THE TAXONOMY, BIOGEOGRAPHY AND BIOLOGY OF COW AND FRILLED SHARKS (CHONDRICHTHYES:HEXANCHIFORMES)

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ABSTRACT

This study was undertaken to investigate the taxonomy, biogeogaphy and biology of cow and frilled sharks (Chondrichthyes: Hexanchiformes). This taxon comprises two families, four genera and six extant species. The hexanchoids are a distinctive group of sharks characterized by six or seven paired gill openings, a single dorsal fin and an anal fin. Adult males of this group lack a siphon sac, but have in its place, a clasper sac. This structure, which develops along the claspers, is unique to the Hexanchiformes. Hexanchoid sharks are widely distributed in area and depth. This group ranges from coastal bays and harbors along the open coast out across the continental shelf and down along the slopes to considerable depths. They occur from the equatorial zone to sub-polar regions. However, little is known about the ecology and life history of these sharks. Intraspecific variation of meristic counts were generally low for the Hexanchidae, but high for the Chlamydoselachidae, indicating that subpopulations, subspecies or even additional, new species exist within this family.

Based on the indicators used in this study, maturity in male frilled sharks was attained at 916 mm TL, perlon sharks between 700 and 800 mm TL, sixgill sharks approximately 3140 mm TL, bigeyed sixgill sharks at about 1250 mm TL and sevengill sharks at approximately 1550 mm TL. Male reproductive success did not appear to be seasonal since males were found to contain viable sperm all year round.

Female perlon sharks begin maturing between 950 mm and 1100 mm TL. Gravid females and newborns were absent from the other size classes and it is suspected that they aggregate in different locations to those of adult males and non-breeding females. Adult females are known at 4210 mm TL and immature at 3500 mm TL, However, a more accurate estimate of the size at maturity is wanting. Newborn sixgills were caught off southern Namibia during mid- to late summer over three successive seasons. The occurrence of gravid females carrying term embryos during spring months and newborns during the summer months suggests a late spring or summer pupping period. Sixgill and sevengill sharks give birth in areas of high primary productivity. Energetically, this is advantageous for the newborns to be placed in an area with an abundant food source. The rapid growth rates of sixgill and sevengill sharks over the first year would enhance their survivorship since neither species has many predators. The number of female sevengills entering the breeding population is regulated to ensure that some portion of the population is reproductively active at any one time. The "staggering" of females which enter into the breeding population in any given year indicates a two year reproductive cycle. Fecundity estimates for 19 specimens with a largest egg diameter of at least 40 mm indicates a litter size of 67 to 104. The recapture of an adult female sevengill in approximately the same location in which it was tagged suggests that the same individual sharks may return to the same breeding grounds.

As with any predators, sharks tend to exploit advantages over their prey. The hexanchoids, especially the sevengill, have evolved complex foraging strategies including social facilitation whereby they actively hunt in packs for large prey species.

Sharks of the order Hexanchiformes, although lacking the diversity of the major shark orders, nonetheless play an integral role in the marine environment. The group's success can be attributed to their apical trophic position. In most habitats in which they occur, hexanchoids have no comparable competitors since equivalent sized sympatric squaloids and carcharhinoids feed at a lower trophic level.

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As children, most of us have heroes that we idealize and want to be like. For me, as a child and adult, that hero has always been my father, to whom I dedicate this dissertation.
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CHAPTER 1

INTRODUCTION

Sharks, rays and chimaeras are related groups of cartilaginous fishes included in the class **Chondrichthyes**. It is now generally accepted that sharks, or selachians (superorders **Squalomorphi**, **Squatinomorphi** and **Galeomorphi**) and rays, or batoids (superorder **Batoidea**) form a monophyletic group, sharing a common neoselachian ancestor. The interrelationships of the sharks and rays with the chimaeras (subclass **Holocephali**) however, remain uncertain (Compagno 1973, 1977; Maisey 1984).

The sharks are a highly evolved and extremely well-adapted group of fishes, having persisted in some form for at least the last 400 million years. Studies on the life histories of this remarkable group have, however, been limited. The extreme diversity of their bony fish counterparts, the teleosts (class **Osteichthyes**), has tended to focus attention away from the relatively less-diverse and less numerous sharks and their relatives.

The role of chondrichthyians has often been ignored in marine community studies, yet they are apical predators and as such perform an integral role in their environment. Furthermore, in order to do so, they have evolved highly developed and specialized means by which they feed, reproduce and survive.

Current taxonomy recognizes eight orders of sharks (Compagno 1973, 1977), with 30 families and approximately 370 species. The batoids are an even more diverse group with five orders, 17 families and at least 550 species. The chimaeras consist of a single order, three families, and 31 or more species. These numbers are continually being revised as new species are described.

Orders of Sharks

'Major' Shark Orders - Carcharhinoids

Of the eight shark taxa, four may be considered major orders because of their numbers and diversity of species, while the other four are minor orders. The Order **Carcharhiniformes** is by far the predominant group, with eight families and comprising over 55 percent (209 species) of the total number of shark species. The characteristics of this group include two spineless dorsal fins, five paired gill slits, movable nictitating lower eyelids and a long mouth extending behind the eyes. According to Compagno (1988), these sharks are far less diverse morphologically and biologically than the other major shark orders. This conclusion was based on a lack of specialized characteristics or unusual trophic adaptations within this group. In general, this hypothesis holds true with regards to morphology, since most carcharhinoid families are externally less distinct from one another than are members of, for example, the lamnoid or orectoloboid families. Obvious exceptions are the hammerhead sharks (**Sphyrnidae**) with their bowplane cephalofoils, and the swell sharks (Cephaloscyllium, **Scyliorhinidae**), which have a unique ability to gulp air.

In terms of their life histories, however, the carcharhinoids show extreme specialization. For example, along the east coast of southern Africa at least 15 species of Carcharhinus are known to occur (Compagno, Ebert & Smale 1989) and although morphologically similar, each occupies a specific niche within this ecosystem. Notable features of the Carcharhinus species in regard to their general distribution and the habitat occupied by this group in the south-west Indian Ocean have been described by Bass, D'Aubrey and Kistnasamy (1973). Comparison of two large Carcharhinus species, the dusky, C. obscurus, and Zambezi, C. leucas, illustrates how morphologically similar congeners have relatively diverse life histories. Adult dusky sharks usually occur along the deeper waters of the outer continental shelf. Seasonally, they range close inshore to give birth. The juvenile dusky sharks remain in this nearshore environment for the first few years of life. Once they begin to mature, the dusky sharks move offshore and join the adult populations. In contrast, the Zambezi shark is a coastal species that migrates up rivers and into estuaries to give birth. The young Zambezi sharks remain in these estuaries until they begin to mature. In the state of Florida, U.S.A., Snelson, Mulligan and Williams (1984) found that only juvenile and adult bull

(=Zambezi) sharks occupied the nursery area, whereas adolescent individuals were excluded. Both species may be categorized as sympatric or allopatric to each other depending on the life stages and microhabitat utilization. Juvenile dusky sharks and adolescent and adult Zambezi sharks occupy similar habitats, but the latter is a higher trophic level predator which preys heavily on juvenile dusky sharks. Studies by Van der Elst (1979) showed that Zambezi sharks were significant predators on juvenile dusky sharks along the Natal coast. The removal of Zambezi sharks by large mesh shark nets has resulted in an increase in numbers of juvenile dusky sharks, which prey heavily on commercially valuable teleost fishes.

The complexity of all 15 Carcharhinus species, each successfully adapted to this ecosystem, suggests a group of sharks that has radiated into most available niches. The habitat, prey preference, reproductive strategy and behavior of each species varies according to life stage. Thus Carcharhinus has managed to invade a broad range of niches, especially in the tropics, and considering the inclusion of the other carcharhinoid groups, further enhances the dynamics of the ecosystem.

'Major' Non-carcharhinoid Orders

The three major non-carcharhinoid orders (**Squaliformes**, **Orectolobiformes**, **Lamniformes**) all have members that are far more heterogeneous than the Carcharhiniformes. Morphologically these groups are diverse, while biologically they occupy a wide range of habitats. The lamnoid and orectoloboid families are especially distinct from each other.

The Order **Lamniformes** is a small (in terms of species) but highly diverse shark taxon with seven families, four of which are monotypic, and 15 species. The sharks in this group are large with a "typical" shark shape. They have two spineless dorsal fins, an anal fin and five paired gill openings. The mouth is long and there are no nictitating membranes. The lamnoids have not radiated into the same range of niches as carcharhinoids, but each member has particular morphological adaptations especially suited to its life history. The basking shark (**Cetorhinidae**) and megamouth shark (**Megachasmidae**) are giant filter-feeding species, each of which occupies a distinctly different habitat. The two species can be contrasted with the warm-blooded, high-speed mackerel sharks (**Lamnidae**) which include the mako shark, Isurus oxyrinchus (probably the fastest swimming shark) and the white shark, Carcharodon carcharias, the marine superpredator. Prey preferences for this group include small to large teleosts, cephalopods, cartilaginous fishes, marine mammals, sea birds and marine reptiles. The thresher sharks (**Alopiidae**) have elongated caudal fins that are nearly as long as the body and used to stun schooling bottom and pelagic bony fishes. The bizarre-looking goblin shark, Mitsukurina owstoni (**Mitsukurinidae**), is a deepwater species, unlike any other shark, and a specialized benthic inhabitant.

The lamnoids, though small in number, are all fairly wide ranging species. They have representatives within all major ecosystems and appear to compete on an equal, and in some cases higher, trophic level than most carcharhinoids. Lamnoid success can be attributed to their highly specialized morphological adaptations and life history strategy.

The Order **Orectolobiformes** is a small, diverse group of sharks with seven families and 33 species. These are the only sharks that combine two spineless dorsal fins, an anal fin, nasal barbels, a short mouth situated well in front of the eyes and five paired gill openings. This order includes many specialized bottom dwellers, such as the dorso-ventrally flattened wobbegongs (**Orectolobidae**) and the near eel-like carpetsharks (**Hemiscylliidae**). Another specially adapted member of this order is the filter-feeding, oceanic whale shark (Rhincodon typus), which is also the largest living fish. The orectoloboids, despite their distinctive morphological appearance, are generally restricted to warm temperate or tropical inshore waters. They fill the gap in the ecosystem left vacant, for the most part, by the carcharhinoids. The closest analog to the reef-dwelling orectoloboids is the swell shark, one of the few morphologically specialized carcharhinoids. Interestingly, in those areas where both swell sharks and bottom-dwelling orectoloboids occur, the former group inhabits deeper water. This suggests an obvious trophic adaptation that benefits both groups. Several orectoloboid species may for example, inhabit a typical inshore tropical reef. Members of the families **Parascylliidae**, **Hemiscylliidae** and **Brachaeluridae** are generally small and specially adapted to feeding on small reef fishes, crustaceans and other invertebrates. Larger species such as those members of the **Ginglymostomatidae**, **Orectolobidae** and **Stegostomatidae** feed on larger prey items such as fish, crabs, lobster and cephalopods. The wobbegongs, with their powerful jaws and fang-like teeth are especially adept at ambushing unsuspecting prey. The nurse sharks (**Ginglymostomatidae**) have a well developed suction mechanism whereby they may quickly inhale small reef fish or invertebrates. Swell sharks by comparison, do not have any of the special feeding adaptations exhibited by the orectoloboids. Thus it appears that the more generalized swell sharks have been replaced in nearshore tropical reefs by several diversely specialized orectoloboid species.

The Order **Squaliformes** is the second largest group of sharks with three families and at least 83 species. This is a predominantly deepwater group that, with continued investigation, will probably expand to 100 species or more. The characteristics of this group include two dorsal fins (many with spines), no anal fin, cylindrical bodies, short mouths, long snouts and five paired gill openings. The teeth are moderately differentiated, many species having powerful jaws adapted for cutting. The squaloids have several specialized adaptations and include species with bioluminescent organs and others that are specialized oceanic pygmies. The oceanic cookie-cutter shark, Isistius sp., for example, is an ectoparasite on large bony fishes, oceanic sharks, cetaceans and pinnipeds, while the deepwater Portuguese shark, Centroscymnus coelolepis, parasitizes deep diving cetaceans. This order has both some of the smallest and largest living shark species. The spined dwarf pygmy shark, Squaliolus sp., reaches a maximum total length (TL) of 20 cm while the giant sleeper shark, Somniosus sp., grows to at least 7 m. Squaloids are the only sharks that are known to inhabit the cold Arctic and Antarctic polar waters. The squaloids have radiated mainly into deepwater and oceanic habitats where the carcharhinoids are less abundant.

'Minor' Shark Orders

Of the remaining four 'minor' orders, three (**Pristiophoriformes**, **Squatiniformes** and **Heterodontiformes**) are morphologically conservative and appear to be restricted in their choice of habitat.

The saw sharks (Order **Pristiophoriformes**) are a minor group with a single family (**Pristiophoridae**), two genera and five or more species. This is an unmistakable group that is easily distinguishable by its elongated and flattened rostrum, edged with slender, sharp lateral teeth and a long pair of rostral barbels in front of the nostrils. These sharks have two dorsal fins, no anal fin, short transverse mouths and small cuspidate holding teeth in both jaws. The genus Pliotrema differs from Pristiophorus by the presence of six paired gill openings instead of the usual five. The maximum size range for these sharks is between 1 and 1.5 m TL. They occur at moderate depths on the continental shelves and slopes down to 915 m depth (Compagno 1984a). These sharks appear to be most common on mud, sand or gravel bottoms. The saw-like snout is used for attacking small fishes and cephalopods.

The angel sharks (Order **Squatiniformes**) are a small, highly distinctive group of sharks with one family (**Squatinidae**), a single genus and at least 13 species. They are ray-like in external morphology with mottled dorsal surfaces and large pectoral fins that extend over the ventrally directed gills. Unlike rays, however, the fins are not fused to the sides of the head. There are two dorsal fins, no anal fin and a caudal fin with the lower lobe longer than the upper. The mouth is terminal with sharp impaling teeth in both jaws. The maximum size for this group is 2.4 m TL but most species are less than 1.5 m TL. They are shallow to moderately deep water species of the continental shelves and slopes from the intertidal down to 1390 m depth (Compagno 1984a). Angel sharks are often observed half buried on sand or mud bottoms. They are adept at ambushing prey, which consists largely of small fishes, crustaceans, cephalopods, gastropods and bivalves.

The horn sharks (Order **Heterodontiformes**) are a minor group with one family (**Heterodontidae**), a single genus and eight species. These are the only sharks that combine two dorsal fin spines and an anal fin. They have large, thick heads with a broad crest over each eye, short pig-like snouts, and short transverse mouths with enlarged, flattened crushing teeth posteriorly and smaller cusped teeth anteriorly. The maximum size attained by these sharks is 1.6 m TL. Horn sharks inhabit shallow to moderately deep water from the intertidal out to 275 m depth (Bass, D'Aubrey & Kistnasamy 1975). They are often seen by divers, hiding in caves and crevices on rocky reefs during the day. The highly differentiated dentition and head structure of horn sharks are specialized adaptations for feeding on hard shelled invertebrates (Compagno 1988).

All of these 'minor' groups have specialized morphological adaptations and life history strategies that enable them to co-exist with the larger more diverse groups. For example, they tend to occupy shallow-water habitats in temperate seas where the carcharhinoids are less numerous, but are restricted to the outer shelf and upper slopes in the tropics.

The fourth order in this 'minor' category, the cow and frilled sharks (Order **Hexanchiformes**), has two families, four genera and five species. These are the only sharks that combine six or seven paired gill openings, a single dorsal fin and an anal fin. Only the sixgill sawshark, Pliotrema warreni (Order Pristiophoriformes), has more than the customary five paired gill slits, common to all other shark species. However, the sixgill sawshark has two dorsal fins, no anal fin, and has its rostrum flattened into a saw with lateral teeth and rostral barbels. The catshark, Pentanchus profundicolus (Order Carcharhiniformes), has a single dorsal fin, but five paired gill slits. The validity of P. profundicolus is uncertain since it is known only from type material and may merely represent an anomalous individual (Compagno 1988).

The frilled sharks (family **Chlamydoselachidae**) are a monotypic group represented by the frilled shark, Chlamydoselachus anguineus. Frilled shark is the common name usually applied to this species and will be used here. A list of other regional common names that have been applied to C. anguineus is given in table 1.1. The frilled shark is distinctive in having a slender, eel-like body, with prominent keels on the abdomen. The head has six paired gill openings, with the lower ends of the first gill extending across the throat. The snout is extremely short and truncated, the mouth being terminal. The teeth are alike in the upper and lower jaws, with three strong cusps and a pair of intermediate cusplets. The anal fin is larger than the dorsal fin and the caudal fin lacks a subterminal notch. It is a medium-size shark that reaches at least 1.96 m TL (Bass et al. 1975). It is usually caught on or near the bottom in deep water between 120 and 1450 m depth, though it occasionally makes excursions into the water column (Shiobara, Abe & Hioki 1987).

The frilled shark was first described by Garman (1884) from a 1.5 m TL female specimen purchased by the Harvard Museum of Comparative Zoology (MCZ), Harvard University. The exact location of capture is unknown, but it was likely southeastern Honshu, Japan, due to the close proximity of several deep water submarine canyons. Much of the early interest in this species stems from its supposed affinity with the cladodonts (Garman 1884, 1885; Gill 1884). Gudger and Smith (1933) showed, however, that the frilled shark actually possesses many specialized structural adaptations. Neurocranial studies by Compagno (1977) showed a close similarity between the frilled shark, other hexanchoids and squaloids.

The frilled shark's anatomy has been described in detail by numerous authors (Garman 1885; Hawkes 1907; Goodey 1910; Allis 1923; Gudger & Smith 1933; Smith 1937), but these studies were based on Japanese specimens, since their capture outside Japan is uncommon and most of these were deposited in museums and academic institutions. Smith (1967) pointed out that not only did a certain degree of sexual dimorphism exist within the species, but that within each sex there is a wide variation in form. Given the paucity of specimens, knowledge of their taxonomy, biology, and ecology is sketchy.

The cow sharks (family **Hexanchidae**) comprise three genera and four living species. These sharks are characterized by having six or seven paired gill openings, a single dorsal fin, an anal fin and an elongated caudal fin. The genus *Heptranchias* is represented by a single species, *H. perlo*, or commonly referred to as the perlon shark, the name that will be used here. A list of regional common names for this species is given in table 1.2. Perlon sharks can be distinguished by their narrow snout, seven paired gill openings and a mouth that is subterminal and longer than wide. This is the smallest hexanchoid, attaining a maximum length of 1.4 m (Garrick & Paul 1971). It is a moderately deep water species occurring between 27 and 720 m depth (Compagno *et al.* 1989).

The perlon shark was first described by Bonnaterre (1788) from the Mediterranean Sea as *Squalus perlo*. The species was subsequently redescribed several times (see chapter 3 for synonymy) from various localities. Unfortunately most of these descriptions were poor and the supposed differences were owed to changes in allometry and sexual dimorphism (Garrick & Paul 1971). Detailed studies on their anatomy and morphology have never been undertaken.

Two species in the genus *Hexanchus* are recognized, the sixgill shark, *H. griseus*, and the bigeyed sixgill shark, *H. nakamurai*. Sixgill shark is the common name most frequently used for *H. griseus* (and will be applied here) though other vernacular names such as mud shark, cow shark, gray shark, or bluntnose sixgill shark have been used (Bigelow & Schroeder 1948). A list of regional common names for *H. griseus* is given in table 1.3. Bigeyed sixgill shark is the only common name that has been applied to *H. nakamurai* and thus will be used here. Both species can easily distinguished by the presence of six paired gill openings, a subterminal mouth, comb-like lower anterolateral teeth and a subterminal notch on the caudal fin. The sixgill shark can be separated from its congener by a relatively short blunt snout, broad mouth, smaller eye diameter and a relatively smaller dorsal-caudal space (Bass *et al.* 1975). The sixgill shark has six rows of large lower anterolateral teeth as compared to five for the bigeyed sixgill. The sixgill is the largest member of the family Hexanchidae with a maximum of at least 4.82 m TL (Bolivar 1907) while the bigeyed sixgill is a moderate sized species that grows to 1.78 m TL (Springer & Waller 1969). Both are regarded as deep water species that occur along the outer shelves and upper slopes, but also occasionally come close inshore (Bass et al. 1975; Ebert 1986b, 1988a).

The sixgill shark was originally described as Squalus griseus by Bonnaterre (1788) from an unknown location in the Mediterranean Sea. The species was subsequently placed into the genus Hexanchus that was erected by Rafinesque (1810). Descriptions of additional eastern Pacific Ocean species, H. corinus (Jordan & Gilbert 1880), H. vulgaris (Perez-Canto 1886) and H. griseus australis (De Buen 1960), are probably synonymous with H. griseus (Regan 1905; Bigelow & Schroeder 1948; Compagno 1984a). Detailed descriptions, however, are unavailable to accurately determine any possible regional population differences. Comparison of regional populations, however, will only be possible when detailed descriptions of specimens from various regions are available.

The bigeyed sixgill shark was originally described as a subspecies, H. griseus nakamurai, by Teng (1962) from specimens collected at a fish market in Kee-Lung, Taiwan. Considerable confusion has arisen in the literature since this species has often been misidentified as H. griseus (Nakamura 1936; Desbrosses 1938; Bigelow & Schroeder 1948; Fourmanoir 1961; Cervigon 1966). Springer & Waller (1969) recognized a distinct sixgill species from the Bahamas and described it as H. vitulus without commenting on Teng's (1962) earlier description. Compagno (1984a) commented on the status of these two species, noting that Teng's (1962) work had been cited as an unpublished dissertation, thus invalidating his name. The specific name H. nakamurai, however, has been resurrected for this dissertation based on new information (see chapter 3).

The genus Notorynchus consists of a single species, N. cepedianus. This species is commonly referred to as the sevengill shark (the name that will be used here) or cow shark. A list of additional common names is given in table 1.4. The sevengill shark is easily distinguished by the presence of seven paired gill openings, broad head, large anal fin and spots covering the dorsal surface of the body. The lower jaw has six rows of large anterolateral teeth as compared to five in the perlon shark. The sevengill shark is a large species reaching at least 2.96 m TL (Ebert 1986b). This is the only nearshore, coastal hexanchoid species commonly found in shallow bays, estuaries and just behind the surfline along beaches (Herald & Ripley 1951; Compagno 1984a; Ebert 1986b, 1989).

The sevengill shark was first described by Peron (1807) as Squalus cepedianus based on a specimen taken in Adventure Bay, Tasmania, Australia. Several nominal species of Notorynchus have been described, including the type species for the genus, N. maculatus (Ayres 1855). The main criterion used to separate these species was the number of upper medial teeth (G?nther 1870; Garman 1884; Fowler 1941) or color (Whitley 1931). More recent works by Bass et al. (1975), Kemp (1978), Pequeno (1979), Compagno (1984a) and Ebert (1989), however, have tended to synonymize this genus into a single wide ranging species. Daniel (1916, 1928, 1934) presented an excellent detailed description of Heptanchus maculatus (=N. cepedianus) from California, but his study was based solely on two immature specimens. Comparison of additional material from California and elsewhere is necessary before the taxonomic status of different sevengill populations can adequately be determined.

Although morphologically conservative, the Hexanchiformes have adapted themselves to an extremely broad range of habitats. This is especially interesting since given the low numbers of species in this group, their wide-ranging distribution compares favorably with the more species-rich Carcharhiniformes.

Life History Studies

Studies on the life histories of elasmobranchs have been few (Ripley 1946; Olsen 1954; Springer 1960; Jensen 1966; Ebert 1984, 1989). In the past, elasmobranch research has tended to focus in two directions. Most early research tended to concentrate on elasmobranch anatomy, with emphasis on their "primitive" anatomical condition. Elasmobranchs were considered primitive fishes due to their low diversity in comparison to the numerous teleost species. This early misconception of the shark as a prehistoric misanthrope has been perpetuated to the point where sharks are perceived as 'mindless eating machines'. This general perception of sharks by the public is the cause of what has been the second emphasis in elasmobranch research, shark attack. The misconception of sharks as being primitive and a relic fish group has directed attention away from the fact that sharks are an important and perhaps vital link in the marine ecosystem.

Most life history studies on sharks have concentrated on those species that are commercially important. Examples of some of these studies include those on the sandbar shark, Carcharhinus plumbeus (Springer 1960), soupfin shark, Galeorhinus galeus (Olsen 1954, 1984; Ripley 1946), the spiny dogfish, Squalus acanthias (Ketchen 1975, 1986; Jones & Geen 1977a,b) and the rig, Mustelus lenticulatus (Francis 1980, 1988, 1989; King 1984; King & Clark 1984). Studies aimed at the entire elasmobranch community instead of only the commercially important species are lacking.

A Review of Hexanchoid Literature

The hexanchoid sharks inhabit most marine ecosystems. They are especially prominent in the deep sea ranging from the outer continental shelves and upper slopes down to depths below 2000 m. Hexanchoids are most common in deep tropical waters, but rare in tropical shallow-water habitats. The sevengill is very common in temperate coastal zones while the sixgill is common in deep temperate waters. There are no records of hexanchoids from polar regions but this could be a sampling artifact since no efforts have been made to ascertain the presence or absence of these sharks in such areas.

The seasonal and spatial movement patterns of cow and frilled sharks are for the most part unknown. Sevengills exhibit seasonal movements into and out of Humboldt and San Francisco bays (Ebert 1986b, 1989), while sixgills have been reported to occur in nearshore waters, including bays (Ebert 1986b, 1988a). Detailed tag-release studies for cow and frilled sharks have never been conducted. Approximately 60 sevengills were tagged in

1978 by biologists from Humboldt State University (HSU) of which two were recaptured within 14 days in the same location as they were tagged (Dr. R. Barnhart, HSU, Arcata, California, pers. comm.). In separate studies, sevengills were tagged in San Francisco Bay between 1979-80 (S. Smith, biologist, NMFS, Tiburon, California, pers. comm.), and between 1981-83 (Ebert 1984). Unfortunately, no sevengills were ever recaptured from either study.

Previous attempts to age cow sharks by standard techniques employed for elasmobranchs were unsuccessful (Ebert 1984, 1986a,b, 1989). Age estimates in elasmobranchs are derived from counts of opaque and translucent bands in spines and vertebral centra (Cailliet, Radtke & Welden 1986). A problem with cow and frilled sharks however, is that they lack fin spines and have insufficient vertebral calcification. At present the only means by which growth rates may be determined and age estimates subsequently derived is by tag-recapture or <u>in situ</u> studies with captive specimens. Both these methods have their draw-backs. Tag-recapture studies in the field usually require that large numbers of individuals be tagged, and that long time periods be allowed for sufficient recaptures. Growth rates of sharks raised in captivity do not necessarily reflect those of sharks in the wild (Wass 1973; Gruber & Stout 1983; Casey, Pratt & Stillwell 1985). All sharks of the Order Hexanchiformes are ovoviviparous in their mode of reproduction. The young are retained in the female until they are fully developed. Most of what is known on the reproductive biology of hexanchoids was derived from scientific notes and referred to in the literature in more general works on elasmobranchs (Bigelow & Schroeder 1948; Breder & Rosen 1966). Original research on their reproductive biology is limited (Tanaka, Teshima & Mizue 1975; Tanaka & Mizue 1977; Capape 1980; Ebert 1986a,b, 1989). Virtually no information exists for the frilled or bigeyed sixgill sharks. The frilled shark has received some attention from the monograph volumes published by Gudger and Smith (1933), Smith (1937), and Gudger (1940), and based on data collected by Bashford Dean during his sojourns to Japan in 1900-1901 and again in 1905. Since then very little new data on this species have become available. Most of the available information on bigeyed sixgill sharks is from anecdotal accounts based on one or two specimens (Springer & Waller 1969; Forster et al. 1970; Bass et al. 1975). Information on size at maturity and fecundity in the perlon shark (Tanaka et al. 1975; Tanaka & Mizue 1977; Capape 1980) and sixgill shark (Vaillant 1901; Desbrosses 1938; Branstetter & MacEachran 1986; Ebert 1986a,b) have been reported, but pertinent life history information for these species is lacking. Daniel (1928, 1934) described the general reproductive anatomy of sevengill sharks, though all of his specimens were immature. Herald and Ripley (1951) commented on the sevengill's occurrence in San Francisco Bay and hypothesized that the Bay represents a pupping ground for this species. More recently, Ebert (1989) reviewed the size at maturity, fecundity, and life cycle of the sevengill shark in relation to the ecosystem of two California bays. However, additional research is required to investigate the life cycle of this species outside these bays.

Virtually no data exist on the food habits and feeding behavior of these sharks. Most of the available information comes from generalized accounts for these species. The bigeyed sixgill shark was reported by Forster et al. (1970) to contain the remains of a midwater bony fish, while the sixgill shark has been reported to contain a wide variety of prey ranging from crustaceans and cephalopods to bony and cartilaginous fish species, as well as marine mammals (Bigelow & Schroeder 1948; Backus 1957; Ebert 1986a,b). Scant information on the perlon shark indicates that it is primarily a feeder on bony fish and cephalopods (Bass et al. 1975; Capape 1980).

Most extensive predator-prey studies have involved large land predators, such as the lion, Panthera leo, (Schaller 1972) or spotted hyena, Crocuta crocuta, (Kruuk 1972). Even with these land predators, however, problems arise. For example, many of these animals remain in the bush, thus making observations on them difficult, although their environment is certainly more conducive to field observations than the shark's. Attempting to continuously observe large marine predators, like the shark, is virtually impossible. Very few observations have been made on large sharks feeding under natural conditions (Eibl-Eibesfeldt & Hass 1959; Hobson 1963; Limbaugh 1963; Tester 1963; Ebert 1986b), and most observations on shark feeding behavior has been under artificial situations where bait had been introduced (McCosker 1985; Tricas & McCosker 1985). Observations such as this, under artificial conditions or in aquaria, hardly represent natural feeding behavior.

Objectives of the Study

The hexanchoids are usually considered the most primitive group of neoselachians, though studies by Holmgren (1941) and Compagno (1973, 1977) and Maisey and Wolfram (1984) have shown close similarities to other modern shark groups, e.g. squalomorphs. This is a very poorly known group and one that has frequently been overlooked in favor of the more diverse and 'popular' sharks. Although extremely well adapted, the reasons for the success of this group have never been analyzed. Previous studies on Hexanchiformes have centered on the anatomy (Garman 1885; Goodey 1910; Allis 1923; Daniel 1916, 1928, 1934; Gudger & Smith 1933; Smith 1937; Holmgren 1940, 1941) and interrelationships (Holmgren 1942; Schaeffer 1967; Compagno 1973, 1977; Maisey & Wolfram 1984) of these sharks with other elasmobranch orders, and have not taken into account their life history and ecology.

Given the integral role of these sharks in their environment, a world-wide study on the taxonomy and biology of hexanchoids was undertaken in an attempt to understand the persistence and success of this group.

TABLE 1.1

Common regional names for *Chlamydoselachus anguineus* taken from Boeseman (1973), and Masuda *et al.* (1984).

English-Frilled Shark
French-Requin lezard
Spanish-Tiburon anguila
German-Kragenhai
Norway-Kravehai
Russian-Plascenosnaja akula
Sweden-Krashaj
Japanese-Rabuka

TABLE 1.2

List of the common regional names for *Heptranchias perlo* taken from Bigelow and Schroeder (1948), Boeseman (1973) and Masuda *et al.* (1984).

English - sevengill shark; narrowsnouted sevengill; slender sevengill; sharpsnouted sevengill
Japan - edo-aburazame
France - perlon
Yugoslavia - pas volonja pepeljak
Israel - shevazim
Spain - bocadulce
Greece - carchias
Italy - squalo manzo
Portugal - olho branzo

TABLE 1.3

A list of common regional names for *Hexanchus griseus* taken from Bigelow and Schroeder (1948), Boeseman (1973) and Masuda *et al.* (1984).

France - Requin griset
Spain - Canabota gris
Yugoslavia - pas glavonja
Israel - sheshzim
Greece - carcharias
Sweden - sexbagig kamtandhaj
Italy - squalo capopiatto
Portugal - albafar
Japan - kagurazame
Denmark - Seksgaellet
Norway - kamtannhai
Germany - Grauhai

TABLE 1.4

Common regional names for *Notorynchus cepedianus* taken from Last, Scott & Talbot (1983), Compagno (1984), *Masuda et al.* (1984) and the present study.

Australia - Tasmanian tiger shark
Brazil - cacao-bruxa, meaning witch shark
Japan - ebisuzame
(minami-ebisuzame= *N. pectorosus*)
New Zealand - broad-snouted sevengill shark
North America - sevengill shark, spotted sevengill shark, broad-snouted sevengill shark
Southern Africa - cow shark
Tristan de Cunha Island - brown rock shark

CHAPTER 2
METHODS AND MATERIALS

Material Collected

Field collections of hexanchoids were made in California, U.S.A., Japan, Namibia, South Africa, and Taiwan. The Californian material was collected with the assistance of several commercial and sport fishermen in central and northern California. A small fishery for bay sharks has been operating in Humboldt and San Francisco Bays, targeting among other species the sixgill and sevengill sharks. Sharks from California were taken by gill net, harpoon, long-line, and rod and reel (Ebert 1984, 1986a,b,c 1989). Contacts within the California commercial trawling fleet were helpful in providing specimens of the sixgill shark (Ebert 1986a). In 1987 a nation-wide network was established to collect hexanchoids in southern Africa. Contacts were made with angling clubs and individual fishermen by attendance at fishing competitions where hexanchoids were likely to be caught. Publicity for the project was made through a media campaign involving local newspapers, radio, magazines (Ebert 1986d, 1987a, 1988b) and posters (Figure 2.1) throughout southern Africa. Co-operation and participation on cruises with Sea Fisheries Research Institute (SFRI) aboard the R/V Africana and the Cape Town based trawling fleet Pescanova, were especially helpful in the collection of the deeper living species. Additional material for comparative taxonomic study was provided by several individuals, institutes, and museums. A list of the museum material examined is provided under the appropriate species sections. Institutional acronyms following Leviton et al. (1985) and abbreviations for personal field numbers for material examined are listed in Appendix 1.

Taxonomy

Considerable confusion exists as to the precise number of hexanchoid species. Part of the problem results from species being named on the basis of locality, by poor systematic practice, and by a misunderstanding of variation between hexanchoid species. A synonymy of these various species is provided under the species account. Comparison of hexanchoids from various geographical regions has never been undertaken in any detail. Material for this study was collected from a wide range of geographical regions and compared using morphometrics and meristics, and includes fin radial, spiral valve, tooth and vertebral counts, and cranial measurements. Both fresh-caught and museum specimens were examined.

Total length (TL), precaudal length, and total weight were recorded for all specimens taken in the field. A selected number of specimens, depending on geographical location and size (TL), were measured in detail. Morphometric measurements followed a modified version of Compagno (1984a) designed for hexanchids (Figure 2.2). Proportional measurements, expressed as percentage total length, and selected ratios were used to compare regional differences between conspecifics. Meristic counts were taken from skeletal material prepared through dissection and hot-water maceration. The material was rinsed in cold water to remove any extraneous tissue and to prevent the more delicate structures from falling apart from overcooking. The entire vertebral column, paired and unpaired appendages, and neurocrania were prepared by this method. Counts included those of the fin radials, vertebral column, and cranium. Radial fin counts included those of the pectoral, pelvic, dorsal, and anal fins. Due to poor centrum calcification, vertebral counts were taken by counting the basidorsals. The vertebral counts include monospondylous (MP), diplospondylous (DP), and caudal diplospondylous (DC) vertebrae. The position where the haemal arch formed in relation to the monospondyly-diplospondyly transition was noted. Cranial measurements followed those of Compagno (1988) allowing for modifications of the hexanchoid condition (Figure 2.3). Once the skeleton was cleaned, counted and measured it was place in 50% n-propyl or isopropyl alcohol for storage.

Tooth counts were taken from freshly caught and museum specimens, and literature accounts. The dentition of hexanchoids was examined for ontogenetic and sexual heterodonty in each species. Tooth plates were prepared from fresh specimens by dissection of upper and lower tooth series from the right or left side of the jaw depending on which series was in better condition. If the functional tooth was extremely worn or damaged a tooth from the second row was taken. After removal, the teeth were macerated in laundry bleach (5% sodium hypochlorite, NaClO, in aqueous solution) and hot water until all extraneous tissue was removed. Once cleaned, measurements of principle cusp height (PCH), apical length (AP), mesial length (ML), and basal length (BL) were made to determine any changes in heterodonty (Figure 2.4). The number of cusps and cusplets were recorded from various size specimens.

Spiral valve counts were taken and compared within and between species in the order.

All counts were statistically analyzed for mean (x), standard deviation (s.d.), range (R), and coefficient of variation (cv). Counts for upper and lower teeth are separated by a slash (/). The number of specimens examined is represented by an (N).

Biogeography

Knowledge of hexanchoid distribution was based upon field collections, museum records, published accounts, and personal communications from colleagues. Where possible, records of a species from a given location were verified by examination of preserved and freshly caught specimens or from photographs. Verification of species from these locations are noted by the appearance of 'present study' following a literature citation. For example, "sixgill sharks occur along the eastern North Pacific from Baja California to southeast Alaska (Ebert 1986b; present study)," indicates that its distribution was reported by Ebert (1986b) and that specimens from this region were also examined in this study to verify their occurrence. Where a new record is reported here for the first time no citation is made following the statement. Tables condensing the species distribution and its source are given. Maps illustrating the general location and range of the various species are presented.

Habitat

A generalized description of the known habitat for each species is given. Hydrographic data from R/V Africana cruises was especially useful for the deep-water species whose habitat is virtually unknown at the present.

Movement Patterns

Movement patterns of sevengill sharks were studied by tag and recapture methods. A tagging program in California was initiated in 1982 and conducted through 1985 (Ebert 1986b). The tagging effort in southern Africa was a coordinated program with the Oceanographic Research Institute (ORI) which had an established network among the angling community geared towards the conservation of fishes. This program was established in 1984 to encourage anglers to release sharks, rays and bony fishes rather than leave them on the beaches. Among the species tagged was the sevengill shark. Coordination with the ORI program provided an established base from which to further encourage anglers to tag and release sharks and to report their recapture. The tags used were of the sheep ear type or dart tags. Sharks that were caught by rod-reel and could be brought on shore or into a boat were tagged on the dorsal fin with sheep ear tags. Dart tags were used from boats and applied using a pole to 'dart' the sharks as they swam past. Thus the tag location was variable, but always confined to somewhere on the shark's dorsum behind the head.

Growth

Sevengill sharks were measured, when possible, prior to being tagged and released to obtain growth data. When possible, both total length (TL) and precaudal length (PCL) were recorded. Anglers were encouraged to record PCL on all tagged sharks and to remeasure those recaptured (Ebert 1988b).

Reproduction

Determination of the physical maturation status for each animal collected was based on a modified and expanded criteria following Pratt (1979) and Ebert (1986b, 1989). Determination of, and speculation about, behavioral maturation will be discussed.

Males

i) an abrupt change in the relationship of the inner clasper length to TL. Inner clasper length was measured from the apex of the cloaca to the clasper tip. ii) development of the clasper sac and scroll. With the onset of maturation, a large sac-like structure forms along the length of the claspers. The clasper sac is thought to be analogous to the siphon sac of other elasmobranchs. The distal most 3 or 4 pelvic fin radials elongate to form the scroll. The scroll is a diagnostic character in the Hexanchidae only; the Chlamydoselachidae lack a scroll. iii) a sharp increase in the relationship of testes weight and length to TL. iv) the presence of a straight, as opposed to a coiled, epididymis. With the onset of maturation the epididymis enlarges and coils. v) the expulsion of sperm through the genital papilla by applying pressure along the sperm sac. Additionally, sperm smears were taken to verify the presence of mature spermatozoa in the discharged seminal fluid. vi) calcification of the terminal cartilage elements. Terminal cartilage elements appear at the onset of maturity and become fully calcified in the adult condition. This development was considered critical in establishing maturity for cow and frilled sharks.

Based on information derived from these indices, the approximate size at maturity was established by plotting body weight to TL.

Females

Sexual maturity could only be established for females by internal examination:

i) differentiation of the ovaries and ovarian egg development. ii) a rapid increase in the shell gland width to TL relationship. iii) determination of whether the oviducts were pendulous. iv) the presence of fertilized eggs or embryos in the oviducts.

As in males a length-weight relationship was plotted for females to establish the approximate size at maturity.

A simple four point numerical system, based on maturation data was employed for field use. The system is as follows: the number (1)- indicates embryos or fetuses, (2)- juveniles or immatures, (3)- adolescence or mature, and (4)- adults. Sex is denoted by an **M** for males and **F** for females. Numbers followed by (+) or (-) indicate that the animal is in a late or early phase of this stage. For example, M3- is a male which has lost its juvenile characteristics and is starting adolescence, or an F3+ which indicates that this is a late adolescent female that may be entering her first breeding season.

Food Habits and Feeding Behavior

Shark stomachs containing prey items were removed and returned to the laboratory for identification. Stomach contents were identified to the lowest possible taxon. Each prey species was identified and weighed to the nearest 0.01 gram. Various indices have been described for quantitatively expressing the importance of different prey in the feeding habits of fish. In this study an index of relative importance following Pinkas, Oliphant and Iverson (1971) was used to rank prey items. This index is calculated by summing the numerical and weight percentage values, and multiplying by the percent frequency of occurrence. Due to the size of many prey items, the percent wet weight was used instead of percent volume. The equation reads as follows:

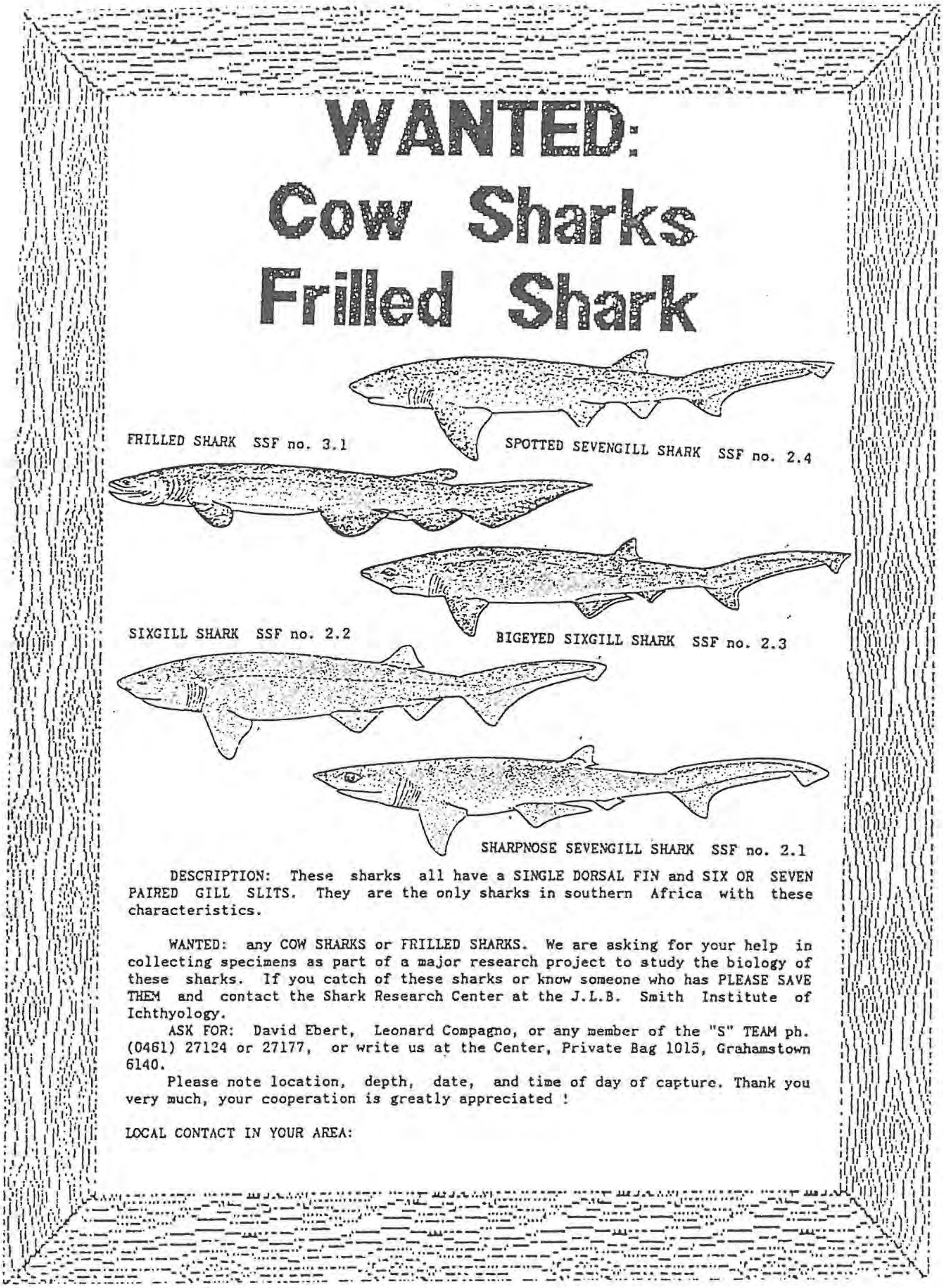
$$(\%N + \%WT)\ \%FO = I.R.I.$$

where:

N = numerical percent
WT = percent weight
FO = frequency of occurrence percent
IRI = Index of Relative Importance.

Data for the sixgill, sevengill and perlon sharks were compared on a regional basis with the major prey categories being grouped at a higher taxonomic level, in order to determine regional differences in the major prey groups. In those species for which adequate data were available, individuals were separated into size classes to determine dietary changes associated with growth.

Most studies on the food habits of sharks merely present data on prey preference. Little or no information regarding the behavior, habitat and life history of the predator or prey is included. Due to the paucity of published data on elasmobranch feeding ecology and predator-prey relationships, observational information on the feeding behavior of the sevengill shark, over a seven year period, is presented. These observations are presented in the context of predator-prey strategies, analogous to those of large land predators on which numerous studies have been conducted.



WANTED:

Cow Sharks

Frilled Shark

FRILLED SHARK SSF no. 3.1

SPOTTED SEVENGILL SHARK SSF no. 2.4

SIXGILL SHARK SSF no. 2.2

BIGEYED SIXGILL SHARK SSF no. 2.3

SHARPNOSE SEVENGILL SHARK SSF no. 2.1

DESCRIPTION: These sharks all have a SINGLE DORSAL FIN and SIX OR SEVEN PAIRED GILL SLITS. They are the only sharks in southern Africa with these characteristics.

WANTED: any COW SHARKS or FRILLED SHARKS. We are asking for your help in collecting specimens as part of a major research project to study the biology of these sharks. If you catch of these sharks or know someone who has PLEASE SAVE THEM and contact the Shark Research Center at the J.L.B. Smith Institute of Ichthyology.

ASK FOR: David Ebert, Leonard Compagno, or any member of the "S" TEAM ph. (0461) 27124 or 27177, or write us at the Center, Private Bag 1015, Grahamstown 6140.

Please note location, depth, date, and time of day of capture. Thank you very much, your cooperation is greatly appreciated !

LOCAL CONTACT IN YOUR AREA:

FIGURE 2.1 - Publicity poster for cow and frilled sharks.

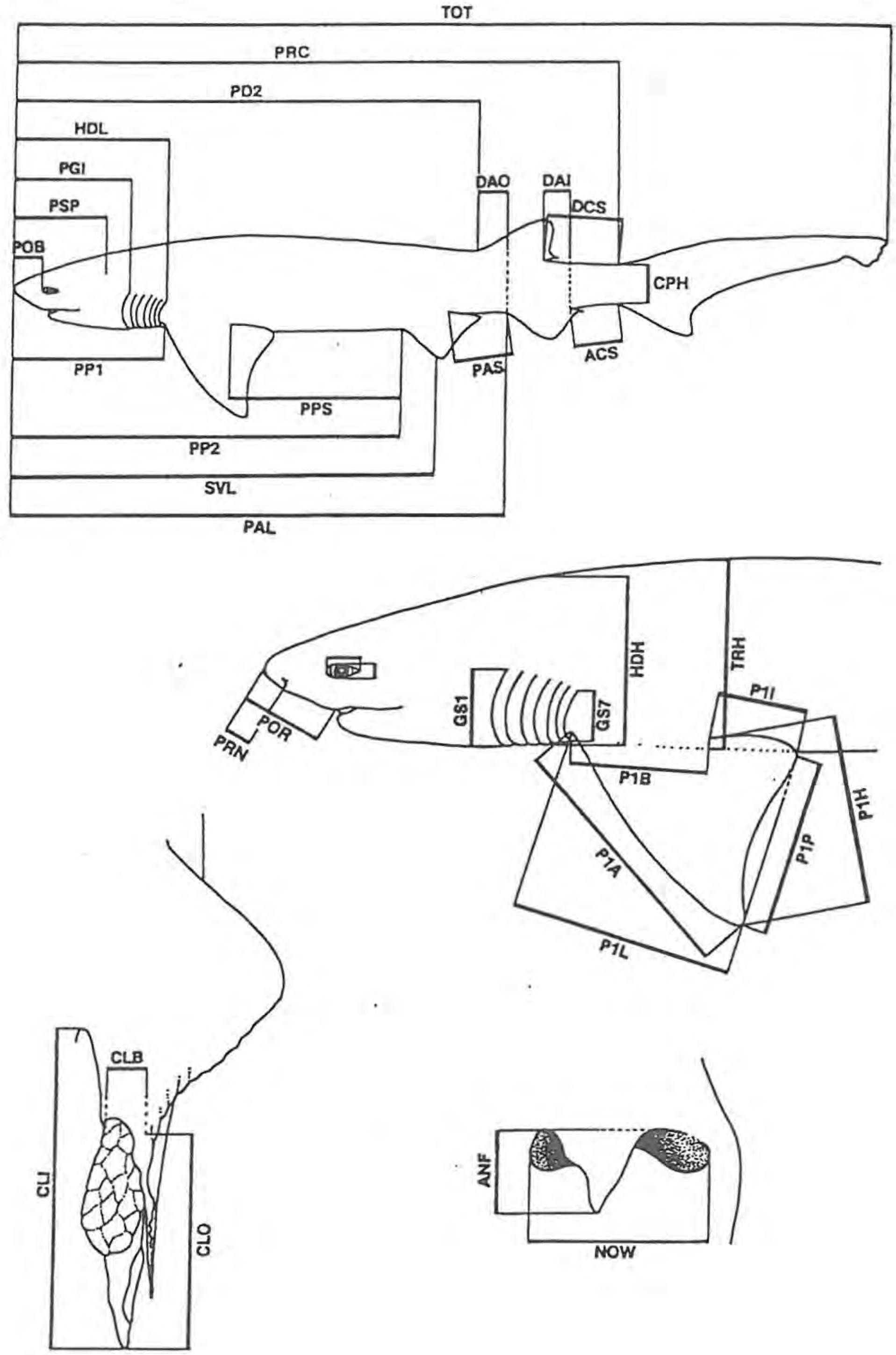


FIGURE 2.2 - Abbreviation code for morphometric measurements.

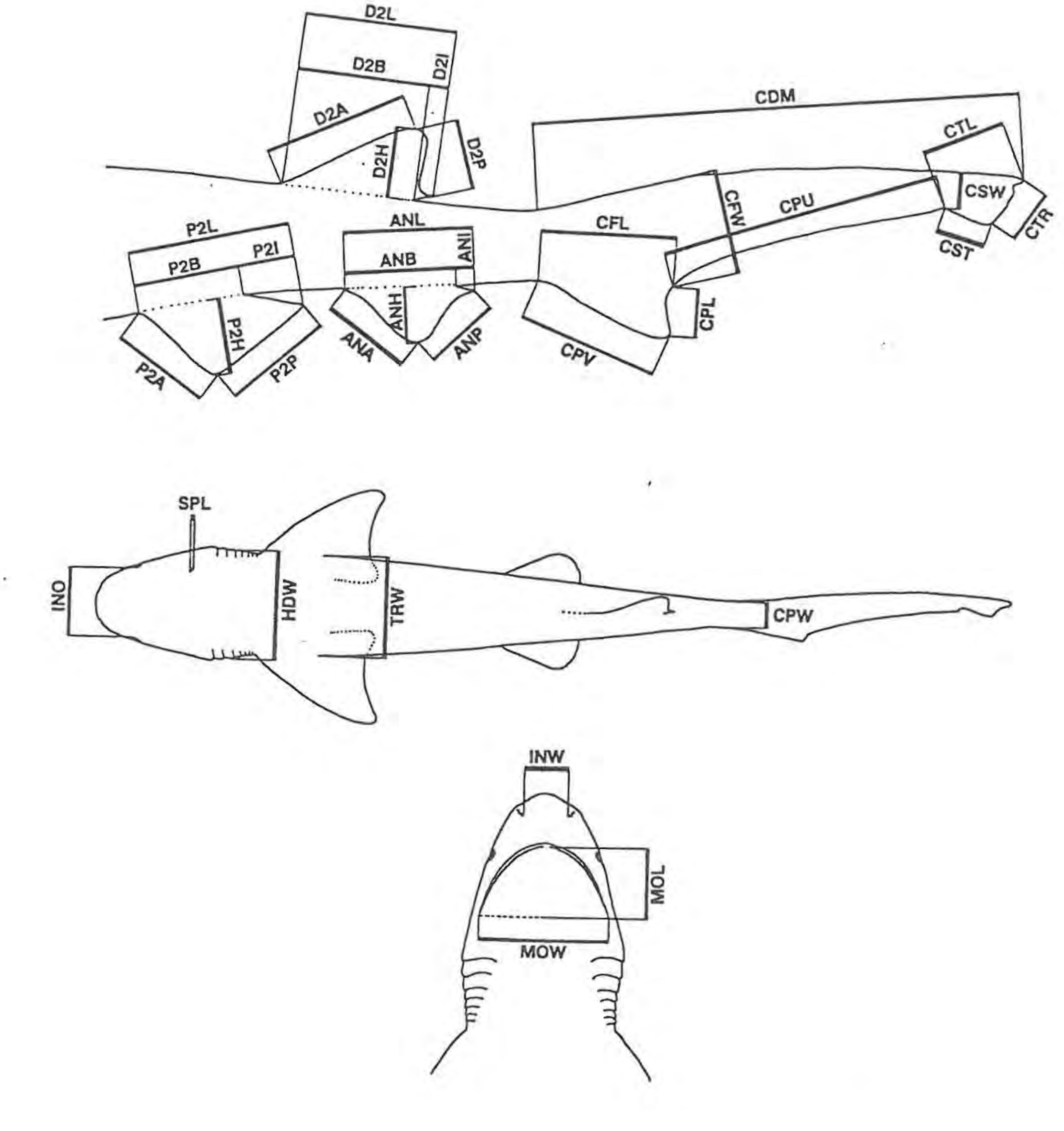


FIGURE 2.2 - Morphometric measurements taken on cow and frilled sharks (continued).

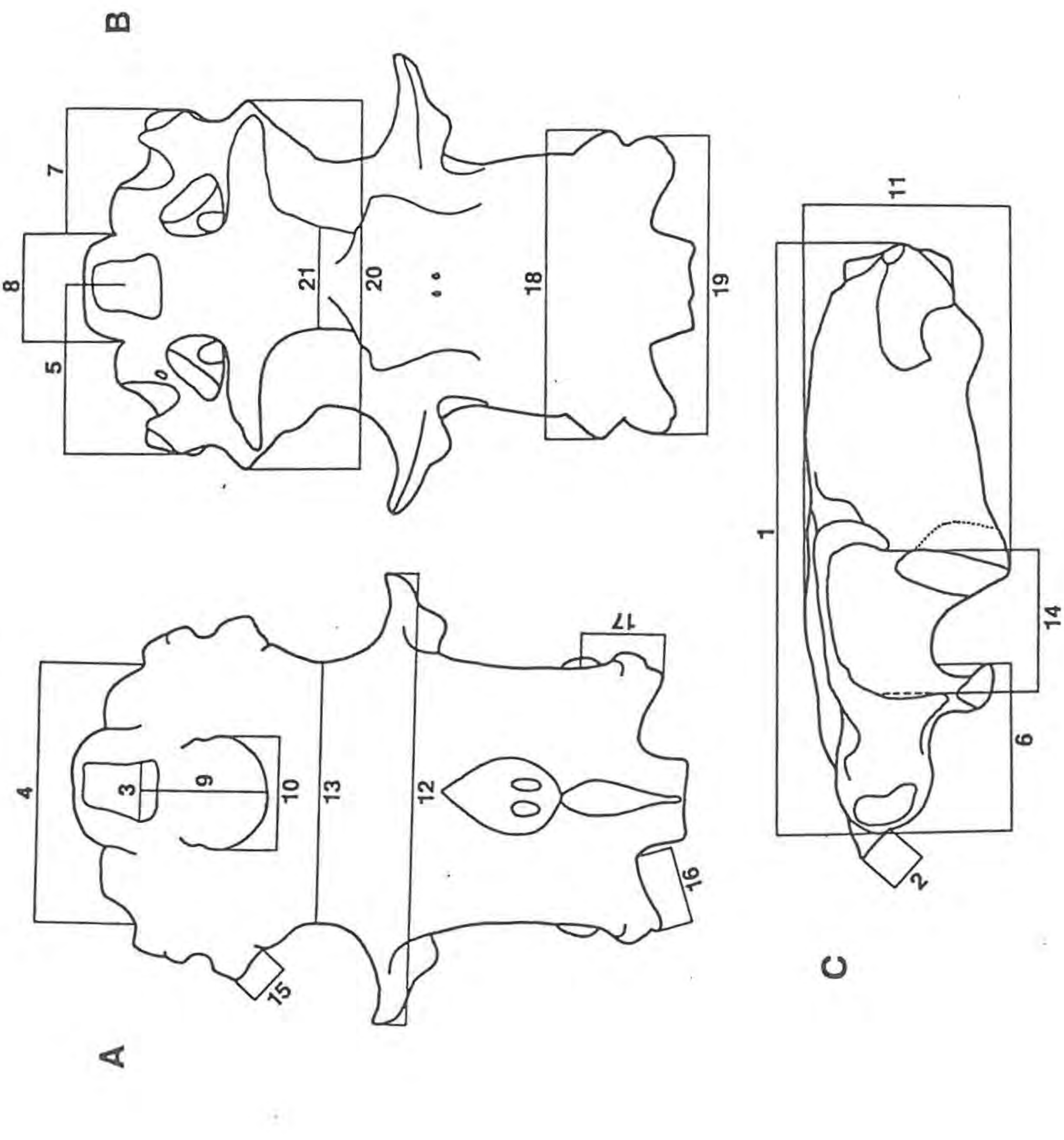


FIGURE 2.3 - Cranial measurements.

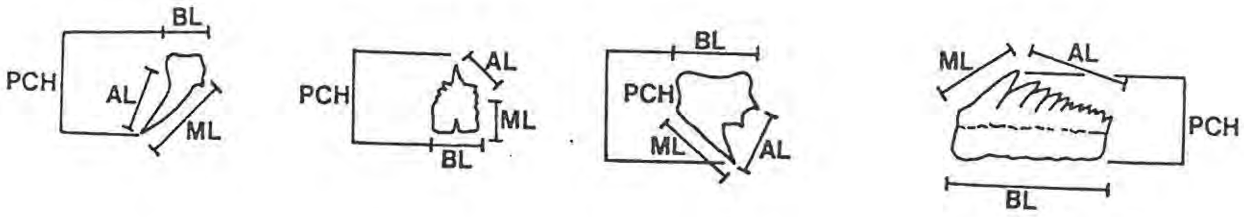


FIGURE 2.4 - Tooth measurements for cow sharks, (AP) apical length, (BL) basal length, (ML) mesial length and (PCH) principle cusp height.

CHAPTER 3
RESULTS

Taxonomy

ORDER HEXANCHIFORMES Comgagno, 1973:
Frilled and Cow Sharks

Order: Hexanchiformes Compagno, 1973, J. Linn. Soc.(Zool.), Lond., 53, suppl. 1: 37p.

Diagnosis:

Sharks of the Order Hexanchiformes are characterized by having a cylindrical TRUNK, not flattened or ray-like. The HEAD is conical to slightly depressed, not expanded laterally, with six or seven pairs of GILL SLITS present on the sides of the head. The posterior most gill opening is located in front of the pectoral fin origin. SPIRACLES are usually present but are occasionally absent; if present they are small and well behind and above the level of the eyes. NOSTRILS are without barbels or nasoral grooves; anterior nasal flaps are short and do not reach the mouth. EYES on sides of head, without nictitating lower eyelids. The SNOUT is short to moderately long, truncated to conical, not greatly elongated or flattened, and without lateral teeth or rostral barbels. The MOUTH is large, arched, and elongated, and extends behind the eyes. LABIAL FURROWS may be present or absent. The TEETH are weakly to strongly differentiated along the jaws, without enlarged anterior or posterior teeth and without any conspicuous gaps or small intermediate teeth between anterior and lateral teeth in the upper jaw. A single spineless DORSAL FIN with its origin set over or behind the pelvic insertion. The relative position of this fin corresponds to the second dorsal fin in other sharks. The PECTORAL FINS are small to moderately large, not expanded and ray-like. PELVIC FINS are small to moderately large, the vent continuous with the inner fin margins. The ANAL FIN is small to very large. The CAUDAL FIN has a long dorsal lobe, with the ventral lobe being present or absent. VERTEBRAL axis is elevated into the dorsal caudal lobe. INTESTINAL VALVE is a spiral type. DEVELOPMENT is ovoviviparous without any yolk-sac placenta. No specialized conditions such as oophagy or uterine cannibalism occurs in these sharks. Litter sizes range from 2 to 108. The ovaries are paired for all species.

A key to the families and species of Hexanchiformes is provided following Compagno (1984a) with modifications stemming from the present study.

KEY TO FAMILIES

1a. Body elongated and eel-like. Six paired gill slits, with first gill slits being continuous across the throat. Mouth terminal on head. Single dorsal fin. Caudal fin lacks a subterminal notch. Teeth are tricuspidate and similar in upper and lower jaws - Frilled sharks .... Family **Chlamydoselachidae.**

1b. Body shape stout, not eel-like. Mouth subterminal. Six or seven paired gill slits; first gill slit does not extend across the throat. Single dorsal fin. Subterminal notch present on caudal fin. High long-cusped teeth in upper jaw, lower teeth are comb-shaped - Cow sharks .... Family **Hexanchidae.**

FAMILY CHLAMYDOSELACHIDAE Garman, 1884: Frilled Sharks

Family: Chlamydoselachidae Garman, 1884: 8.

Diagnosis: The Chlamydoselachidae are a distinctive family with a single living genus and species that has a slender, eel-like body, with prominent keels on the abdomen. The head has six paired gill slits, with the lower ends of the first gill slits extending across the throat. Spiracles may or may not be present. The snout is extremely short and truncated, with the mouth being terminal. The teeth are alike in the upper and lower jaws, with three strong cusps and a pair of intermediate cusplets. The anal fin is larger than the dorsal fin and the caudal fin lacks a subterminal notch.

GENUS CHLAMYDOSELACHUS Garman 1884

Genus: Chlamydoselachus Garman, 1884: 8.

Diagnosis: see family diagnosis.

CHLAMYDOSELACHUS ANGUINEUS Garman, 1884
Frilled Shark
Figure 3.1

Synonymy:

Chlamydoselachus anguineus Garman, 1884a: 47, fig. 5; 1884c: 116;

1884d: 345; 1884e: 484; 1885a: 1, pl. 1-20; 1885b: 536; 1887: 267; 1888: 82, pl. 15; 1899: 41-44, pl. 70; 1913: 14, pl. 59 (figs 4-5), pl. 61 (figs 7-8). Gill, 1884a: 346; 1884b: 524. Davis, 1885: 98, pl. Ayres, 1889: 191, pl. Collett, 1890: 219; 1896: 3,pl 1-2. Rose, 1895: 194. Nishikawa, 1898: 95, text figs 1-3, pl. Palmen, 1898: 25. Dean, 1903: 487. Braganca, 1904: 26. Doflein, 1906: 257, figs. Hawkes, 1906: 959, text figs 1-2, pl. 1-2; 1907: 471, figs. Bolivar, 1907a: 197; 1907b: 207. Stead, 1907: 554. Brohmer, 1908: 621, figs 1-6; 1909: 647, text figs 1-15, pl. 1-4. Ziegler, 1908: 561, figs 1-7. Deinega, 1909: 1, pl. 1-4; 1923: 1, pl. 1-4; 1925: 194, figs. Osorio, 1909: 48. Goodey, 1910: 540, pl. 42-45. Allis, 1911: 511, figs 1-2; 1923: 123, figs. Maurer, 1912: 7, text figs. 1-3, pl. Roule, 1912: 3. Seabra, 1913: 118. Pellegrin & Loppe, 1914: 140. Mertens, 1921: 173. Lozano Rey, 1928: 297, fig. Gudger & Smith, 1933: 243, text figs 1-33, pl. 1-5. Smith, 1937: 333, text figs 1-128, pl. 1-7. Momose, 1938: 2, figs 1-7. Gudger, 1940: 523, text figs 1-33, pl.1-6. Bigelow & Schroeder, 1948: 93. Noble, 1948: 106. Roedel & Ripley, 1950: 39, fig 21. Smith, 1951: 87; 1967: 105, pl. 19-23. Wheeler, 1962: 689. Springer & Garrick, 1964: 83. Trunov, 1968: 137, fig. 3. Miller & Lea, 1972: 34, fig. Boeseman, 1973: 10. Bass *et al.*, 1975: 16, text fig. 9, pl. 6. Domanevskiy, 1975: 1117. Armada, 1977: 9, fig. 1. Nakaya & Bass, 1978: 397, fig. 1. Bass, 1979: 247, fig 1. Timokhin, 1980: 125. Cadenat & Blache, 1981: 5, figs 3-4. Masai, Takatsuj & Aoki, 1981: 257. Castro, 1983: 35, fig. Eschmeyer *et al.*, 1983: 17, pl. 1. Uyeno & Sasaki (in Uyeno, Matsuura & Fujii), 1983: 45, fig. Compagno, 1984a: 14, fig. Maisey & Wolfram, 1984: 170. Masuda *et al.*, 1984: 3, pl. 2. Nakaya, 1984: 293; 1985: 2. Tanaka, 1984: 30; 1987: 4. Taniuchi, 1984c: 18; 1987: 19, fig. Borets, 1986: 3. Lloris, 1986: 87, figs 17-18. Clark, 1987: 221. Hara, 1987: 14. Kobayashi, Tomonaga & Tanaka, 1987: 1. Goto, 1987: 11. Sato, 1987: 20. Shcherbachev, 1987: 38. Shiobara *et al.*, 1987: 7, figs 1-6. Tomonaga, Kobayashi & Tanaka, 1987: 3. Compagno *et al.*, 1989: 19, pl. 2.

Didymodus anguineus Cope, 1884a: 275; 1884b: 412-413; 1885: 878.
Chlamydoselache anguinea Gunther, 1887: 22, pl. 64-65.

Material examined

Chlamydoselachus anguineus, MCZ uncat. (Holotype), ca. 1500 mm TL, female, S.E. Honshu, Japan, only four pieces remaining from specimen; immature gonads and vertebral segments.

Other material examined: see Appendix 2.

Diagnosis: see family diagnosis.

Description: Proportional measurements expressed as a percentage of the total length are given in Appendix 3.

BODY long, slender, eel-like, compressed behind the pelvic fins. Proportional lengths along body axis increase with growth (Figure 3.2). HEAD length to sixth gill opening 1.8 times in pectoral-pelvic space. Head broad, flattened, wider than high, slightly convex. Preoral SNOUT length 0.1 times mouth width. Snout tip broadly rounded, nearly terminal. NOSTRILS lateral, width 5.2 in internarial width, 2.2 in eye length, and 0.3 in third gill opening. EYES rather large, rounded, length about 10.4 times in head length. Proportional eye length decreasing with growth (Figure 3.3). SPIRACLE variably present or absent; if present about 11.6 times in eye length and located about 1.9 eye lengths behind posterior margin of eye. GILL OPENINGS descending in length with the sixth being about 1.4 times the height of the first. First gill opening extending across the throat. Width of third gill opening about 3.2 times in head length and 3.3 times eye length. MOUTH large, width about 2.9 times in head length and 1.2 of head width at mouth corners. Mouth length 0.9 times in mouth width.

TEETH are long, smooth, without serrations and tricuspidate with a pair of cusplets. The teeth are similar in both upper and lower jaws (Figure 3.4). The teeth are slender, curved inwards and set on a broad base which projects behind and interlocks with the tooth base posterior to it, thus it cannot be easily pulled out. Tooth rows range between 19-30/21-27 (Table 3.1), with the number of tooth rows varying between individuals. No apparent regional or sexually dimorphic differences were apparent.

LATERAL TRUNK DENTICLES (Figure 3.5) lanceolate, single

-cusped, with flattened bases. Crown slightly projected above the body with four longitudinal ridges extending from the base to the cusp. Denticle crowns widely spaced.

PECTORAL FINS are of moderate size, broad, rounded and low on body. Both anterior and posterior margins are convex. Pectoral length from origin to rear tip 1.0 times in anterior margin length. Pectorals much smaller than pelvics. Pectoral origin is posterior to sixth gill opening. PECTORAL FIN SKELETON (Figure 3.6) with radials extending about 3.6 times into length of pectoral anterior margin. Radials divided into three to six segments. Propterygium small with no radials, mesopterygium with 5 to 7 radials, and metapterygium with 4 to 10 radials on basal segment and 0 to 4 on metapterygial axis; total radial counts were between 15 and 17 (Table 3.2).

PELVIC FINS large, broadly rounded, with anterior margin 0.9 times pectoral anterior margin. Pelvic anterior and posterior margins convex, with inner margin of males somewhat longer than in females. Inner margin not forming clasper scroll. PELVIC FIN SKELETON (Figure 3.7) is a flattened band of cartilage, slightly concave dorsally and enlarged at the ends. A long basipterygium with three segments from which 20 to 23 radials extend diagonally from its axis (Table 3.3). Pelvic radials have 3 or 4 segments each except for the last two or three which are unsegmented in some individuals.

The CLASPERS (Figure 3.8) have an elongated axial cartilage connected to the basipterygium by an intermediate segment followed by the beta cartilage. In the adult condition the end-style is joined by a terminal cartilage.

The DORSAL FIN is set far back and low, only 1.4 times anal fin height. Anterior margin is rounded and convex with posterior margin. Base is short, 0.4 times dorsal caudal space, height 3.6 times in base, and inner margin 1.0 times in height and 3.6 in base. DORSAL FIN SKELETON (Figure 3.9) has a basal cartilage which is elongate, slightly convex distally and flattened proximally. Basal cartilage radials number between 16 and 32 with each having up to 4 segments (Table 3.3).

ANAL FIN very large, broad, and rounded, height 1.5 times dorsal fin height, base length 1.4 in dorsal base. Anterior and posterior margins rounded and convex. An acute angle formed at the tip of the posterior and inner margins. Base about 0.1 times in anal caudal space. Height 3.2 times in base, 3.1 into inner margin, and 9.9 times in base. ANAL FIN SKELETON (Figure 3.10) composed of an elongated basal cartilage with 20 radial cartilages extending diagonally from it (Table 3.3). Radials with a maximum number of between 4 and 6 segments.

CAUDAL FIN elongated, subtriangular, without a subterminal lobe. Length of dorsal margin 2.8 times in precaudal length, preventral caudal margin 3.2 times in dorsal caudal margin.

Total VERTEBRAL COLUMN counts were 171 for the Namibian specimen and 146 for the Taiwanese specimen; both were adult males. The variability in the MP-DP counts was especially high. The Taiwanese specimen had 72 MP and 21 DP for precaudal counts while the Namibian specimen had 18 MP and 76 DP for the precaudal. The caudal counts (DC) differed widely, with the Taiwanese specimen having 78 and the Namibian frilled shark 52. The transition between the MP and DP for the Taiwan specimen was over the pelvic fins at the 72nd vertebrae, while the transition in the Namibian specimen was just posterior to the pectoral fins at the 18th vertebra.

The NEUROCRANIUM of a 916 mm TL adult male from Namibia was dissected out and measured (Table 3.4).

CRANIUM (Figure 3.11) with short, blunt ROSTRAL CARTILAGE, not hypercalcified in adult. Length of medial rostral cartilage about 19 times in nasobasal length, width across bases of lateral rostral cartilage about 4.9 times in length of medial rostral cartilage. NASAL CAPSULES longer than wide, with rounded edges. Width of cranium across nasal capsules 1.7 in nasobasal length. NASAL APERTURES moderately large and transversely oval, separated by a space 1.8 times their widths. ANTERIOR FONTANELLE large, rounded anteriorly, sub-triangular posteriorly, slightly longer than wide. CRANIAL ROOF 1.3 times orbital length. ORBITAL NOTCHES 1.3 times orbital length. SUBORBITAL SHELVES 0.7 times orbital length. OTIC CAPSULES 0.9 times orbital length.

SPIRAL VALVE turn counts were found to be highly variable and differed by geographical region (Table 3.5). Frilled sharks from Japan had counts ranging from 35 to 46, while Namibian specimens ranged much lower, between 26 and 28 turns. A single Norwegian specimen had 47 while an Australian individual had a high of 49. Those from Taiwan and the North Atlantic fell within the range of the Japanese specimens.

The LIVER is large and extremely oily. It consists of two lobes, one on each side of the body, extending the entire length of the abdominal cavity. The lobes are of equal size and alike in form.

The COLOR of fresh frilled sharks were a dark chocolate brown (Figure 3.12). A thin membranous film covering the shark was rinsed off after death to reveal a dark gray color beneath the membrane. The color of preserved specimens varied from light brown to gray.

DEVELOPMENT is ovoviviparous without placenta. Numbers of young range between 2 and 12 (Gudger & Smith 1933).

ETYMOLOGY: The species name is derived from Greek <u>Chlamydo-</u> meaning a mantle or frill, <u>selachus-</u> meaning a shark, and Latin <u>anguineus</u> meaning snakelike.

REMARKS: The high degree of variability exhibited in this species needs to be assessed critically. Additional skeletal material needs to be examined and compared for differences, especially in spiral valve and vertebral counts. Although the sample size was small, the number of spiral valve turns correlated closely with individuals from similar geographical localities. However, the average number of turns differed widely between geographical regions. The short monospondylous condition observed in the Namibian frilled shark differed greatly from that of a Taiwanese specimen. The MP-DP transition typically occurs in the region over the pelvic fins in most elasmobranchs. The Namibian frilled shark has its MP-DP transition posterior to the free rear tip of the pectoral fins. The only other record for vertebral counts in this species was a partial count of 112+ given by Goodey (1910). In Goodey's (1910) Japanese specimen the MP-DP transition occurred at the 70th vertebra. Unfortunately, frilled sharks are rare at most localities outside Japan and when a specimen is caught it is usually preserved at an institution and cannot be dissected. Therefore, careful examination of the meristics and morphometrics for most of these specimens is lacking.

FAMILY HEXANCHIDAE Gray, 1851:

Cow Sharks

Figure 3.13

Family: Hexanchidae Gray, 1851: 67.

Diagnosis: These sharks are small to very large with a cylindrical, moderately slender to stout body, lacking keels. Unlike most sharks the head has six or seven paired gill slits, with the lower ends of the first gill slits not extending across the throat. The eyes are moderately large and rounded. Spiracles are present though minute. The snout is short to moderately long, conical and slightly pointed to broadly rounded. The mouth is subterminal on the snout and wide. The teeth are differentiated in the upper and lower jaws. The upper anterolateral teeth are small and narrow, with a single main cusp followed by one or more smaller cusplets. The lower anterolateral teeth are very broad, compressed, and comb-like, with a single large cusp followed by a series of smaller cusplets. Both upper and lower jaws have a series of posterolateral commissural teeth which are small and granular. A single dorsal fin set behind the origin of the pelvic fins. A small to moderate-sized anal fin is present. The caudal fin is long, nearly one-third the total length and with a strong subterminal notch.

Remarks:

The Family Hexanchidae has traditionally been divided into three genera, Heptranchias, Hexanchus and Notorynchus, comprised of four valid species. It has been suggested that detailed comparison of these species may reveal that the division of this group based on the number of paired gill slits is invalid (Bass et al. 1975, Garrick & Paul 1971, Springer & Waller 1969), and that H. perlo and H. nakamurai have more in common morphologically, while N. cepedianus is closer aligned to H. griseus. Detailed comparison of these four species in the present study strongly supports the current taxonomic arrangement, with the two sixgill species belonging to a single genus and each of the sevengill species belonging to its own genus.

Key to the Family Hexanchidae:

1a. Six pairs of gill openings .... Hexanchus

1b. Seven pairs of gill openings 3

2a. Snout shorter, blunt and broad. Lower jaw with 6 rows of large, comb-like anterolateral teeth on each side. Dorsal fin base set far back, distance between its insertion and the upper caudal fin origin about equal to the dorsal fin base. Eyes relatively small. Size relatively large, growing to at least 4.82m TL .... H. griseus.

2b. Snout relatively long and pointed. Lower jaw with five rows of large, comb-like anterolateral teeth on each side. Dorsal fin base separated from upper caudal fin origin by a distance much greater than its length. Eyes relatively large. A moderate sized species, reaching up to 1.8 m TL...... H. nakamurai

3a. Snout length more than 1.5 times internasal space. Anal fin small. Body plain or with few large indistinct dark blotches. Eyes relatively large. Lower jaw with five rows of large, comb-like anterolateral teeth on each side. A small hexanchoid species reaching about 1.4 m TL ...... Heptranchias perlo

3b. Snout length less than 1.5 times internasal space. Anal fin large. Dorsal surface of body usually covered with small dark spots. Eyes relatively small. Lower jaw with six rows of large distinct, comb-like anterolateral teeth on each side. Size large, up to at least 3 m TL .... Notorynchus cepedianus

GENUS HEPTRANCHIAS Rafinesque, 1810

Genus: Heptranchias Rafinesque 1810: 13.

Diagnosis: A narrow, pointed head, with seven paired gill slits. The mouth is subterminal and longer than wide. The eyes are large and rounded. Upper and lower teeth differ. The upper teeth have a single large, curved, smooth-edged cusp, with or without several smaller cusplets, while the lower teeth are large and comb-like, with a single high cusp followed by a series of smaller cusplets. The caudal peduncle is long, over twice the length of the dorsal fin base. Caudal fin nearly 1/3 the total length.

HEPTRANCHIAS PERLO (Bonnaterre, 1788)

Perlon shark

Synonymy:

Squalus perlo Bonnaterre, 1788: 10.

Squalus cinereus Gmelin, 1789: 1497. Bloch & Schneider, 1801: 133. Bosc, 1803: 185. Latreille, 1804: 72. Risso, 1810: 24. Desvaux, 1851: 24

Heptrachias cinereus Rafinesque, 1810: 13. Indice Ittiol. Sicil., 1810: 45. Swainson, 1839: 314. Bonaparte, 1839: 9. Icon. Faun. Ital. 1841: 1. Cat. Pesc. Europ., 1846: 17. Costa, 1854-1857: 11; 1871: 87. Gill, 1861: 404. Rey, 1928: 289. De Buen, 1930. Ranzi, 1934: 378, 417.

Monopterhinus cinereus Blainville, 1816: 121.

Carcharias cinereus Cloquet, 1817: 69.

Squalus (*Monopterhinus*) *cinereus* Blainville, 1825: 80

Notidanus cinereus Cuvier, 1829: 390. Lowe, 1837: 194. Bonaparte, 1835. Agassiz, 1843: 218. Cuvier, 1843: 364. Van der Hoeven, 1855: 261. Nardo, 1859-1860: 787. Fitzinger, 1864: fig. 176. Gunther, 1870: 398. Gervais & Boulart, 1877: 195. Reguis, 1877: 53. Heldreich, 1879: 91. Giglioli, 1880: 52. Perugia, 1881: 55. Rochebrune, 1882: 46. Faune Senegambie, 1883-1885: 24.

Squalus (*Notidanus*) *cinereus* Voigt (in Cuvier), 1832: 509.

Heptanchus cinereus Muller & Henle, 1841: 81, pl. 35 (fig. 3). Dumeril, 1865: 437, pl.4 (fig. 1-4). Bocage & Brito Capello, 1866: 15. Miklucho-Maclay, 1870: 12, pl.2 (fig. 1-6). Ninni, 1870: 66. Canestrini, 1871-1872: 43. Gegenbaur, 1872: pl. 21 (fig. 5,6). Hertwig, 1874: 349, pl. 12 (fig. 7,10,13). Doderlein, 1878-1879: 30; 1881: 78. Stossich, 1880: 69. Moreau, 1881: 339. Graeffe, 1886: 447. Carus, 1889-1893: 500. Vieira, 1897: 67. Sicher, 1898: 16. Steinhard, 1903: 6, pl.1 (fig.1-3). de Braganza, 1904: 30, 102. Allis, 1912: 478, figs 1-2. Borri, 1934: 94. Belloc, 1934: 152. Daniel, 1934: 4, 24, 25, 51, 91. Noronha & Sarmento, 1934: 100. Nobre, 1935: 414. Holmgren, 1941: 3.

Heptranchus cinereus Gray, 1851: 68.

Heptrancus angio Costa, 1854-1857: pl.13, 14, fig.3.

Heptanchus (*Heptranchias*) *cinereus* Brito Capello, 1870: 141.

Notidanus (*Heptanchus*) *cinereus*, var. *pristiurus* (var. *aetatis*) Bellotti, 1877: 60.

Notidanus (*Heptanchus*) *cinereus* Lo Bianco, 1899: 542. Imms, 1905: 44.

Heptranchias *deani* Jordan & Starks, 1901: 384. Jordan & Snyder, 1901: 128. Jordan & Fowler, 1903: 595. Pietschmann, 1908: 708.

Hexanchus *cinereus* Seabra, 1911: 195.

Heptranchias *perlo* (Bonnaterre, 1788) McCulloch, 1911; Garman, 1913: 21. Hussakoff, 1919: 9. Fowler, 1936: 27. Norman & Fraser, 1937: 5, fig.8. White, 1937: 40, pl.1e, 4m, 17c, 23b, 29e, f. Tortonese, 1938: 286. Fowler, 1941: 9. Norris, 1941: 23, 37, pl.1 (fig.4); pl. 20 (fig. 79). Howell-Rivero, 1941: 7, pl.3,4. Fowler, 1944: 113, fig. 5. Bigelow & Schroeder, 1945: 92, fig. 30; 1948: 88, figs 10-11. Lindberg & Legeza, 1959: 26, fig. 15-16. Teng, 1962: 33, fig. 6. Springer & Garrick, 1964: 80. Forster *et al.*, 1970: 393. Garrick & Paul, 1971: 1,2. Boeseman, 1973: 8. Pissaro & Sanches, 1973: 3. Tanaka *et al.*, 1975: 15, figs 1-8. Tanaka & Mizue, 1977: 1, figs 1-10. Capape, 1980: 231, figs 1-14. Chirichigno, 1980: 24, fig. 3. Uchida, 1982: 2. Cadenat & Blache, 1981: 17, figs 5-7. Castro, 1983: 40, fig. Uyeno & Sasaki (Uyeno, Matsuurs & Fujii), 1983: 46, fig. Chen, 1984: 51. Compagno, 1984*a*: 17, fig. Maisey & Wolfram, 1984: 170. Mizue, 1984*a*: 42; 1984*b*: 46. Nakaya, 1984: 293. Tanaka, 1984: 30. Taniuchi, 1984*a*: 7; 1984*b*: 11; 1984*c*: 18; 1984*d*: 36. Cappetta *et al.*, 1985: 401. Compagno & Talwar, 1985: 169, fig 1. Nakaya, 1985: 2. Lloris, 1986: 90, fig. 20. May *et al.*, 1986: 82, fig. Yu, 1988: 3. Compagno *et al.*, 1989: 18, pl. 1.

Heptranchias *dakini* Whitley, 1931: 310; 1968: 5. Fowler, 1941: 5. Munro, 1956: 2, fig. 4. Scott, 1962: 19, text-fig.; Scott *et al.* 1974: 23, text-fig.

Material examined:

Heptranchias *deani*, SU 12620 (Holotype), 954 mm TL, adolescent female, Misaki, Japan.

Other material: see Appendix 2.

Description: Proportional measurements expressed as a percentage of the total length are given in Appendix 3.

BODY TRUNK slender and compressed. Proportional lengths along body axis increase with growth (Figure 3.14). HEAD narrow, slightly convex, length to seventh gill opening 0.8 times in pectoral-pelvic space. SNOUT narrowly rounded, length of preoral snout about 1.6 times mouth width. NOSTRILS lateral, about equidistant between snout tip and mouth. Anterior nasal flap expanded as a broadly triangular, corrugated lobe. Nostril width 2.0 in internal width, 2.7 in eye length, and about 0.5 in third gill opening. EYES very large, oval, anterior edge about opposite front of mouth. Eye length about 6.0 times in head length and about 2.0 in height. Proportional eye length decreases with growth (Figure 3.15). SPIRACLE present, but minute. Spiracle located at the level of the upper eye margin, its distance behind the eye about equal to the horizontal diameter of the latter. Spiracle about 15 times eye length and located about 1.1 eye lengths behind the posterior edge of the eye. GILL OPENINGS long, with the first extending from about the level of the spiracle to the throat, but not extending across it as in C. anguineus. Gill openings decreasing in length with the seventh being about 2.3 times the length of the first. Width of the third gill opening about 3.0 times in head length and 2.0 times eye length. MOUTH large, narrowly rounded in front, and about 1.4 times length in width. Width about 2.8 times in head length. LABIAL FURROWS oblique at angle of mouth. Labial furrow originates on upper jaw and extend downward and forward for a short distance onto lower jaw. Lower labial furrow about 1.5 times into upper labial.

TEETH differ in upper and lower jaws (Figure 3.16). First two to four upper anterolaterals smooth-edged, with a single slender median cusp curved rearward. The base of the first two anterolaterals smaller than succeeding teeth. The third or fourth tooth and all subsequent anterolateral teeth with 1 to 3 short cusplets on the outer side. The upper posterolateral commissural teeth small and granular. Lower jaw consisting of one symmetrical medium tooth with a single median cusp and up to three cusplets on each side. The anterolateral teeth with single large cusp followed by up to 11 cusplets. Serrations may be present on the mesial margin in larger individuals. The posterolateral commissural teeth small and granular.

The total number of teeth range between 25-43/09-33 (Table 3.6). The total number of upper teeth increased slightly with growth (Figure 3.17). The upper jaw consisted of 9 to 11 anterolateral teeth per side with no apparent increase in their number associated to growth or state of maturity (Figure 3.18). The posterolateral commissural teeth range between 3 and 12 per side, and appear to increase with growth, thus accounting for an increase in the total number of upper teeth. The total number of lower teeth increased with growth (Figure 3.19). The lower jaw consists of a single medial tooth and five anterolateral teeth which was consistent for all specimens examined. The lower posterolaterals numbered from 1 to 13 per side with an increase in their numbers associated to growth.

LATERAL TRUNK DENTICLES (Figure 3.20) lanceolate, with one large single cusp followed by a single cusplet on each side. The crown slightly projected above the body with three longitudinal ridges extending from the base to the cusp. Denticle crowns imbricate.

PECTORAL FINS relatively small and broad based. Anterior margin weakly convex, posterior margin moderately concave, apex narrowly rounded with free inner rear tip more broadly rounded. Pectoral length from origin to rear tip 1.1 times in anterior margin length. PECTORAL FIN SKELETON (Figure 3.21) with radials extending about 0.5 of pectoral anterior margin length into fin. The radials are divided into 4 or 5 segments, the longest distal segment about 0.8 times length of its proximal segment. Total radial counts ranged from 21 to 25; Propterygium small with no radials, mesopterygium with 9 to 11 radials, and metapterygium with 11 to 15 radials (Table 3.7).

PELVIC FINS slightly higher than anal fin; prolonged rearward in males, partially enclosing the claspers. The inner margins entirely separate posterior to the cloaca in both sexes. Anterior margin slightly convex, apex broadly rounded. Posterior margin straight, apex pointed and free rear tip slightly convex. Pectoral anterior margin 0.4 times into pelvic anterior margin. PELVIC FIN SKELETON (Figure 3.22) consisting of a long basipterygium with two segments from which 20 to 26 radials for females and 19 to 23 radials for males extend diagonally from its axis (Table 3.8). Pelvic radials have 2 to 3 segments with the last 2 to 11 being unsegmented.

The CLASPERS are enclosed in a scroll formed by the last 4 radials of the pelvic fins. In adults the clasper sac has three large glands which appear to function when the animal reaches maturity. No spur or spines are present. The CLASPER SKELETON (Figure 3.23) consists of an elongated axial cartilage connected to the basipterygium by an intermediate segment followed by the beta cartilage. In the adult condition the end-style is joined by a terminal cartilage which is calcified.

DORSAL FIN origin set posterior to pelvic free rear tip. Length about equidistant to the pelvic-anal space. The base is about 0.6 times into the dorsal caudal space. Anterior margin slightly convex, apex broadly rounded. Posterior margin concave and narrowly rounded at free rear tip. Dorsal fin high, about 1.5 times base and about 2.8 times inner margin. The DORSAL FIN SKELETON (Figure 3.24) has an elongated basal cartilage which is convex ventrally and slightly concave dorsally where the radial cartilages attach. Between 17 and 21 radial cartilages are attached to the basal cartilage with 3 to 6 segments per radial (Table 3.8).

ANAL FIN small, broad-based, height about 0.5 times dorsal fin height. Origin of anal fin in relation to dorsal fin sexually dimorphic; in females the anal fin originates near the middle of the dorsal fin base, while in males it originates below the posterior portion of the dorsal fin base. Anal fin height about 2.6 times in base, and inner margin 1.6 times in height and 4.2 times in base. ANAL FIN SKELETON (Figure 3.25) comprised of an elongated basal cartilage with between 15 and 21 radials (Table 3.8). Maximum number of radial segments range between 2 and 4.

CAUDAL FIN elongated, dorsal margin moderately convex, length 2.2 times precaudal length. Preventral caudal margin slightly convex, 4.1 times in dorsal caudal margin. Subterminal lobe strongly notched. Upper and lower postventral caudal margins strongly arched. Terminal caudal lobe moderately concave, about 4.5 times into caudal dorsal margin.

Total VERTEBRAL COLUMN counts range between 141 and 159 for specimens from the Mediterranean Sea, Natal, South Africa and Taiwan (Table 3.9). MP counts 33.9-38.6% (35.8%), DP counts 18.6-24.8% (22.5%), and DC counts 40-43.5% (41.6%) of the total vertebral counts and DP/MP ratio 0.5-0.7%, DC/MP ratio 1.1-1.3%. The MP-DP transition occurred between the 52nd and 58th vertebral segments or at about the rib closure.

CRANIAL MEASUREMENTS were taken from a series of Heptranchias perlo from Taiwan and ranging between 592 mm and 1030 mm TL (Table 3.10).

CRANIUM (Figure 3.26) with a long narrow ROSTRAL CARTILAGE, not hypercalcified in adult. Length of medial rostral cartilage about 8.7 times in nasobasal length, width across bases of lateral rostral cartilages about 1.3 times in length of medial rostral cartilage. NASAL CAPSULES longer than wide, with rounded edges. Width of cranium across nasal capsules 4.3 in nasobasal length. NASAL APERTURES large, transversely oval and separated by a space 4.3 times their widths. ANTERIOR FONTANELLE rounded, slightly longer than wide. CRANIAL ROOF 1.8 times orbital length. ORBITAL NOTCHES 13 times orbital length. SUBORBITAL SHELVES 1.4 times orbital length. Length of OTIC CAPSULES 1.5 times orbital length.

SPIRAL VALVE turn counts ranged from 18 to 22 for all specimens examined (Table 3.11).

The LIVER is large, consisting of two lobes, one on each side of the body cavity, extending the entire length of the abdominal cavity. The lobes are of equal size and alike in form. The liver is extremely oily. Percent liver weight increase with size (Figure 3.27).

COLORATION in adult perlon sharks is a rather pale uniform gray, lighter below. Juvenile color patterns are much more brilliant (Figure 3.28). The pectoral and caudal dorsal fin margins are white-edged. The dorsal fin has a black spot at the apex which fades with growth. Most individuals up to one meter in length have some evidence of this black spot, but lose it beyond this size. After preservation these specimens become dark gray to brown.

DEVELOPMENT is ovoviviparous without placental attachment. Number of young range between 9 and 20.

ETYMOLOGY: The species name Hept- for seven and -anchias, from branchias, gill. The name perlo based on the French common name perlon, of uncertain derivation but possibly based on French Perle, a bead or pearl, and perhaps an allusion to the large glowing eyes of this species.

REMARKS: It appears that the number of upper anterolateral teeth is a variable character in this species and not related to life stage (Figure 3.18). Previous studies (Bigelow & Schroeder 1948, Bass et al. 1975, Capape 1980) have reported an increase in the total number of upper anterolateral teeth corresponding to the state of maturity. It appears, however, that these authors had an insufficient sample size to verify this variability. The lower jaw was always found to have a medial tooth and five anterolateral teeth for all specimens examined in this study. Bigelow and Schroeder (1948) noted that some specimens lacked a lower median tooth and may have only four anterolaterals. Similarly, Garrick and Paul (1971) reported that one individual had six lower anterolateral teeth. However, these aberrant tooth counts appear confined to anomalous individuals.

Published vertebral counts of perlon sharks may vary because of the different methods employed in counting them (Table 3.9b). Previous attempts to count vertebrae by x-radiography were not entirely successful due to poor calcification, and x-radiography did not adequately elucidate vertebral segments in the caudal region. This is illustrated in a photograph shown by Garrick and Paul (1971: p. 14; plate 2) of a perlon shark vertebral column. Furthermore, a higher number of calcified vertebral segments corresponding to TL (and perhaps age) was observed. Precaudal counts for western North Atlantic, Mediterranean (Springer & Garrick 1964), Australian and New Zealand (Garrick & Paul 1971) specimens using x-rays were consistent with the findings of this study. However, published caudal counts were slightly lower. Bass et al. (1975) had very low counts for South African and Mozambiquan specimens compared to the count noted above (Table 3.9a) for a vertebral column of a South African specimen prepared by water maceration. The accuracy of Capape's (1980) very low precaudal counts is difficult to assess since his methodology is somewhat vague and uncertain.

GENUS HEXANCHUS Rafinesque, 1810

Genus: Hexanchus Rafinesque, 1810: 14.

Diagnosis: Members of this genus have a broad head, six paired gill slits, moderate to large eyes, a minute spiracle, and 5 or 6 comb-like lower anterolateral teeth. Ontogenic heterodonty and sexual dimorphism are pronounced. A long or short dorsal-caudal space, with the distance from the dorsal fin insertion varying from slightly longer to about twice as long as dorsal base. Moderate sized to large species ranging from 1.8 to 4.8 m TL. Spots or black fin tips lacking. Juvenile coloration brilliant with white fin edges.

HEXANCHUS GRISEUS(Bonnaterre, 1788)

Sixgill Shark

Synonymy:

Squalus griseus Bonnaterre, 1788: 9. Gmelin 1789: 1495. Bloch & Schneider, 1801: 129. Latreille, 1804: 72. Risso, 1810: 37. Naccari, 1822: 24. Nardo, 1824: 261; 1827: 9. Martens, 1824: 408. Trapani, 1838: 16.

Squalus vacca Bloch & Schneider, 1801: 138

Hexanchus griseus Rafinesque, 1810: 14. Swainson, 1839: 316. Muller & Henle, 1841: 80. Heckel, 1846: 91. Busch, 1848: pl. 3 (fig.8). White, 1851: 130. Costa, 1854-1857: 15, 16 (39, 40); 1871: 87. Canestrini, 1861: 267. Guichenot, 1841: 30. Dumeril, 1865: 431, pl.4, fig.9-12. Poey, 1868: 454. Gray, 1868: 76. Brito Capello, 1870: 140. Miklucho-Maclay, 1870: 13, pl. 2 (fig. 8-14). Ninni, 1870: 66. Costa, 1871: 87. Gegenbaur, 1872: pl. 3 (fig. 6,7). Poey, 1876: 398. Brito Capello, 1880: 45. Doderlein, 1881: 76. Moreau, 1881: 336. Carus, 1889-1893: 499. Almeida & Roquet, 1892: 372. Jordan & Evermann, 1896: 19. Jordan &

Evermann, 1900: pl.2 (fig.8). Carruccio, 1896: 165. Vieira, 1897: 67. Sicher, 1898: 16. Huber, 1901: 600, pl. 27, (fig. 1,2). Vaillant, 1901: 202. de Braganza, 1904: 28. Regan, 1905: 571. Bolivar, 1907: 207. Smith, 1907: 30; 1916: 349, 351. Fowler, 1908: 52; (1929), 3, 1930: 484; 1936: 26; 1941: 11. Diaz y Martinez, 1910: 82. Laboissiere, 1910: 6. Seabra, 1911: 195. Roule, 1912: 3. Garman, 1913: 16. Lahille, 1913: 26, 32; 1921: 63. Scharff, 1915: 99. Starks, 1917: 146. Norman, 1922: 319. Marelli, 1924: 544. Barnard, 1925: 22. Rey, 1928: 292. Hickling, 1928: 199. Jordan, Evermann & Clark, (1928), 2, 1930: 11. Hubbs, 1928: 11. Sanchez-Roig, 1931: 18. Baylis, 1933: 322. Belloc, 1934: 151. Borri, 1934: 94. Fraser-Brunner, 1935: 319. Pozzi & Bordale, 1935: 149. Nobre, 1935: 413, pl. 61 (fig.189). Lubbert & Ehrenbaum, 1936: 272, pl. 19 (fig. 239). Howell-Rivero, 1936: 42; 1941: 4, pl. 1, 2. Norman and Fraser, 1937: 5. Desbrosses, 1938: 53. Tortonese, 1938: 286. Holmgren, 1941: 9. Bigelow and Schroeder, 1945: 94, fig. 31; 1948: 80, fig. 9. Phillipps, 1946: 5. Roedel & Ripley, 1950: 40, figs 22-23. Herald & Ripley, 1951: 326, fig 146. Roedel, 1953: 12, fig. 4. Backus, 1957: 246. DeBuen, 1960: 8. Teng, 1962: 27, fig. 4. Lynch, 1964: 259, figs 1-5. Miller & Greenfield, 1965: 857, fig. 1. Smith, 1965: 38, fig. 1. Cervigon, 1966: 923. Hureau, 1969: 1151. Springer & Waller, 1969: 159, figs 5,6,7. Wheeler & Blacker, 312. Forster *et al.*, 1970: 391. Bane & Bane, 1971: 20. Miller & Lea, 1972: 34, fig. Hart, 1973: 27, fig. Pissaro & Sanches, 1973: 8, fig. 1. Bass *et al.*, 1975: 8, fig. 5. *Bass et al.* 1980: 176. Chirichigno, 1980: 24, fig. 1. Robbins *et al.*, 1980: 11. Cadenat & Blache, 1981: 20, fig. 8. Castro, 1983: 37, fig. Eschmeyer *et al.*, 1983: 19, pl. 1. Chen, 1984: 51. Compagno 1984*a*: 19, fig. Ebert, 1984: 1; 1986*a*: 135, fig. 1; 1986*b*: 437, fig. 8. Gilat & Gelman, 1984: 259, fig. 4. Maisey & Wolfram, 1984: 170, fig. 1. Mizue, 1984*a*: 42. Mizue, 1984*b*: 46. Otake, 1984: 64. Tanaka, 1984: 30. Taniuchi, 1984*c*: 18. Borets, 1986: 3. Branstetter & MacEachran, 1986: 156, fig. 3. Clark, 1986: 681, figs; 1987:

225; 1988: 731. Lloris, 1986: 88, fig. 19. Menni, 1986: 425. Randall, 1986: 176, fig. 3. Robbins *et al.*, 1986: 17, pl. 2. Hongxi *et al.*, 1987: 19. Yu, 1988: 3. Compagno *et al.*, 1989: 18, pl. 1.

Monopterhinus griseus Blainville, 1816: 121.

Notidanus griseus Cuvier, 1816: 128. 1829: 390. Bory de St. Vincent, 1829: 597. Voigt, 1832: 509. Bonaparte, 1835: pl. 55 (fig. 1). Agassiz, 1835-1838: 92, pl. E (fig. 2-4). Lowe, 1837: 194. Bonaparte, 1839: 9. Cuvier, 1843: 362, pl. 115 (fig. 1). Couch, 1846: 1337. Bonaparte, 1846: 17. Sassi, 1846: 131. Nardo, 1847: 111. Owen, 1853: 91. Machado, 1857: 8. Nardo, 1859-1860: 787. Gemellaro, 1864: 122. Bocage & Brito Capello, 1866: 15. de la Blanchere, 1868: 371. Gunther, 1870: 397. Canestrini, 1872: 43. Lawley, 1875: 60, 65, pl. 4 (fig. 1). Gervais & Boulart, 1877: 194, pl. 74 (fig. 18). Delfortrie, 1878: 253. Doderlein, 1878: 30. Day, 1880-1884: 304, pl. 158 (fig.2). Stossich, 1880: 69. Perugia, 1881: 55. Graeffe, 1886: 447. Gunther, 1887: 207. Anderson, 1894: 182. Traquair, 1896: 159. Phillipi, 1901: 304. Bolivar, 1907. Gunther, 1911: 809. Ehrenbaum, 1927: 7.

Notidanus vacca Cuvier, 1817: 28.

Squalus (Monopterhinus) griseus Blainville, 1825: 77.

Notidanus monge Risso, 1826: 129. Bory de St. Vincent, 1829: 597.

Hexanchus corinus Jordan & Gilbert, 1880: 352; 1881: 30; 1883: 62. Bean, 1881: 267. Jordan, (1885), 1887: 792. Jordan & Starks, 1895: 788. Jordan & Evermann, 1896: 19. Rep. U.S. Comm. Fish. (1895), 1896: 213. Starks, 1911: 163. Garman, 1913: 17. Halkett, 1913: 39. O'Donoghue, 1926: 41. Jordan, Evermann & Clarke, 1930: 11. Townsend, 1931: 169. Walford, 1936: 24. Barnhart, 1936: 7.

Notidanus vulgaris Perez Canto, 1886: 8. Phillipi, 1887: 554, pl.6 (fig. 1). Quijada, 1913: 112.

Notidanus (Hexanchus) griseus Werner, 1904: 286. Ehrenbaum, 1930.

Hexanchus griseus australis De Buen 1960:

Material examined:

Hexanchus corinus, USNM 27369 (Holotype), 1030 mm TL, 48° 22'N, 124° 36'W, Neah Bay, Washington State, U.S.A.

Other material: see Appendix 2.

Diagnosis: A heavy-bodied shark, with a large blunt snout and six paired gill slits. The mouth is broadly rounded and subterminal. The dorsal fin is set far back, with the dorsal-caudal space being short, about equal to the dorsal fin base. The upper and lower teeth differ, the uppers have one large, single, curved, smooth-edged cusp, followed by up to four smaller cusplets. The lower teeth have a distinctive comb-like shape with a large high cusp followed by up to 13 smaller cusplets. The eyes glow a luminescent green in life. A noticeable pale light line follows the flank along the lateral line from midway up the tail to about the pectoral fin base. The upper and lower postventral caudal margins are weakly arched to nearly straight. Color when fresh ranges from a dark dirty gray to chocolate brown above; below the color may range from light to very dark.

Description: Proportional measurements expressed as a percentage of the total length are given in Appendix 3.

A stout BODY tapering posteriorly to become compressed laterally behind the pelvic fins. Proportional lengths along body axis increase with growth (Figure 3.29). HEAD flattened above, length to sixth gill opening 0.9 times in pectoral-pelvic space. Preoral SNOUT broadly rounded, short and blunt, length about 2.0 times mouth width. NOSTRILS lateral, but closer to snout tip than to mouth. Nostrils small, oblique, with anterior nasal flap anterior margin expanded as a subtriangular lobe with a blunt tip. Nostril width 4.1 in internarial space, 2.8 in eye length, and 2.0 in third gill opening. EYES large, oval, about 6.9 times in head length. Eye height 1.8 times into eye length. Proportional eye length decreases with growth (Figure 3.30). SPIRACLE present, but very small, located at the level of the upper eye margin, about opposite the mouth corners. Spiracle about 9.0 times eye length, located about 1.5 eye lengths behind posterior margin. GILL OPENINGS long, with the first extending from about the level of the spiracle to the throat, but not extending across it as in Chlamydoselachus anguineus. Gill openings decrease in length with the sixth being 1.5 times the length of the first and 0.8 of the third. Width of the third gill opening about 3.8 times in head length and 1.7 times eye length. MOUTH very large, rounded, about 2.0 times length in width. Mouth width about 1.7 times in head length and 1.1 times head width at pectoral origin. LABIAL FURROWS present, well developed especially in the lower jaw. Lower labial 1.0 times into upper labial.

The TEETH are noticeably different in upper and lower jaws (Figure 3.31). Upper jaw usually with a pair of medial teeth, but occasionally only one is present. The medial teeth have one single large, smooth-edged cusp, without serrations. The first anterolateral has a large single, smooth-edged cusp curved slightly rearward. The next seven to nine anterolaterals have a large single cusp with one to nine small cusplets; the number of cusplets increases with growth. Serrations are present from the second to ninth anterolaterals. Posterolateral commissural teeth are small and granular. Lower medial and anterolateral teeth with a very distinctive comb-like shape. A single symmetrical medium tooth with a single median cusp and up to three cusplets on each side. Anterolateral lower teeth have a single large cusp followed by 6 to 13 smaller cusplets; the number of cusplets increases with growth. Serrations may be present on the mesial cusp margin especially in larger individual sharks. The posterolateral commissural teeth are small, the first one to three having a tiny cusp followed by one or two smaller cusplets. The remaining posterolaterals are granular without any cusps or cusplets.

The upper dentition consists of one or two medials, 6 to 9 anterolaterals, and 8 to 28 posterolateral commissural teeth. The lower dentition consists of a single medial tooth and six anterolateral teeth; posterolateral commissural teeth ranged between 7 and 28. Total tooth counts range between 26-46/20-38 for all specimens examined (Table 3.12). A high variability in the tooth count range was related to growth changes. The total number of upper (Figure 3.32) and lower (Figure 3.33) teeth increase with growth. Growth related tooth counts were due to increases in numbers of posterolateral tooth rows.

ONTOGENIC HETERODONTY is very pronounced in the sixgill shark. Both upper and lower teeth show an increase in the number of cusps along the apical length and serrations along the mesial edge (Figure 3.34). This increase is related to growth and maturity in the animal. The lower anterolaterals are especially noticeable as the base and mesial length elongate with growth and sexual maturity. The cusp height of the anterolateral teeth increases at the onset of sexual maturity in males, but not females (Figure 3.35). However, the mesial edge of these same teeth lengthen in mature females, but not in males.

LATERAL TRUNK DENTICLES (Figure 3.36) tricuspidate, with a prominent medial cusp flanked by a single cusp on each side. These denticles are loosely spaced, with slight overlap. Those denticles along the caudal dorsal margin are enlarged and especially noticeable in newborns.

The PECTORAL FINS are large and broad with the anterior margin slightly convex and longer than the fin length. Pectoral fin length from origin to rear tip 1.1 times in anterior margin length. The apex of the anterior margin and posterior margin is broadly rounded, and the posterior margin is nearly straight. Pectoral fin anterior margin 0.5 times in pelvic anterior margin. Radials of the PECTORAL FIN SKELETON (Figure 3.37) extending about 1.8 times into anterior pectoral fin margin. Total pectoral fin radial counts range from 22 to 25 (Table 3.13) with each radial with between 5 and 7 segments. The propterygium is small with no radials extending from it, the mesopterygium has 10 to 11 radials, and the metapterygium with 12 to 14 radials.

PELVIC FINS with nearly straight margins and rounded apices. Pelvic fin base slightly less than dorsal fin length. Free rear tip elongated in males to form a scroll for the claspers. The PELVIC FIN SKELETON (Figure 3.38) consists of a long basipterygium with two segments from which 21 to 26 radials extend diagonally from its axis (Table 3.14). Each radial has 2 to 3 segments with the last 0 to 6 being unsegmented.

The CLASPERS are enclosed in a scroll formed by the inner and posterior margins of the pelvic fins. A clasper sac is present in adults, but not evident in juveniles. Spur and spines absent. The CLASPER SKELETON (Figure 3.39) consists of an elongated axial cartilage connected to the basipterygium by an intermediate segment followed by the beta cartilage. In the adult condition the end-style is joined by 2 terminal cartilage elements. The last 4 radial segments of the pelvic fins form the scroll which encloses the claspers.

DORSAL FIN origin set about over pelvic fin insertion. The mid-point of the dorsal base about over the anal fin origin. Dorsal with nearly straight anterior margin, a rounded apex and a broadly triangular free rear tip. Dorsal caudal space about 0.5 times dorsal fin base and approximately 0.9 times anal fin base. Dorsal fin height about 0.7 times anal fin height. DORSAL FIN SKELETON (Figure 3.40) has an elongated basal cartilage which is convex ventrally and slightly concave dorsally where the radial cartilages attach. Between 14 and 20 radials (Table 3.14) are attached to the basal cartilage with 3 to 4 segments per radial.

ANAL FIN about as long at base as dorsal fin base, rear margin nearly straight, free rear tip short. Height about 0.7 times dorsal fin height. Anal fin height about 1.9 times in base, and inner margin 1.6 times in height and 3.0 times in base. ANAL FIN SKELETON (Figure 3.41) composed of an elongated basal cartilage with between 14 and 20 radials (Table 3.14). Each radial has 3 to 4 segments.

CAUDAL FIN elongated, about 1/3 the total body length. Dorsal caudal margin slightly convex, length about 2.0 times precaudal length. Preventral caudal margin slightly convex, 3.9 times in dorsal caudal margin. Upper and lower postventral caudal margins weakly arched. Subterminal lobe slightly notched. Terminal caudal lobe weakly concave, about 4.3 times in caudal dorsal margin.

Total VERTEBRAL counts for California and southern African specimens ranged between 118 and 148 (Table 3.15). MP counts 31-39.8% (S.A.), 28.0-40% (CA.), DP counts 14.6-21.2% (S.A.), 17.9-20.6% (CA.), and DC counts 41.7-52.0% (S.A.), 39.8-50.3% (CA.) of total counts. DP/MP ratio 0.5 and DC/MP ratio 1.3. The MP-DP transition occurs between the 42nd and 50th segment (X=45) or at about the rib closure.

A series of NEUROCRANIA from specimens ranging between 681 mm and 3330 mm TL were measured from California and southern Africa (Table 3.16).

CRANIUM (Figure 3.42) with a short blunt ROSTRAL CARTILAGE, not hypercalcified in adult. Length of medial rostral cartilage about 19.7 times in nasobasal length, width across bases of lateral rostral cartilages about 0.3 times in length of medial rostral cartilage. NASAL CAPSULES broadly rounded; width of cranium across nasal capsules 1.5 in nasobasal length. NASAL APERTURES large, oval and separated by a space 0.9 times their widths. ANTERIOR FONTANELLE large, rounded, wider than long. CRANIAL ROOF 1.1 times orbital length. ORBITAL NOTCHES 7.6 times orbital length; width across SUBORBITAL SHELVES 0.5 times orbital length; OTIC CAPSULE length 0.6 times orbital length.

SPIRAL VALVE turn counts (Table 3.17) ranged between 35 and 39 for specimens from all geographical regions.

LIVER is large, oily, consisting of two lobes, one on each side of the body cavity and extending the entire length. The lobes are about equal size and alike in form.

COLORATION of the dorsum varies from a dark blackish-gray to chocolate brown, with lighter shades of each color extreme. The ventral region is lighter, ranging from a pale white to dirty gray. A visible light streak along the lateral line extends from midway up the caudal fin to about the pectoral fin base. This light lateral line is especially visible in those specimens tending toward the grayish extreme, less visible in those with the brown extreme. Coloration in newborns (Figure 3.43) is particularly brilliant with the anterior edges of the fins whitish, including the apex of the dorsal fin and the caudal dorsal margin. Eyes glow a bright fluorescent green in life.

DEVELOPMENT is ovoviviparous without placental attachment. Number of young range between 47 and 108 (Desbrosses 1938; present study).

ETYMOLOGY: The species name hex- for six and -anchus from branchus meaning gill. The specific name griseus, gray, refers to a common coloration of this shark.

REMARKS: Based on the material examined, the sixgill shark, <u>Hexanchus griseus</u> appears to be a single, large widely-ranging species. Comparison of meristics, morphometrics, spiral valve and tooth counts taken from a broad geographical area and size range of individuals support this conclusion. Descriptions of distinct sixgill shark species can be traced to individual variation and a lack of adequate material. Tooth count differences, cusplet numbers, and presence or absence of serrations have been used to separate sixgill species (Jordan & Gilbert 1880; DeBuen 1960). However, ontogenic heterodonty is very pronounced in this species and tooth shape, numbers of cusplets and serrations, and the total number of teeth can be related to the sex, size, and maturity of an individual specimen. Jordan and Gilbert (1880) described <u>H. corinus</u> based on differences noted on the lower anterolaterals which had fine serrations and only six cusplets instead of eight or nine. Regan (1905) examined a series of jaws from the Mediterranean and Atlantic, and compared it with the California <u>H. corinus</u> and a Japanese sixgill shark. He concluded that the number of cusplets varied with the size of the animal and was not a specific characteristic. Subsequent work by Bigelow and Schroeder (1948), and Springer and Waller (1969) failed to reveal any specific tooth differences between European, western Atlantic, and eastern Pacific specimens. In addition to specimens from the North Atlantic and North Pacific, jaws from the South Atlantic, South Pacific and Indian Oceans were examined. The number of cusplets reported by Jordan and Gilbert (1880) corresponds to the number found in other <u>H. griseus</u> of a similar size. The number of serrations increases along the mesial edge with growth, but these counts vary according to the degree of tooth wear. The total number of upper and lower teeth increases with growth. Tooth shape also changes with growth as the apical and mesial margins elongate to accommodate the addition of cusplets and serrations, respectively. Careful examination of the teeth, particularly the large lower anterolaterals, can indicate the approximate size, sex, and maturity of an individual specimen.

In several published accounts of <u>H. griseus</u> (Gunther 1870;

Nakamura 1936; Desbrosses 1938; Bigelow & Schroeder 1948; Chen 1963; Cervigon 1966) this species was inadvertently confused with the much smaller *H. nakamurai*. Numbers of cusplets for similar-sized *H. griseus* and *H. nakamurai* differ, the latter species having more cusplets. The large lower anterolateral teeth of all specimens of *H. griseus* examined numbered six, confirming previous accounts. The only exception was noted by Bigelow and Schroeder (1948) who reported individuals with only four. They also reported that the lower medial tooth was absent in some specimens, but all individuals in this study had this tooth and no other accounts were found to support Bigelow and Schroeder's (1948) findings. The subspecies *H. griseus australis* from Chile, described by De Buen (1960) has five larger lower anterolaterals, which suggest that it may have been a *H. nakamurai*. However, the measurements given by De Buen (1960) were found to fit those of *H. griseus* and not *H. nakamurai*. Unfortunately the holotype for this species was lost (Compagno 1984). Additional Chilean material examined all corresponded to *H. griseus* in morphology, including the presence of six large lower anterolaterals. Based on the present evidence *H. griseus australis* appear to be an aberrent specimen and should be regarded as a junior synonym of *H. griseus*.

HEXANCHUS NAKAMURAI Teng 1962

Bigeyed Sixgill Shark

Hexanchus griseus (*partim*) Gunther, 1870: 397. Nakamura, 1936: 7, pl. 1 fig. 1. Desbrosses, 1938: partim fig. Bigelow & Schroeder, 1948: 80, figs 8-9. Fourmanoir, 1961: 8, text figs 3-4, pl. 1. Cervigon, 1966: fig 375.

Hexanchus griseus nakamurai Teng, 1962: 30, fig. 5.

Hexanchus griseus Chen, 1963: 6.

Hexanchus vitulus Springer & Waller, 1969: 159, figs 1-4. Bass *et al.*, 1975: 9, text fig. 6, pl. 2. Compagno 1984*a*: 20, fig. Compagno *et al.*, 1989: 18, pl. 1. Robbins *et al.*, 1986: 17, pl. 62. Boeseman, 1973: 8. Castro, 1983: 38, fig. Cadenat & Blache, 1981: 22, fig. 10. Forster *et al.*, 1970: 390. Tortunese, 1985: 137. Kemp, 1978: 61, pl. 12. Maisey & Wolfram, 1984: 170. Yu, 1988: 3.

Hexanchus nakamurai Boeseman, 1984: 74, fig.

Material examined:

Hexanchus vitulus, USNM 200674, **Holotype**, 1500 mm TL, adult male, Bimini, Bahamas.

Hexanchus vitulus, USNM 200675, **Paratype**, female, Bimini, Bahamas.

Hexanchus griseus nakamurai, TFRI 2515 (Holotype) Lost ?

Other material: see Appendix 2.

Diagnosis: A thin-bodied shark readily distinguished from its larger congener by a narrower head, large eyes, five large lower anterolateral teeth, a long slender dorsal caudal space, with the distance from the dorsal origin to upper caudal origin being at least twice the length of the dorsal fin base. The dorsal fin originates about midway over the pelvic fin base. The upper and lower post ventral margins form a strong arch. The color in life is a uniform pale brown without a light line extending along the lateral body trunk. The trailing fin edges are white in some specimens.

Description: Proportional measurements expressed as a percentage of the total length are given in Appendix 3.

BODY TRUNK slender, tapering to caudal peduncle. HEAD moderately flattened, narrow, and pointed. Proportional lengths along body axis increases with growth (Figure 3.44). Head length to sixth gill opening 1.0 times pectoral-pelvic length. SNOUT narrow, rounded, length of preoral snout 3.6 times mouth width. NOSTRILS nearer the snout than to the forward edge of the mouth, inner posterior part with single valve-like anterior nasal flap. Nostril width 3.6 in internal width, 3.4 in eye length, and about 0.8 in third gill opening. EYES very large, rounded, orbits longer than high, their lengths about equal to length of snout in front of eye; anterior edge of orbit in advance of mouth. Eye length about 4.8 times in head length. Proportional eye length decreases with growth (Figure 3.45). The eyes glow a bright fluorescent green in life. SPIRACLES small and slit-like, their greatest diameter about 5.5 times in eye length. GILL OPENINGS number six with each successive gill opening becoming progressively shorter from the first to sixth gill; sixth gill opening is about 1.7 times the length of the first. Width of the third gill opening about 3.8 times in head length and 1.3 times eye length. MOUTH very large, strongly arched, mouth length 2.0 times into mouth width. Width about 2.3 times in head length. LABIAL FURROWS not visible when mouth is closed, but visible when open. Lower labial about 0.6 times into upper labial length.

TEETH differ in upper and lower jaws (Figure 3.46). Upper jaw with two medial teeth each having a single high smooth-edged cusp, without serrations or cusplets. The first anterolateral has one single large smooth-edged cusp. The next six to seven anterolaterals have a single large cusp with one to five smaller cusplets. The number of cusplets increases with growth. Serrations are present on the mesial edge. Posterolateral commissural teeth are small and granular. Lower jaw with a central medial tooth and a central cusp followed by 3 to 5 cusplets on each side. A single cusp variably high or short depending on sex and maturity. Anterolaterals with a single cusp followed by 6 to 10 cusplets along the apical length. Serrations are present along the mesial length. The cusp is variably high or short depending on sex and maturity. Posterolateral commissural teeth are small and granular.

The total number of teeth ranges between 25-33/09-30 for all specimens examined (Table 3.18). An increase in the total number of upper jaw teeth was observed (Figure 3.47). The number of medial teeth was two followed by seven or eight anterolateral teeth per side. The upper posterolateral commissural teeth numbered between 7 and 15. No apparent increase in the total number of lower jaw teeth was observed (Figure 3.48), but there is considerable variation not correlated with sized. The lower jaw always consisted of a single medial tooth followed by five anterolateral teeth per side. The number of posterolateral teeth ranged between 4 and 19.

SEXUAL DIMORPHISM is strong in this species with the upper and lower anterolateral tooth cusp of adult males becoming higher than those of adult females (Figure 3.49). The increased cusp height only occurs at the onset of sexual maturity in males.

LATERAL TRUNK DENTICLES small, closely imbricate, with a strong central ridge and two short lateral ridges, apical points not strong (Figure 3.50). A series of 1 to 3 enlarged denticles on the upper surface of the caudal dorsal margin.

PECTORAL FINS broad and short, their anterior margins slightly convex, lateral origins below and posterior to midpoint of sixth gill opening. Posterior margins slightly concave, tips rounded and triangular. Length about 1.1 times in anterior margin. PECTORAL FIN SKELETON (Figure 3.51) with radials extending about 2.2 times in pectoral anterior margin length into fin. The radials are divided into 6 segments. Propterygium small without radials, mesopterygium with 10 radials, metapterygium with 16 radials; total radial counts 26 for a single specimen.

Male PELVIC FINS long, with the posterior margin forming a scroll around the clasper. Anterior margin nearly straight, posterior margins straight in females, but slightly concave in males due to scrolling of the clasper folds. Pectoral anterior margin 0.3 times into pelvic anterior margin. PELVIC FIN SKELETON (Figure 3.52) consists of a long basipterygium with two segments from which 23 radials extend diagonally from its axis. Each radial with 3 segments, except for the 4 posterior-most radials which are unsegmented.

CLASPERS with a long axial cartilage and basal segments combined with a calcified terminal cartilage in adult males. The last 4 radial cartilages form the clasper scroll. Spurs and spines are absent. The CLASPER SKELETON consists of an elongated axial cartilage connected to the basipterygium by an intermediate segment, followed by the beta cartilage. The end style is joined by a terminal cartilage element in adults.

DORSAL FIN origin set above pelvic fin midbase. Anterior margin of dorsal fin nearly straight, apex rounded subtriangular, posterior margin slightly concave. Base length 0.7 times into dorsal caudal space. Height about 1.5 times base. Inner margin about 2.8 times height and 4.3 times base. DORSAL FIN SKELETON (Figure 3.53) with an elongate basal cartilage which is convex ventrally and slightly concave dorsally where the radial cartilages attach. One specimen had 13 radials attached to the basal cartilage, each with 3 segments per radial.

The ANAL FIN is small and subtriangular at apex; both anterior and posterior margins straight. Height of anal fin 0.5 times dorsal fin height and about 2.4 times in base, anal base 2.1 times in anal caudal space, anal inner margin 1.3 times in height and 3 times in base. ANAL FIN SKELETON (Figure 3.54) composed of an elongate basal cartilage with 13 radials, each consisting of 3 segments.

CAUDAL FIN elongated, slightly convex, about 1.9 times precaudal length. Preventral caudal margin slightly convex, about 4.3 times into caudal dorsal margin. Subterminal lobe strongly notched. Upper and lower postventral caudal margins strongly concave. Terminal caudal lobe moderately concave, about 4.4 times into caudal dorsal margin.

A VERTEBRAL COLUMN count was made on a single specimen from Taiwan. The counts were 57 MP, 30 DP, and 68 DC. The rib closure occurred at the 54th centra. The transition between MP-DP occurred three centra beyond the closure of the rib cage. The percentage of the total number of vertebrae was MP 36.8%, DP 19.4% and DC 43.9%. Ratios were 0.53 DP/MP and 1.19 DC/MP. Only by removing the vertebral column could accurate counts be determined.

NEUROCRANIUM from a 482 mm TL juvenile male from Taiwan was dissected out and measured (Table 3.19).

CRANIUM (Figure 3.55) with short blunt ROSTRAL CARTILAGE, not hypercalcified in adults. Length of medial rostral cartilage about 29.8 times in nasobasal length, width across bases of lateral rostral cartilages about 0.2 times in length of medial rostral cartilage. NASAL CAPSULES large and rounded, width across about 3.8 in nasobasal length. NASAL APERTURES large, oval, and separated by a space 1.6 times their widths. ANTERIOR FONTANELLE rounded, slightly longer than wide. CRANIAL ROOF 1.4 times orbital length. ORBITAL NOTCHES 6.7 times orbital length. SUBORBITAL SHELVES 1.1 times orbital length. OTIC CAPSULES 1.5 times orbital length.

Intestine of the SPIRAL VALVE type with the number of valve turns ranging from 22 to 27 (Table 3.20).

LIVER is large and very oily. It consists of two lobes, one on each side of the body cavity, which extend the entire length of the abdominal cavity. The lobes are of equal size and alike in form.

COLOR is a light pale brown to gray with no conspicuous markings other than trailing white edges on fins; slightly lighter below. Juvenile coloration (Figure 3.56) with white trailing fin edges on the pectoral, pelvic, and the dorsal fin tips. Caudal fin white edged along the caudal dorsal margin, upper post ventral margin, and the subterminal lobe. A black spot is located at the tip of the caudal fin. No light lateral line is present.

DEVELOPMENT is ovoviviparous with a litter size of 13 to 26.

ETYMOLOGY: The generic name is derived from the Greek Hex- for six, -anchus or branchus for gill. The specific name is in honor of Dr. H. Nakamura.

REMARKS: Teng (1962) described the subspecies Hexanchus griseus nakamurai from Kee-Lung, Taiwan in his Ph.D thesis. Approximately 100 copies of his work were published in Japan by Ogawa Press, Maizuru, Kyoto Prefecture, with copies being available to the general public (K. Nakaya, professor, Hokkaido University, Japan, pers. comm.). The question has arisen as to whether or not this should be regarded as a valid publication. According to the International Code of Zoological Nomenclature (1985; Article 8a), printing for general distribution, qualifies it as a publication. Thus, H. nakamurai would appear to be a valid species name. The question remains as to whether the very similar H. vitulus is a distinct species or a synonym of it. Unfortunately, the holotype and paratype of H. nakamurai, which was held at the Taiwan Fisheries Research Institute (TFRI) in Kee-Lung, has been lost. However, comparison of the holotype of H. vitulus to Teng's (1962) description, and excellent illustrations of his H. griseus nakamurai by Y.T. Yang, to Taiwanese material of H. nakamurai confirm that these two species are synonymous. Therefore, since Teng's (1962) H. nakamurai has precedence over Springer and Waller (1969) the former should be resurrected as the valid scientific name for the bigeyed sixgill shark.

GENUS *NOTORYNCHUS* Ayres, 1855

Type Species: *Notorynchus maculatus* Ayres, 1855, from San Francisco Bay, California (Ayres 1855: 1: 72-73).

Synonymy

Squalus cepedianus Peron, 1807: 337.

Squalus platycephalus Tenore, 1810: 241, 258.

Notidanus indicus Agassiz, 1835, pl. E (fig. 1); 1838: 92; 1843: 217. Gunther, 1870: 398. Hutton, 1873: 271. Day, 1878: 723, pl. 189 (fig. 4). Johnston, 1882: 138; 1890: 38. Gilchrist, 1902: 165.

Heptanchus indicus Muller & Henle, 1841: 82, pl 32. Bleeker, 1860: 58.

Notorynchus maculatus Ayres, 1855: 72-73. Gill, 1862: 495. Jordan & Evermann, 1896: 17; 1900, pl.2 (fig. 7). Byers, 1940: 23. Roedel & Ripley, 1950: 41, fig. 24-25. Herald & Ripley, 1951: 325. Herald, 1953: 241, fig. 2. Clemens & Wilby, 1961: 17. Herald 1968: 412. Russo & Herald, 1968: 215. Bane & Bane, 1971: 21, fig. 8. Miller & Lea, 1972: 34, fig. Hart, 1973: 28, fig. Welton, 1974: 3, fig. 1D. De Wit, 1975: 110. Compagno, 1977: 308. Gotshall *et al.*, 1980: 223. Robins *et al.*, 1980: 11. Ebert, 1984: 1-57; 1985: 58-59, fig. 1; 1986*c*: 246.

Notorynchus borealis Gill, 1864: 150.

Heptranchus indicus McDonald & Barron, 1868: 371, pl. 32 (figs 1-6). Castlenau, 1872: 217. Haswell, 1880: 96; 1884*a*: 88, pl. 1 (fig. 5); 1884*b*: 381, pl. 10 (fig. 1,2). Ogilby, 1889: 179.

Heptranchus griseus McDonald, 1873: 312.

Heptranchias maculatus Jordan & Gilbert, 1880: 353.

Notidanus (*Heptranchus*) *indicus* McCoy, 1880: 16, text figs A, B, pl. 43 (fig. 2).

Heptranchias pectorosus Garman, 1884*b*: 56. Lahille, 1928: 299, figs 1, 2; Fowler, 1941: 7. Smith, 1965: 39. Yu, 1988: 3.

Notidanus ferox Perez Canto, 1886: 7-8; (in Philippi) 1886: 23, pl. 6 (fig. 2). Philippi, 1886: 555-556. Reed, 1887: 23. Quijada, 1913: 112. Bigelow & Schroeder, 1948: 87. Bahamonda & Pequeno, 1975: 6.

Heptranchias haswelli Ogilby, 1897: 62.

Notidanus medinae Philippi, 1901: 303. Bahamonde & Pequeno, 1975: 6.

Heptranchias indicus Waite, 1907: 6. McCulloch, 1911: 2.

Notorynchus indicus Zeitz, 1908: 289.

Heptranchias platycephalus (Tenore, 1810) Lahille 1928: 300, 302.

Notorynchus platycephalus Garman, 1913: 18. Lindberg & Legeza, 1959: 27, fig. 17. Masai, 1963*b*: 27.

Heptranchias spilotus Lahille, 1913: 26, figs 1-3, pl. 8 (fig. 1).

Notorynchus pectorosus Garman, 1913: 20. McCulloch, 1919: 219, pl. 6 (fig. 3a). Waite, 1921: 10 (fig 5). Waite, 1923: 24, three figs. Phillips, 1924: 259, fig.1. Barnard, 1925: 21, pl. 1. Sadowsky, 1970: 33, fig. 1. Menni, 1975: 83; 1986: 427. Smith, 1975: 10; Mennis & Garcia, 1985: 1, figs 1-3.

Heptranchias indicus: Thompson, 1914: 134.

Heptanchus maculatus Daniel, 1916: 349; 1928: 4, fig. 12; 1934: 1, fig. 12.

Notorynchus ocellatus Devincenzi, 1920: 97.

Notorynchus platycephalus: Fowler, 1925: 188. Masai, 1963b: 27.

Notorynchus griseus (McDonald, 1873) McCulloch, 1929: 3.

Notorynchus macdonaldi Whitley, 1931*b*: 138, pl. 20, figs 3-5. Phillips, 1935: 236, fig. 1.

Notorynchus cepedianus Whitley, 1934: 181, 197; 1940: 70, figs 4, 50, 51; 1968: 5. Clemens & Wilby, 1946: 51, fig. 11. Graham, 1953: 62. Scott, 1962: 19. Teng, 1962: 36, fig. 7. Scott, Glover & Southcott, 1974: 23. Bass *et al.*, 1975: 14, fig. 8, pl. 5. Guzman & Campodonico, 1976: 207-210. Kemp, 1978: 74, pl. 13, fig. 2. Pequeno, 1979: 254. Chirichigno, 1980: 24, fig. 2. Castro, 1983: 38, fig. Eschmeyer *et al.* 1983: 19, pl. 1. Compagno, 1984*a*: 22, fig. Maisey & Wolfram, 1984: 170, fig. 1. Ebert, 1984: 1; 1986*b*: 1, figs 1-7; 1989: 1, figs 6. Mizue, 1984*a*: 42. Praderi, 1985: 3. Branstetter & MacEachran, 1986: 156. May *et al.*, 1986: 492. Paust & Smith, 1986: 28, fig. 6. De Silva, 1987: 61. Compagno *et al.*, 1989: 18, pl. 1. Galvan-Magana *et al.*, 1989: 77.

Heptranchias cepedianus Smith, 1965: 38, fig. 2.

Notorynchus maculatum Roedel, 1953: 13, fig. 5.

Material examined:

Notorynchus borealis, USNM 110920 (Holotype), dried jaws only, Nisquilly, Washington State, U.S.A.

Notorynchus pectorosus, MCZ 801 (Holotype), 391 mm TL, juvenile male, Patagonia.

Other material examined: see Appendix 2.

Diagnosis: A stout heavy-bodied shark, with a large broad head. Seven paired gill slits, decreasing in length from the first to seventh. Small rounded, eyes. Nostrils nearer the snout tip than to the mouth. Mouth very large, heavy jawed, rounded. Teeth differ in upper and lower jaws. Upper jaw may have 1 to 4 medial symphysial teeth followed by 5 to 8 anterolaterals. Lowers are comb-shaped with a single cusp followed by 2 to 6 smaller cusplets. The mesial cusp margin has serrations which increase with growth. Pectoral fins are large, sub-triangular, and broad; pelvics much smaller than pectorals. A single dorsal fin set far back. Caudal peduncle from dorsal fin insertion to origin of caudal fin short about the length of dorsal fin base. Caudal upper and lower margins weakly arched. Color in life ranges from an olive to silvery gray or reddish brown background, scattered with black spots on the dorsum. Spots are usually present, but may be absent. Ventral color is usually an off white to cream.

Description: Proportional measurements expressed as a percentage of the total length are given in Appendix 3.

A stout, heavy-BODIED shark, with a broad head. Proportional lengths along body axis increases with growth (Figure 3.57). HEAD length approximately 0.9 times into pectoral-pelvic space. SNOUT broadly rounded, length of preoral snout 2.6 times mouth width. NOSTRILS lateral, but much nearer the snout tip than the mouth. Anterior nasal flap subtriangular, tip rounded. Nostril width 4.5 in internal width, 2.8 in eye length, and 0.5 in third gill opening. EYES are sub-rounded, slightly longer than high; length 1.6 times height. Eye length about 7.7 times in head length. Proportional eye length decreases with growth (Figure 3.57). SPIRACLES present, but small; about 10.8 times eye length. Eye-spiracle length about 1.7 times eye length. The MOUTH is very large, broadly rounded and about 2.2 times length in width. Width about 1.7 times in head length. LABIAL FURROWS at angle of mouth. Upper 0.9 times into length of lower.

TEETH differ in upper and lower jaws (Figure 3.59). Medial teeth with a single smooth-edged cusp. Anterolaterals with a large, low set cusp followed by 3 to 6 smaller cusplets. The mesial edge of the cusp is serrated. Posterolaterals are small and granular. Lower medial with a central cusp followed on either side by 2 to 4 cusplets. Anterolaterals comb-like, apical length with 2 to 6 cusplets, mesial margin serrated. Posterolaterals small and granular.

Total tooth counts variable, ranging between 21-42/20-37 for all specimens examined (Table 3.21). Total tooth counts for upper jaw increase with growth (Figure 3.60). Upper jaw with 1 to 4 medials, followed by 5 to 8 anterolaterals and 4 to 14 posterolaterals. Total tooth counts for lower jaw increase with growth (Figure 3.61). Lower jaw with a single central medial tooth followed by six large anterolaterals. These counts were consistent for all specimens examined. The posterolateral commissural teeth varied with growth, ranging between 2 and 10.

LATERAL TRUNK DENTICLES (Figure 3.62) lanceolate, with one large single cusp. The crown is slightly elevated above the body with three prominent longitudinal ridges extending from the base to the cusp. Denticles slightly overlapping. Caudal dorsal margin denticles large, rounded, occurring in a series of about three rows, most pronounced in juveniles.

PECTORAL FINS large, broad based, anterior margin nearly straight, rounded at apex with posterior margin. Posterior margin slightly concave, narrowly rounded at tip with inner margin. Pectoral length from origin to rear tip 1.1 times in anterior margin length. PECTORAL FIN SKELETON (Figure 3.63) with radials extending about 1.6 of pectoral anterior margin length into fin. Total pectoral radial counts ranged between 23 and 27 (Table 3.22). Propterygium small with no radials extending from it, mesopterygium with 11 or 12 radials, and metapterygium with 12 to 15 radials (Table 3.22). The maximum number of segments per radial was 6 or 7.

PELVIC FINS small, nearly triangular, 0.5 times into pectoral fin length. Anterior margin nearly straight. Posterior margin slightly concave in females, strongly concave and elongated in males due to clasper scroll. The PELVIC FIN SKELETON (Figure 3.64) consists of a pelvic girdle from which a long basipterygium projects posteriorly with between 21 and 26 radials extending diagonally from its axis (Table 3.23). Each radial consists of 3 to 4 segments with the last 3 to 7 radials being unsegmented.

The CLASPERS are enclosed in a scroll formed by an elongation of the last four pelvic fin radials. In the juvenile, the clasper appears as a flexible stem of cartilage. Adults have an elongated calcified stem with three terminal cartilage elements. The CLASPER SKELETON (Figure 3.65) consists of a long axial cartilage connected to the basipterygium by two basal segments and dorsal to them is the beta cartilage. At the terminus of the axial cartilage (and only in adults) are three strongly calcified terminal cartilage elements.

The DORSAL FIN is set far back, with its origin about over insertion of pelvic fins; base about 5.4 times in caudal dorsal margin. Anterior margin convex, broadly rounded at apex. Posterior margin concave. Dorsal fin height 0.9 times into anal fin height. Dorsal fin base about 0.6 times into dorsal-caudal space; height about 1.5 times into dorsal fin base. DORSAL FIN SKELETON (Figure 3.66) consists of an elongate basal cartilage which is convex ventrally and slightly concave dorsally where the radials attach. Between 15 and 19 radial cartilages (Table 3.23) are attached to the basal cartilage each with 4 to 6 segments.

ANAL FIN small, origin about below dorsal fin insertion, height about 0.7 times dorsal fin height. Anal fin height about 1.8 times in base, and inner margin 1.7 times in height and 2.9 times in base. ANAL FIN SKELETON (Figure 3.67) composed of an elongated basal cartilage with between 14 and 17 radials (Table 3.23). Each radial has 1 to 4 segments.

CAUDAL FIN elongated, about 1/3 entire body length; dorsal margin moderately convex, length 2.1 times precaudal length. Preventral caudal margin slightly convex, 3.8 times in dorsal caudal margin. Subterminal lobe strongly notched. Upper and lower postventral margins weakly arched. Terminal caudal lobe moderately concave.

VERTEBRAL COLUMN counts were made on specimens from California and South Africa. The total vertebral counts for 8 California specimens were 123-130, while the range for 29 Southern African specimens were 127-157 (Table 3.24). The percent MP for California was 40.4-45.9% and for Southern Africa 31.8-44.5%, the percent DP for California was 10-18.2% and for Southern Africa 11.7-19.1%, and the percent DC for California was 40.3-44.7% and for Southern Africa 42.5-52.9% (Table 3.24). The DP/MP ratios for California was between 0.2 and 0.5, and for Southern Africa between 0.3 and 0.6. The DC/MP ratios for California was between 0.9 and 1.1, and for Southern Africa between 1.0-1.6. The MP-DP transition ranges between the 50th and 57th vertebrae, i.e. about 4 to 11 vertebral segments beyond the closure of the haemal arches.

NEUROCRANIA were taken from a series of specimens ranging between 854 mm and 2420 mm TL (Table 3.25).

CRANIUM (Figure 3.68) with a short broadly rounded ROSTRUM, not hypercalcified in adult. Length of medial rostral cartilage about 8.7 times in nasobasal length, width across base of lateral rostral cartilage about 1.25 times in length of medial rostral cartilage. NASAL CAPSULES about as long as wide, with rounded edges. Width of cranium across nasal capsules 4.3 in nasobasal length. NASAL APERTURES large, oval, and separated by a space 4.3 times their widths. ANTERIOR FONTANELLE broadly rounded and oval. CRANIAL ROOF 1.84 times orbital length. ORBITAL NOTCHES 13 times orbital length. Width across SUBORBITAL SHELVES 1.37 times orbital length. Length of OTIC CAPSULES about 1.46 times orbital length.

SPIRAL VALVE turn counts range between 14 and 17 for all specimens examined (Table 3.26).

LIVER is large, consisting of two lobes, one on each side of the body cavity. The liver is known to produce high concentrations of vitamin A (Byers 1940). Percent liver weight increase with the shark's growth (Figure 3.69).

COLOR varies from a pale to silvery gray or a reddish-brown above, white below. Black spots usually present on back and sides, but may be absent. Sevengills kept in captivity at the Monterey Bay Aquarium (MBA) were observed to lose their spots within several weeks of placement in display tanks (G. van Dykhuizen, aquarist, MBA, pers. comm.). White spots occasionally found on back and sides can be attributable to a fungus. Juvenile coloration quite striking with the trailing fin edges and dorsal fin apex being white (Figure 3.69). The caudal fin has a prominent black strip extending from the caudal peduncle to the fin tip. The enlarged dermal denticles of the caudal dorsal margin are a conspicuous white, as is the ventral margin and subterminal lobe. Albino (Herald 1953) and piebald (Ebert 1985) colored individuals are occasionally captured.

DEVELOPMENT is ovoviviparous without placental attachment. A single gravid female contained 82 embryos (Ebert 1986b, 1989).

ETYMOLOGY: The species name is derived from the Greek Noto- meaning spotted, -rynchus meaning snout, and cepedianus named in honor of Lacepede.

REMARKS:

Based on current evidence, it appears that Notorynchus is a monotypic genus represented by N. cepedianus. The highly variable number of teeth in sevengills has been the subject of much debate as to whether more than one species is represented. Examination of 55 California specimens revealed that 51% possessed a single medial tooth, 44% had two medials, and 5% had three medial teeth. In addition, examination of sevengills at three San Francisco Bay fishing derbies indicated that the number of medial teeth was a variable character and did not correspond to any particular size or sex. Compagno (1984a; pers. comm.) independently examined jaws of sevengills from California and concluded that this was a variable characteristic. Similarly, Bass et al. (1975) in southern Africa, Kemp (1978) in Australia and Pequeno (1979) in Chile independently arrived at the conclusion that N. cepedianus was a monotypic species. Even though Smith (1965) listed both N. cepedianus and N. pectorosus as occurring in South African waters, no specimens were observed with 2 or more upper medial teeth. Examination of ca. 400 additional specimens from angling competitions in southern Africa failed to uncover any specimens with more than a single upper medial tooth. Individuals with additional upper medials may occur in this region, but if so, are rare. It is interesting to note that the Pacific Ocean populations have a variable number of upper medial teeth, but Atlantic and Indian Ocean populations lack this characteristic. Australian, Californian, Japanese and New Zealand specimens were found to have between 1 and 4 upper medial teeth. However, from examination of numerous specimens and published accounts (Sadowsky 1971; Menni 1975; Menni & Garcia 1985) revealed no evidence or records of sevengills with more than a single upper medial tooth from the Atlantic or Indian Oceans.

Another variable character was vertebral counts. The precaudal counts for Californian and southern African specimens were consistent, but the caudal counts differed widely. Since the only California specimens examined were small (< 1 m TL), and no southern African individuals of a similar size were compared, it may be that caudal vertebral numbers change with growth. This is known to occur within the Scyliorhinidae (Compagno 1988). This discrepancy may also be due to population differences as is the case of the soupfin shark, Galeorhinus galeus, which has higher vertebral counts in California than South African (Compagno 1988). The MP-DP transition for both California and southern Africa occurred between the 50th and 57th vertebrae. Daniel (1928) reported that the MP-DP transition took place at the 55th vertebra in a single California specimen. The similarity of the MP-DP transition for both locations tends to support the conclusion that the DC vertebrae were varied with size.

Biogeography

Frilled Shark

The frilled shark has a scattered but circumglobal distribution in boreal to temperate and sub-tropical waters (Figure 3.71; Table 3.27). The frilled shark has been reported from both sides of the North Pacific Ocean. In the Eastern North Pacific the one confirmed Californian specimen was taken in a drift gill net, at a depth of 20 m, over water in excess of 1500 m deep (Noble 1948; present study). There are unconfirmed reports of frilled sharks being caught off the Channel Islands of southern California, and in particular San Clemente (S.P. Applegate,Instituto de Geologia, Mexico, pers. comm.). Reports of a second frilled shark taken from California waters (Roedel & Ripley 1950) could not be confirmed. In the central Pacific Basin, they have been taken off the Milwaukee Seamount, Northwestern Range and Colahan Seamount, Hawaiian Range (Borets 1986). Frilled sharks are especially abundant around the deep submarine canyons of Sagami and Suruga bays off SE Honshu, Japan (Tanaka 1985; Taniuchi 1987; present study). South of Japan this species has been caught in the Okinawa Trough of the East China Sea (Nakaya 1985) and from off Taiwan. The Taiwanese records are based on three specimens which were examined in April 1988. The three specimens were an adult male, 1250 mm TL, Ta-Chi (24° 50'N, 121° 50'E), ca. 300 m depth, 12 April 1988; adult male, 1410 mm TL, Tung-Kang (22° 26'N, 120° 30'E), March 1988; adult female, 1571 mm TL, Cheng-Kung (23° 06'N, 121° 22'E). These are the first confirmed records for this species from Taiwanese waters. In recent years deep sea exploratory fishing for orange roughies, Hoplostethus atlanticus, around Australian waters has resulted in an increased knowledge of the deep fauna. One of the less common species that is regularly caught in deep exploratory trawling there is the frilled shark (L.J.V. Compagno, South African Museum, Cape Town, pers. comm.). The frilled shark was originally reported from Australian waters by Stead (1907), but was based on rather dubious evidence, a skull and vertebral column. Later, Bass (1979) confirmed its occurrence from New South Wales. Frilled sharks are fairly common in New Zealand waters between depths of 600 m and 1200 m (Nakaya and Bass 1978). The frilled shark has been captured off Chile in the south Eastern Pacific Ocean (Armada 1977).

Although Indian Ocean records are scarce, the frilled shark has been caught in oceanic waters off the Transkei coast (Timokhin 1980), and off the Natal (R. White, fishermen, Natal, South Africa, pers. comm.) and Cape (Smith 1951; M.M. Smith, former director, J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa, pers. comm.) coasts. Those from the Transkei coast were taken in depths of between 1230 and 1400 m, while the Natal specimen was caught in about 300 m depth by a ski boat fisherman. The Cape record for this species was based on a report by Smith (1951) from an angler at Port Alfred. Unfortunately, the specimen was discarded before its identity could be confirmed. As a result, this record is considered dubious since the continental shelf is very broad in this area and it seems unlikely that this species would occur so far out of its normal range. It may be that this particular specimen was ill, disabled, or at least disoriented when caught. Thus, this record is only tentatively included on the distribution chart.

Frilled sharks are particularly common in the Northeastern Atlantic, especially off the Faeroe Bank. During a series of experimental trawls in this region during the late 1950's, approximately 50 frilled sharks were taken from 300 trawls. This is far less than the large number of squaloids taken in the area, which consisted mainly of the genera *Centroscyllium*, *Deania* and *Oxynotus* (A. Wheeler, former curator, BMNH, pers. comm.). Elsewhere in the Northeast Atlantic, frilled sharks occur from Madeira to the Shetlands and the Varanger Fjord, Norway; along the Iberian Peninsula, to the Straits of Gibraltar and from the Northwest African coast (Collett 1896; Wheeler 1962; Golovan & Pakhorukov 1986; present study). In the southeastern Atlantic, they range from off Angola southwards to Namibia (Smith 1967; Trunov 1968; Domanevskiy 1975; present study). The only frilled shark record from the Western Atlantic is from Suriname (Uyeno & Saski 1983). Exploratory research along the upper continental shelf of this area and around the Caribbean Sea by the BCF/NMFS program failed to catch any additional frilled sharks, although other hexanchoids were caught. It may be that frilled sharks are, at best, rare in the Caribbean.

Perlon Shark

The perlon shark is a moderately deep water species with a circumglobal distribution in tropical, subtropical and warm temperate regions (Figure 3.72; Table 3.28). In the western Pacific Ocean basin, this species occurs off the Japanese Islands of Hokkaido, Honshu, and Kyushu (Mizue 1984a; Tanaka 1984; Taniuchi 1984a,b; present study). It is also known from Ogasawara Island (Taniuchi 1984c), the Yellow Sea (Chu et al. 1960), and East China Sea (Hongxi et al. 1987) extending from Okinawa (Mizue 1984b) southwards to Taiwan (Teng 1962; present study). The perlon shark has not been recorded from any of the central Pacific Basin islands including Hawaii and the Philippines, nor is it known from the eastern North Pacific. In the South Pacific it is commonly taken off the eastern Australian states of New South Wales, South Australia, Tasmania and Victoria (Garrick & Paul 1971; Last et al. 1983; May et al. 1986). It occurs off New Caledonia (present study) and New Zealand (Garrick & Paul 1971), but is unknown from any of the other South Pacific islands. In the eastern South Pacific perlon sharks occur off Chile and Peru (Chirichigno 1984; Compagno 1984a).

Perlon sharks occur in the Indo-Pacific off Bali, Indonesia (Compagno 1984a), Western Australia (May et al. 1986; present study), India (Compagno & Talwar 1985) and the Gulf of Aden. It has not been recorded from the east coast of Africa between the Gulf of Aden and Mozambique though it may occur in this region. It is however, a common species from southern Mozambique to Natal, South Africa (Bass et al. 1975; present study), and is known from several island groups scattered throughout the Indian Ocean including Aldabra (Forster et al. 1970), the Comores, Madagascar (Fourmanoir 1961) and the Mascarene Range (Shcherbachev 1987).

In the western Atlantic Ocean, perlon sharks are common along the east coast of North America, from New York to Florida including the Bahamas and Bermuda. They occur throughout the Caribbean from Cuba (Bigelow & Schroeder 1948) and the Gulf of Mexico, to Suriname, French Guiana, and Venezuela (Uyeno & Saski 1983), and extending southwards to Brazil (O. Gadig, Guaruja, Brazil, pers. comm.) and Argentina (Compagno 1984). Perlon sharks occur along the west African coast from Central Namibia and Angola (Pissarro & Sanches 1973; Lloris 1986; present study) northwards through the Gulf of Guinea to the Straits of Gibraltar. In Atlantic European waters they occur from the Bay of

Biscay to the southern coast of England (Cappetta et al. 1985). Perlon sharks are common throughout the western Mediterranean Sea, particularly off Tunisia, France, Malta, and Italy (L. del Cerro, Barcelona, Spain, pers. comm.; J. Abela, fisherman, Malta, pers. comm.; Capape 1980; present study). There are no confirmed records from the eastern Mediterranean.

Sixgill Shark

With increasing exploration of the ocean depths and as the distribution of many deep sea species become available, it appears that one of the most wide-ranging shark species is the sixgill shark. It has been recorded from temperate and boreal areas to the tropical (=equatorial) regions of the world. Sixgills appear to have a circumglobal distribution, occurring from 70°N to at least 42°S latitude (Figure 3.73; Table 3.29). It may even be a polar species, but as limited exploration of the deep fauna has been conducted in this region there are no confirmed records of it from this region. This is probably one of the most broadly distributed and abundant large sharks, comparable only to the blue shark, Prionace glauca, a pelagic species and one which is easier to observe than the deeper-living sixgill.

In the northern Pacific Ocean sixgill sharks occur from the outer coast of Baja California, northwards along the entire eastern Pacific coast of North America to Alaska and across the Aleutian Islands chain to Japan (Compagno 1984a; Ebert 1986b; present study). There are no records of them occurring in the Gulf of California or southwards along the Pacific Mexican and Central American coasts, nor have they been recorded from the Bering Sea. They occur around the Japanese Islands of Honshu, from Choshi to Nagasaki, and Izu (Tanaka 1984; Taniuchi 1984a,b; Mizue 1984a). This species occurs throughout the East China Sea from Okinawa (Mizue 1984b; present study) to Taiwan (Teng 1962; present study) and the Philippines (Otake 1984), and extending into the South China Sea (Chu et al. 1962). The sixgill ranges throughout several Pacific island chains including Enewetak, Marshall Islands (Randal 1986), Palau, Micronesia (L.J.V. Compagno, pers. comm.; present study), the Hawaiian Islands, and the Kimmey Seamount, Northwestern Range (Borets 1986). In the South Pacific, it occurs off the Australian states of New South Wales (Stead 1963), Tasmania (Last et al. 1983) and Victoria (Lynch 1964), and from the deep waters around New Zealand (Phillipps 1946). In the eastern South Pacific, sixgills occur off the South American coasts of Chile (present study) and Peru (Chirichigno 1980), and off the Nasaka Ridge (Golovan & Pakhorukov 1986).

Sixgills range from Sumatra and Malaysia (Stead 1963) in Indonesian waters to the Indian Ocean islands of Assumption, Geyser Reef, Cosmoledo, Madagascar, Comores and Aldabra (Forster et al. 1970; present study). They occur off southern Mozambique and South Africa (Bass et al. 1975; present study), but are unknown from elsewhere along the north eastern African coast.

Sixgills are common in the southeastern Atlantic along the coastlines of South Africa, Namibia, Angola, Ivory Coast and Nigeria and extending into the northeastern Atlantic from Senegal to Iceland and southern Norway (Wheeler & Blacker 1969; Pissarro & Sanches 1973; Bass et al. 1975; Compagno 1984; Lloris 1986; present study). They are particularly abundant around island chains such as the Azores, Madeira and the Canary Islands (Boeseman 1973; present study). This species is also common in the Mediterranean Sea especially around some of the islands such as Crete, Cyprus and Malta and along the coast of France and Spain (Bigelow & Schroeder 1948; Gilat & Gelman 1987; Golani 1986; L. del Cerro, pers. comm.; J. Abela, pers. comm.; present study). It is common along the Mid-Atlantic Ridge and Northwest Atlantic off Newfoundland, and along the eastern seaboard to Florida, including the Bahamas and Bermuda (Compagno 1984a; Backus 1957; Clark 1986; K. Hartel, curator, MCZ, pers. comm.; present study). Sixgills are abundant around Cuba, the Caymans, and throughout most of the Caribbean Sea including the Gulf of Mexico, the deep waters around the Yucatan Peninsula, to Nicaragua, Costa Rica, Venezuela and extending from Brazil to Argentina (Bigelow & Schroeder 1948; Cervigon 1966; Springer & Waller 1969; Clark 1988; Menni 1986; S.P. Applegate, pers. comm.; present study). In the South Atlantic sixgills are found along the Mid-Atlantic islands of Isla de Noronha (A. Amorim, Instituto de Pesca, Santos, Brazil, pers. comm.), Gough and Tristan da Cunha (Roscoe 1979; present study).

Bigeyed Sixgill Shark

The bigeyed sixgill shark ranges in subtropical to tropical waters (Figure 3.74; Table 3.30) between 90 and 600 m depth (Bass et al. 1975). It occurs off the western Pacific islands of Ogasawara (Taniuchi 1984c), Okinawa (Mizue 1984b), Taiwan (Teng 1962; present study), the Philippines (Springer & Waller 1969; present study), and New Caledonia as well as off New South Wales, Australia. There are no records of it from elsewhere in the south or eastern Pacific.

Indian Ocean records for the bigeyed sixgill range from Bunbury, Western Australia, Kenya, southern Mozambique, Natal, South Africa, and from off several island chains including Geyser and Zelee Banks, East of Diego Suarez, Castor and Cordeliere Banks (Forster et al. 1970; Bass et al. 1975; present study). Records of sixgill sharks from off Madagascar (Fourmanoir 1961) and Mauritius (Gunther 1870) were subsequently re-identified as bigeyed sixgills (Bass et al. 1975; present study).

The North Atlantic range of bigeyed sixgills extends from the Bay of Biscay (Desbrosses 1938) and the Straits of Gibraltar to the western Mediterranean as far as Italy (Compagno 1984; Tortunese 1985). There are some questionable records from the Gulf of Guinea which need confirmation. The Eastern Atlantic range extends from Florida and the Bahamas, to the Caribbean including Cuba, Virgin Islands, and from the Caymans to Mexico, central America, and Venezuela (Bigelow & Schroeder 1948; Cervigon 1966; Springer & Waller 1969; Clark 1988; I. Sang, Dept. of Marine Sciences, University of Puerto Rico, Puerto Rico, pers. comm.; S.P. Applegate, pers. comm.; present study). There are no records of bigeyed sixgills from the South Atlantic.

Sevengill Shark

The sevengill shark is a common coastal species of temperate waters (Figure 3.75; Table 3.31). It occurs on both sides of the North Pacific, in the Sea of Japan, along the western Japanese coast line, around the Korean peninsula, Yellow

Sea, and along the Chinese mainland coast as far south as Amoy and Taiwan Island (Chu *et al.* 1960; Teng 1962; Chu 1963; Mizue 1984a; present study). In the eastern North Pacific it occurs from southeast Alaska to the northern Gulf of California (Ebert 1986a, 1989; Galvan-Magana, Nienhuis and Klimley 1989; S.P. Applegate, pers. comm.).

In the southern hemisphere, sevengills occur along all three major continents, New Zealand, and off several smaller islands. Along the South American coastline, sevengills occur from Santos, southern Brazil (where they are rare), southward to Uruguay and Argentina where they are abundant, particularly in the Rio de La Plata area (Menni and Garcia 1985; O. Gadig, pers. comm.; present study). There does not appear to be any break in the population between Argentina and Chile since they are known to occur around the eastern Straits of Magellan (Pequeno 1979). Sevengills occur along the Chilean coast to southern Peru (Chirichigno 1980; present study). Around New Zealand waters sevengills are especially abundant in bays and harbors (Paul 1987). Along the Australian coastline sevengills commonly occur off New South Wales, Victoria, South Australia and Tasmania (Last *et al.* 1983).

In southern Africa sevengills occur from East London on the Southeast Cape Coast to Cape Agulhas and the Cape Peninsula of South Africa, and up the west coast at least to Mowe Bay, Namibia. Although this species has not been confirmed from Angola several of its chondrichthyian faunal associates in temperate southern African waters, such as the gully shark (*Triakis megalopterus*), houndshark (*Mustelus mustelus*) and bull ray (*Myliobatis aquila*) occur at least to Mocamedes, Angola (Penrith 1978) where the cold Benguela Current turns seawards and sevengills are to be expected to occur there. Sevengills are cited here for the first time as occurring on several small island chains in the southern Atlantic; Tristan da Cunha (37° 05′ S, 12° 16′ W) and Gough (40° 18′ S, 09° 56′ W) (V. Peddemors, Natal Sharks Board, Umhlanga Rocks, South Africa, pers. comm.; T. Andrews, Rhodes University, Grahamstown, South Africa, pers. comm.).

There are as yet unsubstantiated reports of sevengills from

India and Sri Lanka. Day (1878) first reported them as occurring from Madras, India, with De Silva (1987) later confirming their occurrence in Sri Lanka. Sevengills are commonly taken along the southern coast of Sri Lanaka and used for their liver oil (De Silva, naturalist, Madapatha, Sri Lanaka, pers. comm.). The distribution of sevengills from this region would place them far outside their normal temperate water habitat and range.

The North Atlantic is the only conspicuous gap in the distribution of sevengills from temperate waters. The absence of sevengills from this region is of interest since the temperate Atlantic waters around northern Europe and America would appear to be suitable for their existence. A faunal associate, the spiny dogfish (Squalus acanthias), occurs on both sides of the north Atlantic, but another, the soupfin shark (Galeorhinus galeus), occurs only on the eastern side. Geologically, this species occurred in the North Atlantic as recently as the Pliocene, ca. 3.5 m.y.a. (D. Ward, palaeontologist, British Museum Natural History, London, England, pers. comm.).

Habitat

Frilled Shark

Habitat information for frilled sharks is scarce, since hydrographic and substratum data are virtually unknown for frilled shark records published to date. Hydrographic data on a frilled shark caught in 434 m depth off southern Namibia indicate that it was in a low oxygen, high nutrient zone (Table 3.32), with a soft bottom substratum. The abundance of frilled sharks between southern Namibia and the Cunene River, Japan and the North Atlantic, coincides with regions of high biological productivity.

Perlon Shark

Very little habitat data are available for the perlon shark. Most specimens were caught in bottom trawls though some were taken on midwater long line sets. Hydrographic data for a single perlon shark captured off Natal are given (Table 3.33) to provide some information on the physical parameters occurring in its habitat. It is a predominantly tropical to warm temperate species.

Sixgill Shark

Hydrographic data for three specimens taken off the west coast of southern Africa indicate that they were in areas of high upwelling (Table 3.34). The bottom water temperature ranged between 6.2 and 9.9 °C and with a high nutrient content recorded in the water samples. All the specimens were juveniles between 681 mm and 1340 mm TL.

Bigeyed Sixgill Shark

The bigeyed sixgill appears to be an epibenthic to midwater species. Off Taiwan this species is usually caught along the upper slopes of several deep trenches that occur around the Island.

Sevengill Shark

Sevengills occur in temperate to warm temperate oceans where the water temperature rarely exceeds 20 °C. They seem to be most abundant where the water temperature lies between 12 and 18 °C. These sharks seem to occur in areas that are associated with upwelling and high productivity. They tend to prefer rocky reef habitat where kelp beds comprising species of Macrocystis, Ecklonia, and Nereocystis, thrive, though sevengills are also caught over sandy and mud bottoms in bays or harbors. Salinity appears to have a profound influence on their habitat selectivity. This is especially true in bays and estuaries which play an important role in their life cycle. For example, during the El Nino event of 1982-83, along the California coast, extraordinary winter rains resulted in high river run off into the bays. The high flow of fresh water lowered the salinity to an intolerable level for many species. Sevengills typically enter these bays in substantial numbers during April to give birth and mate. In 1982-83 however, they appeared several weeks later than usual, at about mid-May, after the rains had subsided and the flow of fresh water runoff had decreased. The sevengill, like many other bay species, relies on certain environmental cues to initiate its movement into bays.

Movement Patterns

Sevengill Shark

A total of 376 sevengills from southern Africa and 36 from California were tagged of which 11 and 1, respectively, were recaptured (Table 3.35). Specimens were at liberty from between 34 and ca. 730 days, and moved from 0 to 379 km. The most interesting recapture was that of an adult female (ca. 3 m TL) from California which had been at liberty for ca. 730 days. This specimen had been dart-tagged in northern Humboldt Bay in May 1984 and recaptured in late April 1986, almost two years later. It is significant that Humboldt Bay is a breeding ground for sevengills and that this particular specimen had been recaptured at the same time of year in almost the same location.

The movement patterns of sevengills in southern African were less clear, with specimens showing no distinctive patterns (Figure 3.76). All sharks were tagged from the shore in areas frequently fished by anglers. Similarly, all but two recaptures were made from shore locations. The depth of capture for the two offshore specimens was not recorded. There appeared to be no correlation between the length of time at liberty and the distance traveled for the southern Africa recaptures. The fastest moving sevengill traveled 2.0 km/day. The time of year when specimens were tagged and subsequently recaptured did not reveal any significant pattern. Unfortunately, the sex was not recorded for any of the recaptured specimens.

Growth

Sevengill Shark

Three tagged sharks were remeasured upon being caught. One specimen at liberty for 359 days grew 89 mm, while the other two showed no signs of growth. Of the two specimens that showed no growth, one had been at liberty for only 34 days, but the other had been free for 538 days. The sex was not recorded upon recapture for any of the specimens.

Reproductive Biology

Frilled Shark

Males

Based on the degree of calcification of the terminal cartilage elements it is concluded that male frilled sharks mature at a minimum size of 916 mm TL. Figure 3.77 shows a sharp increase from a 542 mm TL specimen to a 916 mm TL specimen. The claspers of frilled sharks were not enclosed within a scroll as in the Hexanchidae, but a clasper sac is present in adults. The terminal cartilage elements were calcified in all specimens except one juvenile (542 mm TL) and an embryo (178 mm TL). The juvenile claspers were narrow, stem-like appendages lacking any clasper sac development. The epididymis of adults were enlarged and coiled, and by applying pressure viable sperm were expelled through the genital papilla. The single juvenile examined was a museum specimen which was not dissected for examination. Unfortunately, no additional juvenile or adolescent specimens were available for study. Thus the onset of maturity is difficult to determine in this species.

Females

No fresh specimens were examined during the study. Therefore no further comments on material other than that available in the literature can be made with regards to the maturity of female frilled sharks.

Size

The maximum reported size for males was 1650 mm TL, and 1960 mm TL for females (Gudger 1940). The 542 mm TL specimen from Japan (USNM 161522) is the smallest known free swimming specimen. Gudger (1940) estimated that the size at birth was probably between 508 mm and 610 mm TL. This estimate was based in part, on a 610 mm TL free swimming female (Collett 1890) and an embryo measuring 390 mm TL that still had a large yolk sac of ca. 80 mm in diameter (Gudger and Smith 1933). The 542 mm TL specimen had a very recognizable umbilical scar present suggesting that it was not very old at capture. The 610 mm TL specimen reported by Collett (1890) also had a very recognizable umbilical scar. Based on the limited available evidence it is suggested that parturition occurs, on average, at about 500 mm TL.

Perlon Shark

Males

Males mature between 700 mm and 800 mm TL. All males over 800 mm TL were considered mature. The smallest adult measured 746 mm TL, while the largest adolescent was 783 mm TL. The clasper length increased rapidly between 700 mm and 800 mm TL (Figure 3.78). Adult males had a sticky, mucous substance on the claspers which appeared to act as an adhesive, restricting the clasper's mobility. Calcification of the terminal cartilage elements appear to be the last criterion met before maturity was attained in this species.

Testes weight increased rapidly between 700 mm and 800 mm TL (Figure 3.79) and may be considered a reliable indicator of maturity. However, testes length to TL increase was gradual and not considered a good indicator of maturity (Figure 3.80). No seasonal change in testes weight was observed and viable sperm appeared to be present year-round. Viable sperm were expelled from the genital papilla in both adolescent and adult specimens rendering this an unreliable indicator of maturity. The epididymis of adult specimens was highly convoluted, but only slightly coiled in adolescents. Coiling begins anteriorly in early adolescence and increases steadily throughout this stage of development.

Size

Figure 3.81 shows the length-weight relationship for 19 males between 345 mm and 1069 mm TL. The largest male examined measured 1069 mm TL, and is the largest specimen on record.

Females

Females matured between 965 mm and 1100 mm TL. The largest egg diameter for specimens › 965 mm ranged between 8 mm and 28 mm (Figure 3.82). Maturing ova (10 mm in diameter) were present in one specimen 891 mm TL, while the ovaries of an 871 mm TL specimen were undifferentiated. An adolescent measuring 980 mm TL contained numerous small non-yolk follicles, a narrow uterus (4 mm width), and a shell gland width of 9 mm. The two largest females, 1130 mm and 1185 mm TL, had smaller eggs (10 mm and 18 mm in diameter, respectively), but enlarged oviducts and wide shell glands. The shell gland width to TL relationship increased sharply between 840 mm and 965 mm TL (Figure 3.83). Shell gland width (›10 mm) appeared to be variable, and to be correlated with the size of the largest egg diameter (Figure 3.84). Oviduct width increased rapidly in those specimens over 1000 mm TL (Figure 3.85). The oviducts in the two largest specimens were pendulous and hung loosely. No gravid females were recorded during the study. The total number of eggs combining both ovaries ranged from 15 to 42 (Figure 3.86) for 11 specimens. No reduction in the total number of eggs in relation to the largest egg diameter, was observed (Figure 3.87).

Size

Figure 3.88 shows the length-weight relationship for 36 female perlon sharks. The largest female examined measured 1185 mm TL. The maximum reported size for this species is 1370 mm TL (Garrick and Paul 1971).

The size at birth is approximately 242 mm TL (Tanaka and Mizue 1977).

Sixgill Shark

Males

Males mature at a minimum size of 3140 mm TL. Adult males of this species were rare, only three being recorded during the study and measuring 3140 mm, 3260 mm and 3330 mm TL. Maturation was confirmed in these specimens by calcification of the terminal cartilage elements. Maturity in the 3260 mm TL specimen was based on a pair of claspers examined at the USNM (no. 206071). Another pair of claspers from a 3080 mm TL specimen (USNM 220178) lacked calcification of the terminal cartilage elements as did two additional specimens measuring 2808 mm and 2805 mm TL. The latter three specimens were all considered to be adolescent. No abrupt increase in the clasper length (Figure 3.89) or testes length (Figure 3.90) was observed between specimens 2800 mm and 3200 mm TL. However, testes weight increased abruptly between 2400 mm and 3330 mm TL (Figure 3.91). Viable sperm were found in the 3140 mm and 3330 mm TL specimens, but was not present in a 2400 mm TL specimen; the 2808 mm and 2805 mm TL individuals were both preserved museum specimens which could not be examined for the presence of sperm.

Size

The length-weight relationship was plotted for 48 male sixgill sharks measuring between 675 mm and 3330 mm TL (Figure 3.92). The 3330 mm TL specimen is the largest adult male sixgill on record.

Females

The largest specimen examined (3195 mm TL) had an enlarged epigonal organ and ovaries which were undifferentiated. The shell gland of this specimen was undeveloped. Two additional specimens from the Azores (4050 mm and 4220 mm TL) were observed to have maturing ova ca. 50 mm in diameter (J. Reece, pers. comm.). The weight of these two specimens (350.5 kg and 466 kg, respectively) were considerably less than a pregnant female (4210 mm TL, 555 kg) with term embryos. The ratio of male to female embryos for a 4210 mm TL female was 1:1 with a size frequency of 680 mm to 736 mm TL for males and 680 mm to 722 mm TL for females. Newborn sixgills were caught off Luderitz, Namibia, at approximately the same location over three consecutive summer seasons which indicates that this area between 23° 11'S, 13° 17'E and 27° 04'S, 14° 28'E may be a pupping ground.

Size

A length-weight curve for 72 females ranging in size from 610 mm to 4250 mm TL increased rapidly above 3500 m TL (Figure 3.92).

The size at birth is between 610 mm and 736 mm TL.

Bigeyed Sixgill Shark

Males

Males were immature at 845 mm TL, but mature at 1440 mm TL. No specimens between these lengths were examined to accurately estimate male maturity. Clasper length of specimens between 845 mm and 1440 mm TL increases rapidly (Figure 3.93). The claspers of all specimens › 1440 mm TL had calcified terminal cartilage elements. Insufficient data on other indices of maturity were collected.

Size

The maximum observed size for a male was 1570 mm TL.

Females

Inadequate data were gathered on females to accurately determine the size at maturity.

Size

The maximum recorded size for a female was 1780 mm TL (Springer & Waller 1969). Size at birth is approximately 400 mm TL.

Sevengill Shark

Male Maturity

Sexing of juvenile male sevengills was occasionally difficult to determine, without close examination of the scroll. The claspers remain well hidden within this scroll until late adolescence, when they lengthen. Even at full maturity the claspers are still relatively well hidden within the scroll. As the pelvic fins elongate, however, to accommodate the claspers, the distal most 4 to 5 fin radials also lengthen to form the scroll. A sharp increase in the ratio of clasper length to TL occurred between 1500 mm and 1600 mm TL (Figure 3.95). This rapid change in clasper length continued up to approximately 1800 mm TL. The change in clasper length to TL beyond 1800 mm TL appeared to reflect the animal's natural growth. With maturity, the claspers lengthen and become stiff and hard. Those of juveniles, however, are short, soft and flexible. The most noticeable change in clasper morphology was the development of the clasper sac which commenced between 1300 mm and 1400 mm TL, and appeared to be fully functional by at least 1600 mm TL. The clasper sac, which can inflate, appears to function in a manner analogous to the siphon sac of other elasmobranchs. Male sevengills measuring over 1550 mm TL with calcified terminal cartilage elements were considered adult. Calcification of these elements was always the last criterion to be met for maturity. The smallest male with calcified terminal cartilage elements measured 1513 mm TL, while the largest adolescent lacking calcification measured 1710 mm TL.

An increase in testes weight occurs between 1550 mm and 1700 mm TL (Figure 3.96). This increase was found to be extremely variable. Testes length showed an inflection at about 1650 mm TL (Figure 3.97). The epididymis undergoes a gradual transformation from juveniles to adults. The epididymis in juveniles was, for the most part, straight and narrow. As the male enters adolescence the anterior portion becomes loosely coiled. This coiling slowly extends down the entire length of the epididymis during adolescence. Specimens in late adolescence (usually over 1500 mm TL), were found to have a highly convoluted epididymis which contained viable sperm. In addition, the sperm sac of many late adolescent sevengills was found to be expanded and contain large amounts of viable sperm which could be expelled through the genital papilla.

Seasonality

Mean monthly testes weight from adult males taken in southern Africa indicates a sharp increase from August to December (Figure 3.98). Mean monthly testes weight, ranged from 101 gm in April to 293 gm in December. The monthly range in testes weight was extremely broad, with considerable overlap between these weights.

Size

Figure 3.99 gives the length-weight relationship for 352 males ranging from 391 mm to 2430 mm TL. The heaviest male weighed 79.5 kg and measured 2420 mm TL. The maximum TL recorded for a male was 2480 mm TL, but no weight was taken for this individual.

Female Maturity

Females matured at a size in excess of 2180 mm TL. Two distinct size classes of ovarian eggs containing yolk were observed in specimens between 2180 mm and 2438 mm TL (Figure 3.100). The largest egg diameter increased noticeably in 14 of 31 specimens examined measuring between 2180 mm and 2438 mm TL. The largest egg diameter range was 32 to 77 mm for one group, and 8 mm to 25 mm in the other. All specimens were collected during the late summer and autumn months.

Both ovaries appeared to be functional in all maturing and adult females. The number of large eggs (› 40 mm in diameter) per ovary varied with either the right or left ovary containing slightly more eggs than the other. Individuals differed as to which ovary contained more eggs. The right ovary contained 7 to 17 more eggs in 3 specimens, while the left ovary had 2 to 26 more eggs in 15 specimens.

The total number of eggs from both ovaries (› 20 mm in diameter) decreased in relation to the largest egg diameter (Figure 3.101). This decrease appeared to stabilize once the largest egg diameter reached over 40 mm. Most ovaries with a largest egg diameter of only 20 mm contained large numbers of very small ova. The exact number was difficult to determine and only those over 10 mm diameter were counted.

Fecundity estimates were based on the number of large ovarian eggs (› 40 in diameter) present in 19 females. The number of maturing eggs ranged from 67 to 104. No developing embryos or fertilized eggs were observed.

The shell gland remains undeveloped, and measuring less than 10 mm in width until the onset of maturity (Figure 3.102). At approximately 2200 mm TL the shell gland rapidly increases its width to over 25 mm wide. This rapid widening of the shell gland occurred in 10 of the 20 specimens between 2200 mm and 2438 mm TL.

The rapid change in shell gland width occurred in those specimens with enlarged eggs › 32 mm in diameter (Figure 3.103). This relationship was observed in specimens over 2200 mm TL. The largest shell gland width in relation to the largest egg diameter was variable in those individuals with eggs › 32 mm in diameter.

The uteri for specimens between 2200 mm and 2438 mm TL were straight and narrow. The uteri of individuals over 2500 mm TL hung loosely and were pendulous. In those specimens with enlarged ova (› 40 mm diameter), and broad shell glands a series of longitudinal folds were observed to extend the length of the uteri. The precise function of these longitudinal folds is uncertain, but they may increase the surface area of the uterus as eggs are ovulated. Longitudinal folds were only observed in late maturing animals.

Copulation

One instance of copulation was observed in this species (Mr. J.P. Walters, Walvis Bay, Namibia, pers. comm.). It was about midday and the sky was clear. Neither animal showed any activity or interest in the ski boat as it circled. The swimming pair were observed about 200 m from shore at the surface in water ca. 3 m deep. The pair swam slowly at the surface, making very little water movement. The male's jaws were clamped tightly to the female's flank, just behind the pectoral fin. The body, from head to vent, of each shark was side by side with the male's slowly sagging down below the female. The posterior half of the male was wrapped under the female. It was impossible to determine whether one or both claspers were inserted. The TL of these animals were estimated to be about 1800 mm TL for the male and ca. 2600 mm TL for the female.

Scarring

Biting wounds observed in males and females were determined to have come from three sources; bites inflicted by other sharks, aggression bites inflicted by conspecifics, and mating bites. The first two types will be dealt with in the feeding section (3.7).

Male courtship bites were identified as such by the location of the wound and the time of year. Male scarring consisted of slashes and tooth cuts between the dorsal and caudal fins (Figure 3.104). Longitudinal scratches anterior to the dorsal fin were observed in some specimens. All wounds were superficial and had no apparent adverse effects on these individuals. These bite marks were observed during the spring and summer months in Humboldt and San Francisco bays.

Female wounds occurred in three main locations; the pectoral fins, along the body flanks, and around the pelvic fins. The types of bite marks appeared to be either semi-circular jaw impressions or tooth punctures (Figure 3.104). Both types of wounds appeared to be deeper and more severe than those inflicted on males. Specimens with fresh wounds were observed during the late spring and early summer months. Large females (› 2500 mm TL) were often heavily scarred, showing evidence of healed wounds. These bite marks were observed in adult and late adolescent specimens.

Seasonality

Adults and juveniles were the two dominant age classes observed in Humboldt and San Francisco bays during the spring and summer (Table 3.36). Adolescent males and females were uncommon in these bays. After June, juveniles were the dominant class to occur at least through September. A decrease in juvenile abundance usually occurred after the first heavy autumnal rains, as the runoff reduced the salinity in these bays.

Size

Figure 3.105 gives the length-weight relationship for 324 females ranging between 337 and 2960 mm TL. The 2960 mm TL female is the maximum known size for this species. The smallest free swimming juvenile measured 337 mm TL, while a term embryo measured 450 mm TL; size at birth is assumed to be within this range.

Food Habits and Feeding Behavior

Frilled Shark

Examination of fresh and preserved material yielded some information on the food habits of this species. A 916 mm TL specimen from Namibia contained a partially digested cat shark, Apristurus sp., measuring approximately 265 mm from the cranial base to the caudal region. Another Namibian specimen, measuring 1025 mm TL, contained skeletal remains of a digested cartilaginous fish, possibly a member of the Scyliorhinidae. Finally, the stomach of a North Atlantic specimen contained the remains of an unidentified cartilaginous fish species.

Examination of fresh specimens revealed that the jaws and buccal cavity are highly distensible, suggesting that the frilled shark is capable of ingesting quite large prey. The inwardly projecting, needle-sharp teeth further indicate that this is a highly specialized feeder. In addition, the abdomen is elongate and the stomach distensible, further indicating that this predator is capable of ingesting fairly large prey.

Perlon Shark

Cephalopods and teleost fishes were the only prey items recorded for eight perlon sharks from southern Africa (Figure 3.106). Due to the advanced state of digestion, identifications could not be made for any of the prey items. The diet of 28 Taiwanese specimens consisted primarily of teleosts with crustaceans and cephalopods being of secondary importance (Figure 3.107). Thirteen prey species were identified including seven teleost, five shrimp and one crab species (Table 3.37). The main fish species consumed were *Trichiurus lepturus*, *Trachurus japonicus* and lanternfishes (Myctophidae), all of which are known to occupy an epibenthic to mesopelagic habitat. Of the crustacean species identified, all were either epibenthic or mesopelagic species.

Sixgill Shark

Thirty-six sixgill sharks containing prey items were captured and examined in southern Africa, and were found to have fed mainly on teleosts and cephalopods (Figure 3.108). Secondary prey items included cetaceans and pinnipeds, with cartilaginous fishes and invertebrates of minor importance. A total of 15 prey species were identified with teleosts representing 10 species, cephalopods at least 2 species, and one species each of gastropod, crustacean, cetacean and pinniped (Table 3.38). The primary species consumed were *Merluccius* sp. and *Toderodes angolensis*. The gut contents of 19 sixgills from California were examined and in contrast to southern African sharks, were found to feed primarily on cartilaginous and teleostean fishes (Figure 3.109). Cartilaginous fishes were the most important prey group with an I.R.I. of 2896 followed by teleost fishes with 2714 (Figure 3.106). Cetaceans and agnathans were of minor importance, while pinnipeds were found on a single occasion. A total of nine prey species were recorded (Table 3.39) with *Squalus acanthias* observed on three occasions. Elsewhere, a sixgill from Chile and measuring 930 mm TL, contained two *Octopus* sp. and a 4220 mm TL female specimen from the Azores had the remains of a 25 kg swordfish, *Xiphias gladius*.

A breakdown of the food habits by size classes revealed dietary changes in this species which appeared to be associated with growth. Newborn and juveniles ranging from 681 mm to 970 mm TL preyed exclusively upon teleosts and cephalopods (Figure 3.110). Those specimens measuring between 1005 and 1470 mm TL primarily consumed teleosts and chondrichthyians, and secondarily preyed upon cephalopods (Figure 3.111). Teleost and cephalopods were the main prey groups for specimens between 1588 mm to 1946 mm TL with cetaceans being of secondary importance (Figure 3.112). The largest size group for which data were available (2000 mm to 3195 mm TL) revealed that teleosts and cetaceans were the primary prey groups (Figure 3.113), while chondrichthyians and cephalopods were of secondary importance. Inadequate data were available for larger size groups, but from the information available, it appears that the size and type of prey increases with growth. Cetaceans become increasingly important and larger, while more active teleosts such as swordfish were captured by large specimens (> 4000 mm TL). One additional record of sixgill predation on cetaceans comes from a photograph of a bottlenose dolphin, <u>Tursiops truncatus</u>, with a sixgill bite taken out of it. The bite radius suggested the shark was > 3 m TL. Predation on conspecifics was not observed in any size class.

Predator size in relation to prey size may play an important role in determining hunting success. At least two Atlantic torpedo rays (<u>Torpedo nobiliana</u>) with sixgill shark scars were examined. One torpedo ray, with a DW of 315 mm had a bite radius of 101 mm from a sixgill estimated to be 1000 mm TL (Figure 3.114). This particular species of torpedo ray is an active epibenthic predator and was most likely attacked while swimming off the bottom. The attacking shark had apparently seized the ray directly on its electric organs and had received a shock. The size relationship between predator and prey suggests that the torpedo ray was able to fend off the shark's attack. A larger sixgill may have been more successful. The exhibited attack pattern was typical of other hexanchid attacks on batoids, with the shark first disabling the ray with a bite through the pectoral disc and then consuming it.

Bigeyed Sixgill Shark

Two Taiwanese specimens were found to contain prey items. A 845 mm TL male contained the remains of an unidentified teleost, while a 482 mm TL male contained a crustacean, a ribbon fish, *Trichiurus lepturus*, and some algae. One potential prey species that can be added to this list is a new species of torpedo ray, *Benthobatis* sp., which was collected from Tung-Kang, Taiwan in 1988. This species is currently being described (Compagno and Ebert, in prep.). The specimen had a bite wound on its left dorsal margin (Figure 3.115). A "V-shaped" bite pattern was observed on the dorsum while the bite pattern on the ventral surface was rounded. The shape and pattern of the bite indicated that the attack had been made by a juvenile bigeyed sixgill of approximately 480 mm TL. The predation bout was unsuccessful, possibly prevented by an electrical discharge from the *Benthobatis*. Judging by the extent of the wound, the bigeyed sixgill was able to secure a fairly good grip on the *Benthobatis* before releasing it.

This predation bout reveals some insight into predator-prey interactions between these species. *Benthobatis* is a benthic species that probably remains buried in the sediment for most of the day, as do many of its family, the Narcinidae. This observation suggests that either the shark was able to detect the prey hidden in the substrate and seize it, or that the *Benthobatis* spends at least some of its time swimming off the bottom. *Benthobatis* and other narcinids have very small mouths, which they use to prey upon benthic infaunal organisms. Indeed, the specimen from Taiwan contained parts of several polychaete worms which it probably caught using its distensible jaw apparatus. A larger shark may have been successful in this predation bout.

Sevengill Shark

A total of 443 sevengills stomachs were examined with 241 (54%) containing prey items. The high number of sevengills with empty stomachs is probably due in large part to these sharks everting their stomachs when hooked, thus expelling their contents. On numerous occasions a hooked shark was brought up the surface with its stomach hanging out of its mouth. With such animals it was not possible to determine conclusively whether any stomach contents were present, since this species is known to evert its stomach even when empty.

Prey Preference

Prey preference within four sevengill size classes showed a distinct increase in chondrichthyian and pinniped prey with growth. Those specimens measuring less than 999 mm TL appear to feed mainly on teleosts, though the sample size was small (Figure 3.116). The 1000 mm to 1499 mm TL size class consumed slightly more teleosts than chondrichthyians (Figure 3.117). Chondrichthyians were the most important prey group for specimens over 1500 mm TL, with pinnipeds becoming an increasingly important prey group (Figure 3.118). Those specimens measuring over 2000 mm TL fed primarily on chondrichthyians, with pinnipeds replacing teleosts as the second most important prey group (Figure 3.119).

Geographical Variation

Analysis of the important prey groups and species from California, Namibia, and South Africa revealed distinct differences between these regions.

California. Specimens were collected primarily from Humboldt Bay and San Francisco Bay, with little representation from open-coast sites in California. Only 15 specimens were recorded from the open coast during this study. Unfortunately, those specimens had been eviscerated by fishermen prior to examination and no stomach contents were available.

A total of 175 stomachs were examined with 55 (43 %) containing prey items. Chondrichthyians and teleosts were the predominant prey groups (Figure 3.120), with the other prey groups being of minor importance. Sixteen prey species were identified from Californian waters. Chondrichthyians were the most common prey items and were identified to species level (Table 3.40). The bat ray, Myliobatis californica, and brown smoothhound shark, Mustelus henlei, were the highest in percent number and occurrence of any individual prey. Bat rays were slightly higher in percent weight than brown smoothhound sharks. The identified teleost prey species occupied a wide range of habitats and ranged from fast swimming pelagic salmon, Oncorhynchus sp., coastal nearshore and bay species like the perch, Phanerodon furcatus, to small bottom dwelling species, e.g. members of the Cottidae. The single marine mammal species recorded, the harbor seal, Phoca vitulina, was ranked fourth in importance. When compared as a prey group to the teleosts and chondrichthyians, pinnipeds were of minor dietary importance. All sevengills examined with harbor seal remains were large individuals (over 268 cm TL) and were recorded from Humboldt Bay. Invertebrates were of minor importance in the diet of sevengills from California. The only two invertebrate species observed were the dungeness crab, Cancer magister, and giant Pacific octopus, Octopus dofleini.

Southern Africa

The stomach contents of 139 South African and 129 Namibian sevengills were examined. Of the stomachs examined, 98 (71 %) from South Africa, and 88 (68 %) from Namibia contained prey items. Samples from South Africa were taken between East London and St. Helena Bay. Sampling along the coastline of Namibia was limited to Luderitz Lagoon and waters north of Swakopmund. Sampling was restricted due to the diamond mining industry which controls much of the Namibian coast line and prohibits access, and because of limited ship time for collecting material.

South Africa. Chondrichthyians were the most predominant food item found in sharks from South Africa (Figure 3.121). Chondrichthyians represented 49 % of the prey species recorded and made up 51.2 % of the total prey weight. Chondrichthyian remains occurred in 50 % of the stomachs examined. Of the 40 prey items observed 18 were chondrichthyian (Table 3.41). The most common prey species were an endemic group of catsharks, genus Poroderma, and the wide ranging hound shark, Mustelus mustelus. The striped catshark, P. africanum and the leopard catshark, P. pantherinum, are common coastal temperate water species which range from the Eastern Cape Province to Saldanha Bay on the west coast. It is interesting to note that, west of Cape Agulhas, P.

africanum was the more common prey species, while east of Cape Agulhas, P. pantherinum was the more abundant prey item. Teleosts were the second most important group off South Africa. Numerically, they contributed 31.5 % of the total food ingested and occurred in 28.6 % of the stomachs examined. No single teleost species as consumed in abundance. Marine mammals were of minor importance in the diet of South African sevengills, with the Cape fur seal, Arctocephalus pusillus pusillus, observed seven times and cetacean remains being recorded on seven occasions. The only cetacean remains identified to species were of a juvenile dusky dolphin, Lagenorhynchus obscurus, estimated to have been ca. 800 mm TL. This dolphin had been eaten in February, which is the calving season for these dolphins. Invertebrates and algae were of minor importance and contributed very little to any of the individual indices. The algal remains were most likely ingested along with the Poroderma egg cases since this species tends to lay its eggs on algae.

Namibia. Cape fur seal, A. pusillus, was the predominant prey species found in sevengills from this area (Figure 3.122). This prey species contributed the highest percent number, weight, and frequency of occurrence of any prey species recorded (Table 3.42). Cetaceans were the only other marine mammal species found to occur in the diet of Namibian sevengills. Chondrichthyians and teleosts were important secondary prey groups; teleosts had a slightly higher I.R.I. to chondrichthyians (1657.3 to 1610.5). Ten chondrichthyians and eight teleosts made up 18 of the 26 prey species recorded. The hound shark, Mustelus mustelus and conspecifics were the two most frequently consumed chondrichthyian species. Sevengills were found to have consumed conspecifics on at least four occasions. Sea barbel, Galeichthys sp., and maasbanker, Trachurus trachurus, were the two most frequently consumed teleosts. Invertebrates and algae were of minor importance. Invertebrates were found to occur on eight occasions, but comprised very little in percent number or weight. Algae was observed in a trace amount on one occasion along with shy shark, Haploblepharus pictus, egg cases.

Subdivision of the Namibia data into two regions, the

Luderitz area and the area north of Walvis Bay to mile marker 72 reveals that seal predation was much higher in Luderitz (Figure 3.123). This illustrates the versatility of this predator at optimizing the available food resources. The majority of pinniped colonies are located in the general vicinity of Luderitz. In Swakopmund, no pinniped colonies are located in close proximity to areas sampled.

Analysis of individual sampling areas reveals a distinct difference in the predominant prey groups. Chondrichthyians and teleosts were the most important prey groups for the California sample, while chondrichthyians and pinnipeds were respectively the most important prey groups for South Africa and Namibia (Figures 3.120, 3.121 & 3.122). In all areas, invertebrates and algae were of minor dietary importance.

Hunting Behavior

Based on observations of sevengill feeding behavior, at least four distinct foraging strategies were identified. Each particular strategy, or a combination of one or more, were employed depending on the size and type of prey being subdued. Further studies may reveal additional feeding strategies.

Burst Speed (Figure 3.124). Sevengills typically swim with a very slow, sinuous, almost lethargic motion. This swimming behavior, which has been observed both **in situ** and in aquaria, gives an illusion of a sluggish animal. These sharks have often been seen swimming slowly and paying very little attention to the numerous potential prey species around them. Then, without any indication, one would attack a particular individual prey item. This pattern was observed when sevengills attacked leopard sharks, T. semifasciata, in Humboldt Bay, California. These attacks were very purposeful, with the prey having no time to take flight.

In one observed predatory bout, a leopard shark was swimming near a mud bank in water approximately 30 to 40 cm depth. The attack was initiated by a sevengill from a distance of 30 m. The predator sevengill, measuring ca. 2.7 m TL, 'streaked' past several other leopard sharks at its intended victim as the attack unfolded. By the time the prey shark sensed the attack and began to take flight, it had been seized with a powerful and fatal bite. The force of the attack caused the predator to beach itself on the shallow mud flats with the prey dangling out of its mouth. The sevengill quite agilely managed to wriggle itself back into the water and swim off.

The prey appeared to have been killed by the initial bite which severed the spinal cord. An interesting observation from this attack was that the predator had passed several other individuals of the same species, but seemed to have 'targeted' one in particular. Nothing in the prey's behavior appeared to differ from that of any other leopard sharks swimming in the area.

Ambush Strategy (Figure 3.125). Sevengills seem to be most active nocturnally and on days when the sky is overcast. On clear sunny and warm days, they tend to stay in the deeper water of bays and lagoons. It appears that foraging under conditions of poor lighting favors these predators. Perhaps many of the fast swimming prey species recorded in their diets were more vulnerable in low visibility water. In Humboldt Bay, these sharks can be observed foraging on shallow water mud flats during spring tides in the early morning hours before sunrise. Usually after sunrise, they move into the deeper channels of the Bay. Sharks captured during this time typically had a full stomach. In Luderitz Lagoon, Namibia, extensive shore fishing during daylight hours on calm days shows very little or no activity. Yet, after sunset, these sharks became quite active and were observed to approach the shoreline. Sevengills were caught during daylight hours by fishing in the deeper channels from a boat where the sharks could be baited to the surface. Shark fishermen in St. Helena Bay on the west coast of South Africa also noticed an increase in sevengill activity after sunset or on overcast days.

Besides being nocturnal predators, sevengills seem to prefer water that is very discolored or turbid. Along the South African coast-line fishermen tend to concentrate for these sharks in areas where "brown water" is produced by a strong Southeast wind. The "brown water" is caused either from an upwelling bloom of phytoplankton (predominantly Annulus birostratus) in southern Africa, or by sediment disturbance such as that caused by river runoff, tidal flux or wave action. Where patches of brown water occur, sharks seem to concentrate in these areas, and feeding activity is high. On several occasions, when the writer was attending beach fishing competitions, a change in the wind direction brought discolored water in nearshore. When this discolored water was within casting distance anglers would concentrate in these spots and catch sevengills.

On one occasion, at Cape Agulhas, an onshore wind blowing at ca. 20 knots, pushed a patch of "brown water", in this case from a plankton bloom, nearshore into the surf. Over a period of 90 minutes, 37 adult male sevengills were caught along a 50 m stretch of beach. Sixty minutes after the first shark was caught, the wind changed to a N.W. direction and blew off shore. After a further 30 minutes the brown water had pushed offshore and the sharks stopped biting.

Bays are typically areas in which river runoff and mixing of water masses during spring tides causes the water to become very turbid. During a spring tide, bays become extremely turbid and visibility is poor. In San Francisco and Humboldt bays, when the tide goes 'slack' during a spring tide series, sevengills becomes quite active. This 'slack' water, with suspended particulate matter in the water column, may decrease visibility such that an acute hunter would be at an advantage. Field observations on sevengills suggest that they are acute hunters in turbid conditions, which probably explains their increased hunting activity and success.

Although this species may not necessarily aggregate every time brown water occurs, this observation suggests that they favor such conditions for hunting.

Stealth (Figure 3.126). There is no doubt that sevengills are able to take fairly swift swimming prey, but there is considerable speculation as to how these reputedly clumsy, slow swimming sharks manage to do so. An obvious way would be to scavenge fish that had been injured or lost to an angler. However, the frequency with which fast swimming prey species were encountered seems too high to be accounted for by scavenging alone. Observations in aquaria and in the field reveal that these sharks may catch fast swimming prey by gliding almost motionlessly and undetected to investigate a potential food source. Observations of this behavior from vantage points both above and below the water in captivity and in the field reveal that these sharks can propel themselves by slight undulatory motions of the tail fin. By positioning their large pectoral fins slightly downwards, these sharks can navigate with very little obvious body movement. Such behavior would be advantageous for predators moving within striking distance of unsuspecting prey. Once within striking distance, the predator could make a quick dash and overtake the prey before it had a chance to take flight. A young Cape fur seal, A. pusillus, was attacked in Luderitz Lagoon by a large (ca. 2.4 m TL) sevengill which had glided up from beneath and seized it. The young seal did not appear to have sensed the shark's presence until it had been grabbed (D. van Zyl, fisherman, pers. comm.). The seal's inability to detect the shark's presence reflects an effective hunting strategy.

Social Facilitation (Figure 3.127). Sevengill sharks are both solitary and social hunters. In solitude, they may search for small to medium sized prey, or in a pack, hunt larger prey. Thus, they able exploit a wider spectrum of prey resources. The way in which this species groups to form a hunting pack and what, if any, stimuli initiate the behavior, are unknown. These sharks hunt socially, for example, when preying upon adult Cape fur seals which form part of their stomach contents along with juvenile seals. These seals are large animals which can weigh up to 300 kg. It is unlikely that an individual sevengill would attempt to or could succeed in subduing a large seal. Co-operative feeding behavior however, is more likely to succeed, and has in fact, been observed (Pedro, fisherman, St. Helena Bay, South Africa, pers. comm.; D. van Zyl, pers. comm.). A typical attack pattern on a seal begins when a group of sharks form a loose circle around it. Attempts by the seal to escape are prevented by the pack which gradually tightens its circle around the prey. Eventually one or more sharks bite the seal, which stimulates the rest of the pack to converge on it. Once the attack has been initiated, the rest of the group quickly join in to get their share of food. Unlike some predators, for example a white shark or a lion, which can subdue large prey items, such predation by sevengills may require a cooperative effort. Other large prey that may have been taken in this manner include large individuals of the bat ray, M. californica, larger spotted gully sharks, Triakis megalopterus, small cetaceans and conspecifics. These attacks usually take place at dusk or on overcast days when the water is dark.

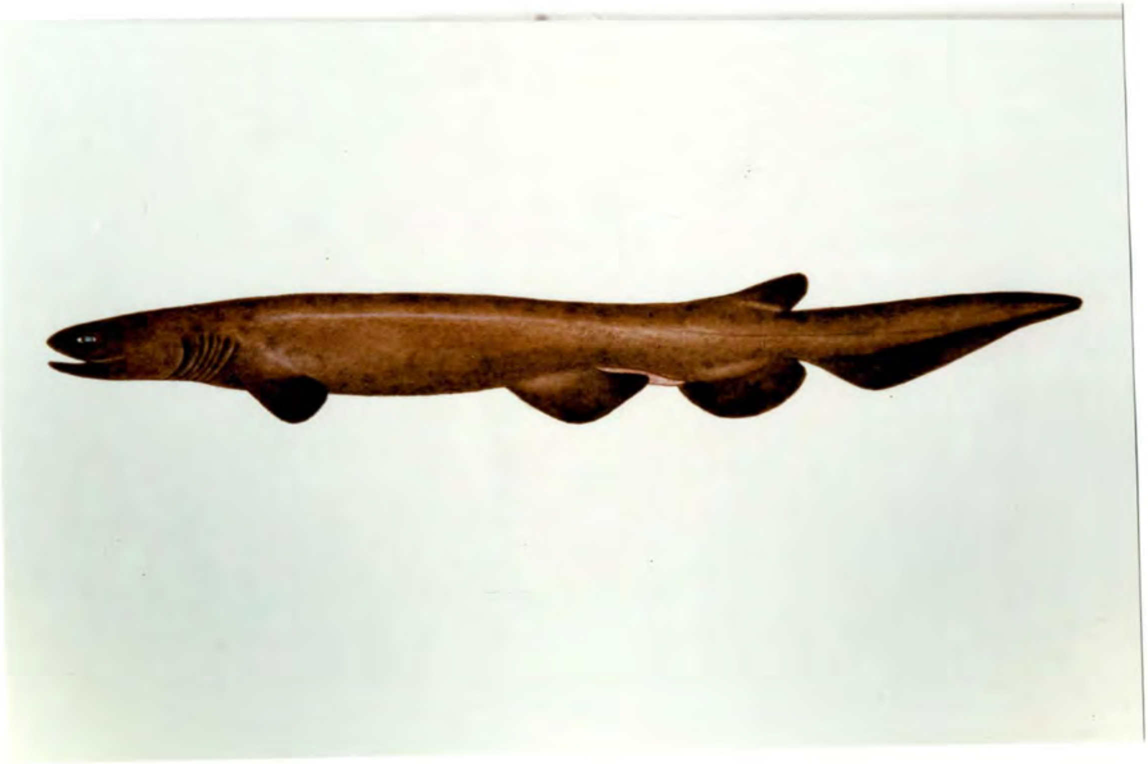


Figure 3.1 Chlamydoselachus anguineus Garman

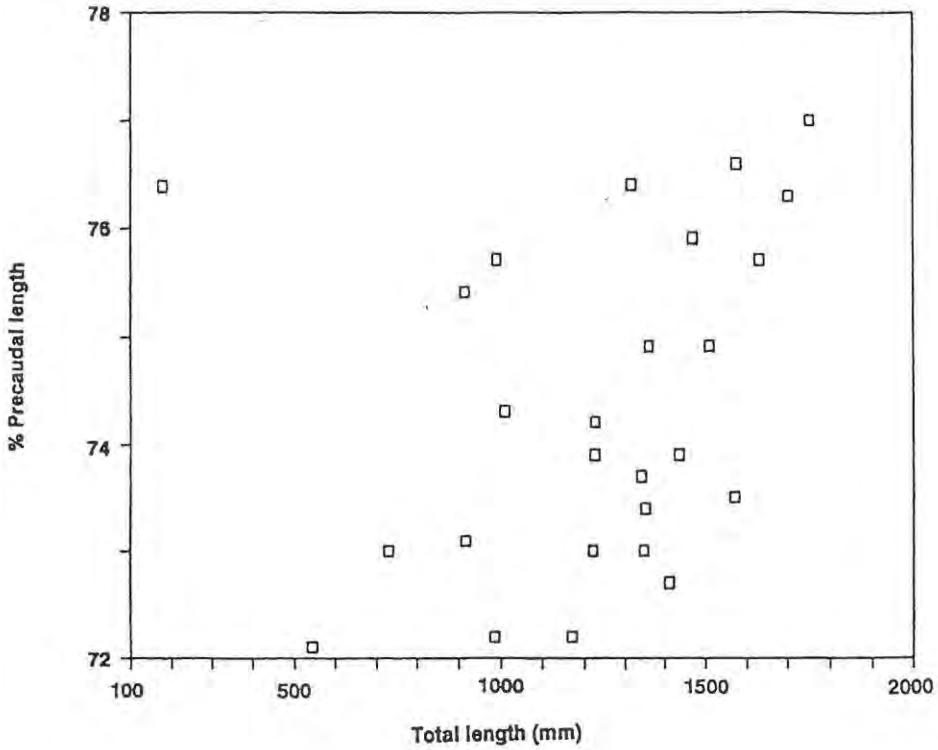


Figure 3.2a - Proportional lengths of snout tip to precaudal length in <u>Chlamydoselachus</u> <u>anguineus</u>. Y= 73 + 0.001x, r^2= 0.8, n= 26.

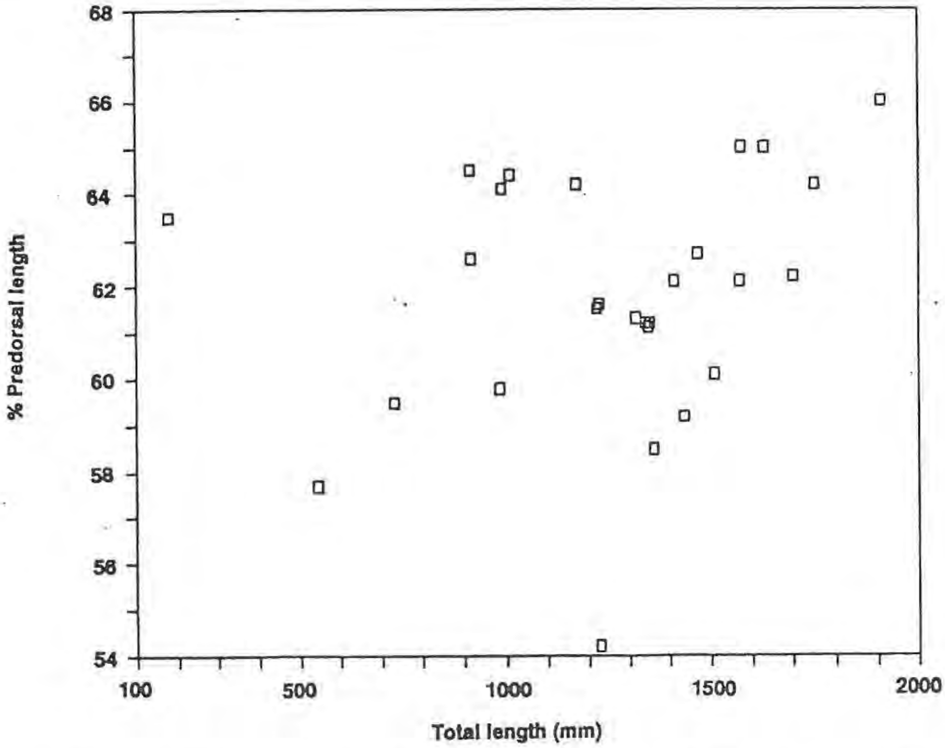


Figure 3.2b - Proportional lengths of snout tip to dorsal fin origin in <u>Chlamydoselachus</u> <u>anguineus</u>. Y= 60 + 0.001x, r^2= 0.1, n= 27.

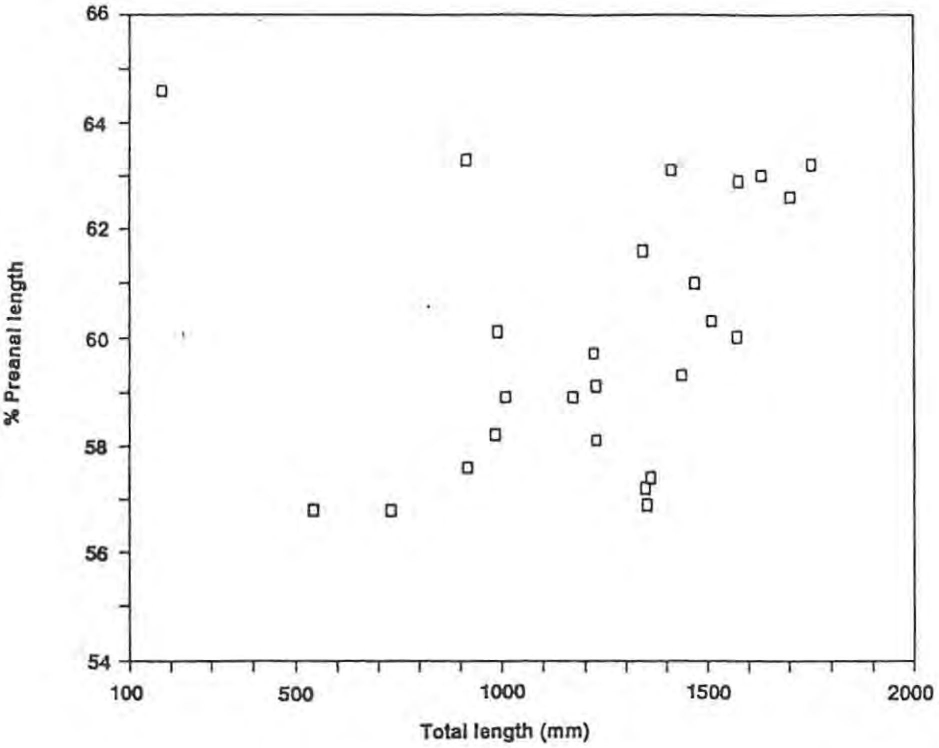


Figure 3.2c - Proportional lengths of snout tip to anal fin origin in Chlamydoselachus anguineus. Y= 58 + 0.001x, r^2= 0.04, n= 25.

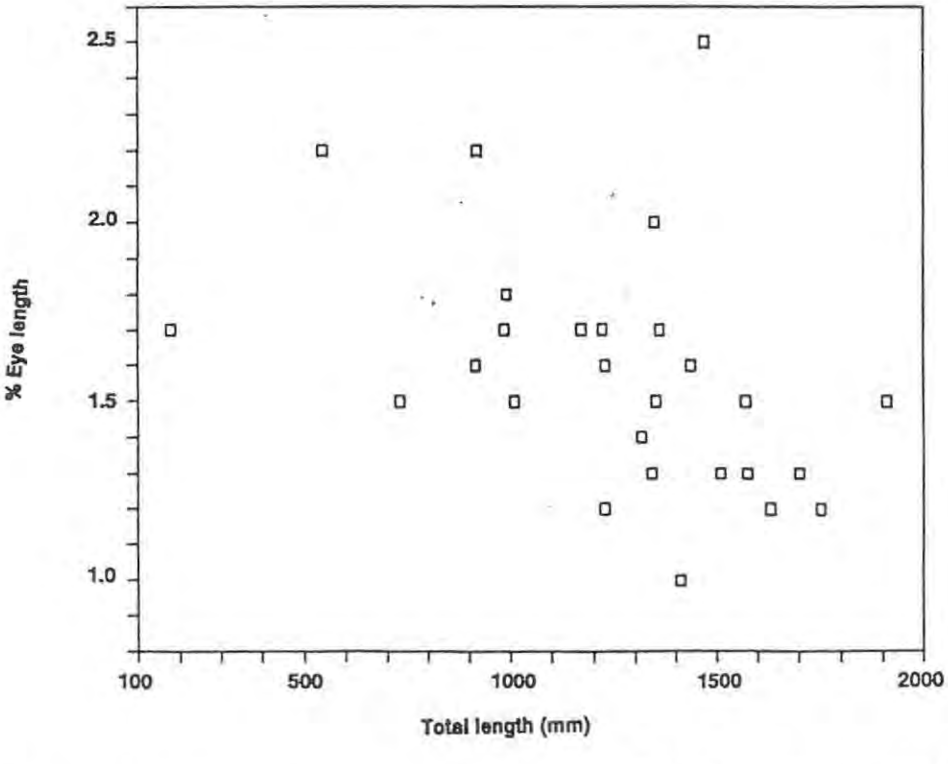


Figure 3.3 - Proportional lengths of snout tip to eye length in Chlamydoselachus anguineus. Y= 2 + 0.003x, r^2= 0.2, n= 27.

Figure 3.4 *Chlamydoselachus anguineus* teeth

Figure 3.5 Lateral trunk denticles of *Chlamydoselachus anguineus*

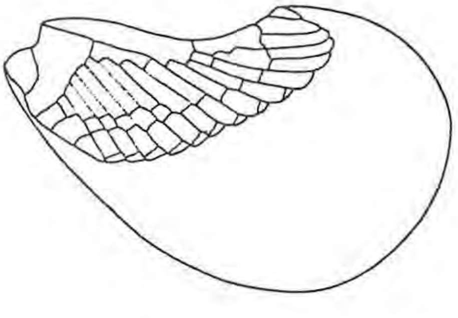


Figure 3.6 Pectoral fin skeleton of *Chlamydoselachus anguineus*

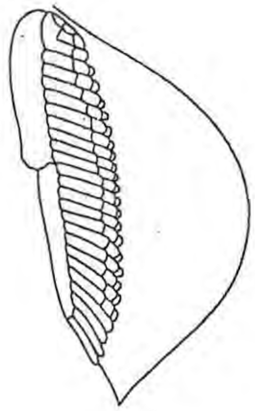


Figure 3.7 Pelvic fin skeleton of female *Chlamydoselachus anguineus*

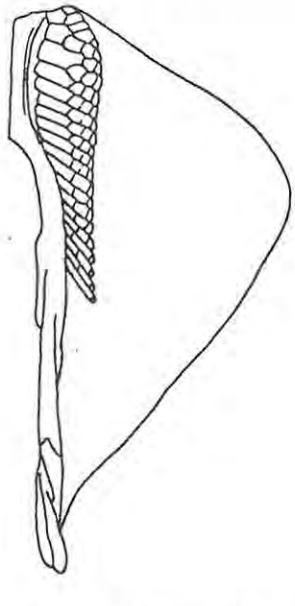


Figure 3.8 Pelvic fin and clasper skeleton of *Chlamydoselachus anguineus*

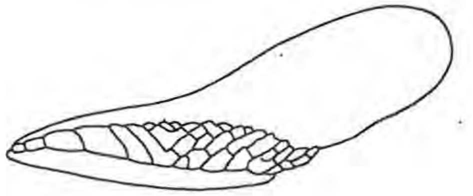


Figure 3.9 Dorsal fin skeleton of *Chlamydoselachus anguineus*

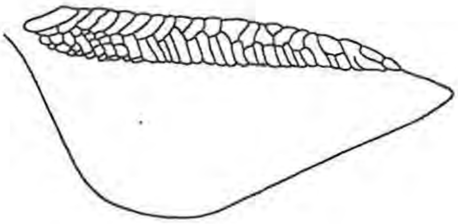


Figure 3.10 Anal fin skeleton of *Chlamydoselachus anguineus*

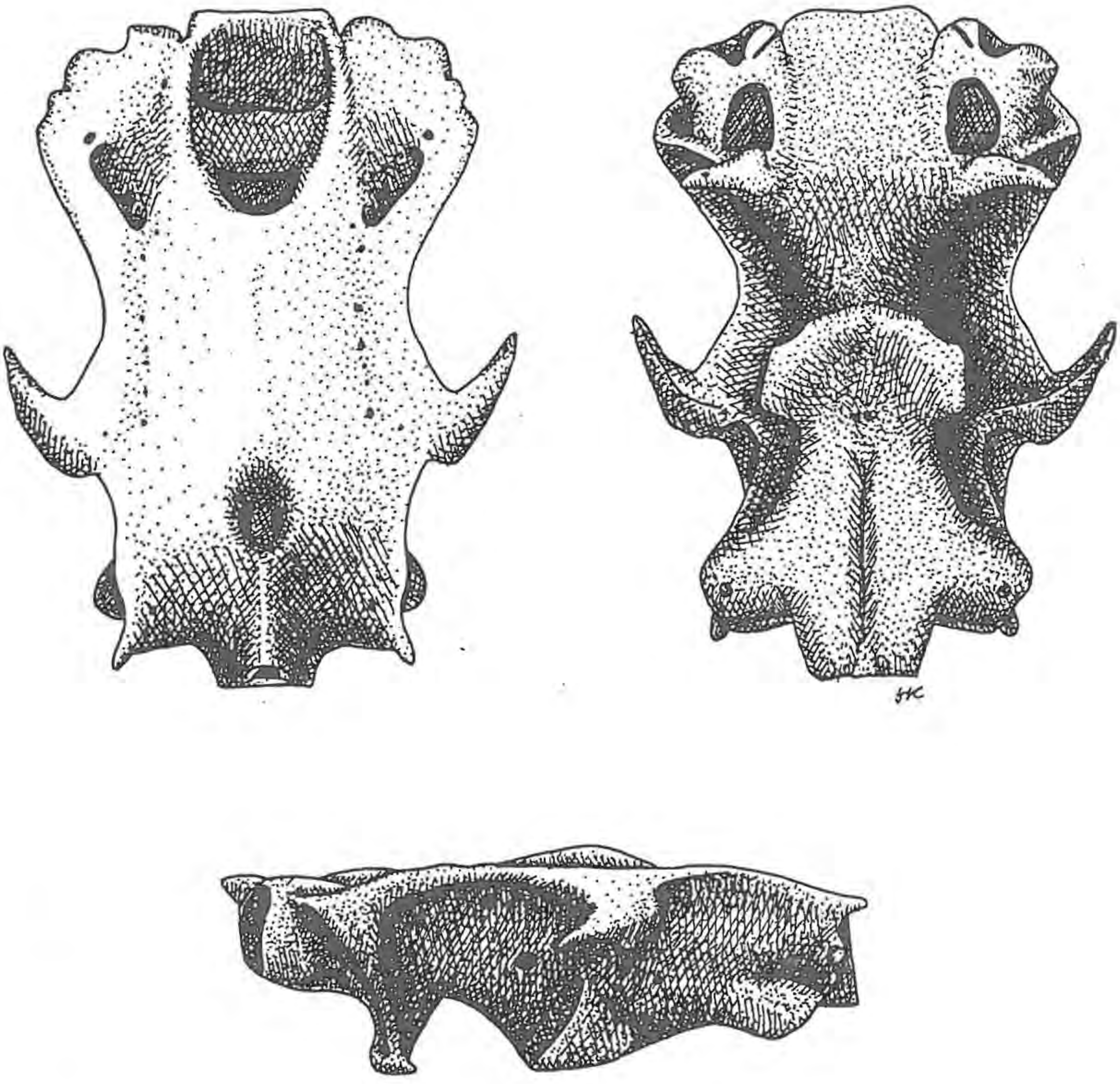


Figure 3.11 Cranium of Chlamydoselachus anguineus

Figure 3.12 Color pattern of <u>Chlamydoselachus</u> <u>anguineus</u>

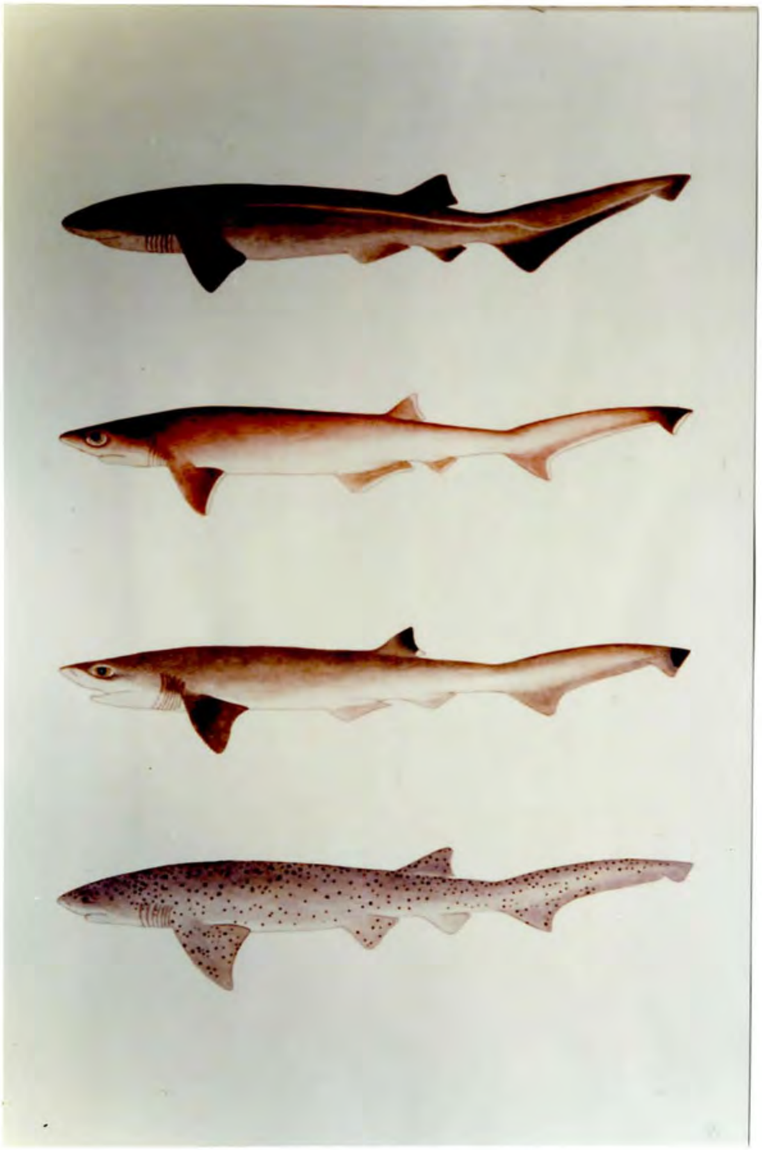


Figure 3.13 The Family Hexanchidae

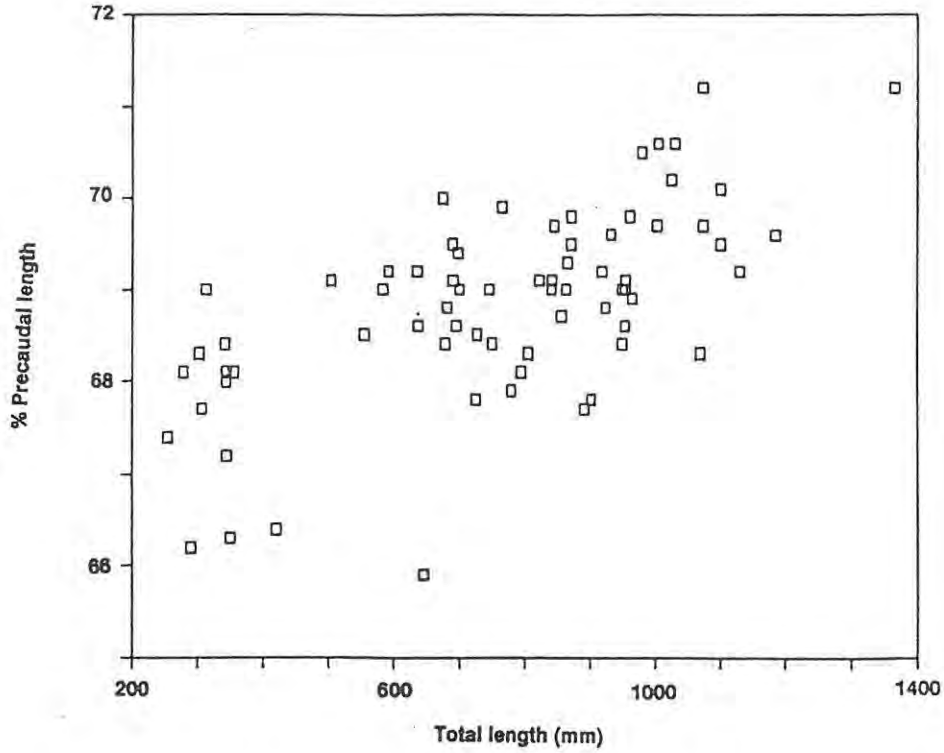


Figure 3.14a - Proportional lengths of snout tip to precaudal length in Heptranchias perlo. Y= 67 + 0.003x, r^2= 0.4, n= 71.

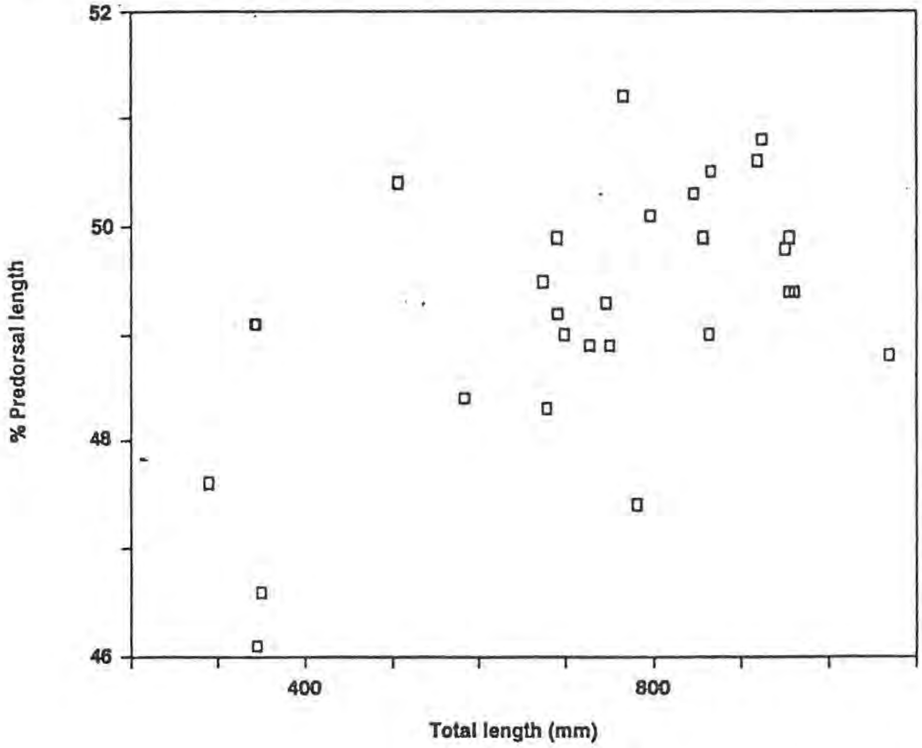


Figure 3.14b - Proportional lengths of snout tip to dorsal fin origin in male Heptranchias perlo. Y= 47 + 0.003x, r^2= 0.3, n= 29.

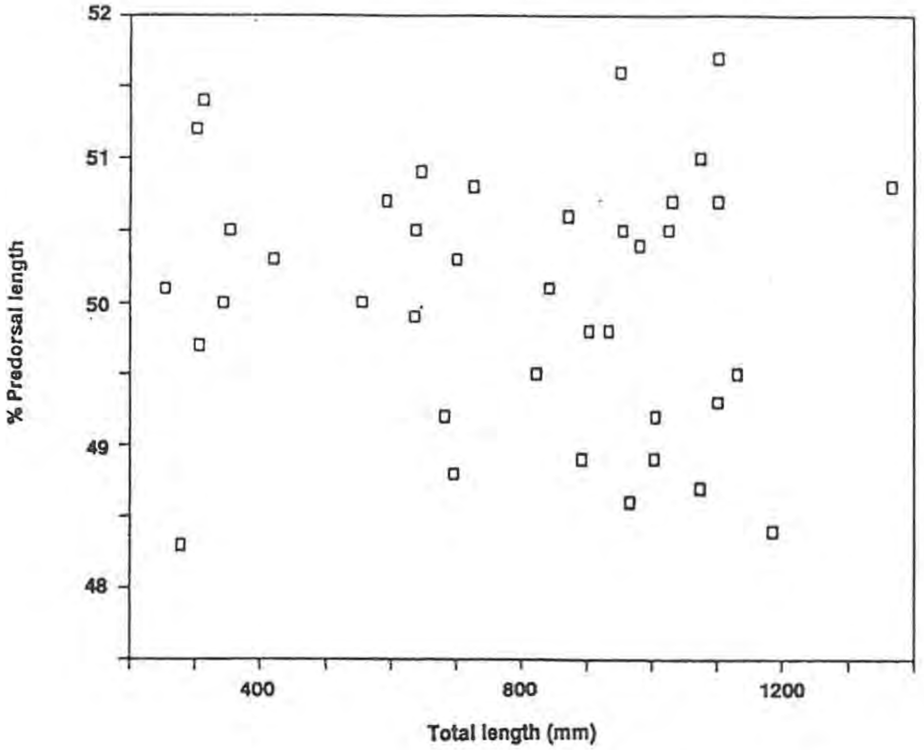


Figure 3.14c - Proportional lengths of snout tip to dorsal fin origin in female Heptranchias perlo. $Y= 49 + 0.002x$, $r^2= 0.2$, $n= 40$.

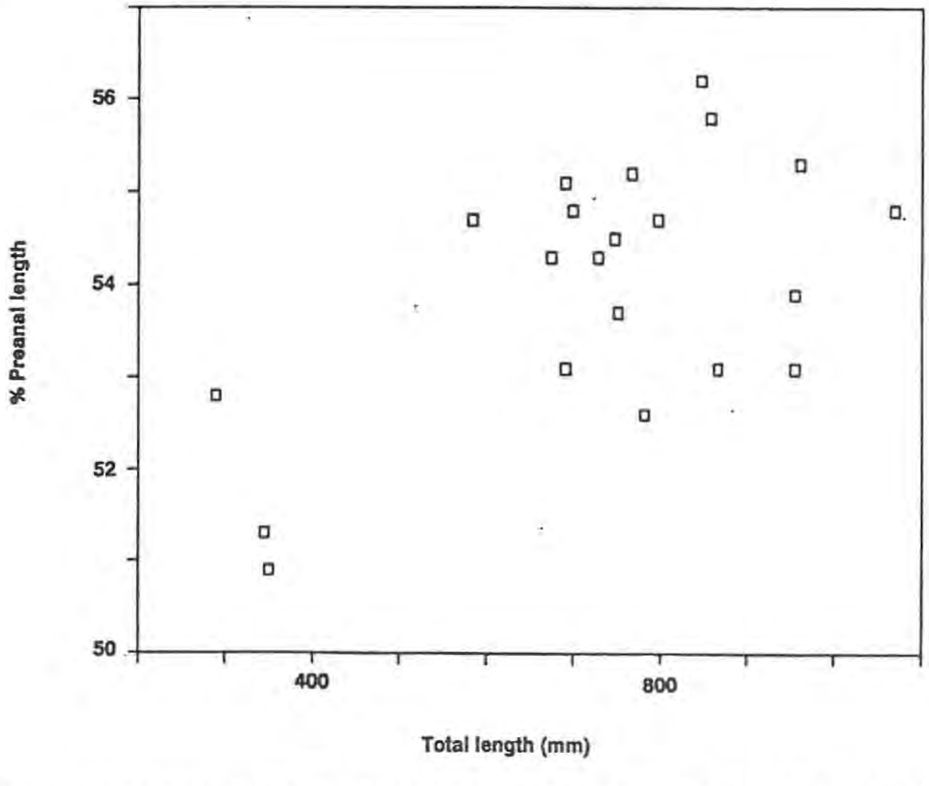


Figure 3.14d - Proportional lengths of snout tip to anal fin origin in male Heptranchias perlo. $Y= 51 + 0.004x$, $r^2= 0.3$, $n= 20$.

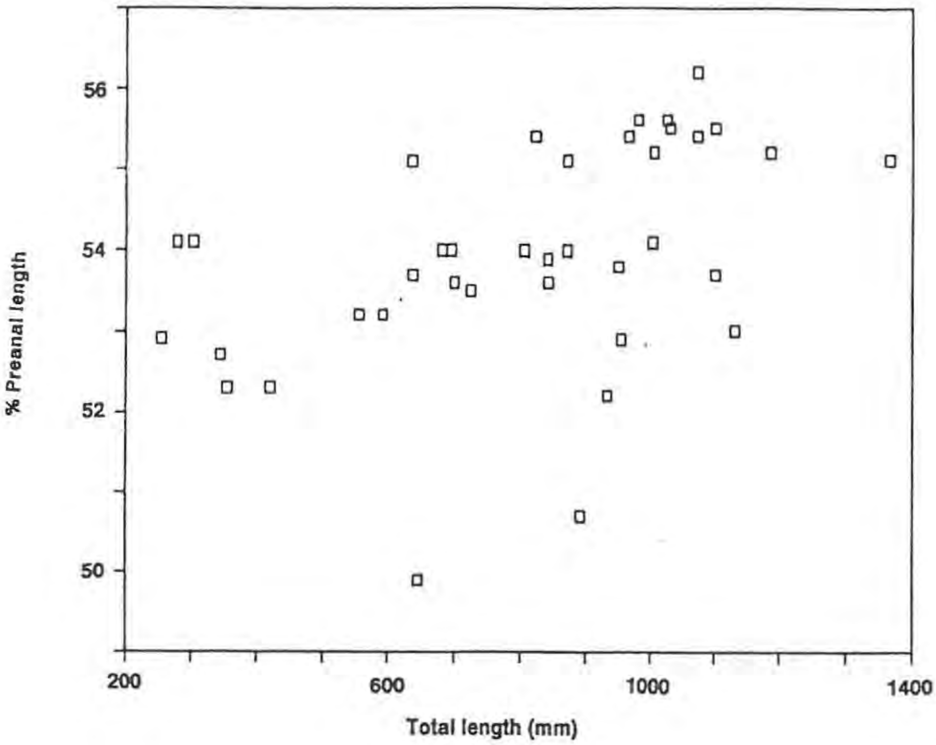


Figure 3.14e - Proportional lengths of snout tip to anal fin origin in female Heptranchias perlo. Y= 52 + 0.002x, r^2= 0.2, n= 39.

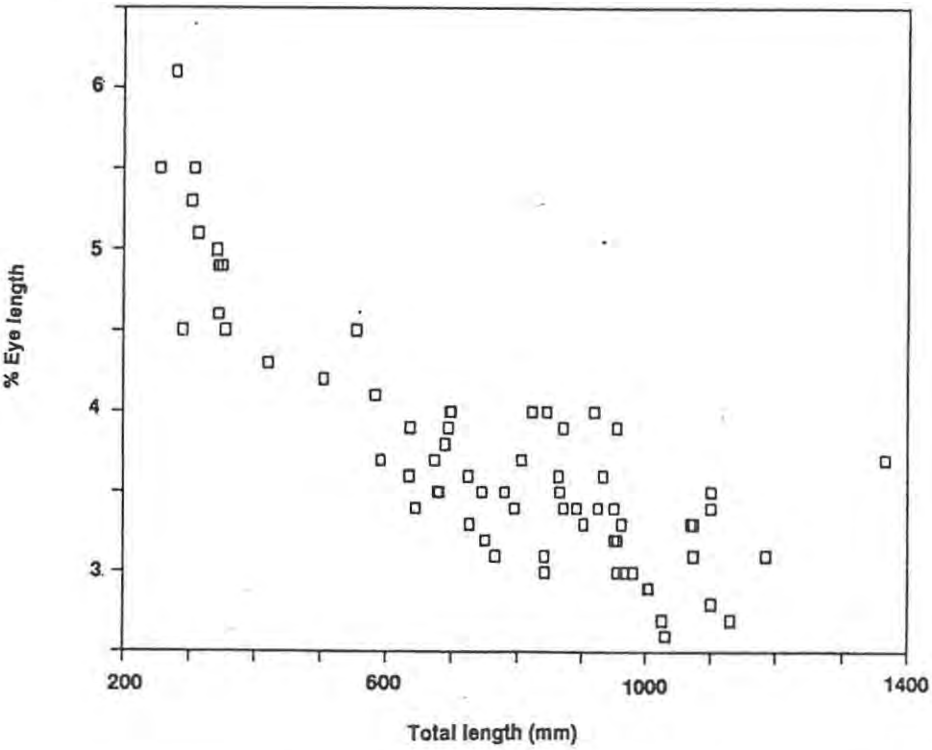


Figure 3.15 - Proportional lengths of snout tip to eye length in Heptranchias perlo. Y= 5.5 + 0.002x, r^2= 0.7, n= 70.

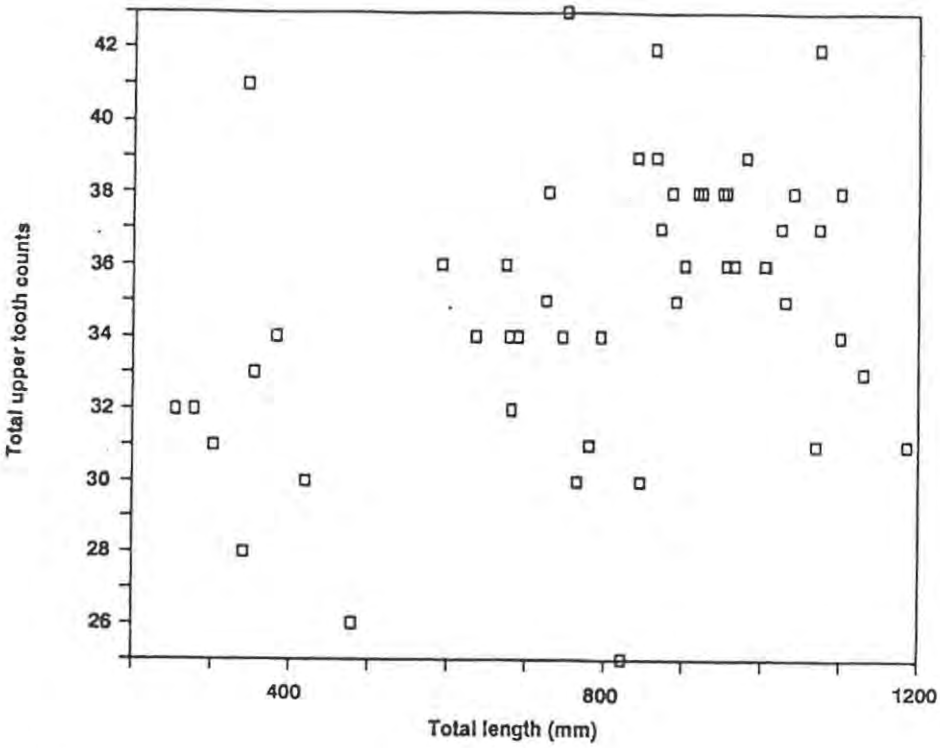


Figure 3.17 - Heptranchias perlo: total number of upper teeth in relation to TL. r^2= 0, n= 50.

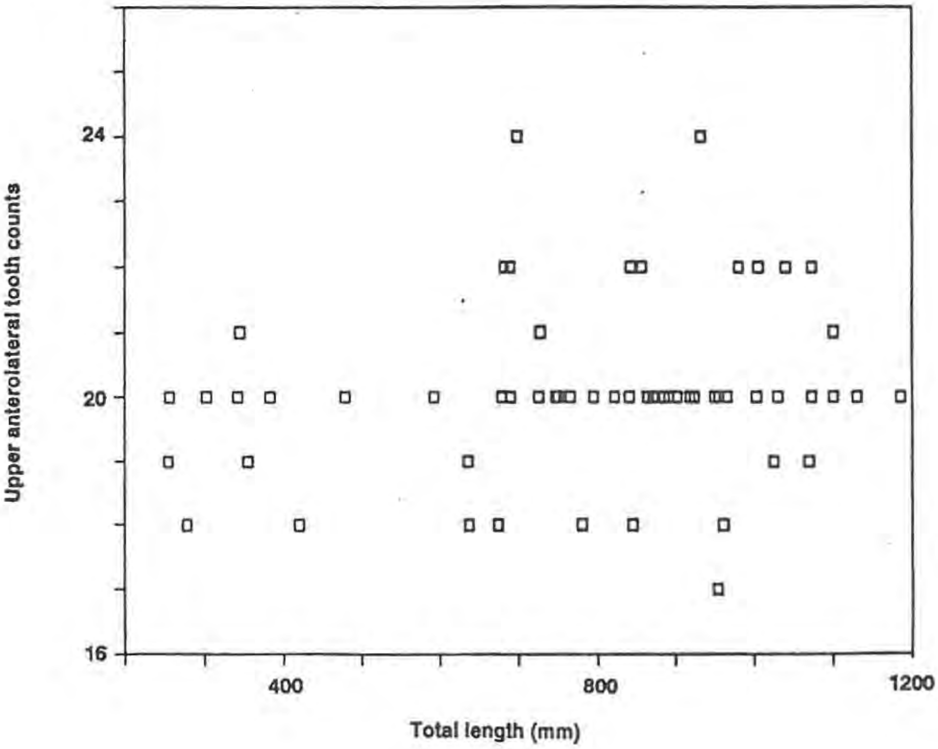


Figure 3.18 - Heptranchias perlo: total number of upper anterolateral teeth in relation to TL. r^2= 0, n= 60.

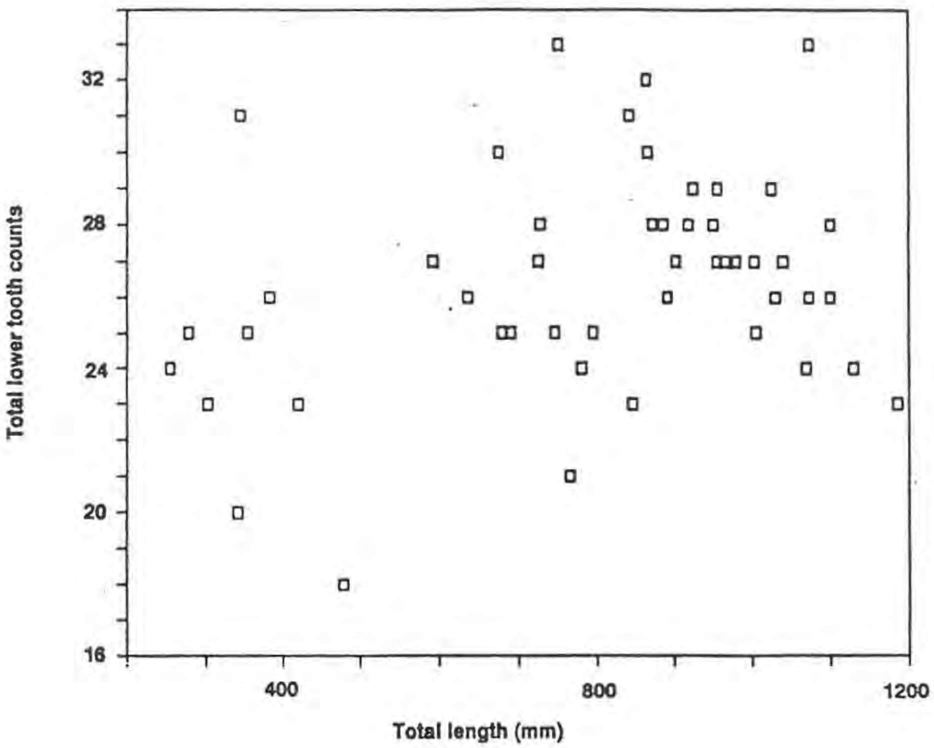


Figure 3.19 - Heptranchias perlo: total lower tooth counts in relation to TL. $r^2= 0$, n= 50.

Figure 3.20 Lateral trunk denticles of *Heptranchias perlo*

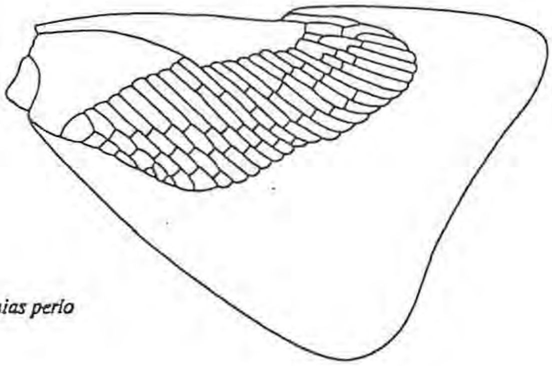


Figure 3.21 Pectoral fin skeleton of *Heptranchias perlo*

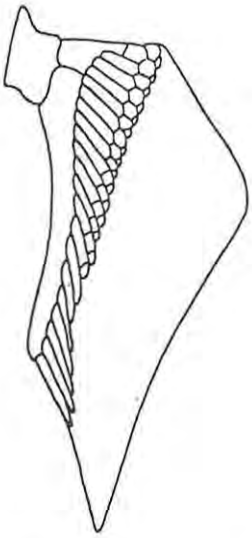


Figure 3.22 Pelvic fin skeleton of female *Heptranchias perlo*

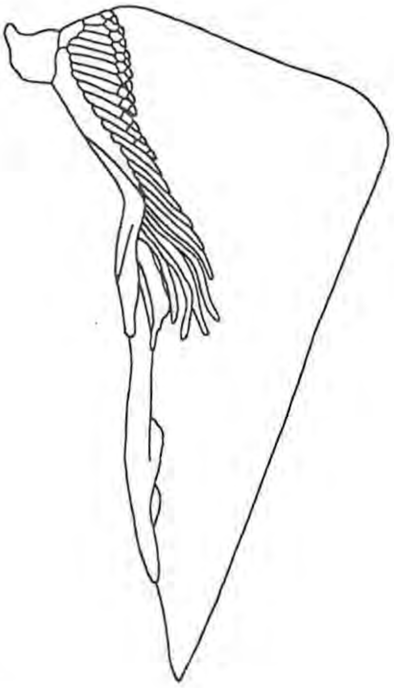


Figure 3.23 Pelvic fin and clasper skeleton of *Heptranchias perlo*

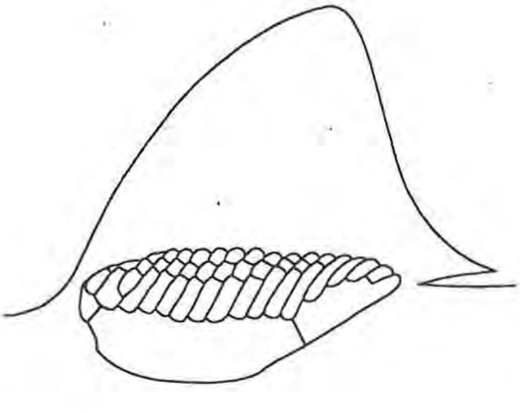


Figure 3.24 Dorsal fin skeleton of *Heptranchias perlo*

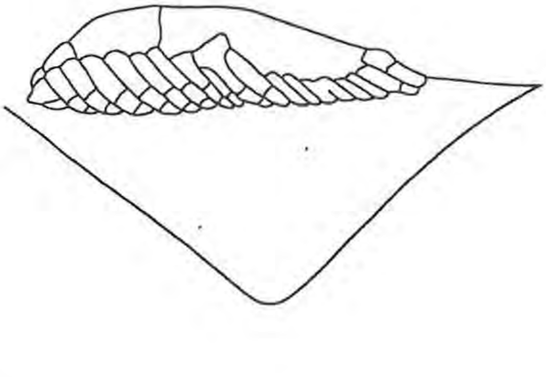


Figure 3.25 Anal fin skeleton of *Heptranchias perlo*

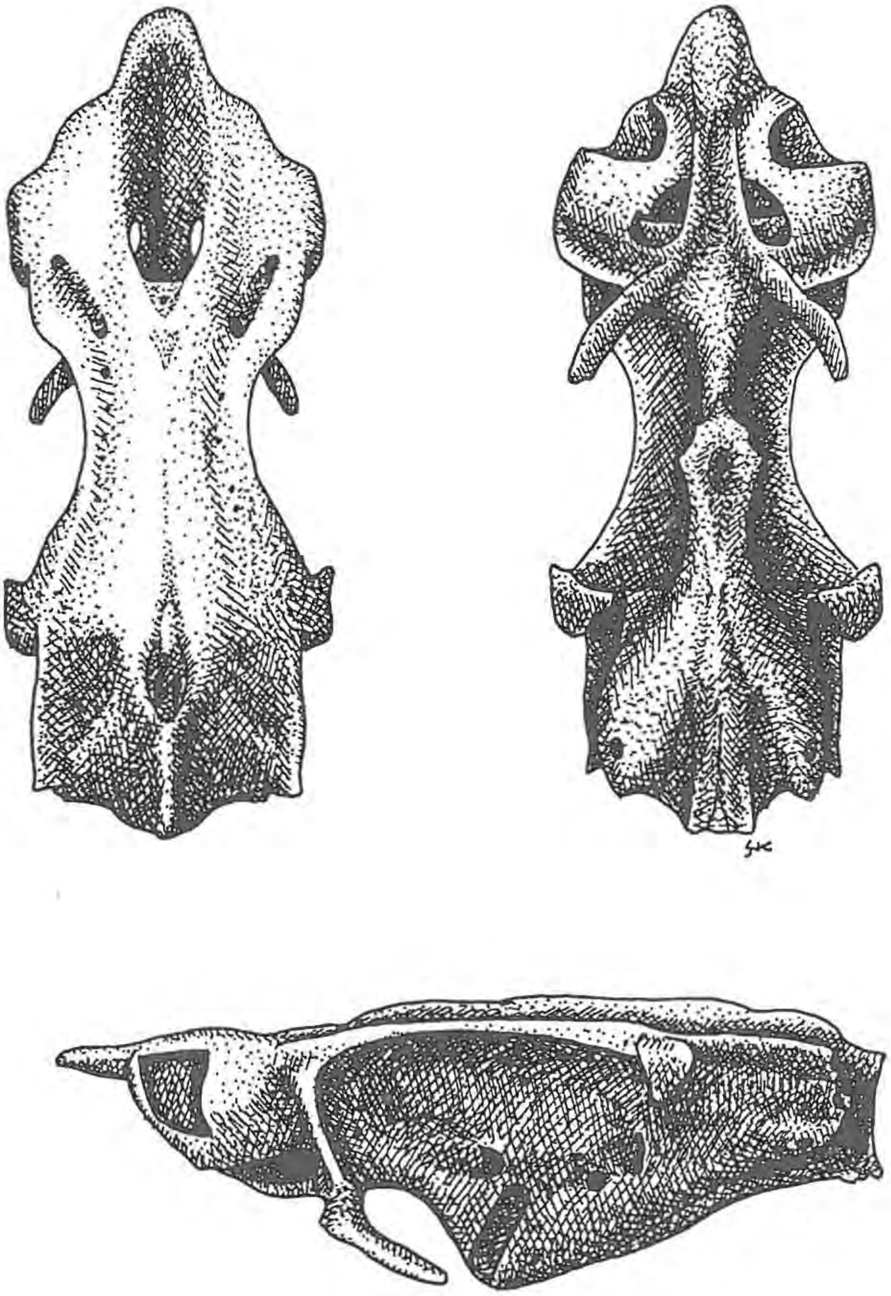


Figure 3.26 The cranium of Heptranchias perlo.

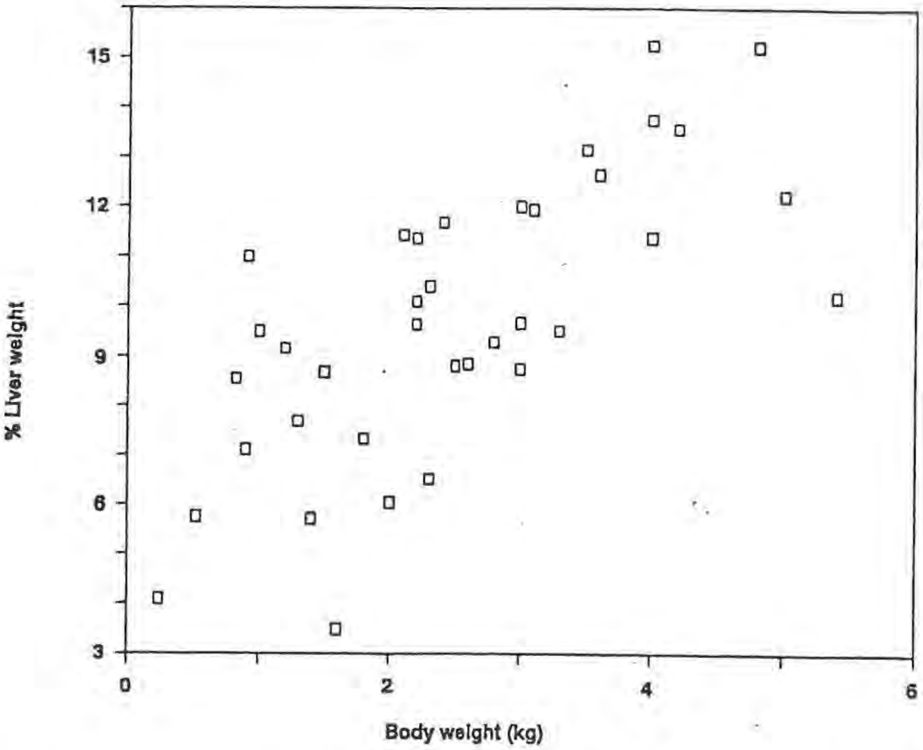


Figure 3.27 - Proportion of liver weight to body weight in Heptranchias perlo. $Y= 0.5 + 0.001x$, $r^2= 0.7$, $n= 37$.

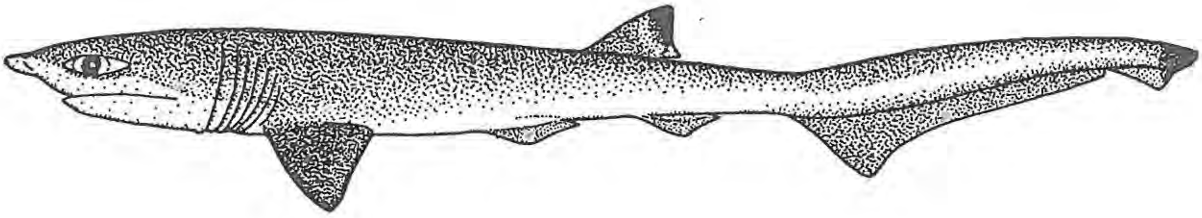


Figure 3.28 - Color pattern of newborn Heptranchias perlo.

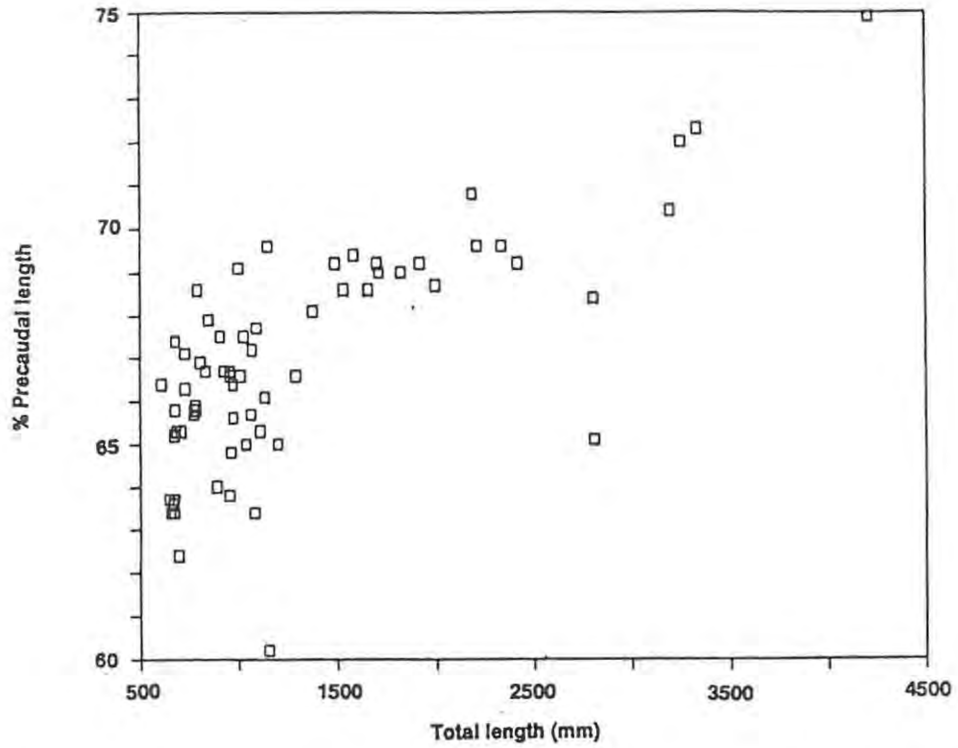


Figure 3.29a - Proportional lengths of snout tip to precaudal length in Hexanchus griseus. $Y= 64 + 0.002x$, $r^2= 0.5$, $n= 66$.

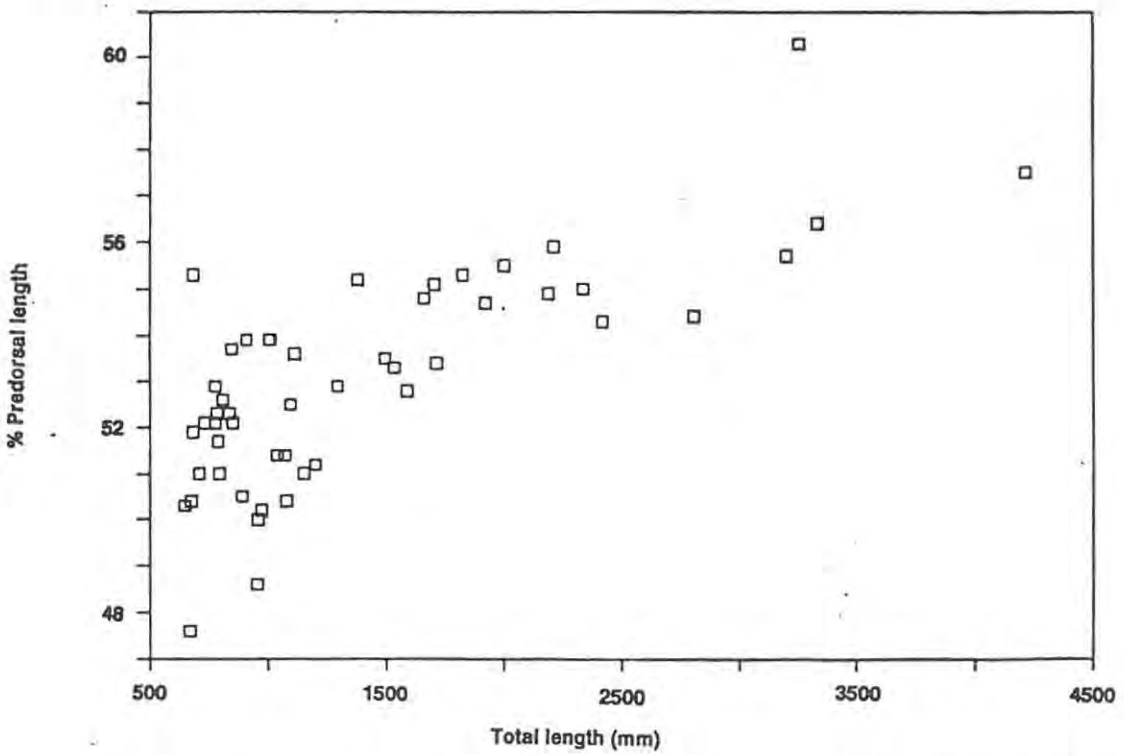


Figure 3.29b - Proportional lengths of snout tip to dorsal fin origin in Hexanchus griseus. $Y= 50 + 0.002x$, $r^2= 0.5$, $n= 58$.

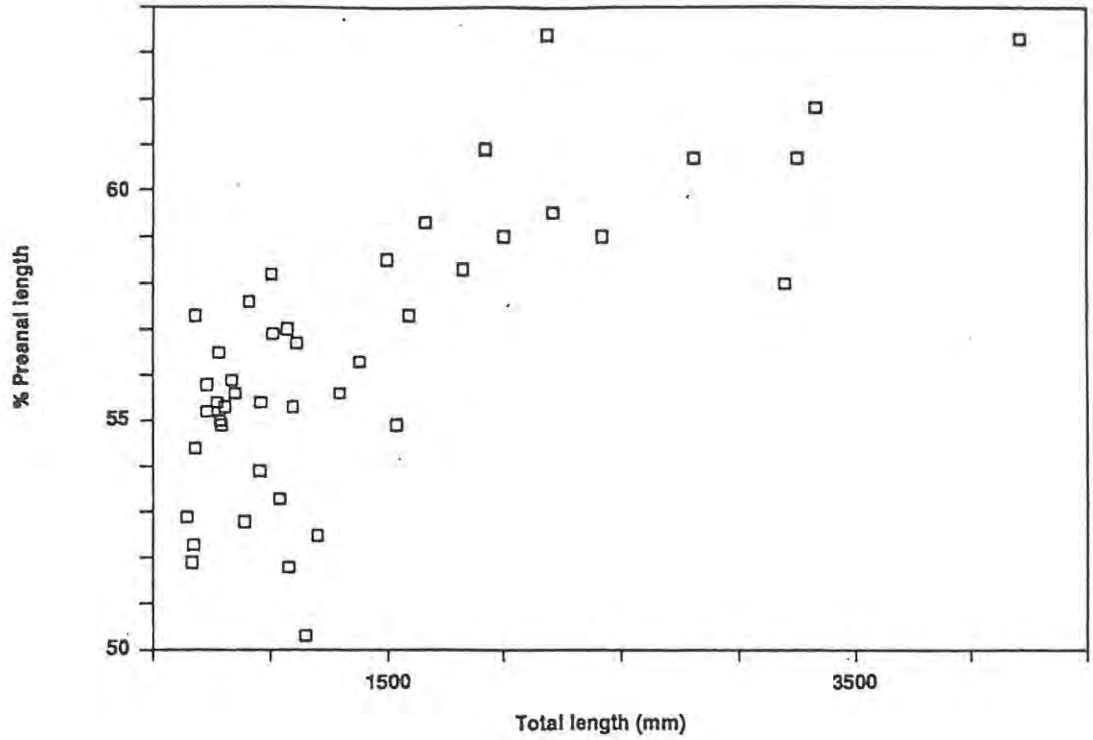


Figure 3.29c - Proportional lengths of snout tip to anal fin origin in <u>Hexanchus griseus</u>. Y= 53 + 0.003x, r^2= 0.5, n= 52.

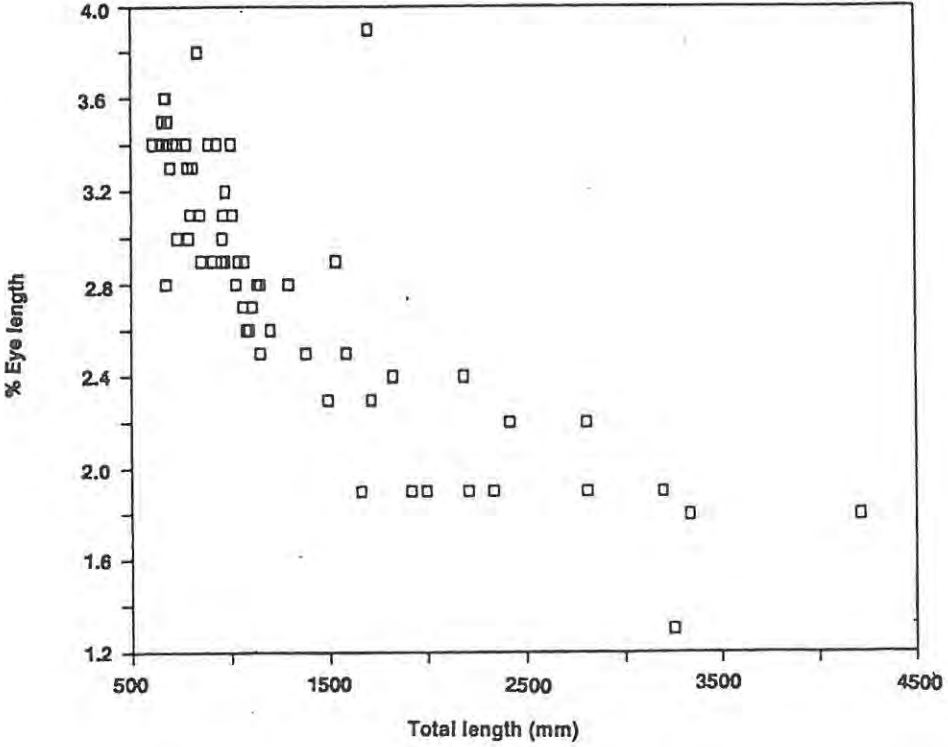


Figure 3.30 - Proportional lengths of snout tip to eye length in <u>Hexanchus griseus</u>. Y= 3.6 + 0.0006x, r^2= 0.7, n= 66.

Figure 3.31 Hexanchus griseus teeth (upper and lower as shown).

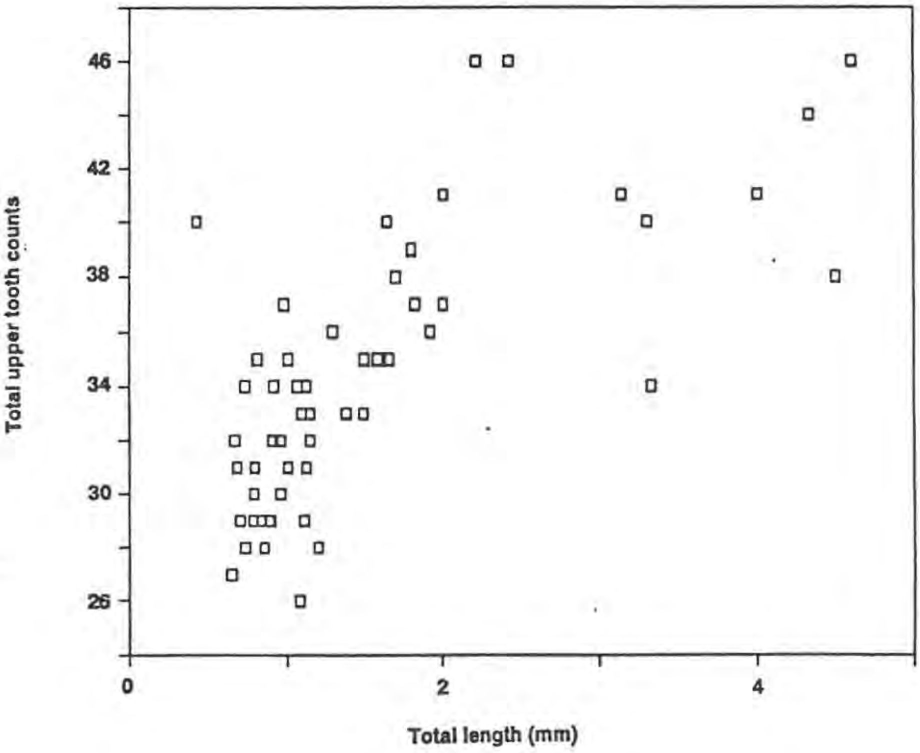


Figure 3.32 - Hexanchus griseus: total number of upper teeth in relation to TL. Y= 29 + 0.004x, r^2= 0.5, n= 56.

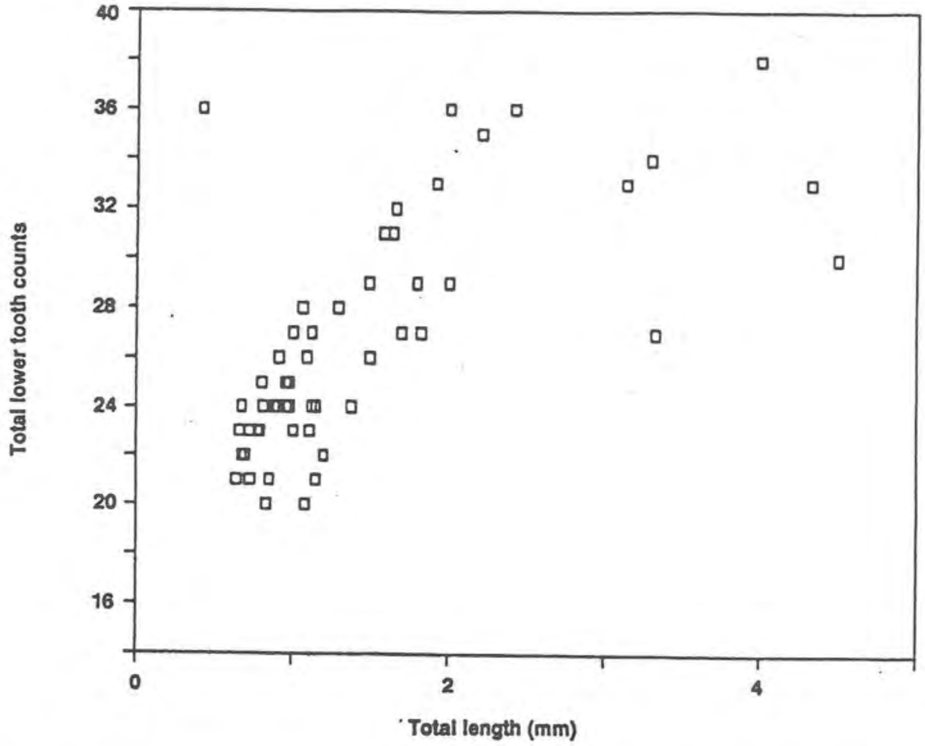


Figure 3.33 Hexanchus griseus: total number of lower teeth in relation to TL. $Y= 21 + 0.004x$, $r^2= 0.5$, $n= 55$.

Figure 3.34 - Ontogenetic heterodonty in Hexanchus griseus. A, 681 mm TL.

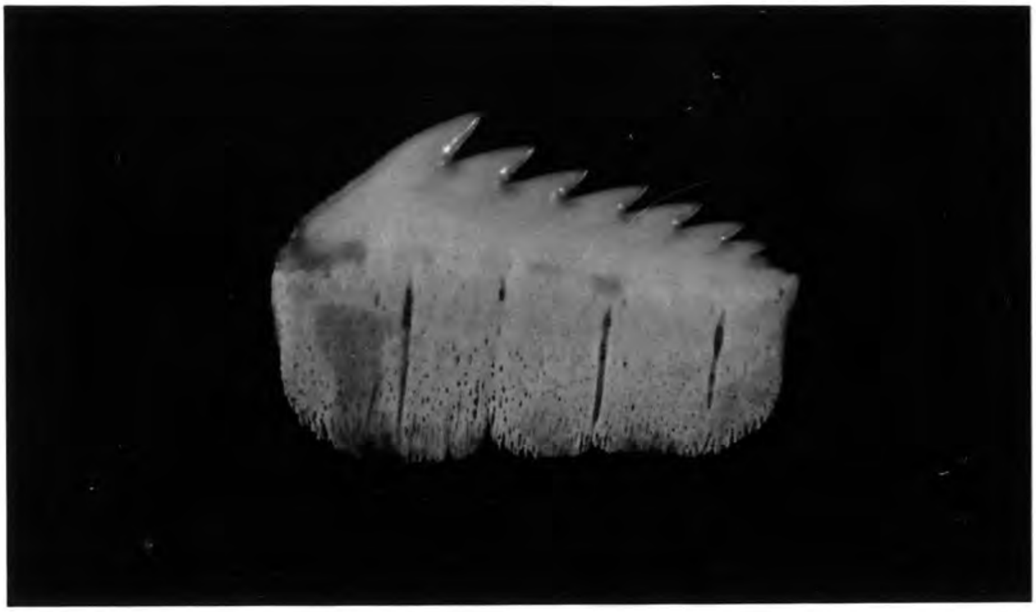


Figure 3.34 - Ontogenetic heterodonty in Hexanchus griseus. B, 1380 mm TL.

Figure 3.34 - Ontogenetic heterodonty in Hexanchus griseus. C, 2805 mm TL.

Figure 3.35 - Sexual dimorphism in Hexanchus griseus. A, 3330 mm TL adult male.

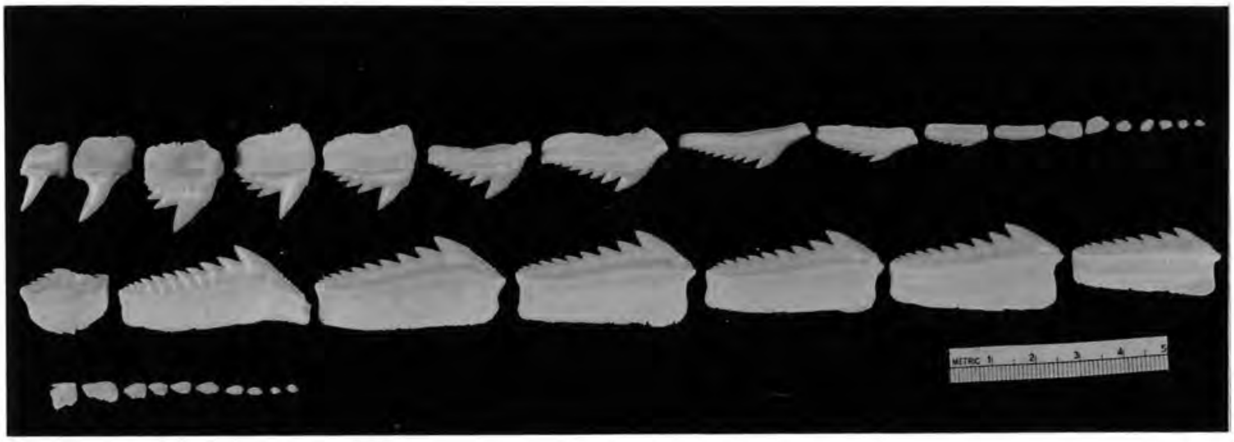


Figure 3.35 - Sexual dimorphism in Hexanchus griseus. B, 4210 mm TL female.

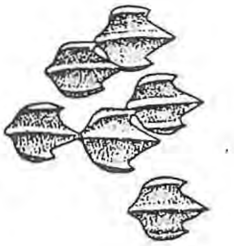


Figure 3.36 Lateral trunk denticles of *Hexanchus griseus*

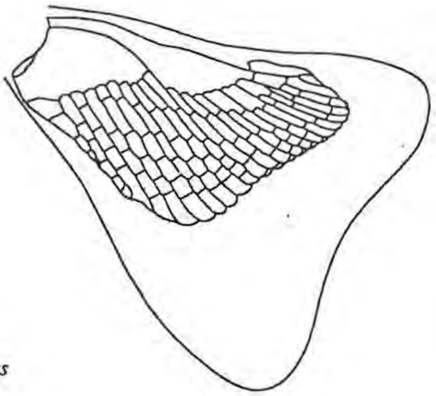
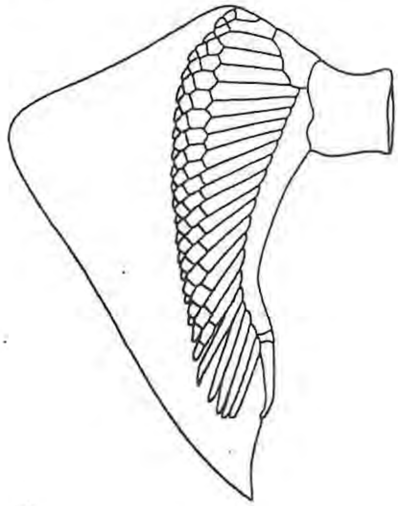


Figure 3.37 Pectoral fin skeleton of *Hexanchus griseus*

Figure 3.38 Pelvic fin skeleton of female *Hexanchus griseus*



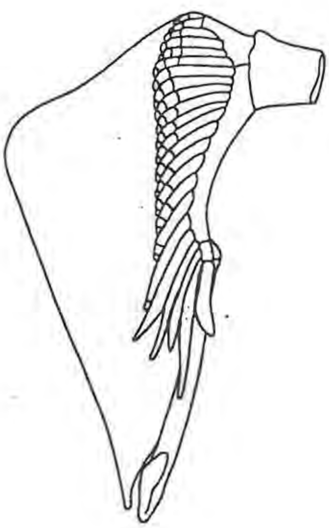
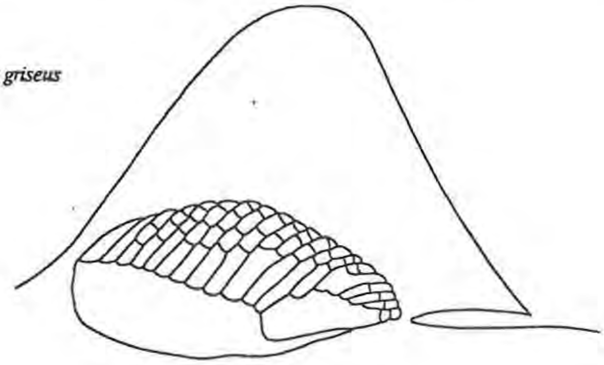


Figure 3.39 Pelvic fin and clasper skeleton of *Hexanchus griseus*

Figure 3.40 Dorsal fin skeleton of *Hexanchus griseus*



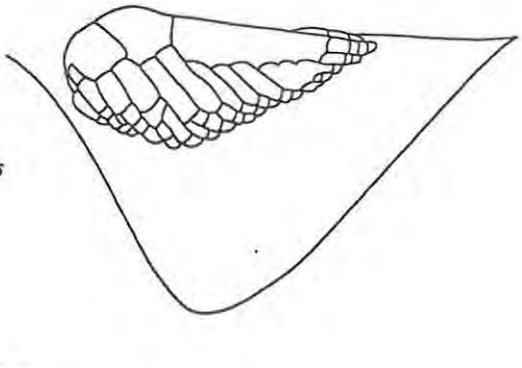


Figure 3.41 Anal fin skeleton of *Hexanchus griseus*

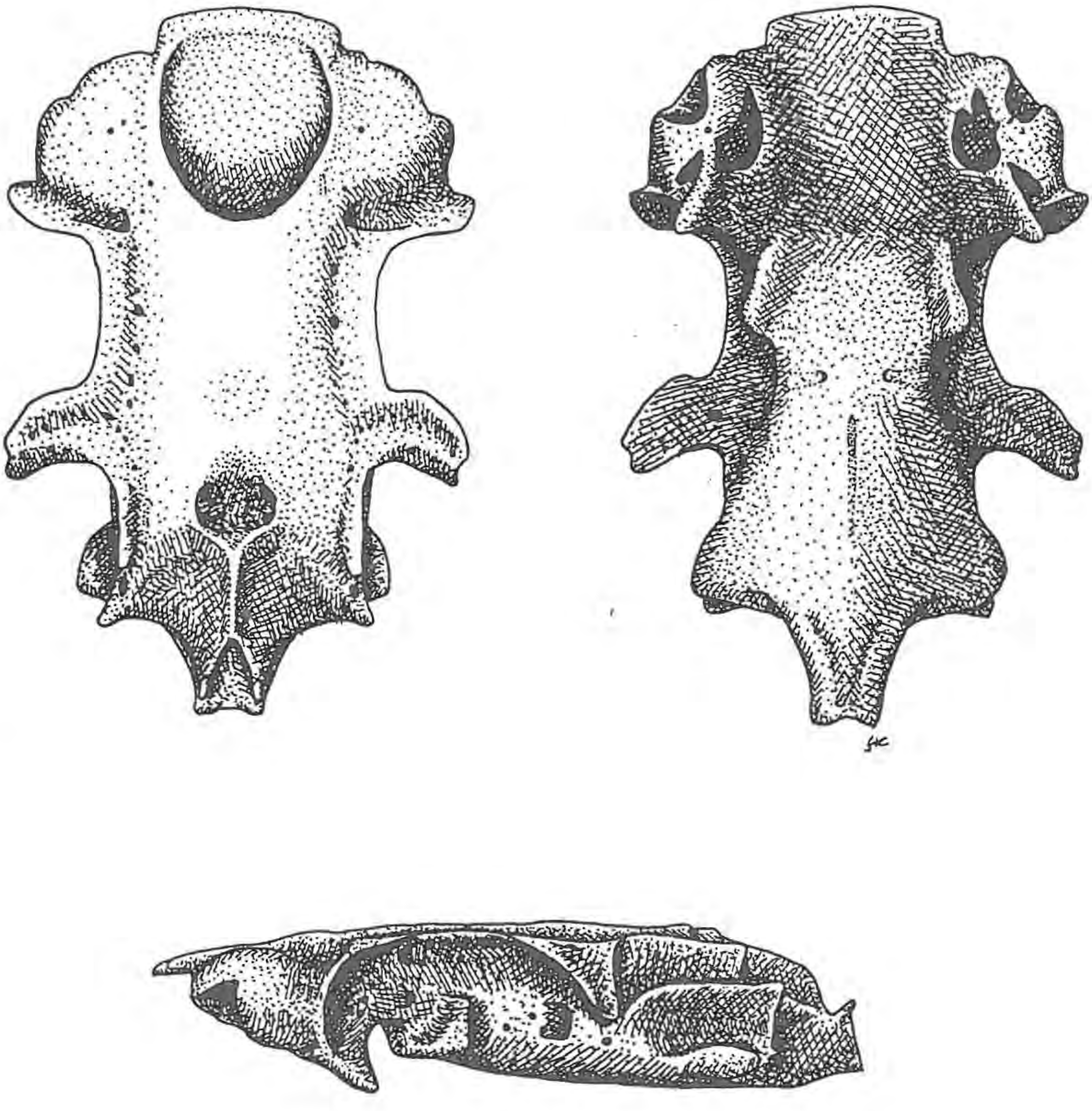


Figure 3.42 - The cranium of Hexanchus griseus.

Figure 3.43 - Color pattern of newborn Hexanchus griseus.

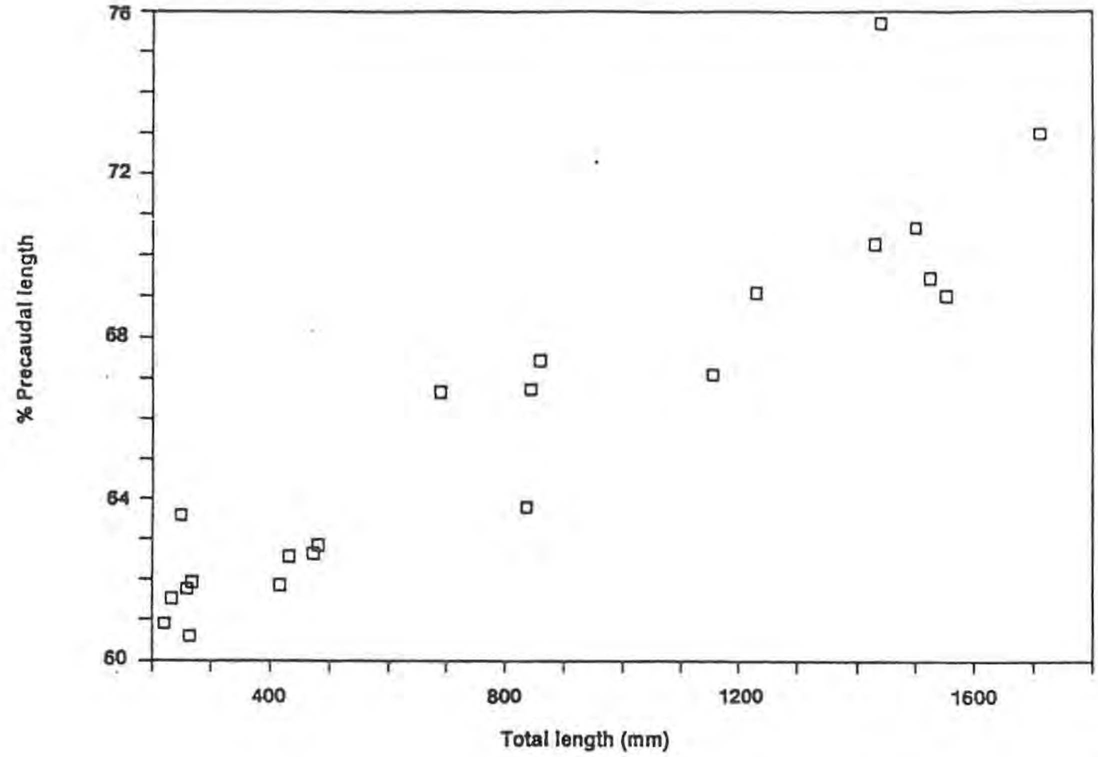


Figure 3.44a Proportional lengths of snout tip to precaudal length in Hexanchus nakamurai. Y= 62 + 0.005x, r^2= 0.6, n= 22.

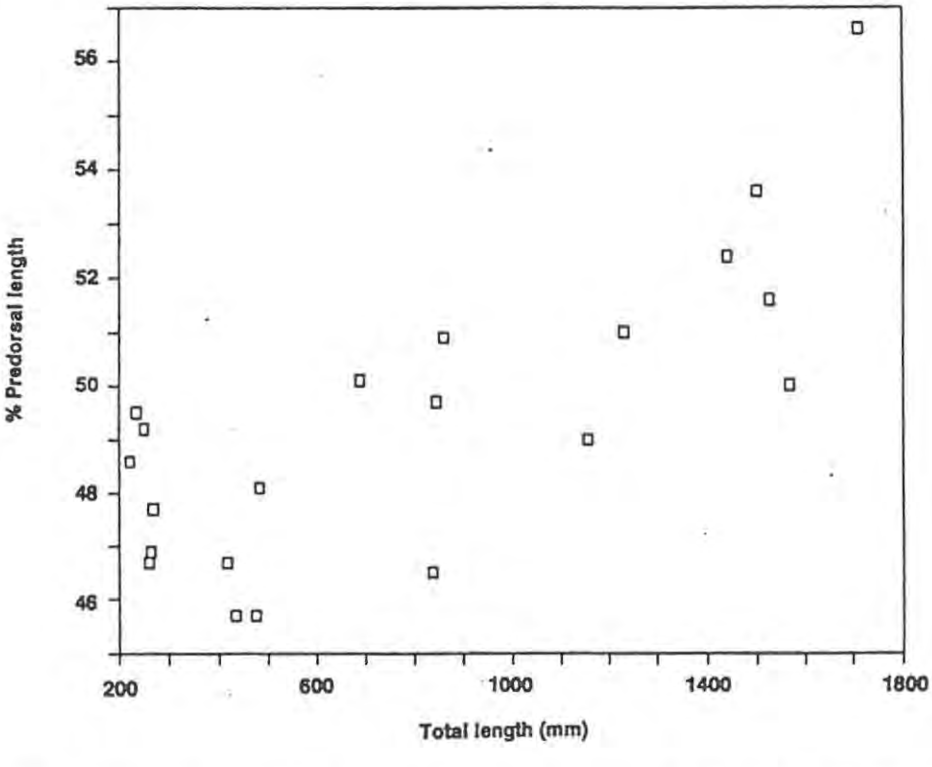


Figure 3.44b - Proportional lengths of snout tip to dorsal fin origin in Hexanchus nakamurai. Y= 46 + 0.004x, r^2= 0.6, n= 21.

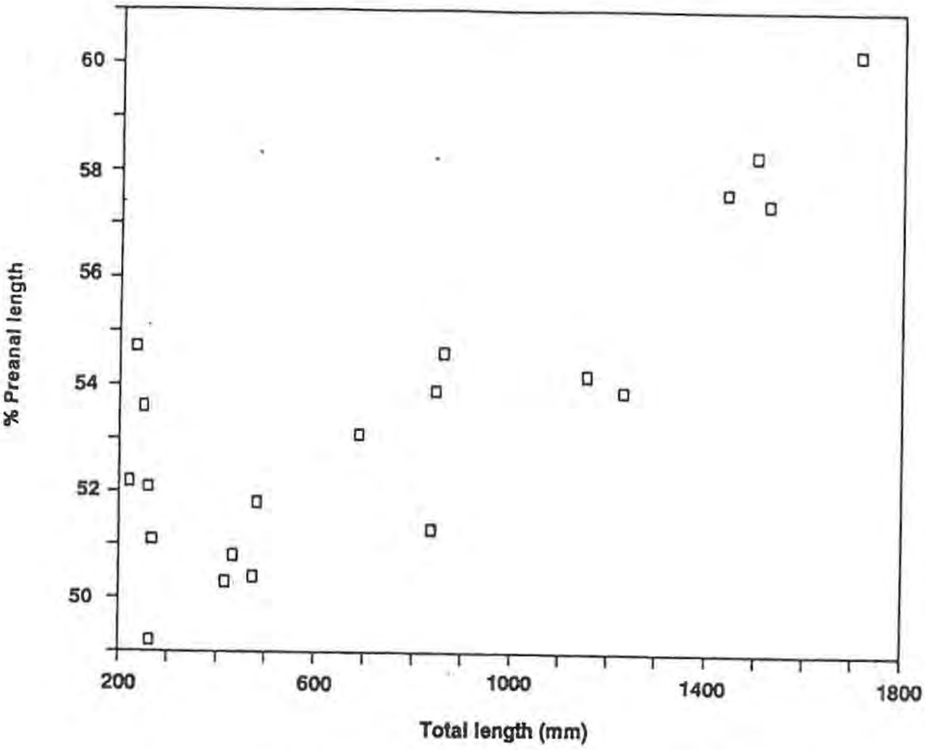


Figure 3.44c - Proportional lengths of snout tip to anal fin origin in Hexanchus nakamurai. Y= 50 + 0.005x, r^2= 0.7, n= 20.

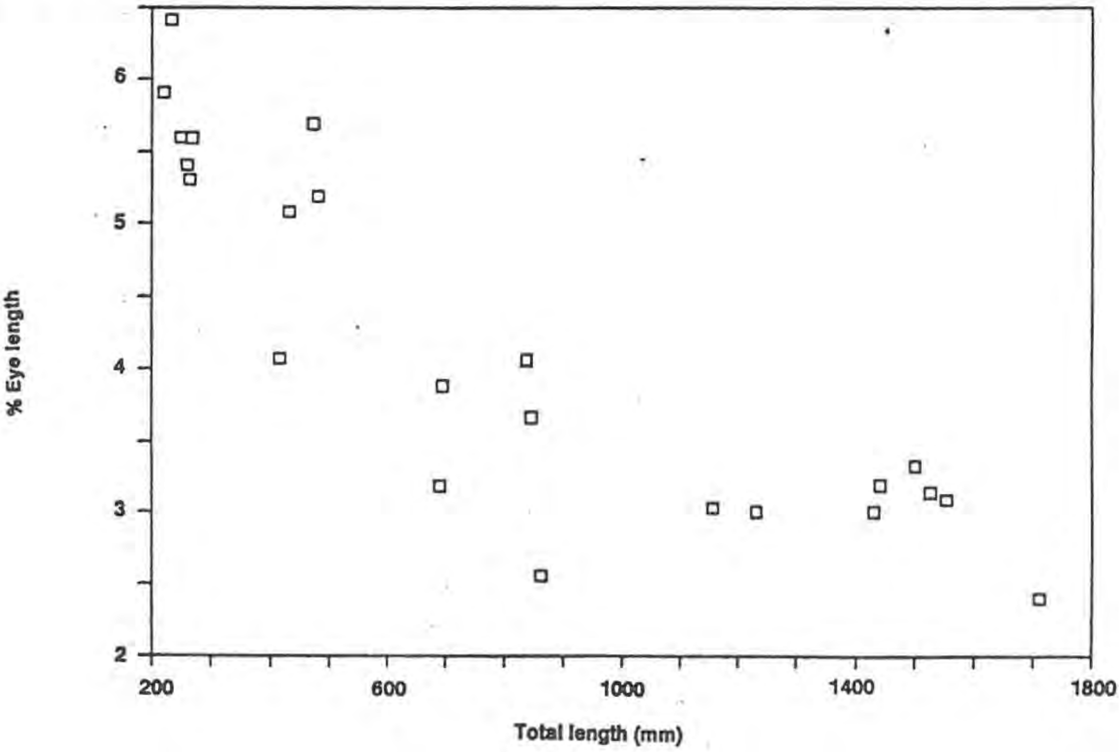


Figure 3.45 - Proportional lengths of snout tip to eye length in Hexanchus nakamurai. Y= 6 + 0.002x, r^2= 0.8, n= 21.

Figure 3.46 - Teeth of Hexanchus nakamurai (upper and lower as shown).

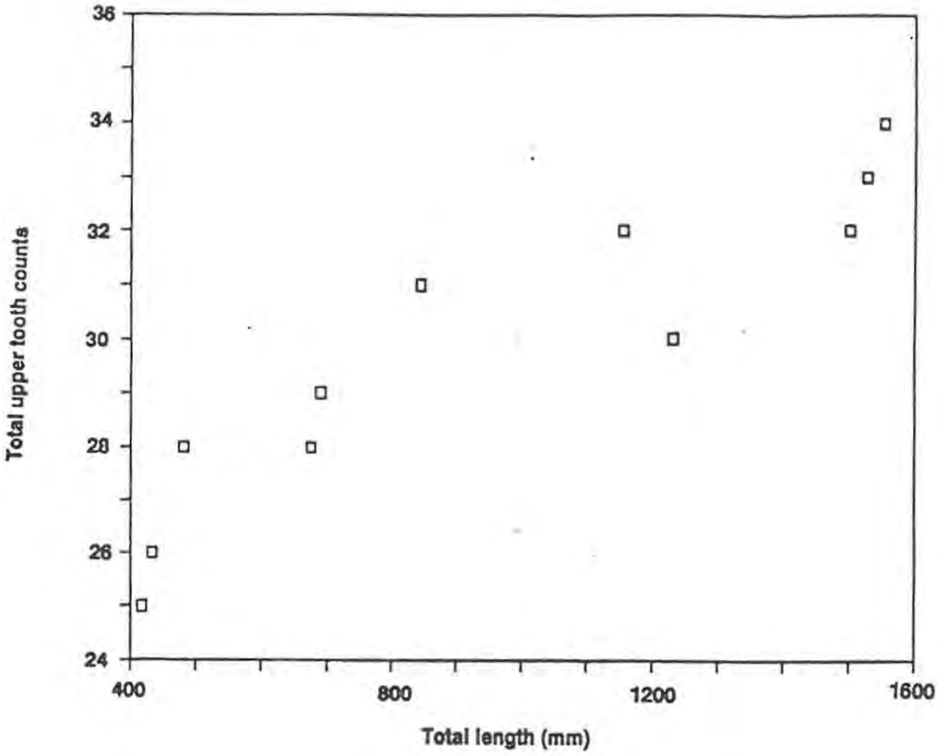


Figure 3.47 - Hexanchus nakamurai: total number of upper teeth in relation to TL. r^2= 1.0, n= 11.

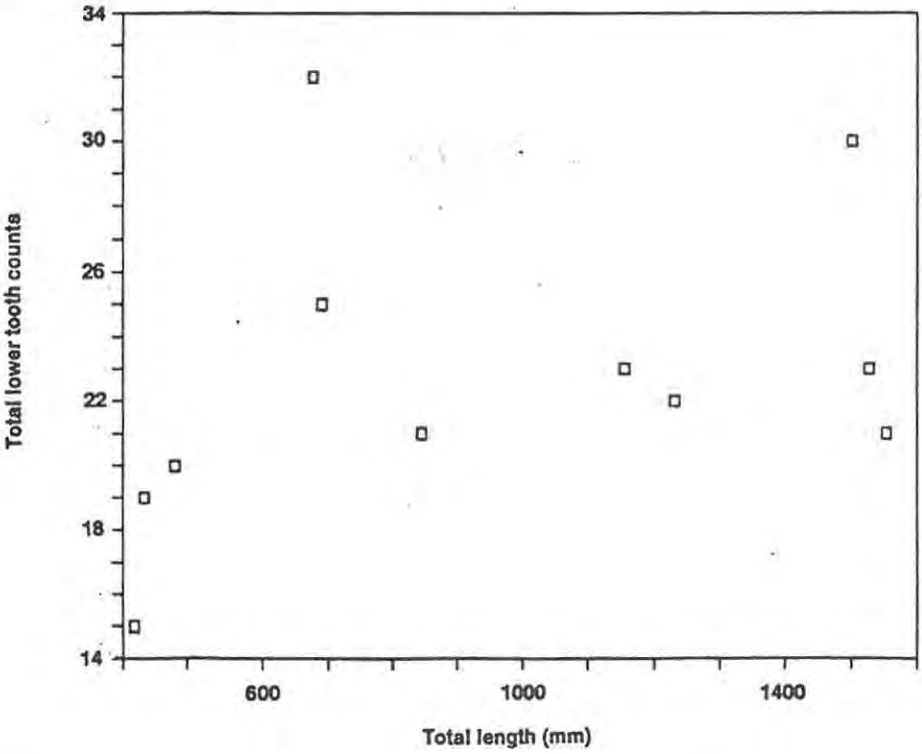


Figure 3.48 - Hexanchus nakamurai: total number of lower teeth in relation to TL. r^2= 0, n= 11.

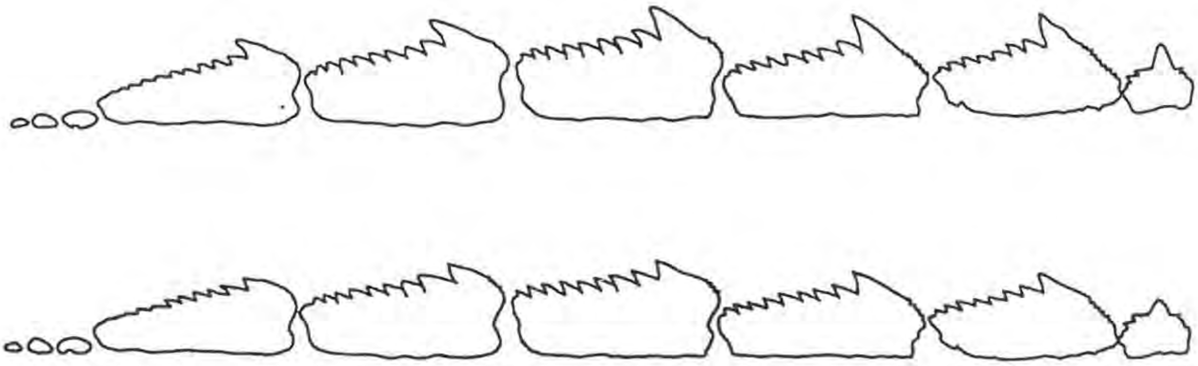


Figure 3.49 - Sexual heterodonty in Hexanchus nakamurai: lower anterolateral teeth of adult male (above) and lower anterolateral teeth of adult female (below).

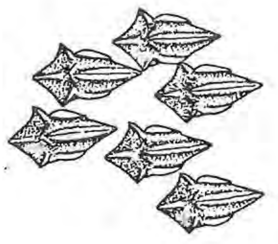


Figure 3.50 Lateral trunk denticles of *Hexanchus nakamurai*

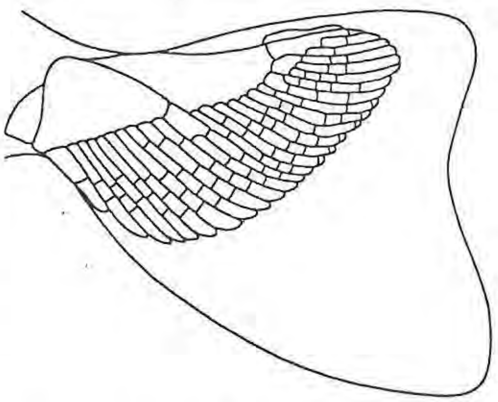
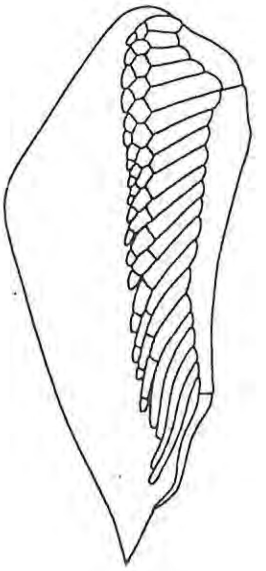


Figure 3.51 Pectoral fin skeleton of *Hexanchus nakamurai*

Figure 3.52 Pelvic fin skeleton of *Hexanchus nakamurai*



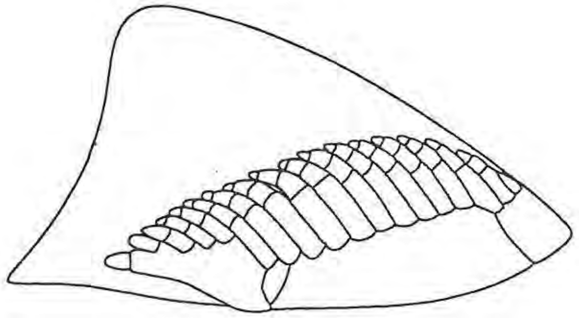
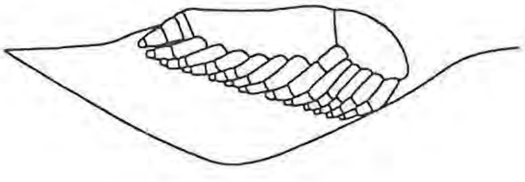


Figure 3.53 Dorsal fin skeleton of *Hexanchus nakamurai*

Figure 3.54 Anal fin skeleton of *Hexanchus nakamurai*



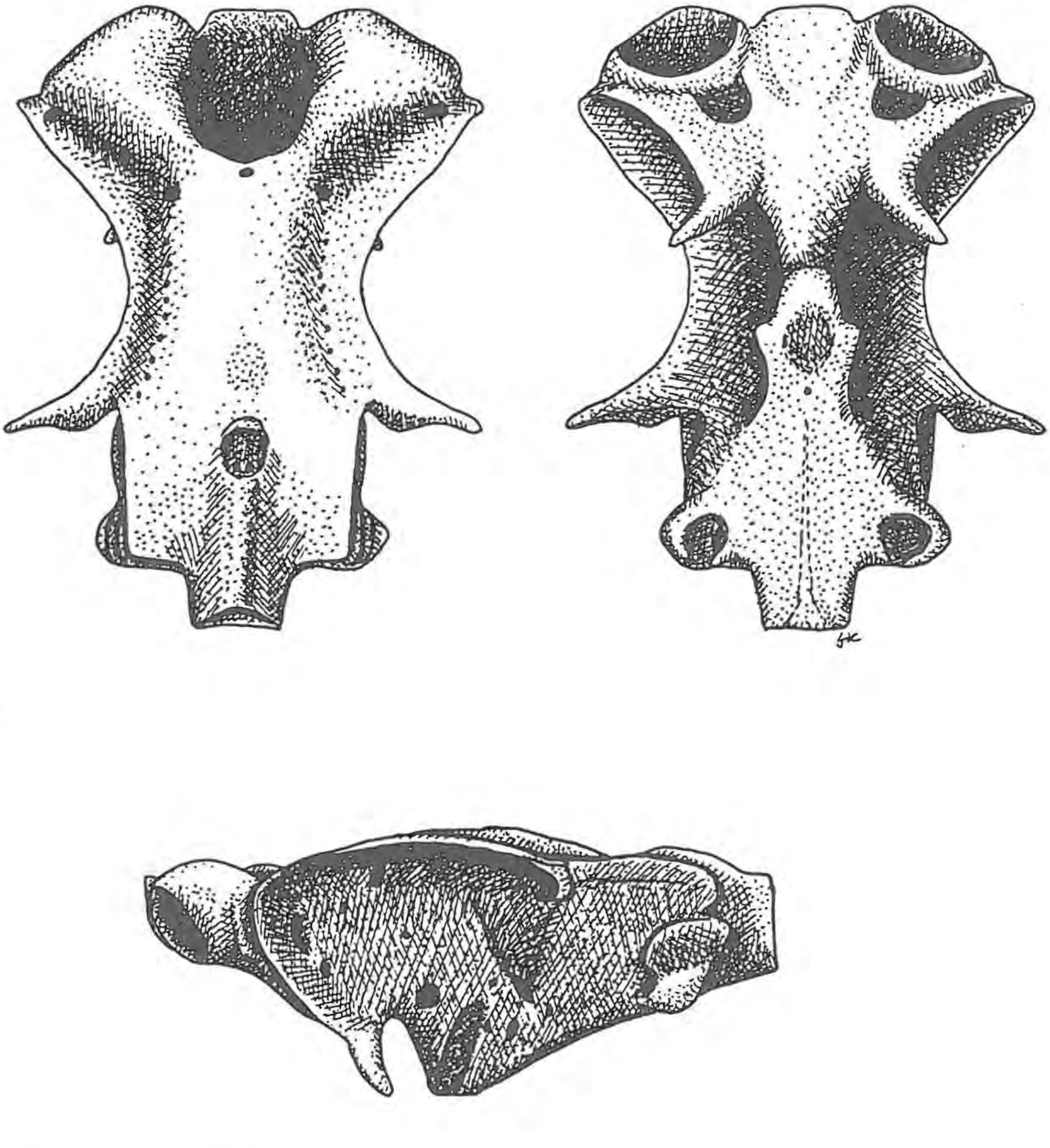


Figure 3.55 - The cranium of <u>Hexanchus</u> <u>nakamurai</u>.

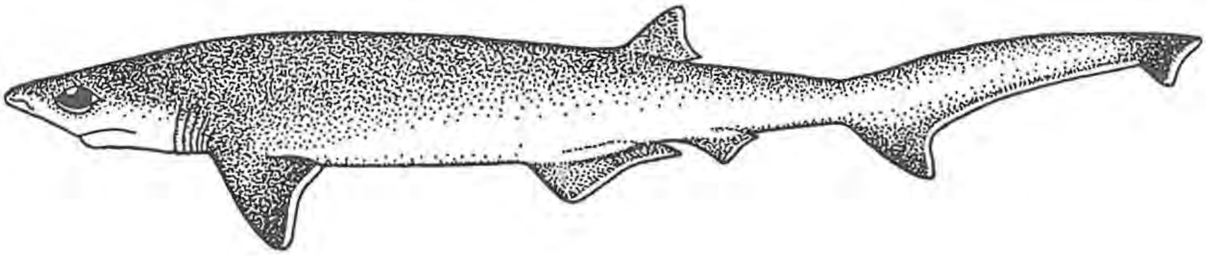


Figure 3.56 - Color pattern of newborn Hexanchus nakamurai.

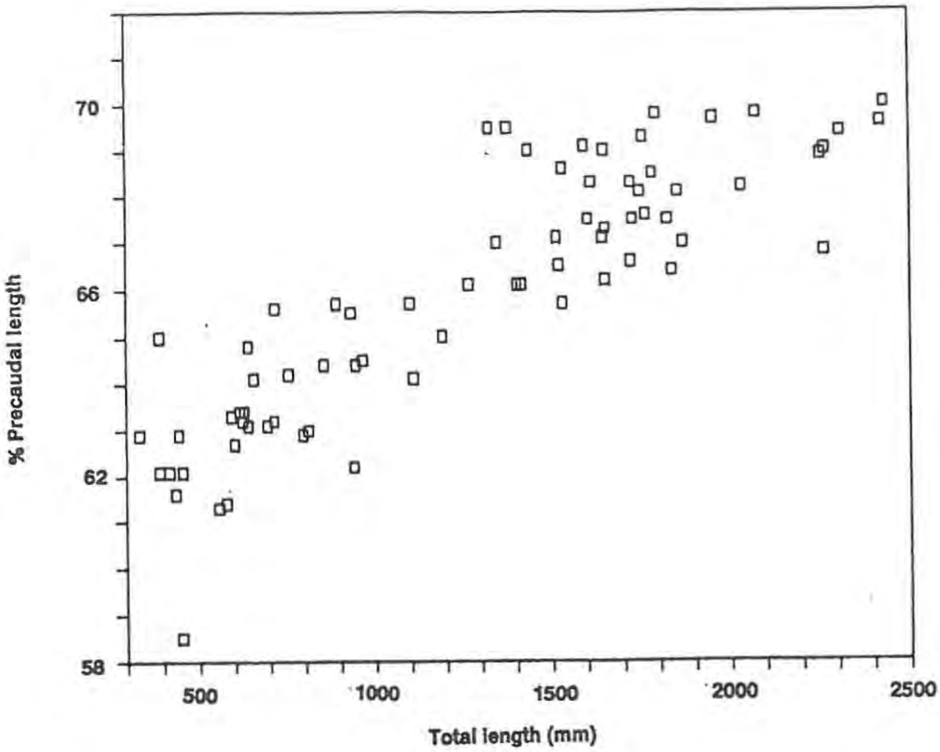


Figure 3.57a - Proportional lengths of snout tip to precaudal length in <u>Notorynchus cepedianus</u>. Y= 61 + 0.004x, r^2= 0.8, n= 72.

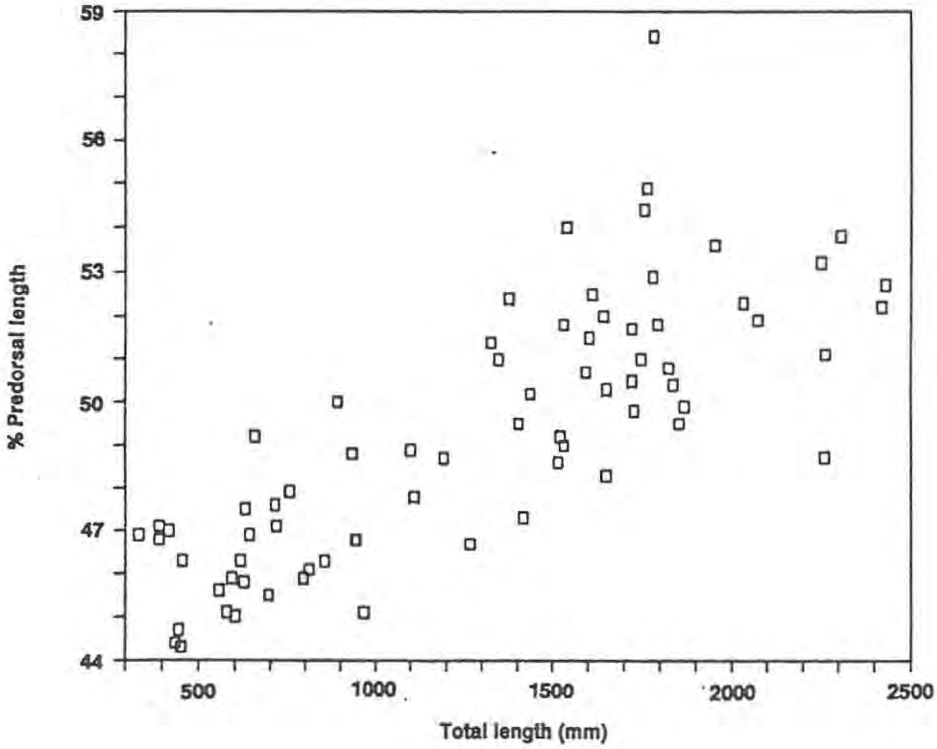


Figure 3.57b - Proportional lengths of snout tip to dorsal fin origin in <u>Notorynchus cepedianus</u>. Y= 44 + 0.004x, r^2= 0.6, n= 73.

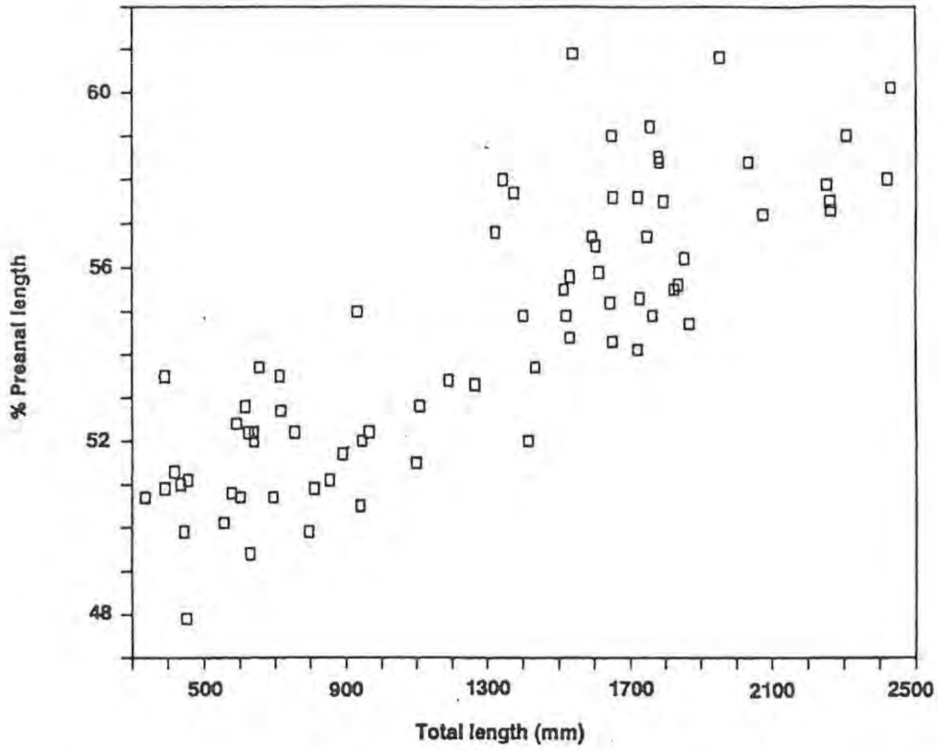


Figure 3.57c - Proportional lengths of snout tip to anal fin origin in Notorynchus cepedianus. Y= 48 + 0.004x, r^2= 0.7, n= 74.

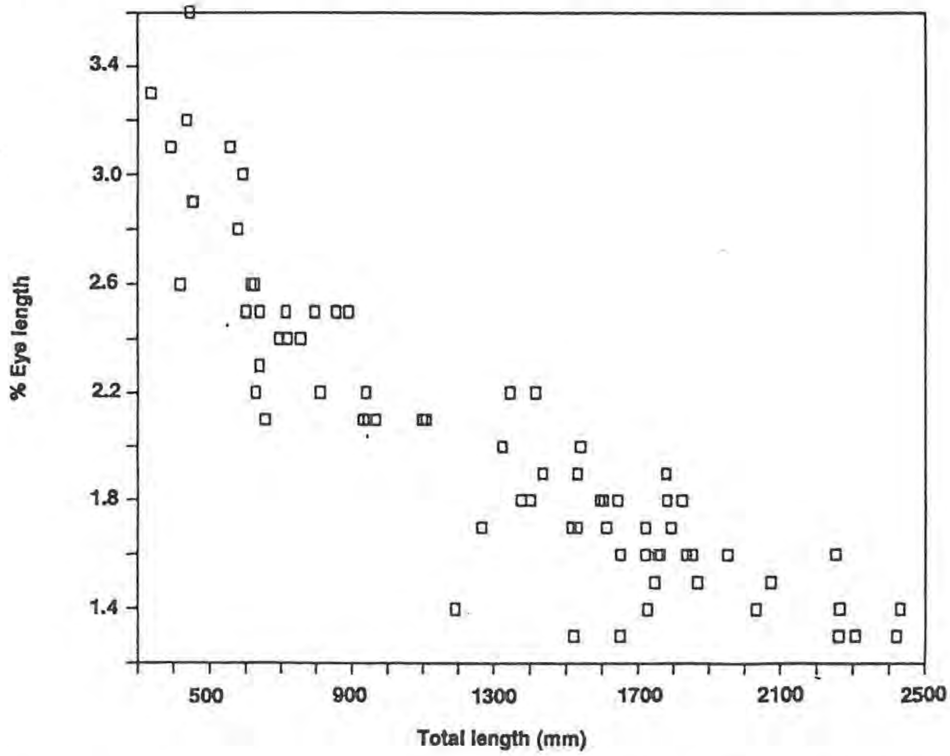


Figure 3.58 - Proportional lengths of snout tip to eye length in Notorynchus cepedianus. Y= 3 + 0.0008x, r^2= 0.8, n= 73.

Figure 3.59 - Teeth of Notorynchus cepedianus (upper and lower as shown).

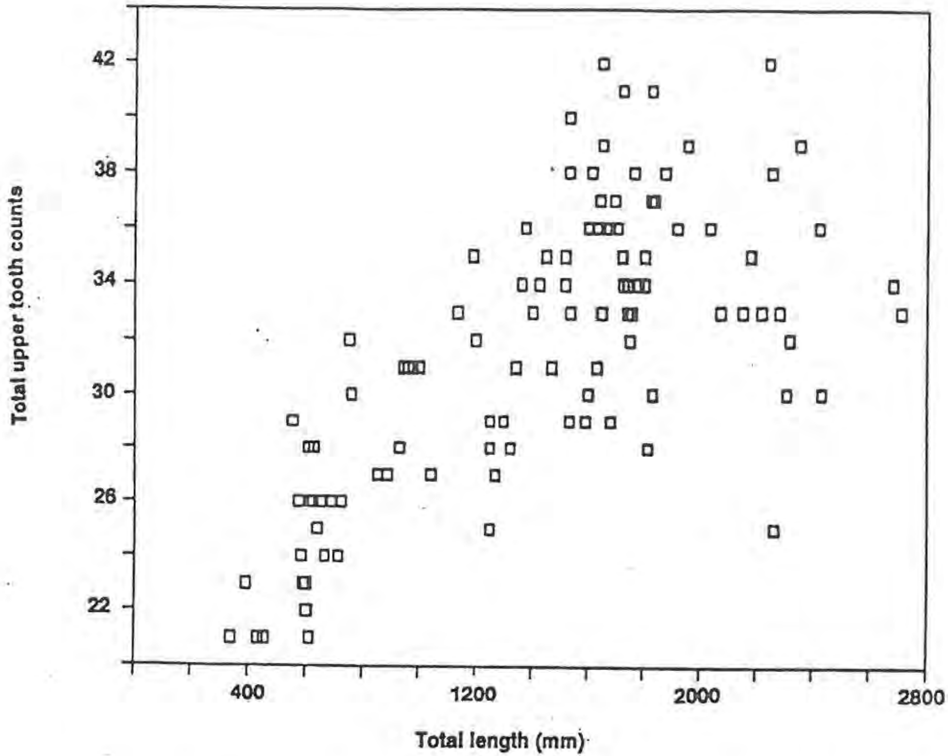


Figure 3.60 - Notorynchus cepedianus: total number of upper teeth in relation to TL. Y= 23 + 0.006x, r^2= 0.5, n= 109.

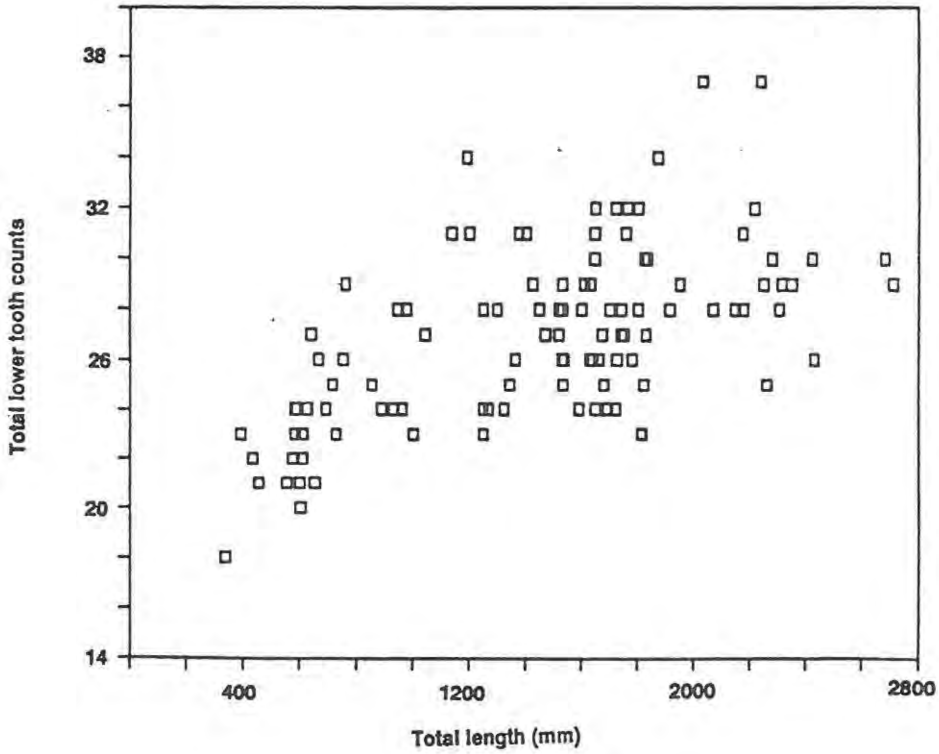


Figure 3.61 - Notorynchus cepedianus: total number of lower teeth in relation to TL. Y= 21 + 0.004x, r^2= 0.4, n= 109.

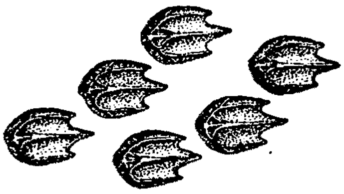


Figure 3.62 Lateral trunk denticles of *Notorynchus cepedianus*

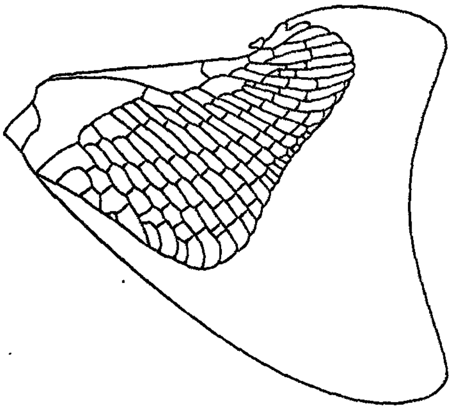
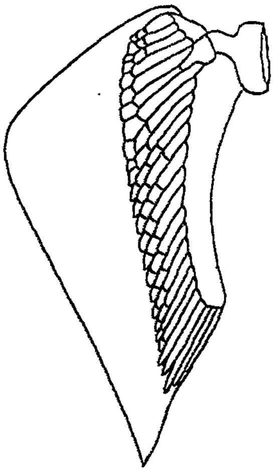


Figure 3.63 Pectoral fin skeleton of *Notorynchus cepedianus*

Figure 3.64 Pelvic fin skeleton of female *Notorynchus cepedianus*



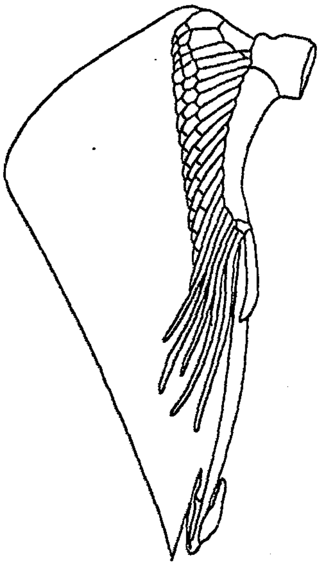
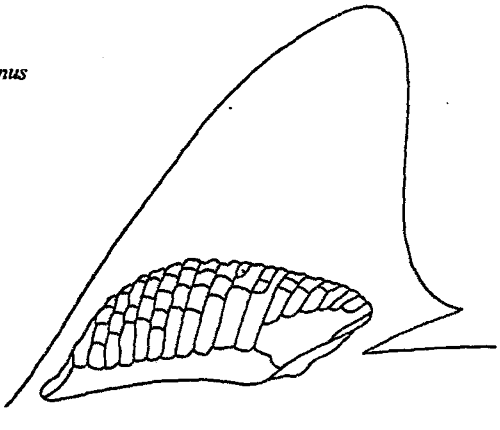


Figure 3.65 Pelvic fin and clasper skeleton of *Notorynchus cepedianus*

Figure 3.66 Dorsal fin skeleton of *Notorynchus cepedianus*



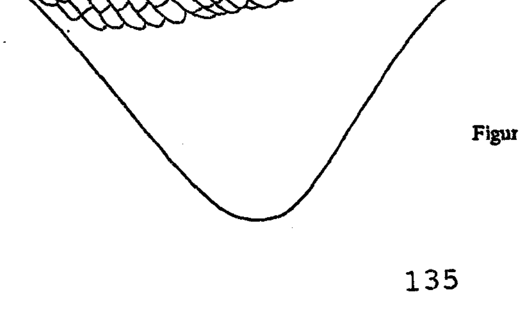


Figure 3.67 Anal fin skeleton of *Notorynchus cepedianus*

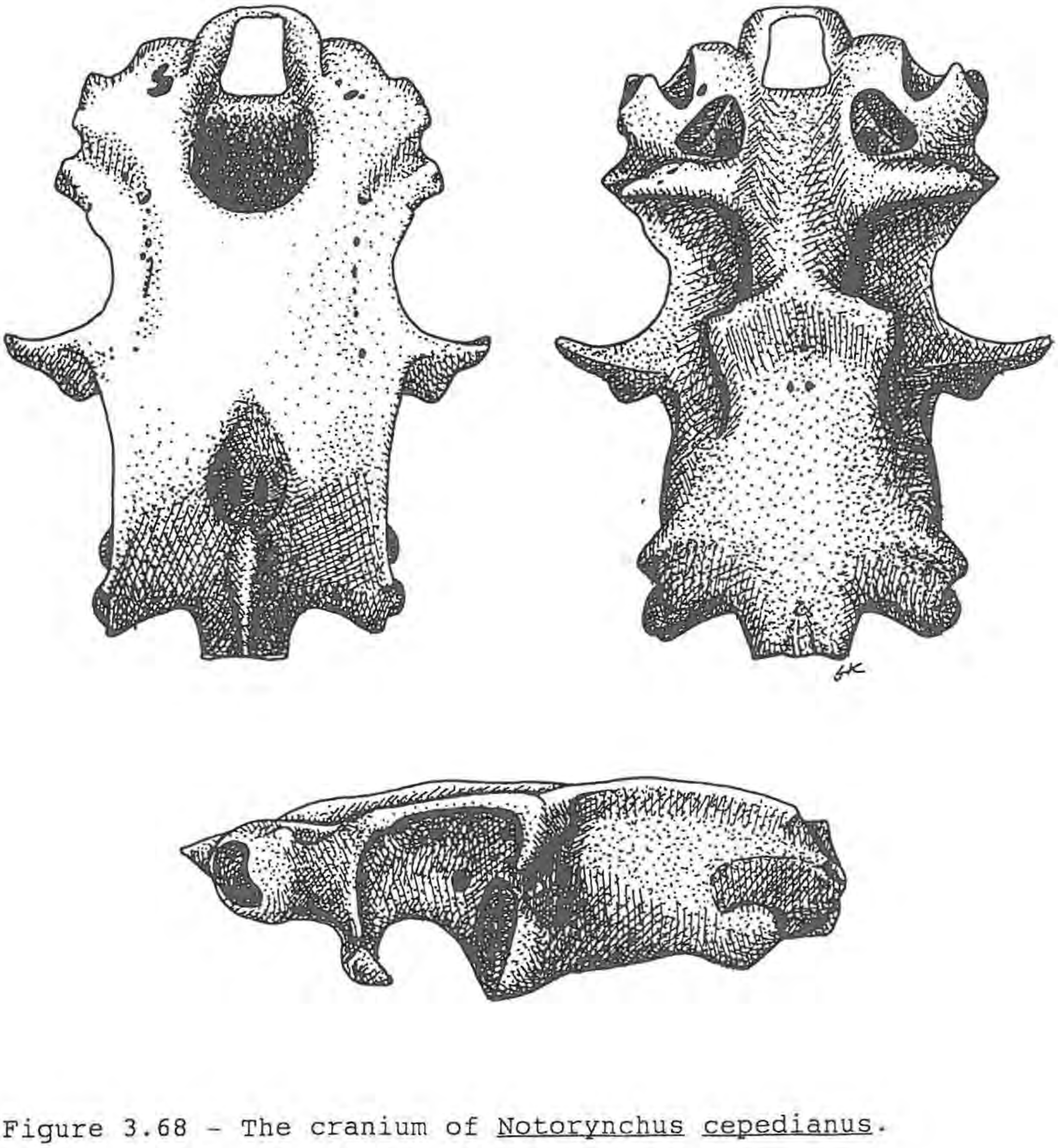


Figure 3.68 - The cranium of Notorynchus cepedianus.

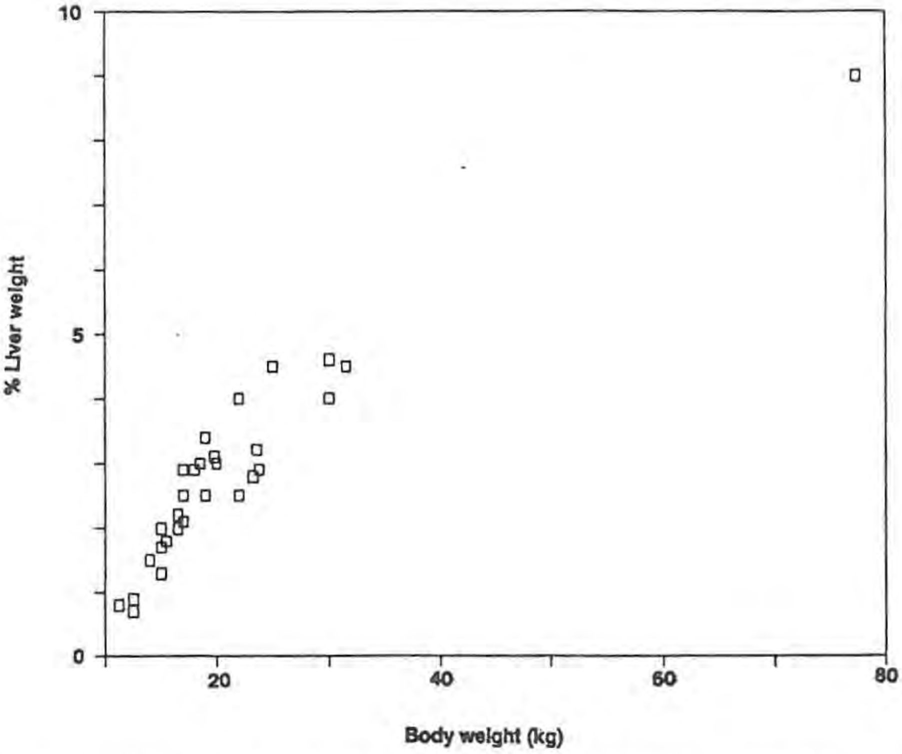


Figure 3.69a - Proportion of liver weight to body weight in male Notorynchus cepedianus. Y= 11 + 0.008x, r^2= 0.8, n= 30.

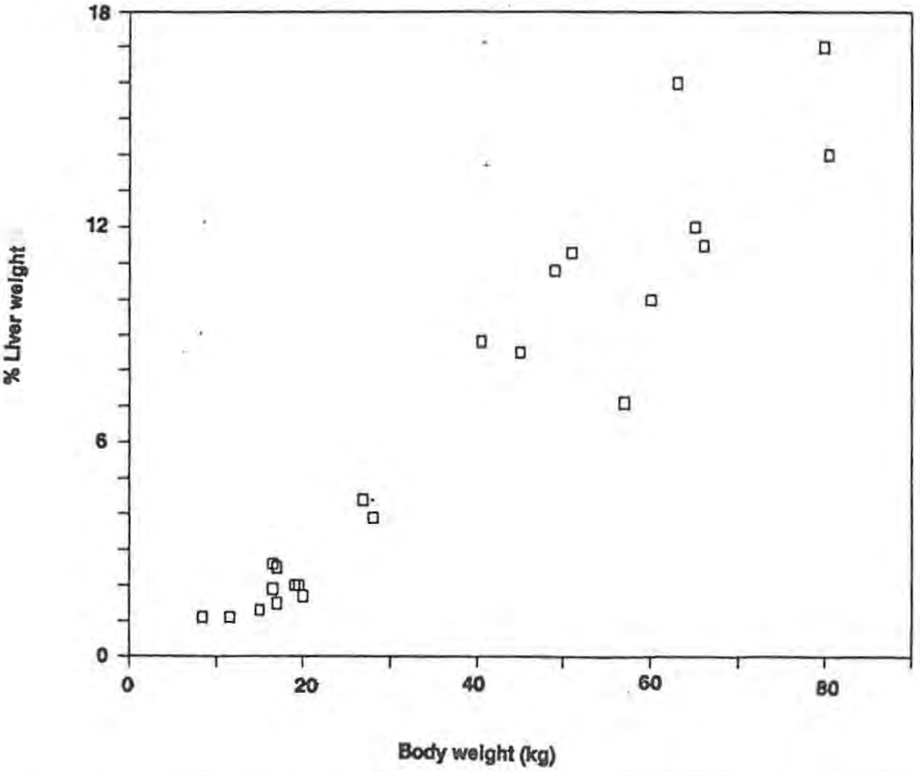


Figure 3.69b - Proportion of liver weight to body weight in female Notorynchus cepedianus. Y= 20 + 0.014x, r^2= 0.8, n= 24.

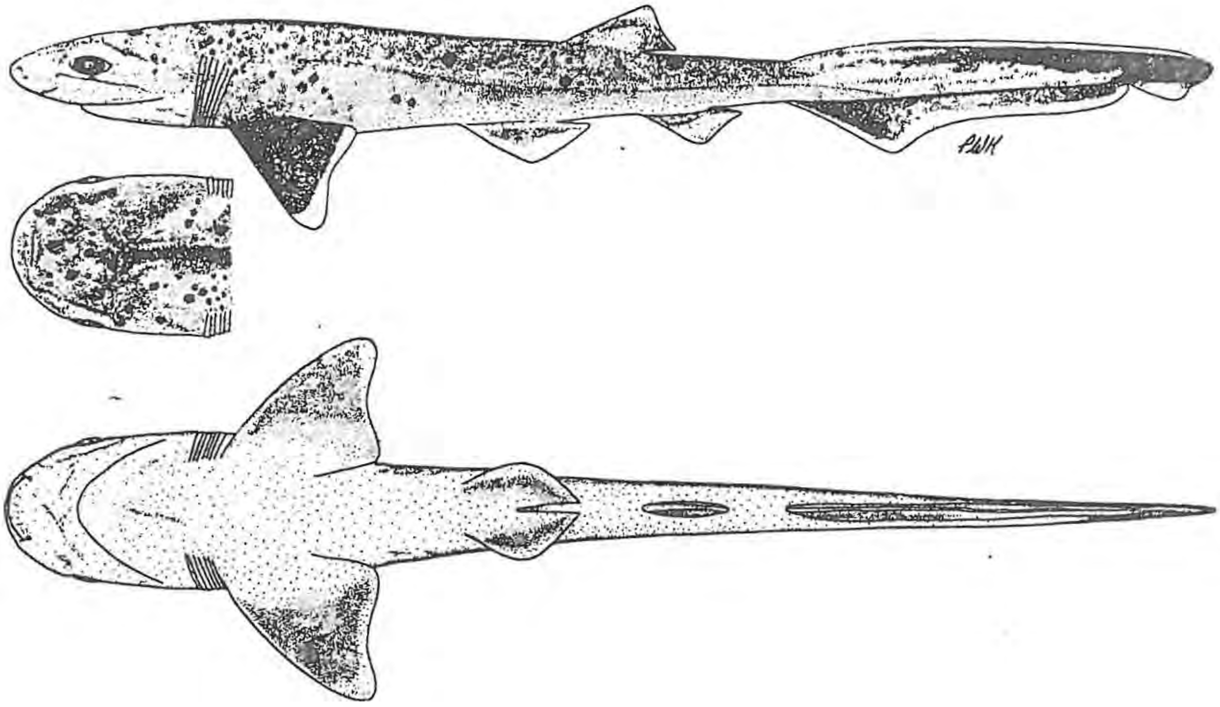


Figure 3.70 Color pattern of newborn Notorynchus cepedianus.

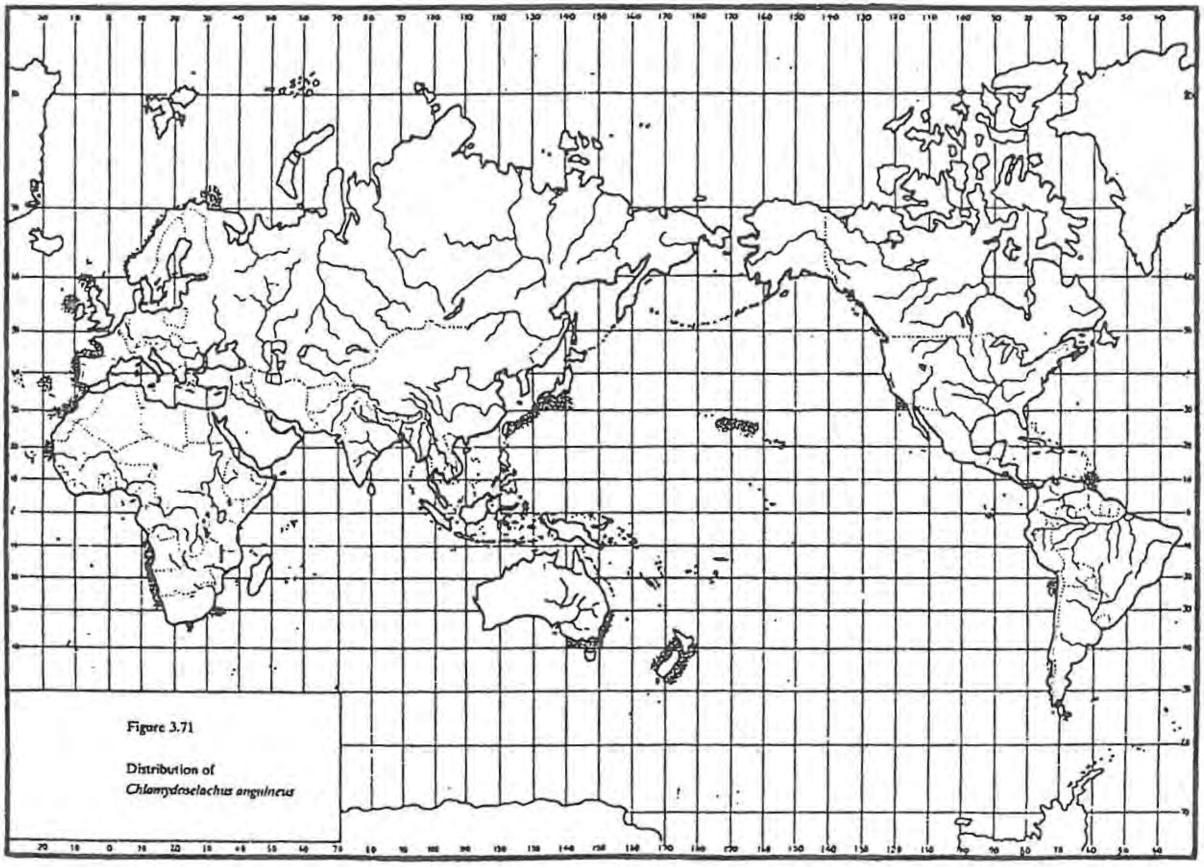


Figure 3.71

Distribution of *Chlamydoselachus anguineus*

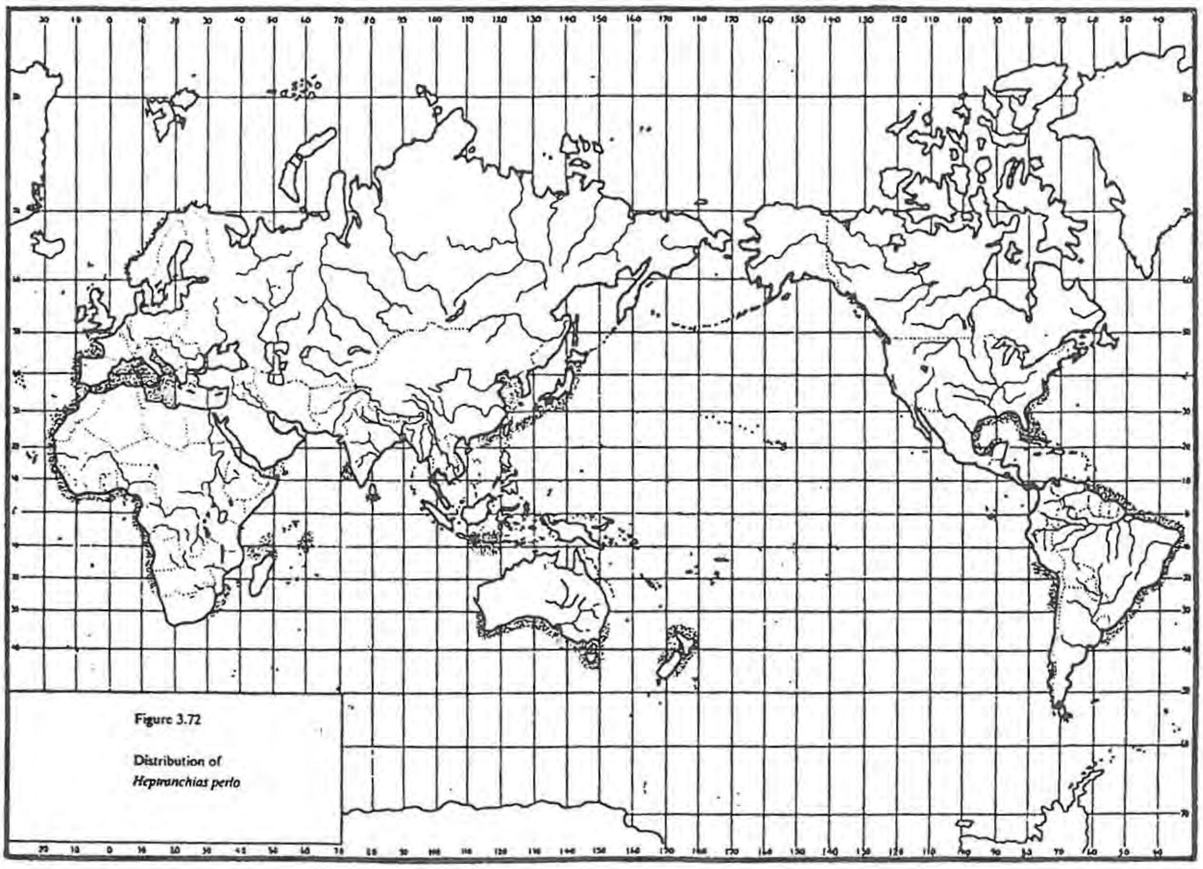


Figure 3.72

Distribution of *Heptranchias perlo*

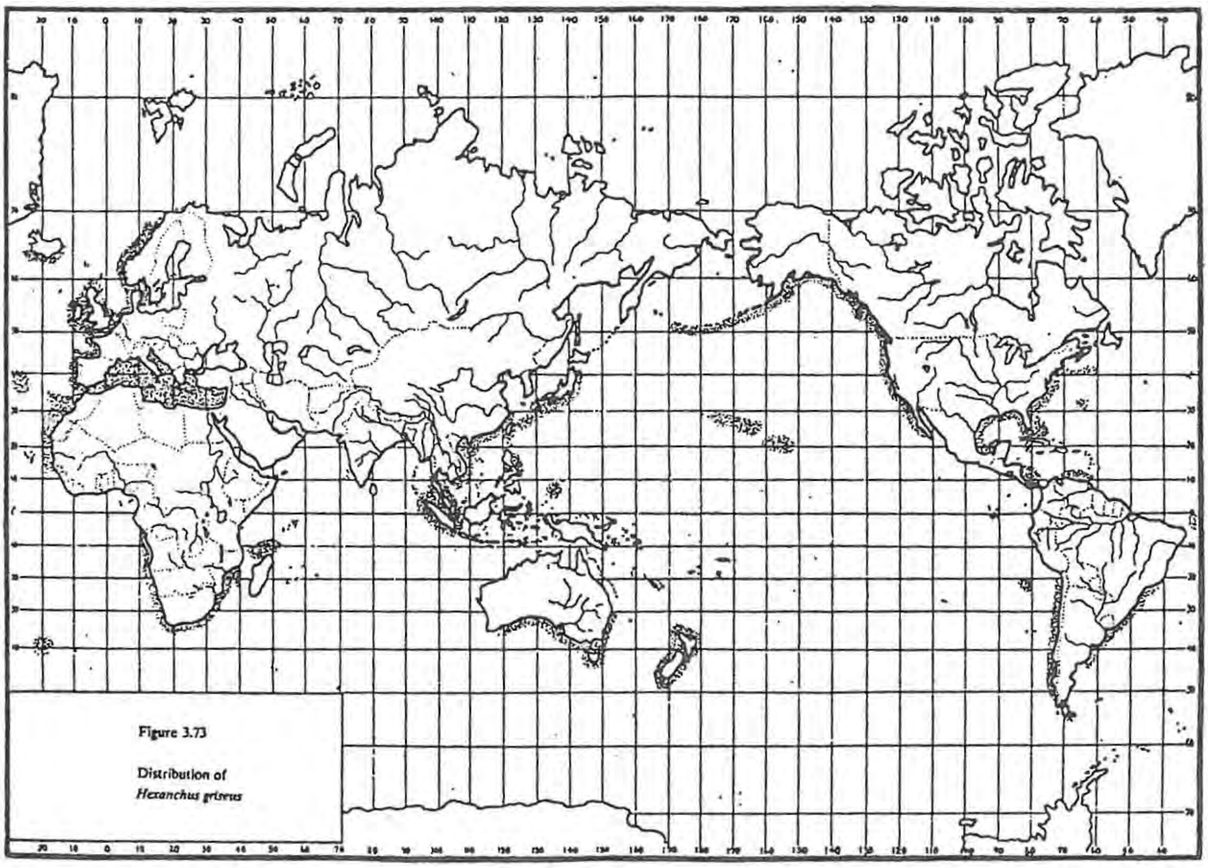


Figure 3.73

Distribution of *Hexanchus griseus*

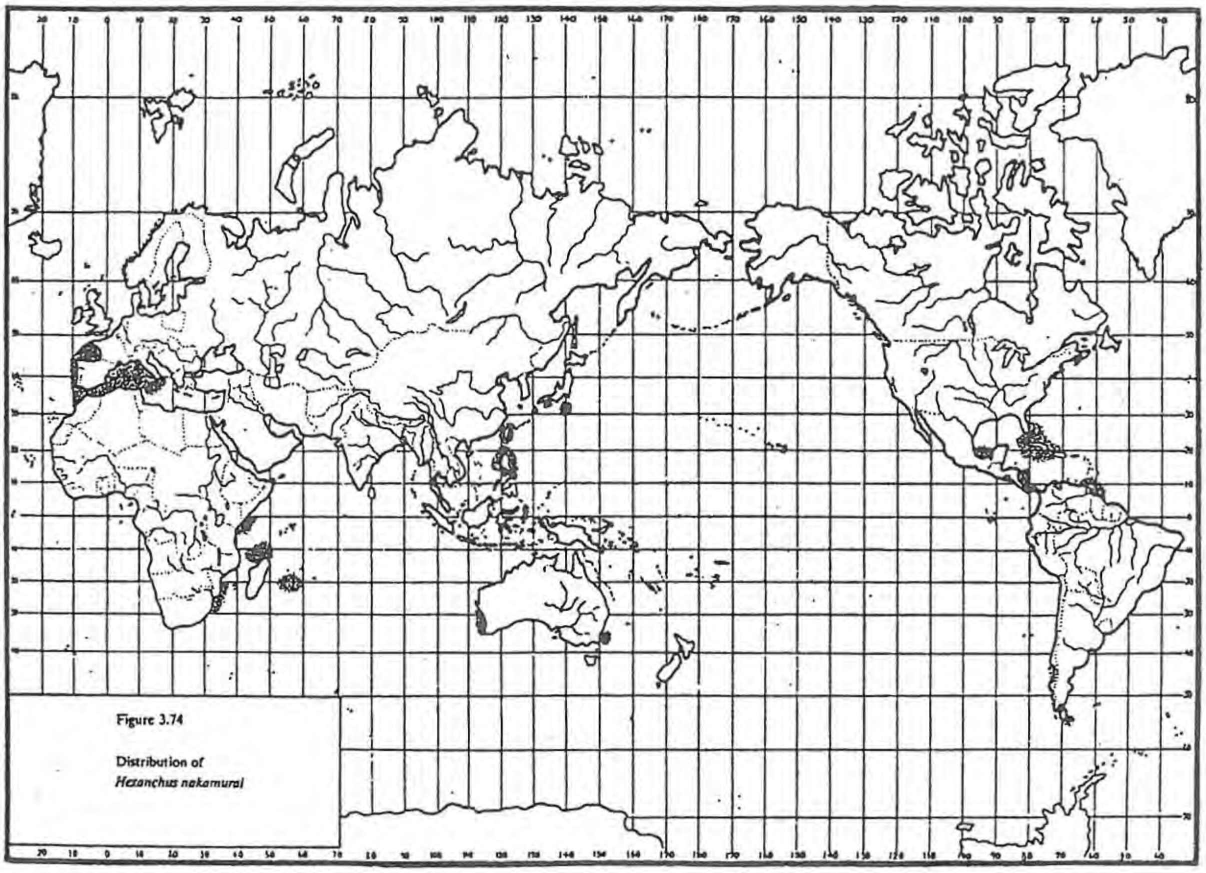


Figure 3.74

Distribution of
Hexanchus nakamurai

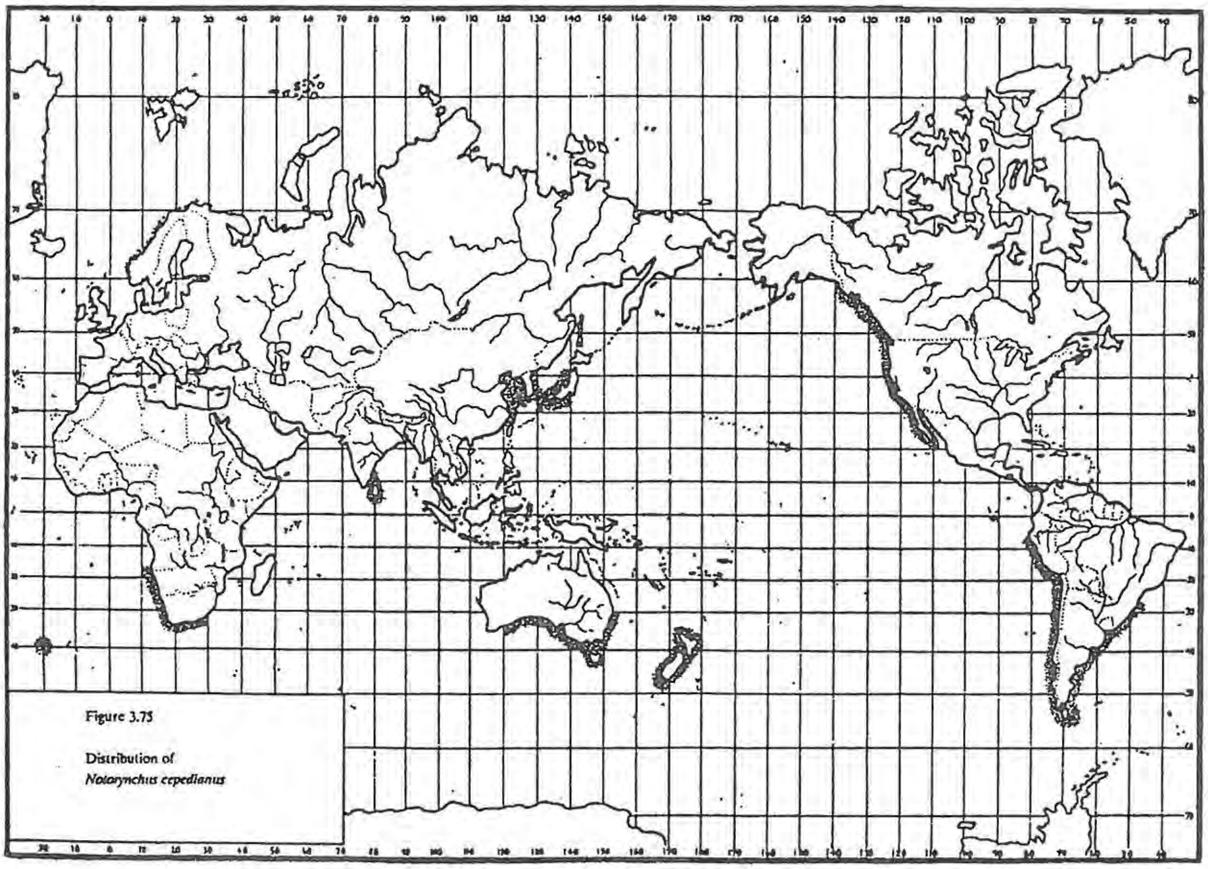


Figure 3.75

Distribution of
Notorynchus cepedianus

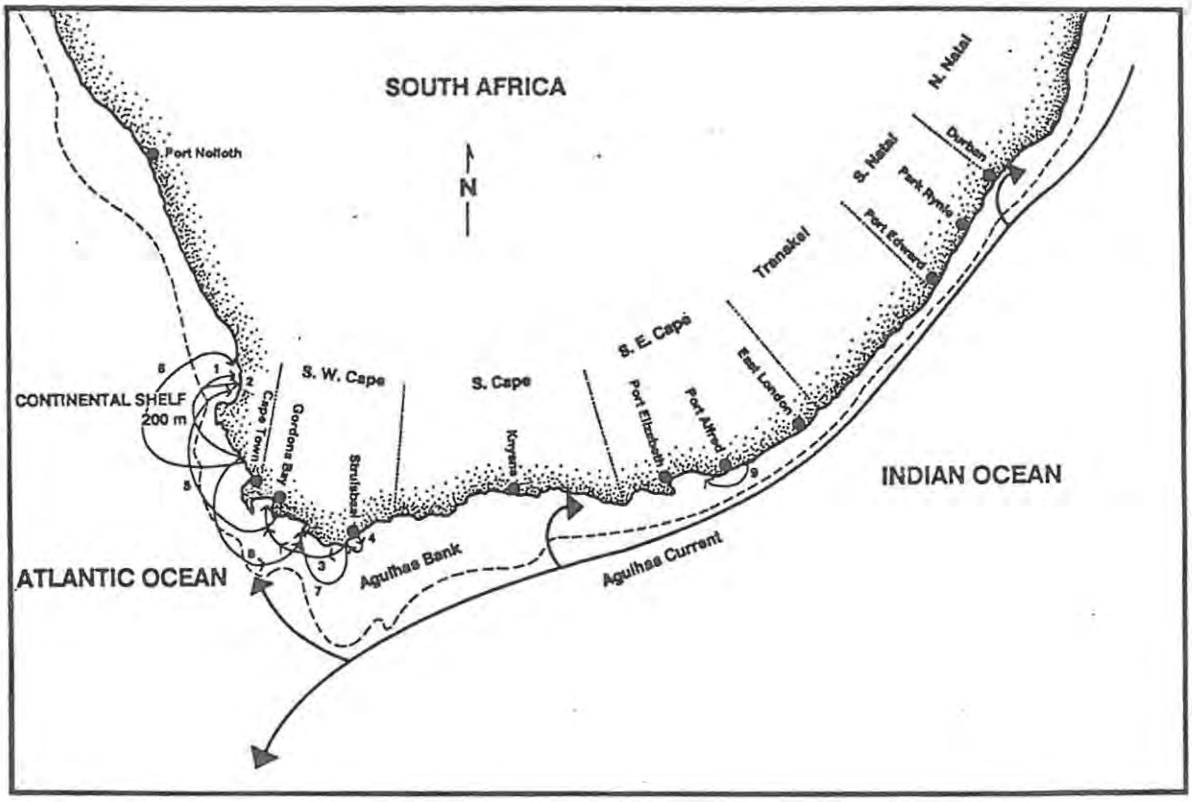


Figure 3.76 - Movement patterns of <u>Notorynchus</u> <u>cepedianus</u> along the Cape coast of Southern Africa.

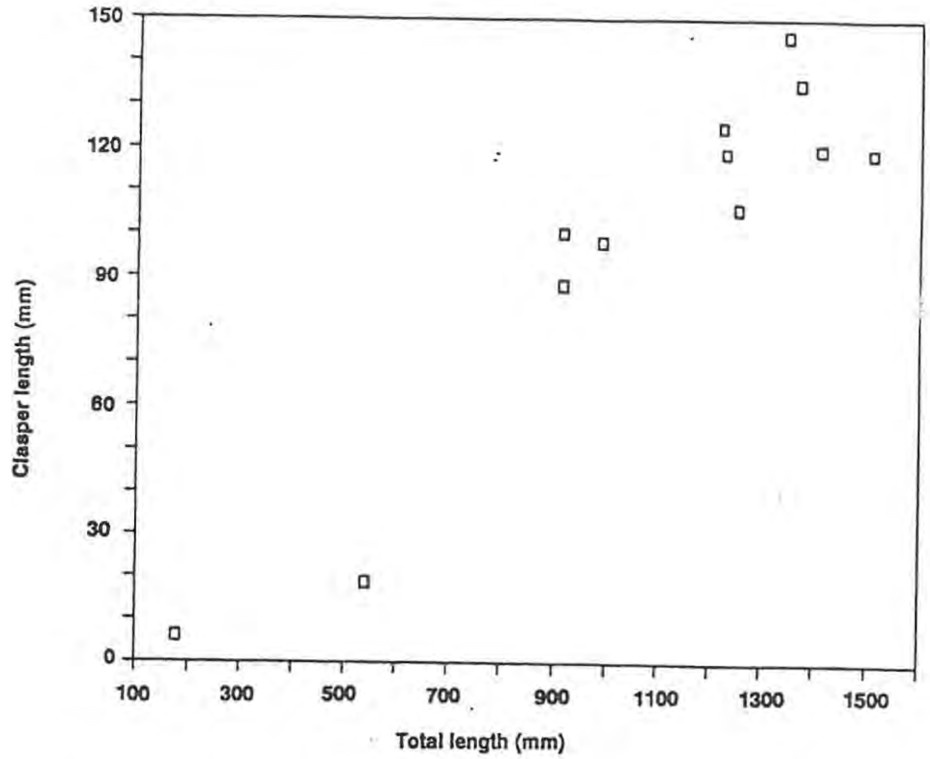


Figure 3.77 - Relationship of inner clasper length to TL in Chlamydoselachus anguineus.

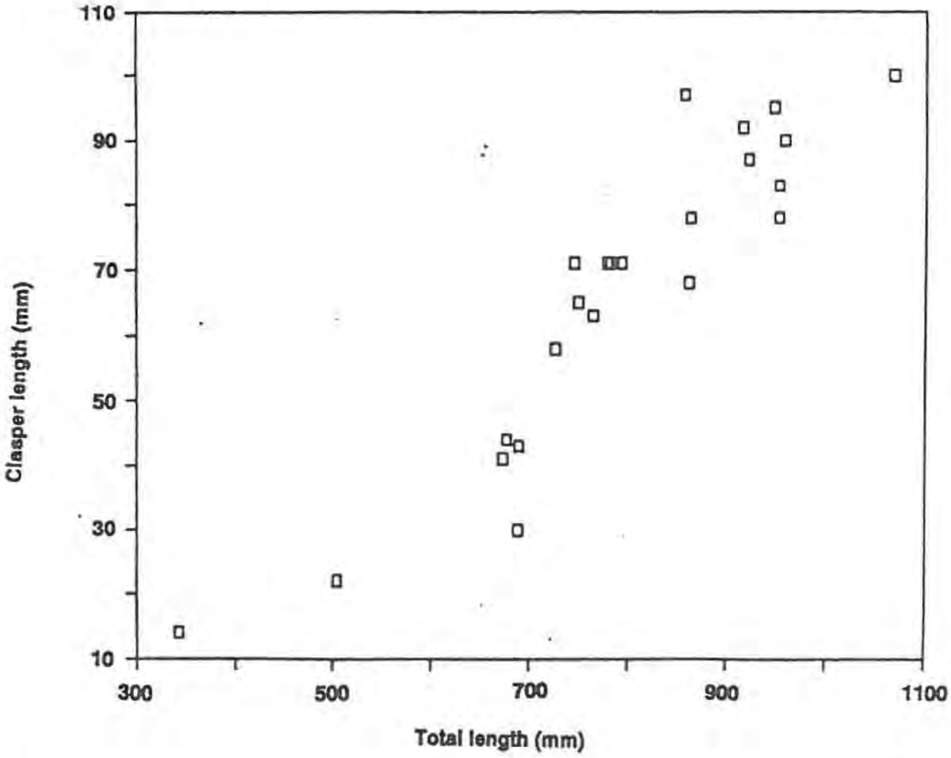


Figure 3.78 - Relationship of inner clasper length to TL in Heptranchias perlo.

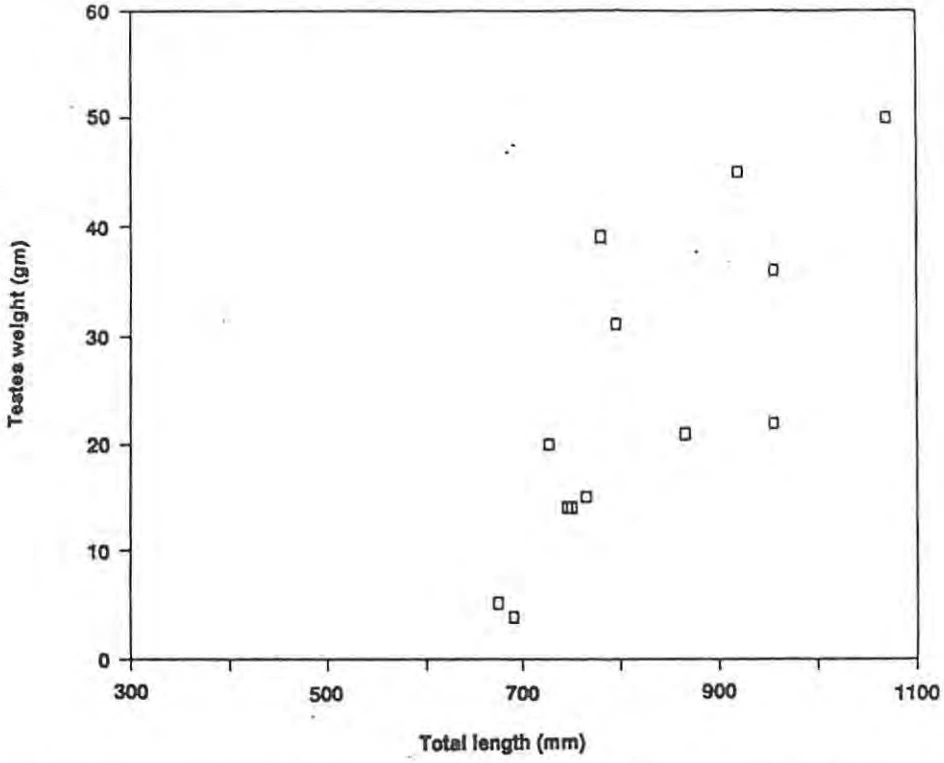


Figure 3.79 - Relationship of testes weight to TL in <u>Heptranchias perlo</u>. Wt.= $(4.9 \times 10^{-12})L^{4.3}$, $r^2 = 0.8$, n= 13.

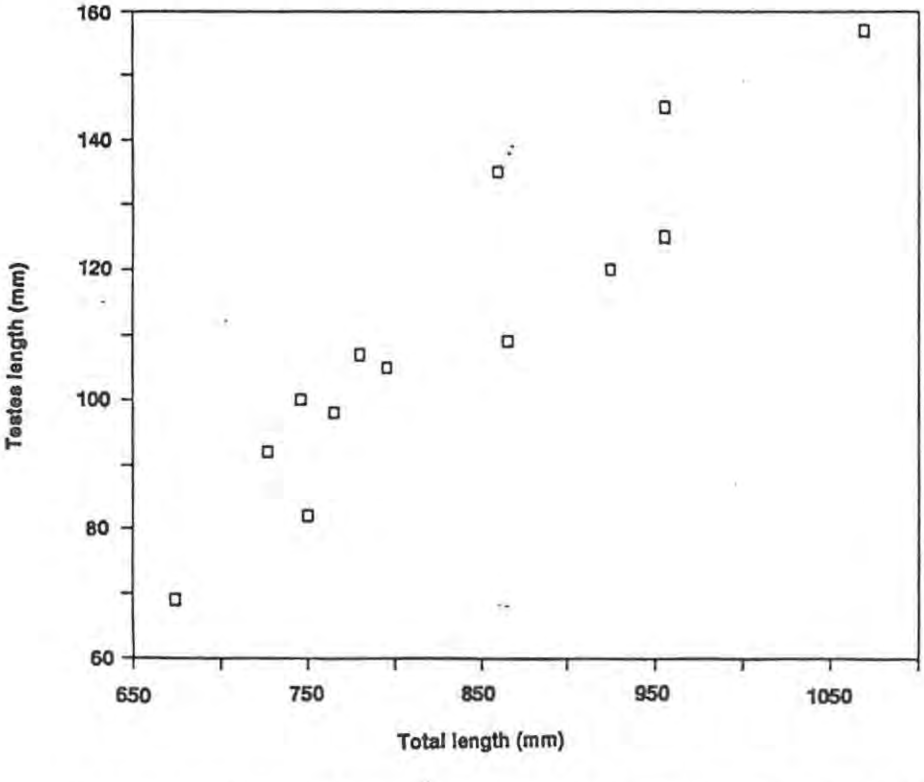


Figure 3.80 - Relationship of testes length to TL in <u>Heptranchias perlo</u>. $Y = 68 + (0.2)x$, $r^2 = 0.9$, n= 14.

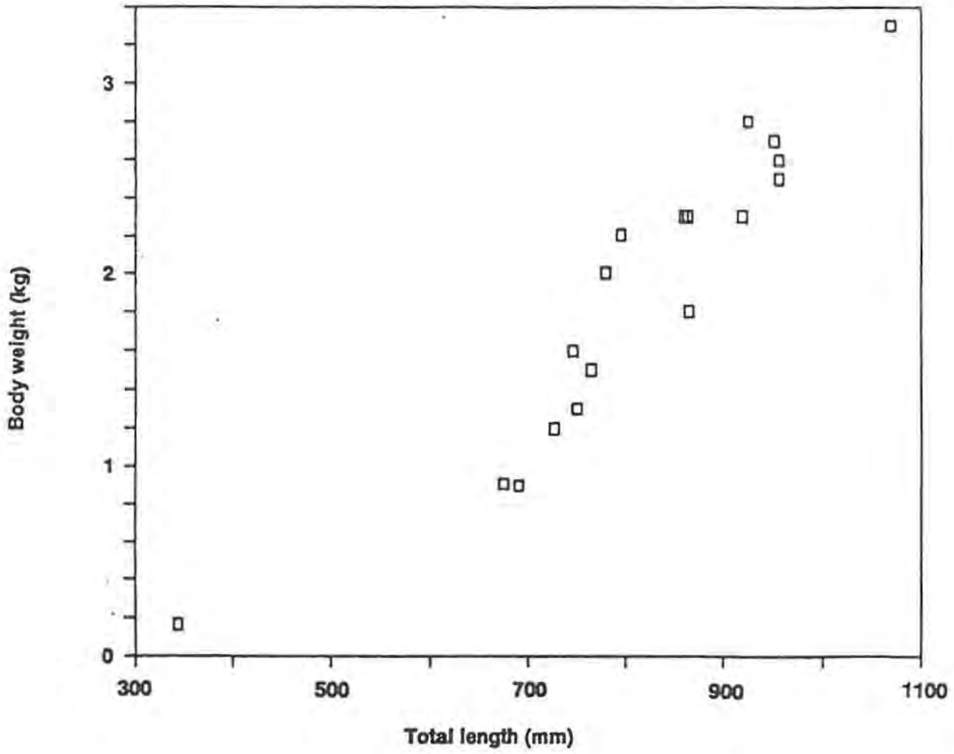


Figure 3.81 - Relationship of body weight to TL in male <u>Heptranchias perlo</u>. Wt.= $(5 \times 10^{-8})L^{2.6}$, $r^2= 1.0$, n= 18.

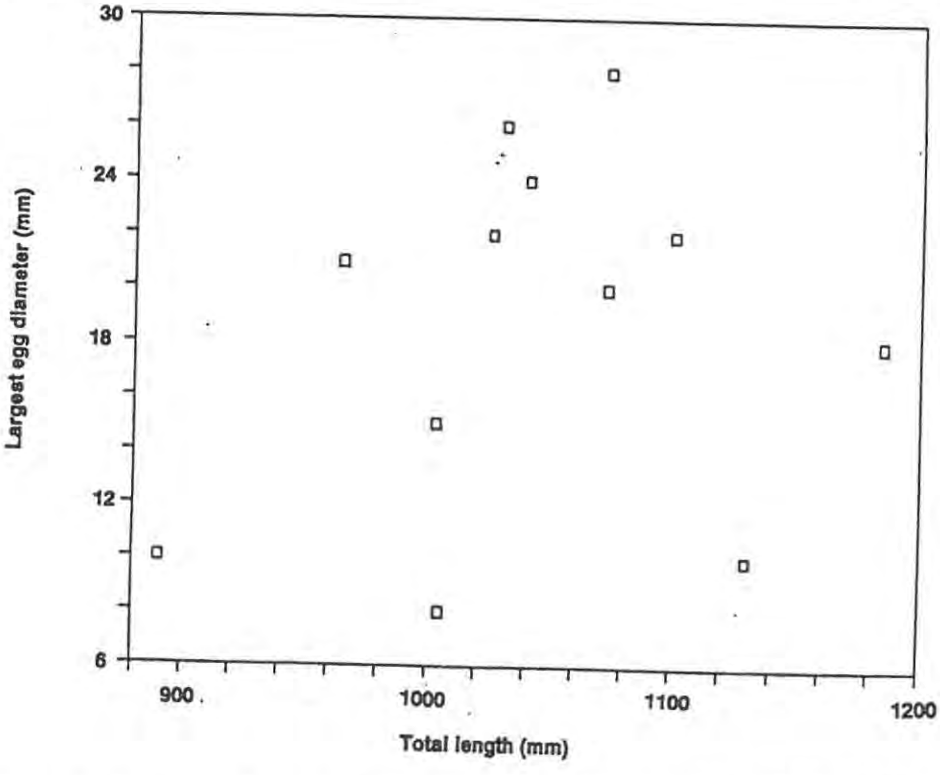


Figure 3.82 - Relationship of largest ovarian egg diameter to TL in <u>Heptranchias perlo</u>.

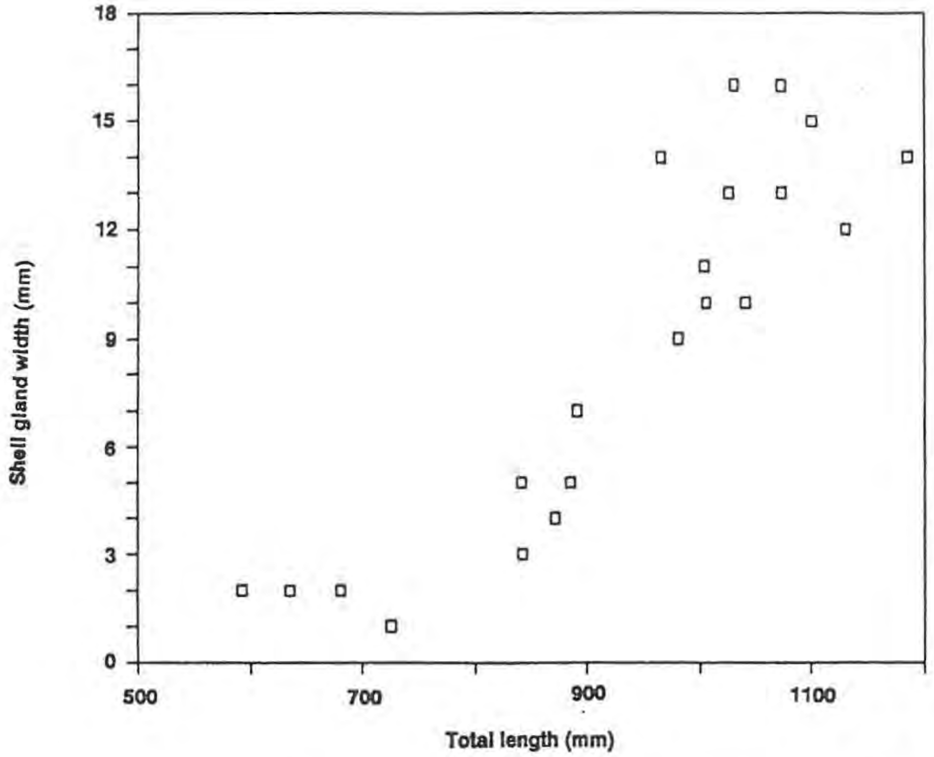


Figure 3.83 - Relationship of shell gland width to TL in Heptranchias perlo.

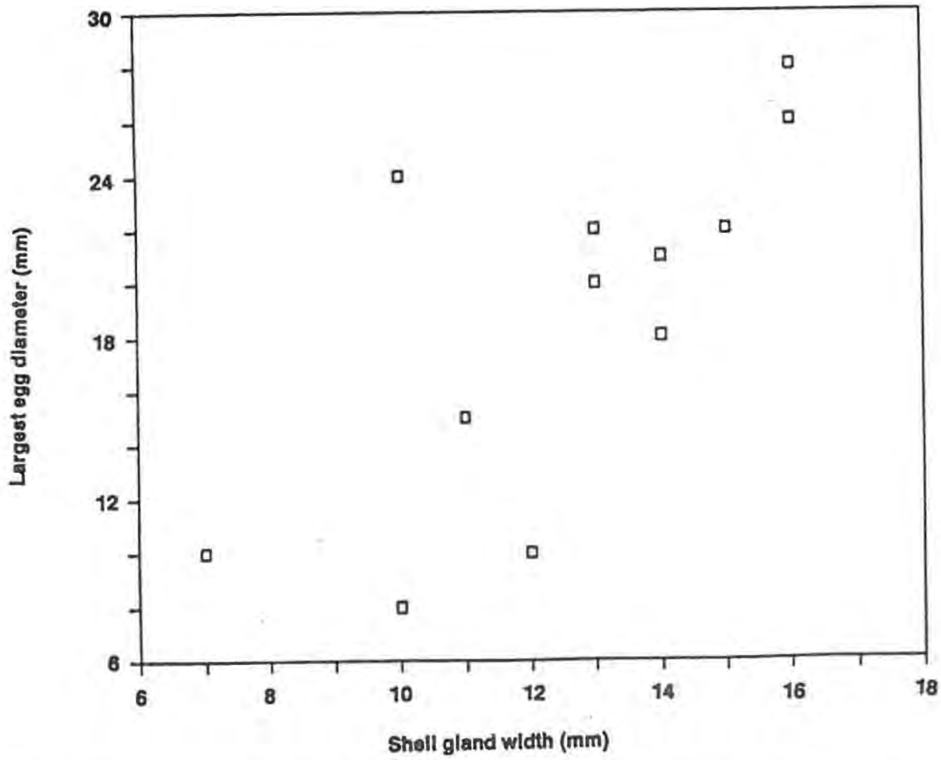


Figure 3.84 - Relationship of shell gland width to largest ovarian egg diameter in Heptranchias perlo.

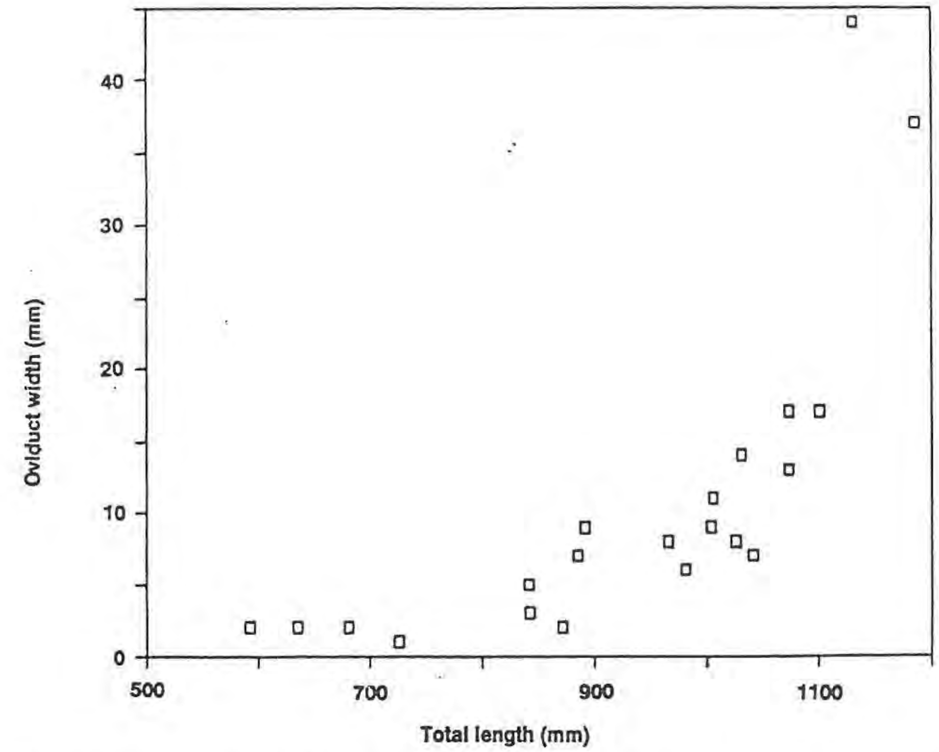


Figure 3.85 - Relationship of oviduct width to TL in <u>Heptranchias perlo</u>.

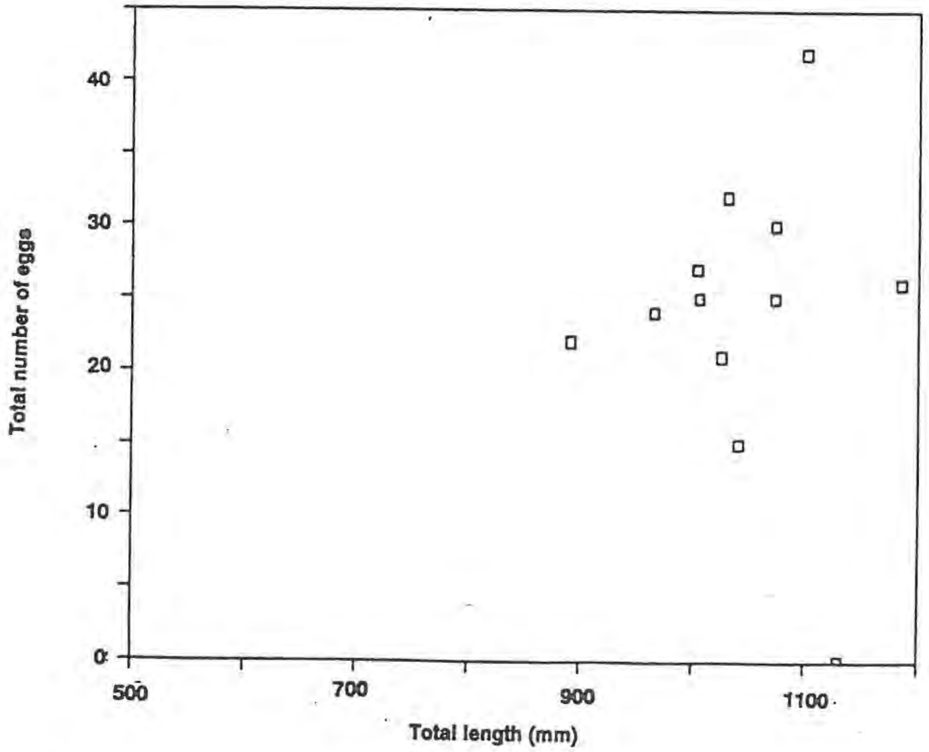


Figure 3.86 - Relationship of total number of ovarian eggs to TL in <u>Heptranchias perlo</u>. Y= 4.5 + (3.2 x 10^{-13})x, r^2= 0.9, n= 21.

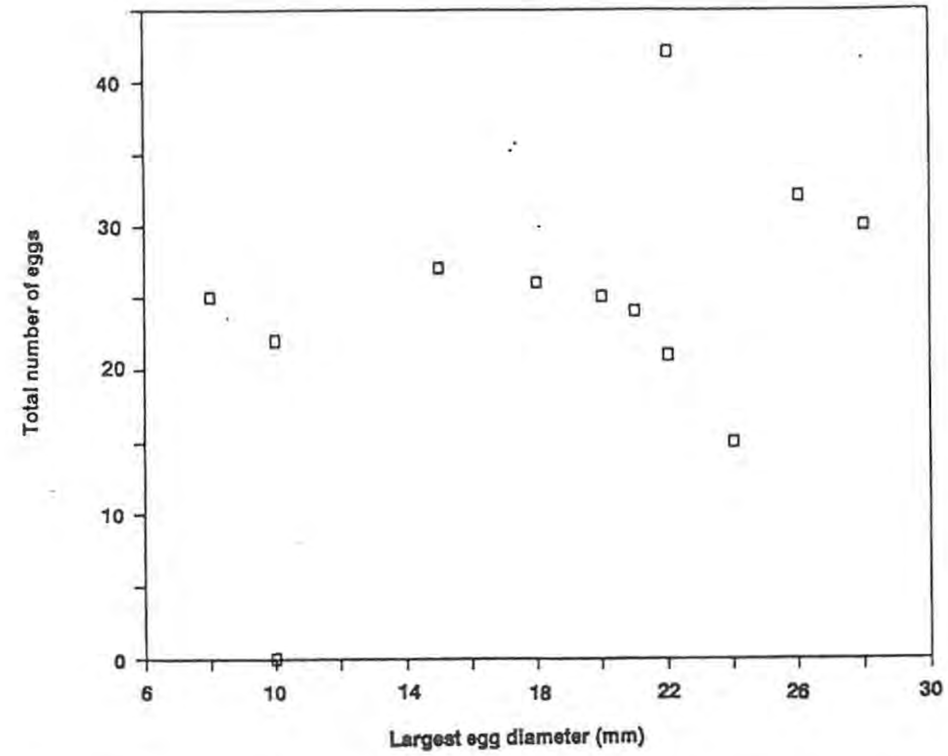


Figure 3.87 - Relationship of total number of ovarian eggs to largest ovarian egg diameter in Heptranchias perlo. $Y= 9.5 + (0.8)x$, $r^2= 0.2$, $n= 11$.

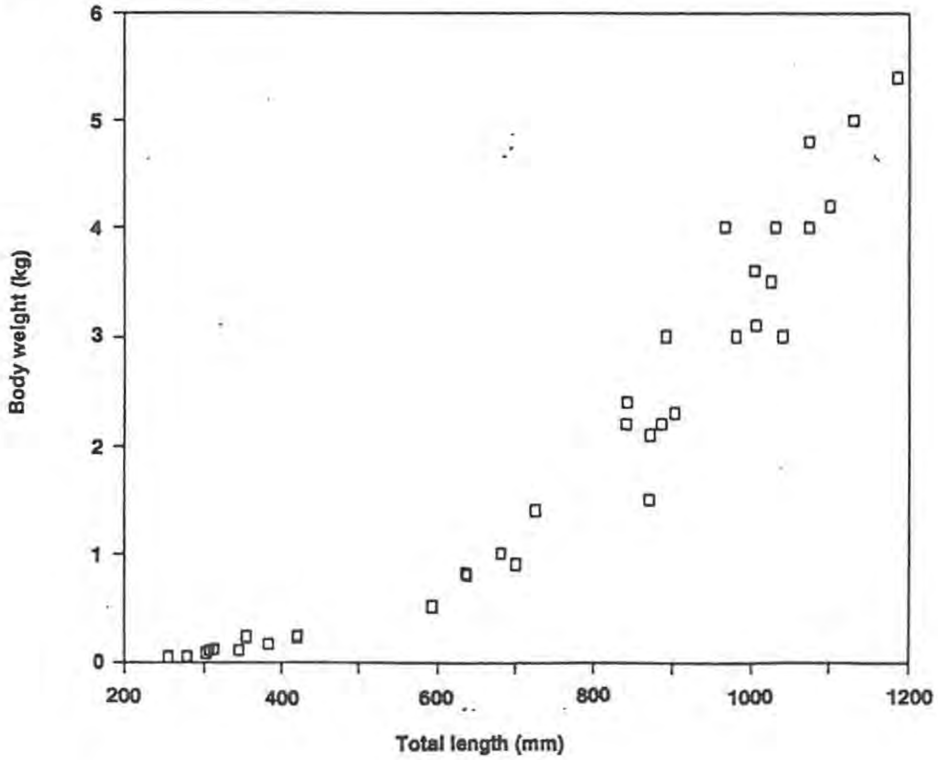


Figure 3.88 - Relationship of body weight to TL in female Heptranchias perlo. $Wt.= (6.7 \times 10^{-9})L^{2.9}$, $r^2= 1.0$, $n= 35$.

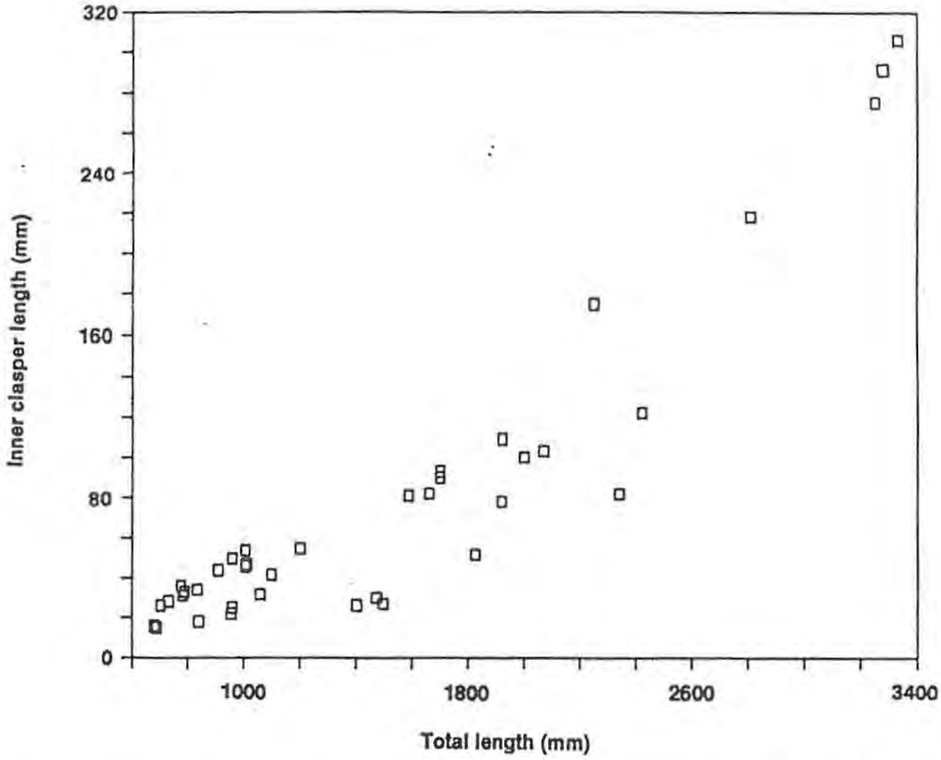


Figure 3.89 - Relationship of inner clasper length to TL in Hexanchus griseus.

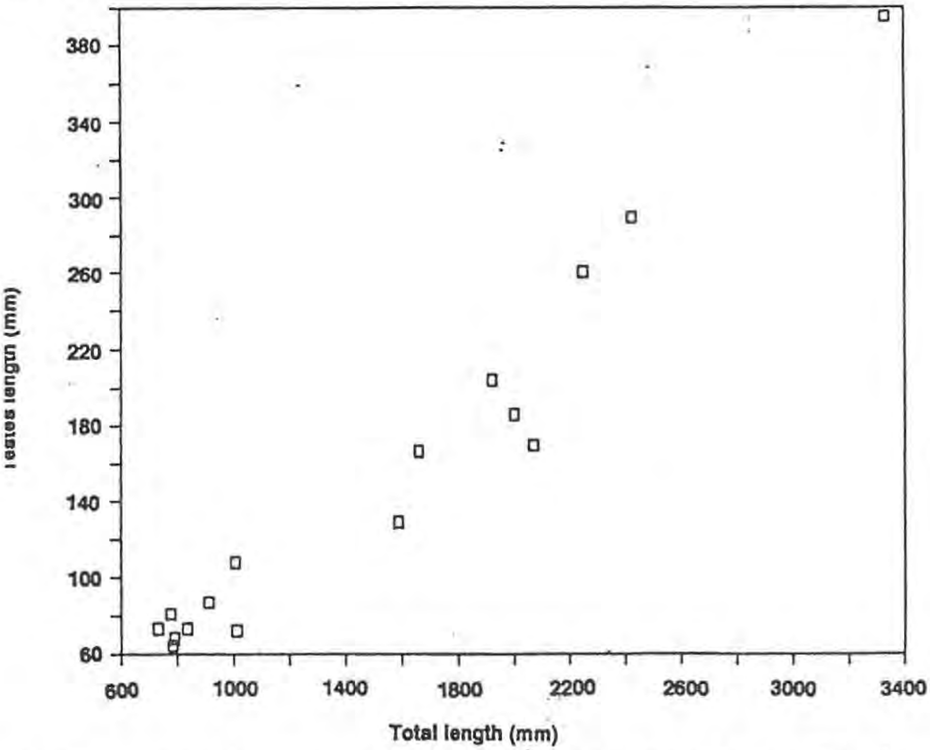


Figure 3.90 - Relationship of testes length to TL in Hexanchus griseus. $Y= 31 + (0.1)x$, $r^2= 1.0$, $n= 16$.

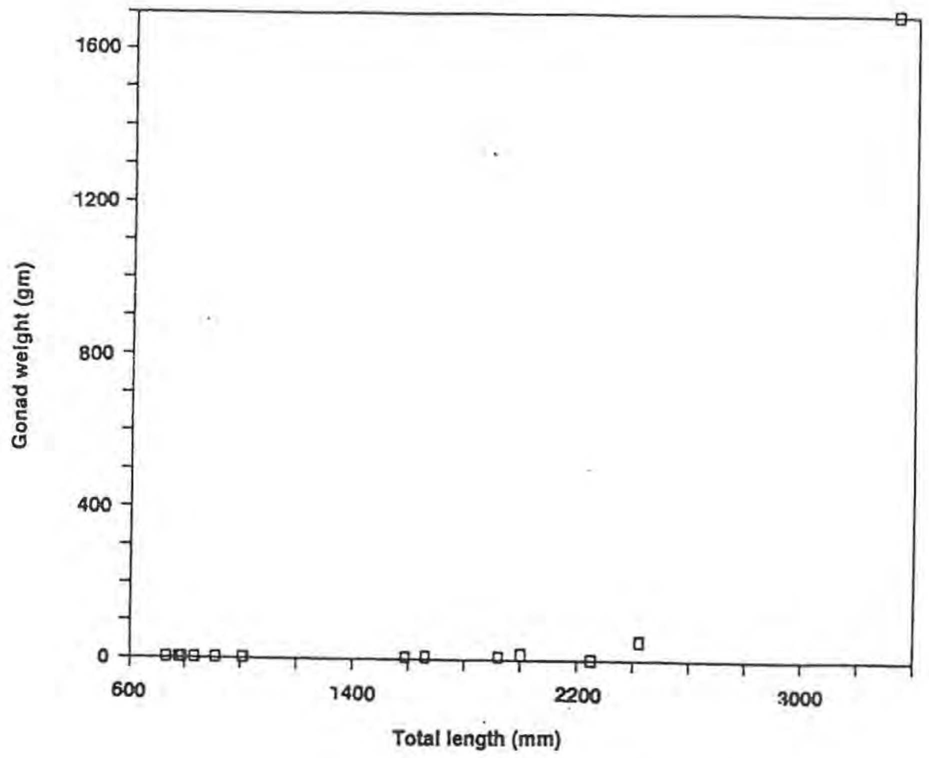


Figure 3.91 - Relationship of testes weight to TL in <u>Hexanchus griseus</u>. Wt.= $(1.4 \times 10^{-10})L^{3.5}$, $r^2 = 1.0$, n= 36.

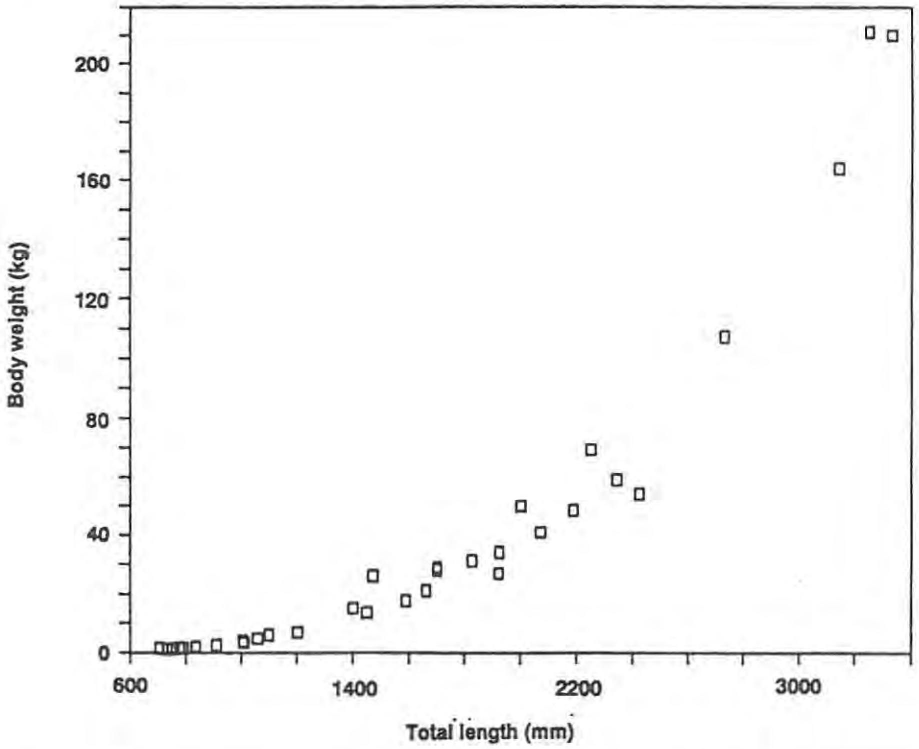


Figure 3.92 - Relationship of body weight to TL in male <u>Hexanchus griseus</u>. Wt.= $(3.3 \times 10^{-13})L^{4.2}$, $r^2 = 0.9$, n= 14.

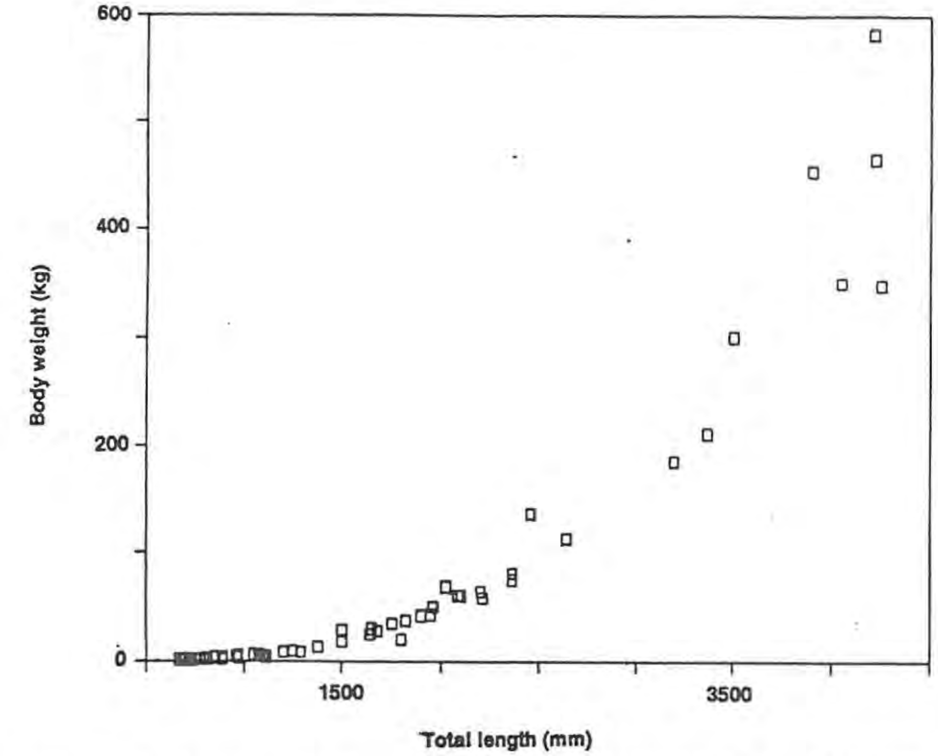


Figure 3.93 - Relationship of body weight to TL in female Hexanchus griseus. Wt.= $(1.7 \times 10^{-10})L^{3.5}$, r^2= 1.0, n= 59.

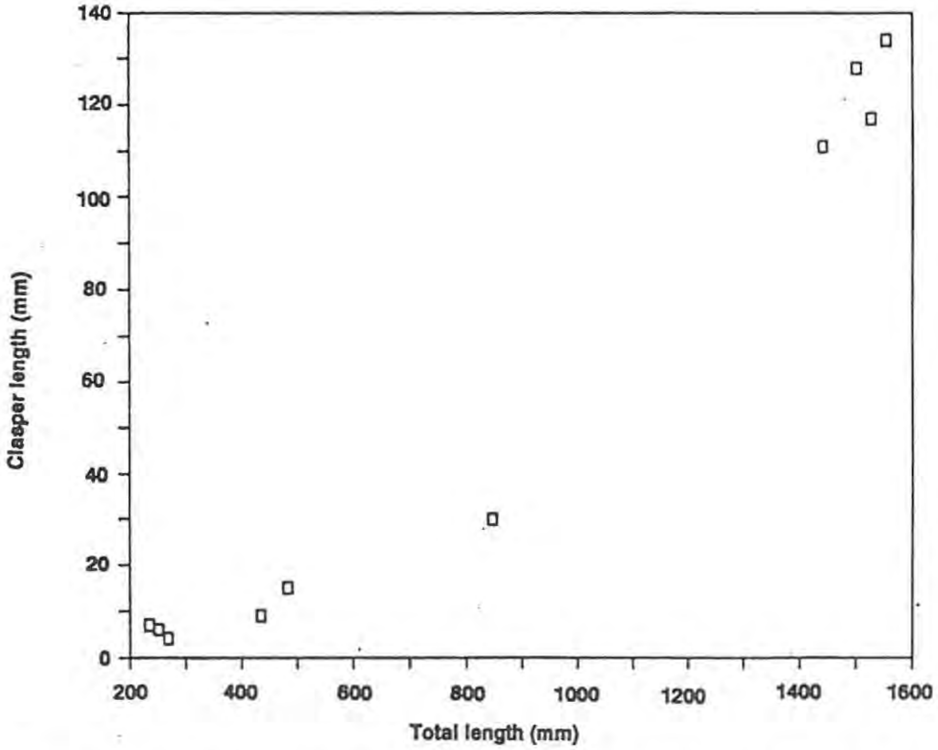


Figure 3.94 - Relationship of inner clasper length to TL in Hexanchus nakamurai.

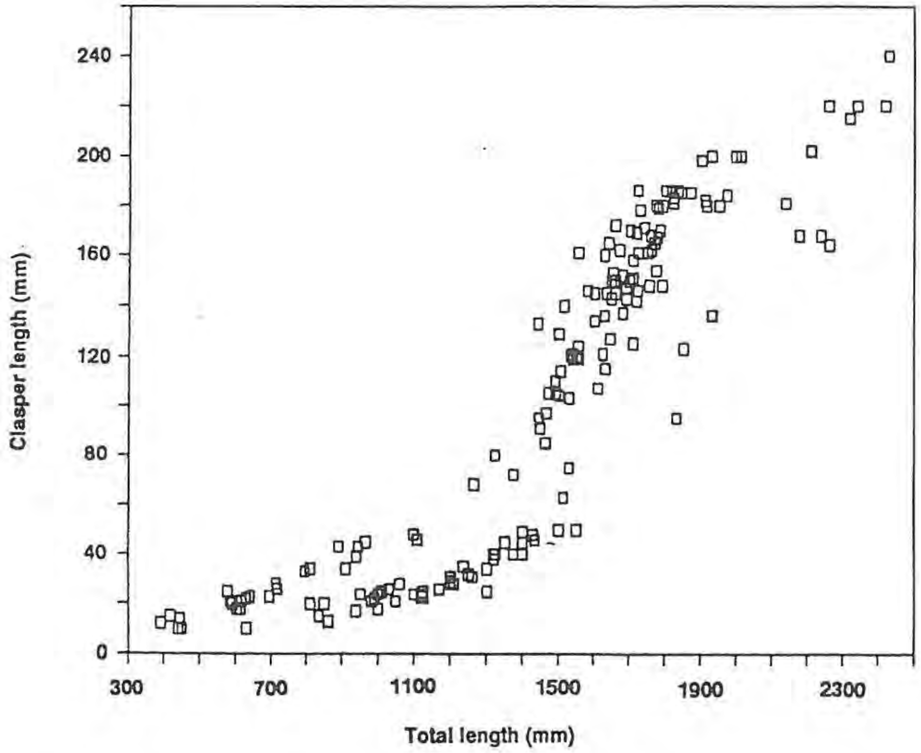


Figure 3.95 - Relationship of inner clasper length to TL in Notorynchus cepedianus.

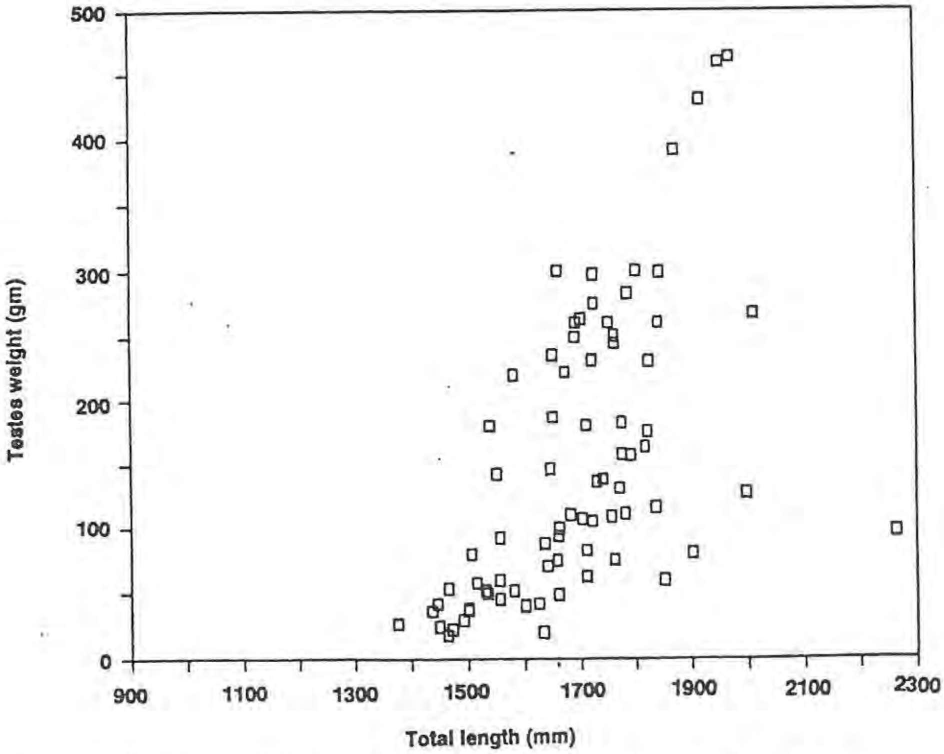


Figure 3.96 - Relationship of testes weight to TL in Notorynchus cepedianus. Wt.= $(1.2 \times 10^{-18})L^{6.2}$, r^2= 0.7, n= 76.

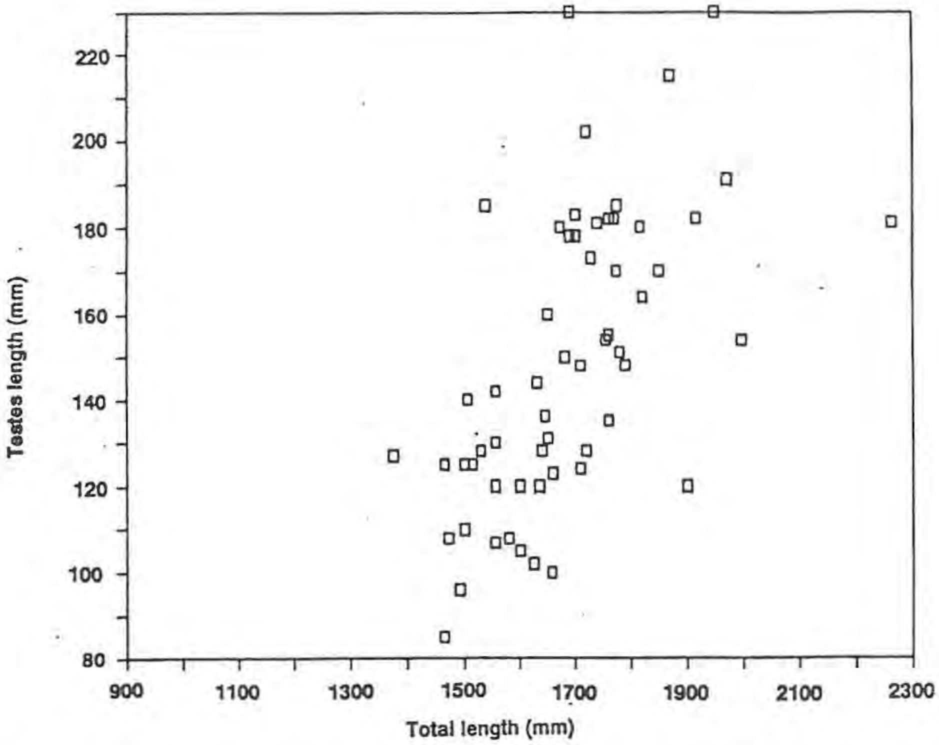


Figure 3.97 - Relationship of testes length to TL in <u>Notorynchus cepedianus</u>. Y= 70 + (0.1)x, r^2= 0.4, n= 58.

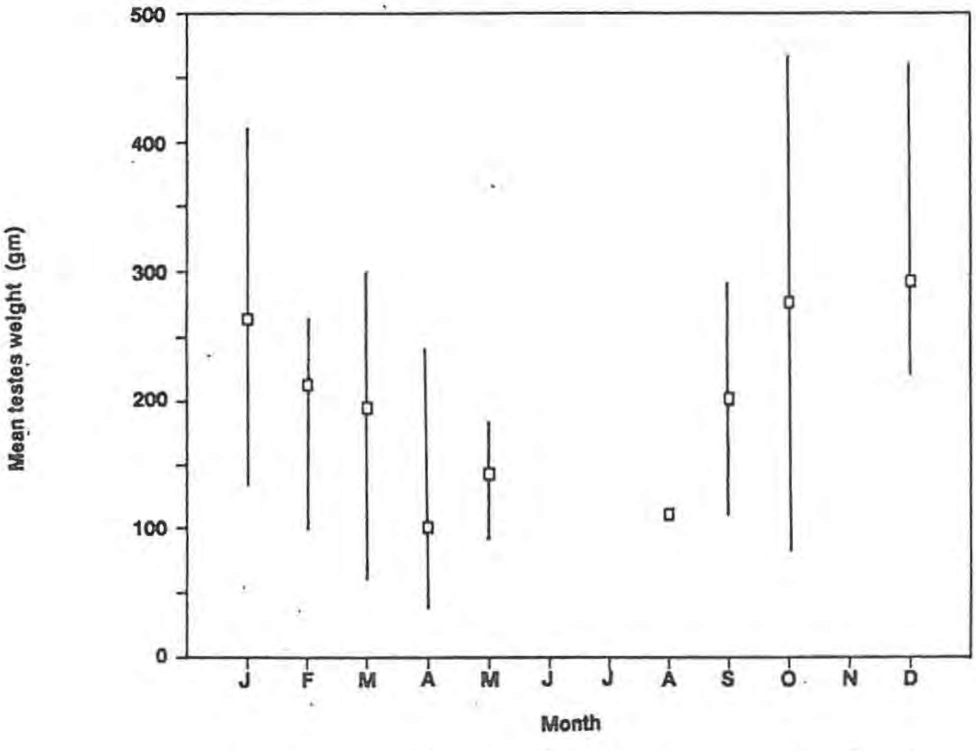


Figure 3.98 Mean monthly testes weight in <u>Notorynchus cepedianus</u> (bars represent the range).

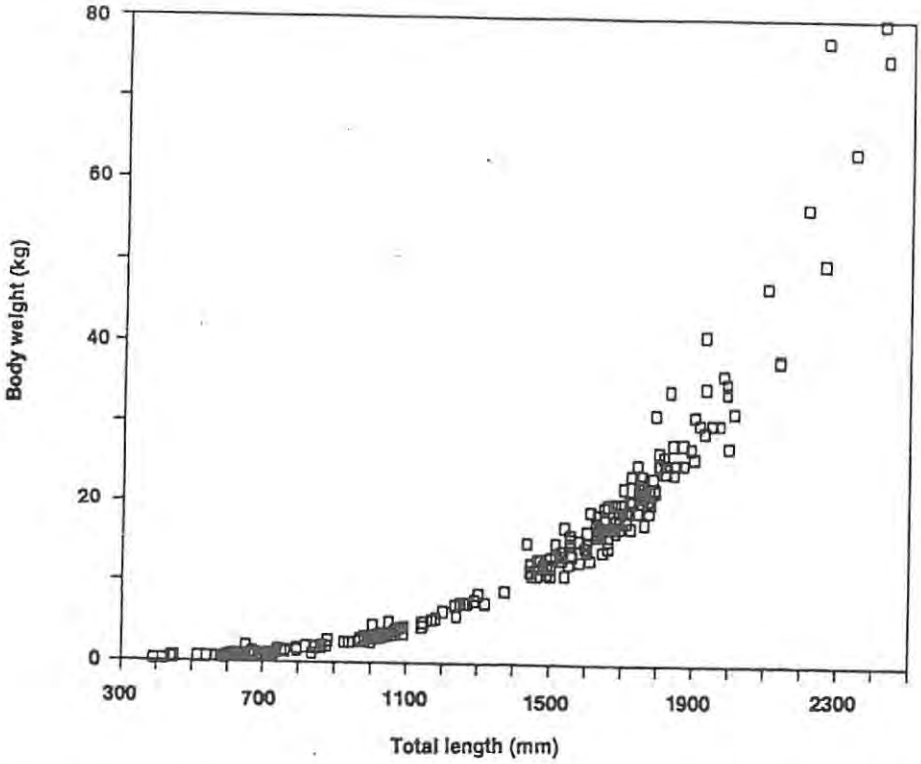


Figure 3.99 - Relationship of body weight to TL in male Notorynchus cepedianus. Wt.= $(5.3 \times 10^{-10})L^{3.3}$, $r^2 = 1.0$, n= 260.

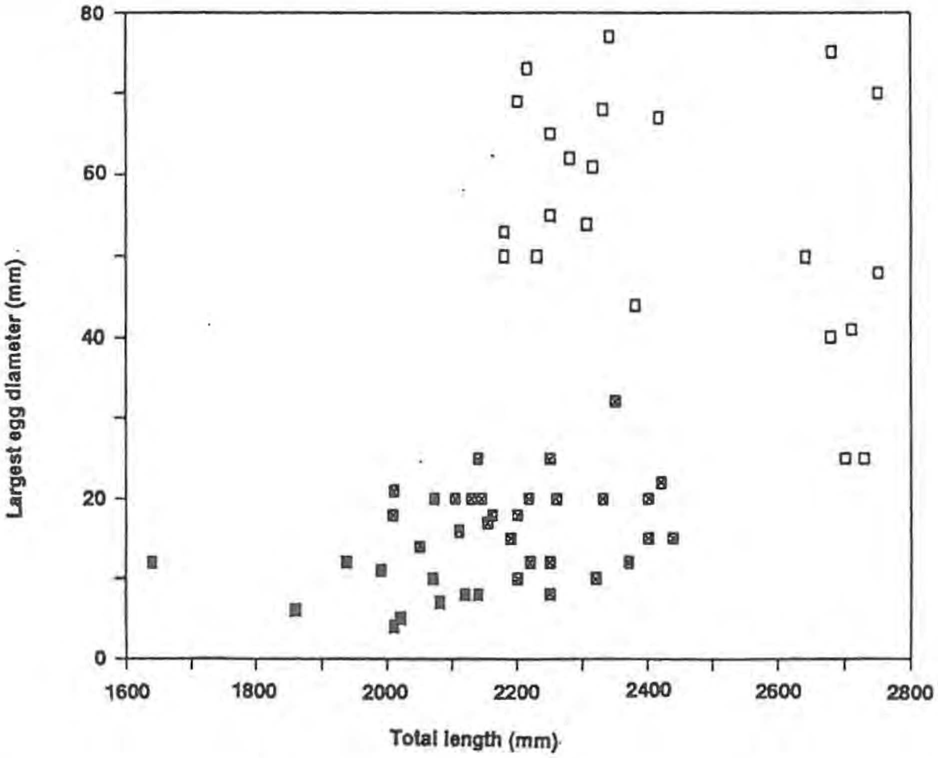


Figure 3.100 - Relationship of largest ovarian egg diameter to TL in Notorynchus cepedianus (■, adolescent, ⊠, non-breeding adult, □, breeding adult).

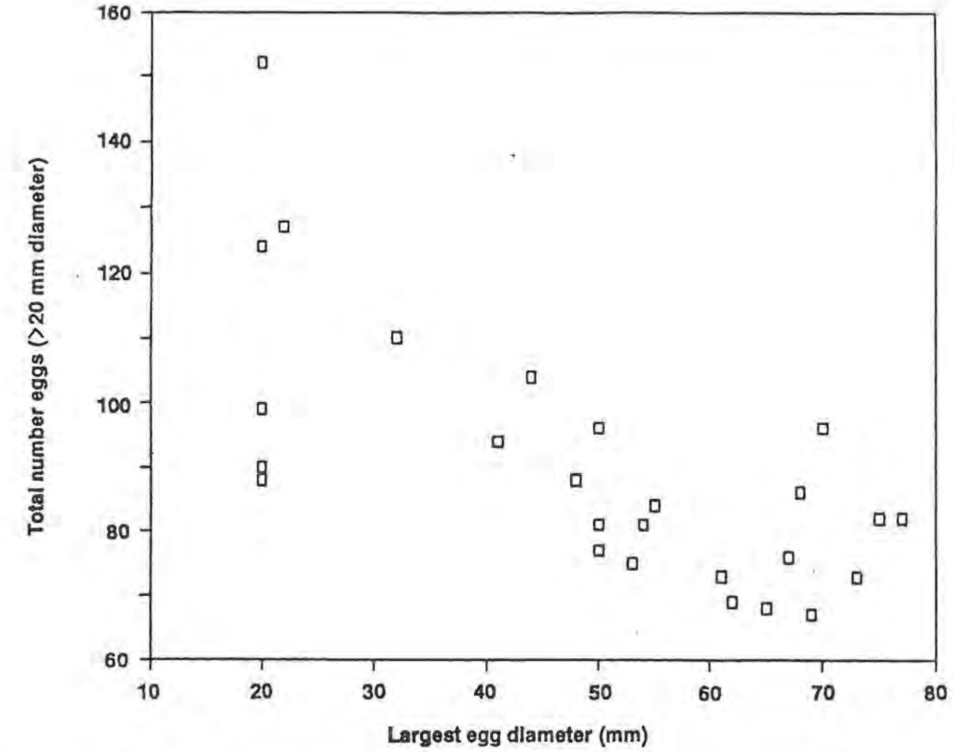


Figure 3.101 - Relationship of total number of ovarian eggs to largest egg diameter in Notorynchus cepedianus. Y= 126 + (0.7)x, r^2= 0.5, n= 26.

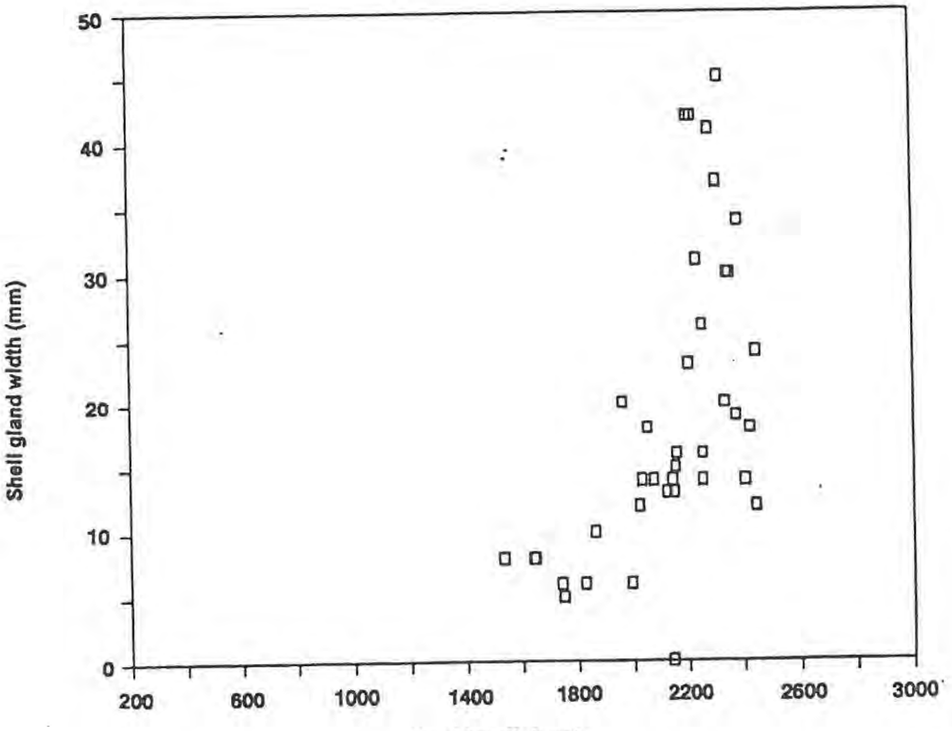


Figure 3.102 - Relationship of shell gland width to TL in Notorynchus cepedianus. Y= 3.6 + (1.4 x 10^{-11})x, r^2= 0.7, n= 36.

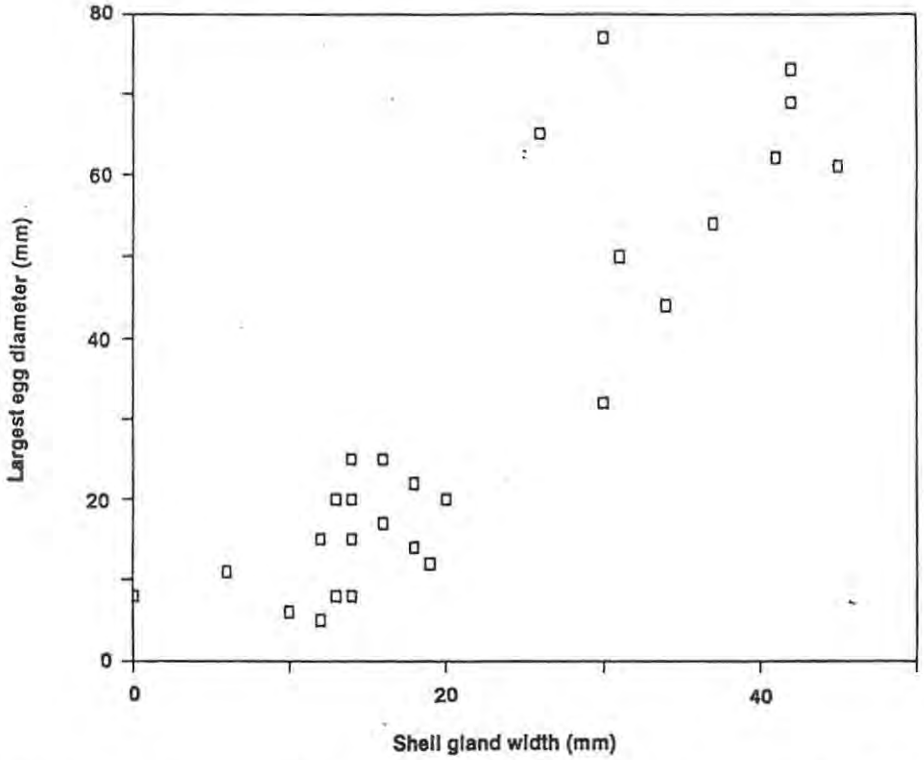
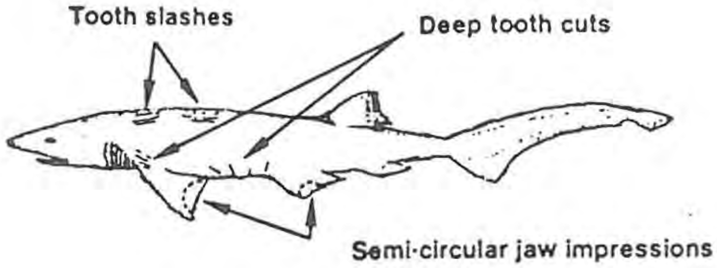
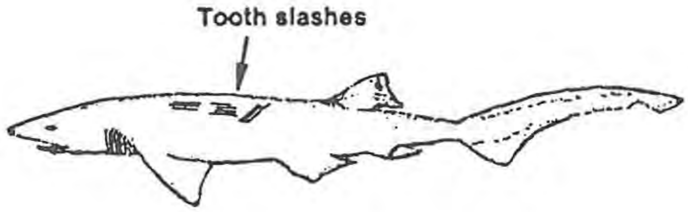


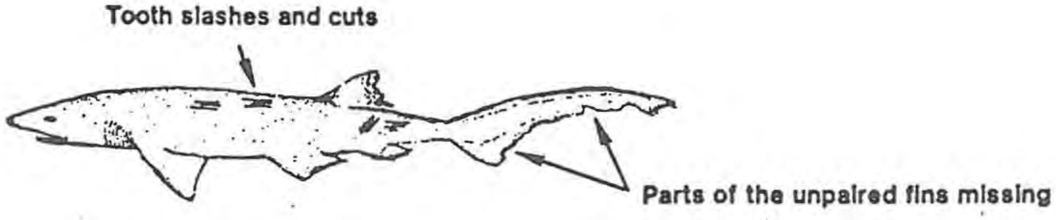
Figure 3.103 - Relationship of largest ovarian egg diameter to shell gland width in Notorynchus cepedianus.



ADULT FEMALE SEVENGILL



ADOLESCENT FEMALE SEVENGILL



ADULT MALE SEVENGILL

Figure 3.104 - Scarring patterns in <u>Notorynchus</u> <u>cepedianus</u> (After Ebert 1986b)

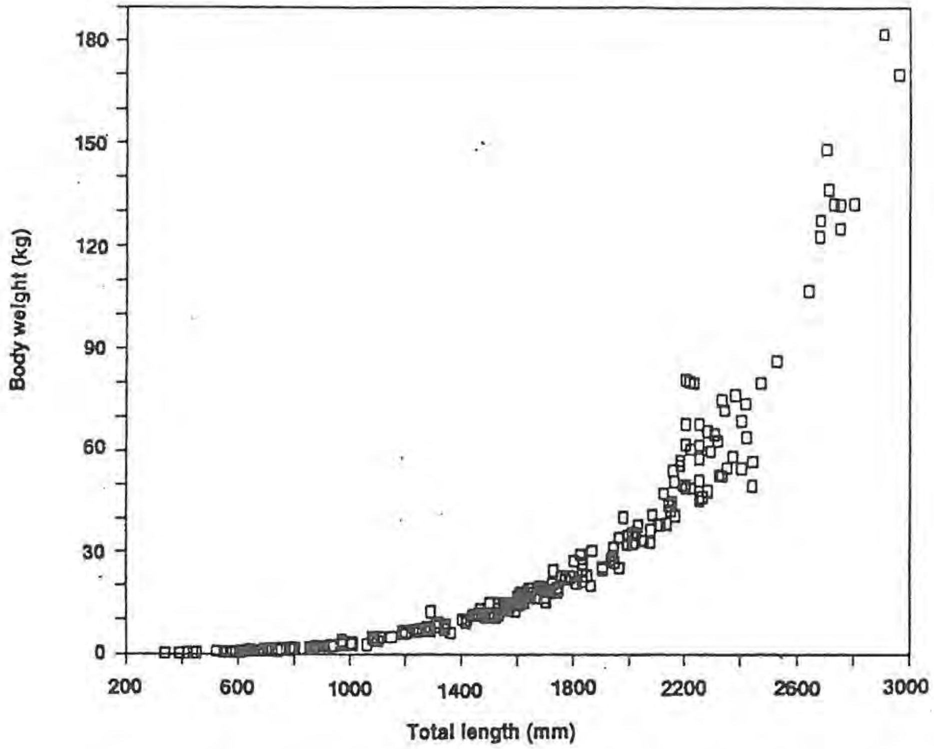


Figure 3.105 - Relationship of body weight to TL in female *Notorynchus cepedianus*. Wt.= 7.1 x 10^{-10})$L^{3.2}$, r^2= 1.0, n= 264.

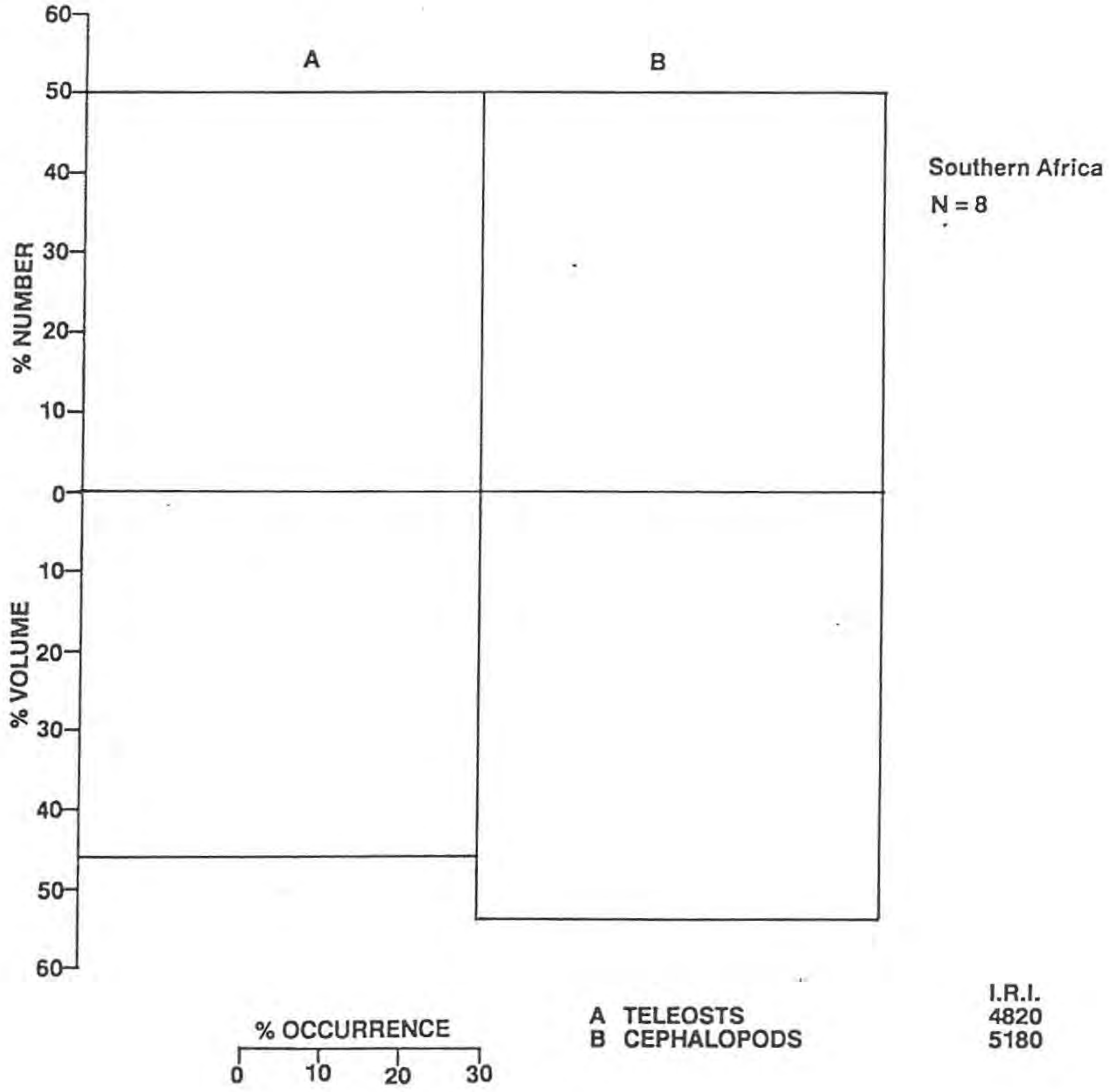


Figure 3.106 - Major prey groups of Heptranchias perlo from southern Africa.

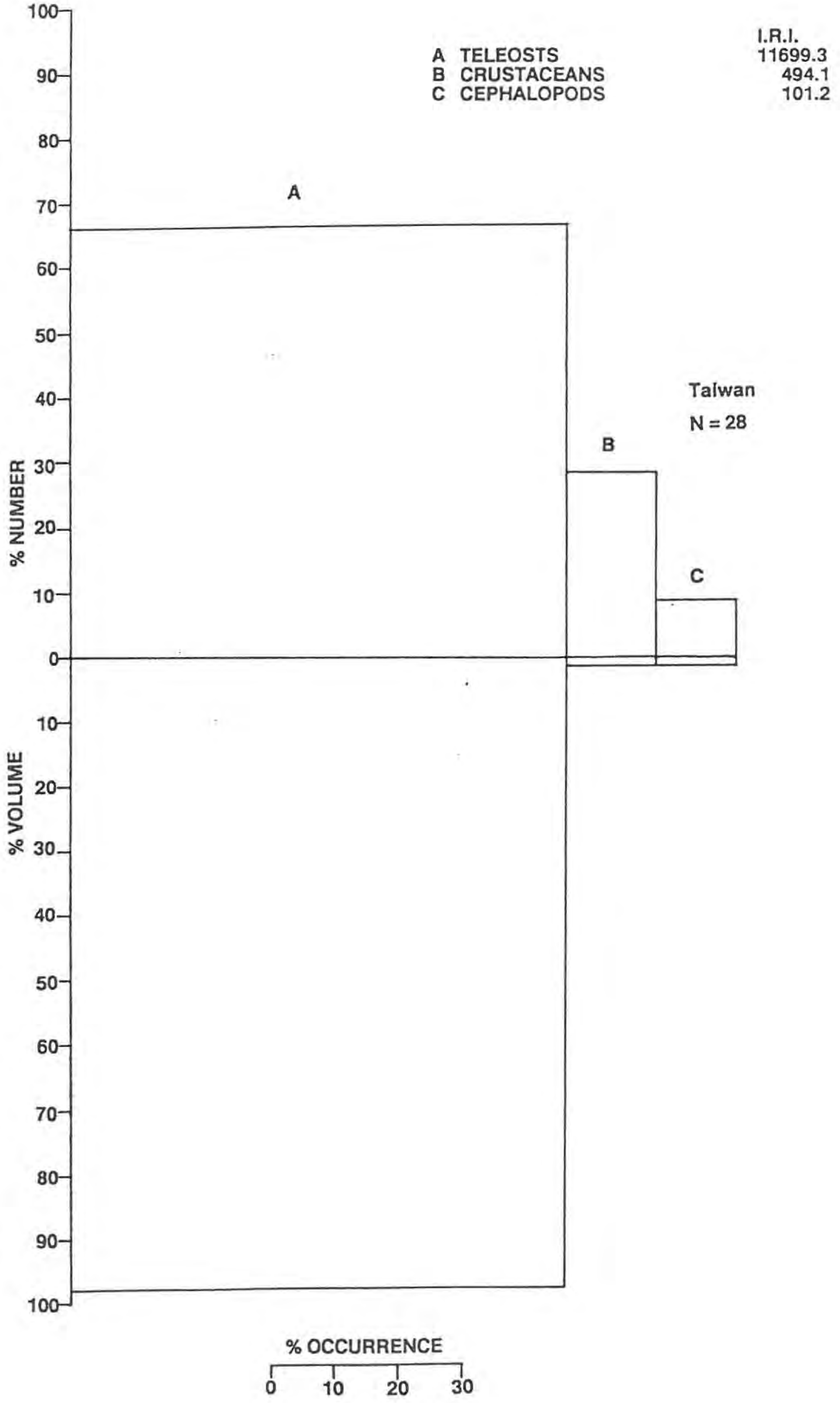


Figure 3.107 - Major prey groups of Heptranchias perlo from Taiwan.

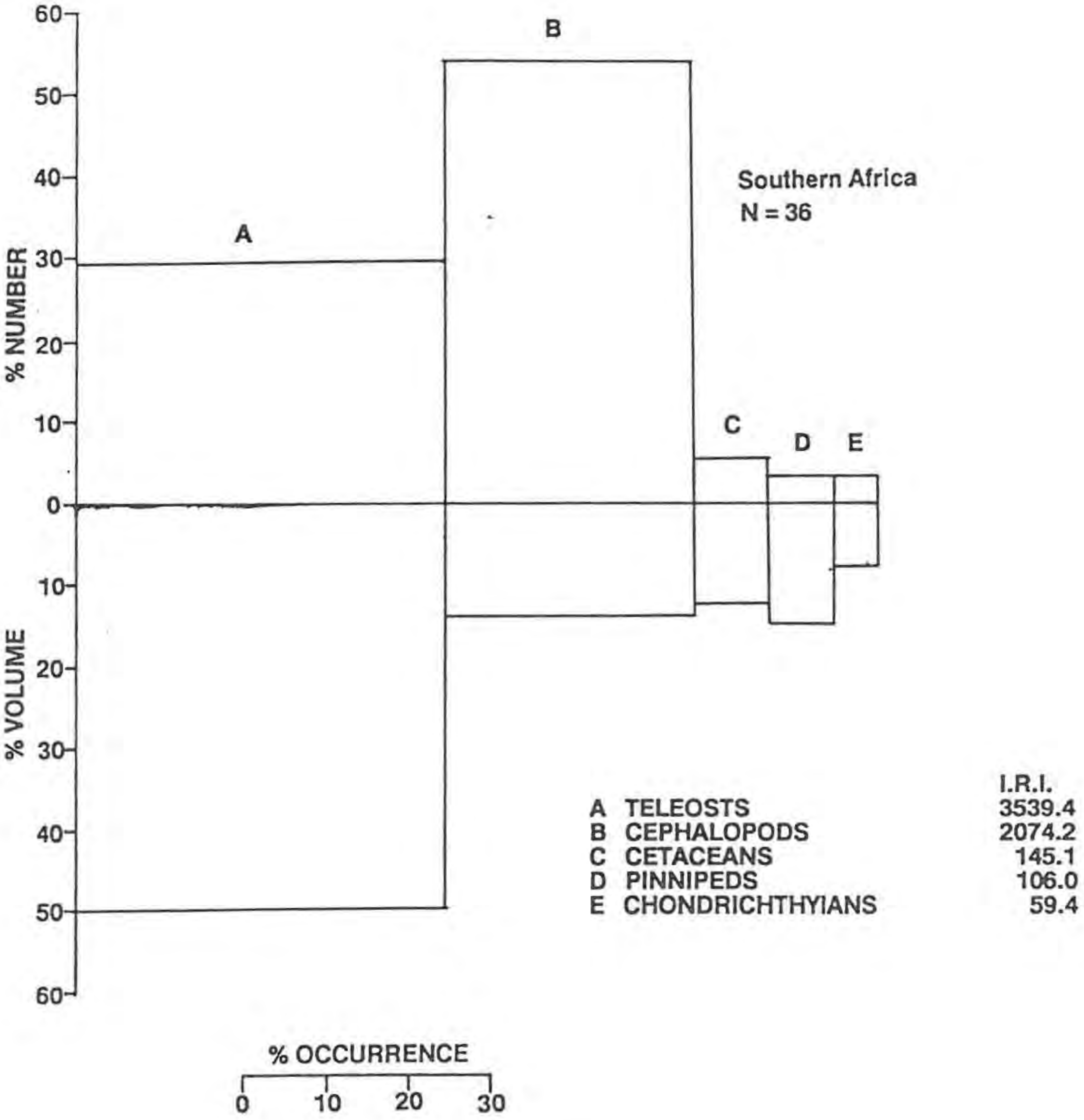


Figure 3.108 - Major prey groups of Hexanchus griseus from southern Africa.

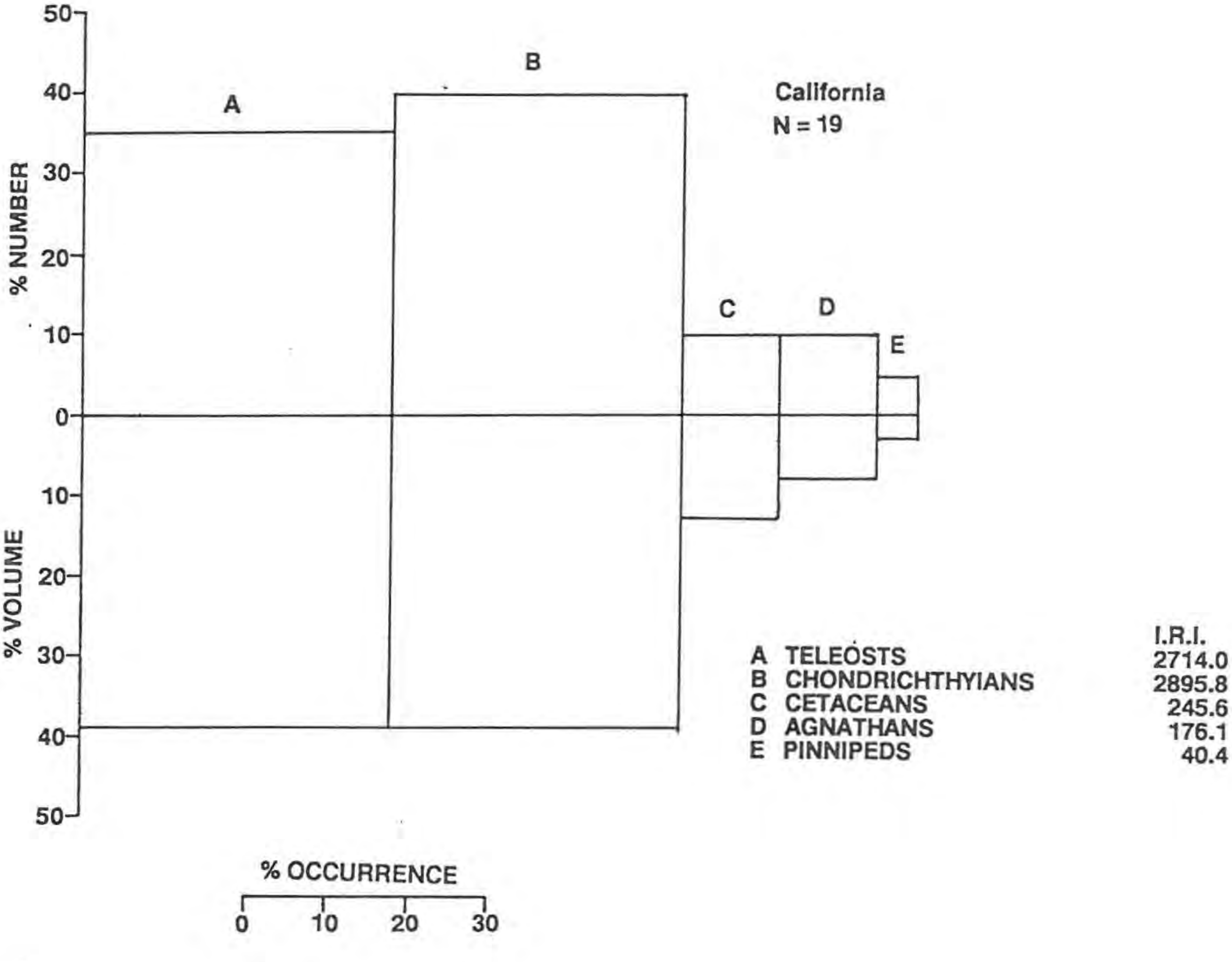


Figure 3.109 - Major prey groups of _Hexanchus griseus_ from California.

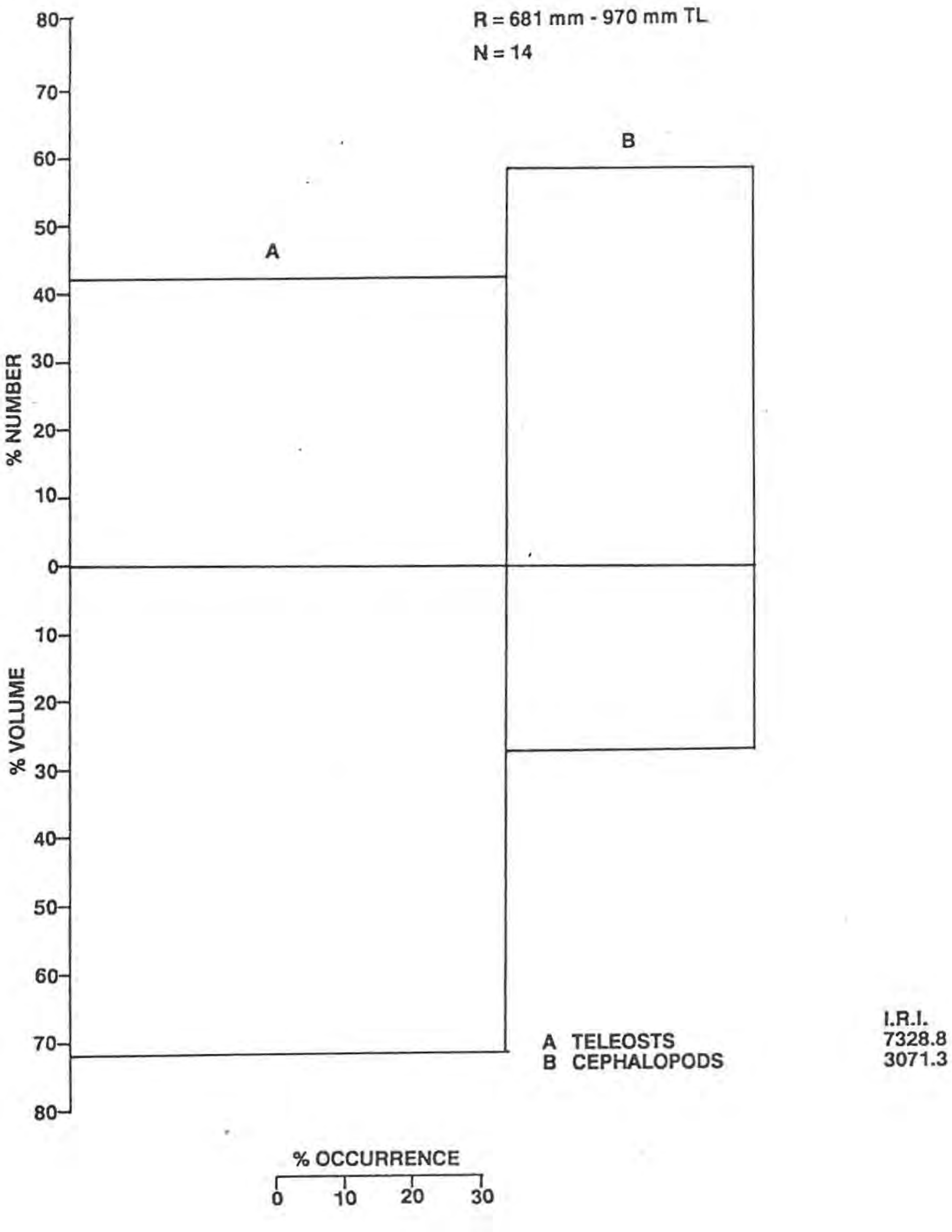


Figure 3.110 - Major prey groups of <u>Hexanchus</u> <u>griseus</u> in the 681 mm to 970 mm TL size class.

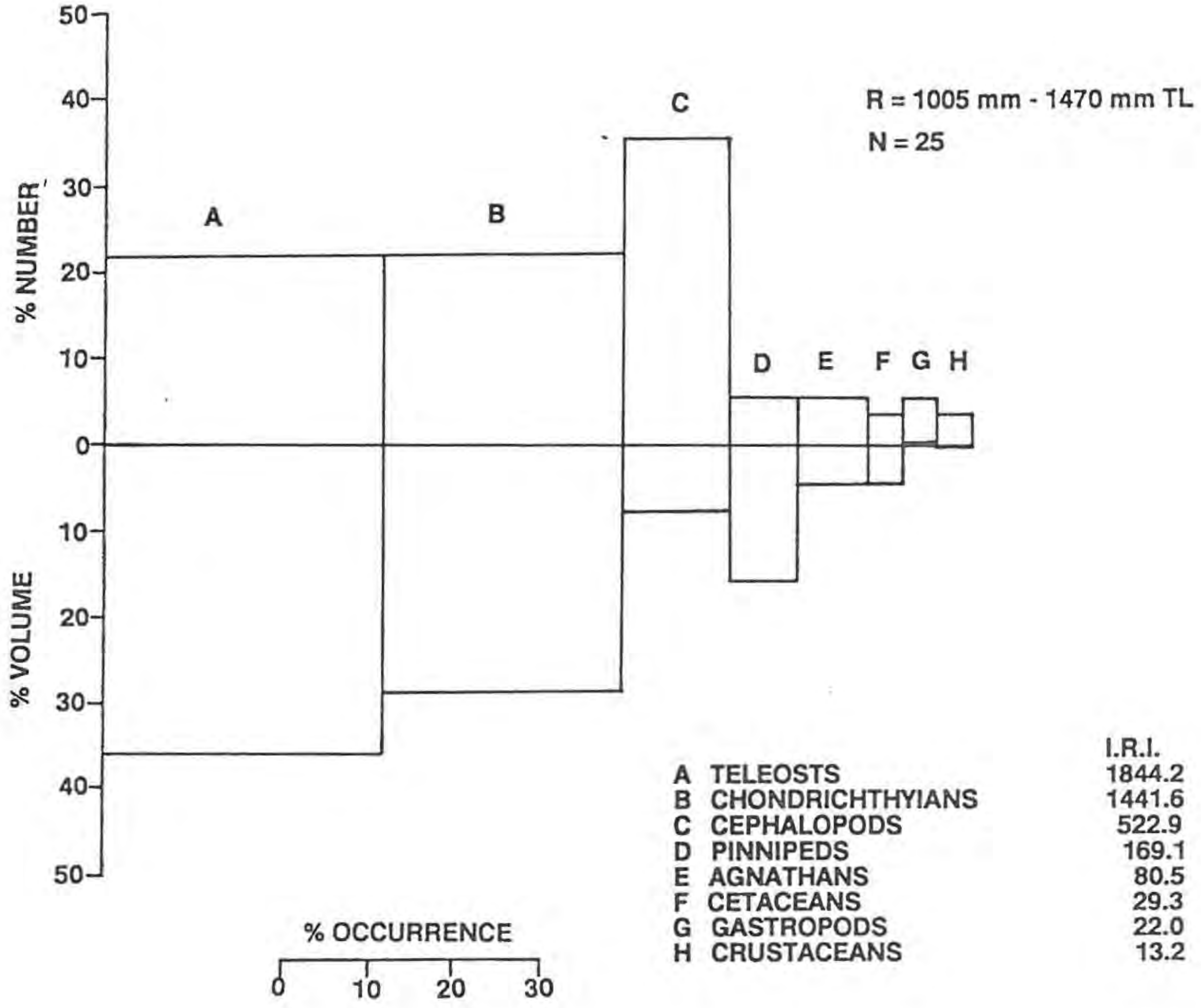


Figure 3.111 - Major prey groups of Hexanchus griseus in the 1005 mm to 1470 mm TL size class.

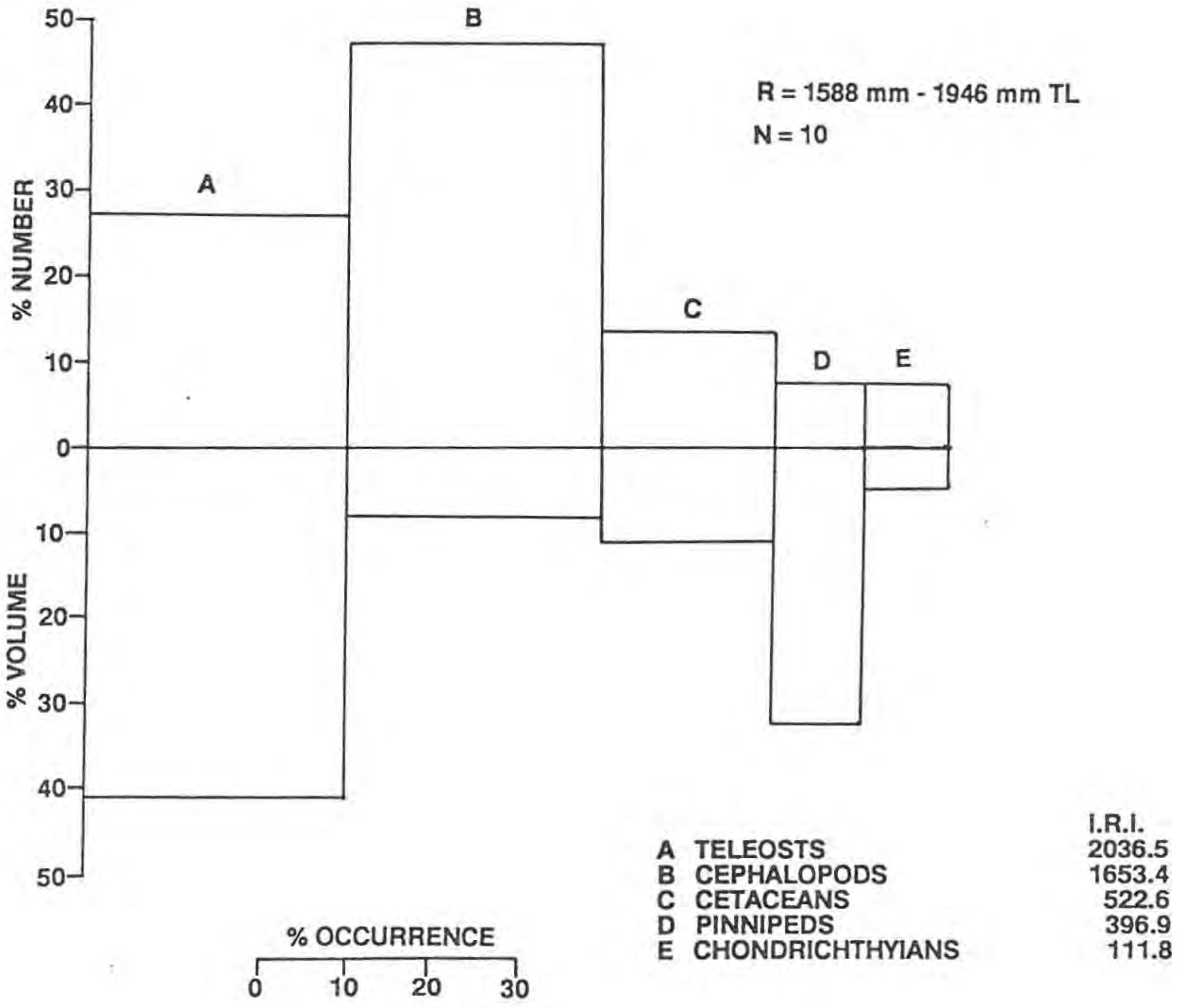


Figure 3.112 - Major prey groups of <u>Hexanchus griseus</u> in the 1588 mm to 1946 mm TL size class.

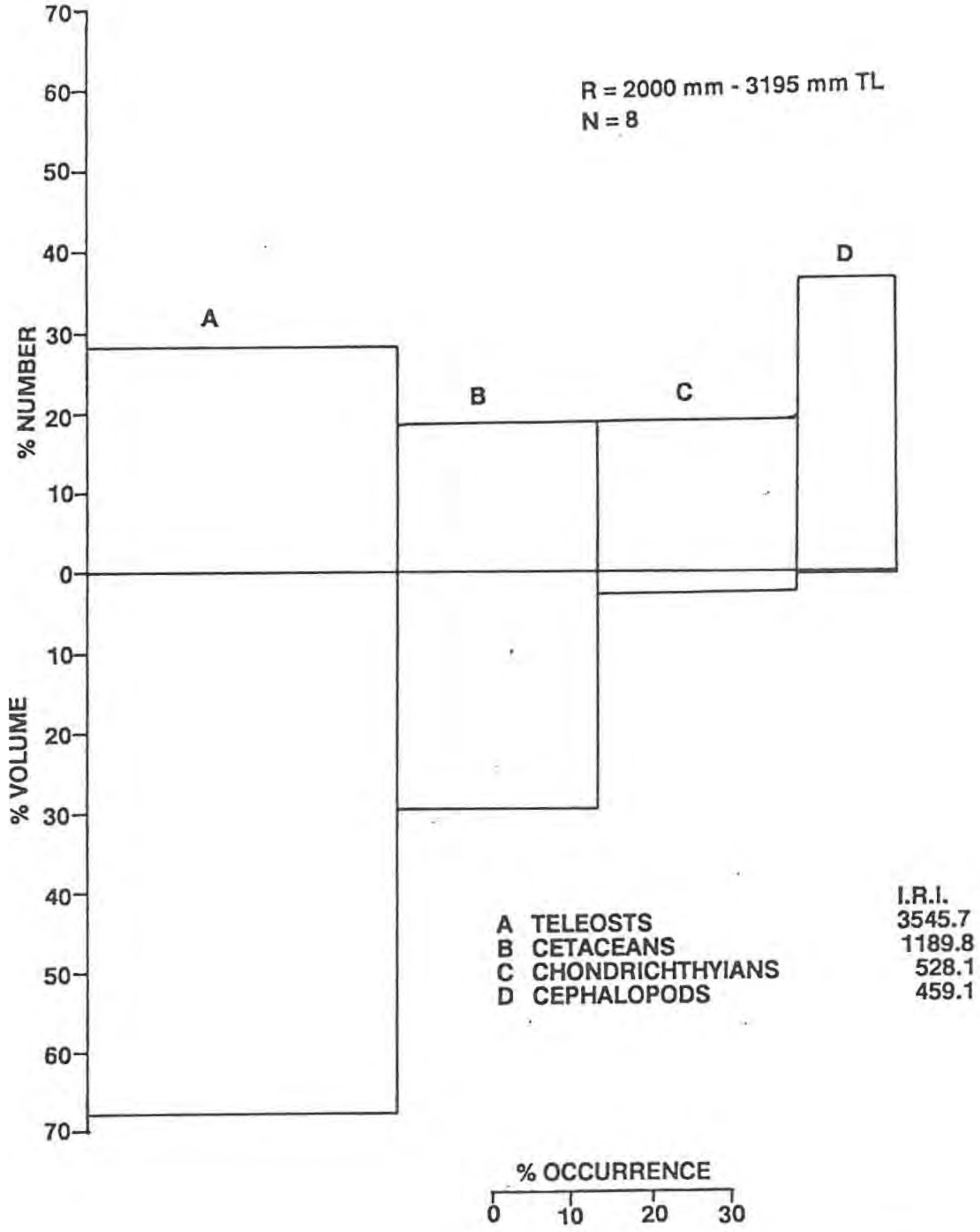


Figure 3.113 - Major prey groups of Hexanchus griseus in the 2000 mm to 3195 mm TL size class.

Figure 3.114 - Scarring pattern of *Hexanchus griseus* on an Atlantic torpedo ray (*Torpedo nobiliana*).

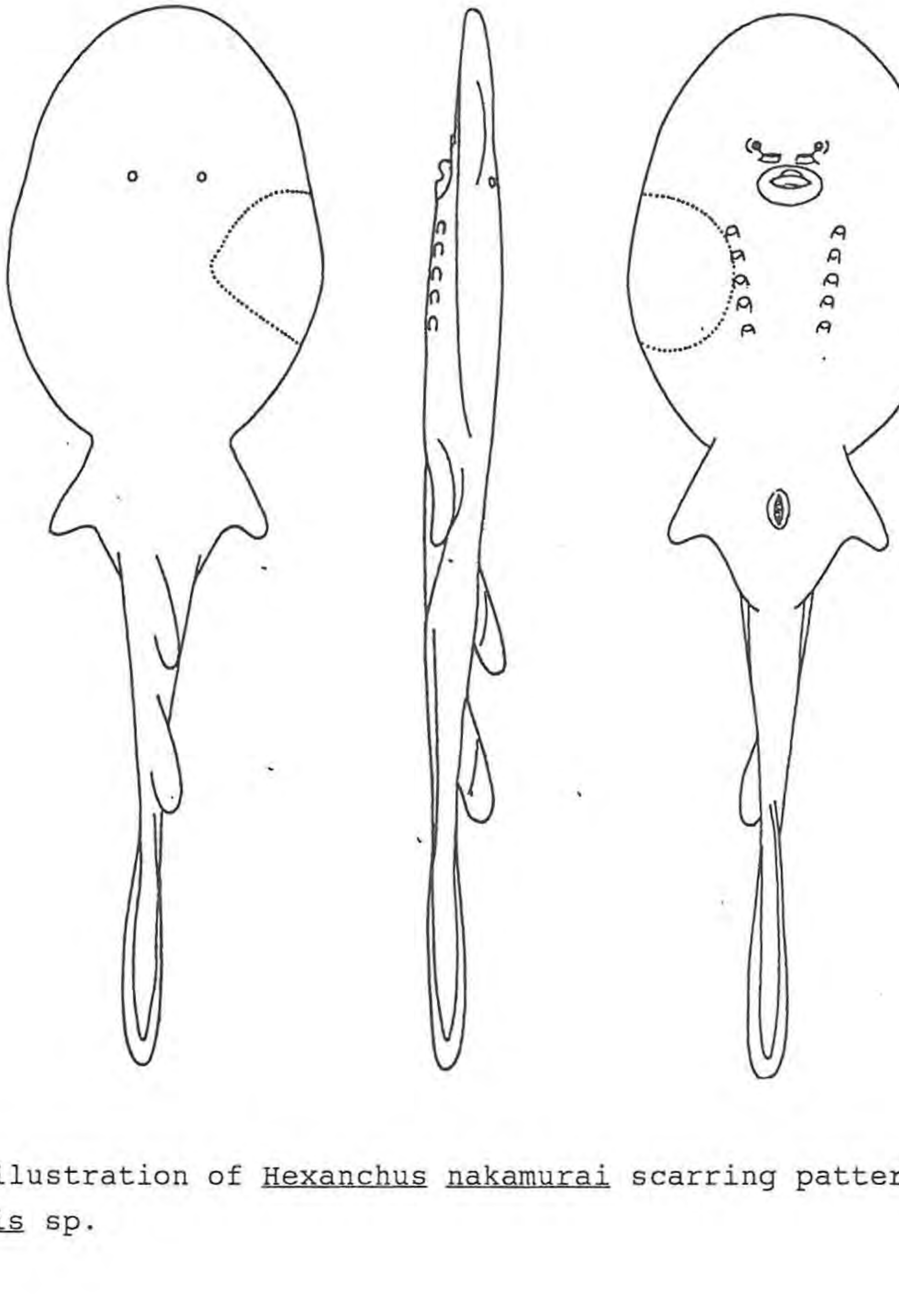


Figure 3.115 Illustration of Hexanchus nakamurai scarring pattern on a Benthobatis sp.

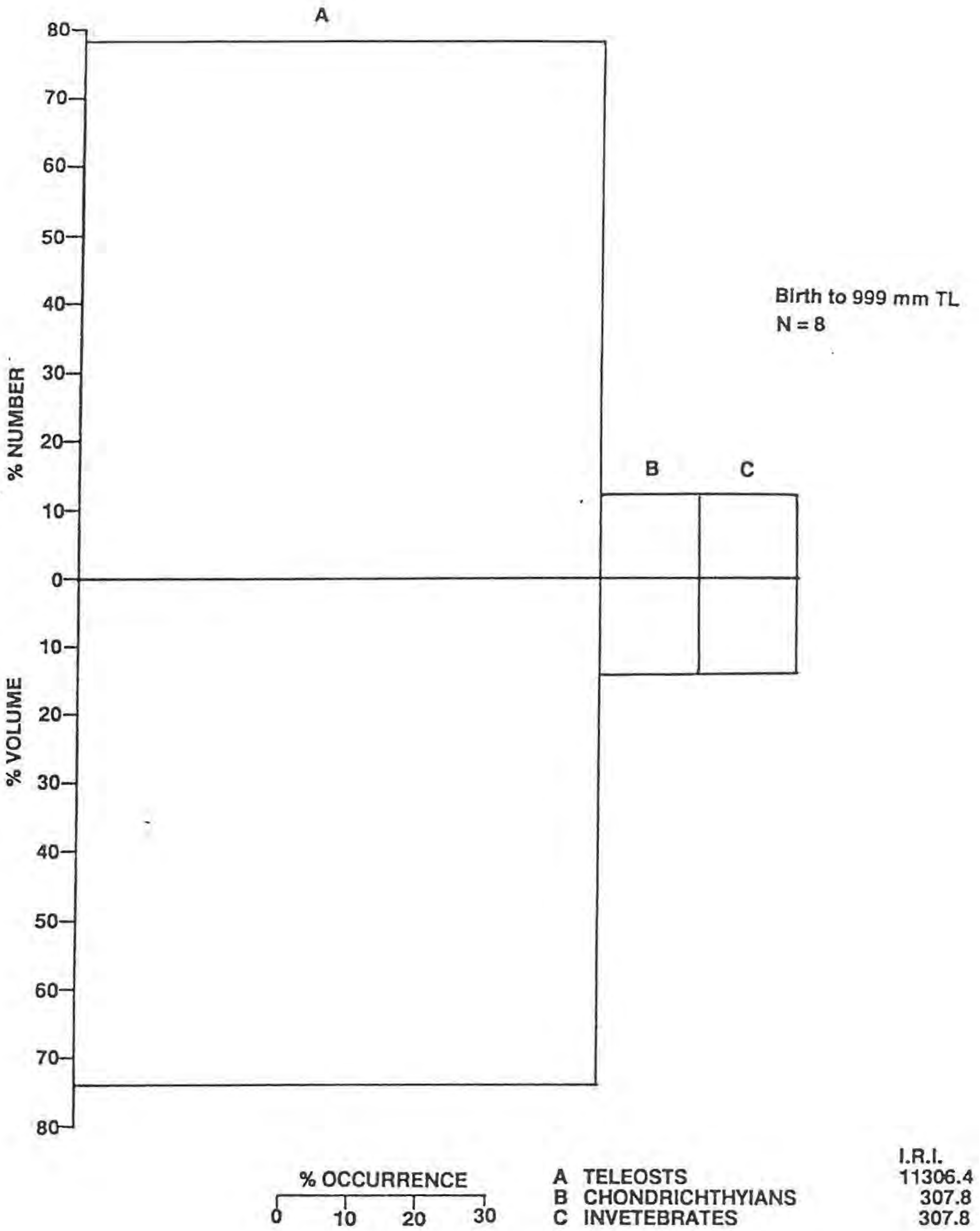


Figure 3.116 - Major prey groups of _Notorynchus_ _cepedianus_ from birth to 999 mm TL.

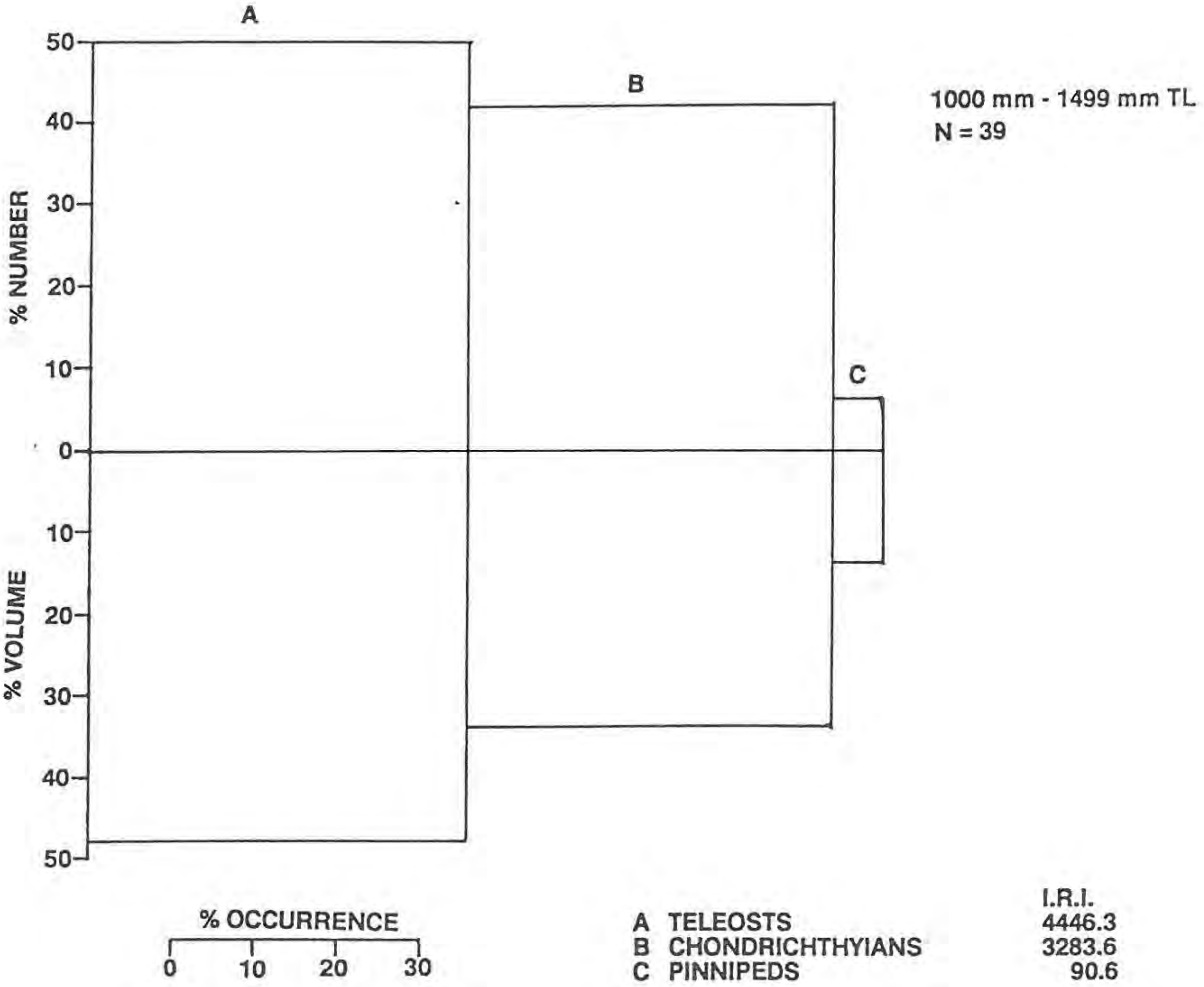


Figure 3.117 - Major prey groups of Notorynchus cepedianus in the 1000 mm to 1499 mm TL size class.

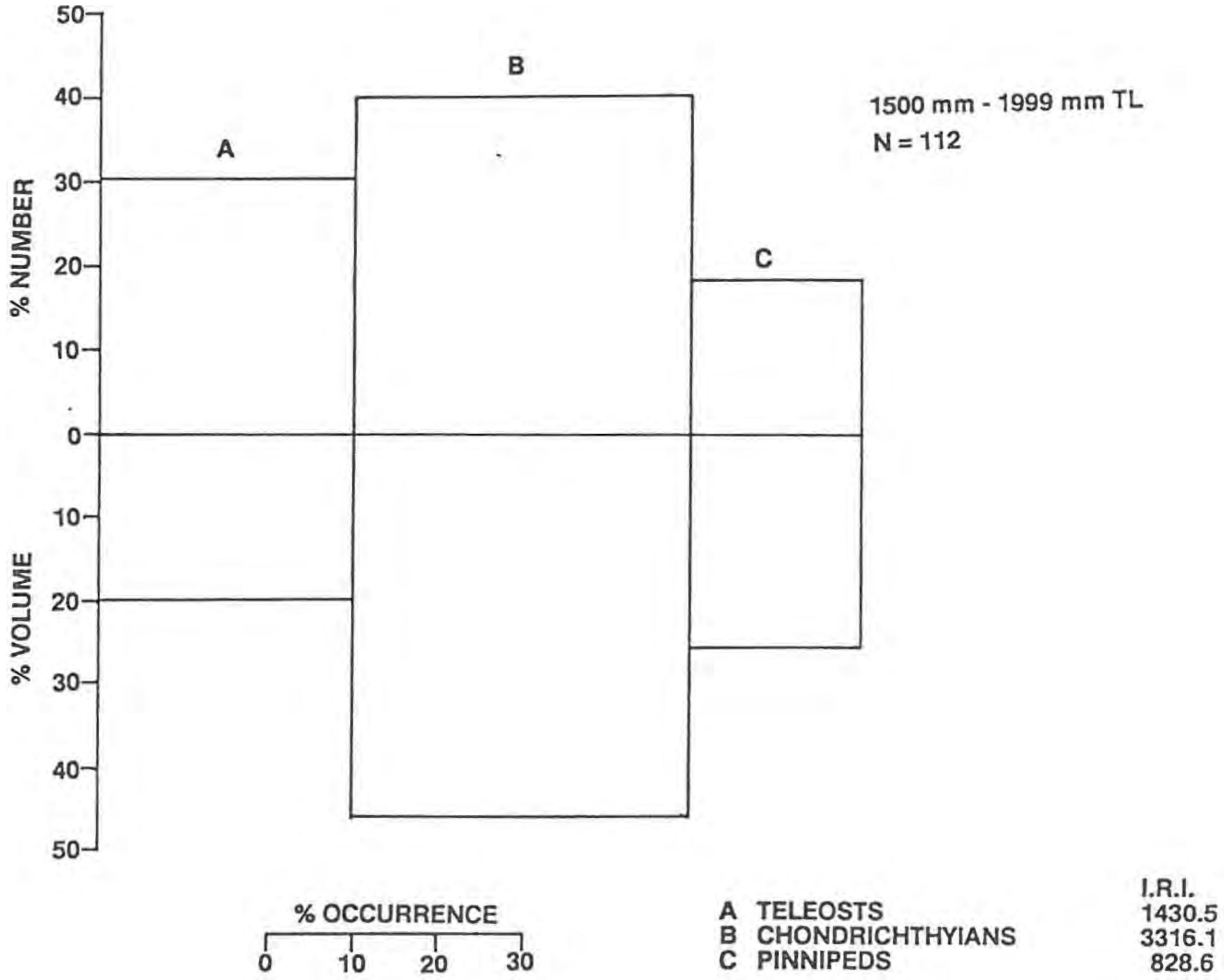


Figure 3.118 - Major prey groups of Notorynchus cepedianus in the 1500 mm to 1999 mm TL size class.

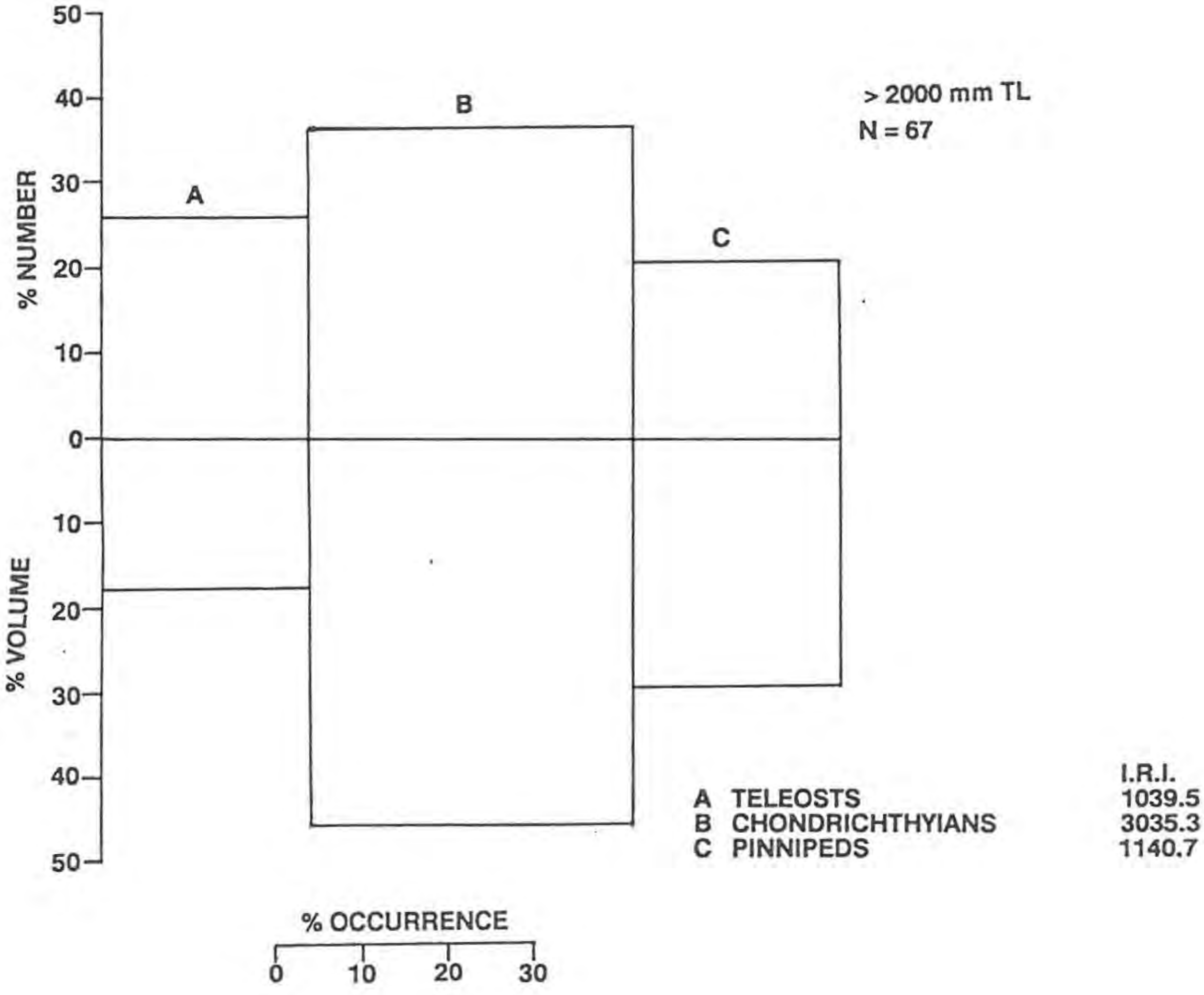


Figure 3.119 - Major prey groups of Notorynchus cepedianus › 2000 mm TL.

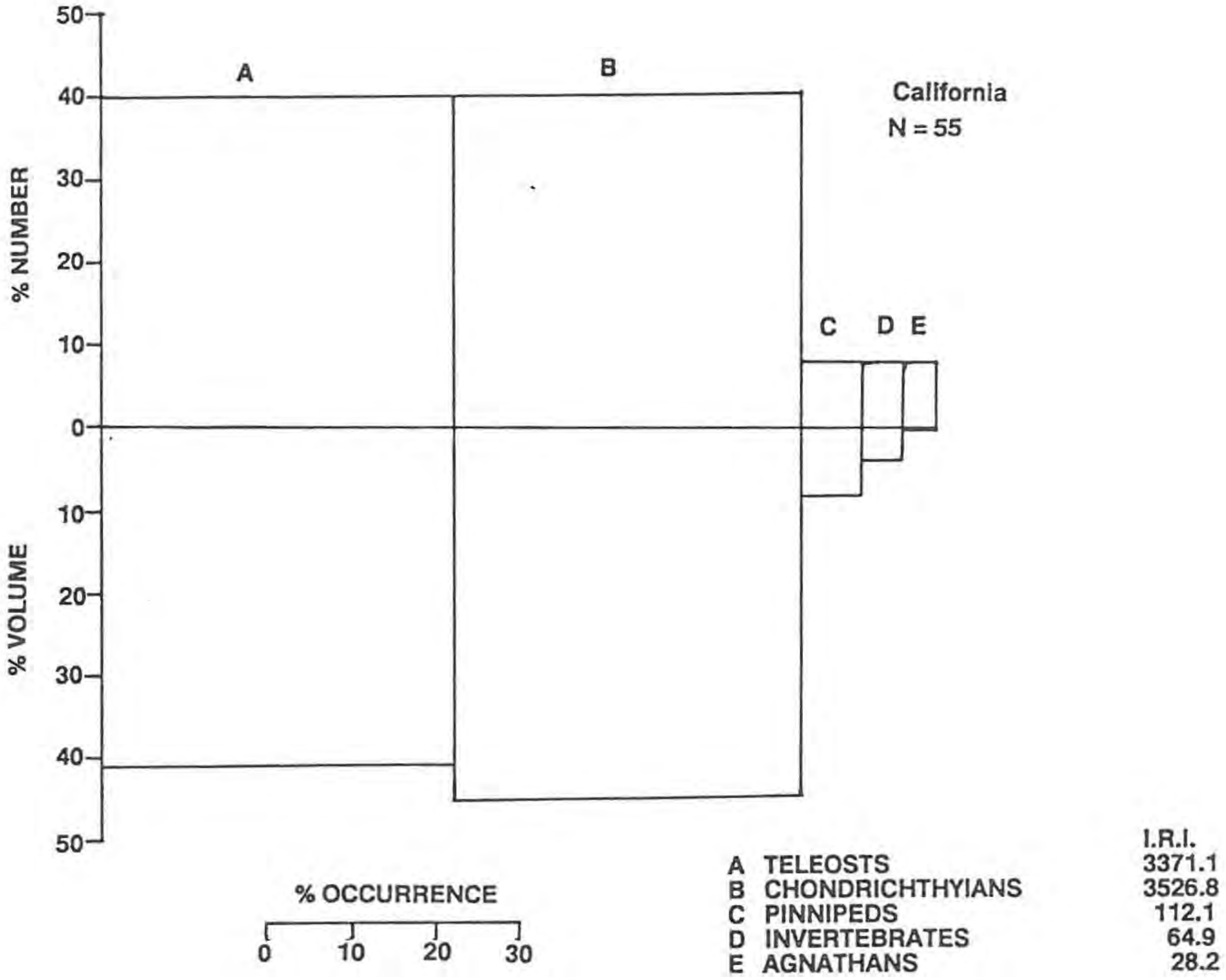


Figure 3.120 - Major prey groups of Notorynchus cepedianus from California.

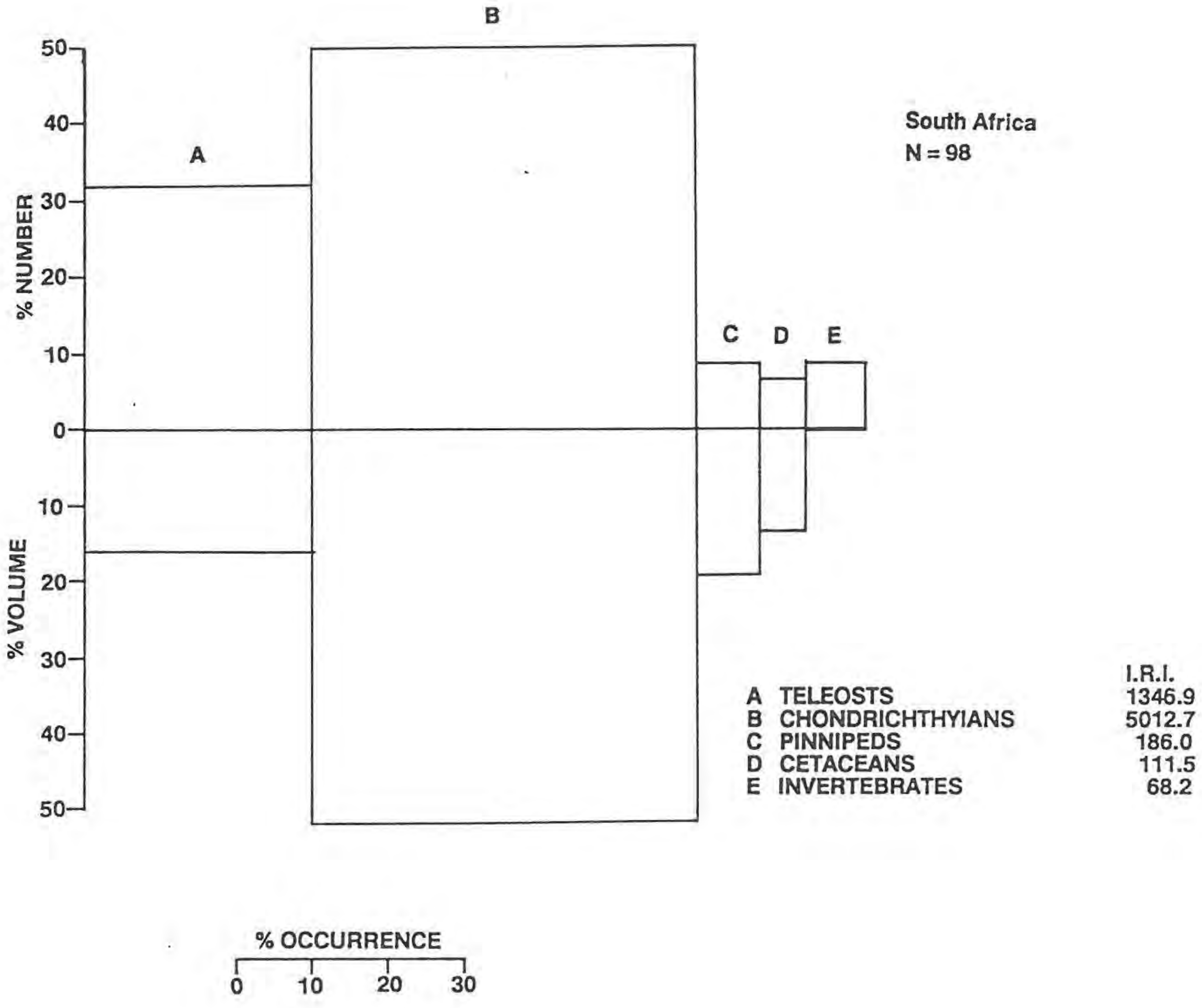


Figure 3.121 - Major prey groups of Notorynchus cepedianus from South Africa.

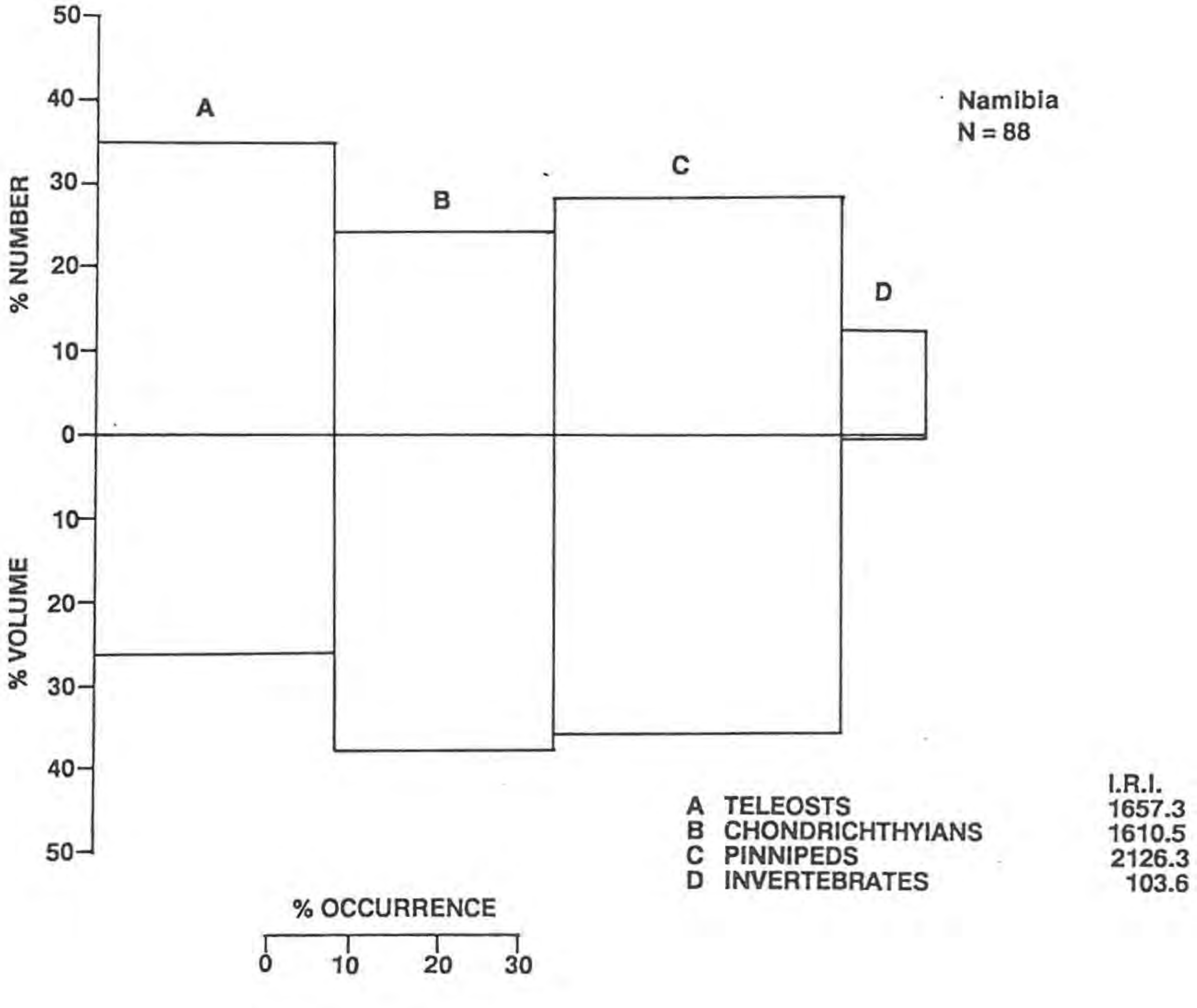
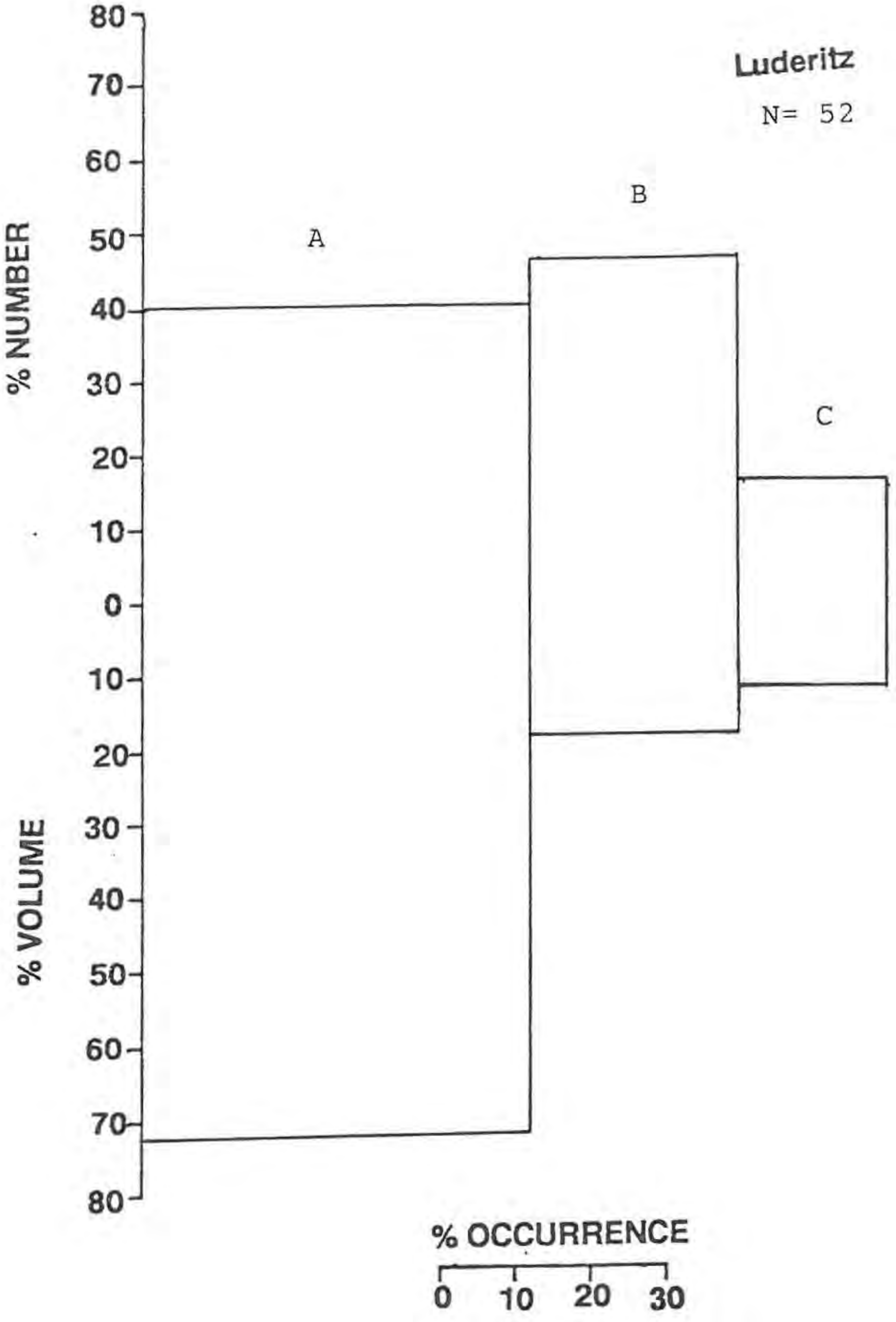
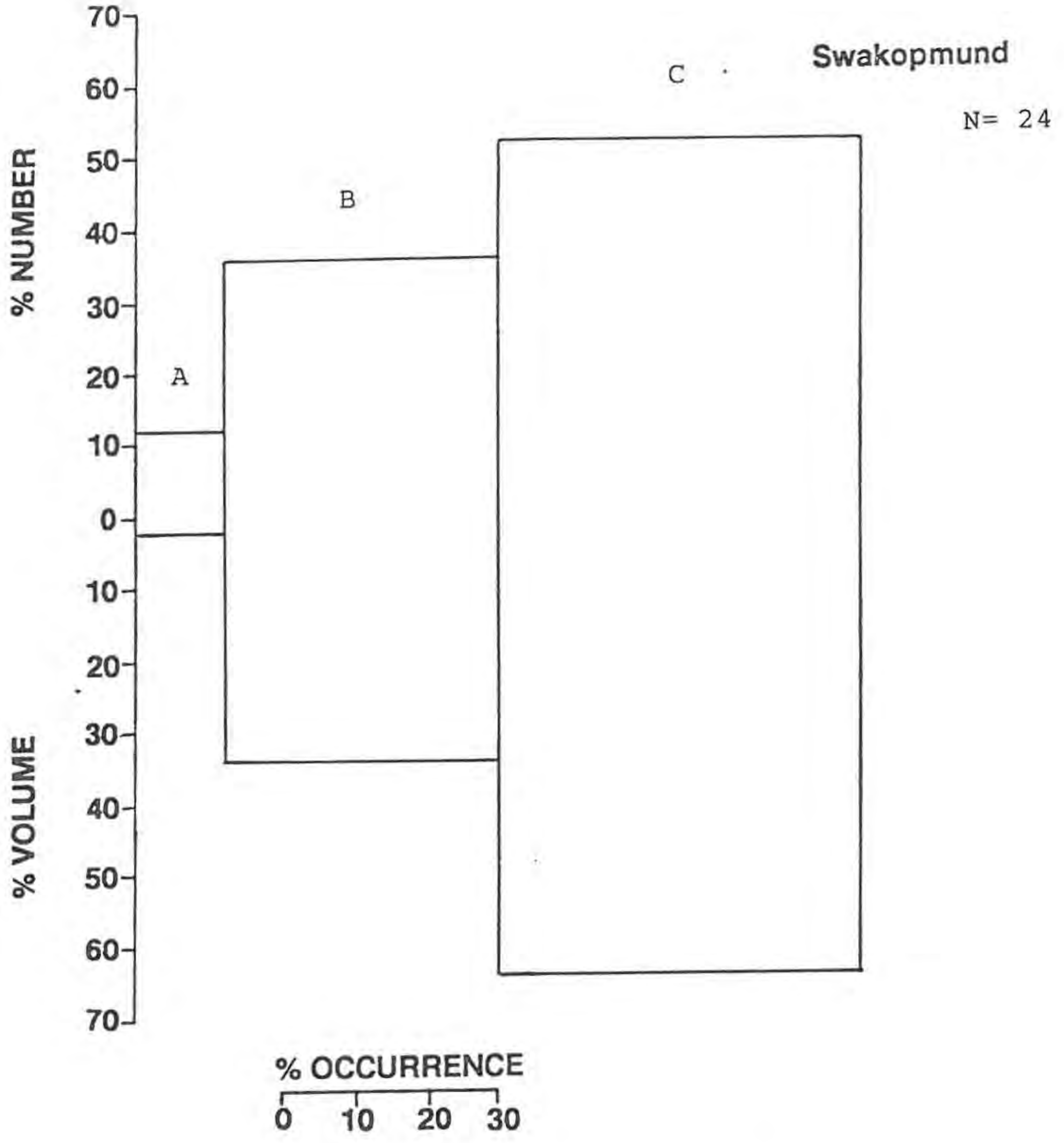


Figure 3.122 - Major prey groups of <u>Notorynchus</u> <u>cepedianus</u> from Namibia.



		I.R.I.
A	PINNIPEDS	5724.6
B	TELEOSTS	1782.7
C	CHONDRICHTHYIANS	531.8

Figure 3.123a - Major prey groups of Notorynchus cepedianus from Luderitz.



		I.R.I.
A	PINNIPEDS	171.1
B	TELEOSTS	2632.5
C	CHONDRICHTHYIANS	5805.0

Figure 3.123b - Major prey groups of <u>Notorynchus</u> <u>cepedianus</u> from Swakopmund.

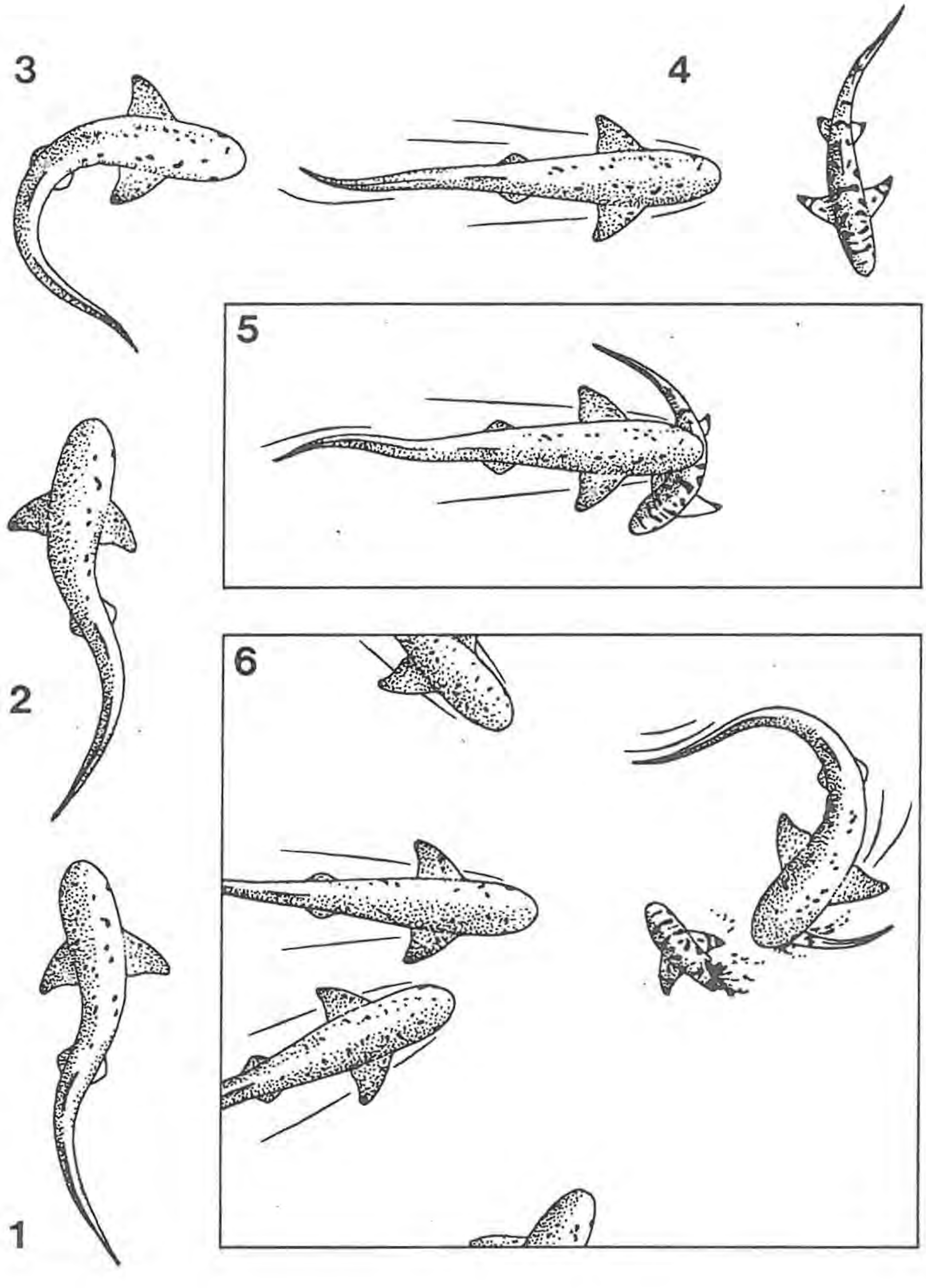


Figure 3.124 - Diagramatic illustration of Notorynchus cepedianus using burst speed to capture prey.

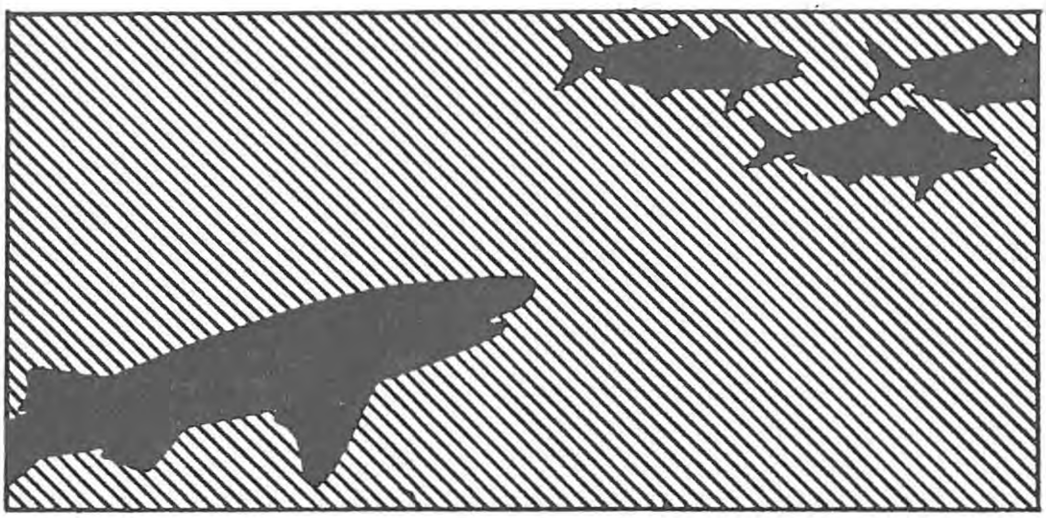


Figure 3.125 - Diagramatic illustration of Notorynchus cepedianus ambushing prey.

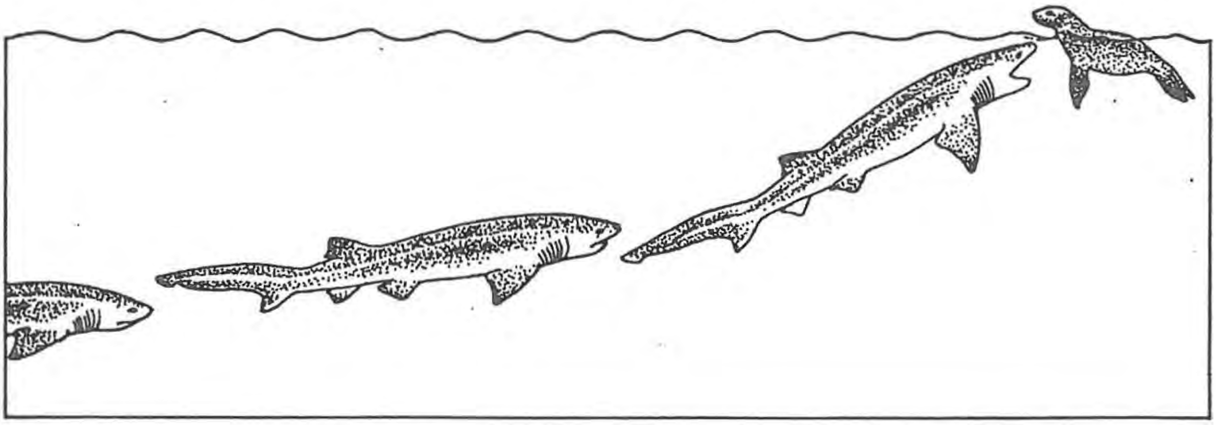


Figure 3.126 - Diagramatic illustration of Notorynchus cepedianus stalking prey.

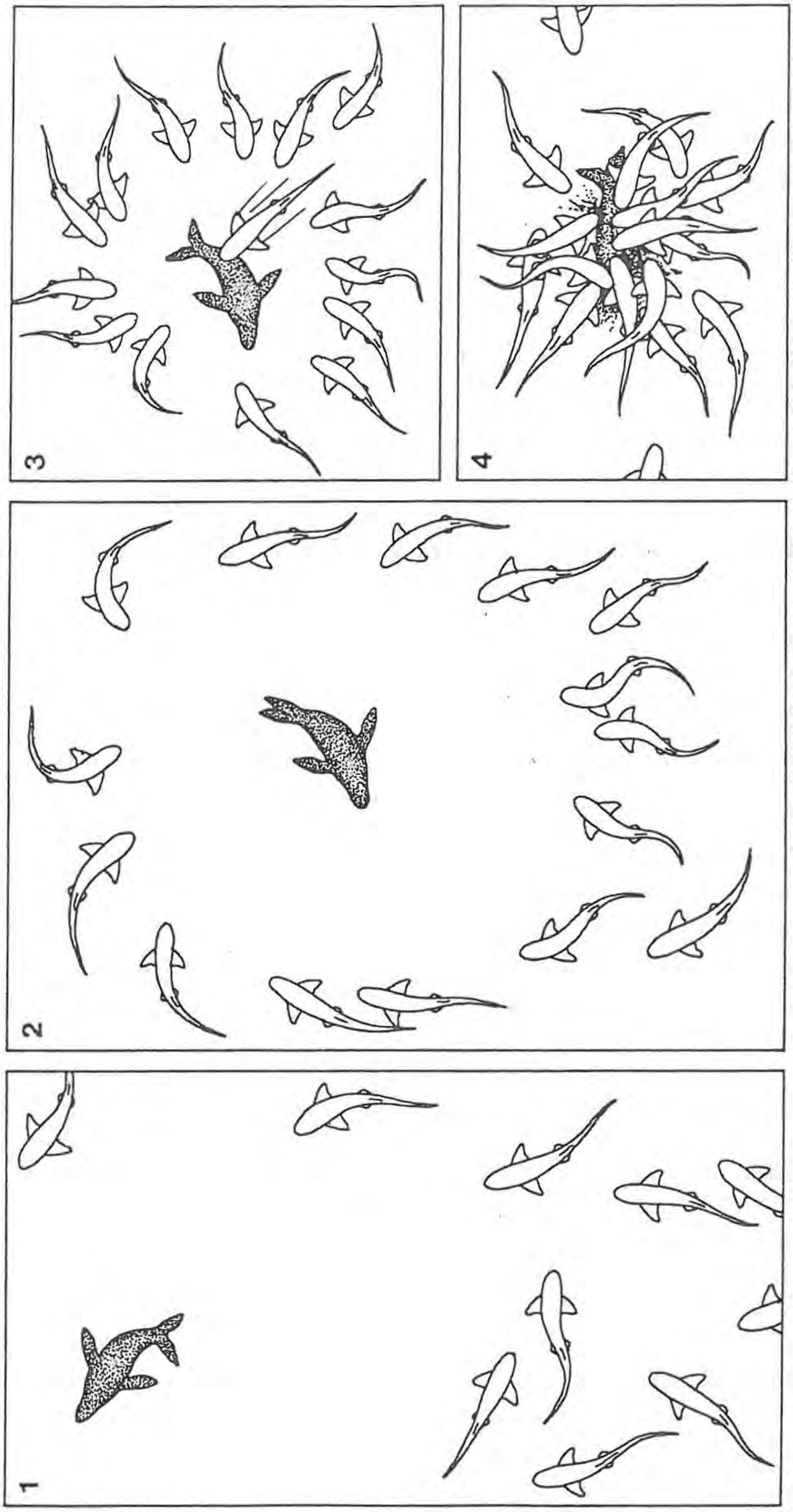


Figure 3.127 - Diagramatic illustration of Notorynchus cepedianus feeding by social facilitation.

TABLE 3.1

Total tooth counts of *Chlamydoselachus anguineus*.

REGION	N	R	$\overline{X}$	s.d.	CV	SOURCE
Angola	1	24/23	-	-	-	1
Australia	1	26/25	-	-	-	2
California	1	25/23	-	-	-	1
Iberia	1	26/25	-	-	-	3
Japan	13	19-28/21-27	24.7/24.4	2.2/1.9	9.0/7.8	1, 4, 5, 6, 7, 8
Namibia	4	28-30/24-27	28.8/25.3	2.3/1.9	9.4/7.8	1
New Zealand	4	24-27/21-26	24.8/23.3	1.3/1.9	5.3/8.3	9
North Atlantic	4	22-25/24-29	23.0/26.0	1.0/2.0	4.0/9.0	1
Norway	1	23/21	-	-	-	10
Spain	1	23/23	-	-	-	11
Taiwan	3	23-24/23-26	23.3/24.7	0.5/1.2	2.0/5.1	1

Source: 1. present study; 2. Bass 1979; 3. Lozano Rey 1928; 4. Garman 1885; 5. Gudger and Smith 1933; 6. Gunther 1887; 7. Hawkes 1907; 8. Jordan and Fowler 1903; 9. Nakaya and Bass 1978; 10. Collett 1896; 11. Bertrand 1926.

TABLE 3.2

Pectoral radial fin counts of *Chlamydoselachus anguineus*.

REGION	N	R	$\overline{X}$	s.d.	CV	SOURCE
Japan	4					1,2,3,4
mesopterygium		5-6	5.3	0.4	8.2	
metapterygium		9-12	11.0	1.3	11.5	
total radials		15-17	16.3	0.9	5.2	
radial segments		3-5	3.7	0.9	24.7	
Namibia	1					1
mesopterygium		7				
metapterygium		8				
total radials		15				
radial segments		6				
Taiwan	1					1
mesopterygium		6				
metapterygium		10				
total radials		16				
radial segments		4				

Source: 1. present study; 2. Braus 1902; 3. Garman 1885; 4. Goodey 1910.

TABLE 3.3

Anal, dorsal and pelvic radial fin counts of *Chlamydoselachus anguineus*.

REGION	N	R	$\overline{X}$	s.d	CV	SOURCE
Japan						
pelvic fin	5	19-25	22.5	2.3	10.2	1,2,3,4,5
dorsal fin	2	16-32	24.0			3,4
anal fin	2	20	20.0			3,4
Namibia						
pelvic fin	1	20				1
dorsal fin	1	15				1
anal fin	1	30				1
Taiwan						
pelvic fin	1	23				1
dorsal fin	1	9				1
anal fin	1	28				1

Source: 1. present study; 2. Braus 1902; 3. Deinega 1909; 4. Garman 1885; 5. Goodey 1910.

TABLE 3.4

Chlamydoselachus anguineus. Cranial measurements of a 916 mm TL specimen, expressed as a percentage of nasobasal length.

Nasobasal length:	76 mm
Length of medial rostral cartilage:	5
Width between bases of lateral rostral cartilages:	26
Width across nasal capsules:	61
Length of nasal capsule:	24
Width of nasal capsule:	30
Nasal aperture width:	15
Width between nasal apertures:	26
Length from rostral base to edge of anterior fontanelle:	26
Anterior fontanelle width:	24
Cranial height:	24
Basal plate width at orbital notches:	23
Cranial roof width over orbital notches:	39
Width across preorbital processes:	31
Preorbital process length:	14
Width across suborbital shelves:	46
Otic capsule length:	30
Width across otic capsule:	34
Width across preorbital processes:	67
Width across postorbital processes:	68

TABLE 3.5

Spiral valve counts of *Chlamydoselachus anguineus.*

REGION	N	R	$\overline{x}$	s.d	CV	SOURCE
Angola	1	27				1
Australia	1	49				1
Japan	9	35-46	40.8	3.7	9.0	1,2,3,4
Namibia	3	26-28	27.0	0.8	3.0	1
North Atlantic	2	43-46	44.5			1
Norway	1	47				5
Taiwan	2	42-43	42.5			1

Source: 1. present study; 2. Gunther 1887; 3. Hawkes 1907; 4. Smith 1937; 5. Collett 1896.

TABLE 3.6

Tooth counts of *Heptranchias perlo*.

REGION	N	R	$\overline{X}$	s.d.	CV	SOURCE
Gulf of Mexico	1	26/20				1
Mozambique	12	28-42/20-32	35.2/26.4	4.2/3.3	12.0/12.6	1
South Africa	3	31-33/24-25	32.0/24.3	0.8/0.5	2.6/1.9	1
Taiwan	31	30-43/09-33	36.0/26.5	2.9/4.1	8.1/15.5	1
Australia	2	25-30/20-23	27.5/21.5			2
New Zealand	1	34/26				2
Japan	7	23-31/31-33				3

Source: 1. present study; 2. Garrick and Paul 1971; 3. Tanaka et al. 1975.

TABLE 3.7

Pectoral radial fin counts of *Heptranchias perlo*.

REGION	N	R	$\overline{X}$	s.d.	CV
Mediterranean Sea	2				
mesopterygium		10	10.0		
metapterygium		13	13.0		
total radials		23	13.0		
radial segments		5	5.0		
South Africa	1				
mesopterygium		10			
metapterygium		14			
total radials		24			
radialsegments		5			
Taiwan	32				
mesopterygium		9-11	10.1	0.6	5.5
metapterygium		11-15	13.5	0.8	6.1
total radials		21-25	23.6	0.9	4.0
radial segments		4-5	4.5	0.5	11.2

TABLE 3.8

Anal, dorsal and pelvic fin radial counts of *Heptranchias perlo*.

REGION	N	R	$\overline{X}$	s.d.	CV	SOURCE
Mediterranean Sea						
pelvic fin	1	24				1
dorsal fin	1	19				1
anal fin	1	20				1
South Africa						
pelvic fin	1	23				1
dorsal fin	1	18				1
anal	1	17				1
Taiwan						
pelvic fin	32	19-26	22.6	1.4	6.1	1
dorsal fin	32	17-21	18.7	1.0	5.1	1
anal fin	32	15-21	17.8	1.6	9.0	1
Japan						
pelvic fin	1	21				2

Source: 1. present study; 2. Tanaka et al. 1975.

TABLE 3.9

Vertebral counts of *Heptranchias perlo*. A. From columns prepared by hot-water maceration. B. From published accounts.

A

REGION	N	R	$\bar{X}$	S.D.	CV
Mediterranean Sea	1				
mp		51			
dp		24			
dc		66			
total		141			
South Africa		1			
mp		55			
dp		36			
dc		62			
total		153			
Taiwan	32				
mp		52-58	55.0	1.4	2.5
dp		28-38	34.7	2.0	5.7
dc		60-67	63.9	2.0	3.1
total		149-159	153.7	2.5	1.6

B

REGION		PRECAUDAL COUNTS		TOTAL COUNTS		SOURCE
	N	$\bar{X}$	R	$\bar{X}$	R	
Australia	3	92	90-93	146	143-151	1
Mediterranean Sea	1		ca. 85		ca. 130	2
New Zealand	3	91	90-91	144	143-146	1
North Atlantic	3	90	89-90	146	141-151	2
Southern Africa	11	76	72-78	128	125-134	3
Tunisia	5	55	54-55		137-140	4

Source: 1. Garrick & Paul 1971; 2. Springer & Garrick 1964; 3. Bass et al. 1975; 4. Capape 1980.

TABLE 3.10

Heptranchias perlo. Cranial measurements expressed as a percentage of nasobasal length.

Sex	M	M	M	F	F	F
TL	690 mm	727 mm	780 mm	592 mm	842 mm	1030 mm
Nasobasal length:	74.9 mm	77.6 mm	81.0 mm	65.5 mm	90.0 mm	106 mm
Length of medial rostral cartilage:	11.1	11.2	11.7	10.2	11.3	10.8
Width between bases of lateral rostral cartilages:	9.7	10.8	8.1	10.8	10.0	13.5
Width across nasal capsules:	43.1	43.8	40.5	44.4	41.5	42.0
Width of nasal capsule:	16.7	23.2	18.1	20.9	21.5	21.5
Length of nasal capsule:	29.4	26.4	29.3	30.2	28.3	27.1
Nasal aperture width:	18.7	20.6	18.4	22.0	22.4	20.9
Width between nasal apertures:	2.9	3.7	3.7	3.4	4.6	3.8
Rostral base length to edge of anterior fontanelle:	23.6	28.0	26.0	24.3	25.3	26.1
Anterior fontanelle width:	7.6	9.0	8.0	10.5	7.2	7.8
Cranial height:	39.4	39.2	40.4	41.2	38.0	38.1
Basal plate width at orbital notches:	4.1	3.2	4.4	4.9	4.0	4.8
Cranial roof width over orbital notches:	23.1	22.8	22.2	23.7	21.6	21.7
Orbital length:	41.0	42.0	43.2	42.7	43.5	38.9
Preorbital process length:	10.5	17.1	14.9	11.8	14.4	16.4
Postorbital process length:	9.9	9.0	9.8	10.8	10.0	12.0
Width across suborbital shelves:	29.0	30.5	28.8	31.1	29.5	29.5
Otic capsule length:	30.6	28.9	30.9	30.1	29.4	28.3
Width across otic capsule:	28.7	36.7	30.6	32.5	29.0	34.7
Width across preorbital processes:	37.5	36.2	34.6	38.9	34.7	34.9
Width across postorbital processes:	48.3	46.5	46.8	50.8	46.2	43.2

TABLE 3.11

Regional spiral valve counts of *Heptranchias perlo.*

REGION	N	R	$\bar{x}$	s.d.	CV
Gulf of Mexico	1	21			
Mozambique	4	18-22	20.0	1.5	7.3
South Africa	5	20-22	21.0	0.8	3.5
Taiwan	36	19-22	21.0	0.8	4.0

TABLE 3.12

Total tooth counts of *Hexanchus griseus.*

REGION	N	R	$\bar{X}$	s.d.	CV
Australia	1	38/30			
California	29	26-46/20-36	34.1/26.2	5.1/4.1	14.9/15.6
Chile	2	32-33/23-25	32.5/24.0		
Cuba	1	40/34			
Gulf of Mexico	2	40-44/33-34	42.0/33.5		
Hawaii	1	39/29			
Mediterranean Sea	2	28-30/19-21	29.0/20.0		
Southern Africa	27	28-46/20-38	33.9/26.7	4.4/5.0	12.8/18.6
Taiwan	2	33-41/23-29	37.0/26.0		
Washington	1	35/23			

TABLE 3.13

Pectoral fin radial counts of *Hexanchus griseus.*

REGION	N	R	$\bar{X}$	s.d	CV
California	1				
mesopterygium		10			
metapterygium		13			
total radials		23			
radial segments		6			
Southern Africa	19				
mesopterygium		10-11	10.4	0.5	23.4
metapterygium		12-14	12.9	0.7	5.8
total radials		22-25	23.2	0.9	3.8
radial segments		5-7	6.1	0.5	8.4

TABLE 3.14

Anal, dorsal and pelvic fin radial counts of *Hexanchus griseus.*

REGION	N	R	$\bar{X}$	s.d.	CV
California					
pelvic fin	2	21-22	21.5		
dorsal fin	1	17			
anal fin	1	14			
Mediterranean Sea					
pelvic fin	1	22			
Southern Africa					
pelvic fin	19	21-26	23.7	1.2	5.1
dorsal fin	16	14-20	17.7	1.7	9.3
anal fin	15	14-20	15.9	1.8	1.3

TABLE 3.15

Total vertebral counts of *Hexanchus griseus.*

REGION	N	R	$\bar{X}$	s.d.	CV
California	3				
mp		42-52	46.3	4.2	9.0
dp		23-30	26.0	2.9	11.3
dc		60-73	61.3	9.0	14.7
total		128-145	133.6	8.0	6.0
Southern Africa	19				
mp		41-50	45.4	2.2	4.9
dp		18-27	24.7	1.9	7.9
dc		50-77	60.8	6.6	10.7
total		118-148	131.0	7.6	5.8

TABLE 3.16

Hexanchus griseus. Cranial measurements expressed as a percentage of nasobasal length.

SEX	F	M	M	M
TL	681 mm	1100 mm	1920 mm	3330 mm
Nasobasal length:	73.0 mm	108.5 mm	157.0 mm	256.5 mm
Length of medial rostral cartilage:	6.4	5.1	7.6	5.1
Width between bases of lateral rostral cartilages:	21.2	21.0	26.8	16.8
Width across nasal capsules:	59.7	72.8	76.0	65.5
Width of nasal capsule:	28.8	36.4	33.8	32.8
Length of nasal capsule:	34.2	34.1	24.2	41.6
Nasal aperture width:	15.1	23.0	22.3	20.7
Width between nasal apertures:	21.9	27.6	22.3	21.8
Rostral base length to edge of anterior fontanelle:	22.3	28.8	24.2	28.3
Anterior fontanelle width:	7.8	15.2	10.4	13.9
Cranial height:	43.8	38.2	10.8	40.5
Basal plate width at orbital notches:	16.2	13.4	15.3	9.0
Cranial roof width over orbital notches:	40.1	44.2	45.9	48.9
Orbital length:	36.4	35.4	40.1	43.4
Preorbital process length:	31.5	22.1	26.8	24.2
Postorbital process length:	25.3	25.8	25.9	26.5
Otic capsule length:	44.4	42.1	46.5	46.8
Width across suborbital shelves:	50.7	47.5	54.4	56.5
Width across otic capsule:	37.9	38.9	45.2	46.6
Width across preorbital processes:	61.6	60.7	61.1	58.1
Width across postorbital processes:	90.4	74.9	82.0	71.0

TABLE 3.17

Spiral valve counts of *Hexanchus griseus*.

REGION	N	R	$\bar{X}$	s.d.	CV
California	7	35-39	37	1.4	3.8
Chile	1	37			
Mediterranean Sea	1	35			
Namibia	14	35-37	36	0.6	1.7
North Atlantic	1	38			
South Africa	8	35-38	36	1.0	2.7
Taiwan	1	36			

TABLE 3.18

Total tooth counts of *Hexanchus nakamurai.*

REGION	N	R	$\overline{X}$	s.d.	CV
Cuba	1	32/30			
Florida	1	29/25			
Philippine Is.	2	25-26/15-19	25.5/17.0		
South Africa	1	34/21			
Taiwan	5	28-33/9-12	30.8/21.8	1.7/1.2	5.6/5.4
Virgin Is.	1	28/32			

TABLE 3.19

Hexanchus nakamurai. Cranial measurements from a 482-mm TL specimen, expressed as a percentage of nasobasal length.

Nasobasal length:	59.5 mm
Length of medial rostral cartilage:	3.4
Width between bases of lateral rostral cartilage:	14.3
Width across nasal capsules:	55.5
Length of nasal capsule:	26.1
Width of nasal capsule:	26.9
Nasal aperture width:	20.2
Width between nasal apertures:	12.6
Length from rostral base to edge of anterior fontanelle:	30.3
Anterior fontanelle width:	10.1
Cranial height:	31.9
Basal plate width at orbital notches:	6.7
Cranial roof width over orbital notches:	28.6
Orbital length:	40.3
Width across preorbital processes:	47.9
Preorbital process length:	21.8
Postorbital process length:	15.1
Width across suborbital shelves:	35.3
Otic capsule length:	27.7
Width across otic capsule:	26.9
Width across preorbital processes:	47.9
Width across postorbital processes:	63.9

TABLE 3.20

Spiral valve counts of *Hexanchus nakamurai.*

REGION	N	R	$\overline{X}$	s.d.	CV
Kenya	6	25-27	26.0	0.6	2.2
Philippines	2	24-25	24.5		
Taiwan	2	22	22.0		
Virgin Is.	1	24			

TABLE 3.21

Tooth counts of *Notorynchus cepedianus*.

REGION	N	R	$\overline{X}$	s.d.	CV
Argentina	3	21-33/18-28	25.7/23.0	5.2/4.1	20.5/17.7
Australia	2	35-39/28-32	37.0/30.0		
Brazil	1	32/26			
California	55	21-42/20-37	28.4/25.8	4.6/3.6	16.3/14.1
Patagonia[1]	1	22/20			
Peru	1	24/22			
Southern Africa	51	28-42/24-37	34.8/28.0	3.3/2.7	9.5/9.7

[1] Holotype of *N. pectorosus*

TABLE 3.22

Pectoral fin radial counts of *Notorynchus cepedianus*.

REGION	N	R	$\overline{X}$	s.d.	CV
California	3				
mesopterygium		11-12	11.7	0.5	4.0
metapterygium		9-10	9.3	0.5	5.1
total radials		25-27	25.7	0.9	3.7
radial segments		7	7.0	0.0	0.0
Patagonia[1]	1				
mesopoterygium		13			
metapterygium		9			
total radials		22			
radial segments		7			
Southern Africa	18				
mesopterygium		11-12	11.2	0.4	3.6
metapterygium		12-15	13.1	0.8	6.1
total radials		23-26	24.3	0.9	3.7
radial segments		6-8	7.0	0.3	4.3

[1] Holotype of *N. pectorosus*

Table 3.23

Pelvic, dorsal and anal fin radial counts of *Notorynchus cepedianus*.

REGION	N	R	$\bar{X}$	s.d.	CV
California					
pelvic fin	2	22-26	23.5		
dorsal fin	3	17-19	18.0	0.8	4.5
anal fin	3	17	17.0	0.0	0.0
Southern Africa					
pelvic fin	26	21-25	22.6	1.2	5.4
dorsal fin	13	15-19	17.5	1.2	6.6
anal fin	13	14-17	15.5	1.0	6.4

TABLE 3.24

Vertebral counts of *Notorynchus cepedianus*.

REGION	N	R	$\bar{X}$	s.d.	CV
California					
mp	10	50-57	52.7	2.0	3.7
dp	10	13-23	18.4	3.2	17.2
dc	8	50-56	53.2	1.9	3.5
total	8	123-130	125.5	2.3	1.9
Southern Africa					
mp	29	48-57	52.7	2.3	4.3
dp	29	16-28	21.7	2.8	13.0
dc	29	54-82	70.0	8.7	12.4
total	29	127-157	144.4	9.4	6.5

TABLE 3.25

Notorynchus cepedianus. Cranial measurements expressed as a percentage of nasobasal length.

SEX	F	M	M	F	F
TL	854 mm	932 mm	1375 mm	1740 mm	2420 mm
Nasobasal length:	83.8 mm	87.4 mm	131.0 mm	159.5 mm	195.3 mm
Length of medial rostral cartilage:	7.4	13.0	10.5	11.5	14.3
Width between bases of lateral rostral cartilages:	15.8	20.9	16.5	22.8	24.6
Width across nasal capsules:	50.1	65.9	58.8	65.0	65.4
Width of nasal capsule:	30.5	31.0	29.4	33.8	31.4
Length of nasal capsule:	20.6	21.4	24.1	23.8	36.5
Nasal aperture width:	22.6	24.0	24.7	25.3	28.0
Width between nasal apertures:	11.8	13.3	15.4	14.3	11.7
Rostral base length to edge of anterior fontanelle:	27.0	25.2	24.0	25.2	27.7
Anterior fontanelle width:	19.9	19.9	17.7	23.0	22.1
Cranial height:	37.4	36.5	37.4	38.2	38.5
Basal plate width at orbital notches:	17.7	18.4	17.6	17.9	17.2
Cranial roof width over orbital notches:	46.4	49.4	46.6	51.5	58.4
Orbital length:	35.8	35.5	31.1	30.5	31.5
Preorbital process length:	18.5	16.8	23.7	16.9	17.9
Postorbital process length:	17.2	18.5	11.0	21.1	19.2
Otic capsule length:	40.9	41.9	40.0	46.0	49.7
Width across suborbital shelves:	50.7	51.7	50.2	55.4	57.0
Width across otic capsule:	42.4	48.2	45.5	48.7	54.2
Width across preorbital processes:	71.4	72.0	54.3	71.5	72.4
Width across postorbital processes:	80.9	81.0	82.7	86.7	89.1

TABLE 3.26

Regional spiral valve counts of *Notorynchus cepedianus.*

REGION	N	R	$\overline{X}$	s.d.	CV
Argentina	1	16	-	-	-
California	23	14-17	15.5	0.75	4.9
China	1	15	-	-	-
Patagonia[1]	1	15	-	-	-
Peru	1	15	-	-	-
Southern Africa	71	14-17	16.3	0.75	4.6

[1] Holotype of *N. pectorosus.*

TABLE 3.27

Distribution of *Chlamydoselachus anguineus.*

LOCATION	LATITUDE	LONGITUDE	SOURCE
Pacific Ocean			
Pt. Arguello, Calif.	34°23'N	121°03'W	1,2
S.E. Honshu, Japan from	35°30'N	140°00'E	
to	34°00'N	138°00'E	1,3,4
Okinawa Island	26°30'N	128°00'E	5
Taiwan from	25°10'N	121°43'E	
to	22°26'N	120°30'E	1
Milwaukee Seamount, Northwestern Range	31°50'N	172°45'E	6
Colahan Seamount, Hawaiian Range	31°02'N	175°54'E	6
Australia, New South Wales	35°35'S	150°44'E	1,7
New Zealand	42°07'S	170°17'E	8
Chile	37°03'S	73°31'E	9
Indian Ocean			
Oceanic	32°49'S	35°07'E	10
Port Alfred, S.A.[1]	33°36'S	26°54'E	11
Transkei			12
Atlantic Ocean			
South Atlantic.....			
Angola from	12°36'S	13°12'E	1,13,14
to Namibia	26°38'S	15°10'E	15,16,17
North Atlantic.....			
North West Africa	22°09'N	---	18
Maderia from	32°00'N	17°00'E	
to Shetlands	59°50'N	06°30'W	
to Varanger Fjord, Norway	69°45'N	30°00'E	1,19,20
Western Atlantic.....			
Suriname	07°00'N	55°30'W	21
Central Eastern Atlantic.....			
Cape Blanc	20°00'N	18°00'W	14

[1] This record is unconfirmed.

Source: 1. specimen, 2. Noble 1948, 3. Tanaka, 4. Taniuchi 1987, 5. Nakaya 1985, 6. Borets 1986, 7. Bass 1979, 8. Nakaya & Bass 1978, 9. Armada 1977, 10. Timokhin 1980, 11. Smith 1951, 12. R. White, pers. comm., 13. R. Melville-Smith, pers. comm., 14. Domanevskiy 1975, 15. Smith 1967, 16. Lloris 1986, 17. Trunov 1968, 18. Golovan & Pakhorukov 1986, 19. Wheeler 1962, 20. Collett 1896, 21. Uyeno & Saski 1983.

TABLE 3.28

Distribution of *Heptranchias perlo.*

LOCATION	LATITUDE	LONGITUDE	SOURCE
Pacific Ocean			
Japan.....			
from Hokkaido	42°00'N	142°00'E	1,2,3
to Kyushu	32°00'N	129°00'E	4,5
Ogasawara Island	27°00'N	142°00'E	3
Okinawa Island	26°30'N	128°00'E	6
Yellow Sea	36°00'N	123°00'E	7
East China Sea	30°00'N	125°00'E	8
Taiwan from	25°10'N	121°43'E	
to	22°36'N	120°17'E	1,9
New Caledonia	21°00'S	164°00'E	1
Australia.....			
New South Wales	33°55'S	151°10'E	10
Victoria	38°23'S	142°17'E	10
South Australia	35°00'S	135°00'E	11
Tasmania	42°54'S	147°18'E	12
New Zealand	41°17'S	174°47'E	10
Peru	12°06'S	77°20'W	13
Chile	23°40'S	70°23'W	14
Indian Ocean			
Bali, Indonesia	08°00'S	115°00'E	14
India	10°00'N	76°00'E	15
Gulf of Aden	13°11'N	50°22'E	1
Aldabra	09°00'S	46°00'E	16
Western Australia	35°00'S	120°00'E	1,11
Mozambique	24°00'S	36°00'E	1,17
Natal, South Africa	30°00'S	32°00'E	1,17
Mascarene Ridge	10°00'S	60°00'E	18
Sri Lanka	06°00'N	81°00'E	19
Comores Is.	12°00'S	44°30'E	1
Madagascar	13°00'S	48°00'E	20
Atlantic Ocean			
South Ireland	52°20'N	80°00'W	21
Bishop Rock, England	06°30'N	49°55'W	21
Bay of Biscay	44°00'N	04°30'E	21
Strait of Gilbratar	36°00'N	06°00'E	14
West African coast.....			
to Fernando Poo	03°48'N	08°24'E	1
to Ivory Coast	03°43'N	06°53'W	1
to Nigeria	04°00'N	06°00'E	1
to Liberia	06°20'N	10°46'W	1

TABLE 3.28 (continued)

LOCATION	LATITUDE	LONGITUDE	SOURCE
to Angola	17°30'S	11°40'E	1,22
to Namibia	26°38'S	15°10'E	22,23
Argentina	36°00'S	54°00'W	14
Brazil	23°30'S	45°00'W	24
Suriname	07°00'N	55°30'W	25
North Carolina from	34°19'N	75°53'W	
to Florida	25°00'N	80°00'W	1
Bahamas	27°30'N	78°53'W	1
Azores	38°00'N	28°00'W	26
Maderia	33°00'N	17°00'W	26
Mediterranean Sea from	36°00'N	05°00'W	1,27,
to	33°00'N	35°00'E	28,29
Caribbean Sea			
Cuba	23°00'N	80°00'W	1,30
Gulf of Mexico from	25°00'N	95°00'W	
to	29°00'N	83°00'W	1,30
Mexican coast			
to Yucatan Peninsula	20°00'N	95°00'W	31

Source: 1. specimens, 2. Nakaya 1984, 3. Taniuchi, 4. Tanaka, 5. Mizue 1984, 6. Uchida 1984, 7. Chu et al. 1960, 8. Hongxi et al. 1987, 9. Teng 1962, 10. Garrick & Paul 1971, 11. May & Maxwell 1986, 12. Last et al. 1983, 13. Chirichigno 1980, 14. Compagno 1984, 15. Compagno & Talwar 1985, 16. Forster et al. 1970, 17. Bass et al. 1975, 18. Shcherbachev 1987, 19. De Silva 1989, pers. comm., 20. Fourmanoir 1961, 21. Cappetta et al. 1985, 22. Pissarro & Sanches 1973, 23. Lloris 1986, 24. O. Gadig, pers. comm., 25. Uyeno & Saski 1983, 26. Boeseman, 27. Del Cerro, pers. comm., 28. J. Abela, pers. comm., 29. Capape 1980, 30. Bigelow & Schroeder 1948, 31. S.P. Applegate, pers. comm.

TABLE 3.29

Distribution of *Hexanchus griseus*.

LOCATION	LATITUDE	LONGITUDE	SOURCE
Pacific Ocean			
Baja California from	27°40'N	114°62'W	
to Aleutian Islands	52°00'N	173°50'W	1,2
Hawaii	21°30'N	158°00'W	1
Kimmey Seamount, Northwestern Range	34°54'N	170°43'E	3
Japan from	36°00'N	149°00'E	
to	32°00'N	129°00'E	4,5,6
Okinawa	26°30'N	128°00'E	7
Taiwan from	25°10'N	121°43'E	
to	22°36'N	121°43'E	1,8
East China Sea	30°00'N	125°00'E	9
Philipine Is.	15°00'N	120°00'E	10
South China Sea	16°00'N	112°00'E	11
Australia....			
New South Wales	33°55'S	151°10'E	12
Victoria	38°23'S	142°17'E	13
Tasmania	42°54'S	147°18'E	14
New Zealand	41°17'S	174°47'E	15
Nasaka Ridge	21°25'S	81°38'W	16
Chile	42°08'S	73°29'W	1
Peru	12°06'S	77°20'W	17
Enewetak, Marshall Is.	11°30'N	162°15'E	18
Palau	07°30'N	134°30'E	19
Indian Ocean			
Sumatra	00°00'	100°00'E	12
Malaysia	03°00'N	100°00'E	12
Assumption Is.	09°00'S	46°00'E	20
Geyser Reef	12°00'S	46°00'E	20
Cosmoledo Is.	09°00'S	47°00'E	20
Aldabra	09°00'S	46°00'E	20
Madagascar	13°00'S	48°00'E	21
Comores Is.	12°00'S	44°30'E	1
Mozambique	24°00'S	36°00'E	1,22
South Africa from	30°00'S	32°00'E	
to	35°00'S	20°00'E	1,22

TABLE 3.29 (continued)

LOCATION	LATITUDE	LONGITUDE	SOURCE
Atlantic Ocean			
South Africa from	34°00'S	18°00'E	
to Namibia	17°30'S	11°40'E	1,22,23
Angola from	17°30'S	11°40'E	
to	06°00'S	12°00'E	24
Ivory Coast	03°43'N	06°53'W	25
Nigeria	04°00'N	06°00'E	25
Senegal from	15°00'N	17°00'W	25
to Straits of Gilbratar	36°00'N	06°00'E	25
to Bay of Biscay	44°00'N	04°30'W	1
to the Irish Sea	53°30'N	05°30'W	1,26
to Ireland	54°00'N	10°30'W	25,26
to Faeroe Bank	61°00'N	09°00'W	25,26
to Norway	58°00'N	06°00'E	25
to Iceland	63°30'N	20°00'W	25
Azores	38°00'N	28°00'W	1
Mid-Atlantic Ridge	40°00'N	30°00'W	27
N.W. Atlantic from	41°55'N	68°05'W	
to Florida	25°00'N	80°00'W	25,28
Bermuda	33°00'N	65°00'W	29
Venezuela	11°00'N	65°00'W	30
Brazil	23°30'S	45°00'W	25
Argentina	36°00'S	54°00'W	31
Isla de Noroha	03°50'S	32°25'W	32
Gough Island	40°20'S	10°00'W	1,33
Tristan de Cunha	37°00'S	12°30'W	1,33
Canary Islands	28°30'N	14°00'W	34
Maderia	33°00'N	17°00'W	34
Mediterranean Sea			
Entire range from	36°00'N	05°00'W	1,35,36,37,
to	33°00'N	35°00'E	38,39
Caribbean Sea			
Cuba	23°00'N	80°00'W	1,40
Caymans	19°00'N	80°00'W	41
Gulf of Mexico from	25°00'N	95°00'W	
to	29°00'N	83°00'W	42
Mexican coast			
to Yucatan	20°00'N	95°00'W	43
Central America from	15°00'N	80°00'W	
to	10°00'N	83°30'W	42

Source: 1. specimens; 2. Ebert 1986b; 3. Borets; 4. Tanaka 1984; 5. Taniuchi 1984; 6. Mizue 1984; 7. Uchida 1984; 8. Teng 1962; 9. Hongxi et al. 1987; 10. Otake 1984; 11. Chu et al. 1962; 12. Stead 1963; 13. Lynch 1964; 14. Last et al. 1983; 15. Phillipps 1946; 16. Golovan & Pakhorukov 1986; 17. Chirichigno 1980; 18. Randall 1986; 19. L.J.V. Compagno, pers. comm.; 20. Forster et al. 1970; 21. Fourmanoir et al. 1961; 22. Bass et al. 1975; 23. Lloris 1986; 24. Pissarro & Sanches 1973; 25. Compagno 1984; 26. Wheeler & Blacker 1969; 27. K. Hartel, pers. comm.; 28. Backus 1957; 29. Clark 1986; 30. Cervigon 1966; 31. Menni 1986; 32. Amorim, pers. comm.; 33. Roscoe 1979; 34. Boeseman 1973; 35. Del Cerro, pers. comm.; 36. J. Abela, pers. comm.; 37. Golani, pers. comm.; 38. Golani 1986; 39. Gilat & Gelman 1987; 40. Bigelow & Schroeder 1948; 41. Clark 1988; 42. Springer & Waller 1969; 43. S.P. Applegate, pers. comm.

TABLE 3.30

Distribution of *Hexanchus nakamurai.*

LOCATION	LATITUDE	LONGITUDE	SOURCE
Pacific Ocean			
Ogasawara Island	27°00'N	142°00'E	1
Okinawa Island	26°30'N	128°00'E	2
Taiwan from	25°10'N	121°43'E	
to	22°36'N	120°17'E	3,4
Dumaguete, Philippines	09°20'N	123°18'E	3,5
New Caledonia	21°00'N	164°00'E	3
New South Wales, Australia	28°34'S	153°50'E	3
Indian Ocean			
Bunbury, Western Australia	33°20'S	115°34'E	3
Geyser Banks	09°00'S	46°00'E	6
Zelee Bank	09°00'S	46°00'E	6
E. of Diego Suarez	12°00'S	49°00'E	6
Castor Bank	12°00'S	48°00'E	6
Cordeliere Bank	12°00'S	48°00'E	6
Kenya	05°00'S	40°00'E	3,7
Mozambique	20°00'S	30°00'E	7
Natal, South Africa	25°00'S	30°00'E	3,7
Madagascar	12°19'S	49°17'E	8[1]
Mauritius	20°10'S	57°30'E	3
Atlantic Ocean			
Strait of Gilbratar	35°00'N	10°00'W	9
Bay of Biscay	44°00'N	04°30'W	10[2]
Bimini, Bahamas	25°46'N	79°14'W	3,5
Venezuela	11°00'N	65°00'W	11[3]
Mediterranean Sea			
Strait of Gilbratar from	35°00'N	10°00'W	
to Italy	44°00'N	09°00'E	12
Caribbean Sea			
Cuba	23°00'N	80°00'W	3,5,13[4]
Caymans	19°00'N	80°00'W	14
Virgin Islands	66°00'N	18°30'W	3,15
Gulf of Mexico from	25°00'N	95°00'W	
to	29°00'N	83°00'W	3
Yucatan Peninsula	20°00'N	95°00'W	16
Bluefields, Nicargua	12°00'N	83°49'W	5
Point Limon, Costa Rica	10°00'N	83°01'W	5

[1] Specimens were incorrectly identified as *H. griseus*; [2] Based on a drawing in the text; [3] Photograph of specimen misidentified as *H. griseus*; [4] Misidentified as *H. griseus.*

Source: 1. Taniuchi 1984, 2. Uchida 1984, 3. specimens, 4. Teng 1962, 5. Springer & Waller 1969, 6. Forster et al. 1970, 7. Bass et al. 1975, 8. Fourmanoir 1961, 9. Compagno 1984, 10. Desbrosses 1938, 11. Cervigon 1966, 12. Tortonese 1985, 13. Bigelow & Schroeder 1948, 14. Clark 1988, 15. I. Sang, pers. comm., 16. S.P. Applegate, pers. comm.

TABLE 3.31

Distribution of *Notorynchus cepedianus.*

LOCATION	LATITUDE	LONGITUDE	SOURCE
Pacific Ocean			
Baja California from	27°40'N	114°62'W	
to S.E. Alaska	56°00'N	134°00'W	1,2
Gulf of California	31°00'N	114°00'W	3,4
Nagasaki, Japan	32°00'N	130°00'E	5
Sagami Bay, Japan	35°30'N	140°00'E	1
Yellow Sea	36°00'N	123°00'E	6
Chinese Mainland coast			
to Xiamen (Amoy)	24°28'N	118°05'E	1,7
Taiwan	25°10'N	121°43'E	1,8
New South Wales	33°55'S	151°10'E	9
Victoria	38°23'S	142°17'E	9.
Tasmania	42°54'S	147°18'E	1,9
South Australia	34°56'S	138°36'E	9
New Zealand	41°17'S	174°47'E	10
Peru from	12°06'S	77°20'W	
to Chile	54°00'S	70°30'W	1,11,12
Indian Ocean			
South Africa from	34°00'S	18°00'E	
to	33°00'S	28°00'E	1
Sri Lanka	06°00'N	81°00'E	13
Madras, India	13°05'N	80°18'E	14
Atlantic Ocean			
Cape Point, S.A. from	34°00'S	18°00'E	
to Cunene River, Namibia	17°30'S	11°40'E	1
Gough Island	40°20'S	10°00'W	1,15
Tristan Island	37°00'S	12°30'W	1,15
Santos, Brazil from	23°56'S	46°22'W	
to Argentina	54°00'S	70°00'W	1,16,17

Source: 1. present study; 2. Ebert 1986b; 3. Applegate 1979; 4. Galvan-Magana, Nienhuis & Klimley 1989; 5. Mizue 1984; 6. Chu et al. 1960; 7. Chu 1963; 8. Teng 1962; 9. Last et al. 1983; 10. Paul 1987; 11. Chirichgno 1980; 12. Pequeno 1979; 13. R. De Silva, pers. comm.; 14. Day 1878, 15. V. Peddemors, T. Andrews, pers. comm.; 16. O. Gadig, pers. comm.; 17. Menni & Garcia 1985.

TABLE 3.32

Chlamydoselachus anguineus. Hydrographic data for a specimen from Namibia.

Location: 27°23.9'S 14°21.1'E; Date 19 February 1989.

Depth (m)	S°/oo	O_2	N	Si	P	Chl A
2	35.40	4.66	5.5	4.0	0.37	0.5
12	35.27	5.59	1.0	4.1	0.45	0.8
23	35.33	5.60	1.2	4.0	0.47	1.1
35	35.43	5.18	4.0	4.9	0.47	0.7
51	35.28	4.94	11.6	8.1	0.98	0.3
105	35.24	4.62	16.2	11.1	1.25	0.0
157	35.21	4.24	14.5	12.1	1.18	0.0
207	35.23	2.53	18.2	22.5	2.04	0.0
306	35.09	2.74	18.2	16.4	1.81	0.0
434	35.06	1.85	18.2	23.3	2.39	0.0

Key: S°/oo - salinity; O_2 - dissolved oxygen; N - nitrogen; Si - silicates; P - phosphates; Chl A - chlorophyll A.

TABLE 3.33

Heptranchias perlo. Hydrographic data for a specimen from Natal.

Depth (m)	S°/oo	O_2	°C
1	35.30	–	22.45
5	35.29	3.37	22.44
20	35.34	3.37	22.29
40	35.36	3.22	21.28
100	35.46	2.52	16.61
150	35.44	2.77	14.81
210	35.39	2.79	14.30
260	–	–	–

TABLE 3.34

Hexanchus griseus. Hydrographic data for specimens from the west coast of southern Africa.

Location: 32°11.3'S, 17°39.4'E; Date: 12 February 1988

Depth (m)	S°/oo	O_2	N	Si	P	Chl A
3	35.10	6.69	5.7	2.8	0.43	7.5
14	35.12	6.60	3.9	2.3	0.41	7.2
25	35.25	5.07	10.0	6.9	0.87	4.1
36	35.23	4.76	12.1	8.8	1.09	1.2
54	35.22	4.60	14.0	9.2	1.10	1.0
106	35.05	4.32	17.8	12.0	1.33	-
161	34.95	2.86	18.4	29.5	2.09	-

Location: 23°15.5'S, 13°16.8'E; Date: 15 January 1989

Depth(m)	°C	S°/oo	O_2	N	Si	P	Chl A
3	18.7	35.27	5.30	5.5	3.8	0.07	0.2
13	18.7	35.27	5.89	5.3	1.7	0.05	0.3
33	17.0	35.31	5.97	5.7	3.4	0.06	0.4
51	14.5	35.39	4.65	11.1	3.5	0.09	0.5
94	13.2	35.43	3.72	16.3	6.3	0.12	-
133	12.7	35.48	1.94	25.3	11.3	0.17	-
173	12.1	35.41	1.86	25.8	11.0	0.18	-
242	11.7	35.33	1.09	25.8	13.5	0.20	-
315	9.9	35.21	0.85	25.8	12.2	0.24	-

TABLE 3.34 (continued)

Location: 23°36.6'S, 13°5.1'E; Date: 15 January 1989.

Depth (m)	°C	S°/oo	O_2	N	Si	P	Chl A
3	20.1	35.32	5.78	4.9	1.0	0.04	0.4
13	19.6	35.32	5.74	1.7	1.0	0.03	0.4
32	16.4	35.33	5.66	6.2	2.6	0.06	0.5
53	15.4	35.45	4.81	10.3	3.0	0.09	1.3
104	13.5	35.49	3.34	17.8	8.3	0.15	-
205	11.8	35.40	1.44	25.6	11.9	0.20	-
307	9.7	35.17	1.30	25.6	16.4	0.22	-
406	8.0	35.01	1.90	25.6	18.3	0.23	-
554	6.2	34.87	2.27	25.6	23.2	0.24	-

Location: 24°25.3'S, 13°35.3'E; Date: 16 January 1989.

Depth(m)	°C	S°/oo	O_2	N	Si	P	Chl A
3	18.2	35.26	5.95	4.7	2.4	0.05	0.3
12	17.1	35.35	5.89	3.2	2.1	0.05	0.4
33	16.2	35.41	5.73	4.1	2.2	0.05	1.0
52	15.0	35.52	5.22	6.0	3.9	0.06	1.1
105	12.9	35.42	4.25	13.9	6.7	0.10	-
206	11.0	35.28	2.55	24.9	11.4	0.17	-
342	9.4	35.14	1.34	26.0	18.9	0.25	-

TABLE 3.35

Tag and recapture data for *Notorynchus cepedianus*.

Location		Days liberty (km)	Dist. & dir. travelled		km/day
Tagged	Recaptured				
California					
Humboldt Bay	Humboldt Bay	ca. 730	0		0
Namibia					
Bird Rock	Bird Rock	34	0		0
Mile 4	Walvis Bay	538	41	S	0.1
South Africa					
Boskloof	Laaiplek	484	291	N	0.6
Grotto	Laaiplek	359	110	N	0.3
Struibaai	Rooiels	162	211	NW	1.3
Struibaai	Agulhas	49	7	W	0.1
Bontkop	Dwarskerbos	136	160	N	1.2
Mpekweni	Boknesstrand	484	69	W	0.1
Grotto	Dwarskerbos	137	120	N	0.9
Agulhas	Kleinbaai	122	76	W	0.6
West Coast	12 Mile Bank	193	379	SE	2.0

TABLE 3.36

Combined seasonal abundance and maturity status of sevengill sharks

in Humboldt Bay and San Francisco Bay.

	MONTHS											
Maturity	M	A	M	J	J	A	S	O	N	D	J	F
Juveniles	2	9	29	36	4	4	21	4	4	4	0	0
Adolescents	1	0	1	1	0	1	1	3	0	0	0	0
Adults	3	7	16	4	1	1	3	2	0	0	0	0

TABLE 3.37

Prey species recorded for *Heptranchias perlo* from Taiwan.

Teleosts

- *Conger cinereus*
- *Nemichthys scolopaceus*
- *Priacanthus macracanthus*
- *Saurida elongate*
- *Trachurus japonicus*
- *Trichiurus lepturus*
- *Diaphus* sp.
- Myctophidae

Crustacea

- Brachyura
    - *Charybdis bimaculata*

- Macrura
    - *Hymenopenaeus aequalis*
    - *Metapenaeopsis andamanensis*
    - *Systellaspis pellucida*
    - *Pasiphaea* sp.
    - *Sergia* sp.
    - Unidentified Penaeidae

Cephalopoda

- Unidentified cephalopoda

Table 3.38

Prey species recorded for *Hexanchus griseus* from southern Africa.

Cephalopoda
- *Loligo vulgaris reynaudii*
- *Todarodes angolensis*
- Unidentified cephalopoda

Gastropoda
- Unidentifed gastropoda

Crustacea
- Unidentified crustacea

Cartilaginous fish
- *Callorhinchus capensis*
- *Mustelus mustelus*

Teleost
- *Coelorhinchus* sp.
- *Diaphus* sp.
- Myctophidae
- *Engraulis capensis*
- *Sardinops ocellatus*
- *Etrumeus whiteheadi*
- *Scomber japonicus*
- *Helicolenus dactylopterus*
- *Merluccius paradoxus*
- *Merluccius capensis*
- Unidentified teleost

Cetacea
- Unidentified cetacean

Pinnipeda
- *Arctocephalus pusillus*

Table 3.39

Prey species recorded for *Hexanchus griseus* from California.

Aganatha

- *Lampetra tridentata*
- *Eptatretus stoutii*

Teleost

- *Anoplopoma fimbria*
- *Merluccius productus*
- Unidentified teleost

Cartilaginous fish

- *Squalus acanthias*
- *Mustelus henlei*
- *Hydrolagus colliei*
- *Echinorhinus cookei*
- Unidentified cartilaginous fish

Cetacean

- *Eschrichtius robustus*

Pinnipeda

- unidentified seal

TABLE 3.40

Index of relative importance of prey species eaten by *Notorynchus cepedianus* from California.

PREY SPECIES	N	%N	Wt (gm)	%Wt	FO	%FO	IRI
Crustacea							
Cancer magister	2	3.5	170	3.6	2	3.6	25.7
Cephalopoda							
Octopus dofleini	2	3.5	65	1.4	1	1.8	8.8
Agnatha							
Lampetra tridentata	4	6.9	40	0.9	2	3.6	28.2
Chondrichthyian							
Notorynchus cepedianus	1	1.7	20	0.4	1	1.8	3.9
Squalus acanthias	2	3.5	200	4.3	2	3.6	28.0
Mustelus henlei	8	13.8	705	15.0	8	14.6	418.8
Triakis semifasciata	2	3.5	200	4.3	2	3.6	28.0
Myliobatis californica	8	13.8	775	16.5	8	14.6	440.5
Unidentified shark	2	3.5	200	4.3	2	3.6	28.0
Teleost							
Clupea harengus	1	1.7	50	1.1	1	1.8	5.1
Engralis mordax	1	1.7	50	1.1	1	1.8	5.1
Phanerodon furcatus	1	1.7	75	1.6	1	1.8	6.0
Porichthys notatus	1	1.7	100	2.1	1	1.8	7.0
Roccus saxatilus	1	1.7	100	2.1	1	1.8	7.0
Acipenser sp.	1	1.7	100	2.1	1	1.8	7.0
Oncorhynchus sp.	1	1.7	100	2.1	1	1.8	7.0
Sebastes sp.	2	3.5	200	4.3	2	3.6	28.0
Cottidae	1	1.7	20	0.4	1	1.8	3.9
Unidentified teleost	13	22.4	1130	24.0	13	23.6	1098.1
Pinnipedia							
Phoca vitulina	4	6.9	400	8.5	4	7.3	112.1
TOTAL	58		4700		55		2296.1

TABLE 3.41

Index of relative importance of prey species eaten by *Notorynchus cepedianus* from South Africa.

PREY SPECIES	N	%N	Wt (gm)	%Wt	FO	%FO	IRI
Algae							
Unidentified algae	2	1.9	92.6	0.3	2	2.0	4.3
Cephalopoda							
Loligo vulgaris reynaudii	2	1.9	162.0	0.5	2	2.0	4.7
Octopus vulgaris	1	0.9	60.0	0.2	1	1.0	1.1
Crustacea							
Crab	1	0.9	8.2	0.2	1	1.0	0.9
Unidentified Crustacea	2	1.9	8.2	0.2	2	2.0	3.8
Chondrichthyian							
Squalus megalops	8	7.4	1803.1	5.1	7	7.1	89.6
Haploblepharus sp.	3	2.8	267.7	0.8	3	3.1	10.8
Mustelus mustelus	8	7.4	3626.9	10.3	7	7.1	126.8
Poroderma africanum	6	5.6	3791.0	10.8	5	5.1	83.5
P. africanum egg cases	2	1.9	9.0	0.0	1	1.0	1.9
P. pantherinum	5	4.6	1622.6	4.6	5	5.1	47.2
Poroderma sp.	2	1.9	70.2	0.2	2	2.0	4.2
Carcharhinus brachyurus	1	0.9	398.0	1.1	1	1.0	2.1
C. obscurus	1	0.9	300.0	0.9	1	1.0	1.8
Rhinobatis annulatus	1	0.9	350.0	1.0	1	1.0	2.0
Raja sp.	3	2.8	390.0	1.1	3	3.1	11.9
Narke capensis	1	0.9	225.0	0.6	1	1.0	1.6
Torpedo fuscomaculata	1	0.9	78.8	0.2	1	1.0	1.2
Dasyatis marmoratus	2	1.9	718.2	2.0	2	2.0	8.0
Dasyatis sp.	2	1.9	2454.0	7.0	2	2.0	18.1
Myliobatis aquila	1	0.9	1176.3	3.4	1	1.0	4.4
Unidentified shark	4	3.7	357.0	1.0	4	4.1	19.3
Unidentified chondrichthyian	2	1.9	314.4	0.9	2	2.0	5.6

TABLE 3.41 (continued)

PREY SPECIES	N	%N	Wt (gm)	%Wt	FO	%FO	IRI
Teleost							
Pomadasys sp.	1	0.9	314.0	0.9	1	1.0	1.9
Merluccius paradoxus	1	0.9	207.6	0.6	1	1.0	1.5
Conger wilsoni	1	0.9	120.0	0.3	1	1.0	1.3
Galeichthys sp.	1	0.9	78.0	0.2	1	1.0	1.2
Argyrosomus hololepidotus	2	1.9	1100.0	3.1	2	2.0	10.2
Mugil cephalus	1	0.9	27.0	0.1	1	1.0	1.0
Lithognathus aureti	1	0.9	30.0	0.1	1	1.0	1.0
Trachurus trachurus	5	4.6	657.0	1.9	3	3.1	19.9
Atractoscion aequidens	2	1.9	250.0	0.7	1	1.0	2.6
Chrysoblephus cristiceps	1	0.9	58.0	0.1	1	1.0	1.1
Merluccius sp.	2	1.9	955.0	2.7	2	2.0	9.3
Trichiurus lepturus	1	0.9	81.2	0.2	1	1.0	1.2
Sardinops ocellatus	4	3.7	88.8	0.3	1	1.0	4.0
Unidentified teleost	11	10.2	1526.1	4.4	11	11.2	163.2
Cetacea							
Lagenorhynchus obscurus	1	0.9	89.7	0.0	1	1.0	0.9
Unidentified Delphinidae	6	5.6	4440.1	12.7	6	6.1	111.5
Pinnipedia							
Arctocephalus pusillus	7	6.5	6861.0	19.6	7	7.1	186.0
TOTAL	109		35019.0		99		971.8

TABLE 3.42

Index of relative importance of prey species eaten by *Notorynchus cepedianus* from Namibia.

PREY SPECIES	N	%N	WT (gm)	%WT	FO	%FO	IRI
Algae							
Unidentified algae	1	0.9	5.0	0.0	1	1.1	1.1
Bivalvia							
Mytilus sp.	1	0.9	5.0	0.0	1	1.1	1.1
Cephalopoda							
Octopus vulgaris	2	1.8	25.0	0.1	2	2.3	4.4
Unidentified cephalopoda	1	0.9	0.6	0.6	1	0.0	1.0
Gastropoda							
Bullia laevissima	7	6.4	64.8	0.2	3	3.4	22.7
Agnatha							
Eptatretus hexatrema	1	0.9	18.6	0.1	1	1.1	1.1
Chondrichthyian							
Notorynchus cepedianus	4	3.7	1105.6	4.2	4	4.5	35.8
Mustelus mustelus	6	5.5	3065.0	11.6	6	6.8	116.9
Triakis megalopterus	1	0.9	350.0	1.3	1	1.1	2.6
Haploblepharus pictus egg case		4	3.7	17.2	0.1	2	2.38.5
Rhinobatis annulatus	3	2.8	3550.0	13.5	2	2.3	36.9
Raja straeleni	1	0.9	78.4	0.2	1	1.1	1.4
Myliobatis aquila	2	1.8	1200.0	4.6	2	2.3	14.5
Dasyatis marmorata	1	0.9	325.0	1.2	1	1.1	2.4
Callorhinchus capensis	3	2.8	57.5	0.2	3	3.4	10.1
Unidentified batoid	1	0.9	200.0	0.7	1	1.1	1.9

TABLE 3.42 (continued)

PREY SPECIES	N	%N	WT (gm)	%WT	FO	%FO	IRI
Teleost							
Argyrosomus hololepidotus	1	0.9	2700.0	10.2	1	1.1	12.7
Galeichthys sp.	4	3.7	1070.0	4.1	4	4.5	35.1
Genypterus capensis	1	0.9	220.0	0.8	1	1.1	2.0
Lithognathus aureti	1	0.9	700.0	2.7	1	1.1	4.1
Trachurus trachurus	5	4.6	665.6	2.5	5	5.7	40.4
Sardinops ocellatus	2	1.8	89.3	0.3	2	2.3	4.9
Scomber japonicus	1	0.9	256.0	0.9	1	1.1	2.1
Unidentified teleost	23	21.2	1123.1	4.3	9	10.2	259.4
Cetacea							
Unidentified Delphnidae	2	1.8	270.7	1.0	2	2.3	6.5
Pinnipeda							
Arctocephalus pusillus	30	27.5	9180.1	34.8	30	34.1	2126.3
TOTALS	109		26342.5		88		2756.0

CHAPTER 4
DISCUSSION

Taxonomy

The Order Hexanchiformes forms a distinctive group of sharks characterised by six or seven paired gill openings, a single dorsal fin and an anal fin. Adult males of this group lack a siphon sac, but have in its place, a clasper sac. This structure, which develops along the claspers, is unique to the Hexanchiformes. The Chlamydoselachidae are distinguished from the Hexanchidae by having the first gill opening extending across the throat, an eel-like body, similar dentition in both jaws, and absence of a clasper scroll. The members of the family Hexanchidae comprise three genera and four valid species; the perlon shark, Heptranchias perlo, sixgill shark, Hexanchus griseus, bigeyed sixgill shark, H. nakamurai, and the sevengill shark, Notorynchus cepedianus. Intraspecific tooth counts showed a broad overlap ranging from 19-46/09-38 (Figure 4.1). Unlike the frilled sharks all the cow shark species show a remarkable increase in the total number of teeth with growth. Ontogenic and sexual heterodonty is especially pronounced in the genus Hexanchus but less noticeable to non-existent in the two sevengill shark species. Tooth development and morphology may be useful characters for determining the age and stage of maturity of the two sixgill species. Intraspecific meristics between the five hexanchoid species showed a slight gradation for pectoral (Figure 4.2), pelvic (Figure 4.3), dorsal (Figure 4.4) and anal (Figure 4.5) fin radials.

While the Chlamydoselachidae were variable the Hexanchidae could be separated on the basis of MP vertebral counts due to high intraspecific variation between the different cow shark species (Figure 4.6). Spiral valve turn counts appear to be a good taxonomic indicator. The low intraspecific variation of spiral valve turns was consistent within the Hexanchidae, but was highly variable for the Chlamydoselachidae (Figure 4.7). Studies on other elasmobranch groups such as carcharhinoids (Compagno 1988) rajoids (Ishiyama 1958, Stehmann 1970) and squaloids, have shown these groups to have low intraspecific variation. The extreme variation in frilled sharks may indicate that subpopulations, subspecies or even additional, new species exist within this group.

The taxonomic arrangement used in this thesis follows that of Compagno (1977) in placing the cow and frilled sharks within separate families, the Hexanchidae and Chlamydoselachidae, respectively. Suggestions that the sevengilled perlon shark and the bigeyed sixgill were more closely aligned than the bigeyed sixgill and sixgill sharks (Springer & Waller 1969; Bass et. al 1975), appear to be unfounded. The cranial morphologies of the bigeyed sixgill and sixgill sharks are similar, while that of the sevengill shark is sufficiently different to warrant inclusion in its own genus (Compagno 1977). Furthermore, ontogenetic heterodonty is pronounced in the genus Hexanchus, but is virtually non-existent in the two sevengill species.

Results of this study indicate that the family Chlamydoselachidae contains at least two distinct species. Based on morphological and meristic differences (i.e. cranial differences, MP and total vertebral counts, spiral valve counts) between Namibian and western North Pacific forms, it is proposed that the Namibian frilled shark, designated here as Chlamydoselachus "sp. A", is a new and presently undescribed species. Results on the biology of frilled sharks will, however, be referred to C. anguineus in this dissertation. The proposed new species will be described elsewhere.

Biogeography

Hexanchoid sharks are widely distributed in area and depth. This group ranges from coastal bays and harbors along the open coast out across the continental shelf and down along the slopes to considerable depths. They occur from the equatorial zone to sub-polar regions.

The distribution, and particularly that of the deep-water species, may be more extensive than current knowledge indicates. An important aspect of elasmobranch distribution, and one that has usually been overlooked, is their micro-distribution in limited subhabitats within a broad range. It is well known that elasmobranchs tend to segregate by size and sex in part of their range. Any adverse effect on one segment of the population may, therefore jeopardize an entire population. One such effect results from the use of shark nets. The dusky shark, Carcharhinus obscurus, pups in nearshore waters off Natal, S.A. where the newborn remain until the onset of maturity. The principal natural predator on these small dusky sharks is the Zambezi shark, C. leucas, a predominantly coastal species. Zambezi sharks are removed by the shark nets which have too large a mesh size to capture the small dusky sharks (Van der Elst 1979). The seaward movement of juvenile dusky sharks as they mature tends to reduce their chance of capture by shark nets. Thus, the population of small dusky sharks has increased tremendously over the past few decades since the breeding population remains offshore beyond the shark nets. The situation is further complicated by reduction of other macropredatory sharks that eat juvenile dusky sharks and other small shark species. Species such as the houndshark (Mustelus mosis) that prey heavily on invertebrates tend to increase predation pressure on these lower trophic level organisms since their chief predators have been removed. Furthermore, as fisheries for elasmobranchs increase, the targeting of breeding areas will have a devastating effect on the entire population. This is the case in San Francisco Bay where the population structure and dynamics of several elasmobranch species have been adversely affected by the development of a shark fishery.

Environmental and physical factors play an important role in the distribution of many elasmobranch species. For bay-dependent species, manmade changes may affect localized breeding or other aspects of the life cycle. For example, heavy fishing pressure on the soupfin shark (Galeorhinus galeus) in San Francisco Bay between the 1930's and 1980's (Byers 1940; Ripley 1946; Herald & Ripley 1951; Ebert 1986c) reduced their numbers from a high of 16 percent of the total bay elasmobranch population (Smith & Kato 1979) to less than 1 percent by 1984 (Ebert 1986c). The effect of natural occurrences, for example El Nino and manmade pollutants that are discarded into the Bay, on elasmobranch populations are at present unknown and should be further investigated. A better understanding of the conditions preferred by elasmobranch species is important to maintaining healthy populations of these fishes.

Habitat

The hexanchoids occupy a broad spectrum of habitats ranging from temperate nearshore zones extending across the continental shelf to the continental slopes and perhaps on to the abysal plains. These sharks also inhabit both demersal and midwater habitats as part of their life history strategy. For example, catch records indicate that the frilled shark, usually considered a deepwater demersal species, is frequently caught in midwater trawls. Shiobara et al. (1987) reported that 40 percent of the frilled sharks captured in Suruga Bay were taken by midwater trawl between depths of 60 and 140 m. The capture of a California specimen was made at night within 20 m of the surface in water over 1500 m deep (Noble 1948).

Perlon sharks appear to be an outer shelf to upper slope species that is most commonly caught between 100 and 400 m. Their abundance between these depths may reflect local fishing efforts, as in Taiwan where perlon sharks are commonly taken between 100 and 300 m depth. However, Tanaka and Mizue (1977) reported that despite making long line sets between 100 and 600 m deep, most sharks were taken between 200 and 300 m, with no sharks being caught in water less than 100 m deep nor below 500 m.

The sixgill shark is a deep water inhabitant of the outer continental shelves and slopes, including seamounts and submarine canyons, ranging in depth to over 2400 m (Hongxi, Siming, & Guogiang 1987). They seem to occur over bottoms of muddy substrate, but also in rocky areas. In addition to its epibenthic habitat, sixgills occur in the midwater column up to several hundred meters off the bottom in the mesopelagic and epipelagic zones.

The close proximity of a submarine canyon to a bay or the coastline acts as a corridor through which deep-sea species venture into the nearshore zone. Sixgill sharks for example, have been well documented as entering San Francisco Bay (Herald & Ripley 1951; Ebert 1986b; present study) which is at the apex of a large submarine canyon. The high productivity, from upwelling, typically associated with submarine canyons also provides a nutrient rich zone for the juveniles.

The bigeyed sixgill shark typically occurs near the bottom between depths of 90 and 600 m (Bass et al. 1975), making occasional excursions into the nearshore and mesopelagic zones. One specimen taken off Natal, S.A. was caught in a shark net in water less than 10 m deep (Bass et al. 1975).

The sevengill shark is a distinctly coastal species, rarely occurring below a depth of 100 m. The deepest recorded specimen for this study was from 226 m off New Zealand. However, this appears to be an anomalous individual since overwhelming data collected from Australia, California, South Africa, Namibia and New Zealand indicate that it is a nearshore species. Off the California coast, a comparison of gill net catches between 10 and 100 m depth indicate that sevengills were captured at an average water depth of 33 m and that sixgills were caught at an average depth of 77 m (Ebert 1986b). Additional data from a gill net study conducted by the California Department of Fish and Game (Wild 1988) further support the conclusion that the sevengill shark is a nearshore species. Intensive sampling for both species in southern Africa from the surfline down to several hundred meters, revealed that sevengills were common in water less than 70 m, while sixgills were more abundant below this same depth. If the sevengill shark was a deeper occurring species, it should have shown up more frequently than the data indicate.

Movement Patterns

The recapture of an adult female sevengill in Humboldt Bay, in approximately the same location in which it was tagged, indicates that individual sharks may return to the same breeding grounds. The sevengill shark is a seasonally abundant species in Humboldt and San Francisco bays during the spring and summer months (Ebert 1986c, 1989). This increase in numbers coincides with their reproductive cycle (see reproductive biology). The fact that individual elasmobranchs migrate to the same breeding grounds is not surprising, given that extensive studies on teleosts have demonstrated this phenomenon. Elasmobranchs have highly sophisticated olfactory senses which they probably use to locate these breeding grounds. At least two other common northern California shark species appear to return to the same bay on a seasonal basis - the soupfin shark, Galeorhinus galeus, and the leopard shark, Triakis semifasciata.

Knowledge of elasmobranch movement patterns is poor. Long term tagging programs could reveal some useful information, but the day to day or even seasonal habits of sharks need to be investigated. Several studies have attempted to tag sharks with telemetric equipment (Nelson 1978, 1987), in order to follow their movements, but unfortunately the time spent actually following the shark has so far been limited by technological and monetary constraints. Longer term movement data could reveal socially complex and behaviorally dynamic organisms acutely attuned to the environment.

Growth

Juvenile sevengills appear to have a very rapid growth rate during the first few years of life. Evidence to support this hypothesis can be inferred from life history data. Newborn sevengills, pupped between April and May in Humboldt and San Francisco bays, range between 350 mm and 450 mm TL. Length-frequency data from several fishing competitions held in September revealed large numbers of juveniles between 540 mm and 700 mm TL. Close examination of these specimens revealed that they had recently healed umbilical scars. It appears that these juveniles taken in September were born earlier in the same year, probably during April-May. Additionally, growth studies conducted at the Monterey Bay Aquarium (MBA) indicate that juvenile specimens show tremendous growth over the first couple of years (G. van Dykhuzien, aquarist, MBA, Monterey, California, pers. comm.). Juveniles (measuring < 1000 mm TL) held in the aquarium were observed to eat continuously and voraciously, while adolescents and adults tended to feed less frequently. Similarly, a newborn sixgill held in captivity at the MBA showed a rapid growth rate from 700 mm TL (1.4 kg) to 1050 mm TL (5.7 kg) in 300 days.

Energetically, it would be advantageous to place newborns in an area of high productivity, i.e. a bay or upwelling zone, where they would be provided with an abundant food supply. The rapid growth rate of juveniles would enhance their survivorship since a sevengill of over 700 mm TL, or a sixgill of over 1000 mm TL, has fewer predators than a newborn and they themselves are high-ranking predators equivalent to much heavier marine mammals.

Reproduction

Frilled Shark

An intensive study of the biology of the frilled shark is needed. This intriguing species has fascinated anatomists since Garman first described it in 1884. The anatomical literature on frilled sharks is extensive (Garman 1885; Hawkes 1906, 1907, Deinega 1909, 1923, 1925; Goodey 1910; Allis 1923; Smith 1937), but data concerning its basic biology are lacking. Works by Gudger and Smith (1933) and Gudger (1940) provided some insight, but virtually no new data have come to light since then. Recently, however, a group of Japanese scientists published a bulletin providing new information on this species (Tanaka 1987; Shiobara et al. 1987; Hara 1987; Taniuchi 1987). Additional data on the life history of this species are currently being prepared by Dr. Sho Tanaka (Faculty of Marine Science, Tokai University, Japan, pers. comm.) and it is hoped that this will shed some light on this fascinating deep sea shark.

The 916 mm TL specimen reported here is believed to be the smallest adult male frilled shark on record. All specimens described by Gudger (1940) were larger, and no suggestions were made as to the maturity of male frilled sharks.

Maturity in female frilled sharks has been estimated at ca. 1500 mm TL based on the presence of six maturing ova (Gudger 1940). A 1398 mm TL specimen illustrated by Gudger (1940) was immature while a 1550 mm TL specimen was mature. Maturity was based on the presence of large ovarian eggs measuring up to 83 mm in diameter. Gudger (1940) reported that more eggs ripen in the right ovary than in the left and that the left ovary was non-functional in some specimens. This differs from the other hexanchoids, all of which have both ovaries functional. Fecundity has been reported as between 2 and 12 (Gudger 1940). One additional record of embryos for this species came from a specimen caught by a trawler off the Cunene River which gave birth to three embryos on the ship's deck (Dr. A. Payne, SFRI, Cape Town, South Africa, pers. comm.).

The reproductive cycle of frilled sharks has been estimated at two years (Gudger & Smith 1933; Gudger 1940). This was based on the fact that after parturition the ovaries are so reduced that the female needs approximately one year for the large ovarian eggs to develop. The eggs must grow to a size in excess of ca. 70 mm in diameter before they are ready for fertilization. Once the eggs have been fertilized, the gestation period is an additional 12 months. This pattern is similar to that of the sevengill shark which also has large (ca. 75 mm in diameter) ovarian eggs prior to fertilization (Ebert 1986b, 1989). Breeding in Japanese waters is thought to occur between late March and June (Nishikawa 1898). Gudger's (1940) observations on the developmental sequence of embryos through April tend to support this hypothesis, but insufficient data are available to confirm this hypothesis.

Reports of frilled sharks outside Japan are comparatively rare, but of those specimens captured, most are › 1000 mm TL. Very few juvenile specimens have been reported in the literature. This may be a sampling artifact if juvenile frilled sharks aggregate in areas not usually fished.

Perlon Shark

Based on the indicators used in this study, maturity in males occurs between 700 and 800 mm TL. Males were found to be mature at a minimum size of 746 mm TL, but adolescents measuring up to 783 mm TL were examined. All males over 800 mm TL in this study were, however, mature. Late adolescent males were found to have enlarged testes, highly convoluted epididymi, and viable sperm which could be expelled from the genital papilla. The terminal cartilage elements were, however, uncalcified. Calcification of terminal cartilage elements was the last criterion to be met before male perlon sharks were considered mature. Tanaka _et al._ (1975) make no mention of the terminal cartilage elements as indicators of maturity, but their estimates of male maturity correspond with those of this study. Bigelow and Schroeder (1948) estimated that Atlantic specimens matured at a slightly smaller size, between 600 mm and 750 mm TL, although no criteria for maturity are cited (their approximation was based on a single adult male measuring 698 mm TL). Much of their information was derived from the literature and personal communications from Luis Howell-Rivero. As discussed above, the terminal cartilage elements were crucial in establishing maturity for the males. It may be that Atlantic specimens of this species do mature at a smaller size, but more information is required to confirm this hypothesis. Other studies have variously reported male maturity at 950 mm TL from the eastern tropical Atlantic (Poll 1951), 930 mm to 1010 mm TL from the Mozambique Channel (Forster et al. 1970), and › 850 mm TL for Mozambique and South Africa (Bass et al. 1975).

Male reproductive success did not appear to be seasonal. Males collected during this study were found to contain viable sperm all year round. This finding supports those of Tanaka et al. (1975). In addition, the mucous substance secreted by adult males appears to be present throughout the year. The presence of this mucous is unique among hexanchoids and elasmobranchs in general. The mucous is quite sticky and appears to act as an adhesive. What role it plays during courtship and copulation is uncertain, but two possibilities are that it assists in the transfer of sperm into the female, or that it acts as a pheromone.

Female perlon sharks begin maturing between 950 mm and 1100 mm TL. No specimens with embryos or intrauterine eggs were collected, so it was difficult to determine with any accuracy the size at which maturity first occurs. The two largest specimens, 1130 mm and 1185 mm TL, contained eggs only 18 mm and 10 mm in diameter, respectively, yet had the greatest oviduct widths of any specimen examined. The shell glands of these specimens were moderately expanded. The remainder of the specimens (› 965 mm TL) with large eggs had very narrow oviduct widths, but moderate to widely expanded shell glands. A direct correlation could be drawn between egg diameter and shell gland width. Those with larger eggs tended to have a wider shell gland, indicating that the female is approaching ovulation. Tanaka and Mizue (1977) reported a similar finding in comparisons of uterine width and egg diameter. When the eggs reached diameters of between 35 and 45 mm the uterus expanded rapidly. Based on uterine width of the two largest females from this study it appeared that they had recently given birth. The uterine widths of these two females were 37 mm and 44 mm, slightly larger than Tanaka and Mizue's (1977) approximate size of 35 mm. The remaining females appear to have been either inactive or entering their first breeding season. Given the extremely narrow width and constricted condition of the uteri prior to the onset of maturity, the uterus of most adult female elasmobranchs examined were found to be pendulous after at least one reproductive cycle and apparently do not return to their pre-reproductive condition between reproductive cycles. Tanaka and Mizue (1977) estimated maturity to occur between 950 mm and 1050 mm TL for Japanese specimens and Bigelow and Schroeder (1948) estimated about 900 mm for Cuban females. Poll (1951) reported an immature 920 mm TL specimen, and Bass _et al._ (1975) noted an adolescent perlon shark of 890 mm TL. Assuming a minimum size of 932 mm TL for maturity, this would be 68 % of the maximum TL reported for this species. This value fits within Holden's (1974) generalization that females mature between 0.6 and 0.9 of their asymptotic TL.

According to Tanaka and Mizue (1977), perlon sharks in Japanese waters had no definitive breeding season. This assumption was based on the observation that no direct relationship could be established between the diameter of maturing ova and the months of the year. Capape (1980) estimated that gestation lasted for about 10 months in Mediterranean specimens and that females gave birth in November or December. Gravid females of this species have rarely been described in the literature. Tanaka and Mizue (1977) suggested that females may not feed during gestation and would therefore escape capture since their specimens were taken on long-line gear. However, perlon sharks in Taiwan were mainly caught by trawl nets which are not as selective as long-line gear and do not depend on feeding behavior to capture sharks and other organisms. All of the specimens observed from Taiwan fell within the approximate size range as those collected by Tanaka and Mizue (1977) - 500 mm to 1200 mm TL. No gravid females or small juveniles < 500 mm TL were observed. Small perlon sharks measuring between 250 mm and 500 mm TL, if present, should have been taken by these trawlers since lantern sharks (Etmopterus sp.) and catsharks (Apristurus sp.) measuring < 200 mm TL were caught in large numbers. Data from this study and Tanaka and Mizue (1977) reveal that no large perlon sharks (> 1200 mm TL) nor small specimens (< 500 mm TL) were captured from Taiwanese or Japanese waters. Bass et al. (1975) reported several specimens from Mozambique measuring between 270 mm and 420 mm TL, but did not acquire any gravid females. Due to the absence of these two size groups, it is suspected that most gravid females and juveniles aggregate in different locations to those of adult males and non-breeding females that could include becoming pelagic as well.

Fecundity in perlon sharks has variously been reported as between 9 and 20 young by Bigelow and Schroeder (1948), 6 by Cadenat and Blache (1981), and 11 by Tanaka and Mizue (1977). No additional information can be supplied other than that perlon sharks appear to have a larger number of ovarian eggs than their reported fecundity would suggest, one specimen having 42 ovarian eggs. The diameter of these eggs (22 mm to 45 mm) was quite large, suggesting that more than 20 eggs may ovulate at one time. However, it seems unlikely that these sharks would approach the reported litter sizes of the sixgill (maximum 108) or sevengill (at least 82) sharks (Ebert 1986b). From present knowledge it is clear that considerable data are needed to elucidate the perlon shark's reproductive cycle.

Sixgill Shark

Records of adult male sixgills are confined to a single specimen reported by Branstetter and McEachran (1986). The specimen measured 3250 mm TL and was taken in the Gulf of Mexico. Three adult males were obtained for this study. Springer and Waller (1969) reported that a male 3480 mm TL was immature, but did not specify what criteria were used to determine this. The claspers of a 3080 mm TL specimen (USNM 220178) lacked calcification of the terminal cartilage elements and was therefore considered to be adolescent. However, the terminal cartilage elements of a 3140 mm TL specimen were calcified. Since only the claspers of the 3080 mm TL specimen were available for examination additional indicators of maturity could not be assessed. Blue sharks do not show an abrupt increase in clasper length at the onset of maturity (Pratt 1979). This criterion, however, should not yet be invalidated for sixgills since the sample size was small and adult males probably reach a larger maximum TL. Data concerning the maximum TL attained by males and whether they are capable of reproducing year-round will have to await the collection of additional material.

Adult females are known at 4210 mm TL (Ebert 1986a) and are immature at 3500 mm TL (Desbrosses 1938). However, a more accurate estimate of the size at maturity is wanting. A 4050 mm TL specimen contained developing ova, but its weight was 116 kg less than a 4220 mm TL specimen and 205 kg less than a gravid female measuring 4210 mm TL. Another specimen reported by Bass (1979) measured 4250 mm TL, but only weighed 348 kg. Unfortunately no maturity data were given either for Bass's (1979) specimen or a 4330 mm TL specimen reported by Springer and Waller (1969). Size at maturity has previously been reported as 4500 mm TL (Springer & Waller 1969) and based primarily on gravid females measuring between 4520 mm and 4820 mm TL. Except for females containing embryos, maturation data on large (› 4000 mm TL) specimens are obscure. The large variability in weight may be related to the female's stage of development. The weight of adult female sevengill sharks can be highly variable; a 2640 mm TL specimen weighed 106 kg, a 2800 mm TL specimen, 132 kg, and a 2910 mm TL specimen, 182 kg. Similarly large white sharks › 4000 mm TL can be extremely variable with some individuals appearing as slender "snakes" and others as massive "pots". The extreme variability exhibited in the weight of these female sharks may reflect the animal's reproductive condition. Until more specimens between 3500 mm and 4210 mm TL are carefully examined as to their maturation status, maturity is assumed to occur at a size in excess of 4000 mm TL.

The sixgill shark has one of the largest litter sizes reported among elasmobranchs. The fecundity has variously been reported as between 22 and 108 (Ebert 1986a). The number of embryos reported in the literature are 108 (Vaillant 1901), 47, ca. 70, 22 (Desbrosses 1938) and 51 (Ebert 1986a). The 22 embryos reported by Desbrosses (1938) came from a specimen of unknown size and was not examined by Desbrosses himself. The information on this particular specimen was given to Desbrosses by Dr. Lopee'. Since very little information was given there is some doubt as to the identity of the specimen which could have been a bigeyed sixgill shark. Several authors (Nakamura 1936; Desbrosses 1938; Bigelow & Schroeder 1948; Fourmanoir 1961; Cervigon 1966) confused these two species. Since both species are known to occur in this area the specimen with 22 embryos was probably a bigeyed sixgill since a litter size of 22 falls within the range reported for this species. One problem in estimating fecundity in sixgills is that they are known to spontaneously abort their young when captured (Ebert 1986a). This was observed in a 4210 mm TL specimen which aborted her 51 term embryos while being brought on board a ship. The 108 embryos reported by Vaillant (1901) came from a specimen caught in water less than 15 m deep.

Newborn sixgills were caught off southern Namibia during mid- to late summer over three successive seasons. The depth ranged between 300 m and 400 m deep. The newborn sixgills from Namibia were similar in size to term embryos from the 4210 mm TL female. The occurrence of gravid females carrying term embryos during spring months and newborns during the summer months suggests a late spring or summer pupping period. Desbrosses (1938) reported an inshore movement of sixgills during the spring and autumn in the Bay of Biscay. Large females and newborns were commonly caught between depths of 50 and 100 m. From his data, Desbrosses (1938) concluded that sixgills produced two litters of young per year. Similarly, there was an increase in juvenile sixgills along the California coast during the summer and early autumn months. Trawl fishermen have also observed that large sixgills were taken during the summer months, but rarely at any other time. Based on approximate litter size, and size at birth, it is suspected that the gestation period for this species is at least 12 months. Furthermore, there is evidence to suggest that a recently pupped female requires at least one year before she is in condition to mate. Studies on two other species, the frilled shark (Gudger & Smith 1933) and the sevengill shark (Ebert 1989), indicate that both have two year reproductive cycles, and it appears that sixgills have a similar cycle.

The maximum reported size for a female is 4820 mm TL (Bolivar 1907). Assuming that females mature at approximately 4000 mm TL, this represents 83 % of their maximum TL and fits Holden's (1974) generalization that female elasmobranchs reach maturity between 0.6 and 0.9 of their asymptotic length. Circumstantial evidence suggests that females may attain a maximum length of 6000 mm TL, but no specimens of this size have been accurately measured. Literature reports of an 8000 mm TL specimen have now long been considered to be erroneous (Backus 1969). However, specimens in excess of 5000 mm TL would not be unexpected in this species, thus making it one of the larger elasmobranchs.

Bigeyed Sixgill Shark

Information on the reproductive biology of this species is scarce. This has largely been due to confusion of this species with the sixgill shark. Forster et al. (1970) recorded a mature male measuring 1230 mm TL which is the smallest reported TL for an adult, and is probably close to the minimum size for maturity.

Female maturity has been estimated at 1420 mm TL (Bass et al. 1975). A litter of 13 was reported from a single specimen (Forster et al. 1970). Reports of ovarian egg counts range from 7 to 26 (Springer & Waller 1969, Forster et al. 1970). A female sixgill of undetermined TL was reported by Desbrosses (1938) to contain 22 embryos. However, the specimen may have been misidentified, since Desbrosses' (1938) illustration is that of a bigeyed sixgill, and not of its congener, the sixgill shark. Furthermore, a litter size of 22 would fit the range observed for the bigeyed sixgill.

Sevengill Shark

Males

Maturation in male sevengills begins at about 1323 mm TL, and is indicated by coiling of the epididymis. Most males appear mature at approximately 1500 mm TL, as evidenced by their highly coiled epididymis and viable sperm (Ebert 1986b). According to Pratt (1979) production of viable sperm is an indication of adult status. Several other authors (Kauffman 1950; Matthews 1950; Olsen 1954) have also used this criterion to determine maturity. However, results of this study on the internal and external organs of male sevengills have shown that viable sperm can be produced prior to maturation. Thus, other criteria were needed to assess stage of development. The most important and simplest measure of maturity was the extent of calcification of terminal cartilage elements. A 1323 mm TL specimen previously reported as being mature (Ebert 1986b) on the basis of viable sperm and several other criteria for maturity, was subsequently found to have uncalcified terminal cartilage elements. This was also the case in several other late adolescent males, some measuring up to 1710 mm TL. Internally these males were mature, but the intromittent organs (i.e. claspers) necessary to transmit sperm into the female were not yet fully developed. Calcification of the terminal cartilage elements appears to be the final criterion met in distinguishing adult from adolescent males. Calcification of these elements coincided with a rapid increase in clasper length and an increase in testes weight. The increase in testes length to TL relationship occurred at a slightly higher TL (1650 mm TL) than the other indicators. The precise implications of this, if any, are unknown.

Male sevengills have viable sperm throughout the year and appear to be capable of reproducing year-round. Sperm was observed to flow freely by applying pressure to the sperm sac on specimens examined year-round. Lyle (1978) found that in _Carcharhinus_ species, sperm were either not present (as in _C. cautus_ and _C. melanopterus_) or present in small quantities (_C. fitzroyensis_) for three-quarters of the year. The Atlantic stingray, Dasyatis sabina, shows a seasonal fluctuation in testes weight, but viable sperm are present year-round (Snelson et al. 1988). Taniuchi (1988) did not observe any seasonal change in testes weight for the Japanese swellshark, Cephaloscyllium umbratile. The monthly change in sevengill shark testes weight may simply reflect low monthly samples. Additional samples should be collected to verify this possible increase in testes weight. If so, the production of viable sperm would coincide with the predicted ovulation of eggs by females and the occurrence of fresh mating scars on females.

Females

Females have a complex and prolonged maturation period. Small egg follicles (0.5 to 12 mm in diameter) first appear in the ovaries of adolescent specimens measuring between 1860 mm and 2080 mm TL. This observation was consistent for all females except one individual measuring only 1640 mm TL which had small follicles (< 12 mm in diameter). These small follicles develop into maturing ova with yolk in females between 2010 mm and 2140 mm TL. Maturation takes place between 2180 mm and 2438 mm TL. Approximately 45 % or nearly one half of the female population within this size range had enlarged ovarian eggs (> 40 mm in diameter) and an expanded shell gland (> 25 mm wide). Females between 2180 mm and 2438 mm TL are suspected of entering their first breeding season since the oviducts of these specimens were narrow and constricted. The oviducts of all females over 2500 mm TL and which had probably given birth at least once, were pendulous. Those females with enlarged ova and shell glands were deemed most likely to copulate successfully during the forthcoming breeding season. This percentage of females (45%) represented the following season's recruitment into the breeding population. The remaining females without enlarged eggs or an expanded shell gland would therefore enter into the breeding population the following year. Regulation of the number of females entering the breeding population would ensure that some proportion of the population is reproductively active at any one time.

The "staggering" of females which enter into the breeding population in any given year indicates a two year reproductive cycle. A two year reproductive cycle was previously proposed for female sevengills based on several factors including reduction of the ovaries following parturition (Ebert 1986b, 1989). The female requires approximately one year before she is ready to mate. During the year of reproductive inactivity the ovarian eggs develop and enlarge to a diameter in excess of 40 mm. During the following breeding season, those females with enlarged eggs will mate, while those which had mated the preceding year, give birth. Females with large ovarian eggs (› 60 mm in diameter) were observed to bear fresh mating wounds, while other specimens with reduced ovaries had wide pendulous oviducts and healed scars. Females in both reproductive stages were observed in Humboldt and San Francisco bays during April and May of the same year suggesting that both mating and pupping occur in the same location. In addition, it appears that the location where breeding occurs is site specific, and perhaps critical to the sevengill's reproductive biology.

Adult females give birth during the spring in Humboldt and San Francisco bays (Ebert 1986b, 1989). Juveniles and newborns appear to remain in these bays throughout the spring and summer. They probably move out of these bays after the first severe autumn or winter rains when the bay's salinity decreases. Sevengills and other bay elasmobranchs do not appear to be as tolerant of salinity changes as the bull shark (Bass et al. 1975; Compagno 1984) and leave these bays during the winter months (Ebert 1986c). The precise timing of this emigration from the bay is variable, and dependent on the severity of the first heavy seasonal rains. However, the following season, after the rains have subsided, these year-old juveniles appear to return to the bay ecosystem and remain for at least a second season. A similar situation appears to occur in the Rio Plata estuary where juvenile sevengills are abundant during the spring and summer months (Menni and Garcia 1985). The majority of adults appear to leave these bays after June, although some do remain. Snelson et al. (1984) found a similar pattern of occurrence for the bull shark. Juveniles measuring up to 1800 mm TL occurred throughout the year in several Florida lagoon systems, while adults › 2400 mm TL were seasonally abundant. Once the juvenile bull sharks begin to mature they leave the lagoon, and upon reaching adulthood, they return.

Sevengills have one of the highest average litter sizes for all elasmobranchs. One female containing 82 term embryos has been reported (Ebert 1986b), but no additional gravid females were captured during this study. Fecundity estimates for 19 specimens with a largest egg diameter of at least 40 mm indicates a range of 67 to 104. The reduction in total egg numbers, in relation to largest egg diameter, indicates that some eggs are reabsorbed. However, it is unlikely that eggs are reabsorbed after they reach a diameter of 40 mm or more.

Reproductive Success

An aspect of reproductive viability which has been overlooked in elasmobranch studies is the success with which a male or female contributes to the gene pool. Factors such as environmental, physical, physiological, and perhaps even sociological may influence an elasmobranchs ability to successfully reproduce. For example, a rapid increase takes place in the clasper length of male sevengills between 1500 mm and 1800 mm TL, followed by a decrease above 1800 mm TL. Smaller males also, though biologically equipped, may have to compete with larger males for an opportunity to copulate with females. In many species of animals the males must wait until they can successfully compete against other males in order to copulate. For example, a recently matured male sevengill measuring ca. 1600 mm TL may be at a disadvantage, in that it could not compete against a larger male of › 2200 mm TL. The smaller male could be excluded from the breeding population, until such time as it is able to compete. Another consideration is the size of an adult female sevengill in relation to a small adult male. Small males may unable to successfully copulate with a female of nearly twice the size. Additionally, certain pheromones may be needed to initiate courtship behavior. The behavior of chain catsharks, _Scyliorhinus_ _retifer_, during courtship and copulation described by Castro _et_ _al._ (1988) suggests that pheromones play an important role.

Unfortunately, unlike many of the large terrestrial game animals, elasmobranchs live in an environment which is difficult to study. Much of an elasmobranch's life cycle is unknown. It is well known that many elasmobranch species segregate by size and sex. Whether these segregations represent different components of a larger group whereby the adult males, adult females, non-breeding adults, adolescents and juveniles each represent a component, which combines to form a social unit within a given territory remains to be seen. Within this territory, specific breeding grounds may be used by one or several different components of the population. Based on the ground color of sevengills in Humboldt, as opposed to San Francisco bays (Ebert 1985) it is likely that each has its own distinct population. Furthermore, there is evidence that some individuals return to the same breeding ground year after year, as do some large land predators. Alligators are known to return repeatedly to hunt or build a nest at the same spot time and again if they were previously successful (Neill 1972). However, knowledge of the reproductive cycle, and its associated behavior, of elasmobranchs is limited.

Food Habits and Feeding Behavior

Frilled Shark

The frilled shark, though commonly regarded as archaic and primitive, is actually a very specialized predator by virtue of its specialized feeding apparatus. On the basis of the limited available data, it would appear that frilled sharks prey primarily on scyliorhinid sharks though they probably feed on other items of the appropriate size. Taniuchi (1987) reported the remains of an Apristurus japonicus in a Japanese specimen. Unfortunately, little else is known about the feeding habits of frilled sharks to confirm its suspected prey preference. However, predation on scyliorhinids and possibly squaloids and other deepwater sharks, would coincide with suspected movement patterns of both predator and potential prey. Recent evidence has shown that frilled sharks are commonly caught in midwater trawls (Shiobara et al. 1987). Similarly, members of the genera

Apristurus and *Parmaturus* are known to migrate vertically into the water column (Lee 1969; Cross 1988; Ebert, unpubl. data). The elongated abdomen, anguiform tooth arrangement, terminal mouth and distensible very long, narrow jaws, give this species a specialized body arrangement reminiscent of gulper eels (Family Saccopharyngidae) or viperfish (Family Chauliodontidae). No other shark has this body shape. Frilled sharks may be capable of swallowing prey items ranging from 1/3 to 1/2 of their own body length, in much the same way as snakes are able engulf large prey items. The *Apristurus* sp. found in the 916 mm TL Namibian specimen measured 29% of the predator's TL. However, this was only a partial measurement since most of the head and half the tail region had been digested. Forensic examination of the prey item indicated that it had been ingested whole. In life, it would probably have measured closer to 35 or 40 % of the frilled shark's TL. The unique body shape of the frilled shark, apparently optimized for grasping and engulfing prey, and its ability to forage in both demersal and midwater habitats indicate a highly evolved life style that is not remotely primitive. Thus rather than representing a "missing link" in chondrichthyian evolution, frilled sharks are in fact highly specialized predators.

Perlon Shark

The diet of the perlon shark consists mainly of epibenthic and pelagic teleosts which indicates that it forages both near and well off the bottom. Food items such as *Trichiurus lepturus*, *Trachurus japonicus*, *Diaphus* sp., and *Nemichthys scolopaceus* are generally associated with an epibenthic to mesopelagic habitat, as are the crustacean species *Metapenaeopsis andamanensis*, *Sergia* sp., and *Systellaspis pellucida*. The presence of these species indicates that perlon sharks also forage into the mesopelagic zone in search of prey. Mediterranean perlon sharks were reported by Capape (1980) to feed primarily on teleosts, with *Gadiculus argenteus*, *Hoplostethus mediterraneus* and *Trachyrhynchus trachyrhnchus* (all epibenthic inhabitants) constituting the main species. Secondary prey species included several crustaceans, the cephalopod *Sepietta oweniana*, and the lantern shark *Etmopterus* spinax. Bigelow and Schroeder (1948) reported that the perlon shark was a voracious predator on hake, Merluccius sp., from Spanish waters. Interestingly, Trichiurus lepturus, whose distribution extends throughout the Mediterranean Sea was not reported in the diet of perlon sharks from this region. Inferences from stomach contents of epibenthic and mesopelagic prey species indicate that the foraging strategies of perlon sharks involve more complexity than previously thought, and includes catching small mesopelagic fishes and crustaceans as well as larger bottom prey.

Sixgill Shark

The sixgill shark is a large, versatile three dimensional apex predator which can exploit a broad spectrum of prey species and habitats. It is the dominant predator along the outer continental shelves, slopes and possibly the abyssal plains. The individual prey species consumed by this shark reveal a predator whose foraging habitat appears to change with its life stage. Newborn pups tend to forage heavily on demersal teleosts and cephalopods along the outer shelf and upper slopes between 200 and 400 m deep. They also appear to be especially abundant in areas of extreme upwelling, such as those occurring off Luderitz, Namibia. Highly productive areas would ensure an adequate food supply for newborn sixgills which appear to have an extremely rapid growth rate over the first year of life (see section 4.5). Larger juveniles (› 1000 mm TL) move along the slope and onto the shelf, often coming close inshore and occasionally into bays and estuaries (Ebert 1986b, 1988). Juveniles over 1000 mm TL have a fairly catholic diet which includes cephalopods, elasmobranchs, marine mammals and teleosts. Such a broad diet probably enables and encourages juveniles to range over a wider area in search of potential prey. Feeding data for adolescent and adult animals are sketchy since these groups tend to stay on the slopes and possibly in the abysses. Adult females are occasionally captured along the upper slopes and on the shelf, while adult males are noticeably absent. Additional information would be useful in confirming these suspected distributional feeding patterns.

Observations on the occurrence of epibenthic, mesopelagic and epipelagic prey species reveal a predator capable of foraging over a broad range of habitats. On the basis of identified prey species, it appears that sixgills spend considerable time foraging off the bottom. Midwater prey species like swordfish and cetaceans recorded in this study and elsewhere (Bigelow & Schroeder 1948; Backus 1957; Springer & Waller 1969; Ebert 1986 a,b) indicate that sixgills are active hunters in this habitat. Swordfish long-line sets made at several hundred meters often caught large sixgills (Branstetter & McEachran 1986; G. Gilmore, Harbor Branch Foundation, Florida, pers. comm.). Forster _et al._ (1970) reported that 82% of the sixgill specimens they captured were taken between 2.5 and 10 m off the bottom. Bigelow and Schroeder (1948) reported that this species comes to the surface at night to feed.

Energetically it makes more sense for a large (› 4 m TL) sixgill to capture one large prey item as opposed to numerous small items such as cephalopods. The energy expended by a large shark to catch smaller cephalopods might not be cost effective. In addition, the large broad mouth and huge cutting teeth of a big sixgill are not suggestive of a predator that survives exclusively on soft bodied cephalopods. However, by using stealth to approach a swordfish or cetacean, a sixgill could position itself within range to make a short dash and overtake its prey. This has yet to be confirmed, but the possibility exists that sixgills can change their ground color over a short period of time. This would be advantageous for a wide-ranging predator to camouflage itself according to the habitat in which it was hunting. Sixgills range from a dark brown to a dark silvery gray color (see chapter 3, taxonomy). A silvery gray countershaded body would be advantageous for a mesopelagic predator, while darker hues would benefit a demersal hunter. A change in the amount of light penetration may synchronously lighten or darken the ground color of these sharks as they move from one habitat to another. Other elasmobranch species, e.g. _Poroderma pantherinum_ and _Notorynchus cepedianus_, have been observed to alter their ground color over short time periods.

A possible scenario for large sixgills preying on large, active prey runs as follows: a sixgill cruising slowly in the water column detects an object (e.g. a swordfish) basking at the surface. Stealthily, the predator glides in for a closer examination and with only a faint flexure of the tail for propulsion and its large pectoral fins positioned at a $45^{\frac{1}{2}}$ angle for navigation, the predator quietly approaches undetected. The deceptive gray ground color helps to camouflage the predator. The shark's keen sensors detect the stimulus of a swordfish. Then with a quick rush, the sixgill overtakes its victim and, by clamping its huge jaws around the tail stock, disables the swordfish and inflicts massive damage. The sixgill, in quick repeated turns, takes several large chunks of flesh. The prey quickly expires from injuries and loss of flesh and blood. Conspecifics and other predators in the area alerted to the activity, move in to investigate and possibly scavenge a meal.

Bigeyed Sixgill Shark

Bass (1980) suggested that bigeyed sixgills and newborn sixgills were allopatric in the tropics, but that adult sixgills were sympatric with juvenile bigeyed sixgills. His hypothesis was based on the presumed resource partitioning between similar sized sixgills and bigeyed sixgills. With such little feeding data available on bigeyed sixgills, it is difficult to confirm or refute this hypothesis. However, based on records of juvenile sixgills from the Mediterranean Sea and Taiwan it appears that the habitat occupied by these two species is not mutually exclusive. A newborn sixgill measures between 610 mm and 730 mm TL while a newborn bigeyed sixgill is ca. 450 mm TL. If resource partitioning occurs between these two species, it probably takes place on a micro-habitat scale. It is of interest that the teleost prey species of the bigeyed sixgill identified from this study and elsewhere (Forster et al. 1970) are known to occupy an epibenthic or mesopelagic habitat, which in turn suggests that this species forages off the bottom.

Sevengill Shark

Prey Preference

The sevengill shark is a versatile predator feeding on a wide spectrum of prey species including pinnipeds, other sharks (including conspecifics), batoids, cephalopods, cetaceans, gastropods and teleosts. Reported prey species include the California sea lion, *Zalophus californianus*, soupfin shark, *Galeorhinus galeus*, angel sharks, *Squatina* sp., big skate, *Raja binoculata*, rats, *Rattus* sp., and even human remains as carrion (Olsen 1984; Praderi 1985; Ebert 1986b). A large *Octopus* sp. was found in the stomach of a 246 cm TL individual from Gough Island (V. Peddemors, Natal Sharks Board, pers comm.). Praderi (1985) identified 14 prey species from Uruguay, which included the Franciscana dolphin, *Pontoporia blainvilli*, the southern sea lion, *Otaria flavescens* and marine birds. Most published accounts of sevengill feeding habits are limited to anecdotal or generalized accounts. Menni and Garcia (1985) reported the teleost species *Pinguipes* sp. and *Trachurus* sp. as prey from Argentine sevengills, while other authors report that they prey on chondrichthyians and teleosts (Clemens & Wilby 1961; Hart 1973; Bass *et al.* 1975).

It is not surprising that chondrichthyians and teleosts are the predominant prey groups of Californian sevengills since Humboldt and San Francisco bays are an important link in the life cycle of many fish species. In addition to sevengills, many other of chondrichthyian and teleost species spend part of their life cycle in these bays (Green 1975; Smith & Kato 1979; Gotshall, Allen & Barnhart 1980). This congregation of chondrichthyian and teleostean prey offers an abundant food resource that is readily exploited. Prey elasmobranchs including the bat ray, *Myliobatis californica*, brown smoothhound shark, *Mustelus henlei*, leopard shark, soupfin shark, and spiny dogfish, *Squalus acanthias*, are all known to pup in one or both these bays (Bane & Bane 1971; Castro 1983; Ripley 1946; Smith & Kato 1979; Ebert, unpubl. data). Teleost prey species including herring, *Clupea harengus*, jack smelt, *Atherinopsis californiensis*, top smelt, *Atherinops affinis*, rockfish, *Sebastes* sp., striped bass, *Morone saxatilus*, white sturgeon, *Acipenser transmontanus*, white perch, *Phanerodon furcatus*, shiner perch, *Cymatogaster aggregata* and sole, Bothidae use these bays as breeding grounds (Green 1975; Allen *et al.* 1980; Rielly & Moore 1982). In addition to sevengills, leopard, spiny dogfish, and soupfin sharks feed heavily on teleosts in these bays (Herald & Ripley 1951; Russo 1975; Talent 1976, 1982; Castro 1983; Compagno 1984a; Ebert unpubl. data).

Close examination of food habits on a regional basis reveals how opportunistic the sevengill can be in exploiting a plentiful food resource. For example, there is a breeding colony of harbor seals in Humboldt Bay, and predation on these seals was high (Knudtson 1977). Observations on harbor seals in Humboldt Bay reveal that these seals stay out of the water before sunrise when sevengills are present (also K. Bates, fisherman, Eureka, California, pers. comm.). Similarly, the highest concentration of Cape fur seal breeding colonies, 65% of the total for southern Africa (David 1987), occurs in the Luderitz area of Namibia where seal predation by sevengills was high. North of Walvis Bay, where seal colonies are scarce, predation on them was correspondingly low.

Though invertebrates are not important in the diet of sevengills, they are heavily preyed on by the brown smoothhound, which feeds on crabs and shrimp (Russo 1975; Talent 1976, 1982; Ebert unpubl. data), and which also pups in several California bays between late May and June (Bane & Bane 1971; Castro 1983; Ebert unpubl. data). The abundance of crustacean prey provides an ample food supply for juvenile brown smoothhounds, which in turn may be preyed upon by juvenile sevengills. The population dynamics and abundance of crustaceans, mollusks, and other invertebrate species in bays are clearly integral components of these ecosystems.

Feeding data for juvenile sevengills < 999 mm TL are scarce. Reasons for this are uncertain, but two possible explanations are proposed. Virtually all small sharks were caught on rod and reel which would tend to select for those individuals which are foraging and may not have eaten for some time. Also these sharks will evert their stomachs quite easily, especially when gut hooked. Juveniles and newborns are voracious feeders in aquaria (G. van Dykhuizen, pers. comm.) and will eat almost daily while larger adolescent and adult animals may feed only once a week. The high consumption rate of juvenile sharks may indicate that digestion is rapid. Prior to this study, Herald and Ripley (1951) had examined several hundred stomachs of predominantly small sevengill sharks, and found them to be either empty or to contain only bait.

The sevengill shark will on occasion evert its stomach when caught on hook and line. The trauma from a hook is readily apparent, but the possibility exists that they routinely evert their stomach to regurgitate undigested prey remains. Prey species with skeletal parts that do not digest properly (e.g. fin spines) and which may not pass through the intestinal tract easily, may be regurgitated. This species is often found with spines and other indigestible material in its stomach. Although this material may eventually be digested, another means of evacuating any unwanted remains would be by regurgitation.

Feeding Behavior

Studies on the food habits and feeding behavior of large predatory sharks are inherently problematic due to the size of the animals, the difficulty in observing and handling them, and the risks to the investigator. However, available information on the food habits of elasmobranchs is extensive and has typically involved the accumulation of stomach content data. These data are usually analyzed by a number of indices that indicate the important prey items. Only a few studies (Hobson 1963; Tricas & McCosker 1984; McCosker 1985) have attempted to examine the relationship between the predator, its prey, and its associated habitat. General life history information concerning the prey is generally lacking. Such information, however, is important in assessing ways in which predators partition and exploit the available resources.

Observations on feeding behavior of large sharks are few and largely restricted to artificial situations, i.e. sharks feeding on bait (Tricas & McCosker 1984; McCosker 1985; Tricas 1985). Several authors have reported sharks scavenging fish offal and mammalian carrion (Scofield 1920; Limbaugh 1963; Stead 1963; Squire 1967; McCosker 1985; Pratt et al. 1982), but observations of actual predation bouts are few (Bolin 1952; Hobson 1963; Springer 1967; Arnold 1972). It has, however, been reported that the sevengill shark is able to put on exceptional bursts of speed that enable it to overtake and capture the leopard shark, Triakis semifasciata (Ebert 1986b). Such observations provide insight into the behavioral ecology of sharks and suggest how a supposedly slow moving and clumsy shark can catch fast swimming fish or marine mammals. The most obvious way to obtain such prey would be to scavenge on it as carrion or offal. However, an alternative means would be to actively forage on live animals, yet virtually nothing is known about hunting behavior in sharks. Hobson (1963), in a series of experiments, noted that different shark species employed various behavior patterns to subdue their prey.

The popular phrase "feeding frenzy", typically associated with shark feeding behavior, is a misnomer. A frenzy by definition is "delirious excitement" (Morehead & Morehead 1981) a phrase which hardly describes the precision accuracy with which a shark feeds. Sharks feeding on a school of fish for example will purposefully attack selected individuals. The pattern of attack varies according to shark species and their preferred prey. Traditionally, sharks were considered scavengers and unlikely to catch very active prey for themselves. Springer (1963) felt that large sharks were unable to capture healthy prey and had to rely on scavenging injured or diseased individuals for food. Although sharks are certainly known to scavenge (Springer 1963), they are also extremely efficient hunters. Subsequent observations have revealed that many apparently slow and clumsy species are actually very swift and in some cases explosive predators. Myrberg (1987) commented on the ability of oceanic whitetip sharks, Carcharhinus longimanus, to generate extremely rapid bursts of speed over a distance of 30 m in order to subdue prey. The plankton-feeding whale shark, typically seen swimming slowly, was observed by Stafford-Dietsch (1987) to take flight quite rapidly when startled, and slow-cruising basking sharks are reported as jumping out of the water. White sharks, also labeled as slow and clumsy predators (Tricas & McCosker 1984), are frequently caught by kite fishing in South Africa. In kite fishing, a large bait is dangled above the water, several hundred meters from shore. White sharks and mako sharks attacking the bait leap straight out of the water to take the bait. White sharks have been observed to jump at least three meters out of the water to strike a bait (Compagno 1984; T. Hecht, Department of Ichthyology & Fisheries Sciences, Rhodes University, Grahamstown, South Africa, pers. comm.). A photograph of a shark jumping out of the water in a 1968 issue of National Geographic (Kenney; p. 255) is in fact a white shark, while in a more recent issue of this same journal, a white shark was photographed coming out of the water to take a bait (Clark 1981). Fishermen in California and South Africa have described predation bouts in which a white shark attacked and consumed an apparently healthy adult seal. In both instances, the attack came from below and was swift. In the South African attack, the Cape fur seal was alerted to the white shark's presence only seconds before it struck. The estimated size of the shark was 5.5 to 6 m TL (Anon., fishermen, Cape St. Francis, S.A.). The California attack occurred with such speed and precision that the sea lion, Zalophus californianus, apparently never detected the shark's presence. This shark was estimated to be 5 m TL (G. Verhagen, fishermen, Half Moon Bay, CA.). In both predation bouts the initial bite removed approximately the posterior one-third of the seal's body. In each instance, the shark returned immediately and consumed the remaining portion of each seal. Burst speed behavior in white sharks differs from that described in recent accounts of its feeding behavior (Tricas & McCosker 1984; Tricas 1985; McCosker 1985) and illustrates the problems involved with attracting sharks by bait. Based on observations around Dangerous Reef, Australia, Tricas and McCosker (1984) concluded that white sharks were slow, clumsy predators that could be "outswum by a world class swimmer." However, these observations should be treated with caution, since substantial quantities of bait were introduced to attract and maintain sharks around a ship. This is somewhat analogous to driving onto the Serengeti Plains of Africa, tossing beef steaks out the window of a land rover, and waiting for any large predators in the vicinity to take advantage of it. Sharks likewise will take advantage of such a situation, and obtain a meal with minimal energy expenditure.

As with any predators, sharks tend to exploit advantages over their prey. The increased activity of sevengills during times of poor visibility probably puts it at a hunting advantage, especially over any active swimming prey not adapted to these conditions. Springer (1967) commented that in his experience, as a general rule sharks tend to be most active on moonless nights. This is especially true of the tiger shark, Galeocerdo cuvier, which remains in deep water during the day, but moves inshore at night (Springer 1963). Similarly, large land predators, for example hyenas, are known to be particularly active on moonless nights when they would be at an advantage over most prey species (Kruuk 1972).

The stealthy manner in which a sevengill approaches a potential prey item may determine whether or not the hunt will end in success. The greater the distance between predator and prey, the less likely the hunt is to be successful. Schaller (1972) observed that lions, unlike certain other large land predators (e.g. the Cape hunting dog or spotted hyena), cannot sustain a prolonged pursuit and must overtake their prey quickly and in a short distance. Observations on oceanic whitetip sharks which hunt in a clear water environment, have shown them to approach to within a distance of ca. 50 m of a prey species. They are able to get within this distance by slow swimming and by the use of disruptive coloration. Once within striking distance, they can put on an explosive burst of speed to overtake the prey before it has a chance to escape (Myrberg 1987). The white shark with its scombroid-like body form, is an example of a shark which could probably sustain a long distance chase or at least a longer sprint than an oceanic whitetip shark or sevengill. Water resistance and reduced visibility tend to limit high-speed chases by sharks, unlike those of large terrestrial predators such as Cape hunting dogs or spotted hyenas, which can pursue prey for over a kilometer (Kruuk 1972). Stealth would also be advantageous when a shark is confronted by a situation it was uncertain of. A careful silent approach would allow the shark to get within sufficient distance to determine whether it should proceed with an attack. In such approaches, the shark would not alert potential prey to a possible attack. If the object being investigated proved to be a non-prey item, the shark will not have expended unnecessary energy nor placed itself in a potentially disadvantageous situation. While boat or shore fishing, sevengill sharks were often observed to "glide-in" almost motionlessly, to investigate. The stimulus given off by the bait presumably attracted the shark, which prudently investigated the source. Similarly, when bait was deliberately presented to these sharks, they approached cautiously, making very little motion in the water, and initially 'mouthing' the bait as if testing it. They would often glide almost motionlessly to within a few centimeters of an observer before changing the swimming pattern to a slow sinuous pace. A curious behavior pattern exhibited by feeding sevengills is increased activity with increased numbers of sharks. As the numbers of sharks present increases, individual swimming pace quickens and they approach the bait less cautiously. Hobson (1963) noted a similar change in the swimming patterns of grey reef (Carcharhinus amblyrhyncos), blacktip (C. melanopterus) and whitetip reef (C. obesus) sharks with increasing numbers of sharks present. Intraspecific competition between oceanic whitetip sharks and silky sharks (C. calciformis) revealed that when two or more of the same species were competing for the same food item, both would close in without reluctance (Springer 1967).

Sevengill sharks often approach observers, to within a distance of several centimetres, without attacking. The motivation behind such an approach was either investigative or to serve warning to a potential intruder or aggressor. Hobson (1963) described the same behavior in whitetip reef sharks which often passed close by a diver but did not attack. He concluded that this was a warning to potential competitors and not a prelude to an outright attack.

There are several advantages to social hunting which either directly or indirectly affect the ecological success of this species. Feeding by social facilitation allows smaller individuals to feast on prey that they would otherwise not have access to. This strategy also increases the chances of success during a hunt. An adult Cape fur seal, A. pusillus, may weigh up to 350 kg (King 1983), while the largest recorded sevengill weighed a mere 182 kg by comparison (Ebert 1986b). Even a large shark would have trouble subduing an adult seal if hunting alone. A pack of sharks, however, would have little difficulty in disposing of an adult seal. This is clearly advantageous if seals represented an enormous food potential in an otherwise depauperate area. The coastal fish fauna off southern Namibian is fairly depauperate, yet the largest breeding colonies of fur seals occur in this area representing an abundant and underutilized food resource. Species such as the copper shark, Carcharhinus brachyurus, occur further off-shore in oceanic water where teleost prey is more abundant. These sharks, although attaining a greater size than the sevengill, are equipped for feeding on smaller prey items and are not capable of utilizing the seals to any extent. Copper sharks are in fact more trophic equivalents of seals. The sevengill, a coastal species, simply utilizes the most convenient and available food resource that fits within its capabilities as a high-level predator. Springer (1967) suggested that lantern sharks, Etmopterus virens, may hunt in packs since the size of its main prey, cephalopods, would seem much too large for an individual to subdue. Group hunting thus allows smaller individuals to feed on an otherwise unobtainable food source.

Social hunting allows predators to forage over a wider range than possible as an individual. Several sharks may spread out over an area to forage for food. Should one shark encounter a school of fish or carrion for example, its behavior may alert other members in the vicinity. In Humboldt Bay it is quite common to see large concentrations of leopard and brown smoothhound sharks feeding on shallow mud flats. Initially one, and then several, sevengills would appear in the area. It is during this time that predation bouts by sevengills on these smaller sharks were observed. As a solitary hunter, a sevengill will focus on small to medium sized prey, but where possible, will readily adapt to a co-operative feeding situation should large prey become available. The presence of both harbor seal and triakid shark gut content remains in sevengills in Humboldt Bay and elsewhere suggest that they do indeed feed socially as well as solitarily. How the sharks are able to move in a coordinated fashion, and whether prey will be taken by an individual or the group is unknown. Lions stalking large prey watch each other and, by their behavior and body language, will make the appropriate moves in a coordinated fashion to subdue the prey (Schaller 1972). A group of sharks similarly becomes excited if the behavior of one changes from a non-aggressive to aggressive posture, suggesting that some form of communication exists between them.

Prey Selection

The sevengill shark is a very indiscriminate and opportunistic feeder, and will readily forage on living prey as well as scavenge for food. It appears to take whatever is most abundant or readily available within its broad spectrum of suitable prey species. Factors which influence prey selection include:

Prey size . The sevengill shark is a moderate sized species known to reach a maximum total length of 296 cm TL and a weight of up to 182 kg (Ebert 1986b). Although lacking the size and power of the white shark, which is probably the most formidable of modern fish-like vertebrates, the sevengill is, for its size, surprisingly active and able to take prey of considerable size. When hunting alone, this shark will attack and consume small to medium-sized prey. Larger prey species (e.g. pinnipeds) are attacked by the pack rather than individuals. The sheer size of very large species like elephant seals, whales, basking and white sharks, probably protects them from predation by these sharks. On the other end of the prey spectrum, however, sevengills will take quite small prey such as chondrichthyian egg cases, small gastropods and very small teleosts.

Based on examination of stomach contents a consistent pattern emerges for small to medium sized prey items. In instances where the entire remains of a shark or teleost were present, the prey had been cut into halves or thirds, except when the prey was very small in relation to the size of the predator, in which case it was consumed whole. Prey were not always cut cleanly in half, but the initial bite usually severed the abdominal cavity and vertebral column and probably resulted in a quick death. In cases where the prey had been cleanly cut in half, the shark evidently consumed the remaining portion immediately. It appears that if the attacking shark did not do so, any near-by conspecific would scavenge the kill. Such behavior is common in large land predators like lion and hyena, where other near-by predators often chase off the one making the kill, and scavenge its victim (Kruuk 1972; Schaller 1972).

In contrast to attacks on sharks and teleosts, those on awkwardly shaped batoids seem designed to disable and dismember, rather than kill with the initial bite. Evidence to suggest this is that remains of even small to medium sized batoids typically include a section of the wing and the remaining portion of the ray. Even smaller batoids were usually found in two sections with the entire remains present.

Pinnipeds occur throughout the range of sevengills in most areas, though predation is only common where large concentrations of these animals occur, for example breeding colonies. Seals occur in San Francisco Bay, and fishermen have reported finding their remains in sevengill stomachs. However, the majority of breeding colonies are to the north and south of this bay along the open coastline. Predation on pinnipeds was high in Humboldt Bay, which has a breeding colony of harbor seals (Knudtson 1977), even though elasmobranchs and teleost were readily available. Similarly, predation on Cape fur seals was high around Luderitz which has the highest concentration of seal breeding colonies in southern Africa. In other regions where pinniped concentrations occurred, such as around the Cape Peninsula of South Africa, seal remains were found in the stomach of sevengills. The percentage of chondrichthyian remains, however, was much higher. This suggests that size may not be as important a regulating factor in prey selection. Rather it appears that the predator's social behavior has a greater influence in determining prey selection than prey size.

Availability. Prey availability has a profound influence on the food habits and feeding behavior of all predators, and a versatile predator like the sevengill is no exception. The ability to feed on both small and large size prey means that these sharks can exploit several food resources that are unavailable to other large predators. Comparison of the three major prey categories - chondrichthyian, teleost and pinniped - in Humboldt Bay shows that these sharks were fairly non-discriminate in their preference for all three groups, which they preyed upon fairly equally. This indicates that sevengill sharks will readily take any of the three primary prey groups in a localized area, regardless of availability or size.

Along the coast of South Africa, which has one of the richest chondrichthyian faunas in the world, this group was found to be heavily exploited by these sharks. No less than 13 different species of chondrichthyians are preyed upon by sevengills. The three most abundant prey species in this area, the striped catshark, Poroderma africanum, leopard catshark, P. pantherinum and hound shark, Mustelus mustelus, are small to medium-sized sharks. The two catsharks are endemic to the Cape Province of South Africa. Seal colonies in this area have a scattered distribution and were inaccessible for direct sampling. Only in St. Helena Bay were seal remains found in significant numbers.

The predominant prey species in southern Namibia, and in particular around Luderitz, is fur seal. A depauperate elasmobranch and teleost fauna occurs along this stretch of coast from the Orange River to Walvis Bay. For a predator to survive in this environment it must be very mobile and able to travel long distances, or alternately be capable of exploiting whatever food source is available. The Cape fur seal, A. pusillus, is such a food source.

Seasonal changes in prey availability may impose changes in dietary preference in a localized area. At present there is no evidence to suggest that the sevengill varies its diet seasonally. However, other species of elasmobranchs are known to do this, and there is evidence to suggest that these seasonal changes are part of a regular cyclic occurrence. For example, leopard sharks in Humboldt Bay change their diet according to availability during the spring and summer months (Ebert, unpubl. data). During April and early May their diet consists mainly of jack smelt eggs, Atherinopsis californiensis, which are laid on eel grass, Zostera mariannus. From approximately mid-May to June, after most of the fish eggs have hatched, this shark changes diet and feeds predominantly on crab species, Cancer magister and C. antennarius which are readily available. Talent (1982) noticed a similar seasonal change in the diet of leopard sharks based on prey availability in Elkhorn Slough, Monterey Bay.

Density. In any given area the more abundant a preferred species is, the more likely it is to fall prey. The concentration of numerous elasmobranch and teleost species in Humboldt and San Francisco bays during the spring and summer months provides an abundant food resource for larger predators. Sevengills use this food rich environment as a means of providing for their newborn and juveniles. As the concentration of primary prey species declines through the fall and winter months, sevengills leave these bays. The only elasmobranch species which are common in these bays during the winter months are the spiny dogfish (S. acanthias), which feeds heavily on dense schools of spawning herring.

Scavenging. The sevengill is able to take both small and large sized prey by hunting and killing, but in addition will scavenge for food. This shark will readily attack other sharks, including conspecifics, rays or teleosts that have been caught on long-line gear or rod and reel. Sevengills have been observed to follow and harass hooked sharks up to the surface (K. Bates; P. Cowley; R. Russo, East Bay Regional Parks, Oakland, California, pers. comm.; Ebert pers. observation). On one occasion a large (ca. 2.7 m TL) sevengill caught on rod and reel had been brought along side the boat and subdued. While preparing to hoist the shark into the boat, a larger conspecific rose up from below and eviscerated it (T. Roelofs, Humboldt State Univsersity, pers. comm.). Several times while long-lining in San Francisco Bay, the sets had to be left over night due to poor weather and sea conditions. Upon retrieving the gear the following day, the catch usually consisted of shark and ray heads, the rest of the body having been eaten (B. van Gorp, fisherman, San Francisco Bay, pers. comm.) by sevengills. Sharks that have become entangled in gill nets are readily preyed upon, although on one occasion the scavenging shark itself had become entangled in the net (K. Bates and D.A. Ebert pers. observation). Praderi (1985) and Brownell (1975) reported sevengills scavenging on the Franciscana dolphin, Pontoporia blainvillei, that had been caught in shark nets. However, neither could confirm whether these dolphins were taken naturally without the aid of nets. The single reported incidence of human remains being found in the stomach of a sevengill were those of a suicide victim who had jumped off the Golden Gate Bridge (Ebert 1986b). Ainley et al. (1985) noted that sevengills fed on harbor seals as carrion, but made no reference to their feeding on healthy animals. Dolphin remains were recorded from southern African and Californian waters, but it could not be conclusively determined as to how these sharks came by them as prey. Two records of cetacean predation by sevengills occurred on newborns; a dusky dolphin, Lagenorhynchus obscurus, ca. 800 mm TL, and a southern right whale calf, Eubalaena glacialis. Both were in areas where these cetacean species are known to breed, and occurred at the time of year that these species calve (P. Best, marine mammalogist, S.A.M., Cape Town, South Africa, pers. comm.).

Predators will also take advantage of distressed prey. Injured or sick and dying animals give off distress signals that are detected by the acute senses possessed by most predators. This is especially true of sharks. Another means by which a predator may scavenge, and one that has often been over-looked, is research related. Tag and release methods are often used to study an animal's movement patterns. Fish are marked with an identifying tag to distinguish them from the rest of the population. However, such a mark may render it vulnerable to selective predation.

During a national fishing competition outside Swakopmund, Namibia, a 1500 mm TL spotted gully shark, Triakis megalopterus, was caught, measured, tagged and released. When released, the shark was in generally good condition. Several hours later, some of the competition anglers brought the remains of this same shark to the central weigh station. The remains consisted of the head, pectoral fins, and part of the first dorsal fin with the tag intact (Figure 4.8). The bite pattern was identified as that of a sevengill. A possible change in the behavior of the spotted gully shark, due to tagging trauma, could have been detected by these predators, who attacked it. Another example of predation in this manner was observed for a 2900 mm TL mako shark, Isurus oxyrinchus, that had been captured in the shark nets off Natal in August 1989. Upon dissection of the stomach, a small (ca. 900 mm TL) dusky shark, Carcharhinus obscurus, with a yellow tag was found. The C. obscurus had been tagged 11 days before the mako shark was captured. Based on the state of digestion the dusky shark had probably been caught shortly after being tagged. Both incidents indicate that disoriented prey may readily fall victim to any opportunistic predator in the area. For example, a salmon or striped bass lost to an angler, may not be in a fit condition to escape a hungry predator immediately after escaping an angler's dinner plate. Kruuk (1972) noted that wildebeest which had their horn tips painted during a study to follow their movements, were systematically culled from the rest of the herd by hyenas. Apparently the wildebeest with the painted horns were not only easily visible to the observer, but also to the hyenas. The best method of escape from hyena attack, is for a wildebeest to run into a herd of its own kind, where the predators often lose sight of it. However, the horn markings enable the hyenas to keep track of their intended prey. Observations on the escape response of prey species from sharks are few, but it is well known that many fish species school for protection and safety. However, if an individual is marked and stands out from the others, it could make selection easier for the predator.

One final way in which sharks may scavenge, and one that has lead to much misconception concerning shark predation in general, is the discard of human refuse. Most early reports on shark predation mistook scavenging as the primary source of nutrition, since human wastage thrown into the sea tended to attract sharks and other predators. Lack of first hand observations on predation bouts and a blindness and stubbornness born out of traditional prejudice against sharks, has perpetuated this view.

Prey Detection

Research on the sensory biology of elasmobranchs has largely been oriented at isolating one particular sense and extrapolating the entire behavior of a species based on these findings. How the various sense organs integrate into a shark's behavior pattern greatly influences how it may for example, perceive a prey species. The majority of researchers fail to look at these predators as an integrated biological unit composed of several senses all working in co-ordination, thus making the shark a behaviorally complex and effective predator, well attuned to its environment. As with most living organisms, sharks do not simply rely on a particular sense to locate a prey they instead integrate all their senses to locate a specific prey species, a mate, or alert them to a potential danger. Much of this narrowness on the part of researchers to isolate and concentrate on a particular sense organ stem from the preoccupation many had with shark attack.

Field observations on sevengill sharks indicate that their behavior towards a food stimulus differed depending on the environmental conditions and prey behavior. The various foraging strategies used by sevengills reflect an animal that can quickly analyze sensory information as it is received to coordinate its behavior toward the prey. In this way the sevengill can enhance its chances of success during a hunt.

Olfactory. Observations show that once a food stimulus has been introduced these sharks will follow the scent to its source. In Luderitz Lagoon oily fish bait was placed in the water to attract sharks. Usually within 5 to 20 minutes after the bait had been introduced the first sevengill sharks would appear. The sevengills were always observed to approach the bait source from opposite the tidal flow. The distance at which these sharks were able to detect the odor was uncertain due to poor water visibility. The number of sharks increased as long as the food scent could be maintained. In San Francisco Bay the best time to fish for sharks is during spring tides when there is a tremendous change in the water level with the current flowing up to seven knots. It is at the start of a spring tide series that sevengill sharks as well as several other chondrichthyian species seem to feed heaviest. Usually during slack tide most sharks, of all species, were caught. With the rapid movement of water various scents and odors can be quickly dispersed throughout the Bay. It seems likely that movement of these odors in the water column stimulates a period of active feeding for many of the chondrichthyian species, including the sevengill shark.

Most chondrichthyians move into San Francisco Bay during the spring at various times in a sequential migratory pattern (Ebert 1986b). It is impossible to say with present knowledge which biological and physical cues chondrichthyians use to determine when to enter these Bays, but salinity is one probable parameter. During the "El Nino" of 1983 large amounts of fresh water runoff lowered the salinity in these Bays for a longer than normal period. Few sharks were seen in these Bays during April, but by May when the rains had subsided and the river flow decreased substantially, large numbers of chondrichthyians appeared. Hodgson and Mathewson (1978) showed that some shark species can detect odors as small as one part/million and can clearly distinguish salinity differences of the water.

Sharks are well known to have an acute olfactory system (Tester 1963; Parker 1910; Parker & Sheldon 1913; Sheldon 1911). Studies by Parker (1914) showed that dogfish sharks tried to balance the amounts of chemical stimulation they detected on both sides of the snout. These dogfish sharks exhibited directional response to odorous food substances. Tester (1963) demonstrated that blinded blacktip sharks, Carcharhinus melanopterus, were able to spiral down on a piece of bait that had formed an olfactory trail sinking to the bottom. Hodgson (1987) showed the path that sharks take when they have located an odor varies according to species. This suggests that the way in which species perceive scents differs, and that depending on their preferred dietary habits, they will approach the bait in a given manner. The two species cited by Hodgson (1987) provide evidence in support of this hypothesis. The nurse shark, Ginglymostoma cirratum, homes in on a stimulus by criss-crossing through the scent trail toward the greatest concentration. Lemon sharks, Negaprion brevirostris, on the other hand, react to the stimulus by swimming into the strongest water current which they use as their main guide to focus in on the source. These two species have very different life history modes. The nurse shark is primarily a bottom feeder on crustaceans, cephalopods, other molluscs and small reef dwelling fish. The lemon shark by comparison is a more active predator feeding heavily on fishes and only occasionally taking invertebrates, but also sea birds. Hobson (1963) also observed that different species react to baits differently. The white tip reef shark, Triaenodon obesus while very adept at getting prey out of small caves and crevices, had difficulty capturing prey out in the open. The grey reef sharks, Carcharhinus albimarginatus and C. limbatus, on the other hand, had difficulty in prising prey out of crevices but few problems in obtaining prey that was in the open. One point that should be emphasized concerning chondrichthyian feeding behavior is that each species has to be viewed as an integrated biological unit, with special sensory structures that enable them to secure prey from a variety of habitats. Life history strategies of sharks vary, and ways in which food stimuli are perceived will differ accordingly.

Electroreception. Based on observations of sevengill sharks electroreception appears to be an important component in their feeding behavior. Since these sharks typically inhabit water of poor visibility they must have additional senses that enable them to locate prey. When sharks appeared around our boat or along the shore-line to investigate the food source (bait) they would often bump their snouts against the boat or poke their head into cracks and crevices. It appeared that once they had reached the source of the stimulus they had become confused and were trying to identify the source. Observations recorded by divers from Scripps Institute of Oceanography (SIO) note that a sevengill shark was poking its head into cracks and crevices around a reef possibly looking for food (unpubl. data, SIO). This behavior suggests that they may be foraging, especially since electroreception falls off rapidly over distance. Foraging would be especially useful when hunting Poroderma catsharks which inhabit cracks and crevices in reefs. The means by which electroreception functions in the open water is uncertain, but it probably differs from the way it is employed around reefs. Studies have shown that sharks have a threshold gradient of 0.005 V/cm (Kalmijm 1981), which no doubt plays a significant role in their hunting strategy. Field experiments on the dogfish, Mustelus canis (Kalmijn 1978), blue shark, Prionace glauca (Heyer et al. 1981), and the swell shark, Cephalopscyllium ventriosum (Tricas 1982) have all demonstrated that these animals can indeed detect and take prey by use of electroreception.

Field observations of leopard sharks in Humboldt Bay show that these animals, when hunting for prey, swim very close to the bottom substrate. When they apparently detect a food source such as an echurid worm, clam or other mud dwelling organism, they run their snouts into the mud and seize it. By contorting their bodies, they are able to wrench the prey free from the mud and consume it. Since these prey species are for the most part hidden in the mud, the only means by which they could be detected is electroreception. Leopard sharks probably move very close to the substrate since the magnitude of the electric field falls off very rapidly over distance. Other species observed to navigate by electroreception include the brown smoothhound shark. Observations in the field have shown that when this species approaches a gill net, it comes right up to it and at the last moment, jumps the net. Laboratory observations show that they approach the sides of an aquarium and at the last moment preform a 90 degree turn and move up the side of the tank wall (Compagno 1984b; Ebert pers. obs.). Based on the preferred prey of most hound shark species (predominantly crustacean) these sharks must rely on electroreception to detect burrowing sand crabs.

Vision. From a human perspective, the noctural behavior and turbid water habitat that sevengill sharks prefer is so poor in visibility, it would appear that vision plays a small role in the location of prey. However, observations of sevengill sharks suggest that they have some degree of visual acuity. Sevengills are also capable of "spy-hopping" (Figure 4.9), a form of behavior that is well documented in marine mammals, whereby the head is elevated above the water line (K. Bates and G. van Dykhuzien, pers. comm.; Ebert, pers.obs.; Watson 1981). Other sharks that have been observed spy-hopping are the white shark (Readers Digest 1987; Stafford-Deitsch 1987; Taylor 1987), spiny dogfish, ragged-tooth and brown smoothhound sharks. The functions of this behavior in sharks are unknown, but possibilities include predator avoidance and prey detection. Given that the white and sevengill sharks have few natural predators, it seems likely that prey detection is the main objective of spy-hopping in these species. Small species such as the spiny dogfish or brown smoothhound sharks, however, are vulnerable to bird or marine mammal predation, especially when feeding on shallow water mud flats. Spy-hopping would enable these sharks to spot potential predators lurking along the shore-line or circling above them.

A third possibility, and one that has been reported for other apical predators, is that these sharks are familiarizing themselves with a "home range". The concept of a home territory has been well documented in mammals, birds and reptiles (Craighead and Craighead 1956; Jewell 1966; Neill 1972; Hutton 1989), but has never been proposed for sharks. An apical predator familiar with all aspects of its home range is at a decided advantage over its prey and is better suited to defending its territory.

Acoustolateralis, **taste** and **hearing** are other senses that are undoubtedly integrated into a shark's hunting behavior. Further studies are needed however, to examine the integration of all sensory systems.

Prey Behavior

The activity of the prey species affects the foraging and hunting behavior of the predator. The substrate in which a prey species lives, whether it inhabits turbid or clear water, and whether it is nocturnally or diurnally active, all influence which predators it is most vulnerable to. Sevengill sharks use San Francisco and Humboldt Bays as nursery and pupping grounds (Ebert 1986a). During the spring time large females move into these bays to pup and possibly mate. The movement of sevengill sharks into these bays coincides with the occurrence of their major prey species.

The appearance of the various species into the bays is dependent on several biological and physical cues including water temperature and salinity. However, the sequence of appearance is apparently consistent, at least for the elasmobranchs. Gravid bat rays usually appear in the bay about late March, followed by gravid female leopard sharks in April. There appears to be a short period of acclimatization (about two weeks) before the females actually give birth. Groups of these two species are sexually segregated with adult females and adult males remaining in distinctly separate groups. Except for the occasional individual the majority of them appear in these bays approximately three weeks after these other species first appear. This coincides with the birthing of leopard sharks whose pups measure about 18 cm tl at birth. The pupping of leopard sharks takes place on the mud flats usually in eel grass, Zostera marianus. The eel grass is typically high in productivity with fish eggs, small teleosts, crustaceans and numerous other small prey species. This food rich environment is ideal for a new born leopard shark. A group of female leopard sharks will pup simultaneously over a period of no more than two weeks. They pup in late April to early May on average, since it is about mid-May when large numbers of small sevengill sharks begin to appear in the catch. The brown smoothhound sharks also pup between mid-May and early June. This abundance of food is advantageous to both juvenile and adult sevengill sharks. Examination of sevengill sharks as small as 70 cm TL showed young of the year brown smoothhound sharks in their stomachs.

An interesting point to speculate on is whether or not sevengill sharks follow these other prey species groups throughout the year, since both the leopard shark and brown smoothhound occur in discrete populations that move about locally as a group. It would be advantageous for a predator to follow these groups so that a constant food supply would be readily available. Another example of a predominant prey species with a local movement pattern are the catsharks, Poroderma species. These catsharks, which figure prominantly in the sevengill shark's diet in South Africa, are nocturnal animals which are usually in caves and crevices during the day, but which move about quite actively at night. This pattern coincides with that of the sevengill, and may explain their predominance in their diet.

Sevengill sharks as a group, may move about in a localized territory in much the same way as hyena clans or lion prides have a home territory. In this manner, those prey species with a localized movement pattern would be subject to predation by sevengills, whereas more migratory species would only be susceptible to predation by sevengill sharks while passing through a group's territory. Individuals moving independently may be at a disadvantage since they can not prey on larger species, nor do they have the advantages of numerous individuals foraging over a wide area.

Prey Condition

Observations on sevengills attacking unrestrained prey failed to elucidate why any given individual was attacked in preference to another. The predator always appeared to target one particular individual. That aspect of the victim's behavior pattern that may have set it apart from the others was not clear. On many occasions, sevengills were observed to swim in the same area as leopard sharks, paying little attention to them, and with no apparent postural changes prior to an attack. Land predators appear to select potential prey items by observing their behavior. A hyena, for example, will dash into a group of wildebeest and scatter them, while alertly looking around at the fleeing herd, and selecting one to chase. Kruuk (1972) was unable to determine why any given animal was selected in preference to others, when all seemed perfectly healthy. Hyenas, however, are apparently very adept at detecting any deficiencies or unusual behavior in the prey. At other times though, hyenas would walk among wildebeest, zebra and other potential prey items and not attack. From Kruuk's (1972) observations, it appeared that the manner in which the predator approached the prey had considerable influence on the prey's reaction.

Injuries to Sevengill Sharks

Many of the prey items that sevengills feed on appear to inflict injuries that are, in some cases, quite severe. On occasion, these sharks may be seriously, if not mortally, wounded. Examples of injuries include those from highly toxic spines of the sea barbel, Galeichthyes sp. The spines are often found embedded in various body parts. Some spines penetrated into organs such as the liver and gonads, and into the wall of the body cavity. In several instances the spine had been stopped by the outer skin. One individual had a spine that penetrated through the roof of the mouth and into the cranium. The spine did not appear to have impaired the shark's behavior and it was quite healthy when captured. Toxic stinging spines from the blue ray, Dasyatis marmorata and the bull ray, Myliobatis aquila were also found in various regions of the body cavity.

At least two instances of sevengill predation on torpedo rays, Narke capensis and Torpedo fuscomaculata, were observed. Members of the order Torpediniformes are well know for the electrical shock they are capable of discharging when defending themselves or stunning prey. Predator size in relation to prey size favored the sevengill in the two instances, as both rays were consumed in full. As previously discussed, at least two attacks by sixgills and one by a bigeyed sixgill on torpedo rays were thwarted by use of the ray's natural defense mechanism. This demonstrates that a distinct size relationship can exist between predators and certain prey. The prey can utilize its anti-predator mechanisms, but beyond a certain predator size, the defense may not be effective.

Relationship Between Conspecifics

Sevengill sharks occasionally form loosely organized groups which move about as a unit. These aggregations appear to represent non-polarized schooling groups. Reasons for large predators to school seem to be unrelated to protection, since they have very few predators. When foraging for food a large group of organisms would be able to cover a much wider area. If a large amount of food is found, for example a seal or school of fish, then the whole group benefits. Furthermore, a group would be more successful at subduing a pinniped or cetacean than an individual.

Another aspect of sevengill shark behavior, and one previously described in other species of elasmobranchs, is schooling in groups of similar size and sex. Grouping behavior has been noted by Templeman (1944), Ripley (1946), Olsen (1954), Springer (1960), Bullis (1967), Ketchen (1986) and Francis (1988). Sevengill sharks have been observed to school or group: (1) during a two day fishing competition at Cape Agulhas, when 37 adult male sevengill sharks were caught. All sharks were taken on a 50 m stretch of beach within a 60 minute period. The following day another 10 were taken in the same spot over a similar time period. On both days the sharks were caught at approximately the same time of day. (2) Over a three day period, 30 female sevengills (all either juvenile or adolescent) were caught over a 40 km stretch of coastline. The stage of maturity of these sharks ranged from immature to maturing individuals which were probably entering their first breeding season. (3) Adult males (› 2.2 m TL) and females (›2.6 m TL) were observed to aggregate in known nursery grounds during the spring months. This occurred over a four week period with an observed increase in the numbers of sharks during spring tide. (4) Young of the year sevengill sharks tend to form groups. For example, on one occasion in San Francisco Bay between 35 and 40 small newborn sevengills measuring between 40 and 50 cm Tl were caught off Coyote Point during a six hour period.

When sevengill sharks appeared in an area where bait has been introduced smaller individuals between 1.4 and 1.7 m TL appeared first. Initially they cautiously approached the bait, but as more sharks appeared the activity of each individual increased. A solitary individual cautiously inspected a bait, whereas the presence of two or more sharks caused increased activity levels between conspecifics.

During social feeding sevengill sharks seem to exhibit extreme tolerance towards one another. Individuals seem more preoccupied with getting a share of the meal, than in the activities of other sharks. This is logical since an individual could lose out on a meal in chasing off another. However, in a group feeding situation, behaviour of one size class has been observed to influence that of others. For example, in one instance where bait was used, small sevengills moved in to feed. Approximately 30 minutes after the arrival of these sharks, larger individuals (over 2 m Tl) appeared. The presence of the larger sharks drove the smaller individuals out to a peripheral area, approximately 10 m from the focal point where the bait was being introduced. Bait cast out near the periphery would induce smaller individuals to dash in and grab it. The sevengill sharks which moved closest to the bait were all approximately the same size, and fed side by side without much segregation by social dominance.

Sevengill sharks will readily feed on their own kind. For example, when one sevengill shark is hooked, other conspecifics in the area immediately turn their attention from the bait to the distressed individual and begin to attack it. Even during group feeding, if one individual becomes distressed or injured, other sharks will attack it. A 2.4 m TL female, for example, had become entangled in an anchor line, and as it fought to free itself, at least four other large sevengills swam around excitedly. The distressed behavior of the injured shark had excited others in the area which then proceeded to attack it. Similar behavior has been reported in sixgill sharks (Fourmanior 1961).

Cannibalism among sevengills was, however, generally low and only observed among the adolescent age group. Adults and juveniles were never observed to have consumed a conspecific, though on at least 4 occasions adolescent individuals were found to contain sevengill remains. The only instance of cannibalism recorded from within the Humboldt and San Francisco bay breeding grounds was by an adolescent. This may explain why adolescent individuals are usually excluded from the pupping grounds.

In a recent study on the Nile crocodile, Hutton (1989) reported that cannibalism was most predominant among adolescent aged animals. This group is generally excluded from the breeding grounds by larger adult crocodiles, which reduces predation on juveniles. Whether adolescent sevengills are excluded from breeding grounds in the same manner by large adults is not known.

Sevengill sharks inflict scratches and bites on each other that may not be associated with courtship and mating. Longitudinal scratches along the dorsum were common on sevengill sharks in areas where numerous individuals were concentrated. These scars may be the result of social hunting. When attacking large prey, feeding individuals may inadvertently inflict injuries on each other. This hypothesis is based on observations of feeding hyenas which occasionally remove part of an ear or inflict a wound on another clan member unintentionally (Kruuk 1972, Goodall & Goodall 1973). These scars may also be the result of larger individuals attacking smaller ones during predation bouts. White sharks will inflict scars on each other during feeding.

Leopard sharks typically feed in aggregations inside Bays along the California coast. When feeding in these aggregations all individuals are typically of similar size and sex. Extended periods of observations on feeding did not reveal social hiearchy among leopard sharks, though this does not imply that this does not occur, but rather that it did not occur in the group studied. In comparison the white shark has a strict social structure based primarily on size. Larger white sharks will chase off smaller individuals even if the prey carcass is a large whale (Tricas 1985; Pratt et al. 1982; McCosker 1985). Tricas (1985) noted that smaller white sharks remained out at a periphery for up to two hours after a larger individual had left the baited area.

How these groups form and whether they constitute a social unit consisting of similar members is unknown. Tagging studies on leopard sharks in Humboldt Bay suggest that these sharks form discreet social groups composed of the same members that remain together over a period of at least several months. Continued studies on this aspect of chondrichthyian behavior may reveal a far more complex social structure that previously thought.

Sevengill Predators

Sevengill sharks have very few natural predators. Smaller juvenile individuals are probably vulnerable to larger teleosts, larger sevengill sharks, seals, birds and other sharks. However, once they reach adulthood they probably have few predators. The white shark and killer whale (Orcinus orca) are probably the only major predators on sevengill sharks. Four sevengills from Southern African waters bore scars inflicted by a white shark. One attack had obviously occurred recently since although the liver and other internal organs were visible, the individual was still alive when caught (Figure 4.10). The only other species known to have bitten a sevengill shark was a ragged tooth shark ca. 2.4 m tl which apparently grabbed, but subsequently released a 1.7 m tl sevengill shark. Killer whales are sympatric with sevengill sharks throughout most of their range, and although there are no reports of attacks by these whales on sevengills, they are known to eat sharks.

General Remarks

Sharks of the order Hexanchiformes, although lacking the diversity of the major shark orders, nonetheless play an integral role in the marine environment. The group's success can be attributed to their apical trophic position. In most habitats in which they occur, hexanchoids have no comparable competitors since equivalent sized sympatric squaloids and carcharhinoids feed at a lower trophic level. The two larger cow shark species, the sixgill and sevengill, are eurytrophic predators that optimize the available resources. The sixgill shark for example, readily forages in the deep dermersal and mid-water zones, but also in the nearshore environment. Sixgills reduce predation on juveniles by having them remain on the continental shelves and upper slopes. Juvenile sixgills in this habitat have few predators and no similar sized competitors with similar prey preferences. Once the sixgill starts to mature, it moves down onto the slopes where it has no real predators and few competitors. Potential competitors are large squaloids such as the sleeper sharks (Somniosus spp.) which have a relatively small mouth in comparison to the sixgill. The Pacific sleeper shark (S. pacificus) with its dagger shaped upper teeth and low, short oblique lower teeth, large buccal cavity and moderate sized pectoral fins is probably a less active hunter than the sixgill. The sleeper shark probably catches fast swimming prey species by lying in wait and ambushing it. The sleeper shark's large buccal cavity appears to act as a vacuum that inhales prey. Of the deepwater lamnoids (Cetorhinidae, Megachasmidae, Mitsukurinidae and Odontaspididae) none combine the large body size with the large mouth and powerful jaws. The sixgill is also an active predator on other chondrichthyians, whereas the other species tend to feed exclusively on teleosts and invertebrates. The sevengill shark, in the nearshore environment, is very similar to its deepwater congener, the sixgill. The large powerful jaws, broad mouth and social predatory behavior enables it to capture fairly large active prey. In those temperate water areas where it occurs, the sevengill shark is displaced only by the white shark as the dominant elasmobranch predator. Carcharhinoids which are sympatric with it are stenotrophic feeding hound sharks (Triakidae) or cat sharks (Scyliorhinidae) that prey mostly on crustaceans and small teleost. Sympatric requeim sharks (Carcharhinus) also tend to be stenotrophic in their dietary habits feeding mainly on teleosts. The bigeyed sixgill shark is comparable in size to many of the larger gulper sharks (Centrophorus sp.) with the notable exception that it has a much broader mouth and stronger jaws than any of these species. Although its predatory behavior is poorly known, it seems likely that the bigeyed sixgill shark occupies a eurytrophic role among the more diverse and stenotrophic squaloids of similar size.

The frilled shark and perlon shark appear to be more prey-selective predators, capable of foraging over epibenthic and mesopelagic habitats in search of prey. The frilled shark is a specialized hunter unlike any other species. The long abdomen, distensible stomach, anguiliform teeth and distensible jaws enable it to capture fairly large prey such as deepwater squaloids and scyliorhinids. The perlon shark is comparable in size to many of the spiny dogfish sharks (Squalus sp.) and smaller gulper sharks. Its tooth morphology, however, suggests this is a predator capable of grasping and engulfing fairly large prey rather than biting and cutting as do most squaloids.

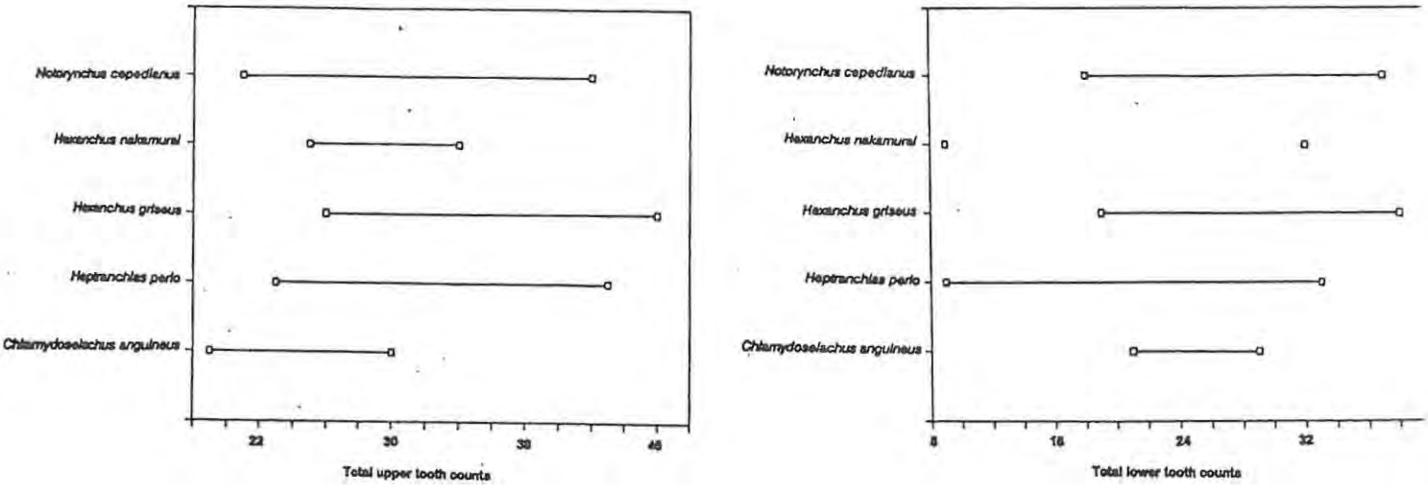


Figure 4.1 - Intraspecific (a) upper tooth and (b) lower tooth counts for hexanchoids.

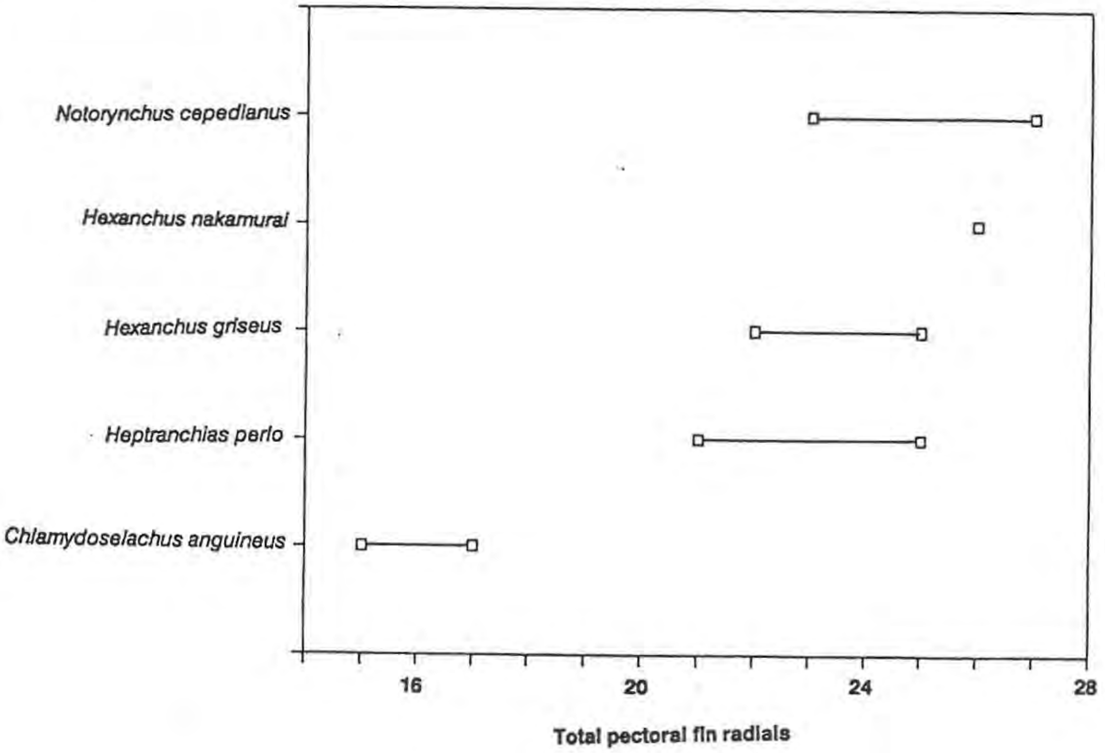


Figure 4.2 - Intraspecifc pectoral fin radial counts.

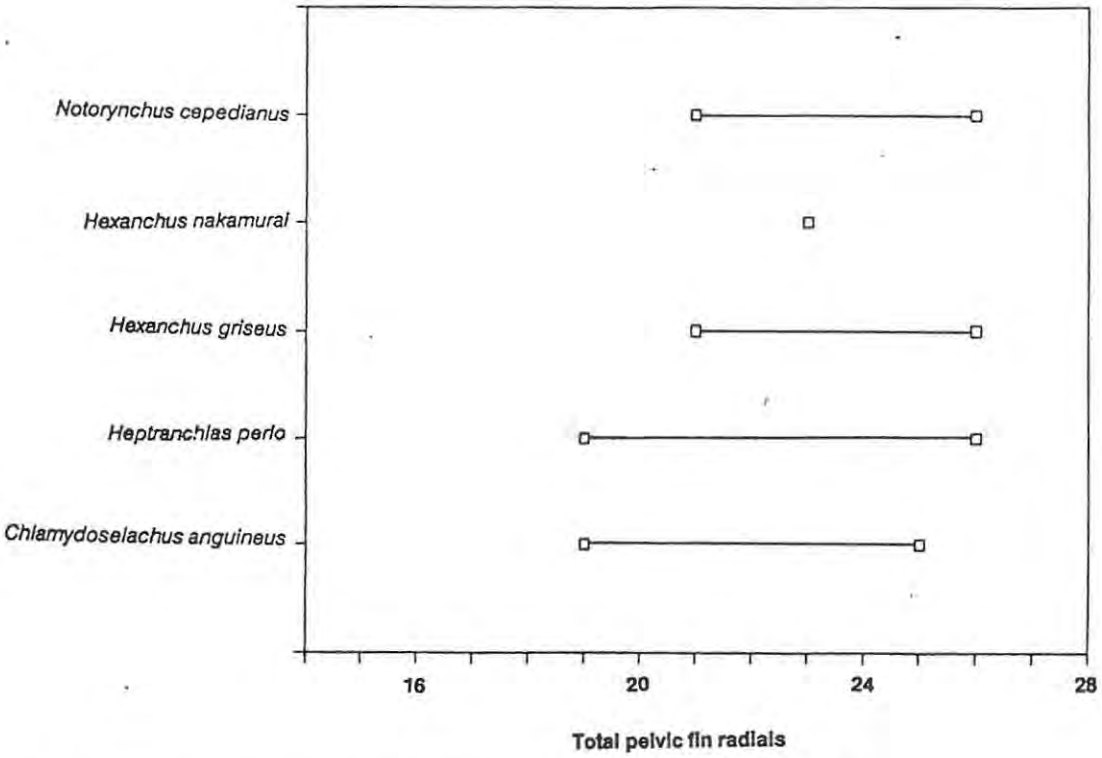


Figure 4.3 - Intraspecifc pelvic fin radial counts.

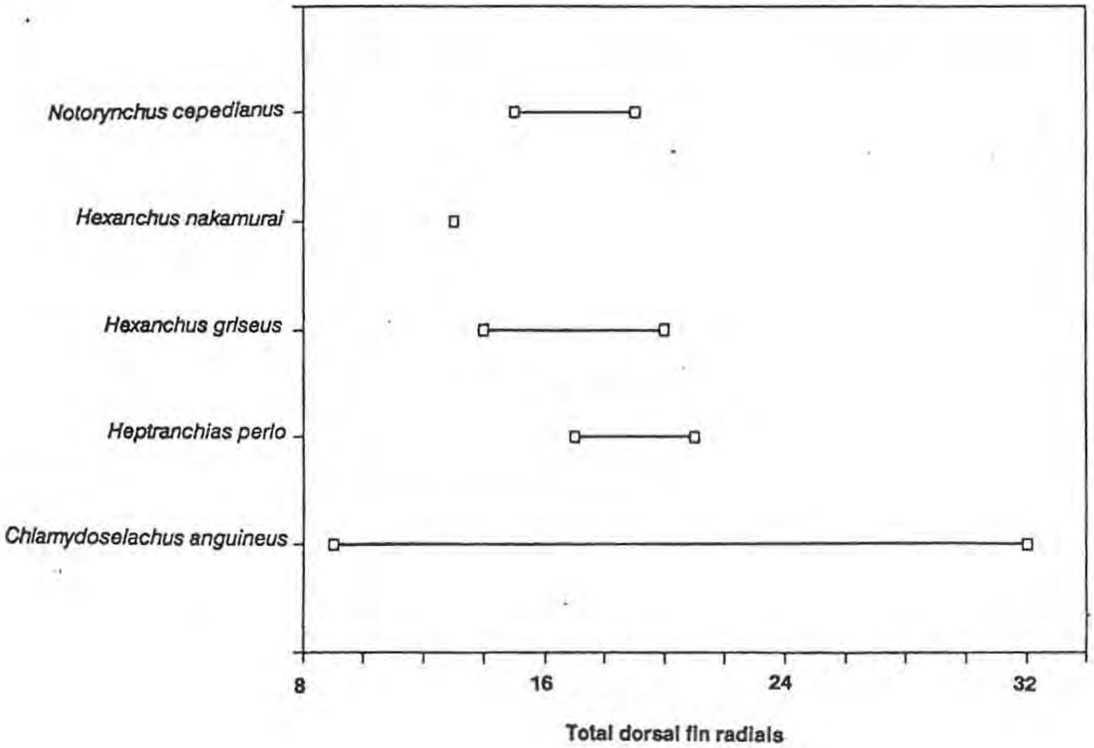


Figure 4.4 - Intraspecifc dorsal fin radial counts.

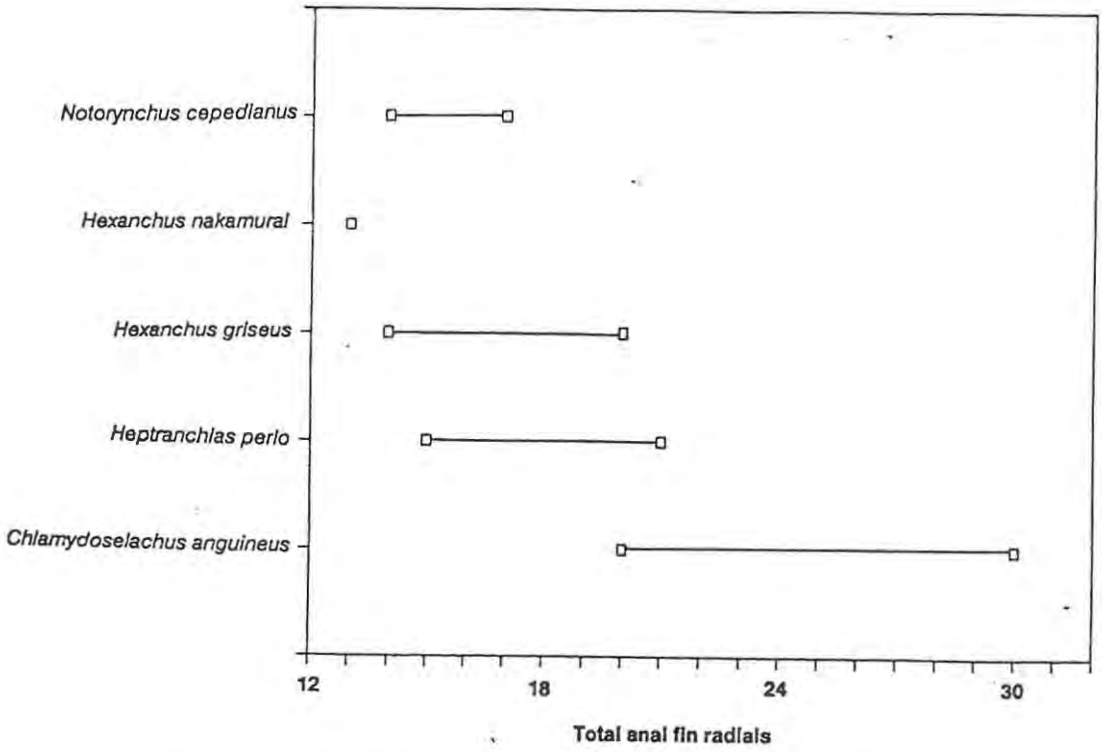


Figure 4.5 - Intraspecific anal fin radial counts.

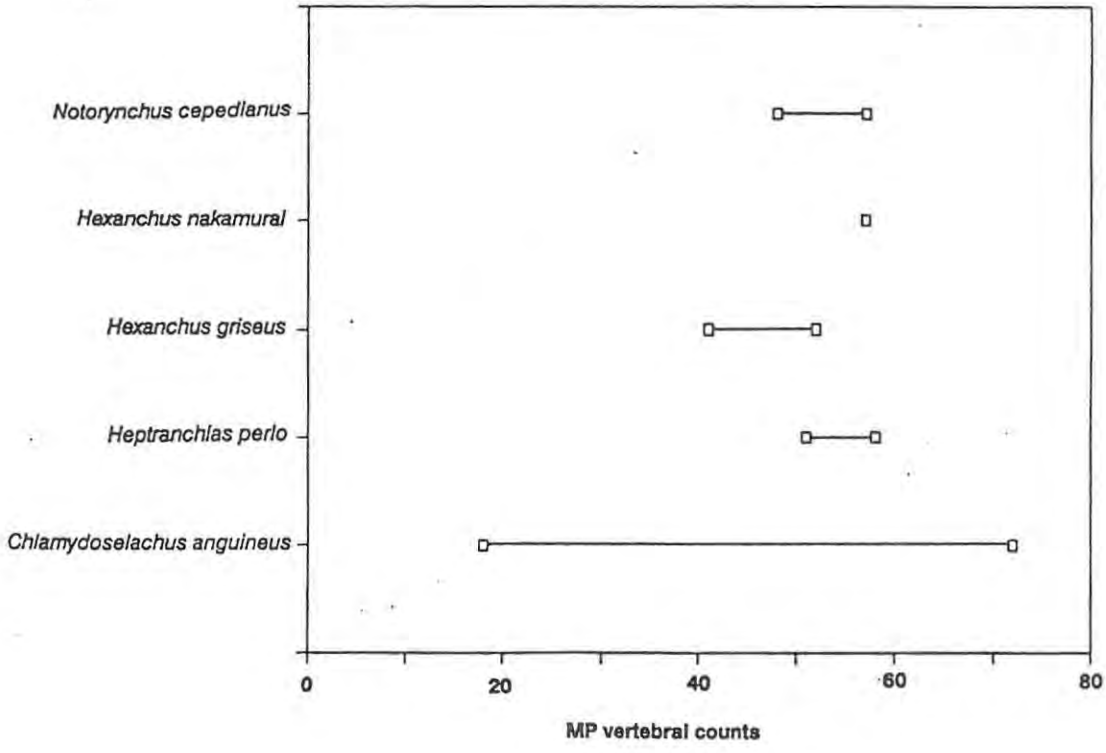


Figure 4.6 - Intraspecific monospondylous vertebral counts.

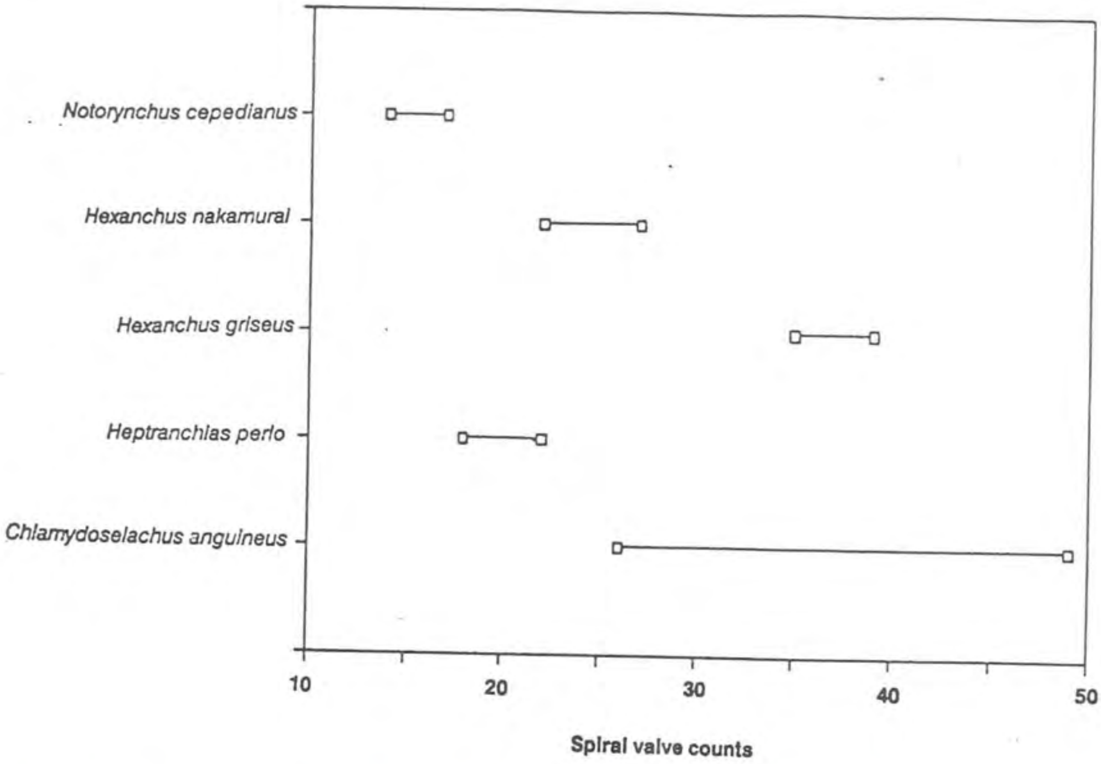


Figure 4.7 - Intraspecifc spiral valve counts.

Figure 4.8 - Remains of a spotted gulley shark attacked by sevengill shark.

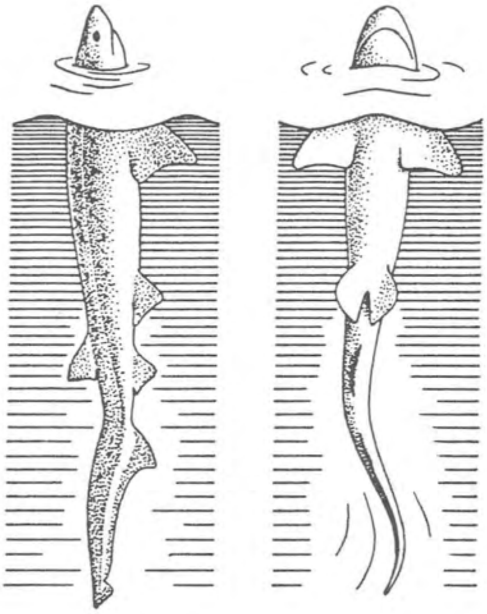


Figure 4.9 - Spy-hopping sevengill.

Figure 4.10 - White shark bite on 1.7 m TL sevengill shark.

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APPENDIX 1

Acronyms for institutional resource collections referred to in the text.

AMS	Australian Museum (Sydney)
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii
BMNM	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
CSIRO	CA Commonwealth Scientific and Industrial Research Organization, Australia
DAE	D.A. Ebert field number
LACM	Los Angeles County Museum of Natural of Natural History
LJVC	L.J.V. Compagno catalogued collection
MCZ	Museum of Comparative Zoology, Harvard
MJS	M.J. Smale field number
MLML	Moss Landing Marine Laboratories, Moss Landing, California
MLP	Museo de La Plata, Argentina
MNHN	Museum National d'Histoire Naturelle, Paris
NMF	National Marine Fisheries College, Kee-Lung, Taiwan
NMNZ	National Museum of New Zealand, Wellington
ORI	Oceanographic Research Institute, Durban
RUSI	Rhodes University, J.L.B. Smith Institute of Ichthyology, Grahamstown
SAM	South African Museum, Cape Town
TFRI	Taiwan Fisheries Research Institute
UF	University of Florida, Florida State Museum
USNM	United States National Museum of Natural History, Washington D.C.
WAM	Western Australian Museum, Perth

APPENDIX 2

List of hexanchoid material examined.

TABLE 2.1

Chlamydoselachus anguineus: material examined.

Australia: CA 4546, 1226 mm TL adult male, N.S.W.; CA 4488, 1310+ mm TL adult male, N.S.W.; CA 4540, 1435 mm TL female, N.S.W.; AMS 17698, 1346 mm TL adult male, N.S.W.; AMS 124101-09, 1360 mm TL female, N.S.W.

Japan: M 158 (0329), 178 mm TL embryonic male; SU 12923, 1468 mm TL female, Misaki, Japan; CAS 12922, 984 mm TL juvenile female, Misaki; BM 1887.3.19.4, 1220 mm TL adult male, Sigamya Bay; MCZ 34247, Yokohama; USNM 161522, 542 mm TL juvenile male, Shimizu; MCZ uncat. (**holotype**), ca. 1500 mm TL, female, S.E. Honshu, Japan, only four pieces remaining of specimen.

Northeastern Atlantic: BM 1961.5.11:1, 1508 mm TL adult male, 59°50'N 06°30'W; BM 1962.7.17:1, 1750 mm TL adult female, 40-45 miles N.W. of Butt of Lewis; BM 1931.5.27:1, 1700 mm TL adult female, 59°10'N 07°04'W, Brierly Bank, Wyville-Thomson Ridge; MCZ 63259, 1300 mm TL, adolescent female.

Northeastern Pacific: CAS 20265, 1630 mm TL female, 34°23'N 121°03'W, 22 miles west of Pt. Arguello, California, U.S.A.

Southeastern Atlantic: RUSI 2423, 915 mm TL adult male, Walvis Bay, Namibia; RUSI 2424, 1010 mm TL female, Walvis Bay, Namibia; SAM 31028, 1170 mm TL female, 19°59'S 11°48'E, off Cunene River, Namibia; DAE 881902, 916 mm TL adult male, 26°38'S 15°10'E, West of Luderitz, Namibia; USNM 203466, 990 mm TL male, 12°36'S 13°12'E, Bahia Farta, Angola.

Taiwan: DAE 881204, 1252 mm TL adult male, 24°50'N 121°22'E, Ta-Chi, Taiwan; DAE 882104, 1571 mm TL adult female, 23°06'N 121°22'E, Cheng-Kung, Taiwan; DAE 882304, 1410 mm TL adult male, 22°26'N 120°30'E, Tung-Kang, Taiwan.

TABLE 2.2

Heptranchias perlo: material examined.

<u>Australia</u>: WAM P. 29037-001, 700 mm TL, juvenile female, 38°40'S 149°15'E, 96 km south of Cape Everhard, Victoria; WAM P. 25782-001, 870 mm TL, adolescent female, 33°29'S 128°27'E, Great Australian Bight.

<u>Gulf of Mexico</u>: GM-1(0328), 478+ mm TL, adolescent female, 27°45'N 95°13.9'W, SSW of Galveston, Texas, U.S.A.; UF 40301-2, 637 mm TL, juvenile female, 26°11'N 96°18.4'W, off the Texas coast, U.S.A.

<u>Japan</u>: *Heptranchias deani*, SU 12620 (**holotype**), 954 mm TL, adolescent female, Misaki.

<u>Mediterranean Sea</u>: USNM 204252, 645 mm TL, adolescent female, Ligurian Sea, Italy; BM 1906.11.12.3, female.

<u>Southern Africa</u> (including Mozambique, Namibia, and South Africa): RUSI 6246, 961 mm TL, adult male, 29°53'S 31°00'E, Natal, S.A.; RUSI 6909, 689 mm TL, adolescent male, 21°40'S 35°30'E, Bazaruto, Mozambique; RUSI 12831, 950 mm TL, adolescent female, Natal, S.A.; RUSI 6065, 420 mm TL, juvenile female, southern Mozambique; RUSI 6255, 255 mm TL, juvenile female, Natal, S.A.; RUSI 6064, 355 mm TL, juvenile female, 25°35'S 33°30'E, Natal, S.A.; RUSI 6067, 345 mm TL, juvenile female, Red Cliffs, Mozambique; RUSI 6066, 279 mm TL, juvenile female, 25°15'S 35°10'E, Natal, S.A.; RUSI 6068, 303 mm TL, juvenile female, Natal, S.A.; DAE 881008, 1069 mm TL, adult male, northern Natal, S.A.

<u>Taiwan</u>: TFRI 101020104, adult male, Kee-Lung; TFRI 101020102, juvenile female, Kee-Lung; TFRI 101020101, adolescent male, Kee-Lung; TFRI 101020103, adolescent male, Kee-Lung; DAE 880904-01, 746 mm TL, adult male, 24°50'N 121°22'E, Ta-Chi; DAE 881104-01, 780 mm TL, adult male, 24°50'N 121°22'E, Ta-Chi; DAE 881104-02, 795 mm TL, adult male, 24°50'N 121°22'E, Ta-Chi; DAE 881204-01, 681 mm TL, juvenile female, 24°50'N

121°22'E, Ta-Chi; DAE 881204-02, 965 mm TL, adult female, 24°50'N 121°22'E, Ta-Chi; DAE 881204-03, 842 mm TL, juvenile female, 24°50'N 121°22'E, Ta-Chi; DAE 881204-04, 727 mm TL, adolescent male, 24°50'N 121°22'E, Ta-Chi; DAE 881204-05, 674 mm TL, adolescent male, 24°50'N 121°22'E, Ta-Chi; DAE 881204-06, 1130 mm TL, adult female, 24°50'N 121°22'E, Ta-Chi; DAE 881604-01, 1030 mm TL, adult female, 24°50'N 121°22'E, Ta-Chi; DAE 880605-01, 955 mm TL, adult male, 24°50'N 121°22'E, Ta-Chi; DAE 880705-01, 865 mm TL, adult male, 24°50'N 121°22'E, Ta-Chi; DAE 880905-01, 891 mm TL, adolescent female, 24°50'N 121°22'E, Ta-Chi; DAE 880905-02, 980 mm TL, adolescent female, 24°50'N 121°22'E, Ta-Chi; DAE 880905-03, 955 mm TL, adult male, 24°50'N 121°22'E, Ta-Chi; DAE 881005-01, 1025 mm TL, adult female, 24°50'N 121°22'E, Ta-Chi; DAE 881205-01, 841 mm TL, juvenile female, 24°50'N 121°22'E, Ta-Chi; DAE 881305-01, 1073 mm TL, adult female, 24°50'N 121°22'E, Ta-Chi; DAE 881405-01, 871 mm TL, juvenile female, 24°50'N 121°22'E, Ta-Chi; DAE 882005-01, 725 mm TL, juvenile female, 24°50'N 121°22'E, Ta-Chi; DAE 882005-02, 765 mm TL, adolescent male, 24°50'N 121°22'E, Ta-Chi; DAE 882005-03, 635 mm TL, juvenile female, 24°50'N 121°22'E, Ta-Chi; DAE 882005-04, 750 mm TL, adolescent male, 24°50'N 121°22'E, Ta-Chi; DAE 882005-05, 690 mm TL, juvenile male, 24°50'N 121°22'E, Ta-Chi; DAE 882205-01, 592 mm TL, juvenile female, 24°50'N 121°22'E, Ta-Chi; DAE 882505-01, 1100 mm TL, adult female, 24°50'N 121°22'E, Ta-Chi; DAE 882605-01, 1005 mm TL, adult female, 24°50'N 121°22'E, Ta-Chi; DAE 882705-01, 1003 mm TL, adult female, 24°50'N 121°22'E, Ta-Chi; DAE 882705-02, 1073 mm TL, adult female, 24°50'N 121°22'E, Ta-Chi; DAE 882705-03, 1040 mm TL, adult female, 24°50'N 121°22'E, Ta-Chi; DAE 882705-01, 1185 mm TL, adult female, 24°50'N 121°22'E, Ta-Chi; DAE 882805-02, 885 mm TL, adolescent female, 24°50'N 121°22'E, Ta-Chi.

West Central Africa: USNM 220194, 290 mm TL, juvenile male, Nigeria; USNM 220193, 345 mm TL, juvenile male, Ivory Coast; USNM 220193, juvenile female, Ivory Coast.

TABLE 2.3

Hexanchus griseus: material examined.

California: DAE 821405-02, 1070 mm TL, juvenile male, 36°50'N 121°55'W, Monterey Bay; CAS 1962-XII:9, 2420 mm TL, juvenile male, 37°40'N 122°21'W, Hunter's Point, San Francisco Bay; CAS 1950-IX:19, 1151 mm TL, juvenile female, 37°36'N 122°19'W, San Francisco Bay; CAS 52981, 955 mm TL, juvenile male, 32°50'N 117°25'W, Bird Rock, San Diego.; DAE 872212-04, 775 mm TL, juvenile female, 36°50'N 121°55'W, Monterey Bay; CAS 11615, 688 mm TL, juvenile male, 37°36'N 122°21'W, San Francisco Bay; DAE 872212-02, 674 mm TL, juvenile female, Davenport; CAS uncat., 1310 mm vertebral column and pelvic fins only, central California.

Chile: USNM 164433, 695 mm TL, Chiloe Is., Quemchi; USNM 164432, 930 mm TL, 41°54'S 73°06' W, Bahia Lin.

Cuba: MCZ 36217, 3330 mm TL, Havana.

Gulf of Mexico: USNM 188048, 4330 mm TL, female, 29°4.5'N 88°29.5'W, off the Louisiana coast.

Hawaii: BPBM 9649, 2805 mm TL, adolescent male, Ala Moana, Oahu Is.; USNM 220178, 3080 mm TL, adolescent male, Oahu; USNM 179770, 2808 mm TL, adolescent male, 21°16'N 73°48'W, Ala Moana, Oahu.

Mediterranean Sea: BM 1866.5.28.5, 675 mm TL, juvenile male, Nice France; USNM 204251, 610 mm TL, juvenile female, Bay of Genoa, Italy.

North Atlantic: BM 1928.9.18.1, 675 mm TL, S.W. Ireland.

Southern Africa: LJVC 861010-01, 681 mm TL, juvenile female, 26°44'S 14°30'E, Luderitz, Namibia; RUSI 6244, 960 mm TL, juvenile male, Walvis Bay, Namibia; RUSI 6245, 853 mm TL, juvenile female, 21°40'S 35°30'E, Bazaruto, Mozambique; RUSI 6180, 680 mm TL, juvenile male, 29°53'S

31°00'E, Durban, South Africa; DAE 872105-01, 1920 mm TL, juvenile male, 26°44', 14°30'E, Luderitz, Namibia; DAE 872710-01, 1005 mm TL, juvenile male, 32°31'S 18°20'E, St. Helena Bay, South Africa; DAE 870209-01, 1588 mm TL, juvenile male, 26°44'S 14°30'E, Luderitz, Namibia; DAE 870209-02, 1660 mm TL, juvenile male, 26°44'S 14°30'E, Luderitz, Namibia; DAE 870409-01, 1095 mm TL, juvenile female, 26°44'S 14°30'E, Luderitz, Namibia; DAE 870409-02, 730 mm TL, juvenile female, 26°51'S 14°31'E, Luderitz, Namibia; DAE 870409-03, 1010 mm TL, juvenile male, 26°58'S 14°29'E, Luderitz, Namibia; DAE 870409-04, 783 mm TL, juvenile male, 26°51'S 14°31'E, Luderitz, Namibia; DAE 870409-05, 910 mm TL, juvenile male, 27°04"S 14°28'E, Luderitz, Namibia; DAE 870409-06, 807 mm TL, juvenile female, 26°51'S 14°31'E, Luderitz, Namibia; DAE 870409-07, 794 mm TL, juvenile female, 26°58'S 14°29'E, Luderitz, Namibia; DAE 870309-03, 730 mm TL, juvenile male, 27°04'S 14°28'E, Luderitz, Namibia; DAE 870309-04, 788 mm TL, juvenile male, 26°58'S 14°29'E, Luderitz, Namibia; DAE 870509-01, 1005 mm TL, juvenile male, 26°44'S 14°30'E, Luderitz, Namibia; DAE 870509-02, 835 mm TL, 26°44'S 14°30'E, Luderitz, Namibia; DAE 870509-03, 776 mm TL, juvenile male, 26°58'S 14°29'E, Luderitz, Namibia; DAE 881202-01, 2000 mm TL, juvenile male, 33°06'S 18°03'E, Langebaan, South Africa; DAE 882202-01, 1380 mm TL, juvenile female, 32°12.6 'S 17°38.4'E, West of Cape Columbine, South Africa; DAE 882506-01, 2210 mm TL, juvenile female, 33°58'S 25°36'E, Eastern Cape, South Africa; DAE 882611-01, 3330 mm TL, adult male, 27°28'S 32°47'E, White Sands, Natal, South Africa; SAM 31027, 4000 mm TL, jaws only, female, 29°53'S 31°00'E, Durban, South Africa.

Taiwan: TFRI 103280, 938 mm TL, juvenile female, 24°50'N 121°22'E, Kee-Lung; Fisheries College of Kee-Lung uncat., jaws only, 2 m TL, 24°50'N 121°22'E, Kee-Lung.

Washington: USNM 110926, 4600 mm TL, Port Ludlow; *H. corinus*, USNM 27369 (**holotype**), 1030 mm TL, 48°22'N 124°36'W, Neah Bay.

TABLE 2.4

Hexanchus nakamurai: material examined.

Australia: WAM P.29521-001, 1440 mm TL, adult male, 32°18'S 115°44'E, continental slope off Bunbury, Western Australia; CSIRO 506/85/23, 474 mm TL, juvenile female, New South Wales; CA 3366, 837 mm TL, juvenile female, New South Wales.

Bahamas: *Hexanchus vitulus*, USNM 200674 (**holotype**), 1500 mm TL, adult male, Bimini; *H. vitulus*, USNM 200675 (**paratype**), female, Bimini.

Florida: USNM 220182, 690 mm TL, juvenile female, 29°32'N 96°30'W, N.W. of Florida.

Kenya: RUSI 4343-01, 259 mm TL, embryonic female, 4°37'S 39°22'E, Shimoni; RUSI 4343-02, 268 mm TL, embryonic male, 4°37'S 39°22'E, Shimoni; RUSI 4343-03, 264 mm TL, embryonic female, 4°37'S 39°22'E, Shimoni; RUSI 4343-04, 250 mm TL, embryonic male, 4°37'S 39°22'E, Shimoni; RUSI 4343-05, 220 mm TL, embryonic female, 4°37'S 39°22'E, Shimoni; RUSI 4343-06, 234 mm TL, embryonic male, 4°37'S 39°22'E, Shimoni.

Philippine Islands: CAS 30642-01, 433 mm TL, embryonic male, 9°20'N 123°18'E, Dumaguete; CAS 30642-02, 417 mm TL, embryonic female, 9°20'N 123°18'E, Dumaguete.

South Africa: ORI 2922, 1553 mm TL, adult male, 29°53'S 31°00'E, Durban, Natal.

Taiwan: NMF 0295, 845 mm TL, juvenile male, 25°00'N 121°50'E, Kee-lung; DAE 881504, 482 mm TL, juvenile male, 24°33'N 121°48'E, So-Au; TFRI uncat., 860 mm TL, juvenile female, 22°26'N 120°30'E, Tung-Kang; TFRI uncat., 1155 mm TL, female, 22°36'N 120°17'E, Liuchiu Island; TFRI uncat., 1526 mm TL, adult male, 22°36'N 120°17'E, Liuchiu Island; TFRI uncat., 1230 mm TL, female, 22°36'N 120°17'E, Liuchiu Island.

U.S. Virgin Island: uncat. 871408, 675 mm TL, juvenile male, 18°38'N 65°03'W, off north coast of island.

TABLE 2.5

Notorynchus cepedianus: material examined.

Argentina: MLP 23-v-84-1, 337 mm TL juvenile female, Mar del Plata; MLP 23-v-84-1, 391 mm TL juvenile female, Mar del Plata.

Australia: CSIRO uncat., 795 mm TL juvenile male, Tasmania; CSIRO uncat., 1415 mm TL juvenile female, Tasmania.

California: CAS 1954-IX:19-01, 585 mm TL juvenile male, 37°36'N 122°21'W, Coyote Point, San Francisco Bay; CAS 1954-IX:19-02, 600 mm TL juvenile male, 37°36'N 122°21'W, Coyote Point, San Francisco Bay; CAS 1954-IX:19-03, 612 mm TL juvenile male, 37°36'N 122°21'W, Coyote Point, San Francisco Bay; CAS 1954-IX:19-04, 603 mm TL juvenile male, 37°36'N 122°21'W, Coyote Point, San Francisco Bay; CAS 1954-IX:19-05, 610 mm TL juvenile female, 37°36'N 122°21'W, Coyote Point, San Francisco Bay; CAS 1954-IX:19-06, 586 mm TL juvenile male, 37°36'N 122°21'W, Coyote Point, San Francisco Bay; CAS 1954-IX:19-07, 546 mm TL, 37°36'N 122°21'W, Coyote Point, San Francisco Bay; DAE 823004, 854 mm TL juvenile female, 37°36'N 122°21'W, San Francisco Bay; DAE 820605, 454 mm TL embryonic male, 37°40'N 122°21'W, Candlestick Pt., San Francisco Bay; DAE 821806, 932 mm TL juvenile male, 37°36'N 122°21'W, San Francisco Bay; CAS 1950-IX:19-01, 655 mm TL juvenile female, 37°36'N 122°21'W, Coyote Pt., San Francisco Bay; CAS uncat., 440 mm TL juvenile male, 37°36'N 122°21'W, San Francisco Bay; CAS 39612, 555 mm TL juvenile female, 37°36'N 122°21'W, San Francisco Bay; DAE 830805, adult male, 40°52'N Humboldt Bay; DAE 830805, adult male, 40°52'N Humboldt Bay; CAS 40577, 600 mm TL juvenile female, 37°36'N 122°21'W, San Francisco Bay; CAS IX:30:1951, 625 mm TL juvenile female, 37°36'N 122°21'W, San Francisco Bay; CAS 1948:XII:3, 640 mm TL juvenile female, 37°36'N 122°21'W, San Francisco Bay; CAS SB:168 (0302), 592 mm TL juvenile male, 37°36'N 122°21'W, San Francisco Bay; CAS 12653, 615 mm TL juvenile male, 37°36'N 122°21'W, San Francisco Bay; CAS 36578, 940 mm TL juvenile male, 37°36'N 122°21'W, San Francisco Bay; CAS 1951-

IX:30-01, 945 mm TL juvenile male, 37°36'N 122°21'W, San Francisco Bay; CAS 1949-IV:18, 965 mm TL juvenile male, 37°36'N 122°21'W, San Francisco Bay; CAS 1950-IX:19-03, 714 mm TL juvenile male, 37°36'N 122°21'W, San Francisco Bay; CAS 1950:IX:19-04, 577 mm TL juvenile male, 37°36'N 122°21'W, San Francisco Bay; CAS 1951-IV:6, 1265 mm TL juvenile male, 37°36'N 122°21'W, San Francisco Bay; CAS 1951-IV:6-02, 809 mm TL juvenile male, 37°36'N 122°21'W, San Francisco Bay; CAS 1950-IX:19-02, 628 mm TL juvenile male, 37°36'N 122°21'W, San Francisco Bay; CAS 1951-IV:6, 756 mm TL juvenile female, 37°36'N 122°21'W, San Francisco Bay; USNM 27191, 451 mm TL, juvenile female, 40°52'N 124°15'W, Humboldt Bay; USNM 27191, 417 mm TL, juvenile male, 40°52'N 124°15'W, Humboldt Bay.

China: BM 1895.5.31.29, 1108 mm TL, juvenile male, Shanghai.

Japan: BM 1939.7.20.2, 1098 mm TL, juvenile male, Sagami.

Namibia: DAE 871204, 1720 mm TL adult male, 14 mi. N. of Swakopmund; DAE 871604, 2420 mm TL adult female, 26°38'S 15°10'E, Luderitz Lagoon; DAE 871604, 1592 mm TL, juvenile female, 26°38'S 15°10'E, Luderitz Lagoon; DAE 871604, 2072 mm TL adolescent female, 26°38'S 15°10'E, Luderitz Lagoon; DAE 871604, 2250 mm TL adolescent female, 26°38'S 15°10'E, Luderitz Lagoon; DAE 872105, 1745 mm TL juvenile female, 22°59'S 14°31'E, Walvis Bay; DAE 880203, 2305 mm TL adult female, 26°38'S 15°10'E, Luderitz Lagoon; DAE 880403, 1344 mm TL juvenile female, 26°38'S 15°10'E, Luderitz Lagoon.

Patagonia: *Heptranchias pectorosus*, MCZ 801 (**holotype**), 391 mm TL, juvenile male.

Peru: USNM 38301, 445 mm TL, juvenile male, Paita.

South Africa: DAE 860910, 1650 mm TL adult male, 33°49'S 26°39'E, Cannon Rocks, Eastern Cape Province; RUSI 76653, 1323 mm TL adolescent male; RUSI 19378, 1777 mm TL adult male, 33°31'S 27°08'E, Fish River, E. Cape Province; RUSI 4679, 1791 mm TL adult male, 33°44'S 25°57'E, Alexandria Coast, E. Cape Province; RUSI 10691, 1754 mm TL adolescent female, 33°23'S 27°20'E, Peddie Coast, E. Cape Province; DAE 860712, 1538 mm TL adolescent male, 33°42'S 26°40'E, Kenton, E. Cape Province; DAE 863112, 1950 mm TL adult male, 33°42'S 26°40'E, Kenton, E. Cape Province; DAE 863112, 1720 mm TL adult male, 33°36'S 26°54'E, Port Alfred, E. Cape Province; DAE 872402, 1375 mm TL adolescent male, 33°36'S 26°54'E, Port Alfred, E. Cape Province; DAE 872402, 1530 mm TL adolescent male, 33°36'S 26°54'E, Port Alfred, E. Cape Province; DAE 870603, 1821 mm TL adult male, 33°42'S 26°40'E, Kenton, E. Cape Province; DAE 872904, 1761 mm TL adult male, Kasougha, E. Cape Province; DAE 871705, 2030 mm TL adolescent female, False Bay, Western Cape Province; DAE 871705, 1530 mm TL juvenile female, False Bay, W. Cape Province; DAE 871705, 1645 mm TL juvenile female, False Bay, W. Cape Province; DAE 871705, 1640 mm TL juvenile female, False Bay, W. Cape Province; DAE 872307, 1362 mm TL juvenile female, 34°12'S 22°08'E, Mossel Bay; DAE 872308, 1610 mm TL juvenile female, Betty's Bay; DAE 872308, 1601 mm TL juvenile female, Betty's Bay; DAE 870830, 1780 mm TL adult male, 43°25'S 19°14'E, Hermanus; DAE 871109, 1701 mm TL adult male, 33°42'S 26°40'E, Kenton; DAE 871010, 1556 mm TL adult male, Cape Agulhas; DAE 871010, 1690 mm TL adult male, Cape Agulhas; DAE 871010, 1970 mm TL adult male, Cape Agulhas; DAE 872510, 1556 mm TL adolescent male, 33°06'S 18°03'E, Langebaan; DAE 872510, 1680 mm TL adolescent male, 33°06'S 18°03'E, Langebaan; DAE 872510, 1600 mm TL juvenile female, 33°06'S 18°03'E, Langebaan; DAE 872510, 1650 mm TL adult male, 33°06'S 18°03'E, Langebaan; DAE 872510, 1630 mm TL juvenile female, 33°06'S 18°03'E, Langebaan; DAE 872012, 1691 mm TL adult male, 33°42'S 26°40'E, Kenton; DAE 872012, 1672 mm TL adult male, 33°42'S 26°40'E, Kenton; DAE 880702, 1700 mm TL adult male, 33°36'S 26°54'E, Port Alfred; DAE 880702, 1705 mm TL juvenile female, 33°36'S 26°54'E, Port Alfred; DAE 882405, 1740 mm TL juvenile female, Algoa Bay.

Uruguay: USNM 87681, 890 mm TL, juvenile male.

Washington: *Notorynchus borealis*, USNM 110920 (**holotype**), dried jaws only, Nisquilly.

APPENDIX 3

List of proportional measurements taken of frilled and cow sharks.

TABLE 3.1 Proportional measurements of *Chlamydoselachus anguineus*, expressed as a percentage of total length.

	ATLANTIC OCEAN									PACIFIC OCEAN														
	ANGOLA	NAMIBIA				NORTH ATLANTIC			NORWAY	CALIF	JAPAN					TAIWAN			AUSTRALIA					
Source	USNM 203466	RUSI 2423	DAE 881902-	RUSI 2424	SAM-31028	BM 1961.5.11:1	BM 1962.7.17:1	BM 1931.5.27:1	Collett 1896	CAS 20265	MLML 158(0329)	USNM 161522	BM 1887.3.19.4	CAS-SU 12922	CAS-SU 1468	DAE 831204	DAE 882304	DAE 882104	CA 4545	Hass 1979	CA 4485	CA 4540	AMS 17698	AMS 124101
Sex	M	M	M	F	F	M	F	F	F	F	M	M	M	F	F	M	M	F	M	M	M	M	F	F
TOT (mm)	990	915	916	1010	1170	1508	1750	1700	1910	1630	178	542	1220	984	1468	1225	1410	1571	1226	1315	1346	1310+	1435	1360
PRC	75.7	75.4	73.1	74.3	72.2	74.9	77.0	76.3		75.7	76.4	72.1	73.0	72.2	75.9	73.9	72.7	73.5	74.2	76.4	73.0	93.9	73.9	74.9
PRN	0.7	1.0	1.1	0.9	1.0	1.6	1.3	1.2		1.2		0.6	1.8	1.4	1.2	0.5	1.1	1.3	1.2	0.8	0.8	0.9	1.1	1.1
POR	0.3	0.4	0.4	0.7	0.5	0.3	0.4	0.4		0.0	0.0	0.6	0.4	0.0	0.3	0.4	0.2	0.0	0.5	0.2	0.3	0.3	0.7	0.4
POB	3.1	3.7	3.1	3.4	2.9	3.3	3.2	3.5		2.8	2.8	3.5	3.7	3.5	3.4	3.0	2.8	3.1	3.1	2.1	2.7	2.4	3.0	2.9
PSP		9.2	8.2	9.8	10.5	7.6	7.0			6.7		8.9		8.4	8.2	4.4			7.3		7.7	6.7	7.8	7.6
PGI	10.9	11.3	10.7	10.6	10.1	10.3	9.5	9.9	10.2	8.4	10.7	11.6	9.4	10.8	9.6	9.1	8.9	8.5	11.7	8.0	12.2	11.6	11.3	11.5
HDL	17.6	17.9	17.5	17.4	17.3	15.9	15.5	14.7	13.6	15.2	20.2	16.2	16.2	15.3	15.7	15.3	13.1	15.6	14.2		15.2	16.1	14.6	14.7
PP1	17.6	17.5	15.1	17.4	17.3	15.9	15.5	14.7	13.6	15.2	20.2	16.2	16.2	15.3	15.7	14.5	13.1	15.0	14.2	14.7	15.2	16.1	14.6	14.7
PP2	46.0	46.1	44.5	48.5	47.0	46.4	50.6	50.0		87.7	51.1	47.0	48.8	46.7	48.4	47.0	47.8	47.4	47.3	46.5	49.0	50.1	48.8	46.0
SVL	52.5	54.1	51.6	55.4	54.0	54.4	58.3	57.6		57.4	54.5	54.2	55.3	53.0	54.5	52.8	52.8	53.1	55.5		56.3	59.1	56.7	55.0
PAL	60.1	63.3	57.6	58.9	58.9	60.3	63.2	62.6		63.0	64.6	56.8	59.7	58.2	61.0	59.1	63.1	60.0	58.1		57.2	61.4	59.3	57.4
PDI	64.1	64.5	62.6	64.4	64.2	60.1	64.2	62.2	66.0	65.0	63.5	57.7	61.5	59.8	62.7	61.6	62.1	62.1	54.2	61.3	61.1	61.0	59.2	56.5
DCS	2.3	2.7	2.2	1.4	1.7	4.2	2.1	3.5		3.3	3.9	2.6	3.4	4.1	4.4	2.6	3.0	3.2	2.3		2.2	2.2	2.6	2.4
PPS	23.5	23.0	24.1	27.7	26.8	26.2	32.0	30.3		31.0	26.4	26.9	28.2	21.8	28.2	29.2	29.8	29.3	30.2	30.2	28.6	31.3	29.3	28.3
PAS	5.7	5.8	4.1	2.2	1.6	3.7	1.7	1.6		2.6	3.4	3.7	2.8	3.0	2.6	3.2	5.3	2.4	0.0	0.0	0.0	0.0	0.0	0.0
ACS	1.0	0.7	1.3	0.2	0.8	1.7	0.9	1.8		1.1	1.7	0.6	2.1	2.0	1.4	2.0	0.9	1.8	0.0	0.8	0.0	0.0	0.0	0.0
EYL	1.8	1.6	2.2	1.5	1.7	1.3	1.2	1.3	1.5	1.2	1.7	2.2	1.7	1.7	2.5	1.2	1.0	1.5	1.6	1.4	2.0	1.8	1.6	1.7
EYH	1.3	1.2	1.4	1.0	1.2	0.8	0.7	0.7	0.8	0.8	1.1	1.1	1.1	0.7	1.1	1.0	0.4	1.1	1.0		1.0	1.0	0.9	0.8
INO	6.2	6.4	5.7	6.0	5.9	4.8	4.9	4.4	4.7	4.2	6.7	7.2	4.5	5.9	5.0	5.1	4.2	3.8	5.5		5.8	5.3	5.2	5.5
NOW	0.6	0.8	0.7	0.7	0.8	0.6	0.6	0.5		0.6	0.6	0.9	0.6	0.9	0.7	0.8	0.8	0.6	0.7	0.7	1.0	0.8	0.8	0.7
INW	3.9	4.8	4.0	4.5	4.5	3.4	3.4	3.5		3.6	3.9	4.2	3.1	3.6	3.3	3.3	2.9	3.1	3.6	3.3	3.4	3.1	3.4	3.3
ANF	0.3	0.5	0.4	0.5	0.3	0.2	0.2	0.2		0.3	0.0	0.2	0.2	0.4	0.3	0.2	0.1	0.2	0.3		0.4	0.2	0.1	0.3
SPL		0.1	0.1	0.1	0.1	0.3	0.2			0.2		0.2		0.1	0.1	0.2			0.2		0.3	0.2	0.1	0.1
FSL		3.1	2.9	5.5	5.6	2.7	2.8		3.0	2.8		3.1		2.9	2.8	0.2			2.6		3.0	2.6	2.2	2.9
MOL	7.1	8.1	6.0	6.9	7.0	7.4	6.6	6.3		5.5	7.3	6.5	6.4	7.3	6.9	5.4	5.7	6.1	6.9	6.4	7.1	6.4	6.7	6.9
MOW	5.1	7.3	4.8	6.5	6.5	5.4	5.7	4.6		4.4	9.0	5.7	4.3	5.3	4.4	5.1	3.4	3.4	6.0	7.6	6.3	6.9	5.5	5.7
ULA	1.1		1.5									1.1	1.1			1.2	0.9	1.1	0.9		1.2	0.8	1.0	1.0
GS1	4.9	5.7	6.8	6.0	8.3	5.4	5.8	4.9		5.8	6.7	3.1	4.3	4.9		6.4	4.5	5.4	4.7	6.3	5.1	6.7	4.9	4.1
GS2	4.9	5.5	6.1	5.5	7.5	5.0	5.1	4.9		5.0	6.2		4.4	4.9		5.3	4.4	5.0	4.4		4.9	5.6	5.1	4.4
GS3	5.1	5.4	5.9	5.4	7.3	5.1	4.7	4.8		4.8	5.6		4.3	4.9		4.2	4.3	4.6	4.4	5.4	4.7	5.2	4.7	4.4
GS4	5.2	5.4	5.5	4.9	6.8	4.9	4.7	4.8		4.6	5.6		4.4	4.8		4.2	4.1	4.6	4.2		4.8	4.7	4.6	4.2
GS5	5.6	5.1	5.5	4.9	6.1	4.6	4.5	4.9		4.5	5.1		4.1	4.8		3.7	3.8	4.5	3.8		4.9	4.2	4.7	4.0
GS6	4.8	4.4	5.0	4.5	4.8	4.0	4.0	4.2		4.0	4.5		3.8	4.3		3.2	3.3	3.9	3.4	4.3	4.7	3.7	4.7	3.7
HDH	7.1	6.2	7.5	6.9	8.6	7.2	7.3	6.1		6.9	8.4	3.9	5.9	6.3		7.0	5.7	6.9	5.3		7.9	7.5	7.5	6.0
HDW	6.6	8.9	6.8	8.4	6.8	5.7	5.0	5.7		4.8	12.9	6.5	5.3	5.6		6.2	6.2	2.8	6.8		7.6	7.1	7.4	7.1
TRH	9.0	8.5	9.1	7.3	10.4	8.0	8.1	5.8	8.6	7.4	8.4	4.4	7.4	7.7		9.7	5.7	7.1	6.6		7.8	8.5	7.9	7.3
TRW	3.7	5.8	7.6	5.4	5.6	5.2	4.1	5.1		5.1	6.2	5.5	5.3	4.8		6.8	5.7	2.9	4.6		5.3	4.2	4.3	4.0
CPH	3.6	4.7	3.8	4.2	4.2	3.4	3.8	3.8		3.5	4.5	4.4	3.1	3.2	3.3	3.4	2.9	3.1	3.0		3.1	3.7	3.0	3.3
CPW	2.1	1.5	1.0	1.2	1.4	1.2	1.1	1.4		1.3	2.8	1.8	1.1	1.2	1.3	1.4	2.0	1.0	1.2		1.3	1.5	1.3	1.1
P1L	9.0	9.6	8.8	9.2	9.2	9.5	8.4	8.1		7.6	7.9	8.1	7.3	8.7	8.3	7.5	6.3	7.3	7.4	8.7	8.2	7.9	7.9	7.9
P1A	8.6	9.2	8.3	7.4	8.8	9.6	9.0	7.8	8.6	7.8	6.7	8.9	7.4	8.3	7.8	7.7	6.7	7.4	8.2	8.2	8.8	8.9	7.2	8.1
P1B	4.3	4.9	4.3	4.6	4.7	4.5	4.5	4.4		4.2	3.9	4.8	3.9	4.6	4.0	4.0	3.7	2.5	4.3	3.5	4.0	4.4	3.9	4.7
P1H	5.6	6.2	6.6	6.3	5.9	5.0	4.9	4.9		5.9	6.7	7.4	4.8	5.7	5.8	6.0	5.5	4.6	4.8		5.6	5.2	5.1	5.4
P1I	4.1	5.2	4.8	5.0	4.7	4.5	4.6	4.5		3.6	5.1	4.6	3.8	4.4	3.8	3.6	3.5	4.6	3.9	5.2	4.8	4.1	3.5	3.2
P1P	5.7	5.6	5.2	4.9	5.3	5.3	5.2	4.4		3.5	3.9	4.1	4.5	4.7	5.0	4.6	2.8	3.5	3.6		5.1	4.2	3.3	3.5
P2L	13.9	15.4	12.6	11.6	12.4	13.6	11.8	12.4		10.6		10.5	13.3	10.8	11.6	12.1	11.4	11.0	13.8	12.8	13.2	14.9	13.1	11.5
P2A	6.9	8.4	6.7	6.6	9.1	7.4	8.4	7.6		6.6		5.7	6.1	7.4	7.8	7.4	5.6	6.7	9.8	6.8	8.2	8.7	9.1	8.9
P2B	13.9	10.7	9.4	9.5	10.3	9.6	10.4	11.3	10.7	9.7		8.5	12.6	8.8	10.4	8.9	8.1	9.9	10.8		9.3	11.1	10.3	10.6
P2H	4.2	6.9	5.2	4.9	5.0	4.7	4.2	4.1	5.1	3.9		4.6	3.7	4.2	5.3	4.4	3.3	3.6	5.2		6.7	6.6	5.1	5.1
P2I		4.8	3.2	2.3	2.1	3.7	1.4	1.2		1.9		2.0	0.5	1.9	1.6	3.1	3.6	1.3	3.2		4.1	4.6	2.0	1.4
P2P	10.1	9.8	9.2	8.0	7.0	8.0	2.0	6.9		6.4		6.6	10.2	6.6	8.4	8.1	7.7	8.1	8.1		7.8	8.0	5.7	6.9
CLO	7.5	9.7	3.6			3.8					1.1	0.9	4.4			3.6	4.1		4.2		5.4	4.4		
CL1	9.9	10.9	9.6			7.9					3.4	3.5	10.2			8.5	8.5		9.7		10.8	10.3		
CLB	1.1	1.9	0.9			0.7					0.6	0.4	0.9			1.3	0.9		1.1		1.0	1.1		
D2L	12.9	10.9	11.8	11.0	10.9	13.1	14.1	13.5		10.4	8.4	17.7	12.7	11.1	9.3	11.7	10.5	11.6	20.1	12.6	13.9	18.6	13.1	16.9
D2A	11.7	10.9	11.4	10.8	10.9	13.3	14.1	13.5		10.4	6.7	17.7	12.7	11.9	9.3	11.7	10.5	11.0	20.0		14.6	18.6	15.5	18.4
D2B	9.7	6.9	8.8	7.6	7.9	9.9	10.3	10.5	9.0	7.4	6.7	15.3	9.8	8.1	6.8	9.5	7.8	8.8	17.9	10.0	10.8	14.7	12.6	14.8
D2H	3.0	3.2	3.3	2.9	2.6	2.9	2.8	2.5	2.4	2.6	2.2	2.8	2.7	2.4	2.9	2.9	2.4	2.2	2.8	2.6	2.3	3.1	3.3	2.9
D2I	3.0	3.1	3.2	3.0	3.0	3.3	4.0	2.9		2.0	2.2	2.0	2.5	3.2	3.1	2.5	2.8	3.1	2.2	2.6	2.6	3.0	2.4	2.0
D2P	2.3	3.0	2.6	2.6	2.3	2.3	2.2	1.8		1.9	3.4	1.8	2.1	2.6	2.6	1.5	2.0	2.2	2.0		2.1	2.3	1.6	2.4
ANL	12.6	13.3	13.6	15.6	14.7	13.7	13.7	13.8		12.9		13.8	13.4	11.7	15.5	13.5	11.1	16.1	15.7		19.2	16.4	16.5	16.2
ANA	6.0	6.1	4.9	8.2	6.2	6.5	6.7	5.3		6.0		11.4	7.0	6.4	5.9	7.7	6.0	7.8	9.7		11.0	11.8	10.0	10.4
ANB	10.3	11.6	12.2	13.6	13.5	12.1	12.9	12.0	12.8	12.0		13.4	12.5	10.8	14.6	12.2	10.8	14.8	14.6	12.6	17.7	15.0	15.5	15.6
ANH	4.2	5.1	5.1	5.0	5.0	4.3	3.9	3.9	3.8	2.9		4.8	3.0	3.7	4.3	3.7	3.1	3.2	4.3	4.2	4.4	4.6	4.9	4.6
ANI	1.4	2.6	1.4	1.7	1.2	1.5	1.4	1.2		1.4		1.1	1.2	1.4	1.2	1.0	0.4	1.2	1.6	1.4	1.6	1.4	1.7	0.9
ANP	8.1	5.8	10.6	4.7	10.5	9.2	9.1	9.1		8.0		5.5	6.9	7.3	11.1	7.2	6.7	11.0	6.4		7.4	6.4	9.1	7.4
CDM	25.4	25.1	26.0	26.7	27.4	26.7	23.9	25.3		24.8		27.3	26.4	26.9	25.1	26.2	27.1	26.3	25.7	23.8	26.1	22.7	25.2	25.6
CPV	7.0	8.5	5.6	8.9	7.9	7.3	6.9	6.6		8.0		8.1	7.8	9.0	7.8	7.7	9.3	5.7	9.8	8.3	10.1	9.9	10.2	9.4
CPU	18.7		24.0		23.1	18.7	17.1	17.1		16.0		17.7	18.0	21.1	19.6	20.3	19.4	18.6	19.4				19.2	
CST	2.0					2.9	2.1	2.8		2.8		1.3	2.2	3.6	2.7	3.0	2.7	2.6						
CTR	1.2		2.1			1.9	1.1	1.5		1.0		2.0	1.1	1.5	0.9	1.1	0.9	1.6						
CTL	2.8					2.0	2.5	3.1		2.7		3.0	2.5	2.8	2.9	3.0	2.1	2.8		4.4				
CFL	11.3		10.5		11.3	9.4	9.5	6.6		7.9		11.8	8.6	9.8	8.8	10.1	9.1	9.1						
DAO	0.0	1.1	3.7	5.0	4.8	0.0	0.8	0.0		2.0	1.1	4.6	1.2	1.2	2.9	2.3	1.3	2.6	4.2		2.0	0.7	0.0	1.3
DAI	0.4	1.4	0.5	1.0	1.5	2.8	0.6	2.2		2.0	0.6	1.7	1.6	1.1	3.4	0.6	3.2	3.0	0.3		2.1	1.0	2.2	1.6

NEW ZEALAND

Nakaya & Bass 1978	Nakaya & Bass 1978	Nakaya & Bass 1978	Nakaya & Bass 1978
M	M	F	F
730	1340	1350	1575
73.0	73.7	73.4	76.6
1.0	1.0	1.3	0.9
3.6	2.9	3.6	2.8
8.4	6.6	7.7	8.2
11.1	9.5	9.3	9.3
16.7	14.5	15.2	14.7
15.8	13.4	14.6	14.2
47.5	49.1	46.5	51.6
54.8	55.7	53.5	58.4
56.8	61.6	56.9	62.9
59.5	61.2	61.2	65.0
1.5	1.3	1.5	1.3
1.0	0.8	0.8	0.6
4.4	3.4	3.4	3.3
0.3	0.2	0.2	0.1
6.4	5.7	6.8	5.7
6.4	5.3	6.2	5.7
9.0	8.1	7.8	7.6
3.8	4.1	4.1	4.1
10.1	9.6	8.5	9.5
11.1	10.5	8.1	7.7
2.6	2.7	2.6	2.4
3.0	2.1	2.5	3.8
12.3	11.8	12.2	11.3
4.5	3.9	4.1	3.6
1.6	1.3	1.3	1.5
27.4	26.0	27.0	23.8

TABLE 3.2 Proportional measurements of *Heptranchias perlo*, expressed as a percentage of total length.

	ATLANTIC OCEAN AND ADJACENT AREAS								
	MED.	I.C.	I.C.	NIG.	G.M.	G.M.	CUBA	CUBA	BRZ.
Source	USNM 204252	USNM 220193	USNM 220193	USNM 220194	GM-1(0328)	UF 40301-2	Garrick & Paul 1971	Garrick & Paul 1971	Barcellos 1957
Sex	F	M	M	M	F	F	M	F	M
TOT (mm)	645	350	345	290	555	637	698	932	583
PRC	65.9	66.3	67.2	66.2	68.5	68.6	69.4	69.6	68.9
PRN	1.9	1.7	2.0	2.1	1.4	2.0	2.0	2.0	
POR	4.3	4.9	4.9	5.5	4.7	6.0	5.0		4.8
POB	4.5	4.3	4.9	5.5	5.4	5.2			5.1
PSP	13.0	13.7	13.9	14.1	13.5	13.2			13.2
PGI	16.7	16.9	17.1	17.6	16.6	18.2			14.2
HDL	20.2	20.3	22.3	21.4	19.3	19.6	20.9	19.1	20.6
PP1	20.2	20.3	22.3	21.4	19.3	19.6	20.9	19.1	20.6
PP2	38.0	38.0	39.1	39.7	40.2	38.6	40.0	38.4	40.0
SVL	40.3	40.9	41.2	43.1	43.4	42.4			45.5
PAL	49.9	50.9	51.3	52.8	53.2	53.7	54.8	52.2	54.7
PD2	44.2	46.6	46.1	47.6	48.6	56.0	49.0	48.3	48.3
DCS	14.9	11.7	12.5	14.5	14.4	15.5			
PPS	14.4	12.3	12.8	15.2	14.6	13.3			14.1
PAS	5.4	6.3	7.0	9.0	6.1	8.2			
ACS	10.2	10.3	8.1	10.0	9.0	10.8			
EYL	3.4	4.9	4.6	4.5	4.5	3.9	4.0	3.6	4.1
EYH	1.4	1.4	2.0	2.1	1.4	1.7			1.5
INO	5.0	7.1	7.0	7.2	5.6	6.0			5.3
NOW	1.2	1.4	1.2	1.4	1.1	1.4			1.0
INW	2.8	3.4	2.9	2.8	2.5	2.8	2.6	2.1	2.7
ANF	0.3	0.3	0.6	0.3	0.5	0.5			
SPL	0.3	0.3	0.6	0.3	0.2	0.3			0.3
ESL	4.5	4.3	4.3	4.1	4.0	3.8			4.3
MOL	7.3	6.9	6.1	7.2	6.7	5.5	6.4	7.1	
MOW	7.4	7.1	7.2	7.6	6.1	5.7	8.0	7.0	
ULA	1.4	2.3	2.0	2.1	2.5	2.8			2.7
LLA	2.0	1.7	1.2	2.1	1.8	1.4			
GS1	5.9	6.6	6.1	6.9	6.5	7.7	5.7	7.2	7.2
GS2	5.9	6.3	6.1	6.9	5.9	7.5			6.7
GS3	5.3	5.7	6.1	6.2	5.6	6.9			5.7
GS4	4.8	5.1	5.8	5.9	4.7	6.3	4.2	5.3	5.1
GS5	4.3	4.3	4.6	4.8	4.3	5.3			4.5
GS6	4.2	3.7	4.1	4.1	3.4	4.1			3.6
GS7	3.1	2.9	3.2	3.4	2.7	3.0	2.6	3.1	2.7
HDH	7.9	8.9	9.6	9.0	8.3	11.6	9.6	10.7	
HDW	9.5	8.9	7.8	9.3	9.4	8.8	8.4	9.1	
TRH		8.3	10.1	9.3	9.5	12.7			
TRW		8.0	7.8	7.9	7.2	8.0			
CPH	4.5	4.0	4.1	3.8	3.8	4.1			
CPW	2.9	2.9	3.2	2.8	2.7	3.1			
P1L	11.2	11.1	11.0	11.0	11.2	11.0			10.8
P1A	12.9	10.6	12.2	12.1	11.5	12.2	11.4	11.4	11.7
P1B	6.0	6.0	6.4	5.9	6.3	5.7			6.0
P1H	9.5	9.7	10.1	8.6	10.8	9.9			8.1
P1I	5.9	5.1	5.8	5.9	4.9	5.7			4.8
P1P	8.2	7.4	7.2	7.2	8.8	9.4	9.6	8.5	8.1
P2L	9.6	8.6	10.4	10.0	8.8	8.6			10.5
P2A	4.3	4.0	4.1	3.8	4.7	4.4			4.5
P2B	8.5	7.4	5.8	6.2	7.6	7.5			6.7
P2H	2.9	2.0	2.3	2.1	2.2	2.8			2.4
P2I	2.2	1.7	4.3	3.8	1.1	1.1			3.8
P2P	5.7	5.7	6.7	5.9	5.2	6.0			7.2
CLO				1.4					
CLI			3.8	3.8					
CLB			0.3	0.3					
D2L	9.5	8.3	9.3	8.3	7.9	8.5			7.0
D2A	9.0	8.3	9.3	8.3	7.6	7.7			7.9
D2B	7.6	6.0	7.2	5.5	5.8	6.1	6.2	6.6	5.7
D2H	4.3	4.3	4.3	3.8	4.5	4.6	4.3	4.5	3.9
D2I	1.9	2.0	2.0	2.1	2.0	2.0			1.4
D2P	4.5	3.4	3.2	2.8	4.5	4.6			3.9
ANL	7.4	7.4	7.8	7.2	7.0	7.7			6.9
ANA	4.7	4.0	4.3	4.1	3.6	3.6			4.1
ANB	5.9	5.4	5.5	5.5	5.4	6.3	5.9	5.9	5.7
ANH	3.1	2.6	2.3	1.7	2.3	2.5	2.2	2.7	2.2
ANI	1.6	2.0	2.0	1.7	1.4	1.6			1.2
ANP	4.3	4.6	4.1	4.5	4.3	5.2			4.6
CDM	33.2	32.6	31.9	31.7	31.2	30.8	30.6	30.4	30.9
CPV	9.1	8.6	10.1	9.0	7.7	8.2	9.0	8.6	8.6
CPL	2.6	3.7	2.6	2.4	2.9	2.7			
CPU	17.5	16.9	17.1	16.6	17.3	18.2			
CST	5.3	4.9	5.5	5.2		4.6			3.9
CTR	5.3	4.0	4.3	4.5		5.2			4.8
CTL	7.6	6.9	7.2	7.2		7.7			
CFL	9.6	10.3	9.6	9.0	7.6	8.3			
DAO	5.6	3.1	6.1	4.1	5.4	6.3			
DAI	5.6	3.4	5.2	4.5	5.2	5.3			

MED. = Mediterranean, I.C. = Ivory Coast, NIG. = Nigeria, G.M. = Gulf of Mexico, BRZ. = Brazil.

INDIAN OCEAN

Source	RUSI 6255	ORI 2551	RUSI 6068	ORI 2530	ORI 2367	ORI 2545	ORI 2536	RUSI 6065	ORI 2466	RUSI 12831	ORI 2531	ORI 2558	ORI 2499	ORI 2458	ORI 2368	ORI 2434	ORI 2417	ORI 2516	ORI 2404	ORI 453	DAE 881008
Sex	F	F	F	F	F	F	F	F	F	F	M	M	M	M	M	M	M	M	M	M	M
TOT (mm)	255	279	303	307	313	345	355	420	902	950	342	344	505	678	689	863	918	924	950	961	1069
PRC	67.4	68.1	68.3	67.7	69.0	68.1	68.1	66.4	67.8	69.0	68.4	68.0	69.1	68.4	69.5	69.0	69.2	68.8	68.4	69.8	68.3
PRN	2.7	2.5	2.0	3.3	3.2	1.4	2.0	1.7	2.5	3.2	2.9	3.2	2.8	2.7	2.9	2.8		2.4	2.5	2.3	2.2
POR	6.7	6.8	6.3	6.5	5.4	5.8	5.1	5.5	5.0	4.7	5.8	6.4	5.0	5.0	4.8	5.1	4.8	4.7	4.7	4.5	4.5
POB	5.9	5.7	5.3	4.9	4.5	5.2	5.6	5.0	4.8	5.5	4.7	4.9	4.4	4.6	5.8	4.6	4.7	4.2	4.3	4.7	5.0
PSP	13.7	15.0	14.1			13.9	13.8	13.0		12.4					13.0					11.6	11.7
PGI	16.8	18.6	17.8	17.5	17.5	15.6	17.1	15.4	15.0	15.7	17.2	17.4	15.6	15.3	16.5	15.2	15.6	15.3	14.9	15.5	15.6
HDL	22.3	21.5	21.4	21.8	21.0	22.0	22.5	19.5	18.0	20.8	18.7	19.7	19.8	18.4	20.0	17.3	19.8	17.8	17.6	18.9	18.8
PP1	22.3	21.5	21.4	21.8	21.0	22.0	22.5	19.5	18.0	20.8	18.7	19.7	19.8	18.4	20.0	17.3	19.8	17.8	17.6	18.9	18.8
PP2	40.3	42.2	42.2	41.6	42.4	41.1	40.8	40.7	40.0	40.0	41.8	42.1	42.1	40.2	41.0	40.6	41.6	42.2	40.2	40.9	41.6
SVL	43.9	46.2	45.5			44.6	42.2	43.0		43.1					44.9					45.7	45.8
PAL	52.9	54.1	54.1			52.7	52.3	52.3		53.8					55.1					55.3	54.8
PD2	47.8	50.1	50.8	49.5	49.2	48.9	49.2	48.8	48.7	50.0	49.1	49.1	50.4	48.3	49.9	49.0	50.6	50.8	49.8	49.4	48.8
DCS	13.7	12.9	12.5	12.3	13.0	13.0	14.9	12.6	13.1	13.3	13.4	12.2	12.8	14.3	12.9	13.4	12.4	12.2	12.2	14.7	13.9
PPS	12.5	14.3	15.5	14.0	15.6	14.4	13.5	15.7	16.6	15.5	15.7	17.1	17.0	16.6	16.9	17.1	11.7	18.7	18.3	17.1	17.5
PAS	5.9	5.7	6.3			6.1	4.8	5.5		6.9					7.7					8.6	7.9
ACS	9.8	9.0	9.2	8.8	7.7	10.7	9.0	9.3	5.8	9.4	8.5	11.6	9.1	9.4	8.7	8.9	8.7	9.1	8.4	9.7	9.0
EYL	5.5	6.1	5.3	5.5	5.1	4.6	4.5	4.3	3.3	3.2	5.0	4.9	4.2	3.5	3.8	3.6	4.0	3.4	3.4	3.3	3.3
EYH	3.1	2.9	2.0			2.3	2.5	2.1		1.4					1.9					1.9	1.6
INO	7.5	6.8	6.3			6.7	6.5	6.9		5.7					7.0					5.7	4.8
NOW	1.6	1.8	1.7	1.6	1.6	1.7	1.4	1.2	1.2	0.7	1.8	1.5	1.6	1.3	1.2	1.3		1.3	1.1	0.9	1.0
INW	3.5	3.2	3.0	3.3	2.9	3.2	3.4	2.9	2.4	3.1	3.2	3.2	2.4	2.7	3.5	2.9		2.7	2.6	2.8	2.5
ANF	0.8	0.7	1.0			0.9	0.6	1.0		0.6					0.6					0.6	0.3
SPL	0.4	0.4	0.3	0.3		0.3	0.3	0.2	0.4	0.1	0.3	0.3	0.6	0.4	0.1	0.3		0.2		0.1	0.3
ESL	3.9	2.5	4.0	4.6		4.1	3.4	3.6	3.9	3.7	5.0	4.7	4.2	4.4	3.5	4.3		4.3	4.5	3.7	3.7
MOL	7.8	6.8	6.9			7.2	7.0	6.9		8.3		9.6			8.3					8.5	5.9
MOW	7.1	7.5	7.6		7.0	6.1	6.2	8.1	8.6	8.0	9.4	9.0	9.5	6.6	10.8	7.0	5.4	7.7	7.9	6.7	6.4
ULA		2.2	2.0			1.7	2.0	1.7		2.3					2.3					2.2	1.9
LLA		2.2	2.0			2.0	2.3	1.9		2.1					2.3					2.1	1.5
GS1	7.8	8.2	9.2	8.1	8.0	8.1	6.5	7.6	7.3	6.2	7.9	7.3	8.1	7.4	7.7	7.0		6.5	6.3	7.1	6.5
GS2	7.1	7.5	8.9	8.1	7.3	7.8	6.2	7.1	7.0	6.0	7.6	7.0	7.9	7.1	7.4	6.4		6.5	6.0	6.3	6.2
GS3	7.1	7.2	8.3	7.8	7.0	7.2	5.9	7.1	6.5	5.8	7.0	6.7	7.7	6.6	7.0	5.9		6.2	5.8	5.7	5.8
GS4	6.3	6.8	7.6	7.2	6.4	6.4	5.1	6.4	6.0	5.4	6.7	6.1	7.1	6.2	5.8	5.6		5.7	5.3	5.1	5.1
GS5	5.5	5.4	6.6	6.2	5.8	5.8	4.8	5.7	5.1	4.8	6.1	5.5	6.3	5.3	5.5	5.3		5.3	4.7	4.4	4.2
GS6	4.7	4.7	5.3	5.5	5.1	4.6	4.2	4.8	4.1	4.1	5.3	4.7	5.0	4.3	4.8	4.8		4.2	3.8	3.5	3.6
GS7	3.9	3.2	4.0	4.2	3.8	3.5	3.4	3.6	3.0	3.1	3.8	3.8	3.8	3.2	3.6	3.4		3.1	3.2	2.7	2.9
HDH	9.4	9.3	10.2			10.4	9.0	8.6		8.2					8.7					9.4	9.4
HDW	8.6	8.2	9.6			8.1	8.5	10.4		9.4					11.1					6.1	8.5
TRH	9.8	9.0	10.2		10.2	10.4	9.6	8.3		8.6				10.9	10.5				9.5	10.4	12.2
TRW	7.1	6.5	8.6		10.8	7.2	5.6	10.0		7.4				11.0	10.0				11.0	7.3	9.4
CPH	4.3	3.6	4.0	3.9	3.8	4.3	3.7	4.0	3.8	3.8	4.1	4.1	4.0	3.8	3.9	3.8		3.7	3.6	3.6	3.1
CPW	3.5	2.9	2.6		2.9	2.9	2.8	3.6		2.8	3.2	3.2		3.2	3.3	3.6		3.2	3.4	2.7	2.4
P1L	10.1	10.3	10.5	11.4	11.1	10.7	10.9	10.7	10.1	9.5	11.1	11.6	11.0	10.7	10.4	10.6	9.8	9.4	9.7	8.9	9.0
P1A	11.7	10.3	11.2	11.7	10.8	11.5	11.8	10.4	11.5	8.8	11.6	11.9	10.6	11.2	11.0	11.2	10.2	10.3	10.7	9.2	9.4
P1B	5.5	5.4	5.6	6.2	5.8	6.4	5.9	5.7	5.8	5.7	6.4	6.1	6.1	6.2	6.5	6.3	5.6	5.3	5.4	6.1	5.7
P1H	7.8	7.9	9.2			8.7	8.7	8.8		8.4					9.9					7.5	8.7
P1I	4.7	5.0	5.0	5.2	5.4	4.3	5.1	5.0	4.4	4.2	4.7	5.5	5.0	4.6	4.5	4.4	4.2	4.1	4.3	3.9	4.1
P1P	8.2	8.6	8.3			8.4	9.3	8.6		8.8					9.6					7.8	7.8
P2L	7.5	7.9	7.9	7.8	9.3	8.4	8.2	7.9	8.5	9.2	8.8	6.7	9.5	11.2	10.5	12.8	14.3	14.0	15.1	14.5	13.4
P2A	3.9	3.6	4.3	4.2	4.2	8.1	4.2	3.6	4.5	4.7	3.5	4.1	4.4	4.3	4.5	4.1	4.0	3.8	4.8	3.5	3.5
P2B	6.7	6.1	6.9			6.7	6.8	6.2		8.0					6.4					6.8	6.6
P2H	2.4	2.2	2.0			2.3	2.3	2.4		2.3					2.3					2.0	2.8
P2I	0.8	1.8	1.0			1.7	1.4	4.0		1.2					4.2					7.6	8.1
P2P	5.9	6.1	5.9			6.4	6.5	6.0		6.8					8.6					11.5	12.2
CLO															2.2					6.5	8.0
CLI											4.1		4.4	6.5	4.4	7.9	10.0	9.4	10.0	9.4	9.4
CLB															0.7					1.9	1.2
D2L	7.8	7.2	7.9	7.8	7.3	7.2	7.9	7.6	7.3	7.4	7.6	8.4	8.1	8.0	7.7	9.3	8.2	7.8	7.7	7.5	7.3
D2A	7.8	7.5	8.3	8.8	7.7	7.2	7.6	7.1	7.4	6.9	7.9	8.1	7.9	7.7	7.4	7.4	7.8	7.1	7.6	7.0	6.7
D2B	5.5	5.4	5.6	6.2	5.8	6.1	5.9	5.5	5.7	5.8	5.8	6.4	6.3	6.2	6.1	6.0	6.4	6.2	5.9	5.7	5.5
D2H	3.9	3.9	4.0	3.9	3.5	3.8	4.2	3.8	4.2	3.8	4.1	4.1	4.0	4.3	4.4	3.9	4.4	4.3	3.8	3.7	4.0
D2I	2.4	1.8	2.3	1.6	1.6	1.2	2.0	2.1	1.7	1.6	1.8	2.0	1.8	1.8	1.9	1.9	1.7	1.6	1.8	1.7	1.6
D2P	3.9	4.3	4.3			4.1	4.2	4.5		4.1					4.8					4.5	4.2
ANL	7.8	6.8	7.6	7.5	7.7	7.2	7.9	6.9	5.9	6.4	7.3	7.0	7.5	7.8	6.8	7.0	7.2	6.7	5.5	6.1	6.5
ANA	3.9	3.6	4.3	4.6	4.2	3.8	4.5	3.6	4.3	3.3	4.4	4.4	4.6	4.6	3.8	3.7	4.0	3.5	4.0	2.9	3.1
ANB	5.9	5.4	5.9	5.9	5.8	5.8	6.2	5.2	6.2	5.3	5.8	5.2	6.1	6.2	5.7	5.6	5.7	5.2	5.3	5.0	5.4
ANH	2.0	2.2	2.3	2.6	2.2	2.0	2.3	1.9	2.4	1.7	2.0	2.3	2.2	2.7	1.9	2.2	2.2	2.2	2.1	1.9	2.4
ANI	2.0	1.4	1.7	1.6	1.9	1.4	1.7	1.7	1.6	1.2	1.5	1.7	1.4	1.6	1.5	1.4	1.5	1.5	1.5	1.5	1.1
ANP	5.5	4.7	5.0			4.9	4.5	4.3		4.3					4.8					4.6	4.8
CDM	32.9	31.8	31.6	32.2	30.9	31.8	32.3	32.6	32.1	30.5	31.5	31.9	30.8	31.5	31.9	30.9	30.7	31.1	31.5	30.1	29.8
CPV	9.8	9.0	7.6	9.1	8.6	8.1	8.5	7.1	8.0	7.2	8.8	8.4	8.5	9.0	8.0	8.3	10.0	8.7	9.5	7.4	7.6
CPL	2.7	2.9	3.0			2.0	3.1	3.3		2.8					3.0					3.4	2.6
CPU	15.6	16.4	16.8		10.2	17.6	18.8	16.9		17.7			9.9		16.4	9.8			10.3	16.8	16.7
CST	5.1	4.7	5.0			4.6	5.6	4.8		3.9					4.2					4.1	4.1
CTR	4.7	6.1	5.0			5.2	5.4	5.2		4.7					6.5					6.1	5.6
CTL	7.8	7.5	7.3	7.5	7.7	8.1	8.7	7.4	7.1	6.5	7.6		6.9	6.9	7.5	7.5	7.6	7.7		7.6	7.6
CFL	9.4	7.9	8.6			7.8	10.4	8.1		7.2					8.0					6.9	6.9
DAO	4.3	4.3	5.0			4.3	4.8	4.3													5.7
DAI	4.3	4.3	5.0			4.3	3.7	4.3													5.5

	PACIFIC OCEAN																			
	TAIWAN																			JAPAN
Source	DAE 882205-1	DAE 882005 03	DAE 881204-01	DAE 882005-01	DAE 881205-01	DAE 881204-03	DAE 881405-01	DAE 880905-01	DAE 881204-02	DAE 880905-02	DAE 882705-01	DAE 882605-01	DAE 881005	DAE 881604	DAE 882705-02	DAE 881305-01	DAE 882505-01	DAE 881204-06	DAE 882805-01	CAS-SU 12620 Holotype
Sex	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
TOT (mm)	592	635	681	725	841	842	871	891	965	980	1003	1005	1025	1030	1073	1073	1100	1130	1185	954
PRC	69.2	69.2	68.8	67.8	69.0	69.1	69.8	67.7	68.9	70.5	69.7	70.6	70.2	70.6	69.7	71.2	69.5	69.2	69.6	68.6
PRN	1.9	2.4	1.8	2.2	2.1	2.0	2.0	2.2	1.7	2.2	1.8	2.0	1.9	2.1	2.1	1.8	1.7	2.3	2.0	2.1
POR	5.1	5.0	4.8	5.1	5.1	4.9	4.9	4.9	4.6	4.7	4.5	4.6	3.9	4.9	4.8	4.4	4.5	4.8	4.5	4.7
POB	5.1	5.2	4.8	5.2	4.9	5.5	4.8	5.4	4.4	4.6	4.2	4.4	4.5	4.7	4.7	4.2	4.9	4.4	3.9	4.9
PSP	12.3	12.9	12.3	12.5	12.0	12.1	11.9	12.6	11.3	11.3	10.9	11.0	11.5	11.4	11.7	11.0	11.1	10.9	10.8	12.9
PGI	15.7	16.0	16.7	16.0	15.2	15.6	14.9	15.7	14.7	14.7	14.0	14.2	14.6	15.0	15.7	14.5	14.0	14.3	13.9	16.1
HDL	19.7	21.1	20.4	19.7	19.5	19.4	18.1	19.7	17.6	17.8	17.8	17.9	18.9	17.8	20.5	17.8	17.1	18.2	18.1	19.1
PP1	19.7	21.1	20.4	19.7	19.5	19.4	18.1	19.7	17.6	17.8	17.8	17.9	18.9	17.8	20.5	17.8	17.1	18.2	18.1	19.1
PP2	39.8	40.9	42.1	40.4	41.1	40.3	40.7	39.0	41.0	42.4	42.1	40.9	40.7	40.6	41.0	41.5	40.0	38.9	42.0	39.3
SVL	43.5	43.6	45.0	44.1	44.3	43.9	45.1	42.3	45.0	46.3	44.8	45.7	43.9	44.6	44.0	45.9	44.0	42.7	45.5	44.0
PAL	53.2	55.1	54.0	53.5	53.9	53.6	55.1	50.7	55.4	55.6	54.1	55.2	55.6	55.5	55.4	56.2	53.7	53.0	55.2	52.9
PD2	49.8	50.8	49.7	48.4	49.9	50.0	50.5	49.3	51.0	51.4	49.8	50.7	51.7	50.9	50.3	51.6	50.1	50.4	50.6	49.5
DCS	14.3	12.4	13.2	12.9	13.4	13.3	11.8	12.3	13.2	14.2	13.8	13.7	12.7	12.9	13.6	13.8	13.3	13.8	13.4	13.7
PPS	16.2	15.7	16.0	16.2	16.4	14.8	17.1	14.8	18.4	16.0	17.8	17.0	16.0	16.8	16.3	17.7	16.4	16.0	18.0	15.5
PAS	6.4	6.1	6.6	6.3	5.6	6.7	6.3	6.2	6.6	6.7	6.5	7.1	8.0	8.3	6.7	7.3	5.5	7.0	6.9	5.8
ACS	10.0	9.0	9.4	9.7	9.3	9.7	9.0	10.9	10.2	9.3	10.3	9.6	9.5	9.9	10.3	9.3	9.5	9.5	10.0	10.4
EYL	3.7	3.6	3.5	3.6	3.1	3.0	3.4	3.4	3.0	3.0	2.9	2.9	2.7	2.6	3.3	3.1	2.8	2.7	3.1	3.9
EYH	2.0	2.2	1.2	1.9	2.0	1.4	1.6	1.3	1.7	1.8	1.7	1.7	1.5	2.1	1.0	1.8	1.4	1.7	2.1	1.7
INO	5.9	6.8	5.3	5.7	5.7	5.7	5.6	5.9	5.2	4.7	4.9	5.1	5.1	5.8	5.0	5.1	5.1	4.7	4.2	4.9
NOW	1.4	1.4	1.3	1.5	1.2	1.1	1.3	1.3	1.1	1.1	1.2	1.2	1.1	1.0	1.2	1.1	1.0	1.0	0.9	0.9
INW	2.5	2.7	2.8	2.5	2.9	2.5	2.5	2.6	2.4	2.2	2.2	2.2	2.2	2.3	2.3	2.3	2.1	2.2	2.1	2.5
ANF	0.5	0.5	0.3	0.4	0.2	0.2	0.3	0.3	0.3	0.3	0.3	0.4	0.2	0.2	0.2	0.3	0.5	0.4	0.3	0.4
SPL	0.5	0.5	0.1	0.3	0.2	0.2	0.2	0.2	0.2	0.1	0.5	0.3	0.2	0.2	0.3	0.5	0.4	0.2	0.4	0.2
ESL	4.4	3.5	3.8	3.3	3.4	3.6	3.6	3.7	3.4	3.7	3.9	3.3	3.4	3.5	3.4	3.3	3.6	3.6	3.4	3.9
MOL	5.2	5.7	5.9	5.1	5.0	6.7	4.8	5.2	4.6	4.7	4.9	4.7	4.0	5.8	4.8	4.3	5.0	6.6	4.6	6.8
MOW	6.8	6.9	6.8	6.9	6.1	8.1	5.9	7.4	6.4	5.9	7.0	7.4	5.9	7.7	5.7	6.8	6.2	6.1	7.2	6.7
ULA	1.7	2.0	2.8	1.8	1.8	2.4	1.4	2.1		1.7	1.7	1.8	1.6	2.4	1.7	1.9	1.7	2.2	1.4	2.3
LLA	1.9	0.8	2.2	1.1	1.2	1.9	2.1	0.9		1.1	1.0	0.9	1.1	1.4	1.0	1.4	1.0	1.3	0.9	1.7
GS1	7.6	5.8	6.8	6.6	7.6	6.5	6.0	7.0	6.2	7.1	7.0	6.7	6.4	7.1	6.7	7.9	6.8	6.5	8.3	5.6
GS2	7.3	5.8	6.5	6.2	6.9	6.3	5.7	6.8	6.1	6.9	7.3	6.5	6.3	6.7	6.4	7.7	6.7	6.4	7.8	5.5
GS3	6.8	5.7	5.9	5.8	6.4	6.2	5.6	6.4	5.7	6.4	7.1	6.0	6.0	6.3	5.8	7.3	6.5	6.0	7.2	5.1
GS4	5.9	5.4	5.3	5.2	5.7	5.6	5.2	5.2	5.2	5.9	6.3	5.4	5.6	5.9	5.3	6.5	5.9	5.8	6.4	5.0
GS5	5.1	4.7	4.7	4.7	4.9	4.9	4.6	4.7	4.5	5.0	6.6	4.8	4.9	5.0	4.8	5.6	5.0	5.4	5.7	4.4
GS6	4.1	3.9	4.1	3.7	4.2	4.0	3.8	4.0	3.9	4.3	4.6	3.6	4.0	4.5	3.8	4.5	4.1	4.3	4.7	4.2
GS7	3.4	3.1	3.2	2.8	2.9	3.2	3.0	3.4	2.9	3.1	3.2	3.0	3.1	3.5	3.0	3.4	3.0	3.6	3.5	3.4
HDH	8.1	8.3	10.2	7.7	11.5	10.4	9.5	12.6	10.2	10.4	12.1	10.3	10.1	10.9	11.7	10.8	10.1	10.6	11.8	7.9
HDW	7.1	9.8	8.8	9.0	9.6	8.6	9.2	8.9	9.6	9.0	9.5	9.8	7.5	8.5	8.0	9.3	9.5	7.3	10.0	10.4
TRH	9.8	9.1	11.4	10.0	13.7	12.2	12.5	16.6	13.7	12.8	15.1	13.2	12.7	13.3	15.8	13.2	13.8	12.0	14.1	
TRW	5.2	8.7	10.4	9.9	11.8	9.4	10.3	11.4	12.1	10.5	11.7	11.4	7.5	9.8	13.9	11.2	12.4	7.6	13.5	
CPH	3.4	3.9	3.8	3.7	4.3	4.0	4.0	4.0	3.9	3.7	3.6	3.9	3.7	3.9	3.9	3.9	3.7	4.0	3.7	4.0
CPW	2.7	3.0	3.1	3.0	3.6	3.2	3.0	2.9	3.3	3.1	3.1	2.9	3.2	3.1	3.3	3.2	3.2	3.1	3.3	2.8
P1L	10.3	10.7	10.1	10.0	9.8	9.6	9.5	9.8	9.4	9.0	9.3	9.2	9.0	9.1	9.7	9.7	9.6	9.7	9.5	9.7
P1A	10.8	12.1	11.3	10.8	10.2	11.4	10.2	10.2	10.6	10.8	10.1	10.1	10.4	9.7	11.2	10.0	10.3	10.3	9.5	11.0
P1B	5.9	6.0	6.2	6.3	6.1	5.7	6.1	6.3	5.7	6.0	6.3	5.9	5.9	6.0	6.2	6.2	6.1	5.2	6.0	6.0
P1H	10.1	10.5	9.4	9.5	9.6	9.7	9.1	9.3	9.4	8.8	8.8	8.4	9.4	8.1	10.0	9.6	8.9	8.6	8.4	9.1
P1I	4.4	4.9	4.3	4.0	4.0	4.0	4.2	4.2	4.2	3.6	3.3	3.5	3.4	3.6	3.8	4.0	3.9	4.7	3.8	4.7
P1P	7.9	7.6	7.8	7.9	8.1	7.7	7.2	8.5	7.8	8.2	6.8	6.8	7.1	7.2	7.5	7.5	7.1	7.9	7.1	8.8
P2L	8.1	8.5	8.5	8.1	8.7	8.1	8.5	8.2	8.8	7.3	7.9	7.8	8.4	8.3	9.3	9.0	8.5	9.6	7.9	9.6
P2A	3.7	4.3	4.3	3.7	4.2	4.0	3.9	3.9	4.1	3.9	3.6	3.6	4.4	3.9	4.3	3.9	3.6	4.2	3.8	3.9
P2B	7.1	6.8	6.6	6.5	6.8	7.0	7.3	7.0	7.8	6.4	6.9	6.5	7.2	7.3	8.3	7.7	6.6	8.1	7.2	8.5
P2H	2.4	2.7	2.1	2.9	3.0	2.9	2.5	3.7	3.1	2.8	2.4	2.8	2.8	2.4	3.3	3.0	2.6	2.8	3.0	2.8
P2I	1.0	1.3	1.6	1.9	1.5	1.1	1.1	1.7	1.1	1.3	1.1	1.1	1.2	1.1	1.1	1.0	1.7	1.5	1.4	1.3
P2P	5.7	6.0	4.0	6.9	7.1	6.2	6.3	7.2	7.0	6.4	6.6	6.3	6.3	6.5	7.4	7.1	7.3	7.3	7.2	7.9
CLO																				
CLI																				
CLB																				
D2L	7.1	7.6	7.8	8.0	8.3	7.8	7.7	7.5	7.6	7.4	7.7	7.3	7.4	7.7	7.4	7.5	7.9	8.4	7.9	8.5
D2A	6.6	6.5	7.3	7.2	7.5	7.8	7.0	7.2	7.0	7.0	7.2	6.3	6.3	7.1	7.2	7.1	7.4	7.8	7.3	7.3
D2B	5.7	5.7	6.0	6.2	6.7	6.3	6.0	5.8	6.0	6.0	6.0	5.5	5.5	6.4	5.4	6.2	6.6	6.9	6.5	6.1
D2H	4.1	4.3	4.1	4.3	4.5	4.0	4.2	4.8	4.5	4.3	3.8	4.1	4.2	3.9	4.6	4.2	4.1	4.5	4.3	4.4
D2I	1.7	1.7	1.8	1.7	1.5	1.54	1.5	1.5	1.5	1.5	1.2	1.3	1.3	1.6	1.7	1.5	1.5	1.8	1.5	2.0
D2P	3.5	4.1	3.8	4.4	4.5	4.0	3.7	4.3	4.4	4.1	3.8	4.0	3.9	4.2	4.4	4.2	4.2	4.8	4.8	5.5
ANL	6.9	6.9	7.6	7.4	7.5	7.2	7.0	7.1	7.0	7.0	6.7	6.5	6.9	7.3	7.1	7.1	7.2	7.6	6.8	8.0
ANA	3.9	3.5	4.1	3.4	3.7	3.9	3.8	3.5	3.3	3.6	3.2	3.0	3.7	3.8	5.6	3.4	3.5	3.9	3.5	3.6
ANB	5.2	5.8	6.2	5.9	5.7	5.7	5.7	5.7	5.6	5.8	5.5	5.6	6.0	6.2	3.8	5.9	5.9	5.9	5.3	6.3
ANH	2.0	2.0	2.1	2.3	2.3	2.1	2.0	2.5	1.9	2.1	2.1	1.8	2.0	2.0	2.6	2.4	2.0	2.4	2.4	2.2
ANI	1.7	1.3	1.5	1.4	1.1	1.2	1.3	1.3	1.5	1.1	1.2	1.1	1.1	1.2	1.7	1.2	1.3	1.7	1.4	1.6
ANP	4.2	4.9	4.8	5.1	5.0	4.4	4.5	5.4	4.9	4.5	4.1	4.9	4.7	4.7	4.9	4.9	4.7	5.6	5.1	5.8
CDM	30.0	31.1	30.2	31.4	30.4	30.5	30.6	32.3	30.4	29.8	30.2	29.6	29.5	29.4	29.2	28.4	30.5	30.9	29.5	31.7
CPV	7.4	7.9	7.9	7.9	7.4	8.3	7.5	8.1	7.2	8.0	7.8	6.9	7.1	7.2	8.5	7.5	7.5	7.9	7.7	7.8
CPL	2.5	3.0	3.2	3.2	3.0	3.3	3.7	2.9	2.9	3.4	3.0	3.5	3.8	3.9	4.5	2.9	2.5	3.7	3.6	5.1
CPU	16.5	16.8	16.0	18.3	16.2	16.8	17.2	17.8	16.9	16.4	16.4	16.5	16.0	15.7	15.0	15.6	16.9	16.9	16.2	16.4
CST	4.6	4.3	4.6	4.0	4.6	4.4	3.7	4.3	4.4	3.6	3.8	3.8	3.8	3.7	4.3	3.9	4.2	3.7	4.1	4.6
CTR	5.2	5.4	5.4	5.0	5.5	5.5	4.8	5.6	4.9	5.3	5.0	5.3	5.8	5.0	5.6	4.7	5.2	5.9	5.7	5.3
CTL	7.3	6.9	7.5	7.0	7.4	7.1	6.1	7.4	7.0	6.8	6.8	7.1	7.3	6.4	7.6	6.5	7.5	7.2	7.3	7.2
CFL	7.1	7.7	7.2	7.6	6.9	7.6	7.1	7.7	6.7	7.1	6.3	6.6	6.9	6.8	7.0	7.0	7.0	7.0	6.3	6.8
DAO	3.7	3.8	3.8	4.6	4.8	3.3	4.0	3.0	4.6	4.1	4.1	4.5	4.0	4.9	5.4	4.2	4.0	6.0	5.0	2.6
DAI	3.9	3.8	3.7	3.4	4.3	3.6	3.6	2.8	4.5	3.9	4.3	4.1	4.0	4.5	5.2	4.2	4.0	5.0	4.9	2.8

	TAIWAN										
Source	DAE 881204-05	DAE 882005-05	DAE 881204-04	DAE 880904-01	DAE 882005-04	DAE 882005-02	DAE 881104-01	DAE 881104-02	DAE 880705	DAE 880605	DAE 880905-03
Sex	M	M	M	M	M	M	M	M	M	M	M
TOT (mm)	674	690	727	746	750	765	780	795	865	955	955
PRC	70.0	69.1	68.5	69.0	68.4	69.9	67.9	68.1	69.3	69.0	69.1
PRN	1.8	2.2	1.9	1.9	2.0	1.8	1.9	2.0	2.2	2.1	1.7
POR	4.7	4.9	4.5	4.8	4.7	4.8	4.9	4.3	5.0	5.0	4.3
POB	5.2	5.5	4.4	4.7	5.1	5.1	5.1	5.2	5.1	5.0	4.6
PSP	12.1	12.1	12.1	11.9	12.4	12.2	12.4	12.4	12.3	12.2	10.9
PGI	15.5	14.7	15.2	15.8	15.3	15.9	16.0	15.4	15.7	16.1	14.4
HDL	19.8	19.5	19.8	19.8	19.2	19.7	18.8	18.8	18.9	19.8	18.8
PP1	19.8	19.5	19.8	19.8	19.2	19.7	18.8	18.8	18.9	19.8	18.8
PP2	41.3	39.1	39.0	40.2	39.6	41.0	39.7	39.4	38.9	38.6	39.0
SVL	45.4	43.0	43.0	43.8	43.6	44.4	45.5	43.7	43.1	41.8	42.9
PAL	54.3	53.1	54.3	54.5	53.7	55.2	52.6	54.7	53.1	53.1	53.9
PD2	49.5	49.2	48.9	49.3	48.9	51.2	47.4	50.1	50.5	49.9	49.4
DCS	13.9	12.7	14.0	13.0	13.2	12.1	13.5	12.8	13.4	13.9	12.9
PPS	16.1	15.9	15.1	15.2	15.0	15.9	15.1	15.3	15.0	13.1	15.0
PAS	8.0	8.7	8.3	7.9	8.0	8.8	7.2	7.4	8.2	8.0	8.9
ACS	9.8	9.7	8.9	10.0	8.5	9.2	10.2	9.9	9.5	9.9	9.6
EYL	3.7	3.8	3.3	3.5	3.2	3.1	3.5	3.4	3.5	3.2	3.0
EYH	1.8	1.6	1.7	2.0	1.7	2.1	1.8	1.4	1.8	1.8	1.7
INO	5.8	6.8	6.1	5.9	5.2	5.5	5.9	5.8	5.1	5.2	5.0
NOW	1.3	1.2	1.2	1.5	1.1	1.2	1.2	1.3	1.3	1.3	0.9
INW	2.7	2.3	2.6	2.7	2.4	2.6	2.6	2.8	2.4	2.4	2.2
ANF	0.4	0.4	0.3	0.3	0.3	0.4	0.3	0.3	0.3	0.3	0.4
SPL	0.1	0.3	0.3	0.3	0.3	0.5	0.3	0.3	0.2	0.2	0.2
ESL	3.7	3.2	3.9	4.0	3.3	3.4	4.0	4.0	3.8	3.9	3.5
MOL	5.5	4.9	5.2	4.7	4.7	5.4	5.5	5.2	5.8	6.0	5.0
MOW	7.4	6.4	6.6	6.7	6.3	6.3	7.3	6.8	6.9	6.1	5.8
ULA	2.4	1.7	2.2	2.1	2.0	2.5	3.2	2.8	1.2	1.8	1.7
LLA	1.6	1.4	1.4	1.6	1.3	1.3	1.3	1.6	0.8	1.6	1.4
GS1	6.2	6.8	6.1	7.2	6.4	6.9	6.5	7.3	6.2	6.7	6.8
GS2	5.9	6.7	5.8	7.0	6.3	6.1	6.3	7.0	6.0	6.3	6.4
GS3	5.6	6.4	5.6	6.6	5.9	5.9	5.5	6.7	5.7	5.7	6.2
GS4	5.0	5.4	5.1	5.9	5.5	5.4	5.0	5.8	5.2	5.1	5.5
GS5	4.5	4.6	4.5	5.0	4.7	4.7	4.5	5.3	4.4	4.7	4.8
GS6	3.9	4.1	4.0	4.2	4.0	4.2	3.7	4.5	3.8	4.0	3.9
GS7	2.8	3.0	2.9	3.1	3.3	3.1	2.8	3.4	2.9	3.1	2.7
HDH	9.6	8.4	9.5	10.0	8.8	9.8	9.4	10.1	8.6	10.0	10.2
HDW	9.2	9.3	9.9	9.7	8.4	9.8	9.7	9.3	7.4	8.5	8.9
TRH	10.8	9.6	11.4	13.2	9.2	11.3	11.7	12.9	10.1	11.8	11.7
TRW	10.9	8.6	10.3	11.3	8.4	9.7	10.1	11.1	7.3	9.2	9.2
CPH	4.0	3.8	4.1	3.9	4.0	3.8	3.8	4.4	3.6	3.9	3.4
CPW	3.0	3.0	2.9	3.5	3.3	3.1	3.2	3.5	2.9	3.1	3.0
P1L	9.8	9.7	10.1	9.9	9.6	9.5	9.6	9.6	9.5	9.2	8.7
P1A	10.8	10.4	11.2	10.7	10.9	10.3	10.6	10.1	10.8	9.9	10.1
P1B	6.1	5.5	5.9	6.3	6.0	5.9	6.3	6.0	5.3	5.8	5.2
P1H	9.9	9.1	9.8	9.0	9.1	9.4	8.8	8.6	9.2	9.1	8.8
P1I	4.3	4.3	4.3	4.2	3.9	4.1	3.8	4.5	4.5	3.8	3.6
P1P	8.6	8.3	7.2	8.2	7.5	8.4	8.6	7.9	7.3	8.6	7.5
P2L	11.2	9.71	12.2	13.4	13.4	12.2	13.7	13.5	13.7	14.1	13.8
P2A	4.0	3.5	4.0	4.3	3.9	3.7	3.8	3.9	4.3	4.4	4.2
P2B	6.1	5.2	6.7	6.6	6.0	7.5	6.0	7.2	6.2	6.8	6.1
P2H	1.9	2.3	2.1	2.3	2.4	2.7	2.7	2.4	2.7	2.7	2.7
P2I	5.3	4.5	5.4	7.4	7.5	5.6	7.6	6.9	7.6	8.0	8.5
P2P	8.5	7.7	9.4	11.3	10.8	10.0	11.1	10.8	11.2	12.3	12.4
CLO	3.6	4.1	5.6	8.2	6.4	5.8	7.4	7.9	6.9	6.9	6.0
CLI	6.1	6.2	8.0	9.5	8.7	8.2	9.2	8.9	9.0	8.7	8.2
CLB	0.7	0.7	1.0	1.1	1.1	1.0	1.4	1.1	1.0	1.4	0.8
D2L	7.7	7.4	7.6	7.4	7.5	7.7	7.7	7.4	7.7	7.0	7.9
D2A	6.7	7.0	7.4	6.6	6.8	7.1	7.6	6.8	7.3	6.4	7.5
D2B	5.9	5.8	5.9	5.8	6.0	6.3	6.2	5.3	6.4	5.5	6.3
D2H	3.9	4.2	4.3	3.8	3.9	4.2	3.7	4.0	4.4	4.2	3.9
D2I	1.5	1.3	1.8	1.6	1.5	1.4	1.3	1.5	1.7	1.4	1.4
D2P	3.6	4.1	3.9	4.3	4.1	3.9	4.0	4.5	3.9	4.5	4.6
ANL	7.0	6.5	7.2	7.4	6.5	6.7	7.3	6.9	6.0	7.0	7.0
ANA	3.9	3.5	3.9	4.2	3.6	2.9	3.5	3.4	3.8	3.6	3.7
ANB	5.8	5.1	5.8	6.0	5.2	5.5	5.8	5.4	5.8	5.9	5.3
ANH	1.9	1.9	1.8	2.3	2.1	2.0	2.2	2.0	2.2	2.4	2.3
ANI	1.3	1.4	1.4	1.5	1.3	1.3	1.3	1.5	0.3	1.5	1.5
ANP	4.2	4.3	4.1	4.6	4.5	4.7	4.7	4.5	3.9	5.1	4.8
CDM	30.5	31.0	31.9	31.3	43.7	31.2	31.7	31.1	31.2	31.4	31.4
CPV	7.9	7.2	7.4	8.2	8.3	8.0	8.1	7.7	8.2	7.9	8.1
CPL	3.1	2.9	3.0	3.1	3.3	3.0	3.3	3.3	3.5	3.4	3.4
CPU	17.0	17.3	18.2	17.5	17.6	17.5	17.3	17.2	17.2	17.0	17.1
CST	4.9	4.2	4.1	4.0	4.1	4.3	4.6	4.4	4.2	4.3	4.3
CTR	5.0	4.8	5.5	5.8	5.2	5.2	5.4	5.7	5.3	5.2	5.2
CTL	7.4	6.7	7.0	7.2	6.9	6.5	7.4	7.4	6.9	7.5	7.4
CFL	7.4	6.7	6.9	7.6	7.2	7.5	7.2	6.9	7.3	7.3	7.2
DAO	4.9	4.9	4.8	4.6	4.0	4.8	4.4	4.4	5.2	4.8	6.0
DAI	4.9	4.2	4.8	4.6	3.2	4.1	4.0	4.4	4.6	4.7	4.8

	PACIFIC OCEAN									
	AUSTRALIA					NEW ZEALAND				
Source	Garrick & Paul 1971	WAM P 29037-001	Garrick & Paul 1971	WAM P 25782-001	Garrick & Paul 1971	Garrick & Paul 1971	Garrick & Paul 1971	Garrick & Paul 1971	Garrick & Paul 1971	Garrick & Paul 1971
Sex	F	F	F	F	M	F	F	F	F	M
TOT (mm)	695	700	822	870	845	805	1100	1100	1365	856
PRC	68.6	69.0	69.1	69.5	69.7	68.3	70.1	69.5	71.2	68.7
PRN	2.2	2.6	2.2	2.8	1.7	2.0	1.8	1.8	2.0	1.8
POR	4.9	4.9	4.6	5.2	4.5	4.0	4.0	3.7	4.0	4.2
POB	5.3	5.6	5.4	5.4	5.1	4.7	4.7	4.8	4.4	4.2
PSP		13.1		13.1						
PGI	15.5	17.0	13.7	16.3	13.1	15.5	15.3	15.7	14.7	15.5
HDL	21.0	20.4	19.3	20.0	18.2	19.6	18.3	18.6	18.1	19.5
PP1	21.0	20.4	19.3	20.1	18.2	19.6	18.3	18.6	18.1	19.5
PP2	40.3	40.0	42.5	41.8	40.6	40.7	42.3		40.8	40.0
SVL		44.3		44.5						
PAL	54.0	53.6	55.4	54.0	56.2	54.0	55.5	55.5	55.1	55.8
PD2	50.5	50.3	51.2	48.9	50.3	50.7	50.5	50.5	50.7	49.9
DCS		13.6		14.6						
PPS		15.3		16.9						
PAS		6.4		7.5						
ACS		9.0		10.2						
EYL	3.9	4.0	4.0	3.9	4.0	3.7	3.5	3.4	3.7	
EYH		2.0		2.0						
INO		6.0		4.3						
NOW		1.0		1.3						
INW	3.0	2.9	2.9	2.9	3.0	2.5	2.7	2.8	2.4	2.7
ANF		0.3		0.3						
SPL		0.1		0.1						
ESL		4.1		3.9						
MOL	6.0	6.1	6.0	5.4	6.0	6.3	5.9	6.2		
MOW	6.5	6.1	6.8	4.9	6.7	5.8	6.2	5.8		
ULA		3.3		2.4						
LLA										
GS1	7.3	6.3	6.7	7.8	7.5	7.2	6.8	7.7	7.1	8.2
GS2		5.7		6.3						
GS3		5.3		5.7						
GS4	5.9	5.0	5.1	5.2	6.4	5.2		5.5		5.8
GS5		4.6		4.5						
GS6		3.7		3.7						
GS7	3.5	2.9	2.7	2.9	3.2	2.9	3.0	3.0	2.6	2.9
HDH	9.9	8.7	8.8	10.0	9.1	9.9	11.2	10.9	8.8	9.3
HDW	10.1	9.0	9.1	7.0	9.1	8.2	8.2	9.0	7.3	8.8
TRH		9.4		10.0						
TRW		9.9		7.6						
CPH		4.3		3.4						
CPW		2.7		2.0						
P1L		10.4		10.1						
P1A	11.4	11.1	11.1	10.6	11.4	10.3	10.3	10.0	8.8	10.2
P1B	6.2	6.4	6.2	6.3	6.0	5.7		5.9		5.8
P1H		5.1		8.5						
P1I		4.4		6.3						
P1P	8.6	8.6	8.3	8.9	8.8	9.3	9.1	8.6		9.3
P2L		9.3		9.5						
P2A	4.5	3.7	4.1	4.3	4.5	4.3	3.9	4.2	4.8	3.7
P2B	7.9	8.1	7.5	8.7	7.0	7.5		7.5		7.0
P2H		2.9		2.8						
P2I		1.0		0.8						
P2P	6.0	7.3	6.8	6.4	9.0	6.8	6.6	6.5	6.8	10.2
CLO										
CLI										
CLB										
D2L		7.3		8.0						
D2A		7.0		7.1						
D2B	6.2	5.7	6.4	6.6	6.3	5.8	7.3	7.1	7.3	5.8
D2H	4.6	4.3	4.0	4.3	4.1	4.0	3.6	4.3	3.5	4.0
D2I	1.7	1.6	1.7	1.6	1.7	1.5		1.7		1.5
D2P		4.3		4.5						
ANL		6.9		7.1						
ANA		3.1		3.7						
ANB	5.7	5.7	6.0	5.9	5.6	5.6	6.0	6.3	6.2	5.5
ANH	2.9	1.9	2.6	2.2	2.6	2.2	2.3	2.4	2.5	2.0
ANI	1.4	1.1	1.3	1.4	1.4	1.2		1.4		1.2
ANP		5.1		4.5						
CDM	31.7	30.1	31.0	28.5	30.3	31.7	29.7	30.3	28.6	31.0
CPV	7.9	7.6	7.9	8.0	7.9	8.1	7.5	7.9	7.7	8.0
CPL		2.6		4.3						
CPU		17.1		17.0						
CST		4.7		4.6						
CTR		6.0		5.6						
CTL		7.9		7.6						
CFL		7.9		7.6						
DAO		4.3		5.2						
DAI		3.7		3.4						

TABLE 3.3 Proportional measurements of *Hexanchus griseus*, expressed as a percentage of total length.

	NORTH ATLANTIC AND ADJACENT AREAS				SOUTHEASTERN ATLANTIC AND INDIAN OCEANS																		
	GULF OF MEXICO	FRANCE	ITALY	IRELAND																			
Source	Branstetter & MacE 1986	BM 1866.5.28.5	USNM 204251	BM 1928.9.18.1	RUSI 6180	ORI 2598	DAE 870309-03	DAE 870509-03	DAE 870409-04	DAE 870304-04	DAE 870509-02	DAE 870409-05	RUSI 6244	ORI 2448	DAE 870509-01	DAE 870409-03	DAE 870209-01	DAE 870209-02	ORI uncat.	DAE 872105-01	DAE 881202-01	ORI 2350	DAE 882611
Sex	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
TOT (mm)	3250	675	610	675	680	707	730	776	783	788	835	910	960	975	1005	1010	1588	1660	1715	1920	2000	2336	3330
PRC	72.0	65.2	66.4	63.4	65.8	65.3	66.3	65.7	65.9	65.8	66.7	67.5	66.6	66.4	69.1	66.6	69.4	68.6	69.0	69.2	68.7	69.6	72.4
PRN		1.5	1.8	1.5	3.2	2.5	1.0	1.0	1.1	1.4	2.5	1.4	3.4	2.4	0.6	1.6	2.0	1.3	2.8	1.1	1.4	2.1	2.1
POR	4.5	4.0	4.4	3.9	5.6	6.1	4.7	4.6	4.2	4.8	5.0	5.4	5.1	5.1	4.0	5.0	4.4	4.5	5.8	3.9	5.3	5.2	5.3
POB	4.3	4.1	4.3	3.7	6.2	4.1	5.9	3.7	4.2	4.2	4.2	4.7	6.3	3.7	3.7	3.8	6.2	3.8	4.3	4.3	4.7	3.9	5.6
PSP		10.7	12.1	10.7	12.0		12.8	11.7	11.8	11.9	11.6	12.0	12.7		10.7	11.7	11.9	11.3	11.4	10.9	11.9		12.0
PGI		15.4	15.4	16.1	15.5	15.8	16.7	15.5	15.7	15.9	15.0	15.7	16.3	15.8	14.4	14.8	16.3	15.0	15.4	19.2	15.7	14.7	15.6
HDL		19.7	18.5	21.9	18.6	18.2	19.7	19.0	18.9	20.0	18.9	20.0	18.2	18.9	19.1	19.8	20.4	18.6	17.3	19.2	20.0	18.4	15.6
PP1	20.0	19.7	18.5	21.9	18.6	18.2	19.7	19.0	18.9	20.0	18.9	20.0	18.2	18.9	19.1	19.8	20.7	18.6	17.3	19.6	20.0	18.4	19.2
PP2	49.2	42.7	40.5	39.3	42.0	42.4	43.6	43.4	43.4	42.8	43.3	45.8	43.8	44.0	45.2	43.2	45.0	45.6	46.3	47.1	47.5	48.3	46.5
SVL		46.2	45.4	43.7	46.7		46.9	48.3	47.8	45.6	48.3	48.7	50.6		48.7	48.6	50.2	50.8		53.9	52.6		5.3
PAL	60.8	55.3	54.6	51.4	54.4		55.8	55.4	56.5	55.0	55.9	57.6	55.4		58.2	56.9	57.3	59.3		60.9	59.0		61.9
PD2	60.3	51.1	50.0	51.6	51.9	51.0	52.1	52.1	52.3	51.7	52.3	53.9	50.0	50.2	53.9	53.9	52.8	54.8	53.4	54.7	55.5	55.0	56.5
DCS	7.2	7.7	8.5	7.4	7.6	7.9	6.8	6.8	8.0	8.2	7.2	7.6	8.9	8.8	8.5	6.7	8.6	7.9	8.3	7.5	8.8	7.9	8.9
PPS	18.2	17.2	16.4	12.7	17.6		17.2	18.4	18.3	16.6	19.4	17.1	18.3	18.7	19.9	17.6	19.7	19.1	21.1	20.5	20.0	23.0	23.4
PAS		5.5	4.4	7.4	6.2		5.5	5.9	5.7	5.7	6.6	5.9	5.3		6.1	6.0	6.8	6.6		5.8	5.3		7.8
ACS		3.9	4.9	3.9	6.0		4.7	4.6	4.7	4.4	4.0	5.2	4.9	4.6	4.7	4.1	4.4	5.3	4.5	3.9	5.0	4.7	5.2
EYL	1.3	3.6	3.4	2.8	3.4	3.4	3.0	3.4	3.3	3.0	3.8	2.9	3.1	3.2	3.4	3.1	2.5	1.9	2.3	1.9	1.9	1.9	1.8
EYH		1.5	1.1	1.9	1.9		2.3	2.1	2.2	1.4	1.0	2.0	1.9		1.7	1.5	1.4	1.6		1.7	1.5		1.2
INO		8.3	7.2	9.2	10.2		9.3	8.6	9.8	8.6	8.6	9.0			7.9	8.1	9.6	9.0		7.6	9.1		8.6
NOW		1.2	1.3	1.3	1.0	1.4	1.2	0.9	1.3	1.1	1.2	1.3	0.9	1.2	1.0	1.2	1.1	1.1	1.2	0.7	1.1	1.1	1.2
INW	4.6	4.6	4.8	4.6	5.0		4.5	4.0	4.2	4.4	4.0	4.7	4.9	3.9	4.0	4.3	4.3	4.4	4.4	4.3	4.8	4.5	4.6
ANF		0.6	0.5	0.6	0.7		0.7	0.4	0.5	0.9	0.6	0.8	0.5		0.5	0.4	0.6	0.5		0.5	0.6		0.5
SPL		0.3	0.2	0.6	0.1	0.4	0.4	0.4	0.6	0.6	0.4	0.3	0.3	0.8	0.4	0.4	0.5	0.3	0.4	0.2	0.3	0.5	0.3
ESL		4.6	4.3	4.6	5.0		4.1	4.1	4.0	4.2	3.5	4.5	4.9	5.1	3.6	4.6	3.9	4.8		4.6	4.6		4.7
MOL		5.3	4.9	5.9	6.2		6.4	5.0	6.0	5.8	5.0	4.8	5.6		5.5	4.9	5.0	5.5	5.9	7.3	5.0		5.6
MOW		8.7	10.5	11.4	13.5	10.3	12.0	11.5	10.9	11.6	10.7	11.2	13.1	13.7	10.1	12.3	13.0	11.4	9.8	13.5	10.7	11.9	11.7
ULA		1.5	1.6	2.1	1.8		2.9	2.6	2.6	2.8	1.9	2.6	2.5		2.4	2.5	2.7	2.7		2.5	2.1		1.8
LLA		1.9	2.5	2.7	2.6		2.6	3.0	2.9	2.4	3.1	3.4	2.7		3.0	3.1	2.5	3.0		2.6	2.9		2.7
GS1	7.2	4.9	6.6	7.0	7.1	7.5	7.1	5.3	5.6	6.1	5.0	7.7	7.0	7.1	7.1	6.6	7.3	8.1	7.6	7.1	8.5	6.4	7.2
GS2	6.5	4.7	6.1	6.1	6.6	7.2	6.3	4.8	5.2	5.6	4.7	7.1	6.8	6.4	6.6	5.9	7.1	7.8	7.8	6.9	7.8	6.5	7.2
GS3	5.8	4.6	5.9	5.3	6.3	6.5	5.8	4.5	4.9	5.1	4.3	6.8	6.4	6.2	5.8	5.7	6.9	7.1	6.8	6.8	7.6	6.2	6.5
GS4	5.4	4.1	5.4	4.9	5.9	5.7	5.1	4.3	4.5	5.1	4.1	6.4	5.7	5.6	5.5	5.5	6.5	6.7	6.1	6.7	7.0	6.0	6.5
GS5	4.9	3.9	4.8	4.7	5.0	5.1	4.7	4.1	4.2	4.4	3.8	5.9	5.4	5.1	5.0	5.1	5.8	6.0	5.4	6.5	6.1	5.6	6.0
GS6	4.0	3.7	4.4	4.1	4.1	4.4	4.2	4.0	4.0	4.1	3.6	5.2	5.0	5.0	4.8	4.7	5.5	5.2	4.5	5.9	5.2	4.9	5.3
HDH		7.6	10.0	10.7	9.6		7.3	6.1	6.4	9.0	6.2	7.7	10.9		6.0	11.1	9.6	8.3		9.1	8.2		12.9
HDW		11.1	9.5	13.2	13.3		13.4	13.5	14.1	14.0	13.8	13.2	14.4		14.5	14.3	14.9	16.2		16.6	16.5		14.7
TRH		8.4	12.0	12.7	11.9		6.2	6.4	6.4	11.9	6.2	7.1	12.7	12.3	6.0		9.8	9.3		9.3	8.8		15.8
TRW		9.9	7.7	11.7	10.7		13.8	12.2	14.1	13.8	13.8	12.0	12.6	14.1	14.1	14.9	13.4	14.7		15.6	17.2		15.0
CPH		3.4	3.6	4.1	3.7	3.5	3.3	3.1	2.8	3.6	3.4	3.1	4.3	4.2	2.9	3.1	3.1	3.5	4.7	3.6	4.1	4.5	4.9
CPW		2.4	2.8	2.8	2.8	2.8	2.1	2.3	2.4	1.9	1.9	2.2	2.9	3.1	2.5	2.3	2.2	2.3	3.7	2.3	2.6	3.6	3.0
P1L	12.8	13.5	11.8	14.1	11.3	12.4	11.5	11.5	11.6	11.2	12.2	11.6	11.7	12.8	12.2	11.7	12.0	12.6	13.1	13.1	13.0	13.1	11.4
P1A	12.3	15.6	13.4	15.3	13.0	12.8	13.2	12.1	12.5	12.6	13.6	13.0	12.5	12.8	13.7	12.7	12.5	13.4	13.1	13.4	14.1	13.3	14.3
P1B	8.9	8.1	7.0	7.9	6.8	7.1	7.3	6.8	7.4	7.0	6.8	7.0	7.8	7.2	7.1	7.1	6.5	7.2	7.5	8.5	8.4	7.8	7.8
P1H		8.7	9.8	9.2	10.2		10.1	9.3	9.5	9.6	9.8	10.4	9.6		10.4	10.3	11.2	9.9		9.6	9.5		11.0
P1I	3.8	5.9	5.2	6.1	4.9	5.4	5.8	5.2	4.3	4.9	4.3	6.2	4.5	5.3	5.6	5.0	5.0	5.4	5.5	4.9	4.6	5.0	3.9
P1P		7.9	8.2	9.6	10.0		8.5	7.9	7.9	8.6	9.0	9.2	8.8		8.4	9.8	10.2	9.3		9.4	10.2		9.6
P2L		10.7	9.3	11.7	9.9	9.2	9.5	10.1	10.0	10.0	10.2	9.7	11.7	11.4	10.7	10.6	12.2	12.0	12.8	12.3	12.3	13.2	15.5
P2A	5.5	6.2	5.4	5.6	6.0	5.9	4.9	5.4	5.1	5.2	5.0	5.5	6.7	6.1	5.7	5.6	6.2	6.3	6.8	5.7	6.3	6.8	8.0
P2B		7.1	7.5	7.6	7.1		6.8	7.0	7.4	7.0	7.1	6.6	7.9		6.2	7.3	8.1	8.6		9.1	6.9		9.2
P2H		3.4	3.6	3.7	3.1		2.9	3.1	2.8	3.0	3.0	3.7	3.0		3.7	3.8	4.0	3.9		3.8	4.3		5.4
P2I		3.4	2.0	4.4	2.6		2.6	3.0	2.6	3.2	3.1	3.2	4.0		3.7	3.8	4.4	4.8		4.0	5.4		6.6
P2P	11.8	6.4	6.1	9.0	6.2		6.6	7.6	6.9	7.0	6.8	7.0	7.9		8.1	8.1	9.4	9.4		9.6	9.5		11.6
CLO		1.3		1.9	0.9		1.4	1.5	1.7	1.5	1.3	1.2	0.9		1.7	1.6	2.4	2.0		2.2	2.3		7.8
CLI	8.5	3.9		3.9	2.4	3.7	3.8	4.6	4.0	4.2	4.1	4.8	2.6	5.1	4.6	4.7	5.1	4.9	5.4	4.1	5.0	7.5	9.2
CLB		0.3		0.4	0.3		0.4	0.5	0.5	0.5	0.4	0.4	0.4		0.5	0.8	0.6	0.6		0.5	0.9		1.3
D2L	10.2	8.6	9.0	9.2	8.7	10.0	8.4	8.5	8.0	8.5	8.3	8.2	9.3	9.8	8.6	8.7	9.3	9.2	10.6	8.7	8.2	9.9	10.1
D2A		7.9	7.7	7.0	7.4	7.5	7.9	7.1	6.8	6.9	6.7	6.9	7.9	7.8	7.1	6.9	7.7	7.8	8.6	7.3	6.4	8.8	8.0
D2B	7.7	6.2	6.9	5.9	6.3	6.2	5.9	5.8	5.6	6.0	5.9	5.9	7.1	7.4	6.5	5.9	6.5	6.8	7.6	6.4	6.3	7.4	7.4
D2H	4.6	3.6	3.4	3.9	4.0	3.8	3.0	3.9	3.3	4.2	3.5	3.8	4.1	3.9	4.0	4.3	3.8	4.5	4.8	4.9	4.8	4.7	5.1
D2I	2.6	2.5	2.6	3.0	2.5	2.5	2.3	2.6	2.8	2.7	2.4	2.4	2.4	2.5	3.1	2.7	3.0	2.4	3.0	2.6	2.3	2.4	2.4
D2P		4.3	3.6	5.0	4.4		4.0	4.1	3.6	3.9	4.3	4.2	4.8		5.1	4.9	5.2	5.2		5.0	4.9		5.3
ANL	8.0	7.1	7.5	7.4	6.9	7.5	6.6	7.0	7.0	6.5	6.6	6.6	7.5	7.4	7.1	7.2	7.0	7.3	8.7	7.3	7.0	7.8	7.5
ANA		7.0	5.1	5.2	5.0	5.4	5.2	4.8	4.2	3.4	4.7	4.7	5.2	5.4	4.6	5.0	4.5	4.8	6.4	4.7	4.6	6.1	5.6
ANB	5.8	4.9	5.6	5.3	5.3	5.5	4.8	5.4	5.2	4.4	4.9	4.7	5.5	5.8	5.3	5.6	5.0	5.3	6.4	5.2	5.2	6.4	5.7
ANH	4.2	3.4	3.3	3.1	2.8	3.1	2.9	2.8	2.7	2.3	2.5	2.6	3.0	3.3	2.5	2.9	2.9	3.0	3.8	3.1	3.2	3.9	3.8
ANI	2.2	1.9	1.8	2.1	1.5	2.0	1.9	1.9	1.8	1.6	1.4	1.9	1.8	1.9	1.6	1.9	2.1	2.1	2.3	2.0	2.3	1.7	2.0
ANP		3.9	4.1	4.4	4.4		3.6	4.1	4.6	2.8	4.0	3.7	4.5		4.2	4.5	4.5	5.1		4.8	4.7		5.3
CDM	28.6	34.2	32.0	35.7	33.2	34.6	34.1	34.4	34.7	34.2	33.7	33.1	33.3	33.5	32.5	34.1	30.8	31.5	30.9	30.4	32.0	30.3	28.4
CPV	7.5	9.0	8.4	8.0	8.2	9.3	9.9	8.6	8.6	8.2	8.9	8.2	7.8	9.2	8.5	9.4	8.6	8.4	9.3	8.9	8.3	9.2	9.0
CPL		3.0	3.4	4.3	2.2		2.9	2.6	3.8	2.5	3.0	3.3	2.3		2.4	3.0	2.1	2.5		3.4	2.0		3.6
CPU		20.1	17.5	18.7	19.2		21.6	22.5	19.1	20.3	19.1	19.8	20.1		17.9	20.6	19.2	18.3		18.0	19.2		16.7
CST		5.6	4.6	5.2	4.6		4.9	4.3	5.6	4.9	5.0	4.4	5.1		4.5	4.5	4.2	4.5		4.0	4.1		3.5
CTR		6.4	6.2	6.4	5.4		5.9	6.3	5.2	6.2	6.6	6.4	6.3		6.2	5.8	5.2	5.4		5.7	5.5		3.9
CTL		8.6	7.9	8.3	7.8	7.8	8.2	7.7	7.9	8.2	8.3	7.5	7.9	7.9	8.2	7.6	6.6	7.5	5.5	6.8	6.8	6.0	5.6
CFL		9.0	9.0	10.4	8.2		9.5	9.1	8.2	9.1	8.3	8.0	7.5		8.7	9.9	8.2	8.2		9.0	5.4		8.1
DAO		3.7	4.3	4.9			3.2	4.0	4.5	3.4	3.0	4.2			5.0	3.9	5.4	3.9		4.8	4.4		6.2
DAI		2.7	3.3	3.6			2.1	2.6	2.7	2.3	1.9	2.6			3.9	2.7	3.6	2.7		3.4	3.6		4.4

Source	DAE 861010	DAE 870409-02	DAE 870409-07	DAE 870409-06	ORI 2492	RUSI 6245	Pissarro & Sanches 1973	DAE 870409-01	DAE 882202-01	ORI 611	DAE 882506	MJS 870127
Sex	F	F	F	F	F	F	F	F	F	F	F	F
TOT (mm)	681	730	794	807	846	853	1040	1095	1380	1705	2210	3195
PRC	67.4	67.1	68.6	66.9	67.9	67.9	65.0	67.7	68.1	69.2	69.6	70.4
PRN	1.2	1.9	1.4	1.5	2.4	3.5	1.6	1.0	2.2	1.2	1.6	1.2
POR	4.8	4.9	4.4	5.0	5.9	5.3	4.8	4.4	5.8	4.5	4.1	3.8
POB	6.5	5.1	3.5	4.3	3.9	6.9	4.5	4.7	5.2	3.6	4.0	3.7
PSP	13.2	13.0	10.8	12.3		12.3		11.5	12.2		11.5	10.5
PGI	16.1	17.1	14.4	16.2	15.6	15.8	14.6	16.0	17.4	15.5	15.8	15.3
HDL	22.6	20.0	19.2	21.0	21.0	20.2	19.7	19.1	17.2	20.3	18.0	19.6
PP1	22.6	20.0	19.2	21.0	21.0	20.2	19.7	19.1	17.2	20.3	18.0	19.6
PP2	45.5	43.8	43.4	44.1	44.6	43.9	43.3	42.5	44.2	45.3	47.9	47.7
SVL	49.9	48.6	46.8	47.8		48.0		47.3	47.6		53.0	51.5
PAL	57.2	55.2	54.9	55.3		55.6	53.3	55.3	56.3		59.5	58.1
PD2	55.3	52.1	51.0	52.6	53.7	52.1	51.4	52.5	55.2	55.1	55.9	55.7
DCS	8.8	8.4	7.9	7.8	7.4	7.4		8.1	7.1	6.7	7.6	8.7
PPS	16.8	17.1	18.3	17.8	16.9	17.5		16.8	18.1	18.1	22.6	53.1
PAS	4.6	4.2	3.8	4.3	6.1	4.0		3.8	4.7		3.8	5.2
ACS	3.5	5.2	6.0	5.0	4.1	6.0		5.9	5.7	4.3	4.9	5.6
EYL	3.5	3.4	3.1	3.3	3.1	2.9	2.9	2.6	2.5	3.9	1.9	1.9
EYH	2.2	1.8	1.5	1.9		2.2		1.3	1.3		1.2	1.3
INO	10.1	9.5	8.3	8.2		10.5		9.1	10.3		8.5	9.2
NOW	0.7	1.4	1.1	1.1	1.5	1.2		1.2	1.1	1.7	1.2	1.0
INW	4.6	4.5	3.8	4.6	4.7	5.5	5.8	4.4	5.1	4.6	4.2	4.2
ANF	0.7	0.7	0.5	0.6		0.7		0.5	0.4		0.5	0.3
SPL	0.4	0.4	0.5	0.6	0.6	0.1		0.5	0.5		0.6	0.4
ESL	5.4	3.8	3.5	4.3	5.2	4.5		4.4	4.0		4.5	5.4
MOL	6.6	5.9	5.8	6.8	4.4	5.7	5.2	5.5	4.7		3.4	6.4
MOW	12.0	10.6	10.9	10.9	12.4	14.5	8.8	10.8	11.7	11.7	11.0	13.1
ULA	3.2	2.6	2.8	2.5		2.0		2.8	2.3		2.0	0.3
LLA	3.8	3.0	3.1	3.6		2.5		3.3	2.8		3.1	2.4
GS1	5.4	5.8	5.5	6.6	7.9	6.7	8.7	7.0	8.3	7.0	8.6	9.7
GS2	5.6	4.9	5.2	6.1	7.7	6.7	8.0	6.5	8.1	6.9	8.5	8.6
GS3	5.3	4.7	5.0	5.8	7.1	6.6	7.4	6.0	7.8	6.8	8.7	8.3
GS4	5.1	4.4	4.3	5.3	6.4	6.2	6.5	5.7	7.2	6.5	7.6	7.4
GS5	4.1	4.2	3.8	5.1	5.9	5.9	5.8	5.2	6.4	6.0	6.7	6.6
GS6	4.0	4.0	3.1	4.7	5.1	4.8	5.2	4.9	5.5	5.3	5.8	6.1
HDH	6.3	8.8	4.8	6.2		11.0		7.8	13.4		11.0	14.1
HDW	10.8	13.2	13.6	13.2		15.7		14.7	13.4		14.9	12.5
TRH		12.7	4.8	6.2		11.7		7.6	14.4		11.6	16.9
TRW		13.1	14.9	13.6		10.7		14.3	14.1		17.1	7.8
CPH	3.4	3.3	3.3	3.6	4.4	4.1		3.5	4.2	4.7	4.5	4.7
CPW	2.9	2.1	2.0	2.1	3.9	3.5		2.3	3.6	4.1	3.1	3.3
P1L	11.3	11.5	11.9	11.5	13.8	12.1		11.8	11.9	13.2	12.8	12.5
P1A	12.0	12.6	11.9	12.5	13.0	11.6	13.7	13.0	12.8	14.0	12.8	12.7
P1B	6.5	7.5	7.1	6.8	7.9	7.7	8.2	7.1	6.8	7.7	7.5	7.5
P1H	9.5	8.4	9.2	10.2		10.1	10.1	11.1	10.0		10.0	8.1
P1I	5.6	5.1	4.8	5.3	5.9	5.6		5.5	6.0	5.5	5.0	5.5
P1P	8.1	7.4	7.6	8.1		9.0	9.8	9.8	9.9		9.3	8.1
P2L	5.3	9.2	9.3	9.4		10.4		10.5	10.5	10.7	10.7	11.4
P2A	4.3	5.2	4.5	5.6		5.6	5.8	5.9	5.4	6.0	5.9	9.4
P2B	6.6	7.0	7.7	7.2		8.6	9.4	8.9	8.4		7.7	7.5
P2H	6.5	3.2	2.0	3.3		2.9		3.6	3.7		3.9	4.4
P2I	1.8	1.9	2.4	1.7		2.1		1.6	2.4		3.2	5.9
P2P	7.8	6.3	6.9	7.1		7.3	8.5	7.8	7.8		7.8	9.1
CLO												
CLI												
CLB												
D2L	6.5	8.6	8.6	8.9	10.2	9.5	8.0	8.7	8.8	9.3	8.9	9.1
D2A	6.6	7.4	6.7	7.3	8.2	8.0		7.4	6.5	7.8	7.6	7.7
D2B	5.1	6.2	6.0	6.2	7.4	7.3	5.8	5.9	6.1	7.2	6.7	7.0
D2H	4.1	4.4	3.7	4.2	4.5	4.6	3.8	4.2	4.2	4.3	4.2	4.9
D2I	4.1	2.7	2.6	2.6	2.8	2.6	2.0	3.0	2.8	2.1	2.3	2.8
D2P	4.1	3.7	4.2	4.3		5.3		4.2	5.3		4.0	5.3
ANL	6.5	7.3	7.4	7.8	8.9	7.6	8.0	8.0	8.1	8.4	7.1	8.3
ANA	5.1	4.9	5.2	5.0	5.8	5.3		4.9	4.9	5.7	4.5	5.8
ANB	5.3	5.3	6.2	5.9	6.5	6.1	5.8	5.8	5.9	6.6	5.4	6.3
ANH	4.7	2.9	2.6	2.0	3.4	2.8	3.8	3.3	3.1	3.7	3.2	3.8
ANI	2.2	1.8	1.6	1.7	2.4	1.8	2.0	1.9	2.1	1.8	2.0	2.1
ANP	5.1	4.4	4.7	4.6		4.8		4.7	5.4		4.3	5.2
CDM	30.8	34.2	33.7	33.4	33.6	32.8	35.1	32.3	32.6	30.7	30.9	29.3
CPV	9.1	8.8	8.6	8.7	9.5	7.4	10.3	8.9	8.0	8.6	6.4	6.9
CPL	3.1	2.9	2.8	2.7		2.5		2.9	3.2		2.9	2.8
CPU	20.7	21.0	21.5	20.0		21.5		19.9	18.4	10.5	18.0	18.8
CST	4.0	4.9	4.5	4.7		4.6		5.0	4.2		3.5	3.4
CTR	6.5	6.2	5.8	6.4		5.6		5.3	6.4		5.0	4.7
CTL	7.6	7.8	7.3	7.9	7.3	6.8		7.8	7.2	6.4	6.3	5.5
CFL	9.4	9.5	8.4	8.7		7.2		8.2	8.4		8.1	7.8
DAO	3.5	3.0	3.8	3.2				3.8	3.2		4.4	4.1
DAI	2.5	2.6	2.4	2.2				2.7	3.3		2.7	3.3

	PACIFIC OCEAN																						
	CALIFORNIA																		HAWAII		AUSTRALIA	CHILE	
Source	LJVC 0413	DAE 872212	MLML uncat.	LJVC 0351	DAE 851107-02	DAE 851306	CAS 1950-IX:19	LJVC 0352	LJVC 0442	LACM uncat.	CAS 11615	CAS 52981	USNM 27369 Holotype	DAE 821404-02	DAE 851107-01	LJVC 0256	LJVC 0350	CAS 1962-XII:9	BPBM 9649	USNM 179770	Lynch 1964	USNM 164433	USNM 164432
Sex	F	F	F	F	F	F	F	F	F	F	M	M	M	M	M	M	M	M	M	M	M	M	F
TOT (mm)	646	674	775	890	1080	1110	1151	1294	1536	4210	668	955	1030	1070	1200	1494	1825	2420	2805	2808	2187	695	930
PRC	63.7	63.7	65.8	64.0	63.4	65.3	60.2	66.6	68.6	74.9	63.6	63.8	67.5	67.2	65.0	69.2	69.0	69.2	68.4	65.1	70.8	62.4	66.7
PRN	2.0	1.3	1.5	1.5	3.1	1.8	1.7	1.5	1.7	2.1	1.0	1.7	1.2	0.7	3.3	1.3	1.9		1.1	1.0	1.9	1.7	1.0
POR	5.4	5.3	5.5	5.1	5.1	6.3	5.0	5.3	4.6	4.3	4.0	3.0	4.0	4.1	5.0	5.0	5.2		4.3	4.3	4.6	4.5	3.2
POB	4.2	5.2	5.3	3.8	4.2	4.5	5.0	4.3	2.5	4.2	5.4	3.2	3.9	5.1	5.0	3.7	4.5	6.0	4.5	4.1		3.2	4.4
PSP	10.3	12.6	13.6	11.3	11.1	14.4	12.1	10.6	9.6	10.8	11.9	10.1	11.3	11.8	12.0	4.6	11.2	11.9	11.2	7.1		10.6	12.2
PGI	12.8	16.6	18.1	13.8	16.2	16.2	16.8	14.2	13.6	15.1	15.4	15.9	15.6	14.7	17.0	14.0	13.4		14.8	12.5		14.0	16.3
HDL	15.7	18.1	22.9	19.1	20.3	20.7	20.3	18.5	18.1	19.3	19.6	19.3	22.1	17.1	20.8	18.7	16.9	18.8	17.1	16.6		17.3	19.7
PP1	15.7	18.1	22.9	19.1	18.5	21.6	20.3	18.5	18.1		19.6	19.3	22.1	17.1	17.9	18.7	16.9	18.8	17.1	16.6		17.3	19.7
PP2	40.0	40.2	43.0	41.0	41.2	44.1	39.0	43.2	43.0		38.1	39.7	45.3	42.5	40.0	45.5	47.1	45.8	46.5	41.1		40.3	39.8
SVL	43.6	45.2	47.7	46.2	46.2	49.0	44.6	47.4	47.9	55.2	43.1	46.3	47.8	46.5	48.3	50.2	51.5		52.2	45.9		44.5	44.9
PAL	52.9	52.3	55.4	52.8	51.8	56.7	50.3	55.6	54.9	63.3	51.9	53.9	56.8	57.0	52.5	58.5	58.3	59.0	60.8	56.3	63.4	49.6	52.2
PD2	50.3	50.4	52.9	50.5	50.4	53.6	51.0	52.9	53.3	57.5	47.6	48.6	53.9	51.4	51.2	53.5	55.3	54.3	54.5	50.6	54.9	46.0	53.2
DCS	8.0	6.8	8.3	9.0	7.9		6.1	7.0	7.0		9.3	8.2	8.9	8.2	7.9	7.7	7.1		7.0	7.8	9.1	9.8	8.1
PPS		13.6	14.9		16.6		11.3				13.1	14.5	18.9	16.9	17.5	18.7				21.0		15.8	15.5
PAS	5.1	3.6	4.0	3.5	5.6	4.1	3.3	4.2	4.4		6.9	5.1	4.4	6.7	6.3	4.4	5.8		6.9	6.9	13.6	5.5	4.8
ACS	5.6	5.6	4.9	4.9	4.2	5.4	4.8	4.9	7.0		4.0	4.7	4.5	4.5	5.4	4.0	4.1		4.3	4.6		5.6	6.0
EYL	3.4	3.6	3.4	3.4	2.6	2.7	2.8	2.8	2.9	1.8	3.6	2.9	2.8	2.9	2.6	2.3	2.4	2.2	2.2	1.9	2.4	3.3	3.4
EYH	1.9	2.1	1.9	2.0	1.4	1.4	1.0	1.8	1.6	1.2	1.3	1.5	1.2	1.3	2.1	1.5	1.4		0.9	0.4		0.9	1.6
INO	9.6	10.5	10.8	10.3			8.7	8.7	9.7		7.9	9.5	8.3	7.8					6.5	6.3		9.8	8.8
NOW	0.6	1.2	1.2	1.1		0.5	1.0	1.0	1.0		1.3	1.0	1.0	1.1			1.0	0.7	1.1	0.8		1.3	0.8
INW	4.2	5.2	5.7	4.3		4.5	4.3	3.9	4.2	4.4	5.1	4.7	4.1	4.1		4.4	4.5	5.1	4.0	3.8	5.0	5.0	4.7
ANF	0.5	0.4	0.4	0.4		0.5	0.4	0.4	0.5		0.6	0.5	0.4	0.6			0.3		0.3	0.4		0.3	0.4
SPL	0.3	0.4	0.4	0.3		0.2	0.3	0.3	0.5		0.7	0.2	0.4	0.5		0.3	0.3	0.3	0.4	0.1		0.3	0.1
ESL		4.6	4.9			5.4	4.6				4.3	4.7	4.1	4.8		4.7			4.7	2.8		3.7	3.9
MOL	3.9	5.3	6.2	6.9	6.0	6.8	4.8	7.5	6.8	7.0	6.6	6.1	5.1	5.3	5.8	4.0	4.4	5.2	5.7	3.3		4.5	4.8
MOW	8.5	12.7	10.9	11.9	10.6	10.3	11.4	11.3	11.9	17.2	11.3	11.7	9.5	9.9	10.8	13.3	10.9	12.8	6.5	6.9	10.6	9.5	10.6
ULA		2.4	1.9			1.4	1.9				2.2	2.1	1.8	2.1					1.6	1.3		1.6	1.4
LLA	1.1	3.3	2.5	3.3		2.3	3.0	2.6	2.1		3.4	3.6	2.6	2.8		2.7	3.0		2.5	2.2		2.3	2.5
GS1	7.0	5.8	5.4	7.9	7.4	7.7	6.9	8.8	8.6	10.6	5.8	6.5	5.6	7.9	7.1	6.7	7.8	7.2	9.3	7.5	11.4	5.0	6.1
GS2	6.3	5.3	5.2	7.4	6.9	7.2	6.6	8.0	7.6	9.5	5.1	6.3	5.4	6.9	6.7		7.5	6.9	8.6	7.3	9.8	4.7	5.7
GS3	6.2	5.0	5.0	7.0	6.5	6.3	6.1	7.3	6.4	8.6	4.5	6.0	5.0	6.3	6.3		6.8	6.6	7.7	6.2	9.6	4.7	5.6
GS4	5.4	4.9	4.8	6.5	6.0	5.9	5.8	6.8	6.3	7.5	4.0	5.2	4.6	5.4	6.3		6.6	6.0	6.6	5.5	9.4	4.5	4.9
GS5	5.0	4.6	4.4	5.6	5.6	5.4	5.5	6.0	5.3	6.7	3.6	4.9	4.4	5.1	5.8		6.0	5.0	5.5	4.8	7.0	4.0	4.5
GS6	4.2	4.2	3.9	5.1	5.4	4.1	5.1	5.0	4.8	5.6	3.4	4.3	4.2	4.7	5.4	5.4	5.2	4.5	4.7	4.1	6.0	4.0	4.3
HDH	5.1	8.8	10.3	7.6		10.8	12.1	8.0	7.2		10.1	9.8	7.3	10.6			8.2		15.9			7.3	11.3
HDW	9.9	15.7	14.1	10.6		9.0	14.1	9.3	9.7		11.3	14.6	10.5	9.8			11.5		7.1			11.7	10.4
TRH		9.9	10.0			10.8	12.4				11.0	10.5				11.3			16.4		11.2	6.5	10.6
TRW		11.4	11.8			10.8	11.6				10.0	13.1		8.5		10.0			9.6		14.5	10.8	9.1
CPH	4.0	3.7	3.7	3.7		3.6	4.3	3.9	4.7		3.1	4.7	3.6	3.4		4.7	4.9		4.4	3.6		3.3	4.0
CPW	3.3	2.5	2.8	2.7		2.3	3.9	2.8	2.7		2.7	3.2	2.0	2.6		2.7	3.8		2.7	2.2		2.6	2.7
P1L	12.3	11.5	12.6	11.6	10.6	10.8	12.9	12.9	13.9		12.2	12.1	13.1	11.8	10.8	14.0	12.3	11.7	11.9	10.4		12.4	12.3
P1A	12.2	12.6	13.4	12.5	10.4	14.4	13.5	13.5	15.4	12.8	13.4	13.2	14.9	13.1	11.2	14.1	13.1	12.4	13.5	11.5		14.7	14.2
P1B	6.8	6.8	7.4	7.0	7.4	7.2	7.4	7.5	8.3	8.4	6.7	6.9	7.7	7.3	7.9	8.0	8.2	7.5	8.6	6.5		7.3	7.8
P1H		11.4	10.1		10.1	9.9	11.5		9.1		9.4	10.5	10.5	10.8	10.2	8.4		7.5	9.6	10.1		11.2	10.1
P1I	5.6	5.3	5.2	4.7	4.2	5.4	5.8	5.4	5.5	4.3	5.1	6.3	5.8	5.3	4.2	6.0	4.9	3.8	4.8	4.0		6.0	6.0
P1P		9.2	10.9	9.9	10.1	9.5	10.4	8.5		9.2	9.7	9.5	9.1	8.9	10.2	8.4	9.0	11.8	9.8	7.9		9.6	9.8
P2L	8.7	10.0	9.9	9.7	10.1	10.3	10.8	9.7	11.0	11.4	11.2	11.9	9.2	11.0	10.6	11.3	12.0	10.7	13.5	12.0		9.8	10.0
P2A	6.2	5.6	5.4	4.9	5.1	5.0	5.9	5.7	5.8	7.1	5.5	6.0	5.6	4.8	5.4		6.0	5.4	6.1	6.4		4.9	5.3
P2B	6.7	8.6	8.0	8.0	9.3	8.6	7.8	8.1	8.2	10.5	8.1	7.9	7.5	7.3	6.7		8.2	6.7	8.0	8.2		6.3	7.6
P2H		3.3	3.6		3.2	3.6	3.3		4.8		3.3	3.9	3.7	3.1	4.0			3.7	5.5	4.3		4.0	3.7
P2I	1.7	2.1	2.6	1.7	2.6	1.8	2.6	1.5	1.5	1.0	3.4	3.7	1.7	3.6	3.3		4.7	4.3	6.7	4.3		3.2	2.3
P2P		6.8	7.2	7.5	8.1	9.0	8.7			9.6	8.2	8.4	6.1	8.1	7.9		9.0	8.3	11.1	8.5		6.8	7.1
CLO											1.3	1.5		1.6		2.5		2.0	3.7	2.5		1.7	
CLI											2.2	2.3		2.8	4.6	1.8	2.8	3.6	7.8	5.5		3.7	
CLB											0.4	0.5		0.3				0.5	1.2	0.6		0.4	
D2L	7.7	8.8	8.6	9.2	8.1	8.6	9.3	8.3	8.9	9.2	8.1	9.3	9.6	8.4	7.9	10.0	9.7	8.5	10.2	7.8		8.8	8.7
D2A	7.0	7.6	6.8	6.7	6.5	7.2	7.6	7.1	7.7		7.5	7.5	8.5	6.4	6.1	7.7	7.2	7.3	8.2	6.2		7.9	6.5
D2B	5.3	6.4	5.9	7.0	5.6	6.3	7.0	6.0	6.3	7.5	6.0	6.8	7.3	5.9	5.4	7.4	7.4	6.9	7.3	5.9	7.5	6.2	6.5
D2H	4.0	3.1	3.9	3.9	4.2	4.1	4.8	4.3	4.3	5.3	3.7	4.7	4.2	4.1	3.8	4.0	4.7	4.3	5.2	3.8	4.4	4.0	3.4
D2I	2.5	2.5	2.7	2.2	2.3	2.3	2.7	2.3	2.3	5.4	2.8	3.1	2.4	2.6	2.5	2.7	2.3	1.6	2.7	2.1		2.9	2.4
D2P	4.0	3.7	5.0	4.5	4.6	5.0	6.0	4.5			4.6	6.1	4.5	4.7	4.6		4.5	4.6	5.2	4.3		3.7	4.5
ANL		7.7	7.7	8.2	6.9	7.7	8.9	7.7	7.9	8.1	7.2	8.2	7.0	7.0	6.7	8.0	7.6	7.2	7.8	7.1		7.1	7.8
ANA		5.0	5.4	5.6	4.2	5.0	5.6	5.2	4.8		5.4	5.4	5.4	4.4	4.2	5.4	4.9	5.5	5.3	4.7		5.2	5.3
ANB	5.6	5.3	6.1	6.3	5.1	5.9	7.0	6.0	6.0	6.5	5.8	6.6	5.4	5.0	5.0	6.0	5.6	5.4	6.1	5.1	5.3	5.2	5.8
ANH	2.6	2.8	3.0	2.9	2.6	2.7	3.1	2.9	3.3	4.1	2.8	3.7	3.4	2.8	2.5	3.3	3.3	3.8	4.4	3.6	3.6	3.6	2.8
ANI		2.1	1.9	1.9	1.4	1.8	1.9	1.8	1.8	6.0	1.6	1.9	1.8	2.1	2.1	2.0	2.0	1.8	2.2	1.9		1.7	1.9
ANP		3.9	4.8	4.0	4.2	5.0	5.6	4.3			4.0	5.3	4.3	4.4	4.2		4.2	4.3	5.0	4.6		3.7	5.2
CDM	35.4	34.4	35.0	33.8	3.24	35.5	36.6	32.6	31.9	25.7	37.4	36.1	33.0	33.4	32.0	31.1	30.4	29.9	29.6	27.8	31.5	35.7	33.3
CPV	9.3	8.2	9.3		7.4	7.2	9.3	8.8	8.1	7.3	10.1	8.6	8.4	8.2	7.9	8.7	7.2	7.1	8.5	7.6	8.0	9.6	8.8
CPL		3.3	2.7		4.6	4.5	3.3		3.1		1.8	4.1	2.0	2.7	4.2				3.6	2.5		2.6	4.4
CPU	24.1	18.1	20.0	24.8	19.4	2.25	22.5	23.1	20.8		20.9	19.8	20.6	18.9	20.8		21.4		19.2	17.6		19.0	18.1
CST	5.6	5.3	4.8	4.0	4.2	4.5	4.9	4.3	3.6	1.7	5.2	4.8	4.2	4.5	4.0		3.8		3.4	3.3		5.2	3.9
CTR	5.7	6.1	6.2	6.5	5.8	5.0	6.1	5.1	5.3		5.8	6.2	5.0	5.2	5.8		5.3		4.1	3.6		6.0	6.1
CTL	7.7	8.3	7.7	8.2	7.4	7.2	8.4		6.5	5.2	8.2	7.7	7.3	6.8	7.5		6.6		5.7	5.3		8.5	7.1
CFL		8.8	8.3		5.1	8.1	9.6				9.9	9.2	9.4	8.1	6.3				8.2	9.8		9.4	8.6
DAO		3.4	3.4			3.2	3.0		2.5		5.5	4.3	3.5	4.7					5.5	3.8		4.2	2.9
DAI		2.4	2.7			2.7	2.4		2.1		3.7	2.8	2.9	3.1					4.1	3.2		2.4	2.3

TABLE 3.4 Proportional measurements of *Hexanchus nakamurai*, expressed as a percentage of total length.

	INDIAN OCEAN								WESTERN PACIFIC										EASTERN NORTH ATLANTIC			
	KENYA						AUSTRALIA	SOUTH AFRICA	PHILIPPINES		TAIWAN						AUSTRALIA		GM	BAH.	VEN.	USVI
Source	RUSI 4343	RUSI 4343	RUSI 4343	RUSI 4343	RUSI 4343	RUSI 4343	WAM P 29521-001	ORI 2922	CAS 30642-02	CAS 30642-01	DAE 881504-01	NMF 0295	DAE 882304	DAE 882804-03	DAE 882804-01	DAE 882804-02	CA 506/85/23	CA 3366	USNM 220182	USNM 200674	Cervigor 1966	DAE 890111
Sex	F	M	M	F	F	M	M	M	F	M	M	M	F	F	F	M	F	F	F	M	F	M
TOT (mm)	220	234	250	259	264	268	1440	1568	417	433	482	845	860	1155	1230	1526	474	837	690	1500	1710	695
PRC	65.4	65.8	67.6	61.7	64.3	65.6	75.6	68.3	61.8	62.5	62.8	66.7	67.4	67.0	69.1	69.4	62.6	63.7	66.6	70.6	73.0	67.3
PRN	1.4	0.9	1.2	2.7	1.5	2.2	2.8	2.2		0.2	1.7	1.2	1.0	1.8	1.4	1.2	1.3	1.6	1.7	1.7	2.9	1.2
POR	5.9	6.4	6.4	5.0	6.4	6.3	5.5	4.9		5.1	6.2	5.4	4.2	5.2	5.0	4.4	7.2	6.0	5.8	5.2	5.5	5.6
POB	3.2	4.7	4.8	4.6	4.5	5.2	5.8	4.6		3.5	4.4	4.0	3.7	4.8	4.3	3.7	4.2	4.8	4.8	4.9		4.6
PSP	13.6	14.5	11.2	11.9	12.5	13.4	13.5	11.7		8.8	13.0	11.7	9.8	11.8	11.3	11.7	14.1	12.3	11.8	12.8		13.2
PGI	16.8	15.8	17.6	15.8	15.5	16.4	16.6	15.3	14.3	13.6	15.5	14.7	11.9	14.8	14.5	14.6	17.5	15.2	15.7	16.6		16.8
HDL	20.9	20.0	21.6	18.1	19.3	19.7	19.3	17.0	17.5	15.2	18.8	18.1	16.0	18.5	18.2	17.6	19.6	18.8	19.5	20.0		18.4
PP1	20.9	20.0	21.6	16.9	19.3	19.7	18.9	17.0	17.5	15.2	18.8	18.1	16.0	18.5	18.2	17.6	19.4	19.1	19.5	20.0	17.5	18.4
PP2	40.9	41.0	40.8	40.5	39.7	41.0	44.0	43.3	39.3	36.2	39.8	40.4	42.4	40.6	41.8	43.2	40.7	39.7	41.3	43.3	45.0	41.9
SVL	44.0	45.7	44.8	42.4	42.8	43.6	48.6		41.0	39.4	42.7	44.9	46.7	44.7	45.6	47.4	43.8	42.7	44.6	47.3		46.0
PAL	52.2	54.7	53.6	52.1	49.2	51.1	57.6		50.3	50.8	51.8	53.9	54.6	54.2	53.9	57.4	50.4	51.3	53.1	58.3	60.2	55.3
PD2	48.6	49.5	49.2	46.7	46.9	47.7	52.4	50.0	46.7	45.7	48.1	49.7	50.9	49.0	51.0	51.6	45.7	46.5	50.1	53.6	56.6	51.1
DCS	11.3	12.3	10.0	10.4	9.1	11.5	13.1	12.3	11.5	11.0	11.6	12.5	11.7	12.2	12.0	12.3	10.1	11.1	10.7	10.2	11.6	11.1
PPS	17.2	17.5	16.8	18.9	15.9	15.6	17.7	20.5	18.9	15.9	16.8	17.6	18.6	16.8	17.8	21.9	16.2	14.9	13.7	20.0		16.7
PAS	5.5	7.7	7.6	4.6	5.7	5.6	8.0	8.7	6.7	7.6	8.1	7.1	6.2	6.2	5.8	7.6	4.6	6.3	6.1	8.1		6.2
ACS	9.5	10.2	10.0	8.1	10.6	7.5	9.0		8.4	8.8	8.9	8.8	8.8	9.0	8.5	8.2	8.6	8.5	8.6	7.5		7.2
EYL	5.9	6.4	5.6	5.4	5.3	5.6	3.2	3.1	4.1	5.1	5.2	3.7	2.6	3.0	3.0	3.1	5.7	4.1	3.2	3.3	2.4	4.0
EYH	3.2	2.6	2.4	3.5	3.4	3.7	2.2		2.4	2.3	2.9	1.7	2.3	1.7	2.2	2.0	2.3	1.4	2.0	1.9		2.0
INO	11.3	8.1	9.6	10.8	9.1	11.1	7.9		9.4	9.0	8.7	6.5	6.9	7.1	8.3	7.0	10.5	9.0	8.0	6.7		8.5
NOW	1.4	1.7	1.2	0.8	1.5	1.1	1.0	1.0		1.2	1.2	1.2	0.8	1.1	1.1	1.0	1.5	1.2	1.3	1.1		1.2
INW	5.0	4.3	4.8	4.6	3.8	3.7	4.4	3.8		3.9	4.6	4.0	3.5	4.2	4.2	3.7	4.9	4.1	4.2	3.9	4.2	4.2
ANF	0.9	0.9	1.2	0.8	0.8	0.7	0.5			0.7	0.6	0.5	0.5	0.3	0.3	0.4	0.4	0.5	0.4	0.3		0.6
SPL	0.5	0.4	0.4	0.4	0.4	0.4	0.1	0.4		0.7	0.2	0.5	0.2	0.2	0.2	0.1	0.4	0.4	0.3	0.4		0.3
ESL	3.2	3.4	3.2	3.5	3.8	3.4	5.8			3.5	3.5	3.7	3.4	4.2	4.5	4.7	3.4	4.4	4.5	4.2		4.3
MOL	6.8	6.4	5.6	6.9	5.3	7.5	6.5	6.4		4.2	3.7	3.7	3.6	4.4	3.9	4.1	4.0	3.9	4.5	6.5	5.8	4.6
MOW	10.4	10.2	9.6	11.9	10.6	12.3	9.9	9.8		8.3	10.0	7.7	5.6	7.0	8.1	8.3	9.3	7.4	9.1	9.4	11.5	9.4
ULA	2.3	2.1	2.0	2.3	1.9	2.6			1.4	1.6	1.0	1.1		1.2	2.0	1.4	0.8	0.5	1.4	1.4		3.7
LLA	2.3	2.1	2.4	1.5	2.3	2.6			2.9	2.3	2.7	2.2		2.5	1.2	2.2	2.3	2.0	2.0	2.7		2.7
GS1	7.7	7.3	7.6	6.6	6.8	6.0	5.9	6.0	5.8	5.3	6.2	5.4	5.3	5.9	4.9	6.1	5.9	5.6	5.5	6.3	8.2	6.3
GS2	7.3	6.4	6.4	5.4	6.4	5.6	5.5	5.6	5.3	4.6	5.4	5.1	5.1	5.5	4.5	5.5	5.5	4.8	5.1	5.9	6.5	6.0
GS3	6.4	6.0	6.0	5.0	5.7	4.1	5.2	5.1	5.0	4.4	5.0	4.7	4.9	5.1	4.1	5.0	4.9	4.7	4.6	5.3	5.7	5.2
GS4	5.5	6.0	5.2	4.6	4.9	3.7	4.7	4.7	4.6	4.2	4.4	4.1	4.1	4.5	4.0	4.3	4.2	4.3	4.2	4.9		4.9
GS5	4.5	5.1	4.4	4.2	4.5	3.0	4.2	4.0	3.8	3.7	3.9	3.4	3.1	3.9	3.7	3.7	3.8	3.8	3.8	4.4	4.5	3.9
GS6	4.1	3.4	3.6	3.5	3.8	2.6	3.2	2.9	3.4	3.0	3.1	2.6	2.4	3.1	2.7	2.9	3.4	3.2	3.2	3.5	3.1	3.3
HDH	8.6	8.1	7.6	7.3	7.6	7.1	9.0		8.6	7.4	10.0	8.8	8.5	8.1	8.7	8.6	8.9	8.8	8.3	10.3		9.2
HDW	11.3	9.8	11.6	11.9	12.1	13.8	12.5		11.5	10.8	11.8	10.6	9.2	10.0	10.4	9.4	12.2	11.2	11.8	8.8		10.8
TRH	8.6	8.1	9.2	8.9	10.2	9.3	9.4		10.0	8.3	11.8	9.0	7.6	9.1	9.8	8.7	10.5	9.4	10.2	11.6	9.3	11.7
TRW	7.7	8.5	8.8	7.7	6.4	10.0	12.5		10.0	8.3	12.4	10.1	8.7	9.1	9.8	9.0	9.1	9.3	10.4	8.0	18.9	8.9
CPH	3.6	3.4	3.2	3.5	3.0	3.4	3.6	3.4	3.4	3.2	3.5	3.7	4.1	3.5	3.4	3.5	3.2	3.5	4.1	3.3		3.2
CPW	2.7	2.1	2.4	2.3	3.8	3.0	2.9	3.6	3.1	2.8	3.1	3.1	3.0	3.2	2.8	3.1	3.4	3.3	3.3	2.5		2.7
P1L	10.0	10.2	9.6	9.7	9.5	9.3	10.4	9.9	9.8	9.7	10.3	9.6	9.0	10.4	10.4	9.1	30.5	30.1	11.1	9.9		10.8
P1A	10.0	9.8	10.0	9.3	10.6	9.3	11.1	10.9	11.2	10.6	11.4	10.5	10.4	12.0	12.6	10.4	10.1	10.7	12.1	11.8	11.7	13.1
P1B	5.9	5.6	5.2	5.4	5.3	5.2	6.7	6.1	6.0	5.5	6.0	6.0	6.3	6.4	6.3	6.2	12.0	11.9	6.4	5.7		5.9
P1H	8.2	6.8	8.0	9.3	8.0	9.0	9.2		9.4	8.3	9.5	8.8	8.5	8.9	10.1	8.3	6.1	6.5	9.9	8.8		11.5
P1I	4.1	4.7	4.4	3.9	4.5	4.5	4.0	3.8	4.8	4.6	4.6	3.9	2.9	4.1	4.0	3.5	9.3	10.0	4.9	3.9	4.6	4.9
P1P	8.6	8.1	9.6	8.9	8.3	10.0	8.6		8.2	9.0	7.7	8.8	6.7	9.4	9.4	7.1	4.6	4.9	9.4	8.7	7.6	10.8
P2L	7.7	8.1	7.6	6.6	7.6	7.8		13.7	6.5	6.9	7.5	8.6	7.3	8.7	8.5	12.9	8.2	9.1	8.4	13.6		8.2
P2A	3.6	3.8	4.0	3.9	4.2	3.7	4.2	5.2	4.1	3.2	3.3	3.7	3.6	4.2	4.1	4.2	7.6	9.6	4.5	5.1		3.6
P2B	5.5	5.6	5.2	5.8	6.4	4.9	6.3		5.0	4.2	4.8	5.9	6.0	7.1	7.2	6.9	3.8	4.1	7.2	7.1		5.6
P2H	2.7	2.1	2.4	1.9	2.7	2.2	2.8		2.2	1.8	1.9	2.4	1.4	2.8	3.1	2.9	5.9	6.3	2.2	2.8		2.7
P2I	2.3	2.6	2.4	1.2	1.5	3.4			1.9	3.0	2.5	3.1	0.8	1.5	1.3	6.6	2.5	2.9	1.6	6.9		2.2
P2P	5.5	6.0	5.2	5.8	5.3	6.3			5.0	4.6	5.2	5.7	4.7	6.4	6.3	10.0	2.3	3.2	5.8	9.7		6.3
CLO		0.9	0.8			0.4				0.7	1.2	1.5				5.4	4.9	6.5		4.7		1.2
CLI		3.0	2.4			1.5	7.7	8.5		1.4	3.1	3.6				7.7				8.5		3.2
CLB		0.4	0.4			0.4	1.4			0.2	0.4	0.1				1.0				1.2		0.3
D2L	6.8	6.4	6.8	6.6	6.1	6.7	7.5	7.7	6.7	6.0	6.0	6.4	5.9	6.5	6.9	6.9	7.4	7.0	7.7	8.1		8.1
D2A	5.9	6.0	6.0	5.8	6.1	6.0	6.7	7.0	6.2	6.0	5.8	5.7	5.6	6.0	6.4	6.1	7.0	6.5	6.5	7.0		6.2
D2B	5.0	4.7	4.4	4.6	4.9	5.2	6.3	6.3	4.8	4.4	5.0	4.9	5.3	5.2	5.6	5.2	6.1	5.5	5.7	6.3	5.4	5.8
D2H	3.2	3.4	4.0	3.1	3.8	3.0	4.2	4.0	3.6	3.5	2.9	3.6	2.6	4.0	4.6	3.5	3.6	3.7	3.9	4.0	4.4	3.7
D2I	1.8	1.7	2.4	1.2	1.1	1.9	1.3	1.5	1.9	1.6	1.0	1.2	0.6	1.6	1.2	1.4	1.5	1.6	2.0	2.4		1.7
D2P	4.1	3.0	4.4	4.2	3.4	3.7	4.2		3.4	3.2	3.3	3.8	2.3	4.1	4.5	3.6	2.5	3.6	4.1	4.7		4.6
ANL	5.9	5.1	5.6	5.8	5.7	5.2	5.6	6.1	5.5	5.1	4.4	5.4	5.6	5.7	6.2	5.8	6.1	6.1	5.2	5.9		5.3
ANA	4.1	3.8	3.2	3.5	3.4	3.0	3.3	3.8	3.4	3.2	2.7	2.8	3.0	3.2	3.4	3.5	3.6	3.7	2.8	3.1		3.0
ANB	4.5	3.8	4.0	3.9	4.5	3.0	4.2	4.5	3.8	3.9	3.3	3.9	4.7	4.3	4.7	4.1	5.1	4.7	3.9	4.0	4.3	3.7
ANH	1.8	1.7	2.8	1.9	1.9	1.5	2.4	2.3	1.9	1.6	1.2	1.9	1.3	1.8	2.2	2.4	1.7	2.3	1.2	2.1	2.1	1.9
ANI	2.3	1.3	1.6	1.2	1.1	1.5	1.7	1.6	1.7	1.2	1.5	1.5	1.3	1.4	1.3	1.7	1.5	1.7	1.3	1.5		1.3
ANP	3.6	3.4	3.6	3.9	3.8	2.6	3.8		3.1	3.2	2.5	3.4	3.0	3.5	3.7	3.7	3.0	3.2	3.2	3.9		3.3
CDM	36.3	32.0	33.6	36.6	37.8	37.3	29.5	31.6	37.4	36.9	36.5	34.3	30.2	32.5	31.8	30.0	39.2	35.9	32.6	29.3	29.5	31.4
CPV	8.2	6.0	7.2	7.3	9.1	7.5	8.7	8.6	8.4	7.9	7.3	6.9	7.1	7.4	8.7	8.1	9.3	9.6	9.0	8.5	8.2	7.8
CPL	3.2	3.4	3.2	2.7	2.7	3.0	4.9		2.6	2.5	2.7	3.1	3.0	2.8	4.1	3.2	3.2	3.5	2.8	3.7		4.5
CPU	19.5	17.9	21.2	21.2	20.4	17.9	18.0		18.7	19.3	21.3	18.2	17.0	18.8	17.8	17.0	20.4	21.9	18.6	15.5		17.7
CST	4.5	5.1	4.0	3.9	5.3	4.1	2.4		6.0	5.1	4.4	3.9	3.7	3.4	3.7	3.0	4.2	4.2	3.6	2.9		3.7
CTR	5.5	4.3	4.0	7.3	6.4	6.0	3.8		6.5	6.0	5.8	5.9	4.3	4.9	5.7	4.9	5.7	4.7	5.9	4.8		6.5
CTL	7.7	7.7	7.2	9.3	9.5	8.2	5.2	6.6	10.3	9.2	8.3	7.9	6.7	6.7	7.3	6.6	8.6	7.4	7.4	6.7		8.2
CFL	8.2	7.3	8.0	8.5	9.5	7.8	7.3		8.2	8.3	7.7	7.2	6.7	6.6	7.2	6.3	8.4	7.8	8.3	6.9		7.5
DAO	4.1	5.6	4.4	4.6	3.8	4.9	7.3		4.8	4.6	4.8	5.3	3.4	4.4	4.0	5.2	4.0	4.9	4.2	5.5		5.5
DAI	3.6	3.4	3.6	4.2	3.0	3.7	4.9		4.3	3.2	3.1	3.8	2.8	3.8	2.8	4.0	3.4	3.8	2.0	3.6		3.7

GM = Gulf of Mexico; BAH = Bahamas;
VEN. = Venezuela; USVI = Virgin Islands.

TABLE 3.5

Proportional measurements of *Notorynchus cepedianus*, expressed as a percentage of total length.

	SOUTH AMERICA										
Source	MLP 23-v-84-1	MLP 23-v-84-1	MCZ 801 Holotype H. pectorosus	USNM 38301	USNM 87681	Sadowsky 1970	Menni 1975	Menni 1975	Menni 1975	Menni 1975	La Hille 1928
Sex	F	F	M	M	M	F	M	F	F	M	F
TOT (mm)	337	391	391	445	890	753	793	710	790	740	2070
PRC	62.9	62.1	65.0	62.9	65.7	65.7	64.3	64.6	66.2	67.1	69.0
PRN	1.5	1.3	1.8	0.9	1.3	1.3	1.0	1.4	0.8	1.1	1.0
POR	5.3	4.9	4.6	4.0	4.8	5.2	4.1	4.3	4.5	4.0	3.0
POB	5.3	4.3	6.1	4.5	6.3	4.4					10.0
PSP	13.1	12.0	13.6	11.9	12.0	11.7					12.0
PGI	17.5	15.1	16.6	13.9	18.2	15.3					16.0
HDL	21.1	17.6	19.7	19.8	20.1	19.6	18.0	19.2	19.7	19.4	16.0
PP1	21.1	17.6	19.7	19.8	20.1	19.5	18.0	19.2	19.7	19.4	
PP2	38.9	38.1	38.4	38.2	38.3	40.8		40.8	42.0		
SVL	41.8	39.9	43.7	40.0	42.8	47.9					
PAL	50.7	50.9	53.5	49.9	51.7	52.4		53.2	53.9		43.0
PD2	46.9	46.8	47.1	44.7	50.0		47.2	48.1	49.1	50.6	54.0
DCS	10.4	10.2	10.2		9.9	10.5					10.0
PPS	13.1	13.0	14.1	14.2	11.8	14.4					19.0
PAS	5.9	6.1	7.4	7.2	7.1						8.0
ACS	6.8	6.4	7.2	5.8	5.6	6.5					6.0
EYL	3.3	3.1	3.1	3.6	2.5	2.5	2.5	2.8	2.6	2.8	
EYH	2.4	1.8	2.0	1.8	1.1	1.0					
INO	11.6	10.0	9.2	9.2	10.7	7.7					
NOW	1.5	1.3	1.8	1.3	1.1						
INW	5.0	4.6	4.3	4.0	4.5	4.2	4.2	4.5	4.8	4.6	
ANF	0.9	0.8	0.8	0.4	0.4						
SPL	0.3	0.3	0.3	0.2	0.3	0.4					
ESL	4.7	4.6	4.6	5.2	5.5						
MOL	7.4	6.1	5.6	5.2	5.1	3.7		6.4	6.7		
MOW	11.9	12.0	10.7	9.7	11.6	9.1	11.0	12.0	11.3	12.8	
ULA	3.0	3.6	2.6	1.8	1.6	2.0					
LLA	3.6	3.6	4.1	1.8	2.9	3.9		2.9			
GS1	6.2	6.4	6.1	3.6	6.0	5.5	5.8	6.1	5.6	5.6	
GS2	5.9	5.9	5.4	3.6	5.5	5.0					
GS3	5.0	5.4	4.9	3.4	4.7	4.7	5.4	5.2	5.0	4.8	
GS4	4.7	5.1	4.6	3.1	4.8	4.3					
GS5	4.5	4.6	4.1	2.9	4.3	3.9	4.5	4.5	4.1	4.0	
GS6	4.2	3.8	3.8	2.7	3.5	3.5					
GS7	3.3	3.1	3.3	2.5	2.7	3.0	3.3	3.6	3.2	3.8	
HDH	7.4	7.9	9.5	5.6	8.8	10.4		9.0	9.3		
HDW	13.1	12.3	11.3	11.7	12.6	10.6	8.9	13.3	12.9	13.5	
TRH	7.7	9.0	10.5		10.7	11.2					
TRW	7.1	10.0	9.5		11.0						
CPH	3.9	3.8	4.1	3.6	4.3	4.1					4.0
CPW	3.0	3.1	2.8	2.2	2.8	3.2					
P1L	12.5	11.3	12.3	12.1	13.4						12.0
P1A	12.8	11.8	12.5	11.7	16.2	12.5		12.6	12.6		
P1B	6.8	7.4	6.6	6.7	6.1	7.8					8.0
P1H	10.4	8.2	12.3	10.6	13.1	9.5					
P1I	5.6	5.9	5.6	5.6	7.9	5.2		5.9	6.0		4.0
P1P	10.7	9.7	10.0	10.3	13.5	9.3		9.4	10.7		10.0
P2L	8.9	9.0	9.0	8.5	10.8						10.0
P2A	5.0	5.1	4.6	4.7	5.8						
P2B	6.8	5.9	6.1	5.2	5.4						7.0
P2H	3.0	2.8	3.1	2.7	3.3						
P2I	2.4	2.6	3.3	3.4	4.9						3.0
P2P	5.0	5.6	6.6	4.9	7.5						
CLO			1.5		1.8						
CLI			3.1	3.1	4.8						
CLB			0.5		0.3						
D2L	8.0	8.4	9.0	7.6	9.3						9.0
D2A	7.1	7.4	7.7	6.5	7.9	7.9					
D2B	5.3	6.1	7.4	5.4	7.0	6.9	6.6	7.4	6.3	7.0	5.0
D2H	3.6	3.3	4.3	4.7	4.0	3.8	3.7	3.9	3.7	3.5	
D2I	2.7	2.3	2.0	2.7	2.5	5.2					4.0
D2P	3.3	3.8	3.6	4.5	4.2	3.7					
ANL	7.4	6.9	7.7	6.7	7.5						
ANA	4.7	4.3	4.3	4.0	4.7	6.0					
ANB	5.6	4.9	5.6	4.3	5.6	6.6	5.3	5.0	5.3	5.2	5.0
ANH	2.7	2.6	2.0	2.0	2.8	2.5		2.9	2.3		
ANI	2.1	1.5	1.5	2.2	1.8	1.6					
ANP	3.6	1.3	4.1	1.1	4.0	3.3					
CDM	36.5	37.1	35.8	35.7	34.3	34.3	35.9	34.3	33.2	32.9	31.0
CPV	8.6	8.7	9.7	8.1	8.1	8.3	8.5	8.1	7.1	8.1	
CPL	3.3	2.3	2.6	2.7	3.5						
CPU	18.4	20.5	22.0	17.8	18.3						
CST	5.6	5.6	4.6	6.1	4.5						
CTR	5.3	5.6	5.1	4.9	4.7						
CTL	9.2	9.0	7.9	8.3	6.9						
CFL	9.2	9.2	9.7	8.5	8.4						
DAO	4.7	4.6	5.6		4.7						4.0
DAI	3.9	4.1	4.9		3.9						4.0

SOUTHERN AFRICA

Source	RUSI 7653	DAE 872402-01	DAE 872402-02	DAE 860712	DAE 860910	DAE 871204	DAE 863112-02	DAE 872904	RUSI 19378	DAE 873008	RUSI 4679	DAE 870603	DAE 863112-01
Sex	M	M	M	M	M	M	M	M	M	M	M	M	M
TOT (mm)	1323	1375	1530	1538	1650	1720	1720	1761	1777	1780	1791	1821	1950
PRC	69.5	69.5	68.6	73.1	67.3	66.6	68.3	67.6	71.1	68.5	69.8	67.5	69.7
PRN	3.2	0.5	0.8	1.2	1.7		1.2	0.6	2.7	1.1	3.2	0.5	0.9
POR	4.7	4.1	4.3	4.7	4.1		4.2	4.3	4.6	3.9	4.5	4.1	3.9
POB	6.3	3.8	4.4	4.6	4.5	4.0	4.2	5.5	5.4	4.4	5.7	3.6	3.9
PSP	12.0	10.9	11.3	11.4	11.4	10.3	10.8	11.1	11.8	10.9	11.5	9.9	10.9
PG1	15.2	14.1	14.4	15.5	14.2	13.4	14.0	14.6	14.9	14.1	13.7	13.6	14.2
HDL	16.8	16.7	17.8	18.5	18.3	17.4	18.4	14.6	20.0	16.9	17.3	18.7	18.5
PP1	16.8	16.7	17.8	18.5	18.3	17.4	18.4	18.3	20.0	18.6	17.3	18.7	18.5
PP2	40.9	43.6	42.5	46.2	40.0	42.1	43.4	41.7	45.0	44.7	44.1	42.4	45.1
SVL	46.1	47.4	46.1	50.4	46.7	46.2	48.2	46.8	48.5	48.2	47.5	46.4	50.5
PAL	56.8	57.7	55.8	60.9	57.6	57.6	54.1	54.9	58.5	58.4	57.5	55.5	60.8
PD2	51.4	52.4	51.8	54.0	50.3	50.5	51.7	50.2	52.9	52.2	51.8	50.8	53.6
DCS	11.6	10.8	9.3	10.7	10.7	10.2	9.9	10.9	11.0	9.4	11.0	10.9	10.5
PPS	14.4	19.6	18.3	20.7	18.7	17.4	18.5	18.4	17.4	20.5	19.8	18.0	20.1
PAS	8.2	8.4	7.7	9.1	8.7	7.8	6.7	7.3	8.7	8.4	6.6	8.0	8.2
ACS	6.9	6.9	6.3	7.3	6.7	6.1	6.6	6.9	6.1	6.7	6.7	6.2	7.2
EYL	2.0	1.8	1.9	2.0	1.6	1.6	1.7	1.6	1.9	1.8	1.7	1.8	1.6
EYH	0.9	1.5	1.5	1.3	1.1	1.2	1.5	1.1	1.2	1.1	1.0	1.3	1.1
INO	8.8	8.4	8.9	9.4	9.1	8.4	8.8	8.6	8.3	8.4	7.8	8.4	9.0
NOW	0.9	1.2	1.2	1.4	1.0	0.9	1.0	1.2	1.1	1.1	0.9	1.1	0.9
INW	4.7	4.5	4.6	4.8	4.6	4.2	4.4	4.5	4.3	4.2	4.6	4.1	4.3
ANF	0.5	0.6	0.5	0.4	1.0	0.4	0.4	0.5	0.5	0.6	0.6	0.4	0.5
SPL	0.2	0.2	0.2	0.3	0.2	0.2	0.3	0.2	0.2	0.3	0.2	0.2	0.3
ESL	5.1	5.2	5.4	5.2	5.5	4.5	4.7	4.7	4.9	4.6	4.7	5.0	4.5
MOL	6.6	6.8	5.1	4.3	5.5	4.1	6.8	5.4	6.7	5.6	6.9	5.2	4.4
MOW	10.6	11.3	11.4	11.4	12.7	10.2	12.8	10.8	12.4	11.1	10.8	11.1	11.3
ULA	2.0	3.2	2.8	2.3	3.3	2.8	3.3	2.8	2.1	3.1	2.5	3.2	3.0
LLA	3.3	2.9	2.9	4.0	3.1	3.5	2.3	3.3	3.3	3.1	3.2	2.7	3.6
GS1	5.4	5.6	6.5	6.5	5.7	4.7	6.3	6.2	6.0	6.1	5.8	6.2	4.6
GS2	5.2	5.4	5.4	6.4	5.7	4.5	5.9	5.8	5.7	5.8	5.2	6.0	4.3
GS3	4.5	4.8	5.2	6.1	5.6	4.1	5.7	5.5	5.2	5.2	5.1	5.8	4.1
GS4	4.5	4.4	4.9	5.5	5.2	4.0	5.1	4.7	4.8	5.3	4.9	5.2	3.9
GS5	4.3	4.1	4.6	5.0	4.8	3.8	4.3	4.4	4.3	5.1	4.8	4.8	3.7
GS6	3.6	3.9	4.4	4.6	4.2	3.4	4.0	4.1	3.8	4.4	4.7	4.3	3.5
GS7	2.9	3.6	3.9	4.0	3.6	2.9	3.8	3.6	3.3	3.9	3.5	3.6	2.8
HDH	7.3	7.3	8.2	8.5	11.0	7.4	7.9	7.6	9.0	10.4	8.3	9.1	6.8
HDW	11.0	13.5	14.4	15.6	13.5	13.5	13.5	12.5	13.3	15.2	12.6	14.0	12.8
TRH		7.2	8.0	8.5	15.2	7.3	8.4	8.0	11.5	10.4	8.7	8.8	
TRW		12.7	13.1	16.9	17.0	14.2	14.0	12.6	11.3	14.6	15.1	14.6	
CPH	3.8	3.7	4.1	3.9	4.2	3.8	4.4	3.7	4.3	3.8	4.1	4.1	4.1
CPW	2.5	3.1	3.5	3.1	3.2	2.9	3.8	3.1	3.5	3.3	3.0	3.5	3.2
P1L	11.9	12.4	12.9	13.1	10.3	12.5	12.7	11.9	13.4	12.3	12.6	11.8	11.3
P1A	13.1	12.4	·14.2	14.6	12.5	14.0	14.0	12.5	15.3	14.2	12.9	13.5	12.4
P1B	7.9	7.6	7.6	8.2	7.9	7.8	6.0	7.6	8.8	7.6	7.9	7.0	7.5
P1H	10.4	10.6	11.8	11.4	11.3	10.5	12.4	11.2	11.5	11.4	9.9	11.6	10.3
P1I	4.5	4.7	5.5	6.0	5.1	5.1	5.4	5.5	5.2	5.3	4.8	5.2	3.8
P1P	10.3	10.9	11.4	11.5	12.2	10.5	11.7	11.2	10.2	10.1	10.3	11.1	10.4
P2L	12.3	10.9	13.7	13.7	7.6	12.6	15.1	14.2	14.9	14.3	13.7	14.7	14.4
P2A	6.5	5.7	6.7	6.3	5.8	6.1	7.3	6.1	6.7	6.0	6.1	5.8	6.7
P2B	7.5	6.9	7.6	7.8	7.5	7.1	6.7	7.8	7.5	7.9	8.1	7.4	6.9
P2H	3.4	3.2	4.6	3.4	4.7	3.6	4.5	3.5	3.7	4.2	3.5	4.1	4.1
P2I	5.2	4.7	6.0	7.2	8.2	6.9	8.5	8.0	7.5	7.4	7.4	8.3	7.8
P2P	7.9	8.5	9.7	11.0	12.4	9.0	11.5	10.8	8.7	11.6	9.5	11.8	11.0
CLO	3.7	3.3	4.1	6.1	6.7	6.4	7.8	7.2	5.0	7.4	5.0	7.9	7.3
CLI	6.0	5.2	6.7	7.9	8.7	8.3	9.8	9.2	9.4	10.1	8.3	10.0	9.3
CLB	0.8	0.7	1.0	1.1	0.5	1.1	1.7	1.1	1.5	1.2	1.2	1.3	0.9
D2L	8.2	8.1	9.3	10.2	8.7	9.1	9.7	9.0	10.4	9.0	9.7	8.7	7.8
D2A	7.9	7.3	8.2	9.0	7.1	8.3	8.7	7.7	9.2	8.3	8.9	8.0	7.8
D2B	6.8	6.5	7.1	8.3	7.0	6.7	7.4	7.0	8.0	7.0	7.7	6.9	6.5
D2H	3.6	3.7	5.0	4.2	4.7	4.1	4.5	4.3	4.6	4.0	4.1	4.3	4.2
D2I	1.7	1.6	2.0	2.1	2.4	2.0	2.1	1.8	2.5	2.2	1.7	2.0	2.1
D2P	3.7	3.9	4.9	4.9	4.9	4.4	4.7	4.6	5.0	4.0	4.4	4.7	4.2
ANL	7.3	6.3	7.1	7.9	7.3	6.7	7.4	7.0	8.3	7.0	7.6	6.7	6.7
ANA	5.0	3.9	4.9	4.7	4.2	4.7	5.2	4.4	5.7	4.6	5.4	4.7	4.4
ANB	6.2	4.9	5.8	6.4	6.1	5.1	6.2	5.4	5.6	5.4	6.2	5.7	5.4
ANH	2.5	2.9	3.1	2.6	3.0	2.0	2.9	3.2	3.7	2.4	2.3	2.9	2.8
ANI	1.5	1.2	2.0	1.8	1.8	1.5	1.7	1.5	2.0	1.7	1.5	1.4	1.5
ANP	3.9	4.0	4.4	4.6	5.1	3.8	4.4	4.4	3.8	4.4	4.2	4.2	4.1
CDM	30.5	32.1	31.0	32.3	31.8	30.9	31.5	32.6	29.8	30.9	31.5	32.1	30.4
CPV	7.2	7.0	8.5	8.1	7.4	8.3	8.5	7.8	9.1	8.0	8.2	8.1	8.1
CPL	2.0	1.6	1.6	1.9		1.9	2.2	2.2	3.0	1.7	2.0	1.6	2.5
CPU	19.3	20.4	19.3	21.1	20.9	20.1	18.9	20.4	17.7	18.8	17.6	19.5	18.6
CST	3.7	3.1	3.6	4.2	3.6	3.3	3.8	3.6	3.9	3.9	3.2	3.1	3.5
CTR	3.8	4.5	4.4	4.2	4.5	4.1	4.2	4.0	3.5	4.0	3.9	4.3	4.5
CTL	6.2	6.1	6.5	7.0	6.4	5.6	6.5	6.6	5.9	6.2	6.2	6.0	6.1
CFL	7.8	6.8	7.8	9.0		3.9	8.1	7.3	7.8	7.7	7.5	7.4	3.9
DAO				6.9	5.2		4.9	6.5		5.6	7.0	6.3	
DAI				4.8	5.9		4.3	4.1		4.6	5.0	4.7	

SOUTHERN AFRICA

Source	DAE 880403	DAE 872307	DAE 871705-06	DAE 871604-01	DAE 872308-02	DAE 872308-01	DAE 871705-08	DAE 871705-07	DAE 872105	RUSI 10691	DAE 871705-05	DAE 871604-02	DAE 871604-03	DAE 880203	DAE 871604-04
Sex	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
TOT (mm)	1344	1362	1530	1592	1601	1610	1640	1645	1745	1754	2030	2072	2250	2305	2420
PRC	67.0	72.0	65.7	69.1	67.5	68.3	67.1	69.0	68.1	69.3	68.2	69.8	68.9	69.4	69.6
PRN	0.7	1.7	1.1	1.1	1.0	1.1	0.7	0.7	1.0	1.0	1.4	0.8	0.8	0.9	0.7
POR	4.5	4.6	3.8	4.8	4.6	4.0	4.5	4.7	4.3	3.6	4.4	4.5	4.4	4.3	4.5
POB	4.5	5.3	5.0	4.1	4.7	4.0	5.4	5.5	4.6	4.3	4.9	4.8	4.5	4.3	4.3
PSP	11.2	12.0	11.5	11.4	11.2	11.2	11.5	12.5	11.0	11.1	10.9	10.9	10.0	10.8	10.6
PGI	14.7	14.2	14.7	14.9	15.0	14.9	14.7	16.5	14.5	13.5	14.2	14.5	13.1	14.7	14.3
HDL	18.8	18.7	17.0	18.9	18.0	18.6	18.2	19.7	17.9	19.0		18.3	17.8	19.1	18.4
PP1	18.8	18.7	17.0	18.9	18.0	18.6	18.2	19.7	17.9	19.0		18.3	17.8	19.1	18.4
PP2	43.9	43.3	0.0	42.7	43.1	42.9	42.4	43.8	42.8	44.2	43.7	43.2	45.1	45.8	45.3
SVL	47.0	48.5	45.3	47.8	44.5	48.4	46.6	44.7	46.8	50.2	47.3	47.5	54.2	50.4	50.4
PAL	58.0	59.5	54.4	56.7	56.5	55.9	55.2	59.0	56.7		58.4	57.2	57.9	59.0	58.0
PD2	51.0	54.1	49.0	50.7	51.5	52.5	52.0		51.0	54.4	52.3	51.9	53.2	53.8	52.2
DCS	10.0	11.4	9.9	9.9	9.7	10.2			10.0	11.2	9.9	9.7	10.0	10.2	11.2
PPS	19.0	16.6	0.0	17.4	17.7	16.8			18.3	18.0	18.5	20.8	20.9	19.1	21.8
PAS	7.7	7.3	6.5	6.3	7.6	5.0	7.2	7.3	6.5	6.7		6.9	6.3	6.4	7.7
ACS	6.7	6.6	6.3	7.7	6.7	7.2	8.2		6.4	6.6	6.8	5.8	6.7	7.8	6.9
EYL	2.2	2.0	1.7	1.8	1.8	1.7	1.8		1.5	1.6	1.4	1.5	1.6	1.3	1.3
EYH	1.3	1.2	1.4	1.0	1.3	1.4	1.3	1.5	1.2	1.2	0.8	1.1	1.2	1.3	1.1
INO	10.0	8.5	8.2	9.2	8.5	8.8	9.3	9.1	8.2	9.1	9.1	8.9	9.3	9.0	9.0
NOW	1.2	1.0	1.2	1.3	1.1	1.1	1.2		1.0	1.1	1.0	1.0	1.1	1.1	1.0
INW	4.5	4.4	4.2	4.4	4.6	4.5	4.5	4.8	4.1	5.1	4.6	4.3	4.4	4.5	4.3
ANF	0.4	0.4	0.6	0.6	0.6	0.6	0.4	0.6	0.5	0.5	0.3	0.5	0.5	0.7	0.6
SPL	0.2	0.3	0.3	0.3	0.3	0.2	0.2	0.2	0.3	0.2	0.2	0.1	0.2	0.2	0.2
ESL	4.8	5.4	5.1	4.8	4.7	5.5	5.0	5.5	5.0	4.9	5.3	4.7	4.5	5.3	5.0
MOL	5.6	6.9	6.2	5.8	5.0	5.5	6.1	7.9	6.5	6.8	5.4	5.1	5.0	4.8	4.8
MOW	11.2	10.9	11.4	11.9	11.2	10.3	12.5	11.6	11.9	12.5	11.9	11.5	12.0	10.4	11.4
ULA	1.9	2.2	2.6	2.5	2.2	2.5			2.9	2.0	3.0	2.9	2.7	2.6	2.8
LLA	3.0	3.3	3.3	3.4	2.5	2.9	2.9	2.9	2.3	3.2	2.9	3.2	3.1	2.7	3.1
GS1	6.4	5.6	6.7	6.5	6.4	6.3	6.1	6.6	5.0	6.6	6.4	5.8	7.3	7.4	8.3
GS2	6.0	4.8	5.9	6.3	5.8	5.7	5.7	6.0	4.6	5.9	6.0	5.3	7.0	6.8	8.0
GS3	5.6	4.3	5.6	5.8	5.5	5.5	5.4	5.8	4.6	5.8	5.6	4.9	6.4	6.4	7.2
GS4	5.0	3.7	5.6	5.7	5.0	4.6	4.6	5.2	4.4	5.3	5.0	4.7	6.0	5.6	7.0
GS5	4.5	3.5	4.8	4.8	4.7	4.6	4.5	4.9	4.0	4.7	4.5	4.3	5.3	5.2	6.0
GS6	4.2	3.2	4.3	4.4	4.2	4.3	4.3	4.5	3.7	4.4	3.9	4.0	4.7	4.5	5.4
GS7	3.7	2.8	3.7	3.8	3.6	3.8	3.6	4.3	3.3	3.5	3.8	3.9	4.2	3.5	4.5
HDH	8.9	7.0	7.5	7.2	9.4	10.9	7.9	8.2	6.4	11.1	9.8	7.2	8.9	13.9	7.9
HDW	12.3	12.3	12.0	11.9	13.4	14.0	13.4	13.7	14.7	15.1	14.3	13.0	15.1	15.2	14.6
TRH	11.2	0.0	7.8	6.9	11.2	12.4	7.9	8.2	6.9	11.4	10.6	8.0	9.0	17.4	8.9
TRW	10.2	10.8	12.4	11.9	12.8	14.0	13.4	12.8	13.8	13.9	14.3	15.5	16.4	16.5	17.1
CPH	4.5	3.5	3.8	4.0	4.4	4.2	4.0	4.1	3.5	4.3	4.1	4.3	4.9	4.6	4.5
CPW	3.4		3.3	3.1	3.2	3.4	3.6	3.0	2.5	3.6	3.3	4.1	3.4	3.5	2.9
P1L	12.6	14.0	12.7	12.7	13.4	13.4	12.8	13.0	13.3	14.0	13.8	12.1	12.7	12.6	12.3
P1A	13.4	15.0	13.3	14.6	13.9	14.3	14.6	13.4	15.3	14.8	14.7	12.8	13.7	13.7	13.8
P1B	7.8	8.7	7.8	7.5	8.4	7.6	8.2	8.2	8.2	8.7	8.6	7.7	8.7	8.7	7.4
P1H	11.9	13.4	11.6	11.3	11.9	12.5	12.3	11.6	12.1	11.6	13.3	10.6	11.3	10.6	11.0
P1I	5.6	5.3	5.2	6.0	5.3	5.4	5.2	5.0	5.2	5.7	6.3	4.8	4.2	4.3	5.4
P1P	10.8	12.5	11.8	9.7	11.9	12.9	11.9	12.2	11.8	10.5	12.6	10.1	10.3	10.9	10.2
P2L	9.2	10.6	9.7	10.1	10.3	9.6		10.0	10.3	10.3	10.3	10.1	10.4	10.1	10.2
P2A	6.2	6.4	6.1	6.7	6.2	6.2	6.7	6.3	6.9	6.8	6.8	6.5	6.4	6.4	6.4
P2B	6.7	9.0	8.6	8.5	8.6	7.6		8.5	8.3	8.3	7.4	8.4	8.2	7.5	7.6
P2H	3.6	3.8	4.2	4.0	4.1	4.4		4.0	4.2	4.6	0.0	3.9	7.8	4.1	4.4
P2I	3.0	1.7	2.3	1.9	1.6	2.6		2.4	2.4	2.4	3.4	2.1	2.7	2.6	3.1
P2P	6.7	7.0	6.5	7.2	7.5	6.8		7.0	6.9	7.4	8.2	6.7	7.2	6.9	7.8
CLO															
CLI															
CLB															
D2L	8.9	9.2	9.7	9.4	9.2	8.6	9.5	9.4	9.0	9.1	10.3	8.7	8.9	9.3	9.2
D2A	8.7	8.1	8.5	8.6	8.0	8.3	8.4	8.4	8.5	8.0		7.7	8.2	8.4	8.3
D2B	6.8	7.7	7.8	7.4	7.4	7.5	7.6	7.5	7.0	6.8	7.6	6.5	7.3	7.6	7.2
D2H	4.3	4.4	5.2	4.4	3.7	4.1	4.3	4.4	4.5	4.4	4.4	4.6	4.9	4.5	4.7
D2I	2.2	1.5	2.0	2.2	2.1	1.6	2.2	2.3	2.4	2.3	3.0	2.0	2.2	2.2	2.1
D2P	4.6	4.8	4.3	4.9	4.7	3.9	4.7	5.0	4.0	4.7		3.8	4.9	5.5	5.0
ANL	6.7	7.6	7.3	7.7	7.9	7.5	7.4	7.0	6.9	8.6	5.7	6.6	6.9	6.5	7.1
ANA	4.6	4.4	4.6	5.0	4.4	4.5	5.2	5.2	4.5	6.0	6.5	4.8	4.8	4.6	4.8
ANB	5.6	6.2	5.6	6.2	6.4	6.7	6.2	5.5	5.3	7.2	3.7	5.4	5.8	5.6	5.5
ANH	2.8	3.1	2.5	2.4	2.7	3.1	2.8	2.9	2.6	3.0	3.1	2.5	3.1	2.8	2.9
ANI	1.6	1.5	1.6	1.8	1.5	1.3		1.7	1.7	1.8	2.0	1.2	1.7	1.5	1.6
ANP	4.5	5.1	4.5	4.5	4.7	4.2		4.7	4.8	4.3		3.6	4.4	4.1	4.2
CDM	32.0	27.3	32.7	31.0	32.7	31.7	32.3	32.2	32.8	31.4		29.5	30.4	30.6	30.2
CPV	8.0	9.5	7.7	7.9	8.5	8.1		8.8	8.8	9.1	9.2	8.0	8.0	8.0	9.0
CPL	2.8	2.9	2.0	2.8	1.6	2.6	2.1	1.9	1.9	1.9		2.6	3.2	2.6	3.0
CPU	19.0	20.0	19.9	18.7	20.3	21.1		19.6	19.2	18.5	19.2	17.8	18.7	19.3	19.5
CST	3.9		3.7	3.6	3.2	3.2		4.1	3.4	3.4		3.6	3.7	3.8	4.0
CTR	4.5		4.1	4.1	5.1	4.3		4.1	4.9	3.9		4.2	3.8	3.9	3.7
CTL	6.8		6.5	5.7	6.7	6.2	6.9	6.1	7.2	5.8		6.1	6.0	5.6	5.7
CFL	8.9	9.9	7.1	8.2	9.1	8.0	7.9	8.5	7.9	7.9	8.4	7.0	7.8	7.4	8.3
DAO	5.0	6.8	5.0	5.8	6.4	5.1	4.5		5.8	4.6	4.1	5.7	4.5	4.6	5.6
DAI	3.1	4.8	2.9	4.4	4.5	4.4	3.7		3.8	4.3	3.6	3.6	3.6	3.3	4.4

	AUSTRALIA				CHINA	JAPAN
Source	CSIRO uncat.	CSIRO uncat.	Kemp 1978	Kemp 1978	BM 1895.5.31.29	BM 1939.7.20.2
Sex	M	F	M	M	M	M
TOT (mm)	795	1415	1520	1648	1108	1098
PRC	62.9	66.1	66.5	66.2	64.1	65.7
PRN	1.4	1.1	1.3	1.6	1.2	1.3
POR	4.9	4.2	3.8	3.8	4.2	3.6
POB	3.9	4.0	4.1	4.4	4.2	4.1
PSP	11.6	10.5	10.2	10.7	10.5	10.3
PGI	15.2	13.4	13.2	13.9	13.9	13.8
HDL	18.6	16.9	16.0	17.1	16.5	17.1
PP1	18.6	16.9	16.0	17.1	16.5	17.1
PP2	37.7	40.6	41.5	40.1	40.2	38.6
SVL	40.3	44.4			44.8	41.4
PAL	49.9	52.0	54.9	54.3	52.8	51.5
PD2	45.9	47.3	49.2	48.3	47.8	48.9
DCS	9.9	10.2	10.3	10.6	9.1	9.5
PPS	13.5	18.4	14.4	15.3	19.2	15.0
PAS	6.5	5.2			7.9	7.8
ACS	5.2	6.4	7.0	6.0	6.0	7.1
EYL	2.5	2.2	1.3	1.3	2.1	2.1
EYH	1.4	1.3			1.3	0.6
INO	9.1	9.0			8.4	8.0
NOW	1.1	1.2	1.1	1.2	1.1	1.2
INW	4.2	4.2	4.4	4.4	4.4	4.1
ANF	0.9	0.5			0.5	0.5
SPL	0.4	0.4			0.3	0.2
ESL	4.7	4.5			4.7	4.4
MOL	6.2	6.4	6.5	6.3	5.1	4.3
MOW	9.9	10.9	12.7	11.8	10.5	10.2
ULA	1.5				2.0	1.5
LLA	2.0	2.5	4.4	4.2	2.7	2.7
GS1	5.9	6.0	5.6	5.4	5.8	4.4
GS2	5.5	5.7			5.1	4.1
GS3	5.3	5.4			5.0	3.9
GS4	5.0	5.0	4.9	4.4	4.7	3.7
GS5	4.4	4.3			4.6	3.5
GS6	4.2	3.8			4.2	3.2
GS7	3.4	3.2	2.8	3.2	3.4	2.8
HDH	9.6	10.5			9.4	8.6
HDW	11.8	12.6			12.0	11.1
TRH	9.2	11.4			10.5	9.0
TRW	8.3	9.9			13.1	8.9
CPH	3.3	3.7			4.1	4.0
CPW	2.4	2.6			2.8	2.8
P1L	12.8	12.7			11.8	11.5
P1A	13.6	13.5	13.7	13.5	12.9	13.3
P1B	7.3	7.6	7.6	7.8	6.9	6.7
P1H	10.4	10.7			9.0	7.9
P1I	6.3	5.7	5.7	5.7	5.2	5.0
P1P	10.1	13.1	11.1	11.4	9.0	7.8
P2L	9.4	9.4	8.9	10.4	10.3	9.4
P2A	4.9	6.7	5.7	6.4	6.3	5.2
P2B	6.4	6.9			6.7	6.1
P2H	3.8	5.2			3.0	2.8
P2I	3.4	3.2			4.4	3.5
P2P	6.2	6.6			7.7	5.4
CLO	1.5				1.7	1.5
CLI	4.2		5.6	6.4	4.2	4.4
CLB	0.4				0.5	0.4
D2L	9.1	11.4			8.5	8.5
D2A	7.5	10.1			7.9	7.5
D2B	6.4	9.0	6.6	7.7	6.3	5.8
D2H	3.9	4.8	4.1	4.3	4.6	3.8
D2I	2.4	2.5	2.0	2.3	2.3	2.4
D2P	4.3	4.9			4.2	4.3
ANL	7.4	8.6			6.2	6.6
ANA	5.8	5.7			4.5	4.1
ANB	6.0	6.5	4.5	6.0	4.9	4.8
ANH	2.6	3.4	2.4	2.7	3.2	3.0
ANI	1.6	1.8	1.6	1.9	1.6	1.6
ANP	3.6	3.7			3.4	3.6
CDM	37.7	33.6	33.7	34.5	35.6	34.6
CPV	10.6	9.2	8.7	9.4	8.3	7.6
CPL	1.3	2.0			3.9	4.6
CPU	21.3	19.9			17.6	18.0
CST	4.7	4.1			3.3	3.3
CTR	4.8	4.1			4.6	4.2
CTL	7.7	6.9	7.5	6.8	6.9	6.3
CFL	9.4	9.6			9.2	8.8
DAO	4.5	5.2			6.2	4.7
DAI	3.3	6.7			3.2	4.1

CALIFORNIA

Source	USNM 27191	CAS uncat.	DAE 820605-01	CAS 1950-IX: 19-04	DAE 872212-05	CAS 12653	CAS 1950-IX: 19-02	LJVC 0485	LJVC 0039	CAS 1950-IX: 19-03	LJVC 0038	CAS 1951-IV: 6-02	DAE 821806	CAS 36578	CAS 1951-IX: 30-01	CAS 1949-IV:18	CAS 1951-IV:6	LJVC 802610	LJVC 802510	LJVC 802710	DAE 851906	LJVC 802810	DAE 850605
Sex	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
TOT (mm)	417	435	454	577	592	615	628	640	694	714	717	809	932	940	945	965	1265	1435	1513	1850	2260	2262	2430
PRC	62.1	61.6	62.1	61.4	63.3	63.4	63.4	64.8	63.1	63.2	65.6	63.0	65.5	62.2	64.4	64.5	66.1	69.0	67.1	68.1	66.8	69.0	70.0
PRN	1.7	1.1	0.2	1.0	1.5	1.1	0.8	0.8	1.2	1.1	0.8	1.0	1.0	1.1	1.5	0.6	1.1	1.3	1.6	1.5	3.1	1.8	1.6
POR	4.1	4.6	3.5	4.0	5.1	4.4	3.7	4.4	4.8	4.5	4.6	4.6	4.3	4.4	4.6	5.0	4.6	4.9	4.8	3.8	4.0	4.7	5.3
POB	5.0	5.5	4.4	4.2	4.7	5.0	4.6	4.8	4.3	5.2	4.5	5.2	4.5	4.4	6.1	5.0	5.0				6.4	0.0	5.6
PSP	12.5	11.7	11.5	10.7	11.8	11.5	11.0	11.4	11.1	11.6	10.7	11.4	10.9	11.6	12.1	11.7	12.7				11.9	0.0	11.5
PGI	14.9	14.0	14.8	14.6	15.4	14.5	13.4	14.4	14.4	15.3	14.4	14.2	14.1	16.0	14.3	15.3	15.4				14.4	0.0	15.2
HDL	18.7	17.9	16.3	19.1	18.4	16.9	16.4	17.5	18.6	19.3	17.7	18.4	16.0	19.1	18.8	19.7	20.0	18.9	19.2	17.8	19.0	16.8	19.8
PP1	18.7	17.9	16.3	19.1	18.4	16.9	16.4	17.5	18.6	19.3	17.7	18.4	16.0	19.1	18.8	19.7	20.0	18.9	19.2	17.8	19.0	16.8	19.8
PP2	37.9	37.5	35.9	36.6	40.2	38.7	37.4	39.1	38.6	38.5	38.9	39.2	41.0	37.0	38.9	39.0	39.4	40.4	44.0	42.4	45.1	43.5	45.3
SVL	42.7	41.1	39.2	40.7	43.8	42.3	40.3	42.3	44.4	41.0	56.9	43.3	44.3	41.2	42.6	43.0	43.3	44.6	48.6	48.6	49.6	48.9	49.8
PAL	51.3	51.0	51.1	50.8	52.4	52.8	49.4	52.2	50.7	53.5	52.7	50.9	55.0	50.5	52.0	52.2	53.3	53.7	55.5	56.2	57.5	57.3	60.1
PD2	47.0	44.4	46.3	45.1	45.9	46.3	47.5	46.9	45.5	47.6	47.1	46.1	48.8	46.8	46.8	45.1	46.7	50.2	48.6	49.5	48.7	51.1	52.7
DCS	10.1	9.4	10.4	9.2	9.6	9.9	10.8	10.6	9.8	8.8	10.3	10.6	10.6	10.3	10.6	10.8	11.1	10.9	9.6	9.2	11.5	9.5	11.1
PPS	13.7	11.0	15.6	11.3	15.2	16.6	14.3	15.3	14.3	13.6	15.1	13.8	17.6	12.7	13.2	13.7	15.1	17.2	18.5	18.4	23.0	18.7	20.2
PAS	6.7	7.1	7.7	8.5	8.1	7.0	5.7	7.0	6.6	7.6	7.7	5.9	7.3	6.4	6.7	6.5	7.7	6.4	6.1	7.0	8.4	6.5	9.9
ACS	7.2	6.9	7.7	5.7	5.2	6.8	7.0	7.8	6.3	7.6	6.6	6.9	6.9	6.1	6.8	7.7	8.6	7.2	5.2	5.4	8.0	5.1	7.8
EYL	2.6	3.2	2.9	2.8	3.0	2.6	2.2	2.3	2.4	2.5	2.4	2.2	2.1	2.2	2.1	2.1	1.7	1.9	1.7	1.6	1.3	1.4	1.4
EYH	1.7	1.1	2.0	1.4	1.2	1.3	1.8	0.9	0.7	1.4	0.8	1.4	1.0	1.4	1.3	0.8	1.3				0.9		0.8
INO	9.6	9.2	8.6	8.5	9.1	8.0	9.2	8.0	7.6	9.0	8.6	8.5	7.0	8.5	6.9	9.4	9.1						7.4
NOW	1.2	1.4	1.3	1.2	1.4	1.3	1.1	1.4	1.2	1.3	1.0	1.2	1.2	0.9	1.3	1.0	1.3	1.0	1.1	1.1	0.9	1.0	1.0
INW	4.1	4.4	4.0	4.2	4.2	4.4	4.5	4.1	4.2	4.5	3.8	4.3	3.6	4.0	4.6	4.9	4.4	4.2	4.2	4.3	4.2	4.0	4.1
ANF	0.5	0.5	0.7	0.5	0.5	0.5	0.3	0.5	0.6	0.7	0.6	0.4	0.3	0.4	0.5	0.4	0.6				0.2		
SPL	0.2	0.5	0.4	0.3	0.3	0.2	0.3	0.2	0.1	0.4	0.3	0.4	0.2	0.2	0.2	0.3	0.2	0.2	0.2	0.2	0.2	0.3	0.2
ESL	4.8	4.1	4.2	4.2	4.7	4.2	4.6	4.8	4.5	4.3	3.8	4.7	4.2	4.4	4.0	4.6	4.6				5.1		5.8
MOL	3.6	5.5	4.6	3.3	4.7	5.5	5.3	5.6	5.2	4.8	5.6	4.3	5.0	5.4	5.8	5.0	4.6	5.2	5.9	5.9	6.6	5.7	7.4
MOW	10.1	9.0	9.7	9.7	10.1	9.9	10.0	10.0	9.5	9.2	9.5	9.4	8.6	9.5	10.1	10.3	8.9	11.6	11.5	11.2	11.9	11.8	10.9
ULA	1.4	1.4	2.2	1.9	2.4	1.6	1.9	2.7	2.0	1.7	2.8	2.0	2.3	1.4	1.9	1.9	2.0				1.5		3.5
LLA	2.2	2.5	2.2	2.4	1.9	2.6	3.0	2.8	2.4	2.7	2.5	2.7	3.3	2.4	2.5	2.6	2.9	3.6	3.7	2.8	3.1	2.3	3.7
GS1	6.0	4.8	5.7	4.9	4.9	4.6	5.4	4.8	4.0	5.3	4.0	4.7	3.4	4.4	5.9	5.8	5.7	5.9	5.4	5.3	6.2	5.9	5.8
GS2	5.3	4.6	5.3	4.5	4.6	3.9	4.5	4.2	3.9	5.0	3.8	4.3	3.3	4.3	5.5	5.4	5.5	5.8	4.5	5.0	6.2	5.5	5.6
GS3	5.0	4.1	4.8	4.0	4.4	3.7	4.1	4.2	3.7	4.8	3.5	4.2	3.0	3.8	5.2	5.1	5.1	5.6	4.4	4.7	6.0	5.3	4.9
GS4	4.1	3.9	4.8	3.8	4.1	3.6	3.8	4.1	3.7	4.5	3.5	4.0	2.9	3.7	4.9	4.7	4.9	5.2	4.2	4.6	5.8	5.0	4.7
GS5	3.8	3.4	4.6	3.6	3.9	3.4	3.7	3.8	3.5	3.9	3.3	3.6	2.8	3.5	4.6	4.2	4.4	4.8	3.8	4.0	5.5	4.3	4.5
GS6	3.4	3.2	4.4	3.5	3.5	3.1	3.3	3.6	3.0	3.6	3.1	3.3	2.6	3.4	4.0	3.8	4.0	4.5	3.6	3.5	4.9	4.1	4.3
GS7	2.9	3.0	4.2	3.1	2.9	2.6	3.0	3.0	2.7	2.8	2.6	3.1	2.4	2.8	3.5	3.0	3.3	4.0	3.4	3.2	4.4	3.3	3.5
HDH	7.7	6.9	7.9	8.5	8.8		8.0	6.4	7.9	7.4	7.4	8.2	6.4	8.8	10.3	8.7	9.0				10.0		8.6
HDW	9.8	10.6	12.6	11.8	11.5		11.3	10.8	11.4	11.2	11.2	10.8	12.0	10.9	11.6	13.0	11.3				15.0		12.8
TRH	9.1	6.2	7.7	8.3	8.3		8.9	9.4	7.8	10.9	9.3	9.3	10.2	8.7	11.1	9.8	10.3	13.9	11.8	12.4	10.4	12.8	9.5
TRW	9.4	8.5	11.2	9.0	8.1		7.8	9.8	8.8	8.8	9.3	9.9	3.6	7.8	9.5	10.9	11.6	12.5	8.9	12.2	12.2	9.8	14.0
CPH	3.8	3.4	3.7	4.0	3.9	3.7	4.1	3.8	3.6	3.8	3.9	3.5	2.1	3.8	4.2	4.2	4.0				5.3		3.9
CPW	2.9	2.5	2.6	2.8	2.7	2.3	2.5	1.9	2.4	2.8	2.5	2.8	12.0	2.7	3.3	3.1	3.1				3.5		3.3
P1L	12.5	11.5	11.7	11.8	11.8	11.5	11.5	11.4	11.7	12.2	11.7	12.0	12.0	12.0	12.1	12.8	11.6				12.4		
P1A	12.9	11.0	11.7	12.5	11.8	11.7	11.5	11.3	11.7	11.9	12.3	12.0	12.3	13.0	12.7	13.9	12.9	14.4	13.0	13.4	11.7	13.3	13.8
P1B	7.0	6.4	7.0	6.6	6.8	9.3	7.2	7.0	6.5	7.6	6.6	7.0	7.5	6.7	7.1	7.9	6.6	6.8	6.9	7.1	7.5	7.5	8.2
P1H	9.8	8.3	8.6	9.9	8.1	8.6	8.6	8.1	9.1	8.7	9.5	9.6	10.0	10.0	9.7	9.9	9.6				11.5		14.2
P1I	5.3	5.3	4.6	5.7	5.6	4.9	5.4	4.4	5.2	4.6	4.5	4.9	4.7	5.2	5.3	5.5	4.9	5.4	4.8	4.7	5.8	4.3	4.1
P1P	8.6	8.5	8.1	9.2	8.4	6.7	7.0	8.0	8.8	9.4	9.2	8.8	9.1	9.4	8.8	9.7	9.2				10.8		8.8
P2L	9.6	9.0	8.8	9.4	9.1	8.9	9.4	8.4	9.4	9.4	8.9	9.4	10.3	9.9	10.2	11.1	11.3	11.3	10.8	12.7	14.8	14.2	15.2
P2A	4.8	4.1	4.6	5.0	4.7	4.6	4.8	4.5	4.9	5.3	5.4	4.6	5.5	5.4	5.3	5.8	6.3	6.3	5.4	6.4	7.3	6.9	7.2
P2B	6.7	5.7	5.7	6.4	6.3	6.0	6.5	6.1	6.1	6.2	6.1	5.9	7.2	6.4	6.3	7.5	7.4				8.8		7.8
P2H	3.4	3.0	2.6	2.8	2.2	2.6	2.7	1.9	2.7	2.8	2.4	3.0	3.2	2.7	2.9	2.6	2.6				6.4		4.9
P2I	3.4	3.2	3.1	2.9	2.7	2.8	2.9	2.3	2.9	2.8	2.8	3.5	3.4	3.4	3.6	3.6	4.0				8.0		8.4
P2P	6.2	6.4	6.2	5.4	6.4	6.3	6.5	4.7	5.3	6.2	5.3	5.9	6.9	6.1	6.3	7.3	6.5				11.5		12.8
CLO	1.4	0.9	1.1	1.2	1.4	1.1	1.3	1.1	1.0	1.3	1.3	1.4	1.6	1.2	1.8	1.7	2.1				8.8		8.6
CLI	3.6	2.3	2.2	2.3	1.7	1.5	2.1	3.6	3.3	2.1	3.6	2.3	3.0	2.4	2.8	2.8	3.6	3.2	4.2	6.6	9.7	7.3	9.9
CLB	0.5	0.5	0.2	0.3	0.3	0.2	0.5	0.3	0.3	0.3	0.4	0.4	0.3	0.3	0.4	0.4	0.4				1.3		1.4
D2L	9.1	7.8	8.6	8.8	9.6	8.9	8.4	9.1	9.4	9.1	8.9	8.3	9.2	9.4	9.5	10.4	9.5				9.7		10.9
D2A	8.4	7.8	7.9	8.3	8.8	8.5	7.3	8.0	8.5	8.4	8.4	8.0	7.5	7.7	8.6	9.7	9.3				8.6		9.5
D2B	7.0	6.0	6.2	6.4	7.3	6.7	6.1	7.0	7.5	6.6	6.7	6.8	6.8	7.0	7.4	7.6	7.4	7.9	8.1	8.6	7.5	8.3	8.8
D2H	4.8	3.2	3.7	3.8	4.4	3.6	3.7	3.8	3.6	4.2	3.9	4.0	4.0	3.7	3.5	4.7	4.7	4.9	4.7	5.2	6.2	5.1	4.9
D2I	2.2	2.5	2.6	2.4	2.5	2.4	2.2	1.9	2.3	2.7	2.2	2.1	2.4	1.9	2.2	2.5	2.5				2.2		1.9
D2P	4.1	3.7	3.1	3.6	3.9	4.6	3.8	3.6	4.0	3.5	3.8	4.3	4.7	4.3	4.4	4.4	4.0				5.1		5.8
ANL	6.2	6.4	5.9	5.9	6.4	6.3	6.7	6.6	6.5	6.2	6.1	6.6	6.4	6.6	6.6	7.4	6.6				6.9		6.6
ANA	4.3	3.2	4.0	4.0	4.2	4.4	4.1	4.5	4.3	3.8	4.3	4.3	4.7	3.9	4.2	4.7	4.8				5.5		4.7
ANB	5.0	3.9	4.6	4.0	4.6	4.9	4.9	5.0	4.9	4.2	4.9	4.3	5.0	5.2	5.2	5.4	5.0	5.6	5.8	6.9	6.0	6.3	4.9
ANH	3.4	2.3	2.4	2.3	2.2	2.0	2.2	2.2	2.2	2.4	2.2	2.2	2.8	2.1	2.4	2.8	2.5	3.6	3.0	3.6	4.2	3.7	3.7
ANI	1.9	2.1	2.0	1.9	1.7	1.8	1.8	1.7	1.7	1.7	1.7	1.9	1.7	1.4	1.7	2.2	1.6				1.3		1.9
ANP	3.6	3.9	3.1	3.1	3.4	3.9	3.7	3.4	3.5	3.4	3.3	3.2	3.6	4.1	3.4	3.8	3.6				4.0		4.1
CDM	37.9	36.6	37.4	38.1	37.2	35.8	34.6	35.2	37.8	35.6	34.9	36.5	34.8	37.8	35.2	35.0	34.8	34.8	32.1	31.9	32.7	31.6	31.1
CPV	7.7	7.6	8.4	7.1	7.6	7.2	7.3	6.6	7.2	6.6	7.8	8.5	8.2	8.0	7.9	8.3	9.1	9.0	8.5	8.8	9.3	9.0	9.5
CPL	2.6	3.4	3.1	2.9	3.0	3.6	2.9	2.5	2.4	3.1	3.1	3.0	2.8	2.8	2.9	2.2	3.5				6.4		6.4
CPU	22.5	21.6	20.9	20.3	21.8	21.3	19.4	20.5	22.3	19.7	20.4	19.9	19.5	22.7	21.2	21.2	20.6				19.9		20.6
CST	4.6	5.7	4.8	4.2	4.2	4.6	3.8	4.2	4.3	4.1	3.8	3.8	4.0	3.4	4.1	4.6	3.6				3.5		2.9
CTR	5.5	5.1	5.7	5.7	5.2	4.6	5.3	4.1	4.8	4.6	4.9	4.9	4.0	4.9	4.9	4.0	4.7				4.0		3.3
CTL	8.6	8.5	8.8	8.3	7.8	8.0	8.0	7.2	7.3	7.4	7.3	7.3	6.4	7.2	7.5	6.7	7.0				7.5		4.5
CFL	8.4	8.0	9.0	7.6	9.1	7.8	8.0	7.2	8.5	7.4	7.8	8.3	8.2	8.5	8.4	9.2	8.5				11.1		9.5
DAO	6.0	5.5	5.3	6.1	6.6	5.9	5.7	5.9	5.6	5.6	6.7	5.6	5.7	5.0	6.6	5.9	7.1				7.3		8.2
DAI	4.3	4.1	4.0	3.6	3.7	4.2	3.2	3.9	3.7	3.6	4.0	4.0	4.3	4.1	3.7	3.8	4.0				5.8		6.6

CALIFORNIA

Source	USNM 27191	CAS 39612	CAS 40577	CAS 1951-IX:30	CAS 1948-XII:3	CAS 1950-IX: 19-01	CAS 1951-IV:6	DAE 823004	LJVC 0176	LJVC 0066	LJVC 802510	LJVC 0065	LJVC 802010
Sex	F	F	F	F	F	F	F	F	F	F	F	F	F
TOT (mm)	451	555	600	625	640	655	756	854	1190	1402	1726	1833	1865
PRC	58.5	61.3	62.7	63.2	63.1	64.1	64.2	64.4	65.0	66.1	67.5	66.4	67.0
PRN	1.3	1.1	1.3	1.1	0.8	0.5	1.2	1.1	0.8	1.2	1.1	1.4	1.7
POR	4.0	4.9	4.8	4.5	4.2	4.4	4.6	4.3			5.2		4.7
POB	4.7	4.7	5.0	5.9	4.5	5.0	5.4	4.7	4.7	4.1		3.9	
PSP	12.2	12.3	11.8	12.0	11.6	12.2	12.4	10.8	11.3	10.8		10.5	
PGI	15.1	15.7	15.2	15.0	15.5	15.6	16.1	14.3	15.0	14.8		14.3	
HDL	18.8	18.0	17.2	18.9	19.4	19.7	18.8	18.5	17.7	17.8	17.4	18.2	16.8
PP1	18.8	18.0	17.2	18.9	19.4	19.7	18.8	18.5	17.7	17.8	17.4	18.2	16.8
PP2	36.1	37.7	38.0	39.7	38.3	41.2	39.4	40.2	41.6	42.3	42.9	44.1	42.1
SVL	40.1	41.4	42.5	43.2	42.5	45.6	43.7	44.3	46.1	45.3	48.1	49.2	46.1
PAL	47.9	50.1	50.7	52.2	52.0	53.7	52.2	51.1	53.4	54.9	55.3	55.6	54.7
PD2	44.3	45.6	45.0	45.8	46.9	49.2	47.9	46.3	48.7	49.5	49.8	50.4	49.9
DCS	8.9	10.3	11.0	10.4	10.6	8.4	10.1	10.9	10.5	10.4	10.1	9.5	10.2
PPS	16.9	11.0	15.5	13.8	12.3	14.0	13.0	16.3	17.6	18.2	18.5	20.5	18.2
PAS	6.4	5.8	5.0	6.7	6.9	5.3	5.8	4.9	5.8	6.3	5.5	5.7	5.5
ACS	8.4	7.7	5.8	6.7	7.3	7.9	7.9	7.1	6.1	6.8	6.2	6.3	6.6
EYL	2.9	3.1	2.5	2.6	2.5	2.1	2.4	2.5	1.4	1.8	1.4	1.6	1.5
EYH	1.8	1.1	1.5	1.0	1.3	1.7	1.2	1.1	0.9	1.3		1.2	
INO	9.5	9.2	8.7	8.5	9.2	9.2	8.9	8.5	8.6	8.5		8.3	
NOW	1.3	1.1	1.0	1.4	1.7	1.4	1.2	0.9	0.8	1.0	0.9	1.0	1.1
INW	4.9	4.3	4.3	4.5	4.4	4.7	4.6	3.9	3.9	3.6	4.3	3.8	4.0
ANF	0.7	0.4	0.5	0.8	0.8	0.5	0.7	0.2	0.3	0.4			
SPL	0.2	0.4	0.2	0.2	0.5	0.3	0.4	0.1	0.1	0.2	0.2	0.2	0.3
ESL	4.4	4.3	4.3	4.5	4.4	4.7	4.5	4.6			0.0	0.0	0.0
MOL	3.8	6.5	5.5	6.6	5.3	6.0	4.8	5.5	10.9	6.1	5.4	6.4	4.9
MOW	9.5	9.4	10.3	10.6	9.7	10.5	9.1	10.0	11.8	11.9	11.5	12.0	12.0
ULA	1.6	1.6	1.7	1.9	1.9	1.8	1.9	1.6					
LLA	2.4	2.3	2.0	2.4	3.3	2.6	2.8	2.5	3.6	2.8	2.7	2.7	2.1
GS1	5.5	4.1	4.2	5.0	4.1	5.8	4.8	3.5	6.7	7.3	5.6	6.2	6.3
GS2	5.5	3.6	4.2	4.5	3.8	5.5	4.6	3.3	6.7		5.3		5.8
GS3	5.3	3.2	4.0	4.2	3.6	5.2	4.5	3.0	6.1		4.9		5.6
GS4	4.7	3.2	3.8	4.0	3.4	4.7	4.0	2.8	5.3		4.8		5.5
GS5	4.2	3.1	3.8	3.7	3.4	4.3	3.7	2.6	5.3		4.4		4.7
GS6	3.5	2.9	3.3	3.4	3.3	4.0	3.4	2.3	4.4		4.3		4.1
GS7	2.9	2.5	2.7	3.0	3.1	3.5	2.9	2.1	3.4	3.6	3.5	3.8	3.7
HDH	7.3	8.8	7.3	8.5	8.0	8.9	9.0	5.9					
HDW	8.6	9.7	11.8	12.0	10.5	13.1	11.0	12.3					
TRH		9.7	8.3	8.2	8.3	9.6	9.7		12.5		12.7	10.6	14.6
TRW		7.9	7.5	9.1	7.5	9.8	9.9	8.3	11.3	11.8	10.0	12.2	13.6
CPH	3.8	4.1	3.8	4.2	3.6	4.0	4.0	3.7	4.4	3.9		3.9	
CPW	2.7	2.7	2.5	2.7	2.3	2.7	3.0	2.7	3.2	3.0		3.1	
P1L	11.5	12.3	11.8	11.8	12.0	11.9	11.5	12.5	12.5	12.3		12.2	
P1A	12.9	12.4	11.5	12.0	12.0	12.5	12.8	13.5	13.4	14.9	13.0	13.7	13.7
P1B	6.2	6.8	6.8	7.0	7.0	6.7	6.7	7.1	8.7	7.6		8.5	
P1H	8.4	7.6	9.2	9.0	9.5	9.5	8.9	9.6					
P1I	5.1	5.0	4.5	5.6	5.2	5.8	5.4	5.6	5.2	5.3	4.7	5.5	4.9
P1P	6.7	9.5	8.5	9.3	9.5	10.2	9.8	9.3	9.6	9.6		9.9	
P2L	9.1	8.8	8.8	8.3	8.9	8.7	9.3	8.8	9.1	10.1	9.6	9.8	9.4
P2A	5.8	5.2	5.3	4.8	5.2	5.0	5.2	5.2	5.6	6.3	6.4	5.9	6.2
P2B	8.0	7.2	6.8	6.2	7.0	6.4	6.9	6.8	7.6	7.8		7.2	
P2H	3.3	2.9	2.8	2.6	3.1	2.6	3.3	2.9					
P2I	2.2	2.0	1.5	1.9	1.7	1.7	2.5	2.1	2.1	3.1		2.6	
P2P	4.7	5.6	5.7	5.4	5.9	6.6	6.2	6.2	6.7	6.0		6.9	
CLO													
CLI													
CLB													
D2L	7.8	8.8	9.3	10.2	9.5	9.2	9.8	9.1					
D2A	7.3	8.5	8.0	9.6	7.3	7.3	8.3	8.5	9.7	8.8		8.7	
D2B	5.1	7.2	7.0	8.0	7.0	6.4	7.4	7.3	7.2	6.8	8.1	6.7	7.7
D2H	4.2	7.2	4.0	4.3	4.1	4.0	4.2	4.6	4.9	5.1	4.7	5.3	5.5
D2I	2.4	2.2	2.2	2.1	2.3	2.1	2.4	2.0	2.0	2.3		1.9	
D2P	3.5	4.1	4.2	4.2	5.3	4.7	4.2	4.3	4.6	4.1		4.4	
ANL	6.0	6.7	6.7	6.9	7.2	6.9	6.9	7.7					
ANA	4.2	4.7	4.3	5.0	4.4	4.7	4.2	5.2	4.8	3.4		4.6	
ANB	4.4	4.9	5.2	5.4	5.5	5.0	5.2	6.0	7.6	5.3	6.4	5.0	6.3
ANH	2.0	2.7	2.5	2.6	2.5	2.6	2.6	2.9	2.8	3.1	3.2	4.1	3.5
ANI	1.6	1.6	1.7	1.8	1.9	1.8	1.9	1.8	1.8	1.9		1.8	
ANP	2.7	3.8	3.2	3.4	4.1	3.7	4.0	4.1	3.9	3.5		4.0	
CDM	37.7	38.9	36.2	36.6	35.9	36.0	35.4	37.0	34.1	33.7	32.3	33.8	31.6
CPV	8.4	7.7	8.0	7.5	7.3		9.0	7.3			8.1		8.5
CPL	3.1	2.2	2.5	3.4	3.6		3.6	3.0					
CPU	21.1	20.2	21.2	20.8	20.2	23.4	20.0	19.9					
CST	4.4	4.7	4.5	4.5	4.1	3.7	3.8	4.0					
CTR	5.5	5.0	4.8	5.4	4.8	5.2	5.2	5.0					
CTL	8.6	8.3	8.0	7.8	7.3	6.7	7.8	7.5					
CFL	10.2	8.6	9.2	9.0	8.9	8.9	8.5	7.4					
DAO	5.1	5.0	5.7	6.4	6.9	4.7	5.8	5.0					
DAI	3.5	3.4	4.2	4.0	4.5	3.5	3.4	3.6					