca. 12 m

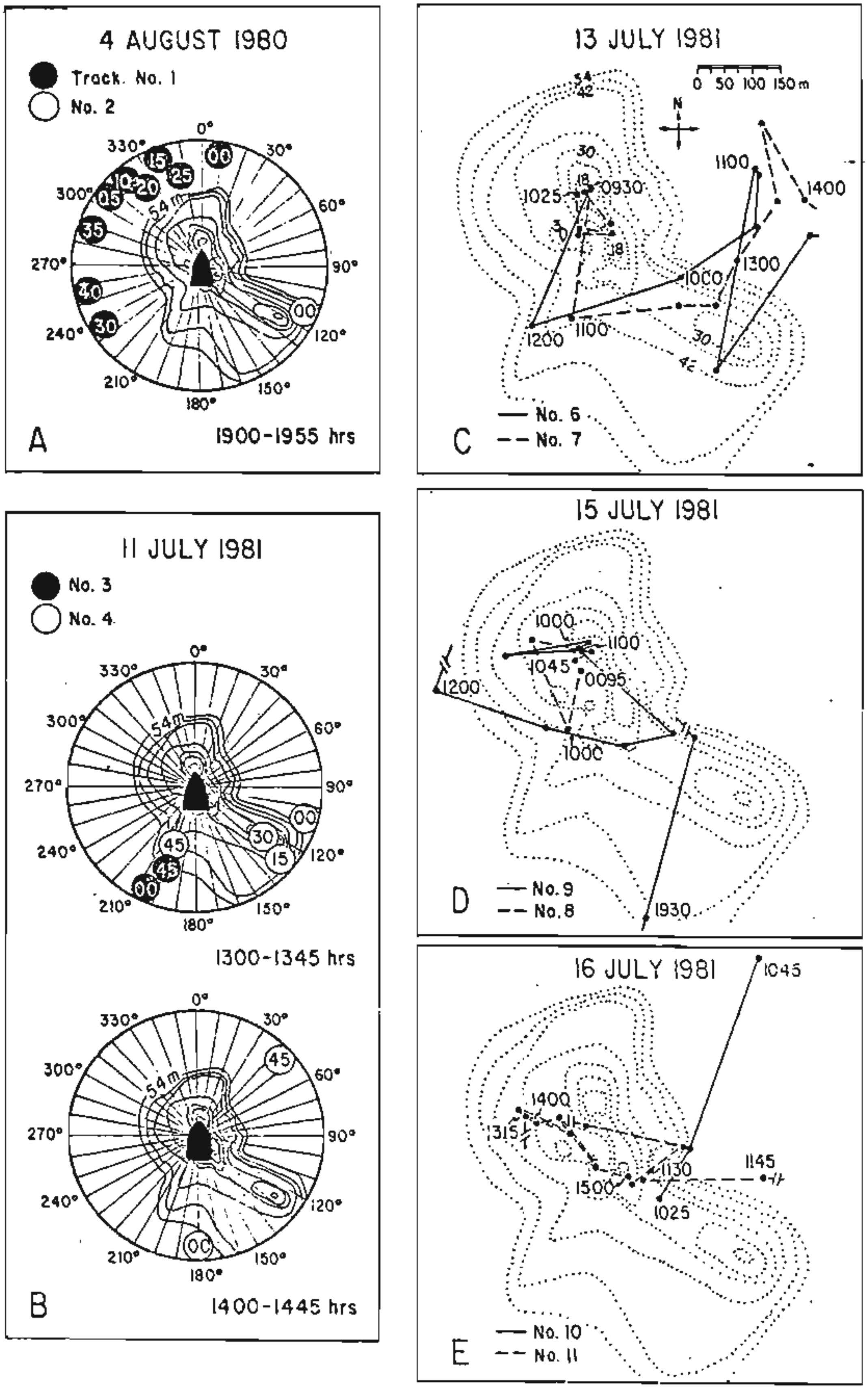
Fig. 10. Swimming depths of hammerhead No. 13 tracked on 14 and 15 September 1981 and bottom depths beneath the shark at 15-min intervals. Note that the tracking was intermittent, and the time abcissa is broken at points to indicate when positions were not taken. The limit of the fathometer's depth scales was 146 m.


14 September 1981
15 September 1981
Time (Hrs)
1300
1500
1700
1900
2100
1100
1300
1700
1900
2100
Depth (m)
0
12
24
36
48
60
72
84
96
108
120
132
146
> 146
Hammerhead "13"
Seamount Bottom
Night
Night

over the seamount. At 1450 and 1645 the shark made small dives to 17 and 30 m. The dives were over deeper bottoms: this may indicate that the shark was along the edge of the seamount ridge. At 1820, soon after sunset, the shark moved away from the seamount. This is indicated by the drop in the bottom depth. The shark moved in a northeasterly direction while making a brief dive to 75 m at 2020 hrs and another to 45 m at 2045 before the tracking was aborted. The shark returned to the seamount on the following day and spent most of the day at a depth of 30 m, possibly along the edge of the seamount as is indicated by the greater bottom depths underneath the shark. Occasionally the shark moved over the ridge as indicated by the shallower bottom depths. At 1245 hrs the shark left its characteristic mid-water position to swim close to the bottom. After sunset the shark again left the vicinity of the seamount in a northeasterly direction and made dives to depths of 65 and 75 m at 2045 and 2145 hrs, respectively. It is unknown whether this scalloped hammerhead was orienting to the thermocline. Frank Carey of Woods Hole Oceanographic Institution tracked a scalloped hammerhead for 24 hrs northeast of Cape Hatteras (pers. comm.). This shark moved slowly within 5 miles of where it was released, and its vertical movements were confined to the mixed layer with the shark making numerous shallow dives but avoiding both the thermocline and surface.

The high variation of sizes of schooling hammerheads at El Bajo Espiritu Santo (chapter 3) indicated that the scalloped hammerheads might leave the seamount to forage in small groups or separately. Differences in size are reflected in differences in swimming performance. For this reason, a large school of sharks composed of individuals with disparate swimming abilities would forage less optimally than small groups composed of individuals with more similar swimming abilities. An attempt was made to determine whether the sharks left the seamount in schools to forage socially by tagging two sharks and simultaneously tracking them. Five paired trackings were attempted during the summers of 1980 and 1981 (Fig. 11). In the first two (A and B), it was possible only to determine simultaneous bearings of the two sharks from the tracking vessel anchored over the seamount. The bearings of the two sharks are shown as shaded and clear circles with the time (in min) enclosed within the circles on a polar plot. The position of the boat and depth contours are superimposed upon the plot. In the first paired tracking on 4 Aug. (A) hammerhead No. 2 left the vicinity of the seamount at 1900 hrs in a southeasterly direction while No. 1 remained longer at the seamount and left at 1940 hrs in a southwesterly direction. Prior to 1900 hrs the bearings of the two sharks were very similar (not shown in Fig. 11) indicating that they might be swimming within a single school. In the second paired tracking on 11 July 1981 (B), the two sharks possessed similar bearings at 1345 hrs possibly indicating that they were within the same school

Fig. 11. Five attempted paired telemetry trackings at El Bajo Espiritu Santo during 1980 and 1981. The former two trackings with the bearings of the two sharks indicated as shaded and clear circles with the time (min) enclosed within the circles. Bathymetric contours are superimposed upon the plots. The latter three trackings consist of the positions of the two sharks (connected by solid or dashed lines) plotted on bathymetric charts.


4 AUGUST 1980
Track. No. 1
No. 2
0°
30°
60°
90°
120°
150°
180°
210°
240°
270°
300°
330°
54m
00
15
25
10
20
05
35
40
30
00
A
1900-1955 hrs
11 JULY 1981
No. 3
No. 4
54m
00
30
15
45
45
00
1300-1345 hrs
54m
45
00
B
1400-1445 hrs
13 JULY 1981
0 50 100 150 m
N
54
42
30
18
1100
1400
1025
0930
1300
1000
1200
1100
30
42
No. 6
No. 7
C
15 JULY 1981
1000
1100
1045
0095
1200
1000
1930
No. 9
No. 8
D
16 JULY 1981
1045
1400
1315
1130
1145
1500
1025
No. 10
No. 11
E

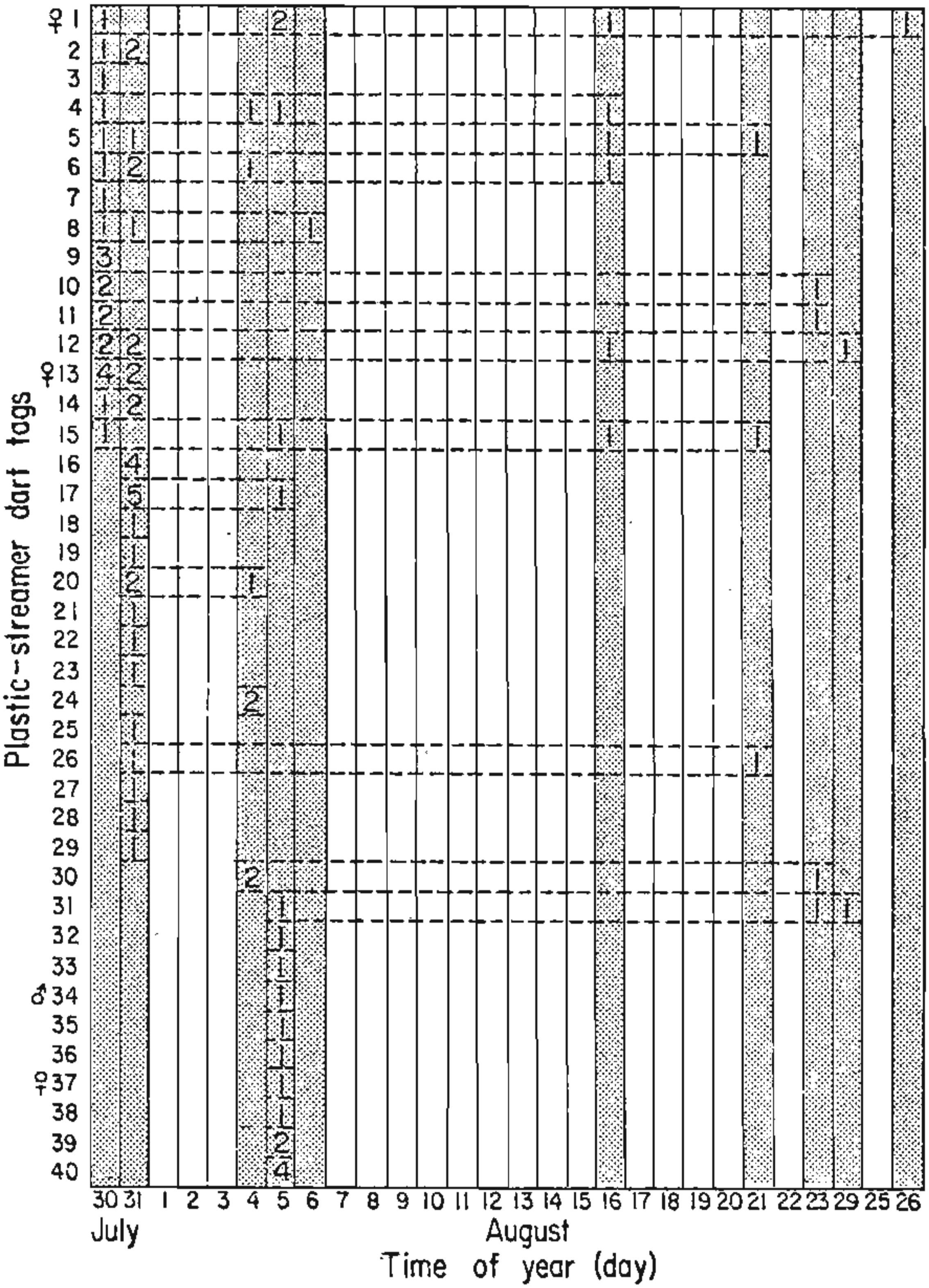
before hammerhead No. 3 departed in a southwesterly direction. Hammerhead No. 4 remained at the seamount longer, and left in a northeasterly direction at 1445 hrs. Positions of the two sharks were determined in the next three paired trackings. In the third paired tracking on 13 July 1981 (C), the two sharks did not remain together prior to departure. Hammerhead No. 6 left the seamount at 1130 hrs in an easterly direction while No. 7 left in a similar direction but later at 1400 hrs. Not only did the position at the edge of the seamount of No. 7 at 1030 hrs differ from the position of No. 6 over the highest pinnacle at 1025, but also a similar positional difference existed at 1100 hrs. In the fourth paired tracking on 15 July (D), hammerhead No. 8 remained momentarily near No. 9 above the seamount ridge before leaving in a southeasterly direction at 1030 hrs. Hammerhead No. 9 swam back and forth along the seamount ridge until it left in a southerly direction at 1930 hrs. Movements from 1200 to 1915 hrs for No. 9 were not included since hammerhead No. 8 was not present on the seamount at this time. And finally, in the fifth paired tracking on 16 July (E), hammerhead No. 10 left the seamount in a northeastely direction at 1045 before hammerhead No. 11 was tagged at 1130 hrs. Hammerhead No. 11 remained at the seamount until 1545 hrs when it left in a northwestely direction. The departure of these sharks at different times and directions, of course, did not prove that the hammerhead were not leaving in schools. If the size of the population of hammerheads at El Bajo Espiritu Santo was large, group composition dynamic, and the departing groups small, the probability of members of four shark pairs (one tagged shark left the seamount before the second was tagged) separating, yet leaving with other sharks would be high. Another approach to determining whether the hammerheads remained in schools at night would be to position the tracking skiff above the telemetered shark and look on the depth recorder chart for the tagged shark and adjacent large targets. Unfortunately, despite several attempts we were unable to position the vessel above the rapidly moving tagged sharks at night.

Marking

One hundred scalloped hammerhead sharks were marked with color-coded, plastic-streamer marks at El Bajo Espiritu Santo during a period from 1979 to 1981. Some marked sharks were never reobserved, or observed only a single time, indicating a steady rate of emigration from the seamount. However, although five other locations in the middle and lower Gulf of California (see chapter 3) were visited on a seasonal basis from 1979 to 1981, none of the sharks marked at El Bajo Espiritu Santo were observed at these locations. Other marked sharks were observed several times over relatively long periods of time indicating a fidelity to the seamount. The chronology of reobservations of 40 marked hammerheads during a 28-day period during July and August 1980 is shown in Fig. 12. The sex of the few sharks sexually identified is noted to the left of their identification numbers. The numbers of reobservations during each day are placed within the cells. Periods over which reobservations were made are indicated by dashed lines. During the ten visits to the seamount, a continuously decreasing number of tagged sharks were seen. This indicated that sharks were emigrating from the site, and not just mixing into local population. If one looks at the reobservations for the first 30 sharks, one finds a steady decrease in observations of 7 on 4 Aug., 5 on 5 Aug., 1 on 6 Aug., 6 on 16 Aug., 3 on 21 Aug., 3 on 22 Aug., 2 on 29 Aug., and only 1 on 26 August. After returning to the seamount for several days, marked sharks were probably moving to other locations were grouping occurred.

Despite the steady rate of emigration, a shark tagged on 30 July 1980 was observed on five different occasions over a 28-day period, and a shark tagged on 30 July 1981 was observed five times over a six week period ending on 26 September. These sharks which were repeatedly seen at the seamount, like the telemetered shark No. 13, probably moved away from the seamount to forage during the night and returned during the following day to swim among the schools at the seamount. Few sexual identifications of marked sharks were made (see Fig. 12); and for this reason, it was not

Fig. 12. Reobservations of marked sharks at El Bajo Espiritu Santo during 28-day period in July and August 1980. Days during which the study site was visited are indicated with shading. Numbers within cells indicate frequencies of reobservations during that day.


Plastic-streamer dart tags
♀ 1
2
3
4
5
6
7
8
9
10
11
12
♀13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
♂34
35
36
♀37
38
39
40
30 31 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 29 25 26
July
August
Time of year (day)

possible to determine whether females remained for longer periods at the seamount than males. This might explain the greater numbers of females in the groups there. Although one of the three marked females was reobserved at the seamount on six occasions over a period of 27 days and the single male was observed only on the same day of marking, the other two females were reobserved only on the same or next day.

One shark marked in August 1979 was observed on the seamount during the same month a year later; another was observed during the same month two years later. Few hammerhead groups were seen at the seamount during the fall, winter, and spring of 1980 and 1981, and those seen did not include the tagged sharks. It is probable that these marked sharks observed on successive years did not remain at the seamount throughout the year, but returned to it after making migratory movements.

DISCUSSION

Hamilton and Watt (1970) divided central place social systems into three overlapping categories. The most socially complex system, characterized by large numbers of individuals with complex communication systems and cooperative behavior patterns was termed a refuging system. Characteristic of such a system are large groups which remain in a small core area during the inactive phase of their diel cycle, and disperse large distances into a large feeding arena to forage either in small groups or as solitary individuals. The composition of such groups is dynamic, and aggressive encounters frequently occur among group members. Animals possessing refuging systems cited by Hamilton and Watt were diverse, consisting of the honey bee (Apis mellifera), the starling (Sturnus vulgarus), the fur seal (Callorhinus ursinus), the baboon (Papio hamadryas), and man (Homo sapiens). Some bony fishes also possess refuging social systems (Reese, 1978) as well as some delphinids (Norris and Dohl, 1980). We will argue that scalloped hammerhead sharks in the Gulf of California possess a refuging social system as well as a few other shark species.

The social system of the scalloped hammerhead resembles that of other refuging species very closely. During day most of the telemetry tagged sharks swam slowly back and forth along the seamount ridge. This core area was small compared to the extensive area of the pelagic environment in which the tagged sharks swam primarily at night. Although hammerhead No. 9 swam slowly during the day within the small km area of El Espiritu Santo for a period of 9.5 hrs, it departed from the seamount at dusk and swam rapidly in a straight line fashion over a distance of 18 km in five hrs (see Fig. 9). During the day the hammerheads at the seamount did not actively forage. Feeding responses were never observed although the sharks were often observed swimming through diffuse schools of potential prey. No feeding responses were directed at bait placed nearby large numbers of hammerheads. Feeding readiness was tested by playing back sounds (attractive to many species of sharks including Sphyrna spp.) and baiting immediately after encountering grouped sharks. Only a few hammerheads were attracted during the tests (Klimley and, 1981). The inactivity of the sharks during the day was also reflected in the smaller distances between subsequent telemetry positions at this time than at night. Hammerhead No. 13 moved 8 km away from the seamount towards the center of the Gulf of California (and probably moved farther since the shark was continuing in this direction when the tracking was aborted) before returning to the seamount on the following day. This tracking together with the continued reobservation of many marked sharks at the seamount over considerable periods of time (see Fig. 11) indicated that a rhythmical dispersion of sharks was occurring from the seamount into the pelagic environment late in the day and back again early in the morning. The separate departures of members of the pairs of tagged sharks indicated that the hammerheads might be leaving either in small groups or as solitary individuals (see Fig. 12). As will be discussed elsewhere (chapter 3), the scalloped hammerhead social system also resembles a refuging system in the highly dynamic composition of its schools and the presence of aggression among group members. Complex communicatory behavior may also exist within the schools.

Such behavior is presently being studied by the principal author.

Other species of sharks also form refuging groups. The gray reef shark was found by Nelson and Johnson (1980) to mill slowly in groups in a small core area of its home range. The feeding motivation of school members was never examined by exposing a school to feeding stimuli such as fish odors or struggling fish sounds, but the sharks appeared uninterested in local fishes which were potential prey. At dusk the gray reef sharks moved away from this core area and presumably foraged, usually in much shallower areas than the daytime core area in Avatoru Lagoon, Rangiroa Atoll. Johnson (1978) presented a diagram of a three-day tracking of a gray reef shark at Rangiroa Atoll. The shark, tagged at a particular location within the lagoon on the first day, returned to this location at the same time both on the second and third days of the tracking. Tracking data from Nelson and Johnson (1980) indicated that the schools broke up at night, but this was not directly observed. While at the core area the gray reef sharks exhibited a diversity of behavior patterns, but these appeared not to be aggressive. Nelson and Johnson (1980) observed that the reef whitetip shark also remained inactive at times in small groups during the day in caves with sandy floors, and the same individuals would repeatedly return to the same caves over several successive days. Randall (1977) on one occasion observed five individuals within a cave. Nelson and Johnson (1980) noted that at dusk the whitetips left their home caves and moved over an area of a square km. Generally, the whitetips did not swim in groups. Little daytime foraging was observed by the reef whitetips by either Randall or Nelson and Johnson, and this convinced them that these sharks were nocturnal feeders. Another possible refuging species is H. portusjacksoni. McLaughlin and O'Gower (1971) found groups of up to 16 bullhead sharks remaining quiescent during the day in caves on a rocky reef. Although the investigators did not follow the sharks at night, they concluded that the sharks swam over both the reef and soft substrates during the night from their diet of benthic invertebrates and lack of activity during the day.

The refuging social systems in these species of sharks may function to optimize energetic output by reducing unessential swimming activity. Energy is conserved during the day as the sharks slowly swim back and forth along the small seamount ridge, yet the sharks can remain at a point central in their feeding area. This point may also be used as a reference for their daily movements. Additional benefits accrued from remaining at the seamount in groups might be the ease with which social activies leading to mating could occur as well as possible protection from predators.

CONCLUSIONS

The scalloped hammerhead shark possesses a refuging social system in the Gulf of California. Individuals most often remain in schools during the day swimming at a single location along a dropoff into deep water. They range widely at night probably within small groups or as individuals presumably to forage in the pelagic environment. At El Bajo Espiritu Santo sharks tagged with ultrasonic telemetry tags swam back and forth along the seamount ridge throughout the day. They did not appear to position themselves at different parts of the seamount when the currents changed from a direction parallel to the ridge to a direction perpendicular to the ridge. For this reason, we do not believe that they were seeking a location where the eddies present enabled them to reduce their effort expended in swimming. During the day distances moved were less than those moved after the sharks departed from the seamount either late during the day or at night. A shark was tracked as far as 8 km from the seamount only for it to return to the seamount on the following day. It is felt that the rhythmical dispersal of scalloped hammerheads at night into the pelagic environment and return to the seamount is common among sharks at the seamount judging from the prompt returns of some telemetry tagged sharks and the repeated observations of marked sharks at the seamount over a relatively long period of time. The separate departures of members of pairs of sharks tracked simultaneously suggested that the hammerheads either fora during the night in small groups or alone. We believe th this social system benefits the hammerheads by ensuring that they remain in the center of their feeding arena while conserving energy during the day when they are not feeding. It is possible that the schooling habit also facilitates social interactions.

ACKNOWLEDGEMENTS

We would like to express our appreciation to all of those who participated in the arduous tracking activities such as S. Brown, F. Galvan, P. Johnson, P.B. Klimley, R. Martinez, S. Michael, R. Rodriquez, J. Teeter, and F. Wolfson. Paul Sikkel helped with the analysis of the telemetry data. We would also like to acknowledge the assistance of the crew of the vessel, Don Jose del Abaroa, and T. Means of Baja Expeditions for being so cooperative and allowing the vessel to remain offshore at night on the seamount. William Newman provided the use of his fathometer/odometer for mapping the seamount topography. Funds for the rental of the Don Jose del Abaroa were provided by the University of California's Ship Fund. Salary support for the authors was provided by the Office of Naval Research (Contract-N00014-77-C-0113: Donald R. Nelson, principal investigator). This report consititutes part of the doctoral dissertation of the senior author at the University of

California, San Diego under the guidance of Richard H. Rosenblatt.

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CHAPTER 5: REPRODUCTIVE MATURITY IN THE SCALLOPED HAMMERHEAD (SPHYRNA LEWINI)

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ABSTRACT

The size of onset of reproductive maturation was determined for scalloped hammerhead sharks caught in the Gulf of California. The minimum size of a mature male hammerhead shark was 163 cm, and all males 218 cm and larger were mature. The indicies of maturity used were a disproportional increase in clasper, testis, and epididymis size in relation to total length and the presence of spermatophores in the ampulla ductus deferens. The minimum size of maturity for female hammerhead sharks of 217 cm was determined from the presence of ovarian eggs in all stages of production and resorption. Wounds and scarring either anterior or lateral to the first dorsal fin occurred more often on females than males. Most of the females possessing these contusions were immature. Thus, these contusions were not the result of courtship behavior as in other sharks but of aggressive interactions between females.

Fall and winter catch samples were too small for indices of recent reproduction such as clasper swelling and

spilling of semen in males and presence of spermatozoa in the uterus of females to indicate whether reproduction in the scalloped hammerhead was seasonal. Multiple peaks indicative of seasonal reproduction were not evident in size frequency distributions of free-swimming sharks and sharks caught by long line and gill net.

INTRODUCTION

Although the male and female reproductive systems have been described for phylogenetically diverse species sharks (Daniel, 1922; Metten, 1941; Matthews, 1950; Teshima and Mizue, 1972; Jensen, 1976; and Pratt, 1979), the onset of reproductive maturity has been described quantitatively for only two carcharhinid species (Jensen, 1976; Pratt, 1979). In the following pages, I will briefly describe the reproductive system of a sphyrnid species, the scalloped hammerhead (Sphyrna lewini), describe changes in its reproductive system associated with the onset of maturity, and determine the range of sizes over which individuals become capable of reproducing. I will also offer some evidence for the lack of seasonality in their reproduction.

METHODS

Sampling

The scalloped hammerhead sharks were caught by myself and local fishermen along the coast of Baja California Sur from the fishing village Juncalito (25 deg 51 min N., 111 deg 19 min W.) to San Jose del Cabo (23 deg 03 min N., 109 deg 39 min W.) in the Gulf of California. The sharks were caught either on bottom long lines or gill nets. This fishing gear has been described in Applegate _et al_. (1979). The gear was deployed over sandy bottoms at depths ranging from 4 to 320 m from just off the coast to distances as far as 16 km at offshore seamounts.

Male Reproductive Anatomy and Indices of Maturity

The reproductive system of the male scalloped hammerhead (Fig. 1) consists of the testis, a long cylindrical organ with rounded ends, embedded in the long, irregularly shaped epigonal organ. Spermatazoa (Fig. 2B) produced in the testis pass through small tubules into the epididymis, a convoluted, tubular organ leading posteriorly to the ductus deferens. The testis begins to produce spermatozoa as the male reaches maturity. The ductus deferens increases in size to store spermatophores (A) formed there once the male reaches maturity. The ductus deferens gradually increases in width as it passes posteriorly on the dorsal surface of the kidney until it enlarges substantially to form the ampulla ductus deferens. It terminates in the urogenital sinus which opens into the cloaca. The

Fig. 1. Diagram of the reproductive system of the male scalloped hammerhead shark (_Sphyrna lewini_).

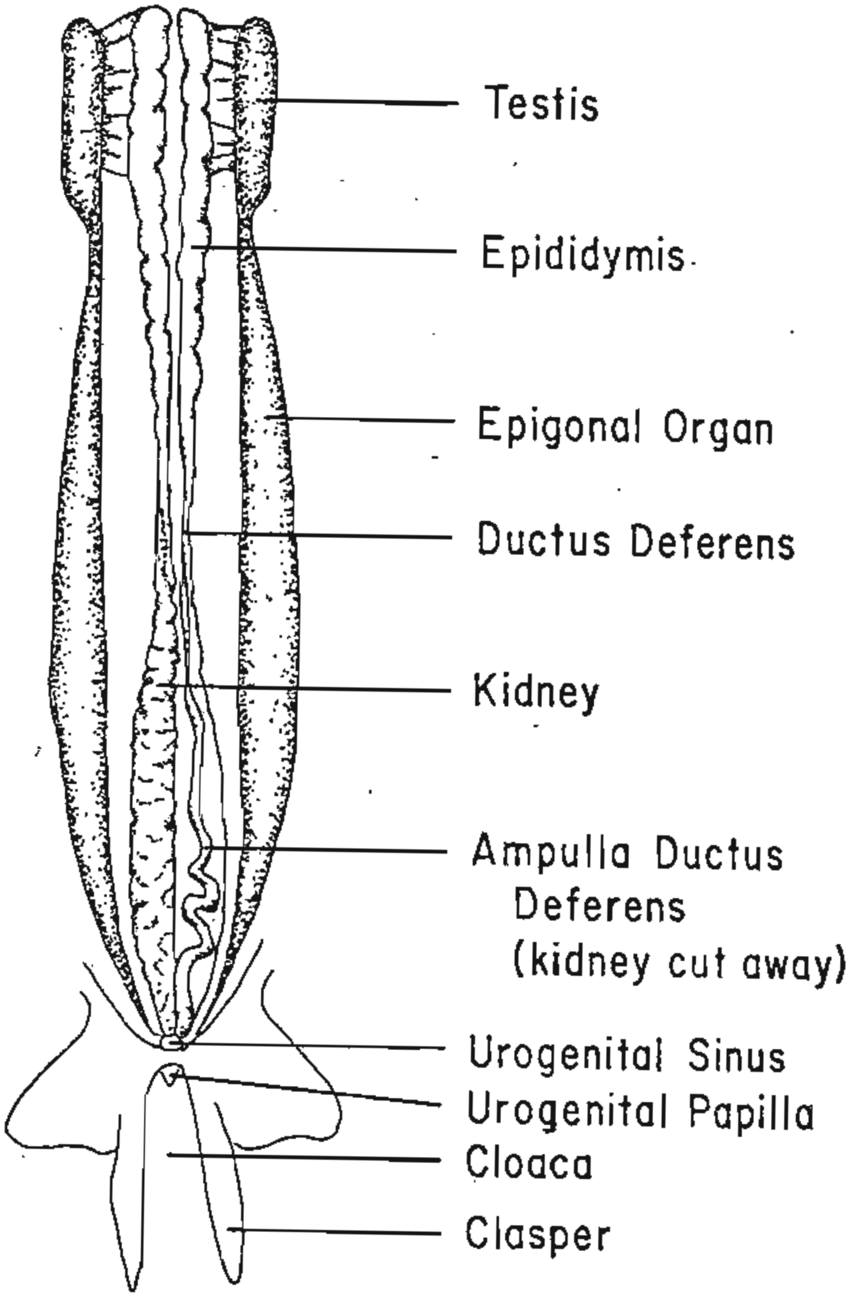
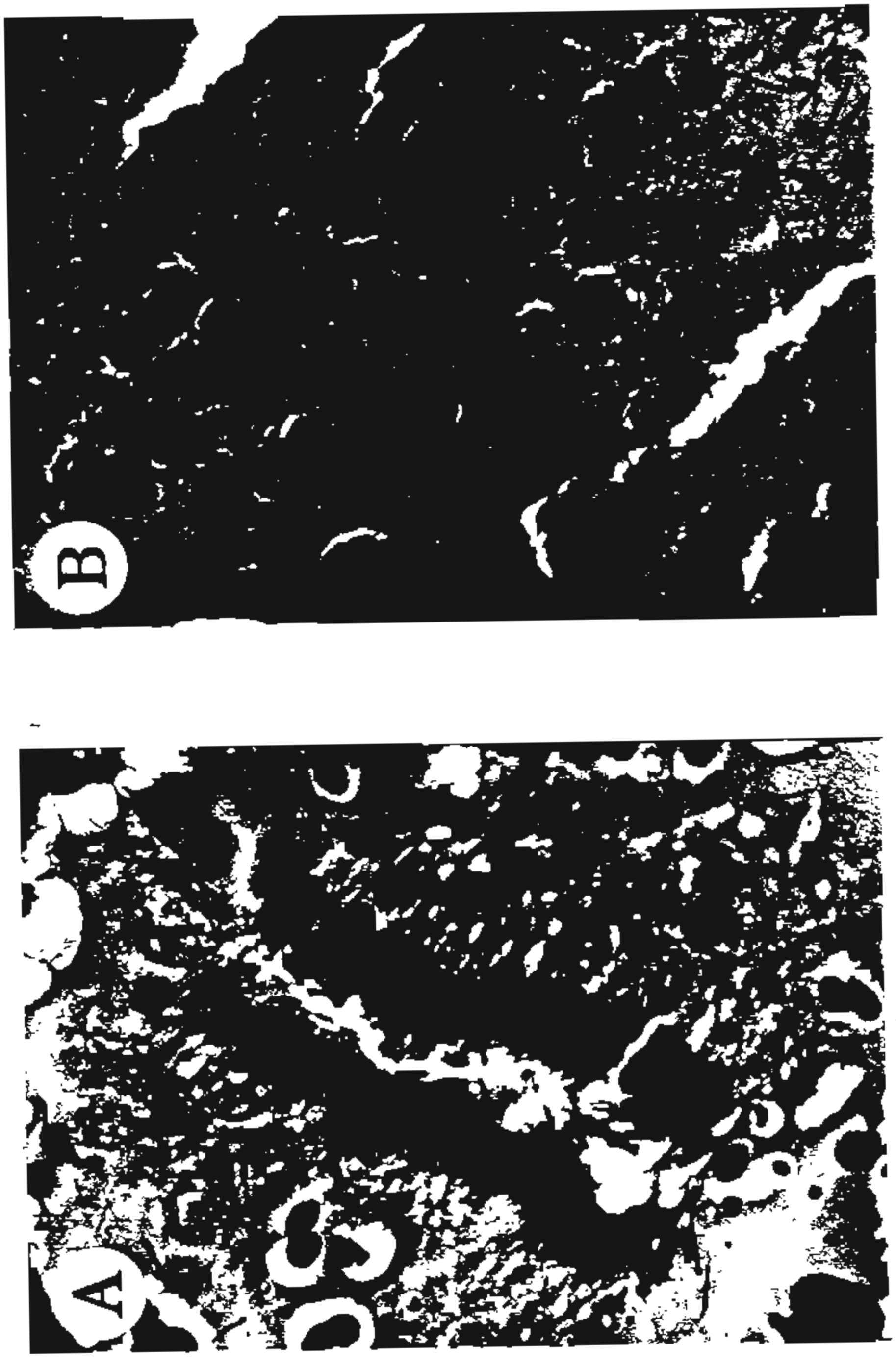

Testis
Epididymis
Epigonal Organ
Ductus Deferens
Kidney
Ampulla Ductus Deferens (kidney cut away)
Urogenital Sinus
Urogenital Papilla
Cloaca
Clasper

Fig. 2. Micrographs of spermatophore (A) and spermatozoa (B) taken from the ampulla ductus deferens of a male scalloped hammerhead shark.


B
A

spermatophores are propelled with water expelled from the subcutaneous siphon sac through the clasper, a scroll-shaped calcified appendage, into the vagina of the female during copulation. For a more detailed description of the reproductive system of the anatomically similar blue shark consult Pratt (1979).

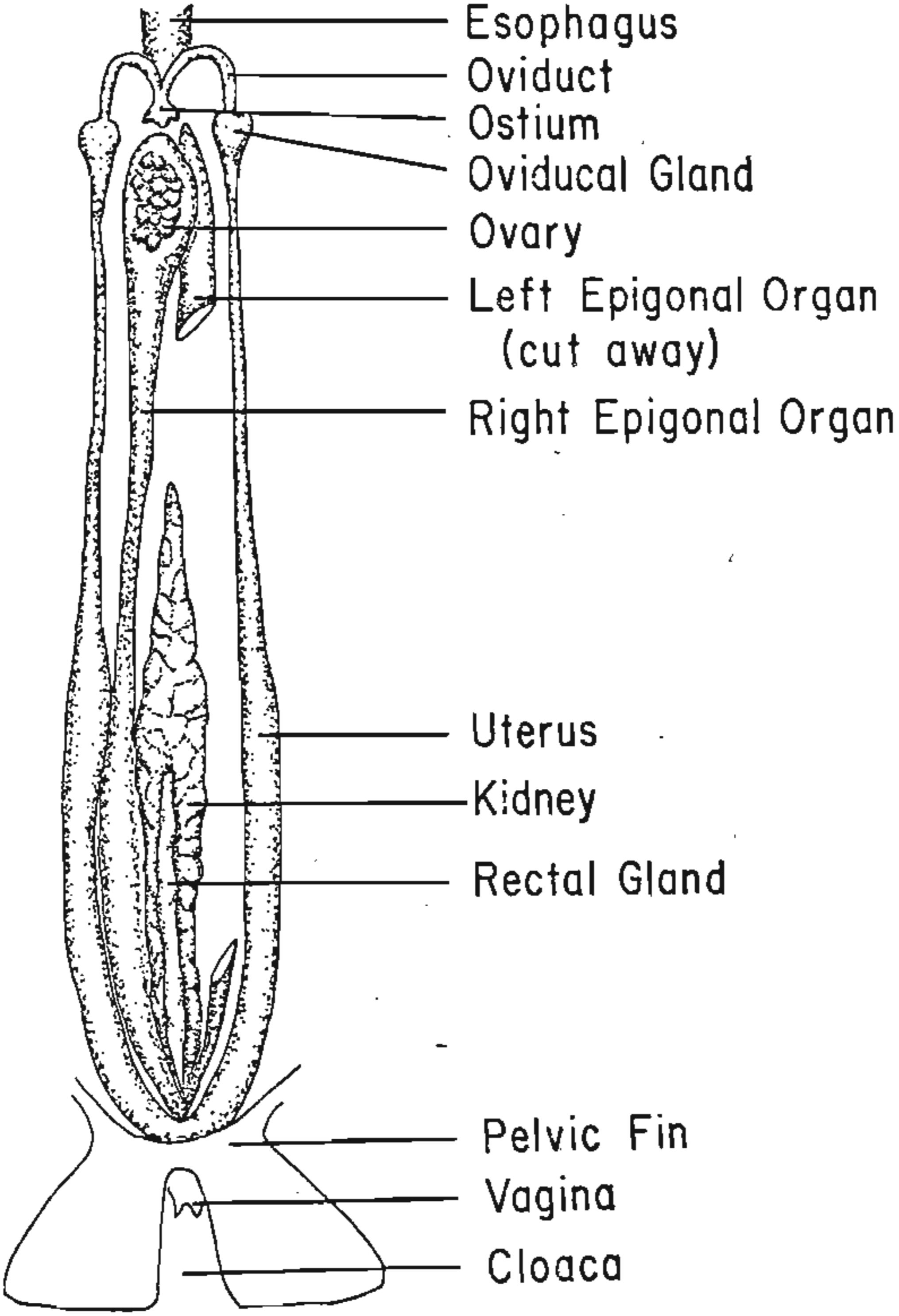
Several anatomical indices of reproductive maturity were utilized to determine the range of sizes over which the male scalloped hammerhead becomes mature. Three indices based on clasper morphology described by Clark and Schmidt (1965) were used. In adult males they noted: 1) the clasper head was fully formed and spreadable into a fanlike pattern, 2) the cartilage proximal to the clasper head was rigid from calcification, and 3) the clasper could be rotated medially so that the distil half of the clasper was perpendicular to the shark's longitudinal axis. An increase in clasper growth in relation to overall body growth was used by Aasen (1961) and Jensen (1976) to identify the onset of maturity in the blue and bull sharks, respectively; but unsuccessfully used by Pratt (1979) in the blue shark. Since the index had been successfully used to determine maturity by some investigators, clasper length (measured from the axil of the right pelvic fin to the tip of the clasper) and total length (from the tip of upper caudal lobe to the tip of the snout) were measured. Although Pratt (1979) was unable to demonstrate an increase in the growth of the testis and the epididymis in relation to total length at onset of maturity, I measured testis length (the distance between its rounded ends) and epididymis width (the maximum width along its length), and plotted them as a function of total length. In order to determine whether these dimensions increased disproportionately with total length at onset of maturity, a dimension of a non-reproductive character was also plotted as a function of length. Mouth width was chosen since it is associated with feeding. Although the presence of spermatozoa were not found by some investigators to be unequivocally indicative of reproductive maturity (Springer, 1960; Clark and Schmidt, 1965; and Bass *et al.*, 1975), Pratt (1979) believed their presence to be indicative of sexual maturity. The presence of spermatophores was determined with the technique of Pratt (1979). The ampulla ductus deferens was disected away from the kidney at its thickest part, cut in a cross-sectional manner, and squeezed so that the seminal fluid would flow onto a slide. The slide was then immersed briefly in Bouin's Fixative in order to preserve the sample and stained with methylene blue prior to examination under a compound microscope in the laboratory.

The claspers were also examined for vascular congestion and spilling of semen upon rotation. These characteristics were believed by Clark and Schmidt (1965) to be indicative of recent copulatory activity. The presence of these characteristics at one time of the year and not at others would imply seasonal reproduction. In order to distinguish such reproduction, I further plotted the total lengths of free-swimming sharks (see chapter 2 for measuring technique) and sharks from fishermen catches in histograms. Periodic peaks in these histograms would reflect seasonal birth peaks. Cumulative percentages over the length range were also plotted on a probability scale in the manner described by several investigators (Harding, 1949; Cassie, 1954; and Bhattacharya, 1967). Separate normal frequency distributions are evident in such a plot as inflections on the resulting curve. If such inflections were due to seasonal birth peaks, they would also be periodic. Size class intervals of 2 cm were chosen in these plots because classes of this size were small relative to the 16 to to 10 cm growth per year throughout the life of Carcharhinus leucas (Thorsen and Lacy, 1982) (growth measurements were unavailable from a sphyrnid shark).

Female Reproductive Anatomy and Indices of Maturity

The reproductive system of the female scalloped hammerhead shark (Fig. 3) consists of a single teardrop shaped right ovary at the end of the elongate, irregularly shaped epigonal organ. Follicles, ova, and corpora lutea are embedded in a dense layer of connective tissue. The function of the flattened epigonal organ, which terminates in the ovary is uncertain. The ostium is a funnel-shaped opening

Fig. 3. Diagram of the reproductive system of the female scalloped hammerhead shark, _Sphyrna lewini_.


Esophagus
Oviduct
Ostium
Oviducal Gland
Ovary
Left Epigonal Organ
(cut away)
Right Epigonal Organ
Uterus
Kidney
Rectal Gland
Pelvic Fin
Vagina
Cloaca

just anterior to the ovary, and it bifurcates into right and left oviducts which lead to the small, heart-shaped oviducal glands. After the oviduct leaves the oviducal gland, it remains small in diameter for a short distance until it expands to become the uterus. The two uteri are attached at their posterior ends to form the common vagina. The vagina is separated from the cloaca by a thin membrane, the hymen. Ova shed from the ovary enter the oviduct through the ostium, pass to the oviducal gland where they are probably fertilized, and develop there for some time before completing their development as embryos with placental attachments in the uterus.

An attempt was made to use several indices to determine the range of sizes over which female scalloped hammerheads reached maturity. Clark and Schmidt (1965) described differences between juvenile, subadult, mature-virgin, and mature-mated females based on the anatomy of the urogenital orifice of the sand (_Odontaspis taurus_), bull, sandbar (_Carcharhinus milberti_=_plumbeus_), tiger (_Galeocerdo cuvieri_, and lemon sharks (_Negaprion brevirostris_). According to Clark and Schmidt, in the young female the vaginal orifice was visible only as a small, pin-sized opening. Depending upon the age and state of maturity of the young female, a thin line passed anteriorly from the genital opening different distances. In the juvenile the orifice was not visible. In the unmated, mature female, the membrane was thin and delicate; in the mature, mated female the membrane was ruptured. Although I carefully examined the urogenital regions of the females to identify such differences, I did not detect such clear anatomical differences in female scalloped hammerheads. The hymens of both large and small individuals were ruptured, and there appeared no correlation between rupture and the presence of mature ova.

Pratt (1979) used the maximum diameter of individual ova in the ovary as an index of maturity in females. Ovum growth increased upon the onset of maturity at a greater rate than overall growth. For this reason, maximum ovum diameter was measured and plotted as a function of total length. Another indicator of the onset of female maturity in some shark species is the presence of wounds and scarring inflicted by males during courtship. Suda (1953) described scars on female blue sharks. He concluded that the scars were the result of reproduction because they were present only at those times when mature ova were present in the ovary and embryos in the uteri of the females. Stevens (1974) also found scarring on females judged reproductively mature. Although female scalloped hammerheads rarely had deep cuts, they often had small, oval contusions where dermal denticles had been scraped off. Both white, recently inflicted wounds and black, past inflicted scarring were sketched on profiles of the dorsal, ventral, and left and right aspects of scalloped hammerheads. Contusions were recorded from sharks photographed while free-swimming and sharks in fishermen catches. The total lengths of some scarred, free-swimming sharks were measured photogrammetrically.

In order to determine whether females had recently copulated, the right uterus was cut in a cross-sectional manner near its base and its anterior end was squeezed to force out its contents onto a slide. The sample was preserved, as described before, and later viewed under a compound microscope for spermatozoa and spermatophores. As an indicator of past copulatory activity, the oviducal gland was cut in a cross-sectional manner at its midpoint, the anterior section squeezed, and the organ drawn across a slide. The slide was later also examined for reproductive products. Due to the presence of spermatozoa in the oviducal gland of gravid females, and the inability of spermatozoa to pass through the uterus to the oviducal gland at this time, Pratt (1979) argued that in the blue shark spermatozoa could remain stored in the gland for longer than 9 to 12 months, the period of gestation.

RESULTS

Male Maturity

General capture information and measurements used indices of maturity and ripeness for 37 male scalloped hammerhead sharks are summarized in Table 1. The anatomical indices did not appear to be accurate measures of maturation. Although most of the larger sharks which were mature by indices such as clasper length and the presence of spermatozoa possessed claspers which were rigid and rotatable with heads that were spreadable (see hammerheads Nos. 1-3, 5-7, and 33 in Table 1), some smaller sharks which were immature by the indices mentioned before possessed these same characteristics (see hammerheads Nos. 15, 22, and 31 in Table 1). For this reason, these were not considered useful indices.

Clasper length, plotted as a proportion of total length, appeared to be most effective in distinguishing mature from immature males (Fig 4A). Clasper length ranged from 4.5 to 16.5 cm over the small total length range of 163 to 170 cm. This large amount of variation in clasper length reflects a period of rapid growth associated with the onset of maturity. Similar, yet slightly less, variation was found over the same body length range in testis length (B) and epididymis width (C). However, similar variation did not occur for mouth width, the non-reproductive character associated with feeding (D). In order to better demonstrate this difference, clasper lengths and mouth widths were converted to percents of their maximum values and plotted together as a function of total length (Fig. 5). Mouth

Table 1. General capture information and indices of maturity and ripeness in male scalloped hammerhead sharks caught in the Gulf of California.

Ident. No.	Date	Length (mm)	Length (mm)	Head Spred.	Clasper Head Rigid	Rotat-able	Swollen	Spills Semen	Testis Length (mm)	Epidy. Width (mm)	Sperm. Am. Duc. Defer.
1	29 July 1980	2440	233	yes	yes	yes	no	no	233	22	yes
2		2140	177	yes	yes	yes	no	no	196	16	yes
3	31 July 1980	1640	165	yes	yes	yes	yes	yes	195	15	yes
4	2 Aug. 1980	1625	80	no	no	yes	no	no	55	10	undet.
5	3 Aug. 1980	2140	180	yes	yes	yes	no	no	216	20	yes
6	4 Aug. 1980	2358	181	yes	yes	yes	yes	no	180	22	yes
7		2058	163	yes	no	yes	yes	yes	209	19	yes
8	5 Feb. 1981	1250	45	yes	no	no	no	no	107	7	no
9		1390	52	yes	no	no	yes	yes	120	8	no
10		1315	40	yes	no	no	yes	yes	90	6	yes
11	7 Feb. 1981	1130	40	no	yes	no	yes	yes	83	5	undet.
12		1285	46	no	yes	yes	no	no	127	10	no
13		1103	40	yes	yes	no	no	yes	96	6	undet.
14		1009	35	no	no	no	yes	yes	87	4	undet.
15	5 May 1981	1460	68	no	yes	yes	no	yes	147	13	no
16	8 May 1981	1007	41	no	no	yes	no	no	80	5	no
17		1110	36	no	no	yes	no	no	79	5	no
18		1010	35	no	no	yes	no	no	70	4	no
19		978	32	no	no	no	no	yes	71	5	no
20		1070	41	no	no	yes	no	no	68	4	no
21		1000	38	no	no	no	no	yes	74	4	no
22		1260	49	no	yes	yes	no	yes	118	4	no
23		1020	30	yes	no	no	no	yes	65	4	no
24		1072	38	yes	no	no	no	yes	71	5	no
25		1010	28	no	no	no	no	yes	66	4	no
26		785	22	no	no	no	no	yes	28	3	no
27		1023	33	yes	no	no	no	yes	78	4	no
28		1010	34	no	no	no	no	yes	69	6	no
29		1020	31	yes	no	no	no	yes	69	6	no
30		1005	35	yes	no	no	no	yes	70	5	no
31	13 May 1881	1655	118	no	yes	yes	no	no	180	14	no
32		1965	54	no	no	yes	no	no	171	5	no
33	13 July 1981	1879	142	yes	yes	yes	yes	yes	198	20	no
34		1185	44	no	no	no	no	no	112	6	undet.
35		1700	45	no	no	no	no	no	111	6	undet.
36		1100	33	no	no	no	no	no	65	5	undet.
37	8 Sept. 1981	1900	186	yes	yes	yes	yes	yes	150	21	no

Fig. 4. Scattergram of three reproductive and one non-reproductive characters as a function of total length. The reproductive characters are clasper length (A), testis length (B), and epididymis width (C). The non-reproductive character is mouth width (D).

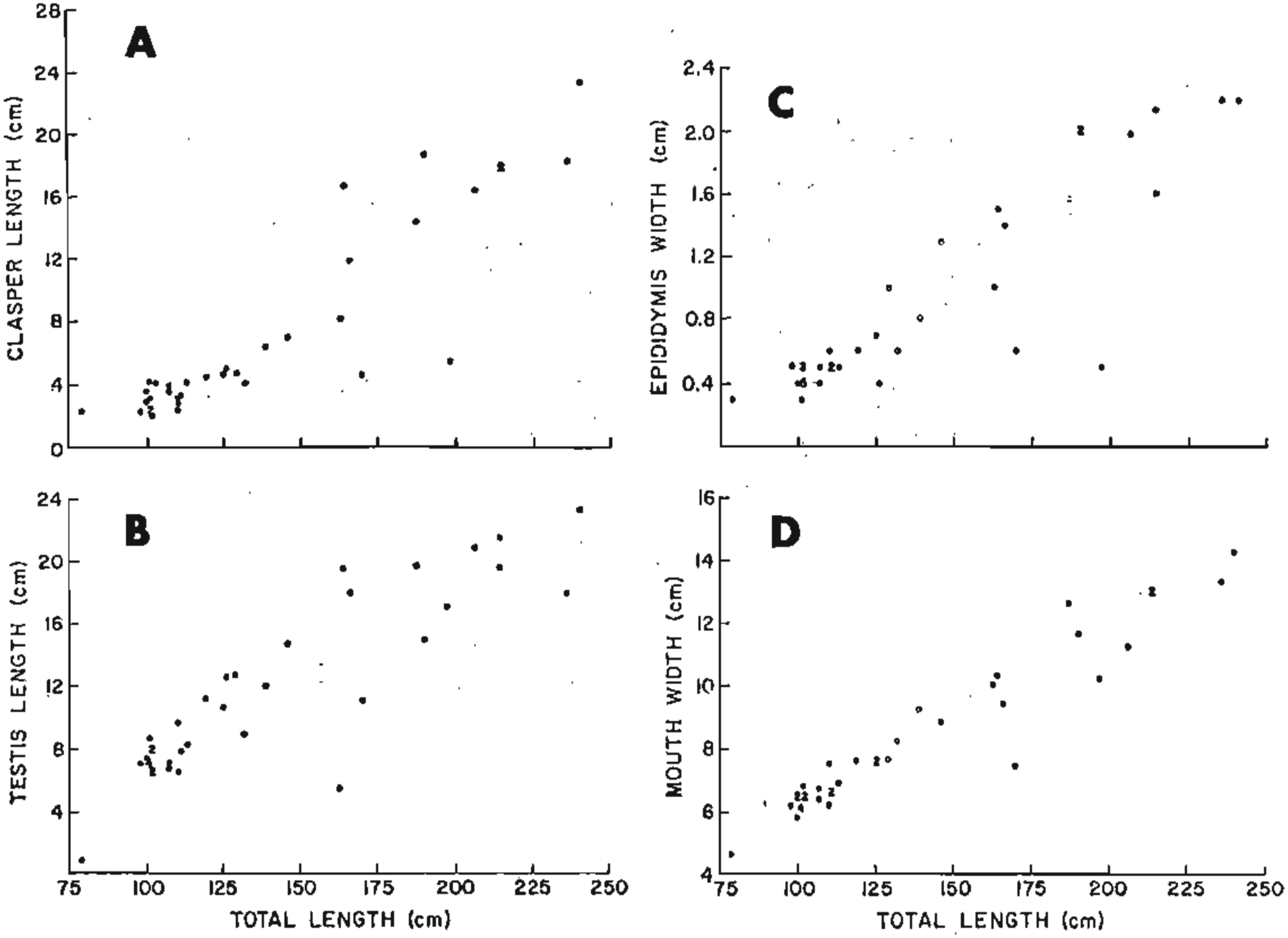
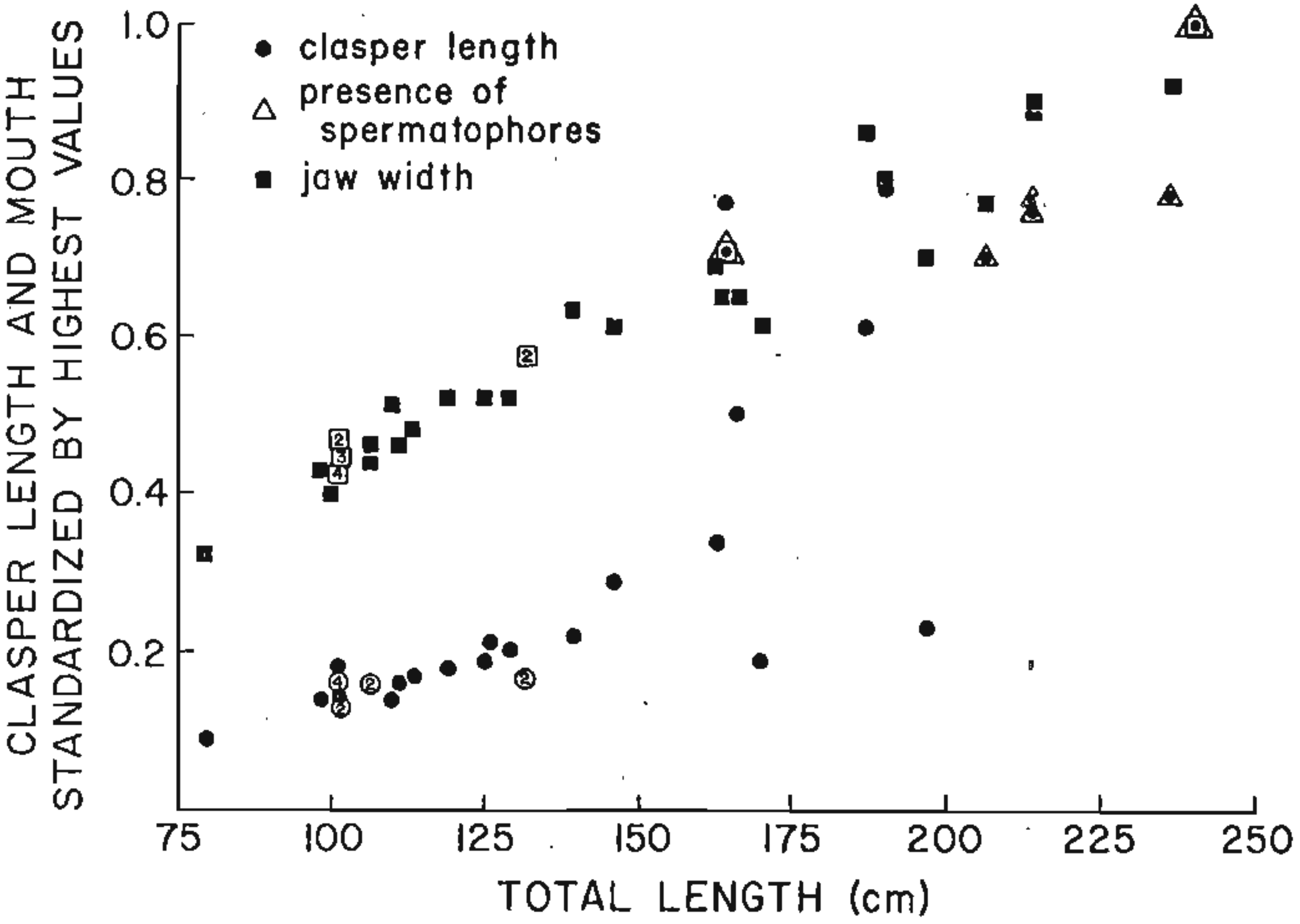

A
B
C
D
CLASPER LENGTH (cm)
TESTIS LENGTH (cm)
EPIDIDYMIS WIDTH (cm)
MOUTH WIDTH (cm)
TOTAL LENGTH (cm)
TOTAL LENGTH (cm)
0
4
8
12
16
20
24
28
2.4
2.0
1.6
1.2
0.8
0.4
4
6
8
10
12
14
16
75
100
125
150
175
200
225
250

Fig. 5. Scattergram of clasper length (circles) and mouth width (squares) standardized by the division by their highest values as a function of total length. Presence of spermatophores indicated by triangles.


CLASPER LENGTH AND MOUTH
STANDARDIZED BY HIGHEST VALUES
1.0
0.8
0.6
0.4
0.2
75
100
125
150
175
200
225
250
TOTAL LENGTH (cm)
● clasper length
△ presence of spermatophores
■ jaw width
2
3
4
2
2
4
2
2

width (squares) increased at a constant rate over the entire range of total lengths. Thus, there was a strong linear relationship between mouth width and total length of the shark (r=0.93). Clasper length (circles), on the other hand, was initially smaller in relation to its ultimate size than mouth width. Clasper length increased at a constant rate until the shark reached a total length of 163 cm, increased more rapidly to 170 cm, and then resumed increasing at the prior rate. This sudden change in growth rate between 163 and 170 cm was reflected in a weaker linear relationship between clasper growth and that of overall growth of the shark (r=0.81). Coupled with the disproportionate change in clasper length over this body length range was the increasing prevalence of spermatophores (triangles) in the ampulla ductus deferens of male sharks at lengths 163 cm and larger. It is believed that male sharks become sexually mature over a range of from 163 to 216 cm.

The indices of recent reproductive activity provided inconclusive results. Four of 11 mature sharks caught during the fall possessed swollen claspers indicative of recent copulation. The two mature sharks caught during the spring did not possess swollen claspers. Two out of nine mature sharks caught during the summer and one caught in the fall emitted semen from their claspers. Two mature sharks caught in the fall did not emit semen from their claspers. Conclusions on seasonal reproduction can be made using these indices only if more mature sharks are examined. It would be particularly instructive to examine sharks caught more southerly along the Sinaloa coast during the fall and winter when mature sharks may not be reproductively active. Seasonal reproduction was not evident in the size-class analysis (Fig. 6). Conspicuous birth peaks were not present in the histograms of shark sizes in classes separated by 16 to 10 cm in either the larger free-swimming sharks (lefthand) or the smaller sharks from fishermen catches (righthand). Neither were the peaks which were present periodic. Conspicuous inflections in the curves for free-swimming (solid circles) and captured sharks (clear circles) did not occur over the smaller sizes as is usually the case for seasonal birth peaks. Furthermore, the weak inflections present were aperiodic. The absence of periodic and discrete peaks and inflections may indicate all year reproduction.

Female Maturity

General catch information and total lengths as well measurements used as indices of reproductive maturity and ripeness are summarized for 26 female sharks in Table 2. Maximum ovum size, plotted as a function of total length, is shown in Fig. 7. The smallest total length of a female scalloped hammerhead with ova in various stages of growth and resorption, indicating one or more generations of egg production, was 217 cm. Only two females had spermatozoa in

Fig. 6. Histograms of size frequency distribution of free-swimming (lefthand) and captured (righthand) scalloped hammerheads in the Gulf of California. Curves of cumulative frequencies on probability scale for free-swimming (solid circles) and captured (clear circles) hammerheads.

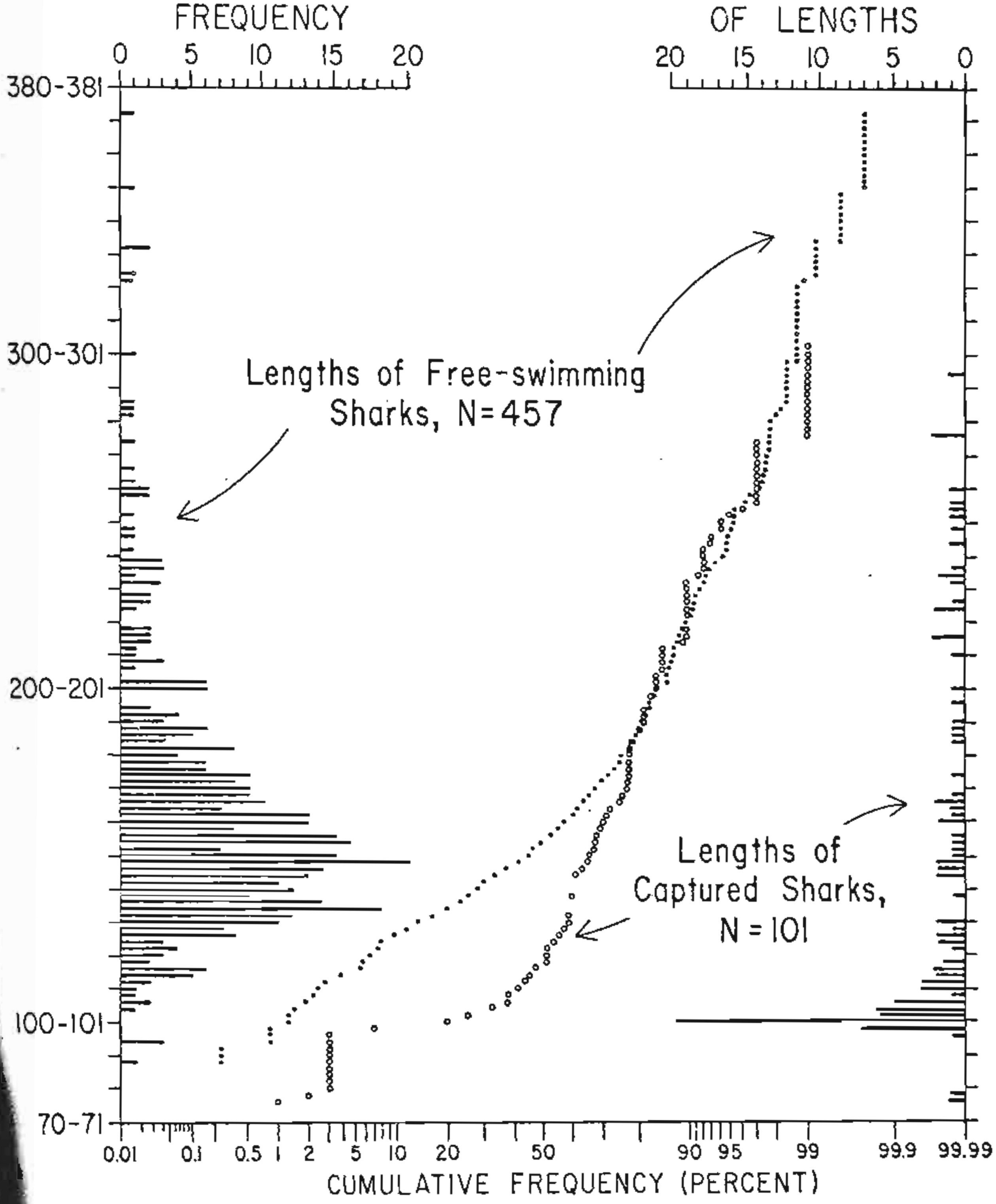
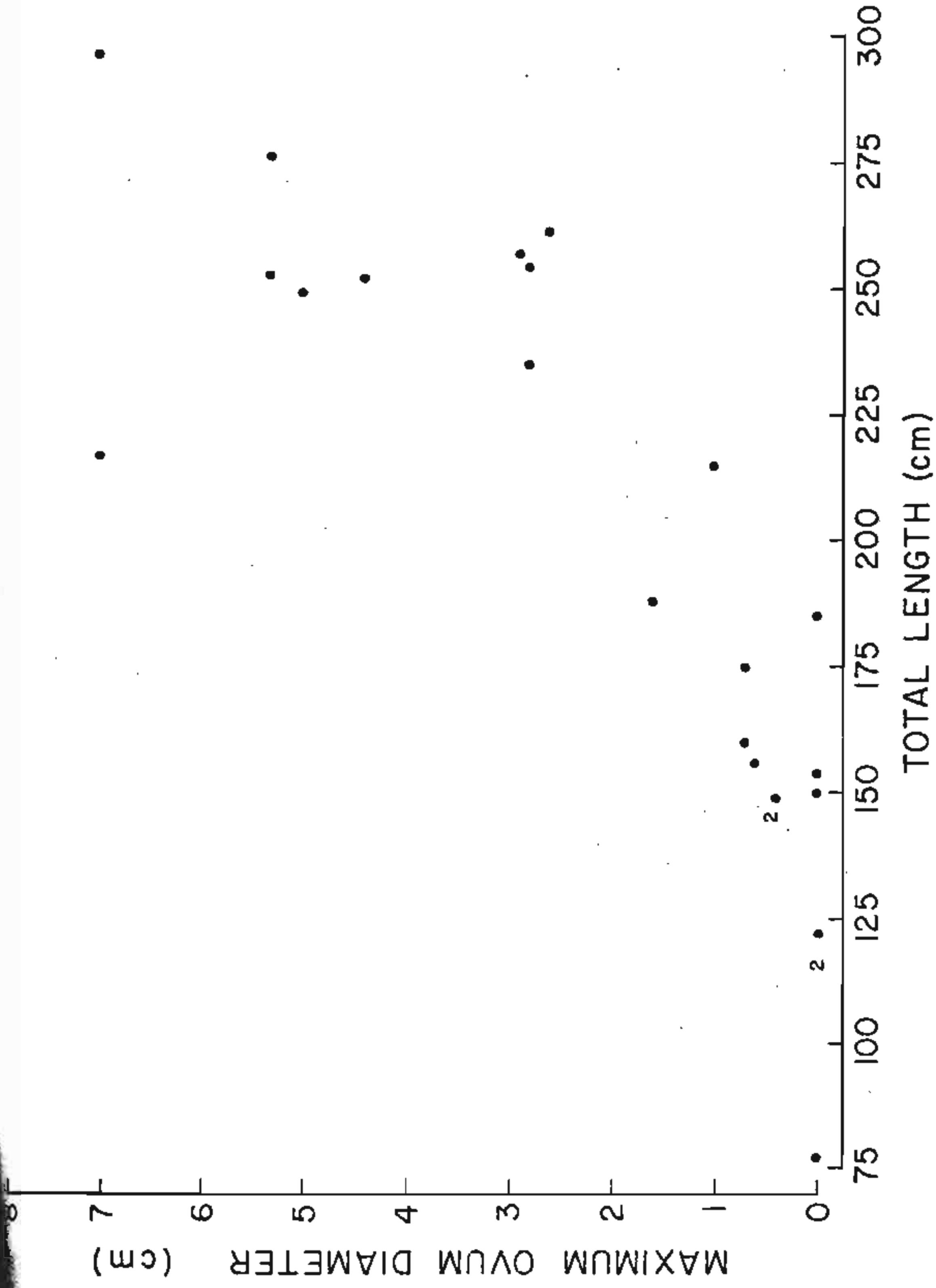

FREQUENCY
OF LENGTHS
0 5 10 15 20
20 15 10 5 0
380-381
300-301
200-201
100-101
70-71
Lengths of Free-swimming Sharks, N=457
Lengths of Captured Sharks, N=101
0.01 0.1 0.5 1 2 5 10 20 50 90 95 99 99.9 99.99
CUMULATIVE FREQUENCY (PERCENT)

Table 2. General capture information and indices of maturity and ripeness of female scalloped hammerheads caught in the Gulf of California.

Ident. No.	Date	Total Length (mm)	Max. Ovum Diam. (mm)	Sperm. in Uterus	Sperm. in Ovid. Gland
1	22 July 1980	2610	26	undet.	undet.
2	2 Aug. 1980	1883	16	undet.	undet.
3	5 Feb. 1981	1163	<1	no	no
4	28 April 1981	1850	<1	no	no
5	4 May 1981	1150	<1	no	no
6	8 May 1981	770	<1	no	no
7	13 May 1981	1450	4	no	no
8		1220	<1	no	no
9		2960	70	no	no
10	14 May 1981	1490	4	no	no
11		1460	5	no	no
12		1563	6	no	no
13		1500	<1	no	no
14		1600	7	no	no
15	13 July 1981	1750	7	no	undet.
16	14 July 1981	1540	<1	no	no
17	29 July 1981	2565	29	no	no
18		2145	10	no	no
19	8 Aug. 1981	2517	44	no	no
20	9 Aug. 1981	2168	70	no	no
21	12 Aug. 1981	2350	28	no	no
22	19 Aug. 1981	2544	28	yes	yes
23		1665		no	yes
24	8 Sept. 1981	2485	50	no	undet.
25		2530	53	no	undet.
26		2760	53	no	undet.

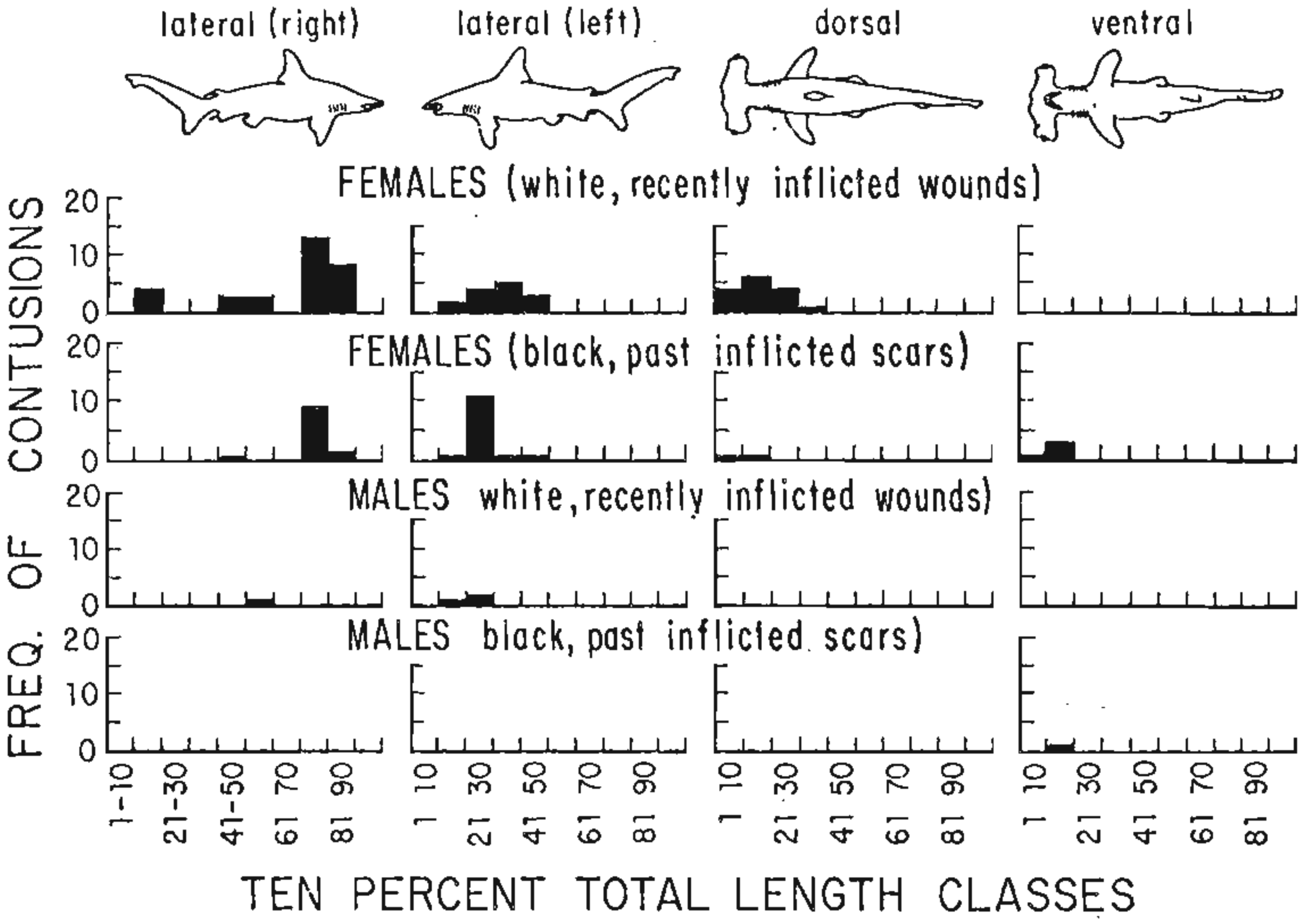
Fig. 7. Scattergram of maximum ovum diameter as function of total length.


MAXIMUM OVUM DIAMETER (cm)
TOTAL LENGTH (cm)
0
1
2
3
4
5
6
7
8
75
100
125
150
175
200
225
250
275
300
2
2

their uteruses. One 254 cm female with an ovum maximum of 2.8 cm had spermatozoa both in her uterus and in her oviducal gland. A 167 cm female with an unknown maximum ovum diameter also possessed spermatozoa in her uterus. The presence of spermatozoa in this small female is enigmatic, possibly it was due to a miscopulation.

Females bore numerous contusions thought at first to be inflicted by males during copulatory activity, as had been observed in other species of shark. Several lines of evidence led to this premature conclusion. The frequencies of white wounds and black scars occurring within 10-percent divisions of different profiles of free-swimming females are shown in Fig. 8. The contusions were recorded from film taken during July and August 1970. Ninety-two contusions occurred on females but only 5 contusions occurred on males. The 18.4:1 ratio of female to male contusions was much greater than the 3.1:1 ratio of females to male sharks at the locations visited during this time (see Klimley and Nelson, 1981). The scrapes occurred non-randomly on the torso. They occurred most frequently anterior or lateral to the first dorsal fin. Females possessing them were not always sexually mature as should be the case if they were precopulatory in nature. Eleven of 16 scarred females were smaller than the smallest sexually mature female of 217 cm judged by the presence of ova of various stages of development.

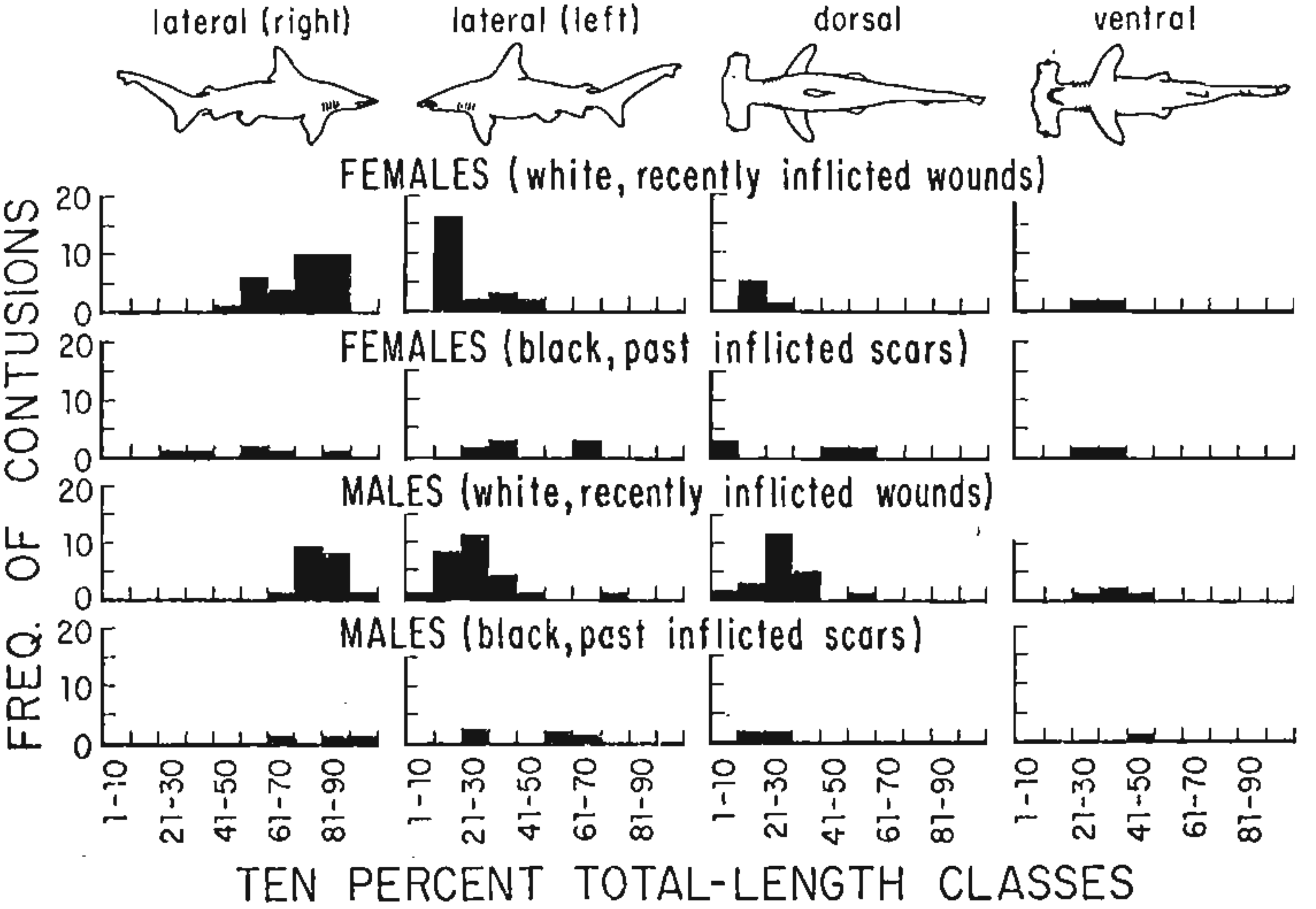
Fig. 8. Frequency of wounds and scars occurring within 10-percent divisions of the total length of free-swimming hammerheads in the Gulf of California during July and August 1979.


lateral (right)
lateral (left)
dorsal
ventral
FEMALES (white, recently inflicted wounds)
FEMALES (black, past inflicted scars)
MALES white, recently inflicted wounds)
MALES black, past inflicted scars)
FREQ. OF CONTUSIONS
20
10
0
1-10
21-30
41-50
61 70
81 90
1 10
21 30
41 50
61 70
81 90
TEN PERCENT TOTAL LENGTH CLASSES

Contusions were also recorded from captured sharks (Fig. 9). Due to observations that the schooling sharks did not respond to feeding stimuli such as bait and low-frequency, pulsed sounds (see Klimley and Nelson, 1981) and the possibility that this absence of feeding might be related to a high level of reproductive motivation overriding the feeding motivation, contusions were expected to be absent in hammerheads caught by long lines and gill nets. These sharks were obviously motivated by hunger. Unexpectedly, contusions were more frequent on these captured hammerheads, and the scrapes were very different in shape, being long rather than oval. The large number of scars in Fig. 9 were recorded from only 3 females and 6 males while a similar number of scars in Fig. 8 was recorded from 31 females and 3 males. Both males and females caught with fishing gear possessed similar numbers of freshly inflicted scrapes, but few past inflicted scrapes. The numerous, freshly inflicted scrapes were probably caused by chafing of the longline leaders on them while the captured hammerheads struggled to escape.

The indices of recent reproductive activity yielded inconclusive information on seasonal reproduction. Of the females judged mature from ovum size, only 1 out of 6 females caught during the summer possessed spermatozoa in their uteri. The single mature female caught in the spring did not possess spermatozoa in her uterus. The two females with full

Fig. 9. Frequency of wounds and scars occurring within 10-percent divisions of the total length of hammerheads captured by long line and gill net in the Gulf of California during July and August 1979.


lateral (right)
lateral (left)
dorsal
ventral
FEMALES (white, recently inflicted wounds)
FEMALES (black, past inflicted scars)
MALES (white, recently inflicted wounds)
MALES (black, past inflicted scars)
FREQ. OF CONTUSIONS
0
10
20
1-10
21-30
41-50
61-70
81-90
TEN PERCENT TOTAL-LENGTH CLASSES

term embryos were both caught in the spring.

DISCUSSION

Based on disproportionate increases in clasper and testis length, epididymis width, and presence of spermatozoa in the ampulla ductus deferens, the minimum length at which males reached maturity was 164 cm (all males 218 cm and larger were mature). This range for the onset of maturity was similar to that found by other investigators. Clark and Schmidt (1965) examined only four scalloped hammerheads for their state of reproductive maturity. A 152 cm male was immature while three other males, ranging in length from 177 to 209 cm, were judged mature. Bass et al. (1975) found that males matured over a range of from 140 to 165 cm. Maturity was determined in these studies, however, on the basis of clasper rigidity, rotatability, and its possession of a fully developed head. These indices which were found to be unreliable with scalloped hammerhead sharks caught in the Gulf of California.

Based on the presence of ova of different sizes, indicating different stages in their development or resorption in individuals of similar lengths, the minimum length at which females reached maturity was 217 cm. This length was slightly less than that which other investigators have found. Clarke (1971) judged a 214 cm female scalloped hammerhead to be immature, but 294 and 304 cm females to be mature based upon the presence of embryos and a flaccid uterus indicative of recent parturition. Bass et al. (1975) found a 212 cm female to be virgin (but possibly mature) and a 307 cm female to be mature based on the presence of distinct ova and the expansion of the uterus to form loose sacs.

The presence of contusions was not an accurate indicator of maturity. Scrapes were present on females as small as 135 cm long. The minimum length of a reproductively mature female was 217 cm. The scrapes appeared to be inflicted during aggressive interactions within the schools.

Although the size class analysis did not demonstrate seasonal reproduction in the scalloped hammerhead in the Gulf of California, Clarke (1971) reported some evidence for seasonal reproduction in Kaneohe Bay, Hawaii. Forty-three adult males with swollen claspers emitting semen and a female with recent wounds (possibly courtship inflicted) were caught between March and September. Two females with full-term embryos were caught during this time period. Hammerhead pup abundance also peaked at this time. However, Clarke cautioned against the assumption that this peak in population size was due to more common pupping only at this time. He believed that the March through October winds could inhibit migration of the pups out of the bay by increasing its turbidity and resulting in a larger population of pups.

CONCLUSIONS

The minimum size of maturity for male scalloped hammerheads of 163 cm was determined with several indices. These were a disproportional increase in clasper and testis length and epididymis width in relation to total length coupled with the presence of spermatophores in the ampulla ductus deferens.

The minimum size of maturity for female scalloped hammerheads of 217 cm was determined from the presence of ovarian eggs in all stages of production and resorption. Contusions were found anterior and lateral to the first dorsal fin on females. These scrapes, however, were often found on females judged immature by the former indices, and were believed to be not directly linked to copulation, but involved in aggressive interactions among females within the hammerhead schools.

An absence of seasonal reproduction was indicated by the absence of birth peaks in size frequency distributions of free-swimming and captured sharks. Inflections due to birth peaks were also not evident in a plot of cumulative percentages on a probability scale.

ACKNOWLEDGEMENTS

I would like to express my gratitude to F. Galvan, R. Martinez, and R. Roderiguez, students at the Centro del Interdisciplinario de Ciencias Marinas, La Paz, Mexico for helping in the examination of the sharks. The Office of Naval Research provided funds for my salary during the study on contract N00014-77-0-01131 (Donald R. Nelson, principal investigator). This report constitutes part of my doctoral dissertation at the University of California, San Diego under the guidance of Richard H. Rosenblatt.

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CHAPTER 6: INSIGHTS INTO HABITAT UTILIZATION FROM FEEDING HABITS OF THE SCALLOPED HAMMERHEAD SHARK (SPHYRNA LEWINI) IN THE GULF OF CALIFORNIA

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ABSTRACT

In the diet of 93 scalloped hammerhead sharks caught in the Gulf of California, cephalopods were most (66.9 percent total index of relative importance [IRI]), fishes next most (31.0 percent IRI), and crustaceans least important (2.0 percent IRI). Sixty-two of the 93 stomachs contained prey. The diet of hammerheads changed as intermediate-sized sharks left a shallow, inshore habitat to school along the dropoff into deep water where they foraged on both inshore and offshore prey. Juvenile sharks fed primarily on benthic and neritic fishes. Intermediate-size sharks still fed on benthic as well as neritic fishes, but in addition fed on an epipelagic cephalopod. Large sharks also fed on neritic fishes but in addition fed on epipelagic fishes and cephalopods and mesopelagic cephalopods. Reflecting the movement of females offshore before males was the greater importance of pelagic prey in the diet of females ($\leq$160 cm long) (33.0 percent IRI) than in the diet of similarly sized males (21.6 percent IRI) and the lesser importance of neritic

prey in the diet of females (37.4 percent IRI) than the diet of males (51.8 percent IRI). The scalloped hammerhead shark is an opportunistic generalist, feeding on numberous items of a wide range of prey species upon encountering them.

INTRODUCTION

The scalloped hammerhead (Sphyrna lewini) makes an ontogenetic movement from a shallow, inshore habitat to an offshore habitat where it can feed upon inshore and offshore prey species. Male and female pups (<87.5 cm) are caught in shallow Kaneohe Bay, Hawaii in equal numbers (Clarke, 1971). Similarly sized pups of both sexes are caught in the bay of La Paz in the Gulf of California. Primarily males in the intermediate size range of 80 to 120 cm are caught outside the bay yet inshore in the Gulf of California (chapter 3). It is believed that females move offshore at smaller sizes than males. Supporting this is the appearance of females of smaller sizes than males in the offshore schools. A delayed offshore movement of males also explains the prevalence of females in the schools. The stomach contents of 93 scalloped hammerheads were examined in order to see if dietary differences occurred not only between sharks of different sizes, but of different sex as predicted by the above-described size and sexual segregation. In addition, dietary differences between sharks caught in two different biogeographical zones in the Gulf of California, different seasons, and different depths were examined in order to eliminate them as confounding reasons for size and sexual differences in diet. Other investigators have described the diet of the scalloped hammerhead in a preliminary manner. Although Clarke described differences between the diets of juveniles and adults, he did not note differences with regard to sex. Bass _et al_. (1975) described the stomach contents of the scalloped hammerhead shark without regard to size or sex.

METHODS

Dietary information was obtained from scalloped hammerheads caught along the coast of Baja California Sur from Juncalito (25 deg 51 min N., 111 deg 19 min W.) to San Jose del Cabo (23 deg 03 min N., 109 deg 39 min W.). The sharks were caught either on bottom long lines or gill nets. The fishing gear utilized is described in Applegate _et al_. (1979).

Stomachs were severed along their longitudinal axes and inverted so that their contents would fall into plastic, storage bags. The stomach contents were temporarily stored in formalin until they were placed in alcohol at the laboratory. Formalin was favored over alcohol because although it may have partly disolved the hard parts, it was less bulky to carry than alcohol. Particular care was taken to ensure that small hard parts such as teleostean vertebral centra and cephalopod beaks just above the pyloric valve were removed from each stomach. Few prey items were whole: mos consisted of only the less digestible hard parts. For this reason, the identification of fishes was often based on neurocranial anatomy using the figures of Gregory (1933), vertebral column anatomy using the figures and key of Clothier (1950), and the urostyle anatomy using the figures of Monod (1968). Identifications of fishes based on hard parts were often corroborated from the examination of specimens of that species in the icthyological collection at Scripps Institution of Oceanography, La Jolla. Rarely were cephalopod soft parts present in the stomachs of sharks. For this reason, identifications of cephalopods were made primarily from cephalopod beak anatomy using the diagrams of Iverson and Pinkas (1950) and the key of Clarke (1962). The collection of a few intact cephalopods allowed me to corroborate most beak identifications. Eric Hochberg of the Santa Barbara Natural History Museum helped with these identifications.

The significance of different prey items in the diet of the hammerhead was determined using the Index of Relative Importance (IRI) of Pinkas (1971):

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

where N is the numerical percentage of prey items, V the volumetric percentage of such items, and F the percentage of stomachs containing such items. The IRI percentages of prey were then plotted in circular diagrams for categories such as location, season, depth, size, and sex of hammerheads. By using this index of dietary significance, the importance of infrequent items of large volumes and frequent items of small volumes were de-emphasized.

As an independent check of the relative significance of different cephalopod prey, the IRI percentages were also calculated by substituting both measured masses and masses regressed from a beak dimension for measured volume. Mass measurements were obtained from curves for different families (Clarke, 1962). The IRI percentages based on the beak dimension differed from those based on measured mass and volume. The IRI percentages changed little when percent mass was substituted for percent volume. The IRI percentages changed more when regressed mass was substituted. With the latter substitution the order of prey items changed with _Moroteuthis robustus_ increasing from 0.9 to 6.7 percent IRI and becoming slightly more important than _Ancistrocheirus leseuri_ which decreased from 10.3 to 5.7 percent. _Dosidicus gigas_, changing from 0.5 to 2.1 percent, became more important than _Octopus_ sp. which increased only from 0.6 to 1.3 percent. In the dietary comparisons, the volume measurements were used. This was because for the few cephalopods for which the mass of the whole cephalopod could be measured and compared to a regressed mass, the directly measured mass differed substantially from the regressed mass. For instance, the mass measured of an individual of the *Mastigoteuthis* sp. was 630 gm, but the mass regressed from the beak dimension was only 240 gm. In another case, the mass measured of an individual *Ancistrocheirus leseuri* was 162.1 gm, but the mass regressed from the beak dimension was only 85.0 gm. Perhaps this inconsistency stemmed from considerable species variability not accurately described by the single regression for each family.

RESULTS

Sixty-two of the 93 stomachs examined contained prey items. Thirty-one species of prey were identified, and these consisted of 21 fishes, 7 cephalopods, and 4 crustaceans. The percent IRI, occurrence in stomachs, number of items, volume, measured mass, regressed mass, and item totals for these categories are presented in Table 1. The scalloped hammerhead shark is a generalist, feeding on many rather than a single dominant species, but upon encountering prey it opportunistically feeds upon several individuals of that species. The most common prey species in the hammerhead stomachs occurred in only 12 percent of the stomachs examined. This cephalopod was *Mastigoteuthis* sp. Only three fish, two cephalopod, and one crustacean species occurred in

Table 1. Percent total of Index of Relative Importance, frequency of occurrence in stomachs, numbers, measured volumes, measured masses, and regressed masses for prey species.

Scient. Name	Common Name	Perc. IRI*	Perc. Occ.	Perc. Num.	Perc. Vol.	Perc. Mass	Perc. Regr. Mass
Cephalopoda							
Masticoteuthis sp.		62.1	12.0	40.2	13.6	12.7	28.2
Ancistrocheirus leseuri		3.7	3.3	2.7	9.1	3.4	17.4
Moroteuthis robustus		0.4	2.2	1.8	<0.1	<0.1	32.3
Octopus sp.		0.3	1.1	2.7	<0.1	<0.1	5.2
Dosidicus gigas		0.2	1.1	1.8	0.2	0.2	16.9
Rossia sp.		0.1	1.1	0.9	<0.1	<0.1	
Vampyroteuthis infernalis		0.1	1.1	0.9	<0.1	<0.1	
Total		66.9	20.8	51.0	22.9	16.3	
Pisces							
Scomber japonicus	chub mackerel	17.0	7.6	8.0	15.2	16.5	
Adioryx suborbitalis	tinsel squirrelfish	3.2	5.4	5.4	0.8	0.6	
Trachurus symmetricus	jack mackerel	2.4	1.1	0.9	21.9	21.8	
Coryphaena hippurus	dolphinfish	2.3	1.1	0.9	20.7	31.6	
Scorpaena sonorae	scorpionfish	2.2	4.4	4.5	0.8	0.8	
Orthopristis inornatus	wavyline grunt	1.2	1.1	1.8	9.2	6.4	
Lythrulon flaviguttatum	Cortez snapper	0.7	1.1	1.8	4.5	2.4	
Sardinops caerulea	sardine	0.3	1.1	2.7	<0.1	<0.1	
Urolophus halleri	round stingray	0.3	1.1	2.7	<0.1	<0.1	
Mugil cephalus	striped mullet	0.2	1.1	0.9	1.3	1.3	
Somberomorus sierra	sierra	0.2	1.1	0.9	0.6	0.7	
Ariosoma gilberti	eel	0.1	1.1	0.9	0.4	0.4	
Stegastes sp.	damselfish	0.1	1.1	0.9	0.4	0.3	
Anchoa sp.	anchovy	0.1	1.1	0.9	0.2	0.1	
Cynoscion sp.	corvina	0.1	1.1	0.9	0.2	0.1	
Hyporhamphus rosae	halfbeak	0.1	1.1	0.9	0.2	0.2	
Engraulididae	anchovy	0.1	1.1	0.9	0.1	0.1	
Epinephalus sp.	grouper	0.1	1.1	0.9	0.1	0.1	
Pleuronectiform	flatfish	0.1	1.1	0.9	0.1	0.1	
Myrichthys tigrinis	tiger snake eel	0.1	1.1	0.9	<0.1	<0.1	
Scorpaena sp.	scorpionfish	0.1	1.1	0.9	<0.1	<0.1	
Total		31.0	37.2	39.5	76.5	83.5	

Scient. Name	Common Name	Perc. IRI	Perc. Occ.	Perc. Num.	Perc. Vol.	Perc. Mass	Perc. Regr. Mass
Crustacea							
Isopoda		1.1	3.2	3.6	<0.1	<0.1	
Penaeus sp.	shrimp	0.6	2.2	2.7	0.1	0.1	
Pleuroncodes planipes	pelagic red crab	0.2	1.1	1.8	<0.1	<0.1	
Stomatapoda		0.1	1.1	0.9	0.1	<0.1	
Total		2.0	7.6	9.0	0.2	0.1	
Miscellaneous							
Pebble		0.1	1.1	0.9	0.1	<0.1	
Total		0.1	1.1	0.9	<0.1	<0.1	
Item Totals		92 guts	112 items	4625 (ml)	4794 (gm)	2721 (gm)	

*Perc. Vol. used in calculation of Index of Relative Importance.

more the 3.0 percent of the sharks examined. The majority of prey species occurred in only 1.1 percent of the stomachs (a single stomach). However, when the hammerhead sharks had prey in their stomachs, they had more than a single prey item. This was reflected in the stomach remains of Mastigoteuthis sp. It was the most important prey species with an IRI percentage of 62.1. This percentage was influenced greatly by the high numerical percentage of 40.1. Six of the eleven sharks which had eaten this species contained more than a single prey individual. In those stomachs with more than a single beak pair, the beaks were in the same state of digestion. Such would be the case if they were eaten at about the same time. It is highly likely that this prey species lives in groups.

Cephalopods (66.9 percent IRI) were more important than fishes (31.0 percent) which, in turn, were more important than crustaceans (2.0 percent). As mentioned before, the IRI is based upon the percent frequency of occurrence of prey items as well as their numerical and volumetric percentages. A moderate volumetric bias was expected from the difference in digestibility between the scale covered teleosts and the naked cephalopods. Less of a bias in the numerical percentage and percent frequency of occurrence was expected because of the large number of identifications based on hard parts. The cephalopods in all but two cases were identified from their species-specific beaks. The fishes were often identified from their skeletal elements. Possibly because of the former bias the fishes possessed a far greater volume (76.7 percent IRI) and mass (83.5 percent IRI) than those (21.9 and 15.5 percent IRI, respectively) of the cephalopods. On the other hand, cephalopods were more important in the other two measures less affected by this bias. The numerical percentage of cephalopods (51.0 percent IRI) was greater than that of fishes (37.2 percent IRI). Although the percent frequency of occurrence of the cephalopods (20.8 percent IRI) was less than that of fishes (37.2 percent IRI), the differential between cephalopods and fishes was less.

The cephalopod component of the diet was less diverse than that of the fishes. This is best seen with IRI percentages calculated separately for each group. The cephalopods consisted primarily of _Mastigoteuthis_ sp. with a IRI percentage of 87.5. Only one other species, _Ancistrocheirus leseuri_, possessed an IRI percentage greater than 1.0, and this was 10.3. The fish component of the diet consisted of 21 species, again dominated by a single species, _Scomber japonicus_, with an IRI percentage of 31.0. However, five additional species possessed IRI percentages over 1.0 with _Adioryx suborbitalis_ 3.2, _Trachurus symmetricus_ 2.4, _Coryphaena hippurus_ 2.3, _Scorpaena sonorae_ 2.2, and _Orthopristis inornatus_ 1.2. The lower diversity of cephalopods than fishes probably reflected the lower faunal diversity of cephalopods in the Gulf of California.

Descriptions in the scientific literature of the daytime and nighttime habitats of the prey species are summarized in Table 2. The cephalopods are primarily pelagic. The two dominant species, *Mastigoteuthis* sp. and *Moroteuthis robustus*, and *Vampyroteuthis infernalis* were mesopelagic. Two more species, *Ancistrocheirus leseuri* and *Dosidicus gigas* were epiplagic. Only the less important species, *Rossia* sp., was benthic. The fishes, on the other hand, were primarily benthic and neritic. The most important species, *Scomber japonicus*, as well as 11 out of the 21 fish species of prey, were neritic. Although some of these species live inshore, many live along the dropoff into deep water at the interface between the neritic and pelagic environments. Only three fish species were epipelagic.

Thompson *et al.* (1979) recognized three characteristic faunal areas characterized by distinctive assemblages of rocky-shore fishes in the Gulf of California. Catches of scalloped hammerheads came from within two of these zones, the Central and Lower Gulf of California. On the Baja Peninsula the Central Gulf of California fauna occurs from Bahia San Francisquito southward to Bahia La Paz excluding Isla Espiritu Santo which is north of La Paz but offshore. The Lower Gulf of California extends from La Paz to Cabo San Lucas. Due to the possibility that stomach

Table 2. Habitats of prey species during day and night with references from which descriptions of diel activity was taken. In some cases, time of the day of habitat occupation was not specified.

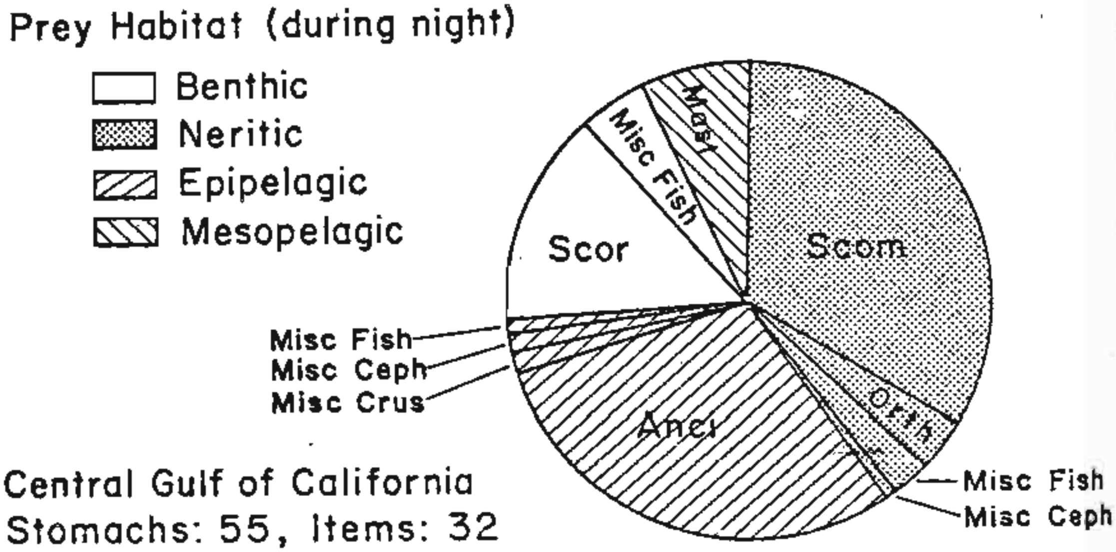
Prey Species	Habitat	Reference
Cephalopoda		
Mastigoteuthis sp.	Daytime:congeners captured deeper than 600 to 700 m. Nightime:some individuals remain at same , others move up to 200 to 600 m depths.	Roper and Young, 1975
Ancistrocheirus leseuri	Night.:one of two species in suborder caught in less than 80 m	Roper and Young, 1975
Moroteuthis robustus	Day. and Night.:captured from a depth range of 100 to 525 m	Roper and Young, 1975
Octopus sp.	Unspecified:intertidal zone to moderate depths	Brusca, 1973
Dosidicus gigas	Night:commonly seen at the surface	Roper and Young, 1975
Rossia sp.	Unspec.:species in suborder are benthic or quasipelagic, spending much of their time (usually during the day) buried in substrate	Roper and Young, 1975
Vampyroteuthis infernalis	Day. and night.:most captures deeper than 600 m	Roper and Young, 1975
Pisces		
Scomber japonicus	Unspec.:captured from surface to 33 m. Schooling.	Miller and Lea, 1972
Adioryx suborbitalis	Day.:hidden in crevices and caves in rocky reef. Night:individuals forage near the bottom. Solitary.	Hobson, 1965
Trachurus symmetricus	Unspec.:captured from surface to 50 m. Schooling.	Miller and Lea, 1972
Coryphaena hippurus	Unspec.:generally in open ocean although frequently visit inshore. Small groups.	Bohlke and Chaplin, 1968
Scorpaena sonorae	Unspec.:remain on sandy bottoms. Solitary.	Thompson *et al.*, 1979
Orthopristis inornatus	Day.:remain in shallow water 2 to 6 m deep in densely packed schools. Night.:disperse over sandy bottom into deeper water. Small groups.	Hobson, 1965
Lythrulon flaviguttatum	Day.:remain in shallow water 2 to 6 m deep in densely packed schools. Night.:disperse over sandy bottom into deeper water. Small groups.	Hobson, 1965
Sardinops caerulea	Unspec.:congener epipelagic. Schooling.	Miller and Lea, 1972
Urolophus halleri	Unspec.:remain on sandy bottom	Thompson and McKibben, 1976
Mugil cephalus	Unspec.:in bays and adjacent to shore. Schooling.	Bohlke and Chaplin, 1968
Scomberomorus sierra	Unspec.:generally pelagic although occasionally inshore. Schooling.	Thompson and McKibben, 1976
Ariosoma gilberti	Day.:remain buried in sand. Night.:moves along the bottom. Solitary.	Rosenblatt, pers. comm.
Stegastes sp.	Day.:close to shore in rocky areas. Aggregating. Night.:remain in crevices and caves. Solitary.	Hobson, 1968
Anchoa sp.	Unspec.:in estuaries, bays, and adjacent to shore. Schooling.	Miller and Lea, 1972
Cynoscion sp.	Unspec.:inshore in shallow water. Schooling.	Thompson and McKibben, 1976
Hyporhamphus rosae	Day.:inshore in shallow water. Small groups. Night.:congener can be dipnetted at surface	Miller and Lea, 1976, Bohlke and Chaplin, 1968

Prey Species	Habitat	Reference
Engraulididae	Day.;inshore. Schools.	Bohlke and Chaplin, 1968
Epinephelus sp.	Unspec.;remain near bottom. Solitary	Hobson, 1968
Pleuronectiform	Unspec.:probably inshore over sandy bottom. Probably solitary.	
Myrichthys tigrinis	Day.;often buried in sand. Night.;among rocks, over sandy bottom, and occasionally near surface. Solitary.	Hobson, 1968
Crustacea		
Isopoda	Unspec.;inshore in shallow water. Solitary.	Brusca, 1973
Penaeus	Day.;buried in sandy bottom. Night.;near bottom. Groups.	Barnes, 1974
Pleuroncodes planipes	Unspec.;found in open sea near surface	Schmidt, 1972
Stomatopoda	Unspec.;inhabit shallow, subtidal region	Brusca, 1973

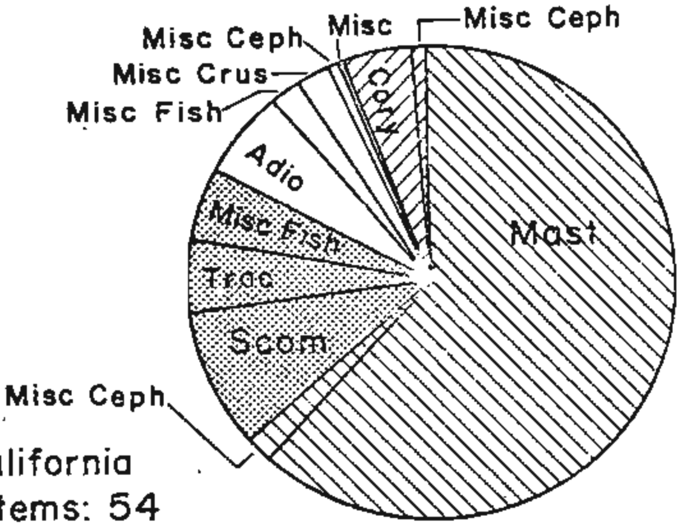
contents might reflect the different faunas present in these two zones, the relative importance of prey from hammerheads caught in the two zones are presented on circular diagrams in Fig. 1. If the percent IRI of the prey species was less than 3.0, it was pooled with similar species. Species were identified by the first four letters (five in Scomberomorus to avoid confusion with Scomber) of the generic name. Pooled species were identified by the first four letters of the name of an inclusive taxon. The diets of the hammerheads caught in the two areas were very different. Both the composition of prey species and their relative significances differed. Scomber japonicus was the most important species (33.7 percent IRI) in the stomachs of hammerhead sharks caught in the Central Gulf, followed by the slightly less important Ancistrocheirus leseuri (30.2 percent), Scorpaena sonorae (14.6 percent), and Mastigoteuthis sp. (7.0 percent). On the other hand, Mastigoteuthis sp. was the most important prey species (62.4 percent) in the Lower Gulf, and also important were Scomber japonicus (9.5 percent), Adioryx suborbitalis (6.2 percent), Trachurus symmetricus (4.7 percent), and Coryphaena hippurus (4.5 percent). The habitats of the prey species are indicated by stippling (neritic), cross-hatching slanting upward to the right (epipelagic), cross-hatching slanting downward to right (mesopelagic), and the absence of either stippling or cross-hatching (benthic). Prey species were ordered by decreasing percent IRI within the habitat, and then these

Fig. 1. Relative importance (as fractions of total Index of Relative Importance) of different prey species for scalloped hammerhead sharks caught in the Central and Lower Gulf of California. Scom=*Scomber japonicus*, Orth=*Orthopristis inornatus*, Anci=*Ancistrocheirus leseuri*, Scor=*Scorpaena sonorae*, Mast=*Mastigoteuthis* sp., Trac=*Trachurus symmetricus*, Adio=*Odioryx suborbitalis*, and Cory=*Coryphaena hippurus*.

INDEX OF RELATIVE IMPORTANCE



Central Gulf of California
Stomachs: 55, Items: 32



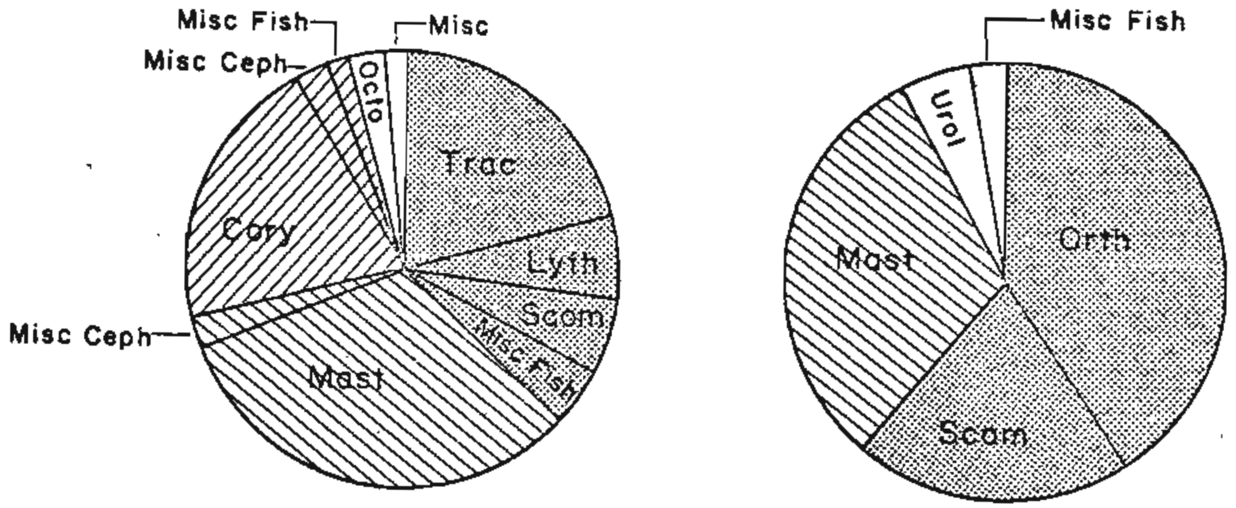
Lower Gulf of California
Stomachs: 42, Items: 54

habitat groups were further ordered by their decreasing percent IRI. For this reason, in the diet of hammerheads caught from the Central Gulf *Scomber japonicus* was followed by the successively less important neritic prey, *Orthopristis inornatus*, miscellaneous fishes, and cephalopods, and all of these neritic species preceded the less important epipelagic species. The IRI percentages of benthic prey species were similar in both Central and Lower Gulf. The IRI percentage of neritic species was only slightly larger in the Central than the Lower Gulf. On the other hand, the IRI percentage of epipelagic prey was greater in the Central than in the Lower Gulf while that of mesopelagic prey was far less in the Central than the Lower Gulf.

The diet of the scalloped hammerhead varied seasonally (Fig. 2). In the summer the sharks fed equally in the neritic, epipelagic, and mesopelagic habitats. At this time, most of the hammerheads caught were either intermediate or large in size. They fed either along the dropoff or pelagically. These sharks fed on several species of fishes in the neritic habitat, *Mastigoteuthis* sp. in the mesopelagic habitat, and *Coryphaena hippurus* in the epipelagic habitat. During the fall smaller hammerheads were caught inshore, and they had fed on *Ancistrocheirus leseuri* in the epipelagic habitat and *Scorpaena sonorae* in the benthic habitat. During the winter small hammerheads were also caught inshore, and they had fed on *Orthopristis*

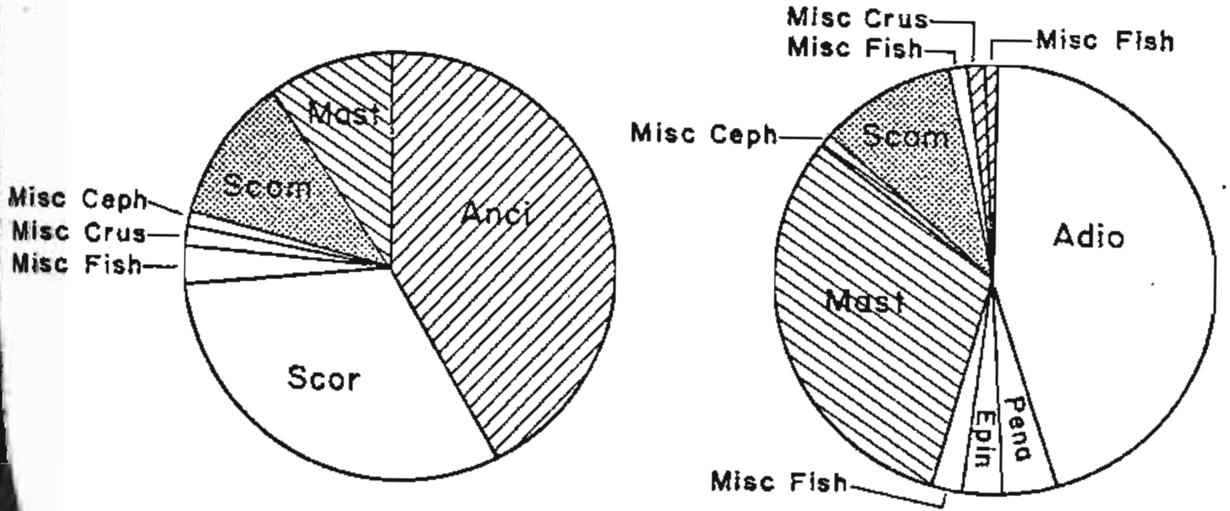
Fig. 2. Relative importance of different prey species for scalloped hammerhead sharks caught at different seasons of the year. Trac=*Trachurus symmetricus*, Lyth=*Lythrulon flaviguttatum*, Scom=*Scomber japonicus*, Mast=*Mastigoteuthis* sp., Cory=*Coryphaena hippurus*, Octo=*Octopus* sp., Ortho=*Orthopristis inornatus*, Urol=*Urolophus halleri*, Scor=*Scorpaena sonorae*, Adio=*Adioryx suborbitalis*, Pena=*Penaeus* sp., Epin=*Epinephalus* sp.

INDEX OF RELATIVE IMPORTANCE



Summer (June, July, Aug.)
Stomachs: 15, Items: 22

Winter (Dec., Jan., Feb.)
Stomachs: 9, Items: 14



Fall (Sept., Oct., Nov.)
Stomachs: 16, Items: 18

Spring (Mar., Apr., May)
Stomachs: 21, Items: 29

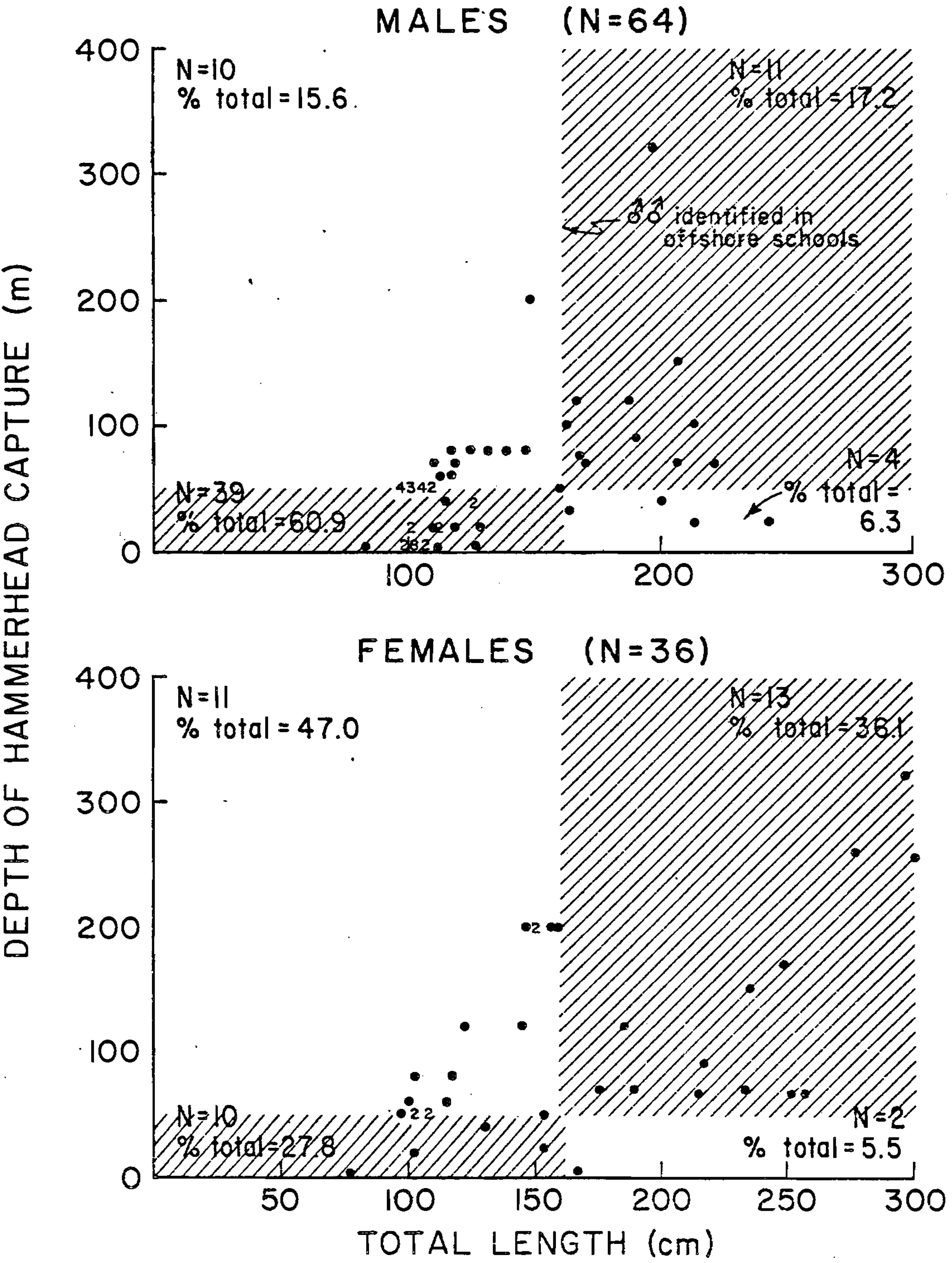
Prey Habitat (during night)

☐ Benthic ▨ Epipelagic
▩ Neritic ▧ Mesopelagic

inornatus and *Scomber japonicus* in the neritic habitat and *Mastigoteuthis* sp. in the mesopelagic habitat. During the spring sharks of varying sizes were caught inshore and offshore, and they had fed on *Adioryx suborbitalis* or the mesopelagic *Mastigoteuthis* sp.

The scalloped hammerhead shark segregates both by size and sex. More intermediate-size males are caught inshore than females, while more intermediate-size females are caught offshore than males. The females in this size range join schools together with larger females and males along the dropoff into deep water. Males move offshore to join the schools only after the grow larger. This size and sexual segregation can be seen when depths of capture of male and female sharks captured by long line and gill net in the Gulf of California are plotted as a function of size (Fig. 3). A larger percentage of small males ($\leq$160 cm total length) of 60.9 percent the total number of males were caught in inshore sets ($<$50 m) than the percentage of small female sharks ($\leq$160 cm) of 27.8 percent. In the deeper water at the dropoffs from offshore islands and seamounts ($\geq$50 m), a larger percentage of small females (47.0 percent) were caught than small males (15.6 percent). These differences are statistically significant (Chi-Square, $p<0.01$). Only small percentages of large males and females, 6.3 and 5.5 percent, respectively, were caught inshore. A smaller percentage of large males (17.2 percent) than that of the females (36.1

Fig. 3. Capture depths of male and female scalloped hammerhead sharks captured by long line and gill net in the Gulf of California as a function of their total lengths. Plot divided into quadrats, and numbers and percentages of the total number of sharks in each quadrat summarized.


MALES (N=64)
N=10
% total = 15.6
N=11
% total = 17.2
♂♂ identified in offshore schools
N=39
% total = 60.9
N=4
% total = 6.3
4342
2
2
282
FEMALES (N=36)
N=11
% total = 47.0
N=13
% total = 36.1
2
2 2
N=10
% total = 27.8
N=2
% total = 5.5
DEPTH OF HAMMERHEAD CAPTURE (m)
400
300
200
100
0
50
100
150
200
250
300
TOTAL LENGTH (cm)

percent) was captured offshore. This may reflect the greater frequency of large females in the offshore schools, and indicate a possible solitary existence for the missing large males.

The diets of the hammerheads caught in the three different depth classes did not indicate exclusive feeding in any particular depth range (Fig. 4). The IRI percentage of prey from different habitats remained relatively constant with increasing depths. However, such a transition from inshore to offshore prey types is evident with increasing total lengths of the hammerheads (Fig. 5). Benthic prey species became less important in the diet of large hammerheads. The second most important prey item, *Adioryx suborbitalis*, and several additional benthic species of fishes and crustaceans comprised 44.0 percent of the IRI total for small sharks (<109 cm TL). The benthic *Scorpaena sonorae*, *Epinephelus* sp., a pleuronectiform teleost, penaeid and isopod crustaceans, and an octopod cephalopod comprised only 13.8 percent of the IRI total of intermediately sized sharks (110-209 cm TL). No benthic prey items were found in the stomachs of large sharks (210-309 cm TL). Neritic prey species remained relatively constant in the three size classes. Such prey constituted 58.6 percent of the IRI for small sharks, 30.9 percent for intermediate sharks, and 44.0 percent for large sharks. The neritic species were almost all fishes except for *Rossia* sp. However, increasing with

Fig. 4. Relative importance of different prey species for scalloped hammerhead sharks caught at depths from <49, 50-99, and >100 m. Mast=*Mastigoteuthis* sp., Scom=*Scomber japonicus*, Adio=*Adioryx suborbitalis*, Anci=*Ancistrocheirus leseuri*, Orth=*Orthopristis inornatus*, Trac=*Trachurus symmetricus*, Lyth=*Lythrulon flaviguttatum*, Cory=*Coryphaena hippurus*, Scor=*Scorpaena sonorae*, Mugi=*Mugil cephalus*, Moro=*Moroteuthis robustus*, Epin=*Epinephalus* sp., Scomb=*Scomberomorus sierra*.

INDEX OF RELATIVE IMPORTANCE

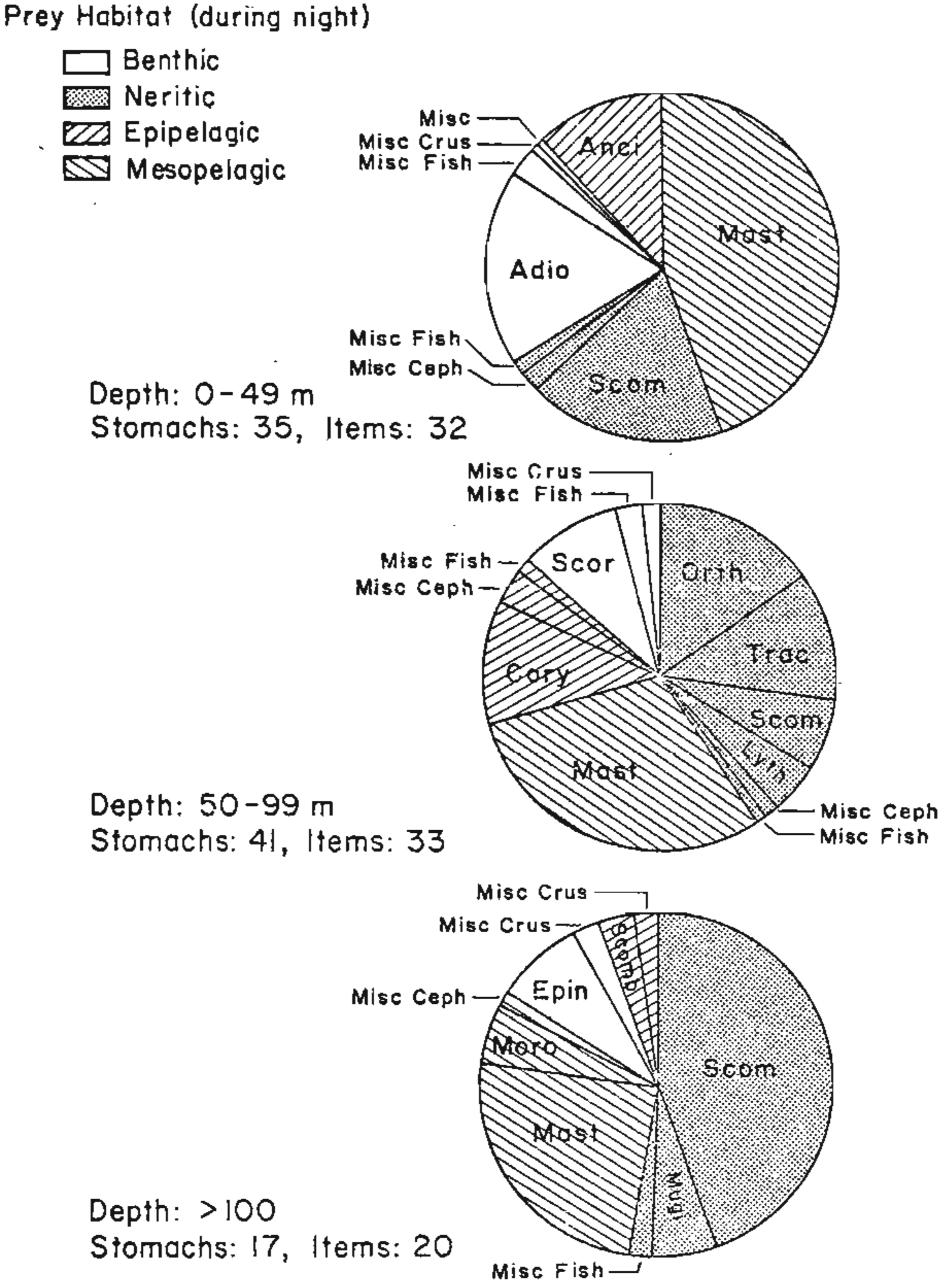
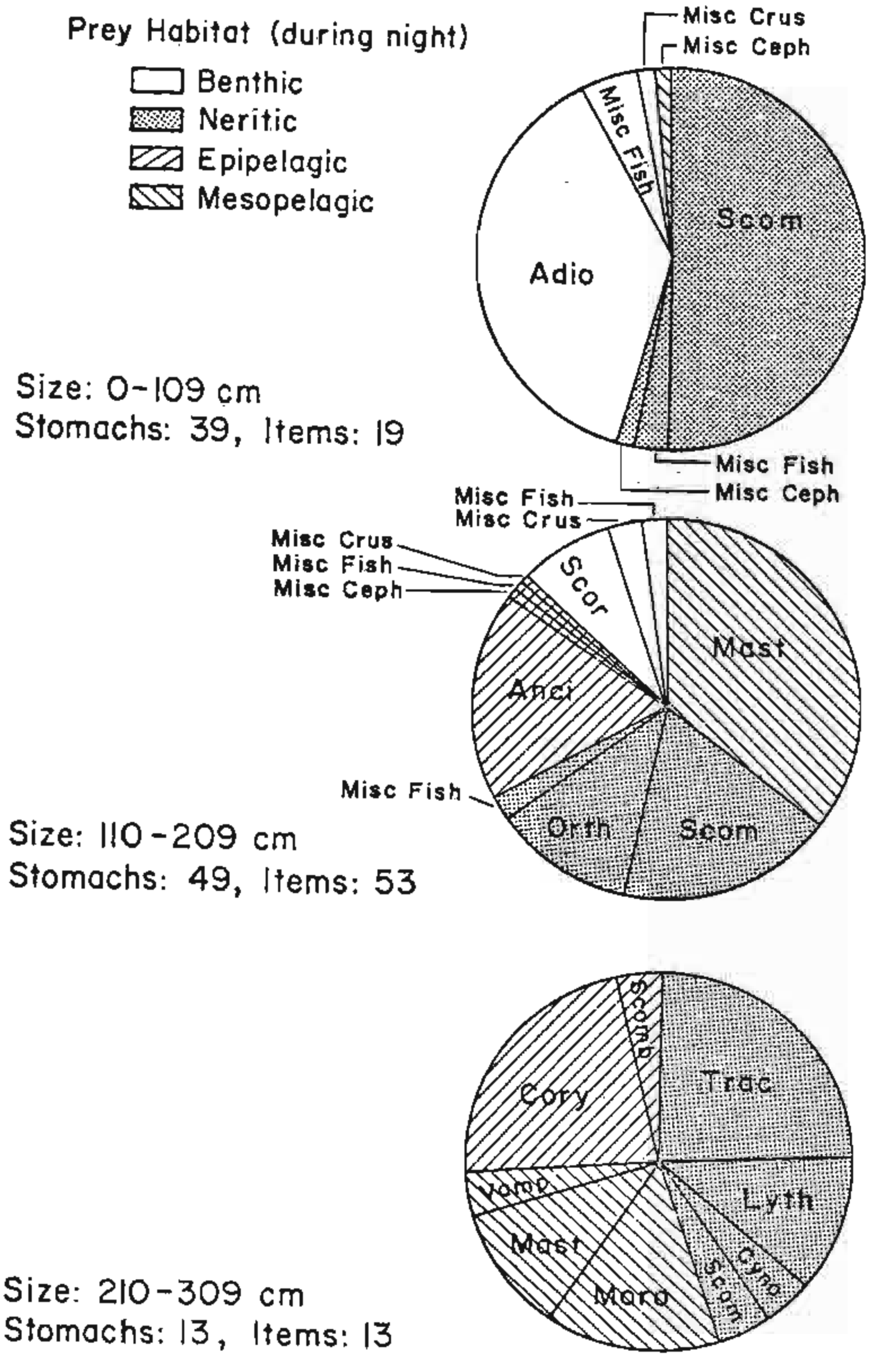


Fig. 5. Relative importance of different prey species for scalloped hammerhead sharks of three size classes, <109, 110-209, and 210-309 cm. Scom=*Scomber japonicus*, Adio=*Adioryx suborbitalis*, Mast=*Mastigoteuthis* sp., Orth=*Orthopristis inornatus*, Anci=*Ancistrocheirus leseuri*, Scor=*Scorpaena sonorae*, Trac=*Trachurus symmetricus*, Lyth=*Lythrulon flaviguttatum*, Cyno=*Cynoscion* sp., Vamp=*Vampyroteuthis infernalis*, Cory=*Coryphaena hippurus*, Scomb=*Scomberomorus sierra*.

INDEX OF RELATIVE IMPORTANCE



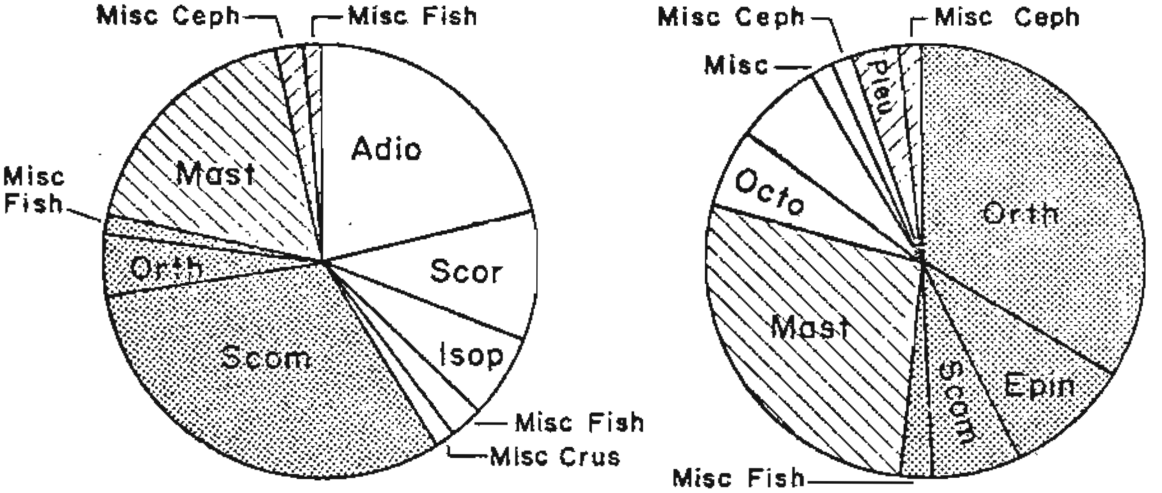
the size of the sharks was the importance of both epipelagic and mesopelagic fishes. Epipelagic prey were not found in the stomachs of small sharks. The epipelagic cephalopod, Ancistrocheirus leseuri, and other cephalopods, fishes, and crustaceans comprised 18.5 percent of the diet of intermediate size sharks. The epipelagic Coryphaena hippurus and Scomberomorus sierra comprised 27.5 percent of the diet of the large sharks. While the mesopelagic Mastigoteuthis sp. comprised only 1.9 percent of the diet of small hammerheads, it increased in significance to 36.3 of the diet of intermediate size hammerheads, and it together with Moroteuthis robustus and Vampyroteuthis infernalis formed 28.5 percent of the diet of the large hammerheads. As described by Clarke (1971), the small hammerhead sharks appeared to shift from a diet of fishes to a mixture of fishes and cephalopods as they became intermediate size sharks. This dietary shift reflected their movement from the shallow inshore habitat to the dropoff to deep water from which they foraged both in the neritic and pelagic habitats.

Small sharks fed less often than intermediate size and large sharks. Prey items were present in 43.6 percent of the stomachs of the small sharks. Prey items were found in 79.5 percent of the stomachs of the intermediate size sharks and 76.7 percent of the stomachs of the large sharks.

If females truly preceded males offshore to enter the schools of scalloped hammerhead sharks there, one would predict that juvenile females would possess fewer benthic prey in their diet and more neritic and pelagic prey in their diet than males. This prediction was born out in the relative importances of of the different prey presented in Fig. 6. Male and female sharks were separated into two size classes, ≤ and >160 cm. This was done to minimize the confounding effect of the dietary differences due to size on a comparison of the diets of males and females. Small sharks fed on more benthic and neritic prey than intermediate size and large sharks (see Fig. 5). If males and females were compared without regard to this bias, the greater occurrence of benthic prey in the diet of males might result solely from their smaller size relative to the females. In the ≤160 cm cm size class benthic prey such as the fishes _Adioryx suborbitalis_, _Scorpaena sonorae_, isopod crustaceans, and other miscellaneous fishes and crustaceans formed 40.9 percent of the IRI total for the diet of male sharks. Benthic prey such as _Octopus_ sp. and miscellaneous fishes and crustaceans formed only 15.1 percent of the IRI total for females ≤160 cm. These females also possessed a larger percentage of pelagic prey than males. Mesopelagic prey formed 27.5 and epipelagic prey 5.5 percent of the total IRI for females; such prey formed 18.1 and 3.6 percent of the total IRI for males. Both males and females >160 cm fed solely on neritic and pelagic prey. The smaller percentage of neritic prey in males may indicate that they spend more of

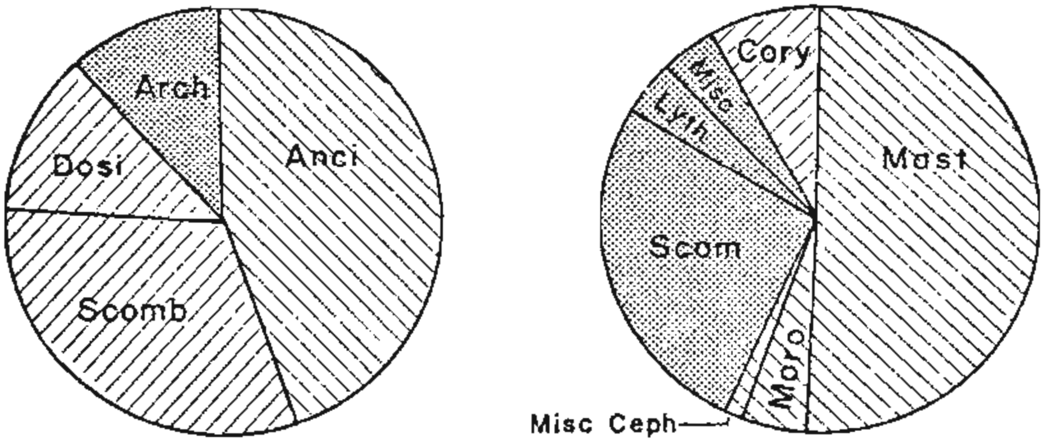
Fig. 6. Relative importance of different prey species for male and female scalloped hammerhead sharks ≤ and > 160 cm. Adio=*Odiorvx suborbitalis*, Scor=*Scorpaena sonorae*, Isop=Isopoda, Scom=*Scomber japonicus*, Orth=*Orthopristis inornatus*, Mast=*Mastigoteuthis* sp., Epin=*Epinephalus* sp., Octo-*Octopus* sp., Pleu-*Pleuroncodes planipes*, Anci-*Ancistrocheirus leseuri*, Scomb=*Somberomorus sierra*, Dosi=*Dosidicus gigas*, Anch=*Anchoa* sp., Moro-*Moroteuthis robustus*, Lyth=*Lythrulon flaviguttatum*, Cory-*Coryphaena hippurus*.

INDEX OF RELATIVE IMPORTANCE



Males, Size ≤ 160 cm
Stomachs: 48, Items: 39

Females, Size ≤ 160 cm
Stomachs: 20, Items: 21



Males, Size > 160 cm
Stomachs: 14, Items: 9

Female, Size > 160 cm
Stomachs: 13, Items: 21

Prey Habitat (during night)

☐ Benthic
▨ Neritic
▨ Epipelagic
▨ Mesopelagic

their life offshore.

There were more prey species characterized as solitary in the diet of the male hammerheads (see Table 2). Solitary species such as Adioryx suborbitalis, Scorpaena sonorae, Urolophus halleri, Stegastes sp., Ariosoma gilberti, a pleuronectiform, and an isopod, penaeid shrimps comprised an IRI percentage of 40.4. In females, on the other hand, the number of species characterized by a solitary social organization was smaller. Myrichthys tigrinis, Scorpaena sonorae, Scorpaena sp., Epinephelus sp., and penaeid shrimps formed only 1.4 percent of the total IRI values. This large difference might also reflect the social nature of the females and suggest a non-social nature for the adult male scalloped hammerheads if the sociality of these sharks was matched with the degree of clumping in their prey species.

DISCUSSION

Scalloped hammerhead sharks in the Gulf of California feed primarily on cephalopods and fishes together with a few crustaceans. Due to the geographical separation of inshore juveniles from the offshore subadults and adults, a change in the diets between sharks of these size classes occurred as smaller sharks fed on benthic and neritic fishes and larger sharks fed on neritic and epipelagic fishes and pelagic cephalopods. Clarke (1971) found fishes and crustaceans in the stomachs of scalloped hammerhead pups less than 87.5 cm long in Kaneohe Bay, Hawaii. These fishes generally occupied a benthic habitat at night as the four most important (measured by frequency of occurrence in stomachs) prey fishes such as scarids, gobioids, labrids, and pomacentrids and crustacean prey such alpheid shrimps, penaeid shrimps, stomatopods, crabs, and isopods. Adults were found to contain in their stomachs either neritic fishes such as _Naso brevirostris_ and _Chanos chanos_ or, more commonly, mesopelagic cephalopods consisting of seven species of oegopsids (_Histioteuthis_ sp. was the most common), two species of ommastrephids, and one pelagic octopod. Bass _et al._ (1975) did not differentiate between prey of differently sized hammerhead sharks. They found the scalloped hammerhead in South African waters to be primarily piscivorous with 80 percent of the stomachs containing neritic fishes such as _Sardinops ocellota_, _Trachurus trachurus_, _Pomatomus saltatrix_, _Elops saurus_, and mullet. Twenty-four percent of the stomachs did possess cephalopods, although the species were not identified. Also present in 8 percent of the stomachs were the benthic crustaceans, _Palinurus_ sp. and _Penaeus_ sp.

The scalloped hammerhead is a generalist among shark species not only in the large number of prey species it feeds upon but also the habitats that it forages in. Twenty-one species of fish prey occurred in 37.2 percent of the stomachs examined (this rather than percent IRI used for comparison to percent occurrence in other shark species), items of 7 species of cephalopod in 20.8 percent, and 4 species of crustacean in 7.6 percent. Twelve neritic species occurred in 24.0 percent of the stomachs examined, 11 benthic species in 18.6 percent, 3 mesopelagic species 15.3 percent, and 6 epipelagic species in 8.8 percent. This relatively equal exploitation of prey from different taxonomic groups and habitats may explain the wide distribution and abundance of this species in semi-tropical and tropical waters (Gilbert, 1967). Large numbers of scalloped hammerheads are caught in the western Atlantic (Rivas and McClellan, 1982), eastern Pacific (Applegate _et al_., 1979), Hawaiian Islands (Clarke, 1971), southwestern waters of Japan (Taniuchi, 1974), and Indian Ocean off South Africa (Bass _et al_. (1975). Other species of sharks are generally confined either to an inshore benthic or neritic habitat or an offshore pelagic environment. For example, a neritic species such as the spiny dogfish (_Squalus acanthias_) feeds mainly upon benthic and neritic fishes. Pelagic fishes and cephalopods comprise the diets of pelagic shark species such as the silky (_Carcharhinus falciformis_) (Strasburg, 1958), pelagic whitetip (_Carcharhinus longimanus_) (Strasburg, 1958), and blue sharks (_Prionace glauca_) (Stevens, 1973; Clarke and Stevens, 1974; and Tricas, 1979). Although the blue shark does feed on some crustacean prey (as much as 12 percent of the stomachs examined by Tricas), the shark feeds primarily on fishes and cephalopods. These prey species are almost all neritic or pelagic. The silky and pelagic whitetip sharks feed almost entirely on pelagic fishes and cephalopods. Although the scalloped hammerhead is more of a generalist than these species, it resembles them in being an opportunist and feeding upon several prey items upon encountering them. The neritic spiny dogfish also feeds opportunistically on a large number of items which are both edible and inedible (Jones and Geen, 1977), and pelagic species such as the silky, pelagic whitetip, and blue sharks similarly feed on almost all available food in their habitat together with inedible items as well (Strasburg, 1958).

Large variations in both prey species composition and habitats occurred with scalloped hammerhead sharks caught from the two biogeographic zones, the Central and Lower Gulf of California, as well as between the four seasons during which sampling was carried out. Similar differences existed in the diets of _P. glauca_ caught at different locations off the coast of England. Clarke and Stevens (1974) found oceanic cephalopods more often in blue sharks caught over deep water in the Bay of Biscayne than in those caught at Looe, over 240 miles (381 km) from the dropoff from the continental shelf into deep water. Tricas (1979) found differences in the the relative importances of cephalopods in the diet of blue sharks during different seasons. _Loligo opalescens_ was more common during the fall and winter months while _Histioteuthis heteropsis_ was more important during the spring and summer months. The blue sharks were probably opportunistically feeding on those cephalopod species present in their habitat, and for that reason changes in prey abundance were reflected in their diet.

The changeover from the juveniles' diet of benthic and neritic prey to the adults' diet of neritic and pelagic prey in the scalloped hammerhead is not unique. Jones and Geen (1977) also found a dietary change related to growth in spiny dogfish. As they grow from young to immature, the percent frequency of occurrence of crustaceans decreased in importance while that of teleosts increased in importance. This was a change from primarily benthic to neritic prey. Little further dietary change occurred as they grew from immature to subadult, and then to mature sharks. No difference in the diet of male and female spiny dogfish as in the scalloped hammerhead were described by Jones and Geen.

CONCLUSIONS

The scalloped hammerhead is an opportunistic generalist, feeding on several prey at a time of a large number of prey species. The juveniles fed primarily on the benthic fish, Adioryx suborbitalis, and the neritic fish, Scomber japonicus. Intermediate size sharks continued to feed upon the benthic Scorpaena sonorae and neritic Scomber japonicus and Orthopristis inornatus, but in addition, they fed on the epipelagic cephalopod, Anchistrocheirus leseuri. Large sharks still fed on the neritic fishes, Trachurus symmetricus and Lythrulon flaviguttatum, but they fed on even more epipelagic fishes and cephalopods, including Coryphaena hippurus and Scombermorus sierra, and mesopelagic cephalopods such as Moroteuthis robustus and Mastigoteuthis sp. Reflecting the movement of females offshore to the the interface between the neritic and pelagic habitats before the males, was the increased importance of pelagic prey in females. Associated both with sharks of large size and the female sex were more prey species which were nocturnally social. This might indicate a greater tendency for adult females to forage socially than juveniles and adult males.

ACKNOWLEDGEMENTS

I would like to thank Felipe Galvan, R. Martinez, and R. Roderiguez, students at the Centro de Interdisciplinario de Ciencias Marinas, La Paz for helping in the collection of stomach-content samples in the field. Identifications of some cephalopos were made by F. Hochberg of the the Santo Barbara Museum of Natural History. Bill Evans provided editorial suggestions which improved the manuscript greatly. The Office of Naval Research provided salary for myself during the study (Contract N00014-77-0-01131 to Donald R. Nelson, Principal Investigator). The National Geographic Society and the

Foundation for Ocean Research provided additional support. This report constitutes part of my doctoral dissertation at the University of California, San Diego under the guidance of Richard H. Rosenblatt.

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CHAPTER 7: SUMMARY WITH DISCUSSION OF FUNCTION OF SCHOOLING IN THE SCALLOPED HAMMERHEAD (SPHYRNA LEWINI)

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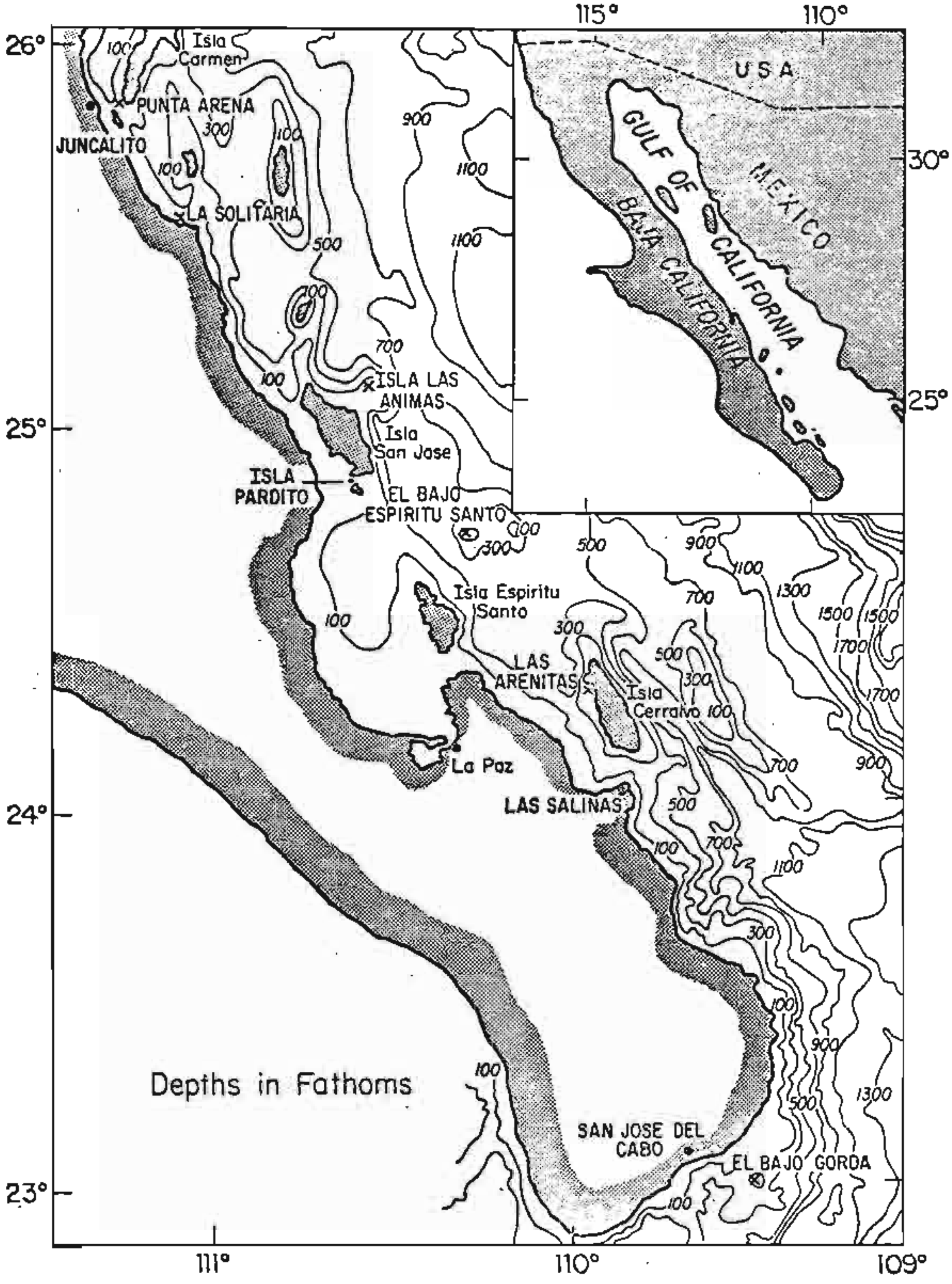
NGS Grant No.: 2204-80

The scarcity of information on the social behavior of sharks comes from only a few studies of an indirect and cursory nature. Some descriptions are based on inferences from fishery catches (Ford, 1921; Olson, 1954; and Jensen, 1965) or incidental observations by airborn or shipboard investigators (Clark, 1963; Springer, 1967; Kenny, 1968; Bass *et al.*, 1975; and Parker and Bailey, 1979). Some of the underwater investigations are preliminary in nature (Eibl-Eibesfeldt and Hass, 1959 and Limbaugh, 1963); others are more detailed such as McLaughlin and O'Gower's study (1971) of bullhead sharks along the coast of Australia and Nelson and Johnson's study (1980) of the reef sharks of French Polynesia. Yet none of these studies delt primarily with the social behavior of the species. It was our intent to enter the habitat of the scalloped hammerhead shark and study the social organization of the species' behavior in detail.

Between July 1980 and May 1981 four expeditions ranging in duration from four to seven weeks were made to the Gulf of California with National Geographic Society support to study the scalloped hammerhead shark. Six locations were visited on a seasonal basis during time periods spanning July and August, October and Novemeber, January and February, and April and May. Using La Paz and Loreto as bases of operations, we repeatedly visited the study sites using our 6.7-m outboard skiff and the 23 m research vessel of the Centro Interdisciplinario de Ciencias Marinas, La Paz.

Study Sites. The six study sites were chosen along the coast of the Baja Peninsula spanning a distance of 378 km over which pronounced seasonal changes in the water temperatures occurred and might be reflected in relative changes in scalloped hammerhead shark abundance at the different sites. Schooling hammerhead sharks had been observed at these locations prior to our seasonal visits either by ourselves or acquaintances. The six locations (marked with crosses) and nearby fishing camps (marked by solid circles) at which hammerhead catches were examined are identified with upper-case lettering in Fig. 1. The sites were along the dropoffs from four islands, Isla Carmen (Punta

Fig. 1. Six study sites (marked with crosses) and four fishing camps (marked with solid circles) visited on a seasonal basis along the Baja Peninsula.


Depths in Fathoms
26°
25°
24°
23°
111°
110°
109°
115°
110°
30°
25°
USA
MEXICO
GULF OF CALIFORNIA
BAJA CALIFORNIA
Isla Carmen
PUNTA ARENA
JUNCALITO
LA SOLITARIA
ISLA LAS ANIMAS
Isla San Jose
ISLA PARDITO
EL BAJO ESPIRITU SANTO
Isla Espiritu Santo
LAS ARENITAS
Isla Cerralvo
La Paz
LAS SALINAS
SAN JOSE DEL CABO
EL BAJO GORDA
100
300
500
700
900
1100
1300
1500
1700

Arena), La Solitaria, Isla Las Animas, and Isla Cerralvo (Las Arenitas), and two seamounts, El Bajo Espiritu Santo and El Bajo Gorda. The bottom topography of these sites was charted with a portable fathometer interfaced with an odometer and compass in order to characterize the habitat of the scalloped hammerhead (Fig. 2). Punta Arena (A), the northernmost site, is located along the southwestern shore of Isla Carmen. It is characterized by a steeply sloped, sandy bottom, dropping to a depth of 110 m before leveling off. Schooling hammerheads were not observed at this site during our four seasonal visits although other investigators had observed them at this location during the spring. La Solitaria (B) is a rocky pinnacle with a gravel slope to a depth of 20 m where large boulders created considerable relief. It rises from a depth of 62 m only 500 m from Punta Pasqual at the head of Bahia Agua Verde. Schooling hammerheads also were not observed at this location by us although such sharks had been observed there by others in the early fall. Isla Las Animas (C) is a large rock jutting out of the sea 10 km northeast of the larger island, Isla San Jose. The island is at the edge of a broad, relatively shallow shelf extending northeasterly from Isla San Jose with a mean depth of 100 m. The bottom abruptly drops to a depth of 1240 m within 3 km from the rock in a northeasterly direction. Small schools of hammerhead sharks (Fig. 3) of up to 40 members were observed seaward of a cluster of rocks east of the island during the summer visit. El Bajo Espiritu Santo (D) is located 17 km offshore

Fig. 2. Bathymetric charts of six study sites (details of charting technique in chapter 4).

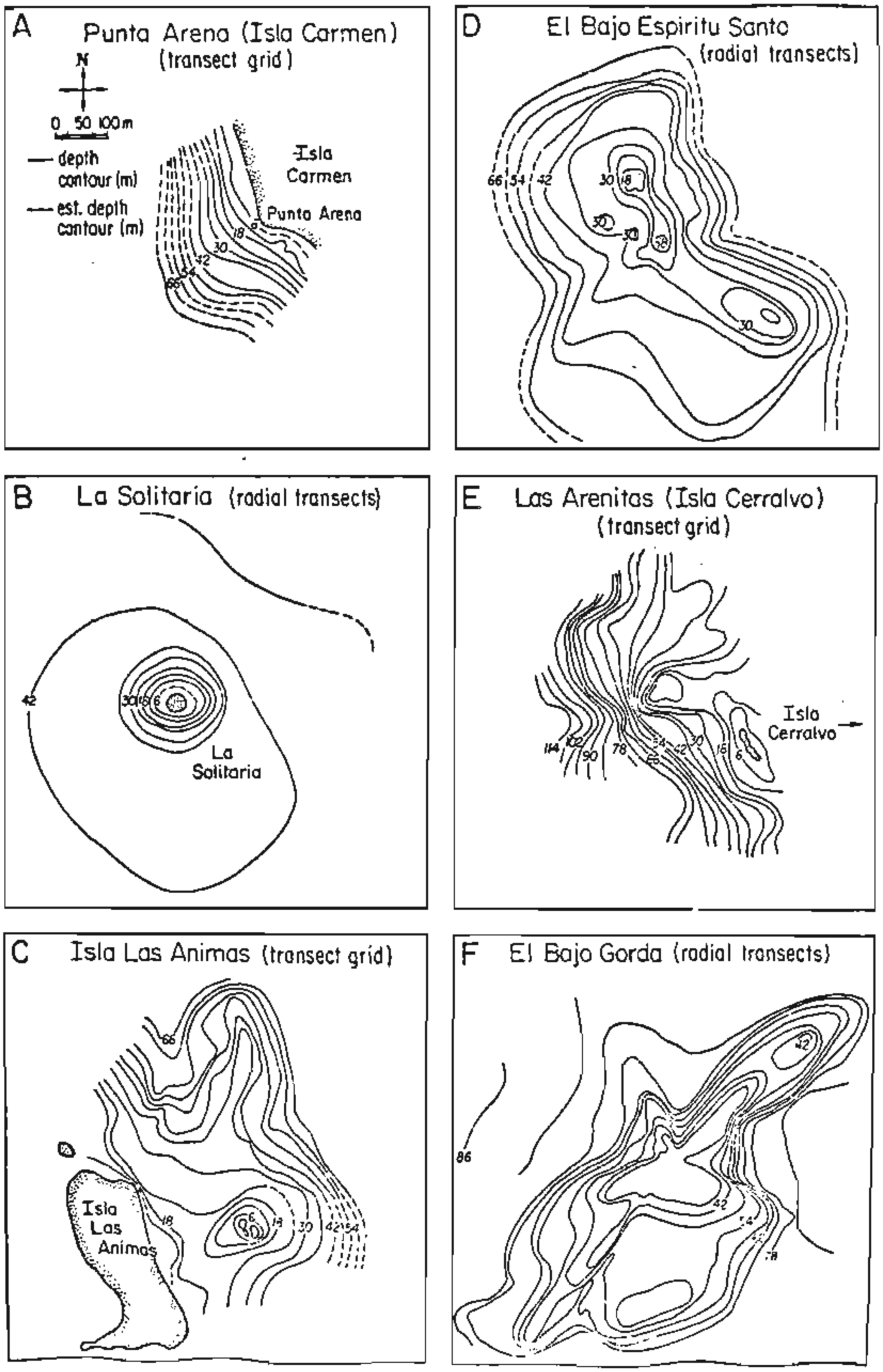
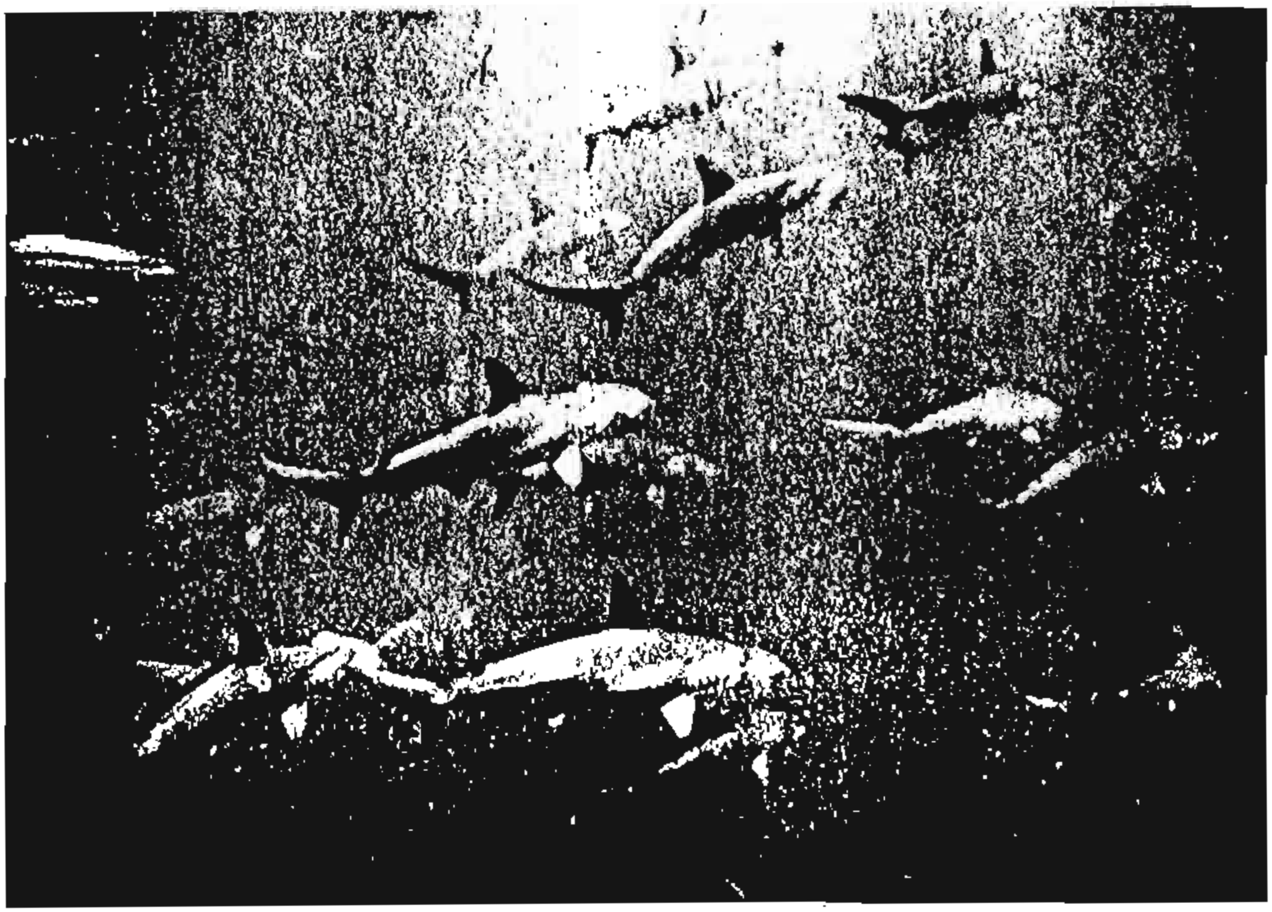

A
Punta Arena (Isla Carmen)
(transect grid)
N
0 50 100m
depth contour (m)
est. depth contour (m)
Isla Carmen
Punta Arena
6
18
30
42
54
66
D
El Bajo Espiritu Santo
(radial transects)
66
54
42
30
18
30
30
30
30
B
La Solitaria (radial transects)
42
30
18
6
La Solitaria
E
Las Arenitas (Isla Cerralvo)
(transect grid)
Isla Cerralvo
114
102
90
78
54
66
42
30
18
6
C
Isla Las Animas (transect grid)
66
Isla Las Animas
18
6
30
18
30
42
54
F
El Bajo Gorda (radial transects)
42
86
42
54
78

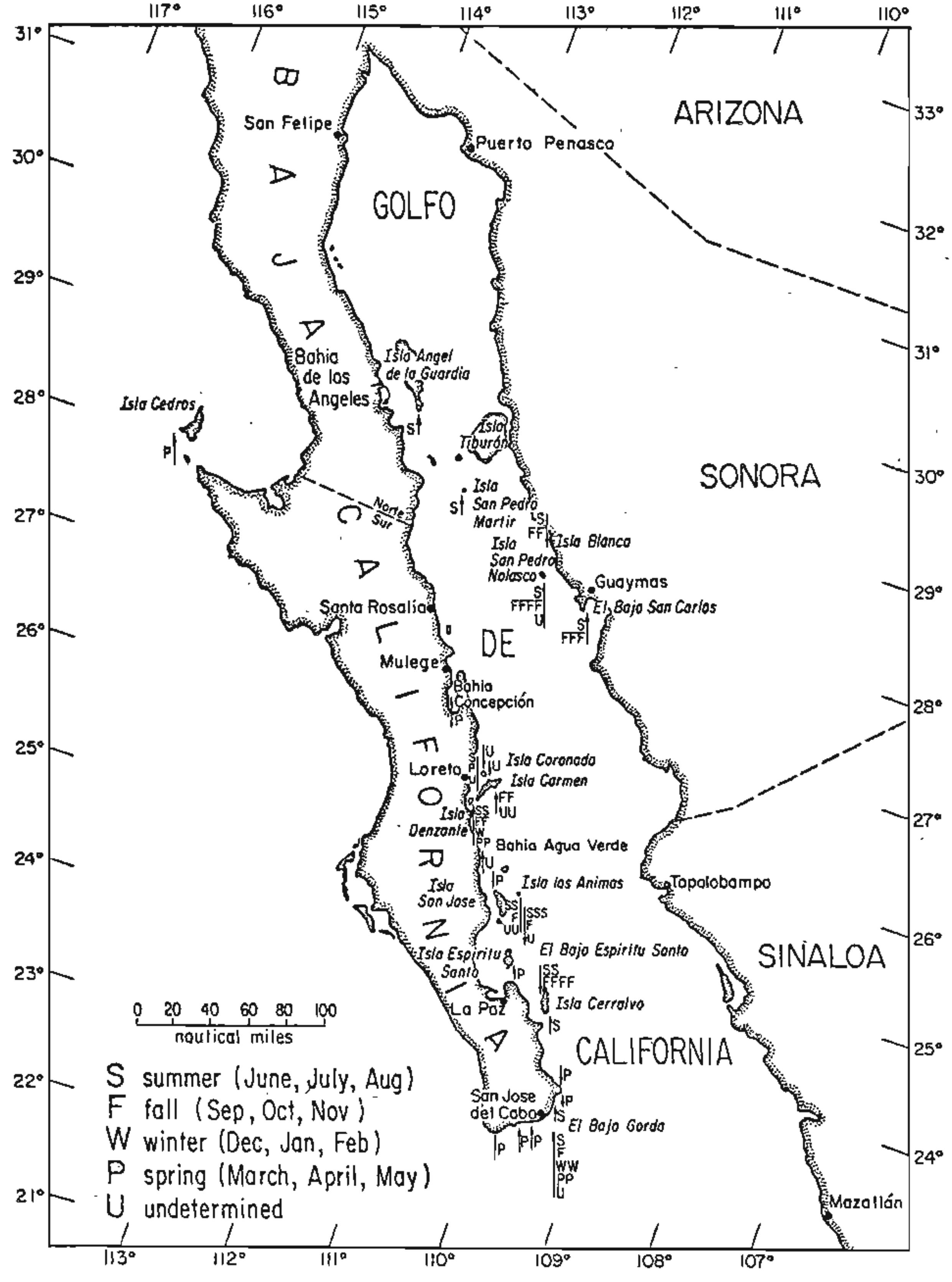
Fig. 3. School of hammerhead sharks. Note orientation of the sharks in the same direction and similar spacing between sharks.



in a northeasterly direction from Isla Espiritu Santo. It consists of a shallow plateau of 1 km in diameter with several pinnacles on a ridge reaching to within 14 m of the surface. This plateau is surrounded by very deep water. This and the other seamount site were inhabited during the summer by a diverse and abundant fauna consisting of loose schools of pompano and small jacks at the surface, large schools of bonito, larger jacks, and snappers in midwater, and large groupers at the bottom. Billfishes, dolphinfish, and large manta rays visited the sites often. The faunas at the islands were slightly less diverse, missing the large oceanic visitors. Large schools of hammerheads with as many as 225 members remained at El Bajo Espiritu Santo during the summer months, and for this reason, much of the research described in this report was conducted at this location. Las Arenitas (E) consists of a dropoff adjacent to a rock only 200 m offshore of the northwestern coast of Isla Cerralvo. Slightly northward of the rock is an elevated rocky reef. The bottom drops off abruptly to the seaward side of the reef, reaching a depth of 376 m within 1.5 km. Although only a few small schools of hammerheads were encountered there during the NGS-sponsored visit during the summer of 1980, schools of up to 50 members in 1979 and 75 members in 1982 were encountered during the summer just off the seaward side of the reef. El Bajo Gorda, the southernmost site, is located 8.5 km southeast of the tip of the Baja Peninsula. It is also a plateau with several pinnacles reaching to within 35 m of the surface. The plateau drops off into deep water on the southern side, yet it is separated by only a small distance of deep water from a broad bank on its northern side which extends southeasterly from the Baja Peninsula. Schooling hammerhead sharks of up to 75 members were encountered there during the summer, and larger groups of up to 225 members during the spring. Characteristic of all of these locations is the proximity of the pelagic environment. The scalloped hammerhead sharks could thus remain during the day at these offshore locations and disperse nightly either into the inshore neritic or offshore pelagic environments.

Our encountering the hammerheads only at the southernmost site during the spring and not at any sites during the winter and late fall indicated that the hammerheads might migrate into the Gulf of California during late spring, remain there during the summer months, and departed during the fall. This possibility was supported when we plotted our encounters and those of other divers as a function of season on a chart of the Gulf of California (Fig. 4). Schooling hammerheads (more than three) were encountered only off the tip of the Baja Peninsula during winter and spring. During the summer they were encountered throughout the Lower Gulf. They were seen in the Lower Gulf as well as at several locations in the Central Gulf nearby Guaymas only during early fall when water temperatures were highest in

Fig. 4. Seasonal occurrence of schools of scalloped hammerheads in the Gulf of California based on observations by the authors and other divers.


117°
116°
115°
114°
113°
112°
111°
110°
31°
30°
29°
28°
27°
26°
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24°
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32°
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26°
25°
24°
113°
112°
111°
110°
109°
108°
107°
ARIZONA
SONORA
SINALOA
BAJA CALIFORNIA
GOLFO DE CALIFORNIA
San Felipe
Puerto Penasco
Bahia de los Angeles
Isla Angel de la Guardia
Isla Cedros
Isla Tiburón
Isla San Pedro Martir
Isla Blanca
Isla San Pedro Nolasco
Guaymas
El Bajo San Carlos
Norte
Sur
Santa Rosalia
Mulege
Bahia Concepción
Loreto
Isla Coronado
Isla Carmen
Isla Denzante
Bahia Agua Verde
Isla los Animas
Isla San Jose
Topolobampo
Isla Espiritu Santo
El Bajo Espiritu Santo
La Paz
Isla Cerralvo
San Jose del Cabo
El Bajo Gorda
Mazatlán
0 20 40 60 80 100
nautical miles
S summer (June, July, Aug)
F fall (Sep, Oct, Nov)
W winter (Dec, Jan, Feb)
P spring (March, April, May)
U undetermined
P
S
S
S
FF
S
FFFF
U
S
FFF
P
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this zone. The inability of ourselves and other divers to observe large hammerhead schools in the Central and Lower Gulf of California during the colder months was reflected in few hammerheads caught at that time by fishermen at Juncalito, Isla Pardito, and Las Salinas (for locations, see Fig. 1).

Function of Schooling

An attempt was made to characterize hammerhead grouping with an emphasis on collecting data which would provide insight into the function of grouping. Five major functional hypotheses are discussed: 1) reproduction, grouping to carry out courtship and/or copulation, 2) defense, grouping for protection, 3) swimming efficiency, grouping at a location where less effort is required to maintain one's position, 4) reference, grouping at a landmark used as an orientational aid, and 5) feeding, grouping to ultimately increase predatory success through cooperation or clumping of individuals where prey densities are highest.

Schooling For Reproduction. In order to evaluate this hypothesis, sharks caught by long line and gill net were examined to determine the range of size over which males and females became mature. The sizes of the sharks swimming within the schools were also measured photogrammetrically. The presence of many subadults in the schools would indicate that the groups were not solely reproductive in nature.

Thirty-seven male scalloped hammerhads ranging from 79 to 240 cm in length were examined for state of maturity. The length of the male's clasper (his intromittent organ) was measured as well as the length of his testis (where spermatazoa are produced) and width of his epididymis (where spermatazoa are stored). These sexual organs all increased in size at a rate disproportional to overall growth in body length over a narrow range of from 163 to 170 cm. Spermatazoa were also found in another storage organ, the ampula ductus deferens, in males generally 170 cm and larger. Based on one or more of these indices, males were judged to become mature over a range of from 163 to 218 cm. Twenty-six females ranging from 77 to 276 cm in length were also examined for their state of maturity. A minimum length of the onset of maturity of 217 cm was determined from the presence of ovarian eggs in all stages of production and resorption. Small contusions either dorsal or lateral to the first dorsal fin were not found to be indicative of recent copulation as in some species of sharks (for account of courtship involving biting in sharks, see Klimley, 1980). These contusions were found on both mature and immature females.

The sizes of free-swimming sharks were measured with a hand-held stereocamera. This consisted of two underwater cameras (Nikonos III) with either 35 or 80 mm lenses (Nikkor) mounted on an aluminum beam with an optical viewfinder and light meter (Sekonic) (Fig. 5 A). The cameras and lenses used in the apparatus were provided by the National Geographic Society. The cameras were fired simultaneously by means of cables which passed through ferrules to a trigger attached to one of the handles. The lengths of the scalloped hammerhead sharks and their spatial relationships to other photographed sharks within the schools were determined by measurements made through a microscope by projecting a scale on to these stereopairs of photographs with a camera lucida (B). The scale to measure the length of the shark from the images of the photographs was obtained from a knowledge of the separation of the cameras and the measurement of the width on the photographs of no overlap in the two images. The measurements required to determine the length of a shark are illustrated in Fig. 6. This method is described in greater detail elsewhere (chapter 2). Photogrammetric measurements of lengths made at Isla Las Animas, El Bajo Espiritu Santo, and El Bajo Gorda are presented in Fig. 7. It was impossible to determine whether males within the groups were immature due to the paucity of male length measurements (solid). One of the two measured males was immature. However, most of the female lengths (stippled) were in size classes smaller than the 218 cm class, in which the smallest reproductively mature females would be placed. This fact together with the absence of copulatory behaviors observed within the schools indicated to us that the sharks were not assembling so that they could carry on courtship

Fig. 5. A. Stereocamera used to measure the lengths of free-swimming hammerhead sharks and their spatial relationship to members of schools. B. Making photogrammetric measurements with a microscope.


A


B

Fig. 6. Stereophotographic pair taken of free-swimming hammerhead shark. Upper photograph was taken by right-hand camera; lower photograph taken by lefthand camera. Measurments of x1 and x2 were made with respect to the lefthand edge of the frame. Measurement 1 was made from the tip of the snout to the tip of the caudal fin. The length was calculated by dividing the product of 1 and the camera separation distance by x2-x1.

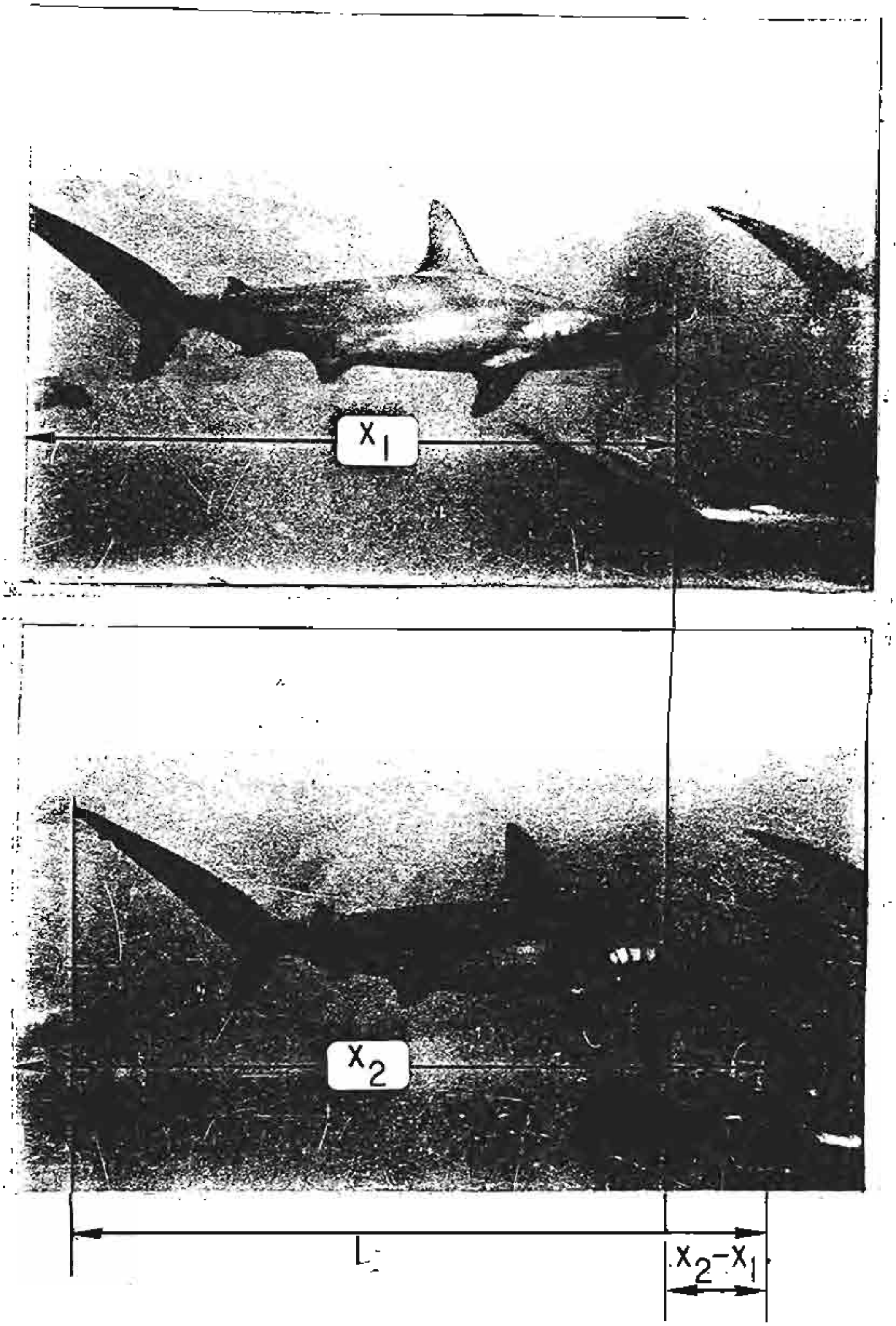
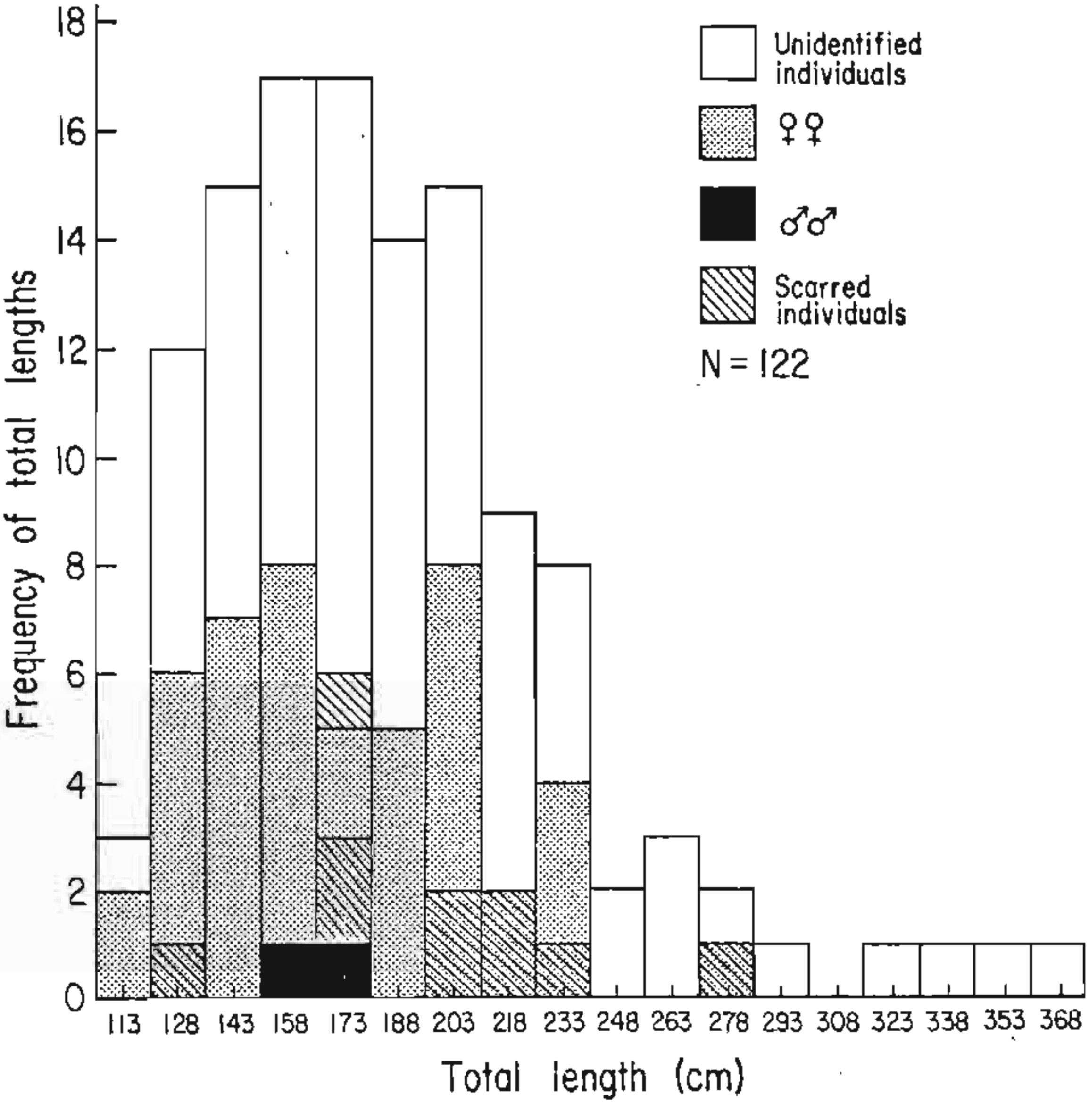

X1
X2
L
X2-X1

Fig. 7. Frequency distribution of photogrammetrically measured lengths of free-swimming scalloped hammerhead sharks pooled from Isla Las Animas, El Bajo Espiritu Santo, and El Bajo Gorda during July and Aug. 1981. Superimposed upon the pooled frequency distribution are those for unidentified (clear) and scarred (cross-hatched) individuals, males (solid), and females (stippled).



Frequency of total lengths
0
2
4
6
8
10
12
14
16
18
113
128
143
158
173
188
203
218
233
248
263
278
293
308
323
338
353
368
Total length (cm)
Unidentified individuals
♀♀
♂♂
Scarred individuals
N = 122

behavior immediately preceding copulatory behavior.

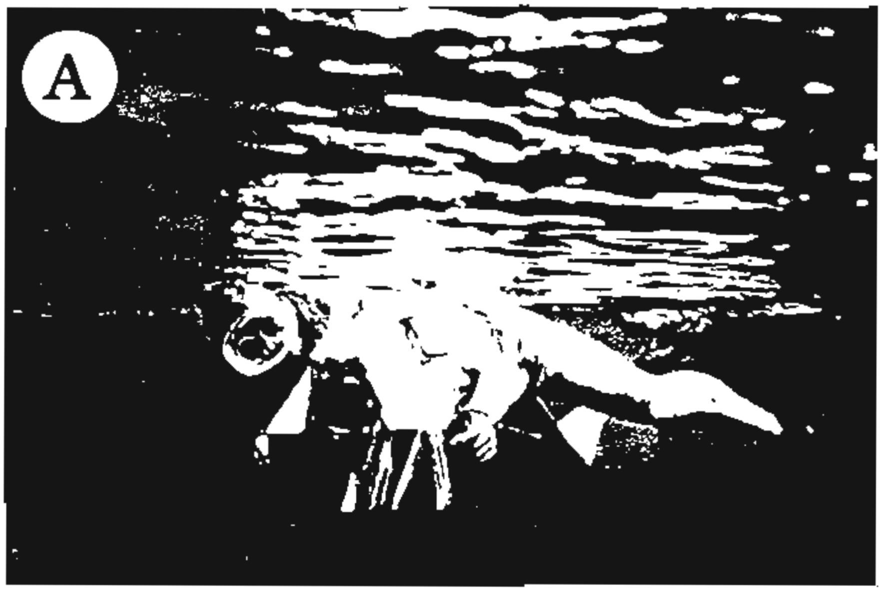
It was hoped that the presence or absence of seasonal periodicity of schooling could be compared with that of reproduction. An asynchrony between the two would eliminate reproduction as a motivational factor behind grouping. An aynchrony was not found. Schooling was observed during all seasons of the year in the Gulf of California although schooling was less common in the winter and spring seasons (see Fig. 4). Little anatomical or histological evidence for seasonality in reproduction existed in the sharks examined during the study. However, enough sharks were not examined at all seasons of the year to draw any strong conclusions from these data. The absence of multiple frequency peaks (corresponding to periodic births) in histograms of lengths of free-swimming and captured sharks may indicate year-round reproduction in the scalloped hammerhead.

However, it is possible that behaviors occurring within the schools might be reproductively motivated in an indirect manner. It was possible to position the measured sharks in an x-y-z cartesian coordinate system with the stereocamera as its origin. If the photographer positioned himself either above or to the side of the school when taking the stereophotograph, the sizes of the sharks along the nearer half of a cross-section of the group could be measured. The distance from the camera to the outermost (nearest to the cameraman) shark was subtracted from the increasing distances on the z-axis to sharks more distant from the cameraman toward the center of the school. Infrequent sharks separated from each other by distances of greater than three body lengths were arbitrarily considered outside of the group and eliminated from the analysis. Although a large increase in the sizes of sharks did not exist on the horizontal plane at Las Arenitas (Isla Cerralvo), a large statistically significant increase did occur on the vertical plane toward the bottom of the group. The lengths of sharks increased 8 cm every 100 cm down into the school. Not only were sharks toward the bottoms of the schools larger, but also they were separated by their nearest neighbors by larger interindividual distances. These increased 18 cm every 100 cm down into the school. At El Bajo Gorda and Espiritu Santo shark lengths increased into the group although it was impossible due to the small sample sizes to determine whether this increase was on the horizontal or vertical plane. Increases in length at these locations were 10 and 12 cm per 100 cm, respectively. Nearest-neighbor, interindividual distances did not increase at these locations. The members of schools at these three locations were primarily females.

Behavioral processes which might bring about segregation of sharks within the schools and scarring on females were described from field observations carried out over a three year period including the four NGS-funded expeditions. In addition, a completely self-contained underwater video system designed by the authors (Fig. 8 A) was utilized to record extensive _ad libitum_ (the whole group videotaped without regard to individual sharks) and focal samples (a single shark videotaped both within and outside of the group), and these samples were viewed repeatedly to form an extensive catalogue of species-typical behaviors (Fig. 8 B). Several aggressive behaviors were described which might explain how the larger females became segregated from the smaller females and how the contusions were inflicted.

Large females suddenly explosively accelerated from their parallel orientation to their schoolmates into a compact, looping swimming path while at the same time rotating on their longitudinal axes 360 degrees. This acrobatic behavior was called Corkscrew-swim. Corkscrew-swim often ended with the shark directing a Hit on another smaller shark dorsal or lateral to its first dorsal fin, presumably leaving a whitish contusion. Females in the vicinity of a shark performing Corkscrew-swim or actually Hit by such a shark often responded by swimming upward to the top or outward to the edge of the group. The withdrawing sharks often shook their heads back and forth twice or three times as they accelerated in what we call Head-shake. These aggressive interactions occurred primarily between females.

Fig. 8. A. Completely self-contained underwater video system. An extremely light-sensitive camera, portable cassette tape recorder, and power supply were placed in this housing, and it could be taken underwater to record two-hour behavioral samples. B. Authors viewing videotape sample aboard research vessel.


A

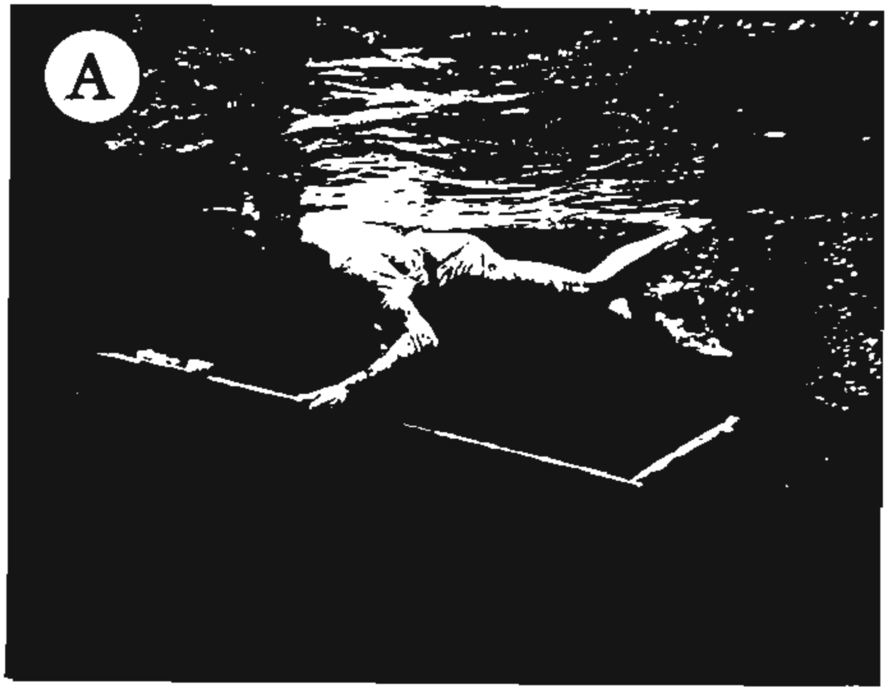

B

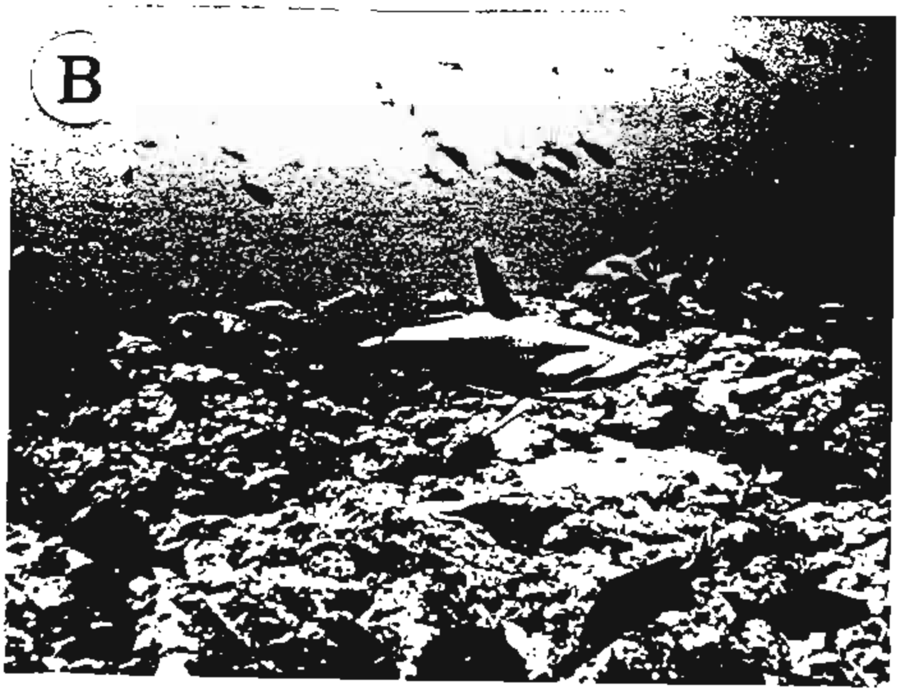
During the summer of 1979 the sex ratios at Isla Las Animas, El Bajo Espiritu Santo, and Las Arenitas averaged 2.7 females to a single male. In following years these ratios were even higher such as 5.5 to 1 in 1980 and 6.1 females to 1 male in 1981 (chapter 3). Males swimming at the top of the groups often attempted to penetrate into the group and reach the larger females nearby the bottom. They accelerated downward explosively thrusting their tails to one side while keeping the anterior part of their torso relatively rigid. The strong tail beats propelled the shark's anterior torso forward and to one side, and for this reason, the behavior was called Torso-thrust. The male's clasper was often visible at this time as the clasper was pivoted at a right angle to the shark's longitudinal axis. It appeared that not all sharks performing Torso-thrust were able to remain within the groups since occasionally a centrally positioned large shark (probably female) performed Corkscrew-swim in response to the intruder's entry, and the intruding shark withdrew to the top of the group while performing Head-shake. We believe that aggressive interactions between females may reflect competition for the few males present at these offshore sites. This possibility will be examined in more detail in the future in a more quantitative study of the behaviors occurring within the schools.

Hamilton and Watt (1970) described three central-place social systems. The most socially complex of these, the refuging system, was characterized by large numbers of individuals with complex communication schemes and cooperative behavioral patterns. Animals with this social system form large groups in a small core area of their home range during the inactive phase of their diel cycle and disperse large distances into their feeding arena during the active phase to forage as small groups or solitary individuals. Hamilton and Watt noted that the composition of these refuging groups was dynamic, and aggressive encounters were common among their members. Animals possessing refuging social systems cited by Hamilton and Watt were diverse, and consisted of the honey bee, the starling, the fur seal, and man. Some species of fishes such as the jacks, grunts, and snappers (Reese, 1978) and some species of cetaceans such as the spinner dolphin (Norris and Dohl, 1980) also refuge.

The scalloped hammerhead shark appears to be a refuging species in the Gulf of California. This was, in part, demonstrated by the use of ultrasonic telemetry. Hammerhead sharks were tagged with small telemetry transmitters (Fig. 9 A) by free-diving into the schools and applying transmitters from the end of a pole spear. The tranmitters were attached to each shark just posterior to its first dorsal fin by a subcutaneous metalic barb. The packages were slightly positively buoyant so that they floated just above the shark's dorsum and did not continuously contact and stress the shark. Although the

Fig. 9. A. Telemetry transmitter used to track movements of sharks. B. Hammerhead with conventional mark swimming above El Bajo Espiritu Santo (photograph taken by T. Rulison).

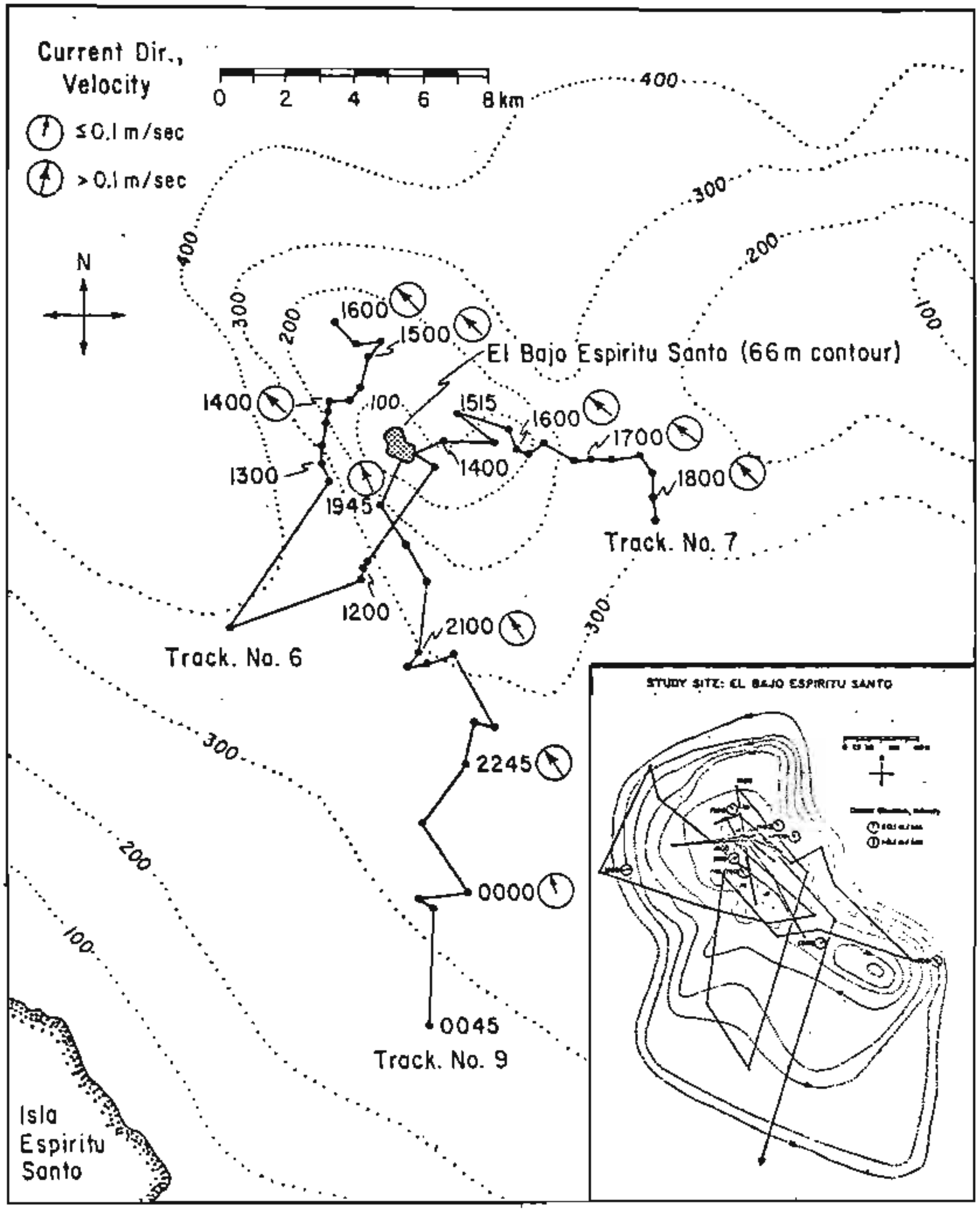

A


B

tagged hammerheads momentarily accelerated once the barb was applied, they soon returned to the schools and remained within them during the remainder of the day. This indicated that they were minimally stressed. During the day most of the tagged sharks swam relatively slowly back and forth along the seamount ridge. This was illustrated by the movements of tagged shark No. 9 which swam up and down the ridge at El Bajo Espiritu Santo from 1000 to 1930 before departing in a southerly direction on 15 July 1981 (inset in Fig. 10). Although the shark swam within an area of a diameter of 1 km for a period of 9.5 hrs during the day, it departed from the seamount at dusk and swam over a distance of 18 km in 5 hrs. The swimming effort at night was even greater than indicated by the distance moved alone since the shark was swimming against a substantial tidal current.

Also conforming to the refuging model was the absence of daytime predation by scalloped hammerheads in the vicinity of El Bajo Espiritu Santo. Feeding was never observed in the vicinity of the seamount although sharks were often observed swimming among diffuse schools of potential prey. No feeding responses were also directed at baits hung just above schools of hammerheads. Feeding readiness on several occasions was tested by playing back sounds attractive to many species of sharks (including *Sphyrna* spp.) and baiting with chum immediately after encountering groups of sharks with only a few sharks attracted (Klimley and Nelson, 1981). Also

Fig. 10. Telemetry trackings of three sharks followed after their departure from the seamount (stippled). Note circles and arrows which indicate current direction and velocity at hourly intervals. Inset of movements of scalloped hammerhead No. 9 over the seamount (indicated with dotted depth contours) is in lower righthand corner.


Current Dir., Velocity
≤0.1 m/sec
>0.1 m/sec
0
2
4
6
8 km
N
400
300
200
100
1600
1500
1400
1300
1200
1945
1515
1400
1600
1700
1800
2100
2245
0000
0045
El Bajo Espiritu Santo (66 m contour)
Track. No. 6
Track. No. 7
Track. No. 9
Isla Espiritu Santo
STUDY SITE: EL BAJO ESPIRITU SANTO

fitting the model was the rhythmical dispersal of sharks into the surrounding pelagic and neritic habitats at night only to return to the seamount during the following day. Although hammerhead No. 9 did not soon return to the seamount, three (or possibly four) other hammerheads did so. For instance, hammerhead No. 13 was tracked ca. 8 km away from the seamount toward the center of the Gulf of California, and it returned to the seamount early during the following day. This coupled with the reobservation of many sharks marked with color-coded, plastic-streamer tags (see Fig. 9B) at the seamount over a period of a month during the summer expedition (chapter 4) indicated that sharks often returned to the seamount after their nightly foraging excursions. The existance of a aggression within the schools of scalloped hammerheads, the schools' dynamic compositions, and the presence of highly stereotyped behavioral patterns, possibly involved in communication (Klimley, 1981) also fit the refuging model.

What could the reason be for gathering into a small core area of the home range during the inactive period of the diel activity cycle? And why should such grouping occur along the dropoff from a seamount or island and not over deep water? In most species the formation of groups at this time is for protection from predation. However, it was possible that other advantages for structured grouping in the scalloped hammerhead could exist such as the matching of fit females with rare males as discussed earlier, to gain a hydrodynamic advantage by remaining in eddies, or perhaps use the seamount as an orientational aid.

Schooling for Protection. This appears to be the least likely reason. Predation of the scalloped hammerheads was never witnessed during the study despite considerable observation by the investigators of the schools. Furthermore, potential predators such as the white shark, *Carcharodon carcharias* (for *Sphyrna* sp. stomach remains see Bass *et al.* [1975]), were rarely caught in the area.

Schooling for Increased Swimming Efficiency. The schooling hammerheads might take advantage of reduced current velocities inside eddies down current from the seamount ridge. If the sharks remained in these eddies, the sharks would not have to swim so fast during the inactive phase of their diel activity cycle. Due to the presence of currents flowing roughly perpendicular to and parallel to the direction of the seamount ridge, it was possible to test whether a change in the direction of the current affected the directions moved by telemetry-tracked sharks. The directions swam between 15 min periods did not differ in a statistically significant manner between the two current regimes. Supporting this conclusion was also the lack of a correlation between the movements at the seamount of hammerhead No. 9 and current directions. These are indicated in small circles following the shark's hourly positions in Fig. 10.

Schooling at Landmark Used As Orientational Aid. The seamount is certainly a conspicous landmark in the pelagic environment to which the hammerheads repeatedly return after extensive movements in the pelagic environment. How do the sharks find their way back to this small spot? The hammerheads may be using geoelectric fields. Elasmobranchs possess sensory receptors, the Ampullae of Lorenzini which are sensitive to electric fields as minute as 0.01 uV/cm (Kalmijn, 1966) and less (Kalmijn, 1982). Such fields are characteristic of ocean currents, and the strengths of these fields are within the sensitivity of elasmobranchs. It is possible that sharks use these fields to locate the seamount. Such fields are induced whenever masses of seawater move through the earth's magnetic field. The presence of the stationary, non-conductive seamount in the moving, conductive seawater masses of the Gulf of California should produce a characteristic field to which the hammerheads could orient. Due to the uniqueness of the seamount's field, the sharks might remain at this location during their inactive phase in order to utilize its characteristic field to remain centrally positioned in the relatively uniform pelagic environment where they feed. It is also possible that they could return to particularly favorable foraging areas better using the seamount as an orientational reference. The testing of this functional possibility was not undertaken during this study, but may be undertaken in the future in collaboration with Adrianus Kalmijn also of Scripps Institution of Oceanography.

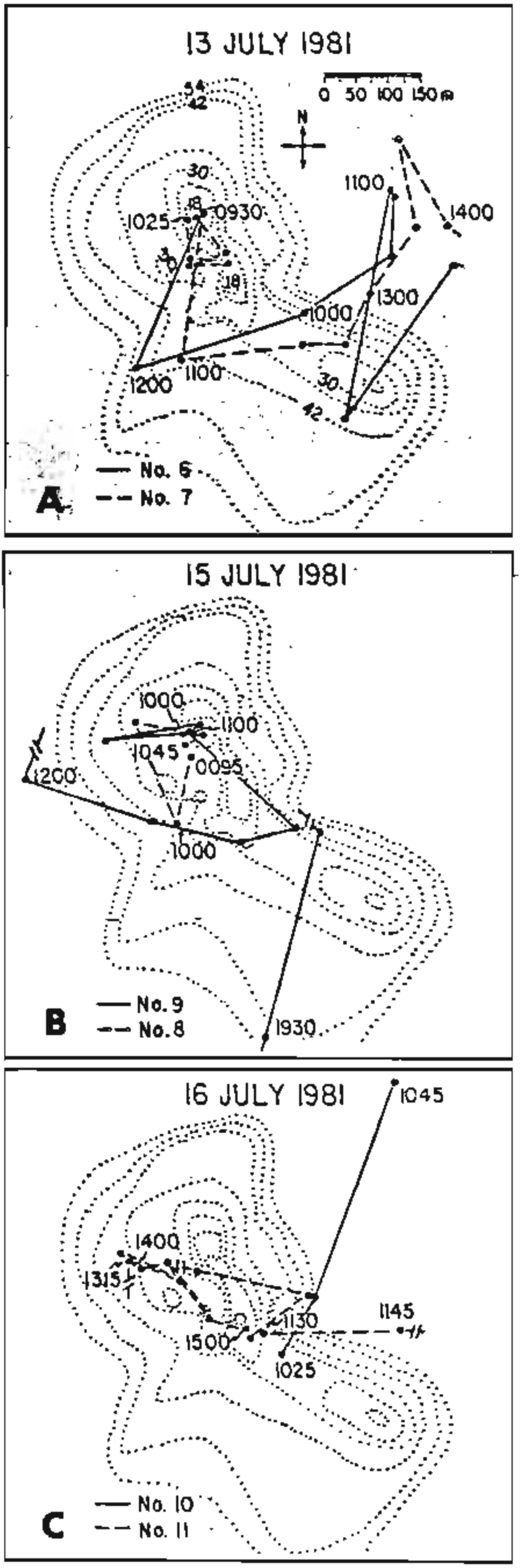
Schooling to Increase Predatory Success. Although predation was not observed in schooling sharks during the day, it is possible that the sharks might remain together during their inactive phase so that they could forage socially during their active period at night. The clumped nature of the prey of adult hammerheads indicated that they might profit by foraging in groups (chapter 6). If prey were clumped, grouped individuals could better exploit the clump once it was encountered. Although the social structure of the cephalopod prey was not known, that of the prey fishes was well known. Intermediate size sharks fed primarily on schooling prey such as the neritic chub mackerel, wavyline grunt, mullet, and anchovy. Large sharks also fed on neritic and pelagic schoolers such as the jack mackerel, the cortez grunt, a corvina, the scud mackerel, the dolphinfish, and the Monterey spanish mackerel.

In order to test whether adult hammerheads foraged socially, an attempt was made to determine whether they left the seamount in groups. On five occasions two hammerheads were simultaneously tagged and tracked to see if they left the seamount together, presumably in a large school. After tagging a single hammerhead, that shark was located, and an attempt was made to dive down into its school and tag an additional shark within the school. Three of the five paired trackings are illustrated in Fig. 11. In all five trackings the two hammerheads left separately. For instance, in paired tracking B No. 8 remained only momentarily nearby No. 9 over the seamount ridge before leaving in a northeasterly direction at 1030 hrs. Hammerhead No. 9 swam back and forth along the seamount ridge (some of these movements are deleted) before leaving in a southerly direction at 1930 hrs. The separate departures of all of the members of the tracking pairs suggested that the sharks probably did not leave the seamount to forage in large groups but more likely in small groups or as solitary individuals. However, this test of whether scalloped hammerheads left the seamount in groups was equivocal. It is always possible that one of the two sharks in each pair departed prematurely due to the stress of the transmitter attachment.

CONCLUSIONS

The scalloped hammerhead possesses a refuging central-place social system. By behaving in this manner they remain during the inactive phase of their diel activity cyle centrally positioned at the interface between the neritic and pelagic habitats. They can then disperse into both habitats to exploit fish and cepalopod resources there during the night. The reason th the scalloped hammerheads may form such highly structured schools at at these locations is not to

Fig. 11. Three paired telemetry trackings performed at El Bajo Espiritu Santo during July 1981 to determine whether scalloped hammerhead sharks departed together within schools.


13 JULY 1981
0 50 100 150 m
N
54
42
30
18
0930
1025
1100
1400
1300
1000
1200
1100
30
42
— No. 6
-- No. 7
A
15 JULY 1981
1000
1100
1045
0095
1200
1000
1930
— No. 9
-- No. 8
B
16 JULY 1981
1045
1400
1315
1130
1145
1500
1025
— No. 10
-- No. 11
C

avoid predation, maximize swimming efficiency, or remain together so that they can forage socially at night, but more likely to carry out social activities. Perhaps the reason why the hammerhead schools form at the seamount rather somewhere else over deep water in the pelagic environment is because the seamount may be a landmark used by the hammerheads to remain centrally positioned within their home range. This functional possiblity will be examined in a future study.

AKNOWLEDGEMENTS

We would like to express our gratitude to the many researchers who participated in the four expeditions during 1980 and 1981 such as S. Brown, J. Barlow, R. Butler, G. Di Sciara, P.B. Klimley, B. Kurtz, J. McKibben, C. Phleger, R. Rosenblatt, T. Rulison, and F. Wolfson. We would also like to thank D. Lluch, H. Nienhuis, F. Galvan, and others from the Centro de Interdisciplinario de Ciencias Marinas (CICIMAR), La Paz for providing the use of their research vessel, the Juan de Dios Batiz, and participating in the joint SIO-CICMAR cruises during which much of this research was carried out. The Office of Naval Research provided salary support for the authors during this time (Contract N00014-77-0-01131 to Donald R. Nelson, Principal Investigator). This report constitutes part of the doctoral dissertation of the senior author at the University of

California, San Diego under the guidance of Richard H. Rosenblatt.

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