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PALEOECOLOGY OF EOCENE ANTARCTIC SHARKS

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A diverse shark assemblage consisting of 17 taxa in 10 families has been collected from the middle to late Eocene La Meseta Formation on Seymour Island, northern Antarctic Peninsula. Paleoecological associations with the diverse shark assemblage suggest a temperate marine environment for the La Meseta Formation with four ecological components: (1) a resident shallow water community dominated by *Carcharias macrota*; (2) a deepwater fauna consisting mainly of squaloid sharks that occasionally entered the La Meseta area from deeper, offshore areas through daily or seasonal vertical migrations; (3) a transitional, eurybathic group of sharks that inhabited both inshore shallow and offshore pelagic and deep areas; and (4) shallow water tropical migrants that occasionally entered the La Meseta area from warmer northern areas.

INTRODUCTION

Hundreds of Cenozoic shark-bearing fossil localities are known throughout the world, and faunal assemblages from many of these localities are described in the literature [*Cappetta*, 1987]. In almost every case, the focus of these studies is on tooth identification and taxonomic designation and, to some degree, on stratigraphy and age correlation. Scant attention, if ever, is given on the ecological relationships of the sharks to other fossils recovered from the locality and between the different fossil shark taxa within. Sharks may have particular habitat or climatic requirements and can be separated into groups depending on the general habitats which they occupy (nearshore, outer shelf, slope, etc.) Thus they can supply ecological information regarding the depositional environment of the fossil locality. Conversely, analysis of invertebrate faunas and sedimentology can supply information about the sharks in a paleoecological context. This study will show the complexities, limitations, and importance in making a paleoecological interpretation of a diverse fossil shark fauna.

At least 17 taxa of sharks within 10 families (Table 1) occur in the middle to late Eocene La Meseta Formation on Seymour Island, Antarctic Peninsula (Figure 1). In contrast to the Eocene, the present-day seas around Antarctica are extremely cold and provide habitat for only a few species of sharks. The squaloid sharks *Somniosus microcephalus* and *Etmopterus lucifer* and the lamnoid shark *Lamna nasus* have been recorded within Antarctic waters; all occur infrequently within the Antarctic Convergence, and none are found in the waters around continental Antarctica [*Svetlov*, 1978; *Compagno*, 1990]. In the late Eocene, however, the waters adjacent to what is now Seymour Island were considerably warmer and had a much more diverse neoselachian fauna with several ecological components (Table 2, Figure 2).

GEOLOGY

Seymour Island lies in the Weddell Sea off the northeastern tip of the Antarctic Peninsula at approximately latitude 64°15′S and longitude 56°45′W, almost directly south of Tierra del Fuego, South America (Figure 1*a*). The stratigraphic sequence of marine sediments on Seymour Island (Figure 1*b*) extends from the Upper Cretaceous (Lopez de Bertodano Formation) through the lower Paleocene (Sobral Formation) and the upper Paleocene (Cross Valley Formation) to the middle and late Eocene (La Meseta Formation) [*Woodburne and Zinsmeister*, 1984; *Sadler*, 1988]. The Eocene beds of the La Meseta Formation are exposed on the northern portion of Seymour Island.

The La Meseta Formation is composed of poorly consolidated marine sandstones, siltstones, clays, and shell beds. Preserved within these strata are the remains of a diverse vertebrate and invertebrate nearshore fauna. The La Meseta Formation is divided into seven numbered units within three sections (Figure 3) [*Sadler*, 1988]. Unit I at the base of the La Meseta Formation is a sequence of unconsolidated fine and silty sands; Unit II is a sequence of highly fossiliferous fine laminated sands and conglomerates; Unit III consists of fine sands with intervals of clays and sandy gravels [*Welton and Zinsmeister*, 1980; *Woodburne and Zinsmeister*, 1984]. Of these seven units, Telm 2–5 contain the bulk of fossil shark localities, and the uppermost units, Telm 6–7, contain no fossil sharks [*Long*, 1992].

TABLE 1. Sharks From the Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula

	Primary Bathymetric Ecology
Hexanchidae	
Heptranchias howelli	deep water
Squalidae	
Squalus weltoni	deep water, transitional
Squalus woodburnei	deep water, transitional
Centrophorus sp.	deep water
Deania sp.	deep water
Dalatias licha	deep water
Pristiophoridae	
Pristiophorus lanceolatus	transitional
Squatinidae	
Squatina sp.	transitional
Stegostomatidae	
Stegostoma cf. *S. fasciatum*	shallow water tropical migrant
Ginglymostomatidae	
Pseudoginglymostoma cf. *P. brevicaudatum*	shallow water tropical migrant
Odontaspididae	
Carcharias macrota	shallow water resident
Odontaspis rutoti	transitional
Odontaspis winkleri	transitional
Mitsukurinidae	
Anomotodon multidenticulata	deep water
Lamnidae	
Carcharocles auriculatus	transitional
Lamna cf. *L. nasus*	transitional
Carcharhinidae	
Scoliodon sp.	shallow water tropical migrant

PALEOECOLOGY

The La Meseta Formation represents a shallow, nearshore, moderate to high-energy depositional environment. Precise depth has not been estimated, but the La Meseta Formation is believed to represent a littoral to shallow sublittoral inner shelf setting. Evidence supporting this interpretation comes from ichnofossils [*Wiedman and Feldmann*, 1988], decapods [*Feldmann and Wilson*, 1988], cirripeds [*Zullo et al.*, 1988], and molluscs [*Zinsmeister*, 1982] and from the sedimentology of the La Meseta Formation [*Sadler*, 1988].

Woodburne and Zinsmeister [1984], *Case* [1988], and *Mohr* [1990] suggested that the terrestrial environment around peninsular Antarctica during the late Eocene was heavily vegetated and had a humid, temperate climate similar to present-day New Zealand or southern South America. The marine environment was also temperate. This idea is supported primarily by the diverse molluscan and arthropod faunas found within the formation [*Zinsmeister*, 1982; *Feldmann and Wilson*, 1989]. Other lines of evidence for a temperate marine environment come from microfossils. The Weddell Sea, adjacent to present-day Seymour Island, began to cool after a period of relatively warm marine temperatures in the Paleocene and early Eocene; by the middle and late Eocene, the marine climate was temperate. Information from calcareous nannofossils [*Pospichal and Wise*, 1990; *Wei and Wise*, 1990] and planktonic and benthic forams [*Stott and Kennett*, 1990; *Thomas*, 1990] confirms this. In a review of fossil penguins from Seymour Island, *Simpson* [1971] also implied that the marine climate at that time was temperate.

A comparison of the fossil shark taxa with those of their closest living relatives and their present distributions show that all of the sharks from the La Meseta Formation were adapted to a temperate marine environment or ranged well within such environments. *Lamna nasus* is widely dispersed in temperate oceans today, even ranging into subpolar regions, and prefers cool-temperate waters [*Svetlov*, 1978; *Castro*, 1983; *Compagno*, 1984, 1990]. Both the extinct *Carcharias macrota* and the living *C. taurus* are (and were) widespread in subtropical, temperate, and cool-temperate waters. Many species of *Squatina* live in tropical to temperate waters, often near the interface with sub-Arctic and Antarctic waters [*Compagno*, 1984]. The range of *Squalus* (*S. acanthias* in this case) in the northern hemisphere extends from subtropical to Arctic waters, including those of Scandinavia, Greenland, and the Bering Sea; *Squalus* in the southern hemisphere is also found in temperate waters [*Compagno*, 1984]. *Dalatias licha* is found in temperate waters off New Zealand, southern Australia, and South Africa, as well as in the cool-temperate waters on both sides of the North Atlantic [*Castro*, 1983; *Compagno*, 1984].

On the basis of the above distributions, as well as the

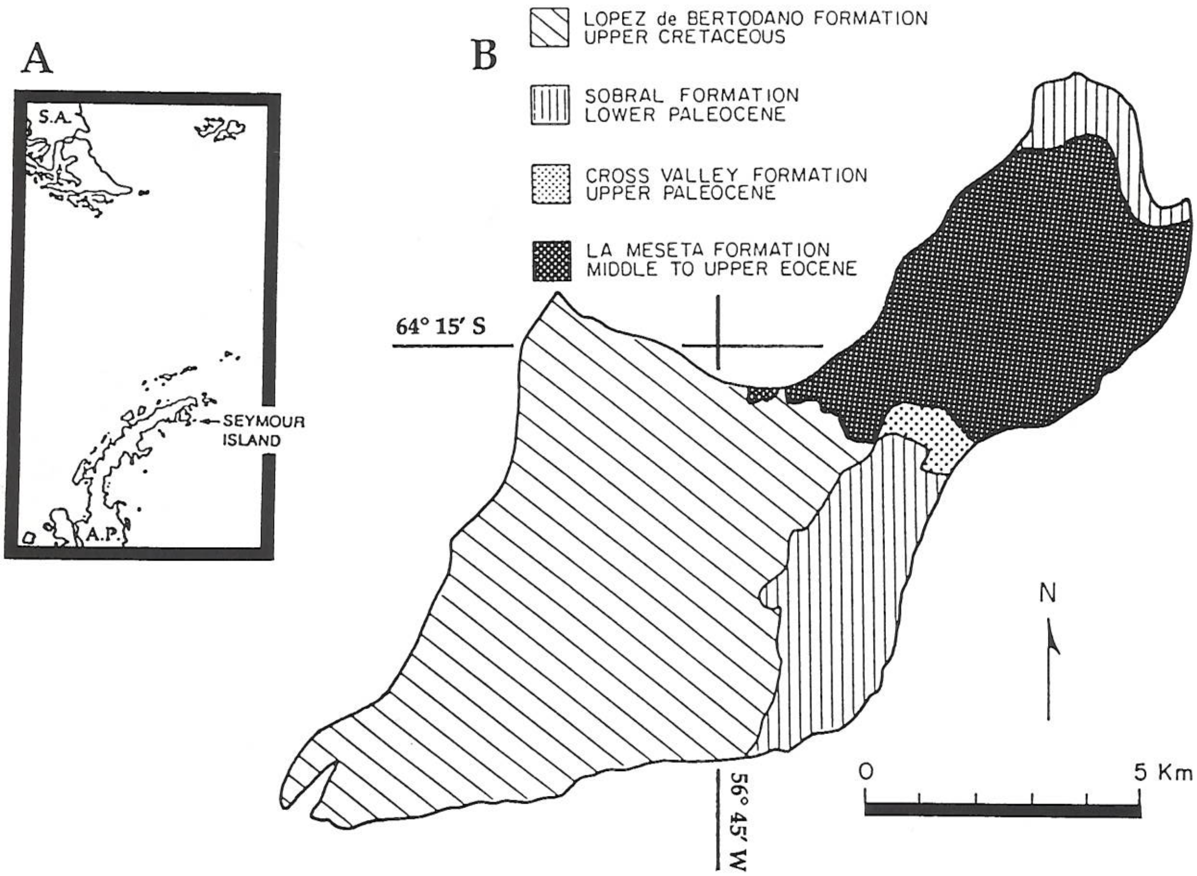

Fig. 1. (*a*) Seymour Island in geographic relationship to southern South America (S.A.) and the Antarctic Peninsula (A.P.). (*b*) Diagram of Seymour Island showing the four geological formations including the La Meseta Formation.

paucity of any Eocene taxa thought to have inhabited warm waters (such as the carcharhinids *Galeocerdo*, *Hemipristis*, *Sphyrna*, *Negaprion*, and *Carcharhinus*), the elasmobranch fauna of the La Meseta Formation seems to be characteristic of a temperate marine habitat. *Kennett and Barker* [1990] estimated the marine paleotemperature of the Seymour Island area, on the basis of oxygen isotope ratios of late Eocene fossil invertebrate shells, to be 8°C for the minimum winter temperature and 12°C for the minimum summer temperature. This temperature estimate is consistent with the water temperature inferred from the late Eocene shark fauna. However, several taxa of warm water sharks are found in the La Meseta Formation, but for reasons given below, these are considered anomalous occurrences.

As part of the paleobathymetric considerations of their geologic occurrences, fossil shark remains can be

TABLE 2. Habitats of Eocene Sharks, La Meseta Formation, Antarctic Peninsula

	Shallow Tropical Migrant	Shallow Temperate Resident	Transitional Temperate Resident	Deepwater Temperate Resident
No. of genera	3	1	6*	6*
No. of specimens	5	591	289	93
Percent of total	0.5	60	30	9.5

**Squalus* is included as both a transitional and a deepwater form, on the basis of other fossil taxa and on modern analogs.

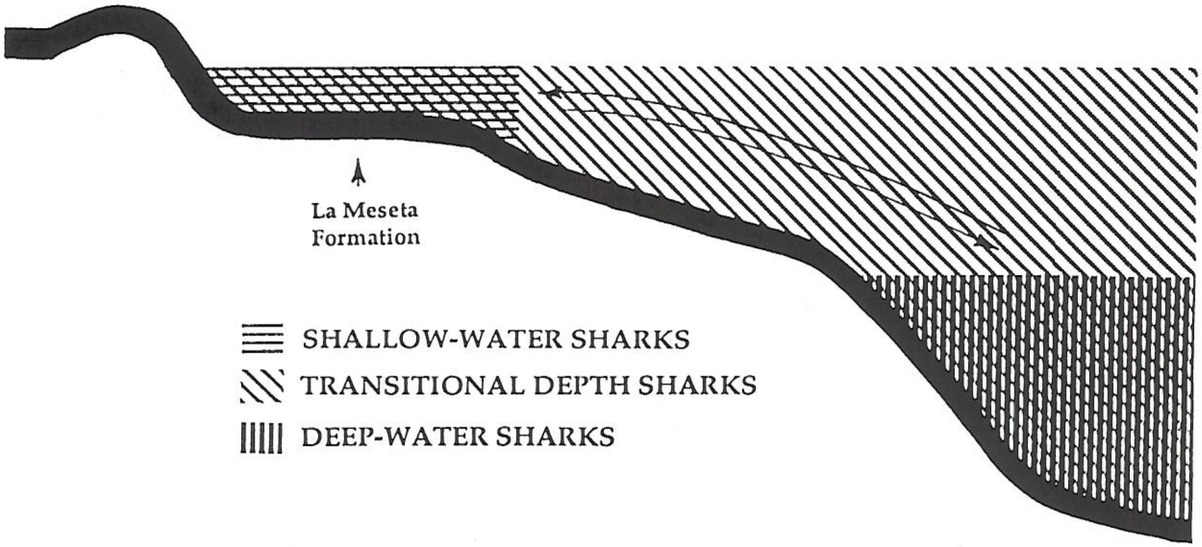

Fig. 2. A hypothetical diagram of a portion of the western Weddell Sea showing the three major shark habitats of the La Meseta depositional environment and adjacent areas. Arrows show the direction of occasional migration by deepwater sharks into the shallow depositional environment. Vertical and horizontal distances not to scale.

used as indicators of the general depth at which they once lived. Inasmuch as sharks can be large and highly mobile aquatic vertebrates, their application for paleobathymetry may not be as precise as those of sessile or limited-ranging invertebrates. However, extant sharks do live within certain depth ranges that are distinct, and these ranges can be compared and summarized with some reliability. In using such ranges to infer paleobathymetry, it is essential to compare the fossils to those of other known fossil sharks and their previously understood paleobathymetric ranges, as well as the depth ranges of living relatives. In doing so with the La Meseta shark fossils, a discontinuity becomes apparent. Although the La Meseta fossils are preserved within a single depositional setting, the sharks lived in different bathymetric and ecological zones. These bathymetric zones include an expected shallow water shark fauna dominated by *Carcharias* and an anomalous deepwater shark fauna characterized by a diversity of squaliform sharks. Complicating matters are several species of sharks that have ranges overlapping these zones. There are also several shark species that may not have been endemic to the La Meseta depositional paleoenvironment but may have strayed in from warmer northern waters. First, however, the shallow water forms will be discussed.

Temperate Shallow Water Residents

Zinsmeister [1979] and *Woodburne and Zinsmeister* [1984] state that the seas around western Antarctica and the Antarctic Peninsula were shallow and geographically extensive. This area, termed the Weddellian Province, extended from South America along both the east and west sides of the Antarctic Peninsula to eastern Australia and contained many small islands with shallow beaches and coastlines. Such habitats were ideally suited for *Carcharias*, whose modern depth range is normally no deeper than several meters. These sharks are most abundant along shallow coastal beaches and in bays, being found most often along the tideline and in the surf zone, although a few individuals may stray to deeper outer shelf waters [*Bigelow and Schroeder*, 1948; *Castro*, 1983; *Compagno*, 1984]. It is not surprising that the overwhelming majority of fossil shark teeth from the La Meseta Formation, 60% of the total sample, are those of *Carcharias* (Table 2). These coastal sharks most probably lived and foraged along the shorelines of the Seymour Island area in the late Eocene.

Temperate Deepwater Residents

A significant number of teeth from the La Meseta Formation (9.5%) are from sharks that are almost strictly deepwater inhabitants today but whose fossils are incorporated into the shallow La Meseta depositional environment (Table 2). These taxa were almost certainly specialized for a deepwater habitat in the Eocene as well; so their occurrence in the La Meseta Formation is noteworthy. These sharks include *Heptranchias*, *Centrophorus*, *Deania*, and *Dalatias*, which presently live on the outer shelf or upper slope at depths of 200 m or more, and *Squalus*, which commonly ranges from shallow water to well below 100 m [*Bigelow and*

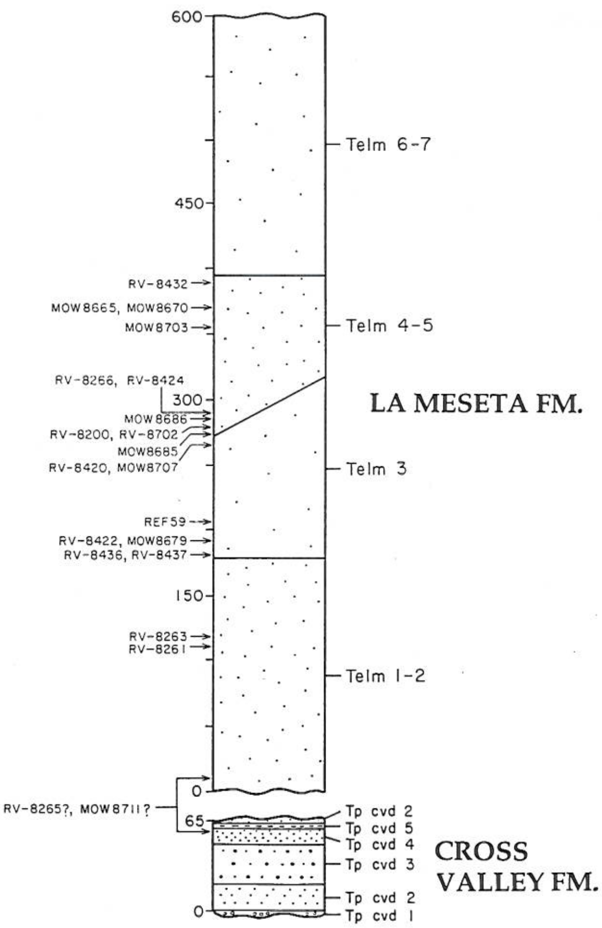

Fig. 3. Stratigraphic column of the La Meseta Formation showing the seven units within three sections and showing the shark-bearing localities. Locality abbreviations are as follows: RV, University of California Riverside vertebrate field locality; MOW, Michael O. Woodburne field locality; REF, R. Ewan Fordyce field locality [from *Long*, 1992].

Schroeder, 1948, 1957; *Compagno*, 1984]. *Cappetta* [1987] regards *Anomotodon* as a deepwater species because it is aligned with the presently deepwater family Mitsukurinidae which live at depths of 200 m to 700 m. The teeth of all of these deepwater species are not exceedingly abundant in the shallow water La Meseta Formation but are too common to be ignored as just anomalous occurrences. There are plausible explanations for their occurrence alongside shallow water coastal vertebrates and invertebrates.

Zinsmeister and Feldmann [1984], *Wiedman et al.* [1988], and *Blake and Zinsmeister* [1988] noted the occurrence of many species of endemic invertebrates from the shallow La Meseta Formation that are restricted to deepwater habitats today. Theoretically, these early forms evolved in south polar latitudes in the early Cenozoic and radiated into deepwater habitats in the late Cenozoic. This scenario does not hold true for the deepwater sharks recovered from the La Meseta Formation. First, unlike the invertebrates, most of the shark taxa were not restricted to the La Meseta area in the Eocene, but had a cosmopolitan or bitemperate distribution by that time [*Long*, 1992]. Second, many of these deepwater shark species are known from strictly deepwater marine deposits, both Eocene and older, elsewhere on the globe [*Long*, 1992; *Welton*, 1979; *Keyes*, 1984; *Cappetta*, 1987]. This indicates they already lived primarily in deep water in the Eocene. In addition, remarkable whole-body preservation of deepwater sharks from the Cretaceous of Lebanon shows that present-day deepwater shark families (Hexanchidae, Squalidae, and Mitsukurinidae, among others) already possessed specialized morphological adaptations for a deepwater existence [*Cappetta*, 1980]. These lines of evidence, in addition to the known bathymetric ranges of their extant representatives, lend support to my contention that these Eocene taxa were inhabitants of deep water and were not shallow water taxa that radiated out into deeper waters in the late Cenozoic, as did many invertebrate groups.

The diversity of deepwater shark species found within the La Meseta Formation suggests the presence of local deepwater habitats. However, *Zinsmeister* [1979] and *Woodburne and Zinsmeister* [1984] claimed that western and peninsular Antarctica was a vast area of islands within a shallow sea. Such a large expanse of relatively shallow coastal water provided an ideal habitat for the shallow water sharks (especially *Carcharias*) and some bony fishes, but not for the deepwater squalomorph sharks. It seems that these deep-dwelling sharks must have lived in adjacent offshore deepwater trenches, canyons, rifts, and outer shelf and slope habitats better suited for them. If so, portions of the early Cenozoic seafloor in West Antarctica during the Eocene must have dropped steeply to sublittoral depths. In the Eocene Weddell Sea, many taxa of deepwater (upper abyssal to lower bathyal) foraminifera have been recovered, proving that deepwater habitats did exist around that area in the Eocene [*Thomas*, 1990]. According to *Woodburne and Zinsmeister* [1984], an extensive subduction zone ran from the western coast of South America down along the present-day Antarctic Peninsula from the mid-Mesozoic to the late Oligocene. This tectonic action could have created a series of deep and lengthy trenches that provided suitable habitat for the deepwater sharks and other deepwater fishes. Also, rifting between Antarctica-Australia and Antarctica-Africa produced many deepwater trenches and basins that would have provided suitable deepwater habitats.

These teeth could not have been reworked from older deposits because they do not exhibit any postdepositional wear or breakage. The teeth of *Centrophorus* and *Deania* are thin and delicate and especially prone to breakage during erosion and reworking. Instead, these teeth were shed and deposited by the deepwater sharks while they were alive in the La Meseta environment. These deepwater sharks migrated into the La Meseta area from adjacent deepwater habitats. Many authors [*Bigelow and Schroeder*, 1948, 1957; *Bass et al.*, 1976; *Castro*, 1983; *Compagno*, 1984; *Compagno et al.*, 1990; *Lavenberg*, 1991] recorded the occurrences of primarily deepwater sharks in relatively shallow water (including a specimen of *Centrophorus* from a depth of 3 m) and suggested that some species may perform vertical migrations. Migration into the shallows could have been for one or several reasons.

Some deepwater sharks and fishes exhibit cyclical daily migrations from deep areas into shallow coastal areas and surface waters and back again. These migrations may be related to the diel movements of the deep scattering layers (DSL), stratified layers of fishes and invertebrates that ascend the water column at night to feed in surface waters and descend into deeper waters with the rise of the Sun [*Dietz*, 1962; *Holton*, 1969; *Lavenberg*, 1991]. Deep scattering layers are found in most of the world's oceans, including the coastal waters off Antarctica [*Dietz*, 1948, 1962]. The vertical depth at which these layers shift within the water column is dependent on the availability and intensity of direct or ambient light within the upper layers of water. The inhabitants of the DSL may protect themselves from predators by concealing themselves in the dark, unlit depths during the day [*Dietz*, 1962]. These organisms are found below the maximum depth that sunlight can penetrate. As the Sun sets and the intensity of sunlight decreases, the DSL rise to the surface, following the ascending depth of visible light, and diffuse into the inner shelf; on dark nights, DSL organisms can be found well into coastal areas [*Dietz*, 1962].

Sharks are a virtually unknown component of the DSL, and their direct relationship to the DSL is unclear. Sharks may follow these layers as they rise and fall through the course of the day, following behind and feeding on the migrating fishes and invertebrates [*Castro*, 1983; *Lavenberg*, 1991]. Large "blob fish" seen on the echograms of the DSL from sounding equipment are suspected to be sharks or large fishes; these "blob fish" are usually seen on the bottom of the DSL as it rises in the early evening [*Dietz*, 1962]. Little is known about sharks in the DSL because deepwater sharks are infrequently caught in trawls and tow sampling through the DSL. These relatively large and mobile organisms may avoid nets designed for smaller and slower deepwater organisms [*Merrett et al.*, 1991]. Like many fishes in the DSL [*Holton*, 1969; *Pearcey et al.*, 1977], sharks may make the vertical migration occasionally, not every day, and therefore would not frequently be captured.

If these deepwater sharks were not directly associated with the DSL, they may have performed diel vertical migrations in much the same way. These sharks probably lived in deeper offshore areas during the day and moved into shallower coastal areas to hunt and feed at night [*Castro*, 1983; *Compagno et al.*, 1990; *Lavenberg*, 1991]. Capture data by *Bigelow and Schroeder* [1957] and others show that many of the shallow depth records are from sharks captured at night, suggesting nocturnal vertical migration. Like the DSL, some deepwater sharks also stay at depths below the level of sunlight penetration and may follow this level to shallower depths in the evening. Some species of deepwater sharks in the families Hexanchidae and Squalidae have an organ on the top of their head called a pineal window (connected to the pineal complex of the brain) that is believed to detect the amount of downwelling ambient light and may serve to mediate vertical migrations [*Clark and Kristof*, 1990, 1991]. It is interesting to note that the two families of deepwater sharks that have a pineal window are the most abundant families of deepwater sharks in the La Meseta Formation.

The proximity of these deepwater areas to the La Meseta Formation is uncertain, but the relative abundance of deepwater sharks and fishes [*Long*, 1991, 1992] suggests that these areas are in relatively close proximity. Vertically migrating sharks need not be fast swimmers, since they would be migrating onshore and offshore for at least 6 hours in each direction, allowing them enough time to move relatively long distances. For example, the DSL descends at speeds of up to 7.5 m/min [*Dietz*, 1962], and *Centrophorus* can swim at speeds of over 2 km per hour [*Yano and Tanaka*, 1986]; so they could travel up to 12 km or more inshore during one vertical migration. Larger squaloid hexanchid sharks (*Dalatias* and *Heptranchias*, respectively) can swim faster and hence travel further in a given time period. Additionally, since the depth of the DSL, and of sharks migrating independently of it, is determined by the depth of sunlight penetration, deepwater organisms would be found at shallower depths for longer periods of time during the almost continual darkness and twilight during the austral summer.

Deepwater sharks may have also entered shallow water on a seasonal basis. *Bigelow and Schroeder* [1948] and *Compagno* [1984] discuss the seasonal movements of *Squalus* and remark that their abundance in coastal areas is due largely to shifts in marine temperature. These sharks avoid water above 15°C, and so they are more numerous in coastal waters during cool seasonal periods. These sharks follow the temperature regime into deeper offshore waters as coastal waters warm with the onset of seasonal change. *Ketchen* [1986] and *Compagno* [1984] also note that pregnant females often migrate into shallow waters to give birth, and *Ketchen* [1986] also states that schools of *Squalus* will periodically swim into upper surface waters and into shallow coastal areas to feed on aggregations of prey.

Transitional Temperate Residents

Several other shark species were transitional between the shallow water and deepwater habitats, based on the ecologies of their living relatives and on the depositional environment of fossil material from other localities. These sharks either had individuals that roamed freely and sporadically between deepwater and shallow water areas without the influence of any particular diurnal or seasonal cycle or had individuals that inhabited particular areas between and including these areas. For example, *Squatina* lives at a depth between 3 m and 1300 meters, but a particular individual may move several hundred meters a day within a particular home range or upslope and downslope [*Compagno*, 1984; *Standora and Nelson*, 1977]. *Squatina* and *Pristiophorus* were primarily benthic in their habits. *Squalus* is regarded as both a deepwater and a transitional taxon, because some extant congeners live in both types of habitats. *Squalus* and both species of *Odontaspis* occupied lower water and midwater depths, and *Lamna* and *Carcharocles* primarily occupied upper water layers both inshore and offshore. All six of these taxa may have ranged freely between the deepwater and shallow water areas and exploited the resources of the habitats in these two zones. The common occurrence of teeth (30%) from these taxa in the La Meseta Formation agrees with this finding (Table 2).

Tropical Shallow Water Migrants

Several species of nonresident shallow water sharks, including *Pseudoginglymostoma*, *Stegostoma*, and *Scoliodon*, occur infrequently in the La Meseta Formation and probably were more common in warmer subtropical or warm-temperate waters to the north. The movements of these sharks into the La Meseta area during the Eocene could have been facilitated by fluctuations of ocean currents or periodic or prolonged warming of coastal waters; or these individuals may have strayed far outside of their normal range. Recent examples of this type of displacement can be seen off the west coast of North America, when warm El Niño currents periodically drive pelagic, inshore, and benthic sharks far into northern areas normally too cool for them. They may stay in these areas for as long as several years until the normal oceanographic condition returns [*Hubbs*, 1948; *Radovich*, 1961; *Karinen et al.*, 1985]. Similar phenomena in the southern hemisphere have been noted by *Velez et al.* [1984] off Peru and by *Compagno et al.* [1989] off southern Africa. These warm water sharks follow the advancing warm water masses into previously cooler areas, but since sharks continually shed their teeth, they will be deposited into their temporary environment and be preserved in the fossil record. The teeth of these shallow, warm water taxa are rare (0.5%, Table 2), and this rarity suggests that the required oceanographic phenomena were also infrequent.

SUMMARY

Most shark paleontologists refer to a collection of shark taxa from a certain locality as an "assemblage," merely a collection of teeth and usually not in an ecological or community context. The paleoecology of the sharks from a particular locality is little discussed aside from a gross generalization of the habitat or climate. As this study shows, a shark assemblage can be a very complex assortment of sharks from many different habitats converging on one specific locality. The La Meseta shark fauna supports many previous observations and interpretations on the paleoenvironment of the western Weddell Sea in the Eocene from invertebrates. More importantly, an understanding of the paleoecology, paleobiogeography, paleobathymetry, taphonomy, and sedimentology of the Eocene western Weddell Sea area is essential for an accurate and meaningful interpretation of the shark assemblage.

On the basis of their extant analogs, the Eocene shark fauna is indicative of a temperate marine climate influenced by periodic short-term warming. In the diverse La Meseta shark assemblage, four distinct ecological groups are represented at this single locality. The dominant ecological group is a shallow water fauna composed almost entirely of *Carcharias macrota* and accounts for 60% of the fossil specimens. The second most abundant ecological group is six genera that are transitional between shallow and deep waters. These account for 30% of the fossil specimens. There are also a significant number of sharks (9.5% of the fossil sample) that live almost entirely in deep water today but are found in the shallow La Meseta Formation in the Eocene. These sharks probably lived in adjacent deepwater areas and migrated into shallow waters on a cyclical diurnal or seasonal basis and deposited their teeth as they fed in the shallows. If this assumption is correct, it is the earliest indication of vertical migration in sharks. Several species of tropical, shallow water sharks (0.5% of the total sample) have also been recovered from the La Meseta Formation, and these are suspected to be migrants from warmer northern waters that entered the La Meseta area during periodic warm water fluctuations.

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