

## Causes and contrasts in current and past distribution of the white shark (*Lamniformes: Carcharodon carcharias*) off southeastern South America

Alberto Luis CIONE<sup>1</sup> & María Julia BARLA<sup>2</sup>

<sup>1</sup>División Paleontología de Vertebrados, Museo de La Plata, 1900 La Plata, Argentina.  
E-mail: acione@museo.fcnym.unlp.edu.ar. <sup>2</sup>Facultad de Ciencias Naturales y Museo,  
1900 La Plata, Argentina.

**Abstract:** The great white shark is a cosmopolitan temperate marine species which is rare in Argentina, Uruguay, and Brazil today. Several publications include the white shark as inhabiting Patagonian waters. However, there is no recent or fossil record of the white shark south of S 38° 30' in the southwestern Atlantic. A tooth found in Quaternary sediments at Pehuencó (S 38° 56'), southern Buenos Aires province, is the southernmost occurrence of the species in the southwestern Atlantic. The occurrence of *C. carcharias* in the Buenos Aires province is another confirmation that the Argentine biogeographic province extends to the south of the Río de la Plata. The present extremely scarce record indicates that there are not permanent living populations in the South American Atlantic coast but occasional transient individuals. However, the abundant fossil and archaeological record suggests that it was much more common in southwestern Atlantic during the late Pleistocene and Holocene than today. This drop in abundance is here mostly attributed to the massive extermination of pinnipeds and cetaceans during the XIX<sup>th</sup> and XX<sup>th</sup> centuries. Patagonian waters, where marine mammals are relatively abundant even today, might be too cold for the species which is mostly encountered between 15-23°C. Besides, another important predator, the killer whale, which also feeds on marine mammals, is frequently found in these waters. Consequently, available evidence suggests that unrestricted hunting of pinnipeds and cetaceans also decimated another animal, a fish.

**Keywords:** *Carcharodon carcharias*, white shark, Argentina, Atlantic, pinniped, cetacean, biogeography.

**Resumen:** **Causas y contrastes en la distribución presente y pasada del tiburón blanco (*Lamniformes: Carcharodon carcharias*) costa afuera de Sud América sudoriental.** El tiburón blanco es una especie cosmopolita en mares templados y que es rara actualmente en Argentina, Uruguay y Brasil. Varias publicaciones incluyen a tiburón blanco como habitando aguas patagónicas. Sin embargo, no hay registro actual o fósil al sur de S 38° 30' en el Atlántico sudoccidental. Un diente hallado en sedimentos cuaternarios en Pehuencó (S 38° 56'), sur de la provincia de Buenos Aires es el registro más austral en el Atlántico sudoccidental. El registro actual de *C. carcharias* en la provincia de Buenos Aires es otra confirmación de que la provincia biogeográfica Argentina se extiende al sur del Río de la Plata. El extremadamente escaso registro actual indica que no hay poblaciones permanentes en la costa atlántica sudamericana sino individuos aislados. Sin embargo, el abundante registro fósil y arqueológico sugiere que fue mucho más común durante el Pleistoceno tardío y el Holoceno. La disminución de la abundancia es aquí principalmente atribuida al exterminio masivo de pinípedos y cetáceos en los siglos XIX<sup>th</sup> y XX<sup>th</sup>. Las aguas patagónicas, donde todavía hay abundancia de mamíferos marinos podrían ser demasiado frías para la especie, que es más frecuente entre 15° y 23 °C. Por otra parte, la orca, que también se alimenta de mamíferos marinos, es frecuente en esas aguas. Consecuentemente, la evidencia disponible sugiere que la caza irrestricta de pinípedos y cetáceos eliminó otro animal, un pez.

Palabras clave: *Carcharodon carcharias*, tiburón blanco, Argentina, Atlántico, pinípedo, cetáceo, biogeografía.

### INTRODUCTION

*Carcharodon carcharias* is a large, predatory shark that has a cosmopolitan distribution throughout temperate seas and oceans and occasionally penetrates tropical zones (Fergusson, 1996; Compagno, 2001; Fig. 1). In the present southwestern Atlantic coasts, *C. carcharias* has been reported on few occasions (Siccardi et al., 1981; Gadig & Rosa, 1996; Soto et al., 1998) al-

though it has been considered to occupy shelf waters from northern Brazil to southern Patagonia (Compagno, 2001; Fig. 3).

Soto et al. (1998) mention that the white shark is known as "puntudo" in Argentina. However, the white shark is so rare in Argentinean coasts that it has no vernacular name (see Menni et al., 1984). In sheer contrast with its present rarity, teeth of *C. carcharias* were frequently found in Pleistocene and Holocene marine beds

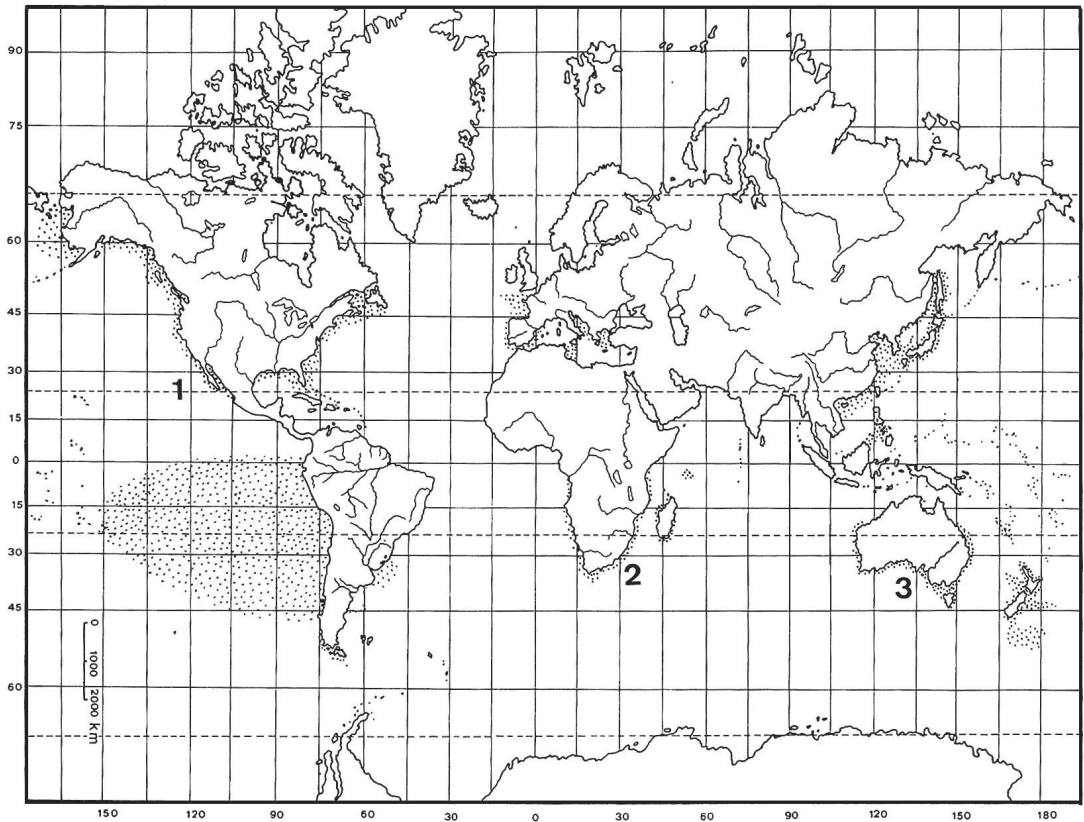


Fig. 1. Distribution of *Carcharodon carcharias* according to Compagno (2001). In shadows the world distribution of the species is shown, whereas 1 (California), 2 (South Africa) and 3 (Great Australian Bight) indicate sites where it is more abundant.

and archaeological sites in Brazil and Argentina (see below). This fossil abundance also contrasts with the comparatively few records of other Pleistocene and Holocene marine fishes in southern South America (see Perea & Ubilla, 1981; Tonni & Cione, 1984; Richter, 1987; Cione & Torno, 1988; Arratia & Cione, 1996; Gadig & Rosa, 1996; Pardiñas *et al.*, 1996; Martínez *et al.*, 1998).

At present, scientists are often preoccupied with biodiversity and its conservation, and *Carcharodon carcharias* is currently protected in many countries (see below). Consequently, understanding of the causes that provoked the important drop in the white shark abundance in the area, may help in protecting this fish in other regions of the world.

In this paper, the present dearth of *C. carcharias* in the southwestern Atlantic in comparison with its Pleistocene and Holocene abundance is discussed and its southernmost distribution is commented on.

#### FOSSIL AND ARCHAEOLOGICAL RECORD OF *CARCHARODON CARCHARIAS* IN SOUTHERN SOUTH AMERICA

Frenguelli (1920, 1922) reported the finding of one tooth of *Carcharodon rondeleti* (= *Carcharodon carcharias*) from the top of the Paraná Formation (formerly named "Entrerriense," early Tortonian, late Miocene, Entre Ríos; Cione *et al.*, 2000; Fig. 3). The material was not preserved but additional teeth are under study by one of us (ALC) at present.

Teeth of *C. carcharias* are fairly abundant in the Pliocene of Chile and Perú (de Muizon & DeVries, 1985; Long, 1993; Suárez & Brito, 2000; Walsh & Hume, 2001; Fig. 3).

In the Estado do Rio Grande do Sul (Brazil), several teeth coming from undetermined Quaternary beds were reported from two localities (Richter, 1987; Sekiguchi, 1994).

In Argentina, Ameghino (1898:243) named (but not depicted) a new species, *Carcharias pampeanus*, from the "Belgranense, Pampeano

medio de La Plata". The short description ("*Carcharias pampeanus* Ameghino con dientes en forma de triángulo isósceles perfecto, de 3 cm de alto por 2 de ancho, de cara interna muy convexa, la externa plana y los bordes dentellados en toda su extensión, con dienteillos muy gruesos..") agrees in size and the coarse serrations with the teeth of *C. carcharias* (see Cione, 1983). However, the original material was not found in the museums where Ameghino worked. The beds assigned to the "Belgranense" are at present correlated with the last interglacial (Illinois-Wisconsin, Isotope Stage 5; ca. 120 ka; Pardiñas *et al.*, 1996; Tonni & Cione, 1999). Other Quaternary teeth of *C. carcharias* have been reported from paleontological and archaeological sites at Pehuencó, Santa Clara del Mar, Centinela del Mar, and Cañada de Arregui in eastern Buenos Aires province (Cione, 1983; Arratia & Cione, 1996; Cione & Bonomo, 2003; Fig. 3).

Teeth of *C. carcharias* are frequently found in early-middle Holocene archaeological sites in the coasts of Rio de Janeiro, São Paulo, Santa Catarina, and Rio Grande do Sul in Brazil (Barbosa & Franco, 1991; Gadig & Rosa, 1996; Fig. 2).

#### SOUTHERN SOUTH AMERICAN BIOGEOGRAPHY

López (1964) recognized three biogeographic provinces in the Atlantic South American coast: West Indian (warm waters; southern boundary at about S 23°), Argentine (warm temperate waters; between S 23° and 41-43°) and Magallanian (northern boundary at S 41°-43°; cold temperate waters; Fig. 3). Balech (1964) provided a more complex biogeographic pattern. However, Balech also considered the Argentine and Magallanian Zoogeographic Provinces, with the boundary between them slightly located to the south of that of López (1964). Some other authors considered that the Río de la Plata is an important biogeographic boundary (eg. Knox, 1960; Briggs, 1974). However, most local authors agree that the Argentine province continues to the south of the Río de la Plata because many northern taxa occur off the Buenos Aires province, and even the Río Negro and Chubut provinces (see Menni, 1983). Confirming this biogeographic pattern, the southernmost known range of *Carcharodon carcharias* is at the latitude of southern Buenos Aires province (in the Argentine biogeographic province) and consequently it has not been reported from the Magallanian biogeographic province (see below).

#### HABITAT AND DISTRIBUTION OF *CARCHARODON CARCHARIAS*

*Carcharodon carcharias* is primarily a coastal and offshore inhabitant of the continental and insular shelves worldwide (Compagno, 1984). The great white shark often occurs close inshore to the surfline and even penetrates shallow bays in continental coastal waters, but also prefers offshore continental islands (Tricas *et al.*, 1997; Compagno, 2001; see papers in Klimley & Ainley, 1996). Notwithstanding their wide distribution, *C. carcharias* is rare in almost all seas, with the exception of some areas such as southern Australia, California, and South Africa (Soto *et al.*, 1998; Compagno, 2001). Catches in some areas have been as many as 50 to 100 per year (South Australia and South Africa) in the past but mostly less in others (Compagno, 2001). It is unknown in many warm and temperate regions notwithstanding that water temperature could be suitable for this species. In spite of the fact that the great white shark ranges from cold and warm temperate areas, there are enough tropical continental and oceanic records to suggest that at least larger individuals have a wide temperature range and penetrate at will into the tropical stronghold of carcharhinid sharks (Compagno, 2001).

Catch data indicate that *C. carcharias* tolerates sea surface temperatures ranging from 7.5°C to 25°C in the Mediterranean, but few records were reported in waters above 23°C (Fergusson, 1996). Casey & Pratt (1985) noted that the 15°C value is an important threshold for great white shark movements in the western North Atlantic, and Cliff *et al.* (1989) considered that the 26°C isotherm was at the upper range of tolerance for this species. Accordingly, white sharks are more common when water temperature is over 14-15°C in the Monterey bay in California (Compagno, 1984). Consequently, the species seems to be most frequently encountered in temperate waters of an isotherm belt of approximately 15-23°C in different parts of the world.

In southwestern Atlantic, *C. carcharias* was reported from Acaraú (S 2° 56'; Estado do Ceará; Brazil; Soto *et al.*, 1998) to Puerto Quequén (S 38° 30', Buenos Aires province, Argentina; Siccardi *et al.*, 1981). Only four individuals were published from Argentina (Siccardi *et al.*, 1981; Soto *et al.*, 1998). There are also two unpublished jaws in Argentinean institutions (MACN-Ict 4544; Puerto Quequén, col. F. Motti, male 3.050 m, 26/12/1952, in the División Ictiología, Museo Argentino de Ciencias Naturales "Bernardino

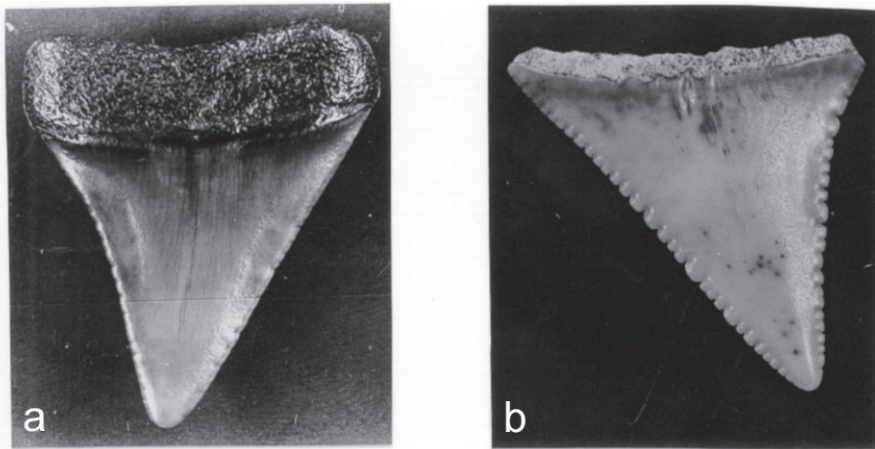


Fig.2. *Carcharodon carcharias* fossil teeth from Argentina: a, Arroyo Ensenada, Entre Ríos province, Paraná Formation, late Miocene. b, Cañada de Arregui, Buenos Aires province; Pascua Formation, late Pleistocene. x2.

Rivadavia,” Buenos Aires. a jaw in exhibition at the Estación Hidrobiológica, Puerto Quequén, Buenos Aires province). Finally, Javier Corcuera observed a juvenile specimen in Puerto Quequén in the spring of 1989.

In Brazil, only 15 individuals were certainly been reported (Gadig & Rosa, 1996; Soto *et al.*, 1998). New data provided by O. Gadig raised the number to 24 for Brazil (Moraes, 2000). Records from Uruguay are unclear (Ximénez, 1962; Carrera, 1991). In a handicraft fair at La Paloma (Uruguay), the author of this paper examined a jaw of an individual supposedly caught in the area. In the southwestern Atlantic, four reports of attacks of *C. carcharias* to humans and cetaceans were published (Siccardi *et al.*, 1981; Soto *et al.*, 1998). The attack to a man in Miramar (Argentina, 1954) was documented by means of a tooth (Elvira Siccardi, personal communication). Consequently, there seems to have been at least 20 certain and more than 10 less probable white shark occurrences might be acknowledged in southwestern Atlantic waters during the XX<sup>th</sup> century.

#### PINNIPEDS IN THE AREA

Pinnipeds and small cetaceans have been considered the main food item for adult *C. carcharias* individuals (Long *et al.*, 1996). Actually, there are very few regions in the world that support white shark populations without a corresponding pinniped population (Ellis & McCosker, 1991; Francis, 1997). The fossil record confirms this association of *C. carcharias* with abundant

pinnipeds (and cetaceans) in several Cenozoic localities such as those of the Pliocene of Chile and Peru (de Muizon, 1981; de Muizon & DeVries, 1985; Long, 1993; Purdy, 1996). Compagno (2001) suggested that pinnipeds are an especially important prey where they are together, especially at seal colonies where pinnipeds are highly vulnerable. However, large white sharks also catch large teleost fishes, sharks and rays, birds, dolphins and marine reptiles, and are presumably capable of subsisting on such other small prey, in areas where seals are uncommon or absent (Compagno, 2001).

Pinnipeds include more than 30 species, divided into three families. In central Argentina, Uruguay and Brazil, the Family Otariidae includes the fur seal *Arctocephalus australis* and the sea-lion *Otaria flavescens*, and the Family Phocidae includes the sea elephant *Mirounga leonina*. Global pinniped distribution is greatly determined by temperature. As general guide, the 20°C summer isotherm in either hemisphere, where it approaches to continental coasts, forms a reasonable pointer to the limits of where one might expect to find seals (King, 1964). However, there are exceptions (e.g. the Monk Seals).

White sharks appear to exhibit an age/size preference for certain foods. This developmental diet reveals a preference for fish in the juvenile white shark (Compagno, 1984). As they increase in size the diet will shift to include other sharks, rays and marine mammals. *C. carcharias* specimens larger than 3 m total length are apparently attracted to regions where pinnipeds are common: Great Australian Bight (Tricas *et al.*,

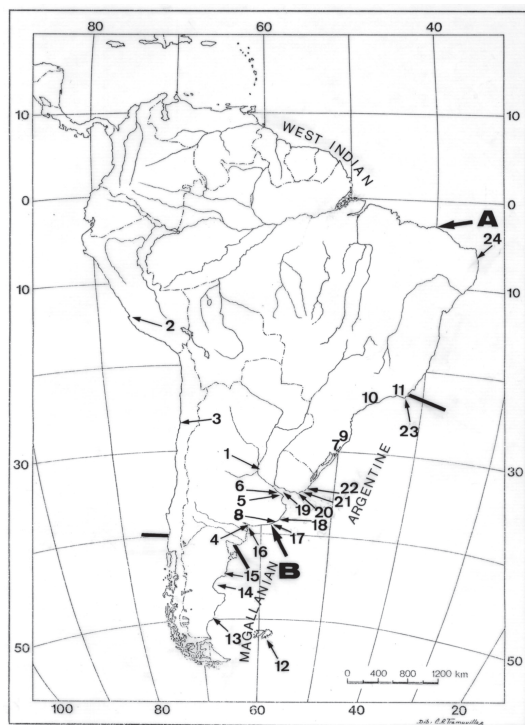


Fig. 3. Records of *Carcharodon carcharias* in paleontological, archaeological and recent localities in South America (see text). Figures in the continent are Miocene to Holocene localities. Miocene: 1, Arroyo Ensenada. Pliocene: 2, Sacaco; 3, Bahía Inglesa. Pleistocene: 4, Pehuencó; 5, Cañada de Arregui; 6, La Plata; 7, Río Grande do Sul. Holocene: 8, Centinela del Mar; 9, Estado do Rio Grande do Sul; 10, Estado da Santa Catarina; 11, Estado do São Paulo; 12, Islas Malvinas (Falkland Islands); 13, Cabo San Francisco de Paula; 14, Golfo de San Jorge; 15, Bahía Camarones; 16, Bahía Blanca; 17, Miramar; 18, Mar del Plata; 19, Río de la Plata; 20, Isla de Lobos; 21, La Paloma; 22, Isla de Torres group, Isla de Marco and Isla Verde and Islote Coronilla; 23, Cabo Frio; 24, Natal. The biogeographical provinces in the South American Atlantic coast according to López (1964) are also depicted.

1997), California (Compagno, 1984; Anderson *et al.*, 1996; Long *et al.*, 1996; see also Carey *et al.*, 1982), and South Africa (Tricas *et al.*, 1997). In California, most shark-bitten pinnipeds were concentrated near haul-out sites (Long *et al.*, 1996). At least in California, prey density appears to strongly affect the distribution of sharks (Long *et al.*, 1996).

## DISCUSSION

### Abundance in southwestern Atlantic

In contrast with their present rarity, the great white shark occurs frequently in Pleistocene and Holocene beds of the Buenos Aires province (Argentina) and Brazil, including archaeological sites. Remarkably, Quaternary records of large sharks that are common today in the Argentinean Zoogeographic Province, such as the odontaspimid *Carcharias taurus* and different species of the carcharhinid *Carcharhinus*, are sparse in Argentina.

During the last Interglacial (Illinois-Wisconsin, Isotope Stage 5; *ca.* 120 ky BP) and the Hypsithermal (*ca.* 7 to 5 ky BP) the sea rose due to higher temperatures that provoked marine transgressions (Petit *et al.*, 1999; Hodell *et al.*, 2001). Isotopic studies ( $^{13}\text{C}$  and  $^{18}\text{O}$ ) confirmed that during the deposition of the Holocene marine beds in eastern Buenos Aires province (Las Escobas Formation; Flandrian transgression, Early-Middle Holocene) water temperature was higher than at present (Aguirre, 1993; Aguirre & Leng, 1996; Aguirre & Zanchetta, 2000). It seems that the higher temperatures were not an obstacle for the relative abundance of *C. carcharias* in Brazil and Argentina during the late Pleistocene and, especially, the Holocene.

In southwestern Atlantic Ocean, the optimal temperatures for *C. carcharias* quoted above are now found between the latitude of Bahía Camarones (S 44° 45'; 15°C isotherm in summer) and to the north of Rio de Janeiro (S 22° 53'; 20°C in winter; Knox, 1960; García, 1992; Figs. 2, 4). However, there are very few records of these sharks in the northern part of this region and none in the southern part at present (Patagonia, see below).

Summer temperatures (and type of coast and water transparency) in Uruguay and Buenos Aires province coasts are surely adequate for the presence of *C. carcharias* (see above) and there is no reason to suppose that there are no suitable nursery areas for *C. carcharias* in the region. Embryos, new born, pregnant or post-partum white sharks have been reported in New Zealand, Australia, Taiwan, Japan, South Africa, the north-east Pacific, the north-west Atlantic and the Mediterranean Sea (Casey & Pratt, 1985; Fergusson 1996). Therefore, parturition probably occurs in many different, mostly temperate, locations world-wide (Francis, 1997).

Specimens of *C. carcharias* were caught at the end of spring and in summer in Argentina (Siccardi *et al.*, 1981; Soto *et al.*, 1998). Moreo-

ver, summer (and in part winter) water temperatures in the area do not differ from those present in southern Australia and even in South Africa where the species is fairly common (Fig. 4).

We suggest that the probable cause of the present rarity of *C. carcharias* should be the falling numbers of pinnipeds (and cetaceans) in our coasts. Certainly, pinnipeds were much more abundant in Argentinean and Uruguayan coasts in the past, but were depauperated by human hunting (see King, 1964; Rodríguez & Bastida, 1998). In the Holocene, they were abundant in the coasts of Argentina and Brazil where they were moderately hunted by natives (see Bryan, 1978; Bayón & Politis, 1996).

Sealing activities began in Uruguay in the XVI<sup>th</sup> century, but commercial harvests in the southwestern Atlantic began later. During the last 200 years, at least 3 million animals were killed there. The XIX<sup>th</sup> century was characterized by intensive exploitation and the uncontrolled harvests during the last quarter of this century made almost all populations become nearly extinct (Ximénez, 1964; Rodríguez & Bastida, 1998). By the turn of XIX<sup>th</sup> century, the small number of seals in the southwestern Atlantic would have not been able to sustain profitable commercial harvests (Allen, 1899 *vide* Rodríguez & Bastida, 1998).

Pinnipeds were apparently exterminated at the Buenos Aires province coast. The more suitable site for pinnipeds in that region appears to be the Mar del Plata area (Rodríguez & Bastida, 1998). There, Francis Drake in 1578, and Juan de Garay in 1581, found huge seal colonies. However, the last reference of seal individuals inhabiting the area previous to more recent times was in 1895 (Rodríguez & Bastida, 1998). A summary of the theoretical population sizes of pinnipeds in the area near Mar del Plata, calculated according to available terrain in relation to seal density values recorded in similar habitats, indicates that *Arctocephalus australis* could have reached a maximum of 165,000 animals, *Otaria flavescens* of 88,000 animals, and *Mirounga leonina* of perhaps 2500 individuals (Rodríguez & Bastida, 1998). During the 1960's, after sealing activities ceased in Patagonia, sea lions gradually began to settle themselves inside the harbour of Mar del Plata and now there is a colony of 600-700 individuals therein and a small colony of fur seals was formed in the Punta Mogotes area (Rodríguez & Bastida, 1998). Out of the Mar del Plata area, pinnipeds are transient in the Buenos Aires province coast north of Bahía Blanca.

There is not a great abundance of pinnipeds in Brazil but in Uruguay there is now a relative

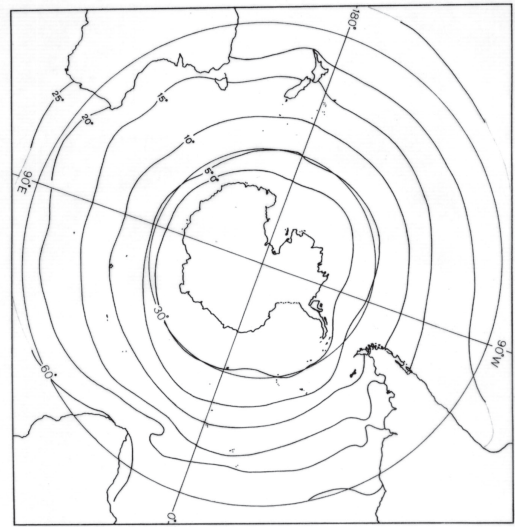


Fig. 4. Summer temperatures in the Southern Hemisphere (modified from Knox, 1960).

abundance of fur seals and a minor number of sea lions in some rookeries (Páez, 2000). As for Argentina, pinnipeds have been strongly exploited (only from 1873 to 1900, 454,500 individuals were killed in Uruguay; Ponce de León, 1999). By the mid of the decade of 1940, populations of sea lion and fur seal populations were greatly depauperated (Ponce de León, 1999). Since 1950, new regulations have reduced the risk of decimation.

Rookeries in Uruguay are the Isla de Lobos group (S 35° 01' - W 54° 52'), near Punta del Este; Isla de Torres group (S 34° 24' - W 53° 46'), near Cabo Polonio; Isla de Marco, near Arroyo Valizas (S 34° 21' - W 53° 45'); and Isla Verde and Islote Coronilla, near La Coronilla (S 34° 26' - W 53° 29'; Ximénez, 1964; Ponce de León, 1999). In the past, there were pinnipeds in many other locations (Ximénez, 1964). At present, Isla de Lobos includes more than half of all individuals occurring in Uruguay (about 300,000). Water salinity is relatively low in the Isla de Lobos, which is located in the mouth of the Río de la Plata (average salinity on surface 1981-1987: about 25‰; Cousseau, 1985; Bazán & Arraga, 1993). This factor might be related to the absence of *C. carcharias* in this location. Attacks to pinnipeds are rare in the San Francisco Bay and Long *et al.* (1996) attribute it to the low salinity of the bay which may deter the presence of white sharks therein. During the late Pleistocene and Holocene transgressions, salinity was much higher in the Río de la Plata area (Cavallotto *et al.*, 1999; Martínez *et al.*, 2000) what explains the presence

of *C. carcharias* in the present coast of the fresh-water sector of the Río de la Plata (Cione & Torno, 1988).

In Patagonia there are several rookeries and the largest number of pinnipeds occurs in the high latitudes of southern Patagonia and Malvinas (Falkland) Islands (Ximénez, 1964). Temperature in Patagonian coasts ranges from 4-8°C in winter to 8-18°C in summer (García, 1992) and could be not as suitable for white sharks as those of more northern waters.

At present, in Patagonian coasts, the only pinniped predator is another mammal, the killer whale or orca (*Orcinus orca*). The orca is a formidable predator that attacks pinnipeds not only in Patagonia but in south Atlantic islands, Antarctica and many other parts of the world. Remarkably, it has been suggested that there may be predation displacement between the orca and white shark (Pyle *et al.*, 1999). The relative abundance of this cetacean could also contribute to the absence of the white sharks in waters of the Atlantic part of the Magallanian biogeographic province where killer whales are more abundant.

Another food item for *C. carcharias* is cetaceans. Where there are concentrations of cetaceans, large white sharks will actively hunt small cetaceans and scavenge on available carcasses of larger species (Long & Jones, 1996). As pinnipeds, cetaceans were much more abundant in Argentinean waters in the past than today (Chebez, 1994). Cetacean bones are frequently recorded in the late Pleistocene and Holocene marine beds in eastern Pampean region. Consequently, before recent times there were a greater number of carcasses available.

Gadig & Rosa (1996) attribute the occurrence of *C. carcharias* in Cabo Frio to the presence of cooler waters related to a coastal upwelling. Brazilian reports of *C. carcharias* are scarce and there are very few records from tropical regions such as the Estado de Ceará (Soto *et al.*, 1998). Individuals reported from Brazil are mostly large, but both fossil and recent records from Argentina correspond to relatively small individuals (probably less than 3 m total length). Compagno (2001) suggested that smaller individuals may be mostly restricted to temperate continental seas. All the specimens quoted by Siccardi *et al.* (1981) from the Buenos Aires province are < 3 m total length. This feature could be related to the southern range in distribution.

Consequently, present evidence suggests that the unrestricted hunt of pinnipeds and cetaceans could have had a secondary effect on the abundance of the white shark in southwestern Atlantic. Actually, the white shark has a rather low

intrinsic rebound potential (Smith *et al.*, 1998) and it also has typically small, localised populations. All this suggests that fishing of any kind should be extremely cautious (Bonfil, 2000). The white shark is the most widely protected shark species in the world. White sharks are also protected by law in several regions such as South Africa, Namibia, Maldives, Australia, the Mediterranean, and part of the United States (Bonfil, 2000). Moreover, it is considered a threatened species by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; see also Tricas *et al.*, 1997).

### Southernmost distribution

Compagno (1984) and Last & Stevens (1994) made maps depicting the distribution of *C. carcharias* as ranging to the Golfo de San Jorge in Patagonia (about S 46°; Fig. 1). Compagno (2001) extends the "certain" distribution even further, to the latitude of the Cabo San Francisco de Paula (about S 49° 30'). However, we do not know of present reports of *C. carcharias* in the western Atlantic Ocean south of S 38° 30' (Puerto Quequén, Buenos Aires province), that is approximately 1150 km to the north of the Cabo San Francisco de Paula (Siccardi *et al.*, 1981; Cione, 1983; Soto *et al.*, 1998; Fig. 3). In the eastern Pacific Ocean coast, *C. carcharias* ranges southward to central Chile, where it seems to be rare (Roberto Meléndez Cortés, personal communication).

A fossil tooth of *C. carcharias* found at Pehuencó, southern Buenos Aires province (S 38° 56'; Cione, 1983) coming from Quaternary marine sediments is the southernmost report in the southwestern Atlantic.

### ACKNOWLEDGMENTS

We would like to thank the Agencia Nacional de Promoción Científica y Tecnológica, Consejo Nacional de Investigaciones Científicas y Técnicas and Universidad Nacional de La Plata for partial support for this project; Roberto Meléndez Cortés, Roberto Menni (referee) and an anonymous referee for the valuable information and comments provided.

### BIBLIOGRAFÍA

- Aguirre, M.L. 1993. Palaeobiogeography of the Holocene molluscan fauna from northeastern Buenos Aires province, Argentina: its relation to coastal evolution and sea level changes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 102: 1-26.
- Aguirre, M.L. & M. Leng. 1996. Variations in the isotopic composition (<sup>13</sup>C and <sup>18</sup>O) of Holocene bivalves

- from the NE bonaerian littoral: possible palaeoenvironmental significance. *Actas XIII Congreso Geológico Argentino y III Congreso de Exploración de Hidrocarburos, Buenos Aires*, p. 127.
- Aguirre, M.L. & G. Zanchetta. 2000. Composición isotópica ( $^{13}\text{C}$  y  $^{18}\text{O}$ ) de moluscos del área costera bonaerense: interpretaciones paleoambientales, *Resúmenes de la Reunión Anual de Comunicaciones Científicas de la Asociación Científica Argentina, Mar del Plata 2000*: 15.
- Ameghino, F. 1898. *Sinopsis geológico-paleontológica, 2° Censo de la República Argentina* 1: 115-228, Buenos Aires.
- Anderson, S.D., A.P. Klimley, P. Pyle & R. Philip Henderson. 1996. Tidal height and white shark predation at the Farallon Islands, California. En D.G. Ainley & A.P. Klimley (eds.), *Great white sharks. The biology of Carcharodon carcharias*, pp.275-279, Academic Press, San Diego.
- Arratia, G. & A.L. Cione. 1996. The fossil fish record of Southern South America. En G. Arratia (ed.), *Contributions of Southern South America to Vertebrate Paleontology*, Münchener Geowissen. Abh.: 9-72.
- Balech, E. 1964. Caracteres biogeográficos de la Argentina y Uruguay. *Bol. Inst. Biol. Mar. Mar del Plata* 7: 107-112.
- Barbosa, D. & T. Franco. 1991. Análise e interpretação dos dentes de seláquios. *Reunião Científica da Sociedade Arqueológica, Brasil* 6: 36.
- Bayón, C. & G. Politis. 1996. Estado actual de las investigaciones en el sitio Monte Hermoso I (Prov. de Buenos Aires). *Arqueología* 6: 83-116.
- Bazán, J.M. & E. Arraga. 1993. El Río de la Plata ¿Un sistema fluvio-marítimo fragil? Acercamiento a una definición de la calidad de sus aguas. En: A. Boltovskoy & H. López (eds.), *Conferencias de Limnología*, pp 71-82, La Plata.
- Bonfil, R. 2000 (active in 2008). En: *Species Identification Sheets, FAO/SIDP - Species Identification and Data Programme. Carcharodon carcharias (Linnaeus, 1758)*. <http://www.fao.org/fiservlet/org.fao.fi.common.FiRefServlet?ds=species&fid=2799>.
- Briggs, J.C. 1974. *Marine zoogeography*, McGraw Hill, New York, 475 pp.
- Bryan, A.L. 1978. Resumo do arqueologia do sambaqui de Forte Marechal Luz. *Arq. Mus. Hist. Nat. (UFMG)* 2: 9-30.
- Carey, F.G., J.W. Kanwisher, O. Brazier, G. Gabrielson, J.G. Casey & H. Pratt. 1982. Temperature and activities of a white shark, *Carcharodon carcharias*. *Copeia* 1982, 254-260.
- Carrera, R. 1991. *Los tiburones del Uruguay (Reconocimiento y aspectos biológicos)*. Museo Dámaso A.Larrañaga, Montevideo, 91 pp.
- Casey, J.G. & H. Pratt. 1985. Distribution of the white shark, *Carcharodon carcharias*, in the western North Atlantic. *Mem. Southern Calif. Acad. Sci.* 9: 2-14.
- Cavallotto, J., R. Violante & G. Parker. 1999. Historia evolutiva del Río de la Plata durante el Holoceno. *Actas del XIV Congreso Geológico Argentino, Salta* 1: 508-511.
- Cliff, G., S.F.J. Dudley & B. Davis. 1989. Sharks caught in the protective gill nets off Natal, South Africa. 2. The great whit shark *Carcharodon carcharias*. *S. Afr. J. Mar. Sci.* 8: 131-144.
- Chebez, J.C. 1994. *Los que se van*. Albatros, Buenos Aires, 604 pp.
- Cione, A.L. 1983. Registros fósiles de *Carcharodon carcharias* (Linné, 1758) (Elasmobranchii, Lamniformes) en Argentina. *Ameghiniana* 20, 261-264.
- Cione, A., M.M. Azpelicueta, M. Bond, A. Carlini, J. Casciotta, M. Cozzuol, M. de la Fuente, Z. Gasparini, F. Goin, J. Noriega, G. Scillato-Yané, L. Soibelzon, E.P. Tonni, D. Verzi & M.G. Vucetich. 2000. The Miocene vertebrates from Paraná, eastern Argentina. En: F.G. Aceñolaza & R. Herbst (eds.), *El Neógeno de Argentina*. Ser. Correl. Geol.14: 191-237.
- Cione, A.L. & A. Torno. 1988. Records of *Pogonias cromis* (Perciformes, Sciaenidae) in Las Escobas Formation (Holocene) in Uruguay and Argentina. Zoogeographical and environmental considerations. *Q. South Am. Antarc. Pen.* 5: 73-82.
- Compagno, L.J.V. 1984. Sharks of the world. An annotated and illustrated catalogue of shark species in date. *FAO Species Catalogue for Fishery Purposes, Rome*, 4 (1), 1-249.
- 2001. Sharks of the world. An annotated and illustrated catalogue of shark species in date. *FAO Species Catalogue for Fishery Purposes, Rome*, 1 (2), 1-269.
- Cousseau, M.B. 1985. Los peces del Río de la Plata y de su frente marítimo. En A. Yáñez-Arancibia (ed.), *Fish Ecology in Estuaries and Coastal lagoons. Towards an Ecosystem Integration*. pp.515-534, UNAM Press, Mexico.
- Ellis, R., & J.E. McCosker. 1995. *Great White Shark*, Stanford University Press, Stanford, California, 504 pp.
- Fergusson, I.K. 1996. Distribution and autoecology of the white shark in the Eastern North Atlantic Ocean and the Mediterranean Sea. En D.G. Ainley & A.P. Klimley (eds.), *Great white sharks. The biology of Carcharodon carcharias*. pp.321-345, Academic press, San Diego.
- 1998 (active in 2008). *Review of the great white shark Carcharodon carcharias*. In the web site: [http://www.zoo.co.uk/~z9015043/gws\\_conserv.html#Distribution](http://www.zoo.co.uk/~z9015043/gws_conserv.html#Distribution).
- Francis, M. 1997. Reproductive strategy of white sharks, *Carcharodon carcharias*. *Shark News* 9, 8-9.
- Frenquelli, G. 1922. Sulla contemporanea presenza del *Carcharodon megalodon* Ag. e del *Carcharodon rondeleti* M.et H. nel Paranense superiore de Entre Ríos (Rep. Argentina). *Boll. Soc. Geol. Ital.* 41: 50-52.
- Gadig, O.B.F. & R.S. Rosa. 1996. Occurrence of the white shark along the Brazilian Coast. En D.G. Ainley & A.P. Klimley (eds.), *Great white sharks. The biology of Carcharodon carcharias*. pp. 347-350, Academic press, San Diego.
- García, O.N. 1992. Síntesis climatográfica de la República Argentina. En M. Iriondo (ed.), *El Holoceno en la Argentina*, Cadinqua, Buenos Aires, 1: 79-103.



- Hodell, D.A., S.L. Kanfoush, A. Shemesh, X. Costa, C. Charles & T. Guilderson. 2001. Abrupt Cooling of Antarctic Surface Waters and Sea Ice Expansion in the South Atlantic Sector of the Southern Ocean at 5000 cal yr B.P. *Q. Res.* 56: 191-198.
- King, J.E. 1964. *Seals of the World*. British Museum (Natural History), London.
- Klimley, A.P. & D.G. Ainley. 1996. *Great white sharks. The biology of Carcharodon carcharias*. Academic Press, San Diego.
- Knox, G.A. 1960. Marine Biology. Littoral ecology and biogeography of the southern oceans. *Proc. R. Soc.* 152: 577-624.
- Last, P.R. & J.D. Stevens. 1994. *Sharks and rays of Australia*, CSIRO Information Services, Hobart, 513 pp.
- Long, D.J., 1993. Late Miocene and Early Pliocene fish assemblages from the north coast of Chile. *Tertiary Res.* 14: 117-126.
- Long, D.J., K. Hanni, P. Pyle, J. Roletto, R. Jones & R. Bandar. 1996. White shark predation on four Pinniped species in Central California waters: geographic and temporal inferred from wounded carcasses. En: D.G. Ainley & A.P. Klimley (eds.), *Great white sharks. The biology of Carcharodon carcharias*. Academic Press, San Diego. pp. 263-274.
- Long, D.J. & R.E. Jones. 1996. White shark predation and scavenging on Cetaceans in the Eastern North Pacific Ocean. En D.G. Ainley & A.P. Klimley (eds.), *Great white sharks. The biology of Carcharodon carcharias*. Academic Press, San Diego. pp. 293-307.
- López, R. 1964. Problemas de la distribución geográfica de los peces marinos suramericanos. *Bol. Inst. Biol. Mar., Mar del Plata* 7: 57-63.
- Martínez, S., M. Ubilla, M. Verde, D. Perea, R. Guerequiz, A. Rojas & G. Piñeiro. 1998. Pleistoceno marino fosilífero en el Uruguay. *Resúmenes del VII Congreso Argentino de Paleontología y Bioestratigrafía, Bahía Blanca*: 129.
- Martínez, S., M. Ubilla, M. Verde, D. Perea, A. Rojas, R. Guerequiz & G. Piñeiro. 2000. Paleocology and Geochronology of Uruguayan Coastal Marine Pleistocene Deposits. *Q. Res.* 55: 246-254.
- Menni, R. 1983. *Los peces en el medio marino*. Estudio Sigma, La Plata, 169 pp.
- Menni, R.C., R.A. Ringuelet, & R.A. Aramburu. 1984. *Peces marinos de la Argentina y Uruguay*. Hemisferio Sur, Buenos Aires, 359 pp.
- Moraes, M. 2000. *Turista ocasional*. [http://www.uol.com.br/nationalgeographic/edicao0500/tuba\\_br.html](http://www.uol.com.br/nationalgeographic/edicao0500/tuba_br.html).
- Muizon, C. 1981. Les vertébrés fossiles de la Formation Pisco (Pérou). Première partie. *Mém. Inst. Franc. d'Études And.* 6: 1-150.
- Muizon, C. & T.J. DeVries. 1985. Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). *Geol. Rund.* 74: 547-563.
- Pardiñas, U., J. Gelfo, J., San Cristóbal, A.L. Cione & E.P. Tonni. 1996. Una asociación de organismos marinos y continentales en el Pleistoceno superior en el sur de la provincia de Buenos Aires, Argentina. *Actas del XIII Congreso Geológico Argentino y III Congreso de Exploración de Hidrocarburos, Buenos Aires*: 95-111.
- Perea, D. & M. Ubilla. 1981. Estudio preliminar de la ictiofauna fósil marina de las costas del Departamento de Rocha, Uruguay. *Resúmenes de las Jornadas de Ciencias Naturales, Montevideo*: 25-26.
- Petit, J.R., J. Jouzel, D. Raynaud, N. Barkov, J. Barnola, I. Basile, M. Bender, J. Chappellaz, M. Davis, G. Delaygue, M. Delmotte, V. Kotlyakov, M. Legrand, V. Lipenkov, C. Lorius, L. Pepin, C. Ritz, E. Saltzman & M. Stievenard. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399: 429-436.
- Ponce de León, A. 1999 (active in 2008). *Pinnípedos de Uruguay*. En: Instituto Nacional de Pesca de Uruguay. <http://www.inape.gub.uy>.
- Purdy, R.W. 1996. Paleocology of fossil white sharks. En D.G. Ainley & A.P. Klimley (eds.), *Great white sharks. The biology of Carcharodon carcharias*. Academic press, San Diego. pp. 67-78.
- Pyle, P., M.J. Schramm, C. Anderson & C. Keiper. 1999. Predation on a white shark (*Carcharodon carcharias*) by a killer whale (*Orcinus orca*) and a possible case of competitive displacement. *Mar. Mammal Sci.* 15: 563-568.
- Richter, M. 1987. Osteichthyes e Elasmobranchii (Pisces) da Bacia de Pelotas, Quaternário de Rio Grande do Sul, Brasil. *Paula-Coutiana* 1: 17-38.
- Rodríguez, D. & R. Bastida. 1998. Four hundred years in the history of pinniped colonies around Mar del Plata, Argentina. *Aqu. Conserv.: Mar.Fresh. Ecos.* 8: 721-735.
- Sekiguchi, F.C. 1994. Distribuição de fósseis pleistocénicos na zona costeira e plataforma continental interna no Rio Grande do Sul. *Acta Geol. Leopold.* 39: 355-364.
- Siccardi, E. 1960. "Cetorhinus" en el Atlántico Sur (Elasmobranchii: Cetorhinidae). *Rev. Mus. Arg. Cienc. Nat. "B. Rivadavia"*, Zool. 6: 60-102.
- Siccardi, E., A. Gosztonyi & R. Menni. 1981. La presencia de *Carcharodon carcharias* e *Isurus oxyrinchus* en el Mar Argentino (Chondrichthyes, Lamniformes). *Physis* 39: 55-62.
- Smith, S.W., D.W. Au & C. Show. 1998. Intrinsic rebound potential of 26 species of Pacific sharks. *Mar. Fresh. Res.* 49: 663-678.
- Soto, J. & W. Nisa Castro-Neto. 1993. Evidência de ataque de tubarão-branco, *Carcharodon carcharias* (Lamniformes, Lamnidae) em toninha, *Pontoporia blainvillei* (Cetacea, Pontoporiidae). *Resúmenes da VI Reuniao Trabalhos Pesca e Pesqueria de tubarões e raias Brasil, Santos*: 323-325.
- Soto, J., W. Nisa-Castro Neto & M. Mincarone. 1998. Sobre a presença do tubarão branco, *Carcharodon carcharias* (Linnaeus, 1758) (Lamniformes, Lamnidae), no Atlântico sul ocidental. *Resúmenes expostos no XI Semana Nacional da Oceanografia, Rio Grande, RS-Brasil*: 323-325.
- Suárez, M. & J.M. Brito. 2000. Una nueva localidad fosilífera con vertebrados marinos del Terciario de Bahía Salado (III Región), norte de Chile. *Resúmenes de las XVI Jornadas Argentinas de Paleontología de Vertebrados, San Luis*: 57.
- Tonni, E.P. & A.L. Cione. 1984. A thanatocenosis of

- continental and marine vertebrates in the Las Escobas Formation (Holocene) of Northeastern Buenos Aires Province, Argentina. *Q. South Amer. Ant. Pen.* 2: 93-113.
- 1999. Pleistocene continental vertebrates from the present marine shelf of Argentina. *Current Res. Pleist.* 16: 134-136.
- Tricas, T.C., K. Deacon, P. Last, J. McCosker, T. Walker & L. Taylor. 1997. *Sharks and rays*. Harper Collins Publishers, London.
- Walsh, S.A. & J.P.Hume. 2001. A new Neogene marine avian assemblage from North-Central Chile. *J. Vert. Paleont.* 21: 484-491.
- Ximénez, I. 1962. Notas sobre elasmobranquios. I. Cuadro sistemático y sinonímico provisional de los selácios de la costa uruguaya. *Rev. Inst. Invest. Pesq.* 1: 35-44.
- Ximénez, A. 1964. Estudio preliminar de la distribución geográfica actual de los pinípedos en América Latina. *Bol. Inst. Biol. Marina, Mar del Plata* 7: 65-72.

Recibido: 16-V-2008  
Aceptado: 24-X-2008