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# Distribution, abundance and biology of the smalltooth sandtiger shark *Odontaspis ferox* (Risso, 1810) (Lamniformes: Odontaspididae)

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**Abstract** The smalltooth sandtiger shark, *Odontaspis ferox*, has a cosmopolitan distribution across warm temperate and tropical waters, and although essentially demersal, it has also been captured pelagically in mid-ocean. The species often occurs inshore at steeply shelving coastal and insular locations, and has now been identified by divers at eight widely separated shallow water sites. In the Southern Hemisphere, most *O. ferox* were caught by trawl on the continental slope, where its bathic range was extended to at least 880 m. Large specimens (>200 cm TL) were found across the whole depth range, but almost all juveniles were caught between 200 and 600 m. The largest recorded male was 344 cm TL, and female 450 cm TL. The few biological data suggest that size at maturity for males is around 200–250 cm TL, and for females 300–350 cm. No pregnant females were recorded but size at birth is probably about 100 cm TL. Nowhere has the species been found in large numbers. Survey and commercial catch data from south-east Australian trawl grounds suggest that numbers of *O. ferox* there have declined since the advent of deepwater commercial trawling in the 1970s. In areas of steep untrawlable terrain, increased gill-netting and longlining are likely to impact on local populations, with mature individuals being particularly vulnerable. Although *O. ferox* is not specifically targeted by commercial fishing activities, its likely very low fecundity make it susceptible to local extirpation, even at seemingly small capture rates. This species is protected off New South Wales and is considered "vulnerable" globally, by the World Conservation Union (IUCN).

**Keywords** Upper slope · Insular · Oceanic · Reproduction · Trawling · Decline

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## Introduction

The smalltooth sandtiger shark, *Odontaspis ferox*, is one of the most enigmatic sharks in the order Lamniformes. It was first described by Risso (1810) as *Squalus ferox* from the type locality at Nice, on France's Côte d'Azur in the Mediterranean Sea, and most early records were from the Mediterranean and North Atlantic. Whitley (1950) described *Odontaspis herbsti* from south-eastern Australia, differentiating it from *O. ferox* mainly on differences in dental formulae, and the absence of pigment spots. Garrick's (1974) account of two specimens from New Zealand cast doubt on any differences in dentition between the species but retained *O. herbsti* for the plain coloured *Odontaspis*. However, Compagno (1984) reviewed the two species and considered that *O. herbsti* was a junior synonym for *O. ferox*. It is known regionally as the ragged-tooth shark or sand shark in North America, bumpytail ragged-tooth shark in South Africa, and Herbst's nurse shark in Australia (Last and Stevens 1994).

Although considered by previous authors as an uncommon to rare species (e.g. Bonfil 1995; Compagno 1984, 2001), *O. ferox* is widely distributed in warm-temperate and tropical seas of continental and insular shelves and upper slopes. The species occurs infrequently but regularly as bycatch in several Mediterranean commercial fisheries and more sporadically so in other parts of the world. It attains a large size, with females reaching at least 410 cm total length (Bauchot 1987; Vacchi and Serena 1997). Despite this impressive size, the increasing incidence of records, and the passage of nearly 200 years of ichthyological study since Risso's description, surprisingly little is known of the biology and ethology of this species. The behaviour of *O. ferox*, other than what has been evaluated by interpreting morphology, stomach contents and records of capture, is essentially unknown.

Geographic and depth distributions of *O. ferox* were summarised by Compagno (1984), Last and Stevens (1994) and Bonfil (1995) and by 1998, about 50 capture records of *O. ferox* had been reported in 36 published papers. There was also a report by Francis (1991) of divers encountering *O. ferox* at the Kermadec Islands, north of New Zealand. We now know of more than 160 captures, with most of the previously unreported records from the Mediterranean Sea and the south-west Pacific; some of the new distributional information was also included in Compagno (2001). There have also been several more diver sightings of *O. ferox* at widely separated locations, including off Lebanon and Malpelo Island, Columbia, where detailed observations of *O. ferox* behaviour were recorded.

This paper reviews the published information and presents new distributional, abundance and biological data for *O. ferox*, and discusses its conservation status. Most of the relatively large number of captures from southern Australia were recorded during scientific trawl surveys and monitoring of the commercial trawl fishery; these data provide a unique quantitative case study of *O. ferox*, and are discussed in some detail.

## Materials and methods

Literature searches were made using Zoological Record and BIOSIS for dedicated citations of the species. Requests for unpublished records were forwarded to researchers working in regions known (or suspected) to be within the global range of this species, and numerous responses were received; these respondents, each with their associated institution or affiliation, are listed in the Acknowledgements. Original data were then collated with information and measurements from museum-preserved specimens, and those literature accounts, which contained sufficient levels of detail for quantitative analyses. Underwater video footage and still photographs, along with photographs of dead specimens, were used to confirm identifications and to describe the colour variability of the species.

The identification of *O. ferox* at dive sites was confirmed by examining photographs. In all morphological respects, the sharks were consistent with earlier published descriptions such as those given by Maul (1955), Daugherty (1964), Garrick (1974), Bass et al. (1975) and Compagno (1984). In practice, *O. ferox* can be distinguished from the similar sandtiger or grey nurse shark, *Carcharias Taurus*, by the larger and more forwardly placed first dorsal fin, and its smaller (relative to the first dorsal) second dorsal fin.

All Australian sharks were measured with the shark lying in a natural position ($TL_{nat}$). Other original measurements follow the protocol for measuring sharks described by Compagno (1984, 2001): total length (TOT) is measured as a straight line value from snout to the upper lobe apex of the caudal fin, after flexing the upper lobe down into line with the horizontal axis of the body. It was difficult to ascertain whether other authors used TOT or $TL_{nat}$, although the latter methodology is more likely for pre-1984 records. For our analyses, we assumed that the two methods generated essentially similar results and for clarity cite all mention of total length in this paper as "TL". Length and weight data from intact specimens were fitted to the non-linear model of the form:

$$\text{Total Weight} = a.(\text{TL})^b.$$

Using SAS Institute's StatView 5.0. Total length was estimated for some accurately weighed specimens, using our generated length-weight regression. We had insufficient comparative data to estimate whole weight for specimens reported only as eviscerated weights.

Reproductive maturity was assessed from direct observations or good descriptions of the reproductive organs. Mature females were those with enlarged ovaries, sometimes with developing oocytes visible, and expanded uteri. Male maturity was assessed by examination and measurement of the clasper outer length (CLO; see Compagno 2001); males with enlarged and/or calcified claspers were deemed to be mature.

## Results

### Geographic distribution

New information was received on more than 30 captures from 12 countries or oceanic locations. Table 1 lists by capture location the 35 published and 26 new records, which included some details of sex, size and capture depth. An additional eight locations where the species was observed by divers are listed in Table 2. In all, *O. ferox* was reported from about 40 regions worldwide (Fig. 1).

### *Mediterranean Sea*

In addition to those included in Table 1, published records for the Mediterranean Sea are from Spain and the Balearic Islands (Lozano Rey 1928), Italy (Giglioli 1880; Tortonese 1956), the Adriatic Sea

**Table 1** *Odontaspis ferox* captures with data used in analyses

| *Capture area* | Date | Sex | TL (cm) | Wt (kg) | Capture depth (m) | Observation/ capture method | Reference/personal communication/specimen registration nos |
|---|---|---|---|---|---|---|---|
| Mediterranean Sea | | | | | | | |
| Italy: Skerki Bank, w. Sicilian Channel | 6-5-1985 | F | 410 | 277[c] | – | Demersal trawl | Vacchi and Serena (1997) |
| Italy: Isola di Linosa, Pelagic Islands | 12-7-1991 | F | 230 | | 10–40 | Bottom-set gillnet | Zava and Montagna (1992) |
| Malta: Xlendi Bay, Gozo I. | 6-3-98 | F | 353 | – | 100 | Bottom-set gillnet | A. Buttigieg, photo |
| Malta: Marsalforn, Gozo I. | July 1999 | – | 400[a] | – | – | – | A. Buttigieg |
| Malta | 5-11-2002 | F | 298 | – | – | Bottom longline | J. Dalli, unpublished MSc. thesis |
| Malta | 14-3-2003 | F | 382 | – | – | Bottom longline | J. Dalli, unpublished MSc. thesis |
| Greece: Sifnos I., Cyclades | 29-9-2001 | F | 165[a] | – | 200 | Swordfish longline | A. Melenkovitch, photo (Fig 3c) |
| Greece: Karpathos I., Dodecanese | 20-6-1968 | F | 340 | – | – | Demersal longline | Ian K. Fergusson data DO-OD/ 0198F |
| Cyprus: off Larnaca | 4-2-1999 | – | 300[a] | 150 | 250 | Bottom-set gillnet | Ian K. Fergusson data: CY-OD/ 0399 |
| Cyprus: Limassol | 1-10-1999 | – | 300 | 200 | 100 | Demersal longline | Ian K. Fergusson data: CY-OD/ 0199 |
| Cyprus: Limassol | 1-10-1999 | – | 160 | – | 100 | Demersal longline | Ian K. Fergusson data: CY-OD/ 0299 |
| Lebanon: off Beirut | 3-4-1964 | M | 283 | – | 100 | – | George et al. (1964) |
| Turkey: Fethiye coast | October 2002 | – | 200[a] | – | – | Demersal trawl | M. Bilecenoglu |
| Turkey: Urla, Izmir Bay | 25-8-2004 | F | 190 | 34 | 30 | Unknown: artisanal | M. Bilecenoglu |

**Table 1** continued

| *Capture area* | Date | Sex | TL (cm) | Wt (kg) | Capture depth (m) | Observation/ capture method | Reference/personal communication/specimen registration nos |
|---|---|---|---|---|---|---|---|
| North Atlantic Ocean | | | | | | | |
| France: Bay of Biscay | 10-1-1930 | M | 141 | 13 | 200–250 | Trawl | Desbrosses (1930) |
| Spain: northern coast | September 1970 | M | 121 | – | – | – | Quèro (1972) |
| Canary Islands: Fuerteventura | 8-3-2000 | F | 374 | 370 | – | Floating, dead | A. Hernandez, photo |
| Canary Islands: Lanzarote | 26-6-1996 | F | 401[b] | 420 | – | Floating, dead | A. Hernandez, photo |
| Azores | 7-5-1997 | M | 344 | – | – | Demersal longline | P. Duarte, photo |
| Azores | 1990s | M | 152 | – | – | Bottom gillnet | Santos et al. (1997) |
| Azores | 1990s | M | 304 | – | – | Bottom gillnet | Santos et al. (1997) |
| Madeira | 26-8-1941 | M | 191 | – | – | – | Maul (1955) |
| USA: North Carolina | 11-8-1994 | F | 340 | 250 | 173 | Demersal trawl | Sheehan (1998) |
| USA: Florida Straits | – | M | – | – | 300–500 | – | J. Castro |
| Mexico: Yucatan Shelf | 7-8-1989 | F | 366 | 289 | 130 | – | Bonfil (1995) |
| Indian Ocean | | | | | | | |
| Maldives | 1996 | M | 310 | – | 300 | Vertical longline | Adam et al. (1998) |
| S. Africa: KwaZulu Natal | 21-10-1966 | M | 111 | 7.3 | | Demersal trawl | Bass et al. (1975) |
| S. Africa: KwaZulu Natal | 2-2-1968 | F | 109 | 8.6 | – | Demersal trawl | Bass et al. (1975) |
| S. Africa: KwaZulu Natal | 7-9-1968 | M | 107 | 6.8 | 400–420 | Demersal trawl | Bass et al. (1975) |
| S. Africa: KwaZulu Natal | 1-4-1972 | M | 110 | 8.6 | 400–420 | Demersal trawl | Bass et al. (1975) |
| Madagascar (north-east) | 1969 | – | 352 | – | – | Demersal trawl | Bass et al. (1975) |
| Ninety East Ridge | 1973 | – | 300[b] | 162 | – | Mid-water trawl | Abe et al. (1981) |
| South-West Indian ridge | March 1982 | – | 292[b] | 150 | 70–80 | Mid-water trawl | Gubanov (1985) |
| South-West Indian ridge | March 1982 | – | 291[b] | 149 | 70–80 | Mid-water trawl | Gubanov (1985) |
| South-West Indian ridge | July 1982 | F | 300 | 145 | 150–180 | Mid-water trawl | Gubanov (1985) |
| South-West Indian ridge | July 1982 | F | 276 | 70 | 140–170 | Mid-water trawl | Gubanov (1985) |
| Melville Ridge | October 2000 | – | 350[a] | – | – | Demersal trawl | Leonard J. V. Compagno - 20001214 |
| North Pacific Ocean | | | | | | | |
| Japan | 22-8-1968 | F | 360 | 311 | 80–90 | Bottom-set gillnet | Abe et al. (1968) |
| Japan | 27-1-2000 | – | 348 | 250[a] | – | – | K. Nagaya |
| Hawaii: south-west Oahu | 9-4-1969 | – | 297 | – | 185–310 | Bottom-set gillnet | Clarke (1972); BPBM 9335 |
| Hawaii: Lisanski | 14-12-1969 | F | 199 | – | 185–310 | Bottom-set gillnet | Clarke (1972); BPBM 9334 |
| USA: southern California | 2-11-1962 | – | 300 | – | 15 | Purse-seine | Daugherty (1964); CAS 27022 |
| USA: southern California | 10-1-1963 | M | 169 | – | 100 | Gillnet | Daugherty (1964); CAS 27023 |
| USA: southern California | 21-11-1968 | M | 275 | 159 | – | Bottom-set gillnet | Seigel and Compagno (1986) |

**Table 1** continued

| *Capture area* | Date | Sex | TL (cm) | Wt (kg) | Capture depth (m) | Observation/ capture method | Reference/personal communication/specimen registration nos |
|---|---|---|---|---|---|---|---|
| USA: southern California | 8-2-1979 | F | 367 | 323[c?] | 175 | Bottom-set gillnet | Seigel and Compagno (1986) |
| USA: southern California | 3-2-1985 | F | 280 | 149 | 40 | Bottom-set gillnet | Seigel and Compagno (1986) |
| Mexico: Gulf of California | 21-5-1994 | F | 364 | 330 | – | "Drift" gillnet | Villavicencio-Garayzar (1996) |
| Mexico: Gulf of California | 1985 | M | 200[a] | – | – | – | A. P. Klimley |
| South Pacific Ocean | | | | | | | |
| New Caledonia: Antigonia Seamount | 21-10-1992 | M | 300[a] | – | 390–420 | Demersal trawl | Stewart (1997) |
| New Caledonia: Jumeaux Seamount | 23-11-1996 | M | 290 | | 295–900 | Demersal trawl | B. Seret; NMNZ P.29397 |
| Louisville Seamount Chain | 15-7-2004 | F | >400 | 800[a] | 883 | Demersal trawl | M. Francis |
| New Zealand: Hawke Bay | 16-10-1972 | F | 231 | 90.7 | 119 | Demersal trawl | Garrick (1974) |
| New Zealand: Hawke Bay | 26-11-1972 | M | 213 | – | 165 | Demersal trawl | Garrick (1974); NMNZ P.5974 |
| New Zealand: Bay of Plenty | 6-12-1985 | F | 152 | – | 525 | Demersal trawl | A. Stewart; NMNZ P 18019 |
| New Zealand: Bay of Plenty | 13-7-1993 | M | 130 | 13 | 220 | Bottom-set gillnet | A. Pederson and A. Christie |
| New Zealand: near Port Taranaki | 1-7-1997 | F | 188 | – | 40 | Bottom-set gillnet | Stewart (1997); NMNZ P.34344 |
| New Zealand: near Port Taranaki | 20-8-2003 | F | 164 | 27[a] | 40 | Bottom-set gillnet | A. Stewart; NMNZ P.38857 |
| Australia: NSW, NE of Gabo Island | 14-5-1948 | M | 168 | 25.0 | 137 | Demersal trawl | Whitley (1950); AMS IB.2136 |
| Australia: NSW, off Newcastle | 23-7-1986 | F | 450[a] | >700 | 400 | Demersal trawl | D. Bagnato (Ken J. Graham data) |
| Australia: NSW, off Eden | 10-4-2000 | F | 368 | 340 | 385 | Demersal trawl | N. Otway |
| Australia: north-east Victoria | 5-3-2004 | F | 300[a] | – | 100–120 | Demersal trawl | Ken J. Graham data; AMS I.43369–001 |
| Australia: NSW, off Ulladulla | 6-5-2004 | M | 280[a] | – | 275 | Demersal trawl | Ken J. Graham data; AMS I.43367–001 |

[a] approximate/estimated

[b] TL estimated from TL-TW regression

[c] eviscerated weight

(Soljan 1975; Morovic 1976; Soldo and Jardas 2002), Malta (Schembri et al. 2003); Greece, Turkey and the Aegean Sea (Economidis 1973; Papakonstantinou 1988; Bilecenoglu et al. 2002), Lebanon (Ben-Tuvia 1971; Mouneimne 1977), Algeria (Moreau 1881; Dieuzeide et al. 1953) and northern Tunisia (Capapé et al. 1976).

In Italian waters, *O. ferox* is occasionally caught by artisanal fisheries in the Tyrrhenian Sea off Calabria (M. Vacchi, personal communication). The species is also caught infrequently in the Adriatic Sea, especially along its Italian coast, but its current status there is difficult to assess because of fishery misidentification with other sharks. Relatively small (<200 cm TL) specimens caught by trawls and deepwater bottom longlines off Croatia are reportedly confused with, and marketed as, smoothhound shark, *Mustelus* spp. (Soldo and Jardas 2002). Juvenile specimens (*ca.* 140 cm and slightly larger) of both *O. ferox* and *C. taurus* have been seen together at

**Table 2** Sites of diver observations of *O. ferox*

| Country | Location | Number of observations | Number of sharks/dive | Estimated size (TL cm) | Depth (m) | Reference/personal communication |
|---|---|---|---|---|---|---|
| Lebanon | Beirut | >10 | 1–5 | >250 | 15–30 | Ian K. Fergusson data |
| Tanzania | Pemba I. | 1 | 1 | >400 | 15 | Leonard J. V. Compagno data; R. Sondhi |
| Australia | Cocos-Keeling I. | 2 | 1 | >350 | 15–30 | B. Hutchins, A. McNeil |
| Columbia | Malpelo I. | >10 | 1–5 | >300 | 30–65 | C. Roessler, D. Perrine |
| New Zealand | Kermadec I. | 3 | 2–6 | >250 | 18–35 | Francis (1991); K. Westerkov, K. Gregor |
| New Zealand | White I. | 1 | 1 | 200 | 25 | C. Duffy |
| New Zealand | Gisbourne | 1 | 1 | 150 | 26 | C. Duffy; www.theeyeonthesea.org.nz |
| Brazil | Fernando de Noronha Archip. | 3 | 1 | >200 | 12–30 | Garla and Garcia Jr (2006) |

Croatian fishmarkets in recent years and several skinned specimens of *O. ferox* were also noted during surveys of commercial fishing activity (A. Soldo, personal communication). In contrast, no recent records are known from the Italian coast of the Adriatic (I. Bianchi, personal communication). Numerous new reports from insular Mediterranean locations are listed in Table 1. The Sifnos Island capture, the smallest Mediterranean specimen in our dataset, was the distinctive "piebald" juvenile shown in Fig. 3C.

Of three recent records of *O. ferox* from the Turkish coast (Table 1), two were observed during a 10-year monitoring of fishery landings along the Turkish coast of the Aegean Sea (M. Bilecenoglu, personal communication), and the third (reportedly *ca.* 400 cm TL) from off Fethiye was identified from a photograph in the local *Sabah* newspaper (15 February 2001). There are no records of *O. ferox* from the Black Sea or the Sea of Marmara. On the Lebanese coast, sharks previously identified as *C. taurus* but now known to be *O. ferox*, are repeatedly seen by divers at the "Shark Land 2" dive-site off Beirut. There are also reports of *O. ferox* being caught in demersal longline and gillnet fisheries off Lebanon, e.g. captures in nets set off Ein Mreisse, on the coast north of Beirut (W. Noshie, personal communication).

The current status of this shark in North African waters of the Mediterranean is patchily known. A small number of specimens, confirmed by preserved dentition, were reported from Algerian fisheries (F. Hemida, personal communication), and literature and contemporary records for Tunisia are equally scant (Capapé et al. 1976; Ian K. Fergusson data). However, it is likely that specimens continue to be landed at Tunisian ports from fisheries operating throughout the Sicilian Channel. We have no reports of *O. ferox* in Libyan or Egyptian waters but it is likely to occur in the slope waters of the southern Levantine Basin.

### *Atlantic Ocean*

Captures have been widespread around the periphery of the North Atlantic Ocean with records from the coasts of Morocco (Cadenat and Blache 1981), northern Spain, France, southern USA and Mexico (Table 1). The French specimen, caught at ~46°N,

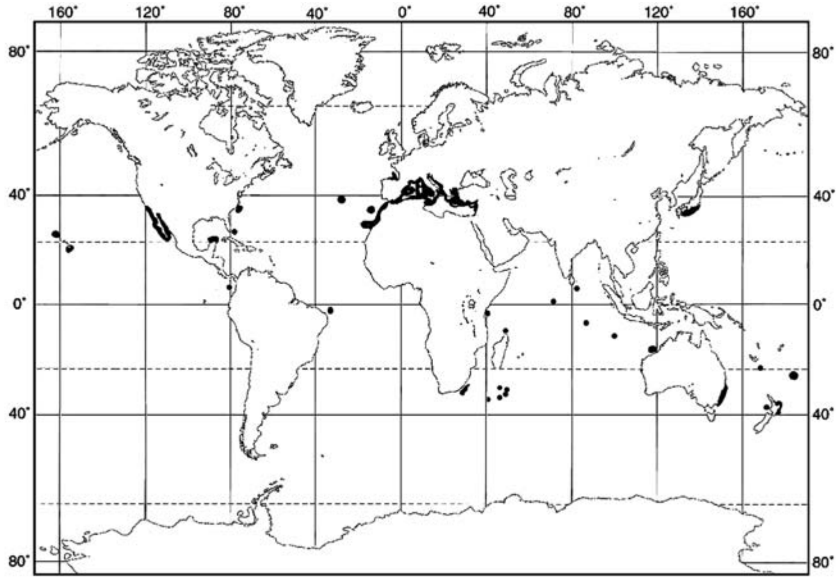


**Fig. 1** Worldwide distribution of *Odontaspis ferox*, combining all sources cited in this paper

4°W in the Bay of Biscay, is the most northerly record for *O. ferox*. There are also several records from oceanic islands and archipelagos in the North Atlantic (Table 1). From the Azores archipelago, four males were caught in gillnets in the 1990s (Santos et al. 1997) and more recently, P. N. Duarte (personal communication) reported two stranded specimens and a moribund (floating) 344 cm male from Sao Miguel, which were conceivably discards from commercial netting. Canary Island records include the large females detailed in Table 1 and three more specimens preserved at the Museo Insular (Brito 1991).

Until recently, there was a sole published record of *O. ferox* from the South Atlantic, a specimen caught off north-eastern Brazil and identified from preserved jaws (Menni et al. 1995). As we completed our paper, Garla and Garcia Júnior (2006) reported a *ca.* 300 cm TL specimen, caught at night by handline at a depth >60 m, from the Fernando de Noronha Archipelago off Brazil (3°52′S 32°25′W). The authors also described encounters with free-swimming *O. ferox* at the same location, with their specific identification supported by photographs.

*Indian Ocean*

Anderson and Ahmed (1993) and Adam et al. (1998) report *O. ferox* from the Maldives where this species is caught on outer reef slopes in bottom-set gillnets at about 100 m, and in deeper water with vertical longlines set for gulper sharks, *Centrophorus* spp., and sixgill sharks, *Hexanchus griseus*. A single record for Sri Lanka is based on a set of jaws collected from a souvenir dealer in Hikkaduwa (Morón et. al. 1998).

South of the equator, a specimen of *O. ferox* was caught by pelagic trawl above the Ninety-East Ridge at ~10°S, 87°E (Abe et al. 1981; Table 1). In March 1995, a large female (3–4 m TL) was recorded on video in 15–30 m at the Cocos (Keeling) Islands (12°S, 97°E) followed by a second sighting of *O. ferox* at the same location in August 1995 (Table 2). The only reported capture of *O. ferox* from Australia's west coast is of a single specimen (>200 cm TL) taken in the 1980s by deepwater scampi trawl, in 300–450 m west of Port Hedland (*ca.* 21°S) (J. D. Stevens, personal communication; Sainsbury et al. 1985).

The presence of *O. ferox* in east African inshore waters was confirmed from photographs, taken in November 2002, of a large female encountered by a diver off Pemba Island, Tanzania (Table 2). Further south, the initial record of *O. ferox* for South Africa was of a specimen caught in Durban Harbour (D'Aubrey 1969), but this report is doubtful as it was not cited in subsequent South African publications (e.g. Bass et al. 1975; Bass and Compagno 1986). However, there have since been several confirmed occurrences from the western Indian

Ocean, including the South African coast, with all but one from offshore or oceanic waters (Table 1). The 352 cm TL specimen from deepwater off northern Madagascar was initially reported by Forster et al. (1970) as *C. taurus* but is now believed to be *O. ferox* (Bass et al. 1975) and more recently, a specimen was caught by a South African trawler on the Melville Bank at *ca.* 38°29′S, 46°46′E; its length was estimated to be between 300 and 400 cm, based on the dimensions of the jaws (Leonard J. V. Compagno data). Specimens reported by Abe et al. (1981) and Gubanov (1985) were caught in 70–180 m by mid-water trawl above the Ninety-East and South-West Indian Ridges (Table 1), presumably in the water column, but no data are given as to the proximity of the nets to the seabed.

*North Pacific Ocean*

Smalltooth sandtiger sharks have been caught across much of the temperate to tropical North Pacific: in the Sagami Sea and elsewhere off southern Japan, off Hawaii, off southern California and in the Gulf of California, Mexico (Table 1). In addition to the 364 cm TL female listed in Table 1, Villavicencio-Garayzar (1996) also reported two other *O. ferox* (with no details) from insular locations in the Gulf of California. Photographs and descriptions by divers have confirmed the species' presence at Malpelo Island off Columbia (Table 2), while recently there have been unconfirmed, but credible, diver reports of this species from the Parque Nacional de Isla de Coco (also known as Cocos Island) at 05°33′N, 87°03′W (J. Stafford-Deitsch, M. deGruy and J. Ruxton, personal communication).

*South Pacific Ocean*

All records of *O. ferox* from the South Pacific are from the western sector (Tables 1, 2, 3).

*New Caledonia and Louisville Seamounts* Two males were caught in deepwater to the south of New Caledonian by the local research vessel *Alis* (Jumeaux Seamount: 23°40.5′S, 168°15.5′E), and by the New Zealand research vessel *Tangaroa* (Antigonia Seamount: 23°25′S, 168°00′E). In July

**Table 3** Details of *O. ferox* captured during scientifically monitored research and commercial trawling off NSW

| FRV *Kapala* | | | | | Commercial vessels | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Date | Sex | TL (cm) | TW (kg) | Depth (m) | Date | Sex | TL (cm) | TW (kg) | Depth (m) |
| 11 7 1975 | M | 155[a] | 15.8 | 360 | 29 1 1994 | – | 317[d] | 200 | 590 |
| 11 7 1975 | F | 114[a] | 7.0 | 360 | 26 4 1994 | | | (120)[e] | 548 |
| 11 7 1975 | F | 122[a] | 8.4 | 360 | 17 5 1994 | – | 115[d] | 8.0 | 523 |
| 11 7 1975 | F | 136[a] | 12.4 | 360 | 20 9 1995 | | | (240)[e] | 150 |
| 16 9 1975 | F | 425[c] | – | 460 | 23 5 1995 | – | 246[d] | 90 | 540 |
| 30 4 1976 | – | 130 | – | 490 | 28 2 1996 | – | 115[d] | 8.0 | 550 |
| 27 5 1976 | – | 152 | – | 595 | 13 3 1996 | – | 134[d] | 13.0 | 590 |
| 9 6 1977 | M | 290 | – | 495 | 13 3 1996 | – | 147[d] | 17.5 | 600 |
| 9 6 1977 | M | 300 | – | 495 | 27 1 1996 | – | 129[d] | 11.5 | 525 |
| 2 8 1978 | – | 292[d] | 150 | 412 | 17 4 1997 | – | 128[d] | 11.3 | 560 |
| 7 8 1979 | – | 123[d] | 10 | 366 | 24 4 2001 | – | 119[d] | 9.0 | 540 |
| 12 4 1989 | F | 267 | – | 850 | 24 4 2001 | – | 123[d] | 10.0 | 540 |
| 16 5 1989 | M | 225 | – | 840 | 24 4 2001 | – | 112[d] | 7.5 | 460 |
| 28 5 1997 | F | 108[b] | 7.3 | 330 | 6 8 2001 | – | 110[d] | 7.0 | 475 |

[a] AMS I.18775–002

[b] AMS I.38629–004

[c] approximate

[d] TL estimated from length-weight regression

[e] combined weight for two specimens (individual weights or lengths not recorded)

2004, a trawler targeting orange roughy, *Hoplostethus atlanticus*, caught a large female (not measured, estimated weight 800 kg) on a Louisville Ridge seamount (38°32.7′S, 168°08.9′W) east of New Zealand; its 883 m capture depth is the greatest recorded for *O. ferox*.

*New Zealand* At L'Esperance Rock, Kermadec Islands, divers observed and filmed at least six *O. ferox* in 30–35 m during October 1986 (Francis 1991), and a photograph depicting two of these sharks was subsequently used to advertise dive-charter operations to the islands (Anon 1993). There were further sightings of large *O. ferox* at the Kermadecs in October 1996 (Table 2).

All mainland New Zealand records are from the North Island with most from the east coast. The first captures were of six specimens trawled in 119–165 m off Hawke Bay in 1972 (Garrick 1974) and since then numerous *O. ferox* have been caught or observed around White Island in the Bay of Plenty. In 1985, 13 adults to about 4.3 m TL were caught by mesh-net at the Volkner Rocks in 175–275 m; five were retained for display in an Auckland aquarium but none survived acclimatisation (C. Thorburn, personal communication). More recent captures were a 1.3 m male (July 1993) and a 1.2 m female (November 1994) that survived in captivity for 11 months (A. Christie, personal communication), and in December 2003, four juveniles between 1.2 and 1.9 m TL also destined for aquarium display (C. Duffy, personal communication). In March 2001, an estimated 200 kg specimen was caught in 280 m, photographed and released alive (A. Stewart, personal communication). Diver sightings of *O. ferox* include a 2.0 m specimen at White Island (April 2001) and a 1.5 m shark seen by D. Freeman (NZ Department of Conservation) while diving in the Te Tapuwae O Rongokako Marine Reserve (38°35′S, 178°14.5′E) in January 2004 (Table 2). The only west coast, North Island, reports of *O. ferox* are of two juvenile females caught in mesh nets set in about 40 m depth south of Port Taranaki (Table 1).

*Eastern Australia* There are 58 recorded captures of *O. ferox* from south-eastern Australia (Fig. 2). The first two Australian specimens were caught by trawlers in 1947 and 1948 between Eden and Gabo Island off southern New South Wales (NSW), and are the type and paratype specimens of Whitley's (1950) *O. herbsti*. Since 1970, *O. ferox* was frequently caught off NSW and eastern Victoria by demersal trawl in outer shelf and upper slope depths during research surveys and commercial fishing (see Tables 1 and 3 for captures with size data). Despite extensive deepwater trawling, none has been reported from around Tasmania and along the southern coast of Australia.

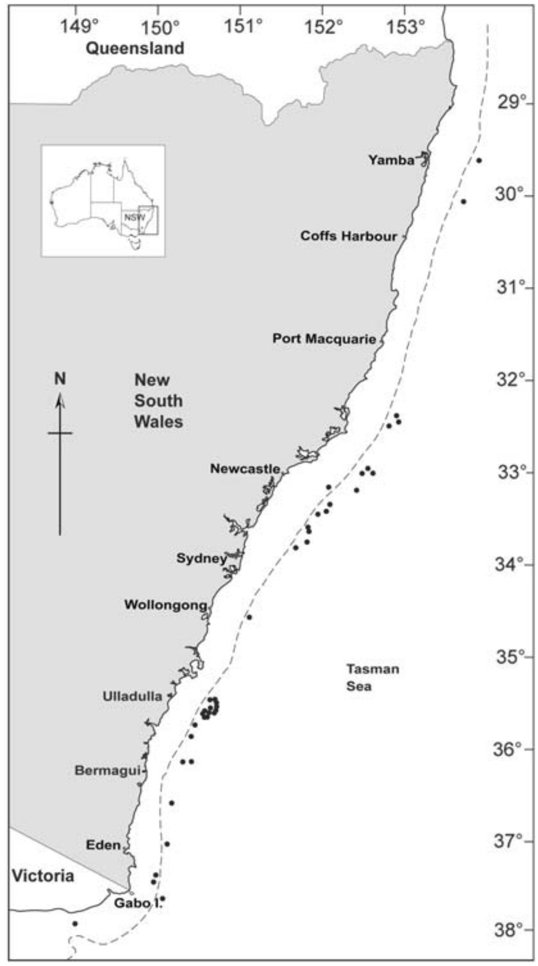


**Fig. 2** Capture locations of *O. ferox* taken by trawl off NSW, Australia. The hatched line represents the 200 m isobath

The NSW records include 36 *O. ferox* caught between 1975 and 1997 during trawl surveys by the NSW fisheries research vessel *Kapala*; these captures were distributed between latitudes 29°32′S and 37°38′S in depths between 300 and 850 m. In 2001, four juveniles were caught in 460–560 m off

Bermagui during a research project on a chartered commercial trawler (Table 3). Between 1993 and 1997, scientific observers onboard commercial trawlers documented catch and bycatch for about 1,600 trawls off central and southern NSW, and eastern Victoria (Liggins 1996, 1997). Twelve *O. ferox* were recorded during the project, including two specimens in 150 m off Newcastle and ten off Ulladulla (Table 3). Other captures of *O. ferox* by commercial trawlers off south-eastern Australia (Table 1) include a female at least 4.5 m TL and weighing in excess of 700 kg (Newcastle Herald newspaper, 24 July, 1986), and a specimen from northeast Victoria that is the shallowest (100–120 m) and most southern (37°53′S, 149°19′E) record for Australia. Despite the species being protected in NSW waters, compliance officers intercepted several headed and eviscerated carcasses of mostly juvenile *O. ferox* at the Sydney Wholesale Fish Market during 2004–2005.

## Regional colour variability

The existence of spotted specimens outside the Mediterranean Sea, including from California (Seigel and Compagno 1986), is supported by observations and photographs of *O. ferox* at Malpelo Island (D. Perrine and C. Roessler, personal communications). As with specimens seen off Lebanon, *O. ferox* at Malpelo exhibited considerable variability in the presence, density and size of spots. The Malpelo sharks were also typified by rather spotty, blotchy pigmentation although mostly without the coarser, black oval blotches seen in most Mediterranean specimens. Whitley's (1950) "*O. herbsti*" was a juvenile (168 cm TL) and its lack of any dark pigmentation is consistent with all small specimens (<2.0 m TL) subsequently examined from NSW waters. Larger specimens caught off NSW, and those free swimming individuals photographed at the Kermadec and Cocos (Keeling) Islands, were predominantly plain brownish-grey dorsally with some showing a scattering of small dark blotches. Figure 3 shows the variable pigmentation seen in *O. ferox*. We believe there may be some regionalised trends controlling the intensity of such pigmentation, much as seen with other species of sharks (e.g. *Carcharodon carcharias*; Ian K. Fergusson and Leonard J. V. Compagno, unpublished data).

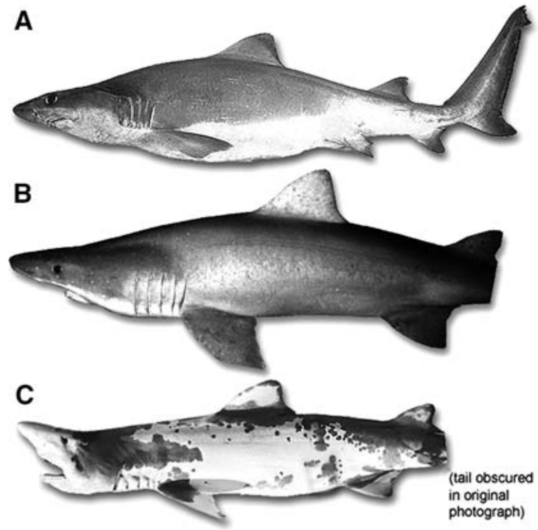


**Fig. 3** Variability in pigmentation observed with *O. ferox*: (**A**) uniformly grey, unspotted juvenile from NSW; (**B**) Moderately spotted, brownish-grey adult from Malpelo Island; (**C**) Extreme "piebald" pigmentation on a juvenile from Sifnos, Greece

## Depth distribution and habitat

Depth data were available for about 90 captured *O. ferox*, as well as diver observations at seven locations, giving an overall depth range for the species of 10–883 m (Tables 1–3). Most specimens from depths less than 300 m were caught inshore on steep, rocky terrain by bottom-set gill-nets and long-lines, and vertical set-lines, whereas the deeper *O. ferox* captures were all by trawl. Although most small juveniles (<150 cm TL) were caught by trawl, the overall size range of specimens caught by the different fishing methods was similar (Fig. 4).

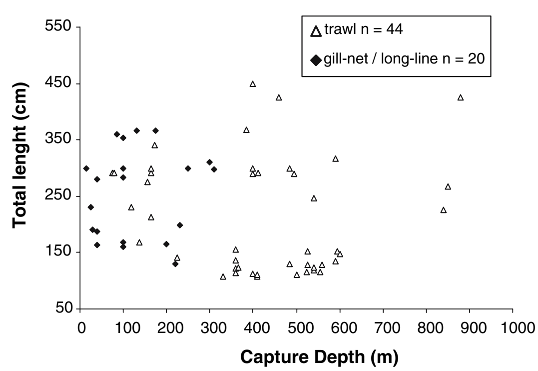


**Fig. 4** Depth distribution of *O. ferox*, plotted as a function of total length

In the Mediterranean Sea, most *O. ferox* were caught nocturnally by gill-nets or lines set on rocky or boulder-strewn seafloors in depths less than 250 m. Capture sites were typically along the coasts of islands lying contiguous to deepwater, near offshore seamounts, or at mainland localities where continental shelves are narrow. Similarly, almost all the *O. ferox* caught in the North Atlantic and North Pacific Oceans, at the Maldives, and around New Zealand's White Island were from insular locations that shelved steeply into depths of several hundred metres. The Volkner Rocks site at White Island, where *O. ferox* was targeted with mesh nets for aquarium display, is described as a deep valley between two pinnacles that rise to 175 and 210 m from the surface (C. Duffy, personal communication). All the dive sites (Table 2) are close to deepwater. At the Kermadec and Malpelo Islands, individuals and small groups of adult *O. ferox* were photographed swimming close to the rocky slopes and associated seamounts. Video footage from Cocos-Keeling Island shows a large female swimming slowly over mainly sandy seabed between coral outcrops, while the small *O. ferox* near Gisbourne, New Zealand, was also seen over the sandy areas of a reef described as "a series of pinnacles encrusted with sponges and bryozoa interspersed with sand" (see Table 2). At the Fernando de Noronha Archipelago off Brazil, Garla and Garcia-Junior (2006) describe the north-western seascape where *O. ferox* have been caught and encountered free-swimming as "...mainly composed of descending slopes with large boulders, and the south-eastern side is characterised by extensive algal-vermetid ridges along rocky shorelines".

The majority of Southern Hemisphere *O. ferox* were taken by trawl on the outer continental shelves or upper slopes of Australia, New Zealand and South Africa, and on or over oceanic ridges in the Indian and southwest Pacific Oceans (Tables 1, 3). Capture depths by demersal trawl were between 100 and 880 m and although *O. ferox* was caught down to 850 m off NSW, none was caught in any of almost 200 trawls in 900–1,250 m (Table 4). Mid-water trawl specimens included four specimens caught in 70–180 m (from the surface) on the Southwest Indian Ridge where the bottom depth is mostly between 200 and 2,000 m, although the tops of some ridges (e.g. Melville Bank) rise to within 50 m of the surface. Similarly, the Louisville Ridge where the specimen in 880 m was captured is a chain of more than 60 volcanoes, most of which rise to within 200–500 m of the surface from the surrounding seabed depths of around 4,000 m (Clark and Anderson 2003). The only captures made in open waters not close to relatively shallow ridges or seamounts were two specimens reported by Abe et al. (1981) from mid-water trawls over the Ninety East Ridge at 10°S 87°E, where bottom depths are between 2,000 and 4,000 m.

By definition, trawling grounds are relatively smooth, open areas of seabed with sand or mud substrate providing habitat for *O. ferox* that greatly

**Table 4** Frequency of *O. ferox* captures during scientifically monitored research and commercial trawling off NSW

| Vessel | Region | Sampling period | Depth range (m) | Number of tows | Number of tows with *O. ferox* | Total *O. ferox* |
|---|---|---|---|---|---|---|
| Overall data | | | | | | |
| FRV *Kapala* | NSW | 1975–1997 | 100–300 | 760 | 0 | 0 |
| FRV *Kapala* | NSW | 1975–1997 | 300–900 | 800 | 28 | 36 |
| FRV *Kapala* | NSW | 1975–97 | 900–1,250 | 189 | 0 | 0 |
| FV *Shelley H* | Bermagui | 1999–2001 | 100–650 | 200 | 3 | 4 |
| Commercial | Newcastle | 1993–1995 | 100–200 | 10 | 1 | 2 |
| Commercial | Newcastle | 1993–1995 | 200–700 | 19 | 0 | 0 |
| Commercial | Ulladulla | 1993–1997 | 200–700 | 319 | 9 | 10 |
| Commercial | Eden | 1993–1997 | 200–700 | 467 | 0 | 0 |
| Commercial | Ulladulla-Eden | 1993–1997 | 25–200 | 800 | 0 | 0 |
| Comparable survey data | | | | | | |
| FRV *Kapala* | Central-sthn NSW | 1976–1977 | 225–630 | 246 | 12 | 14 |
| FRV *Kapala* | Central-sthn NSW | 1996–1997 | 225–630 | 165 | 1 | 1 |

contrasts to the steeply shelving, rocky topography described above. Off NSW, where more than 60 *O. ferox* have been trawled, the continental shelf is mainly 15–25 n. miles wide and gently slopes to the shelf break at around 200 m depth; the upper slope (200–700 m) is narrower (mostly 3–5 n. miles wide) with a gradient between 1:10 and 1:20 (Iwamoto and Graham 2001). While the NSW grounds are interspersed with untrawlable areas of low reef (mainly on the shelf) and smooth-sided ravines along the slope, there are no areas of high reef, pinnacles or seamounts that rise close to the sea-surface near any of the *O. ferox* capture locations.

Few water temperature records are available for *O. ferox* habitats but the data suggest an overall range from about 6°C to more than 20°C. Temperatures at the capture depths are given for the North Carolina specimen in 173 m (17.8°C; Sheehan 1998), the two South-West Indian Ridge specimens in 140–180 m (16.3–17.3°C; Gubanov 1985), and the two Hawaiian captures in 185–310 m (between 18°C and 9°C; Clarke 1972). Seabed temperatures on the NSW upper and mid slopes are generally less than about 12°C with recorded temperatures ranging from 10.1°C in 400 m to 4.0°C in 1,150 m (cf. surface temperatures of 18–24°C). The seabed temperature was 5.5°C during the 850 m trawl that caught the deepest NSW *O. ferox* (Station K890606; Graham 1990). Similarly, trawl headline temperature was 5.8°C at 880 m for the Louisville Seamount specimen. Although surface water temperatures at tropical dive sites frequented by *O. ferox* usually exceed 25°C e.g. Cocos (Keeling) and Malpelo Islands, temperatures below the thermoclines are substantially lower. At Malpelo, temperatures are around 27°C above the thermoclines in 9–30 m[1] but can be as low as 15°C at greater depths[2]. The reports of most *O. ferox* at Malpelo being seen in depths more than 30 m suggest they remain in the cooler waters below the thermocline. Garla and Garcia-Junior (2006) describe the habitat for *O. ferox* at the Fernando de Noronha Archipelago off Brazil as having mean (presumably surface) temperatures of 26–27°C and mean salinity of 36%.

[1] www.bsatravelclub.co.uk

[2] www.divequest.co.uk

## Abundance

Reported captures in commercial fishing gear (and diver sightings) were mostly of small numbers (1–5 sharks) suggesting the species does not aggregate in large numbers, at least in areas or depths exploited by fishers. With no targeted fishing for the species (apart from the occasional mesh-netting at White Island, New Zealand, for aquarium specimens), the only quantitative data relating to the relative abundance of *O. ferox* are from the *Kapala* trawl surveys (Ken J. Graham data) and the scientific study of the commercial fishery (Liggins 1996, 1997) off NSW. The frequency of capture during this monitored trawling is summarised in Table 4.

Although not strictly comparable, *Kapala* and commercial trawlers (with larger gear and longer tow duration) each completed about 1,000 trawls in the 200–850 m depth range, catching, respectively, 36 and 16 *O. ferox*. Almost all captures by *Kapala* and commercial trawlers were of single specimens; multiple captures were seven pairs, and one was of four juveniles. The data show evidence for a decline in relative numbers of *O. ferox* on the NSW slope. Of the 36 *Kapala* captures, 33 were caught between 1975 and 1981 (from 500 slope tows) but only three were taken from about 300 tows between 1982 and 1997. During comparable trawl surveys in 1976–1977 and 1996–1997 (see Graham et al. 2001), there were 14 captures (from 12 stations) from 246 tows in 1976–1977, but only a single juvenile from 165 tows in 1996–1997. On the Ulladulla trawl-ground in particular, *Kapala* caught seven *O. ferox* from 96 trawls in 1976–1977 but only one from 53 trawls in 1996–1997 (Graham et al. 1997). In the 1993–1997 period on the same ground, the average *O. ferox* catch by commercial trawlers was one every 32 tows (Table 4), and when these data are adjusted for gear size and tow duration (to make them comparable to *Kapala* data), the equivalent commercial catch rate was about one shark per 150 tows.

## Biological data

### *Size*

The relationship between total weight (TW, kg) and total length (TL, cm) was plotted from data from 30 intact specimens (18 females, 8 males, 4 unsexed;

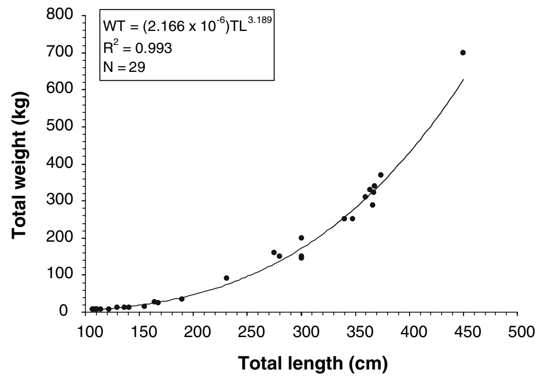


**Fig. 5** Weight-at-length relationship for *O. ferox*, both sexes combined

Tables 1, 3). The 276 cm TL, 70 kg female from Gubanov (1985) was identified as an outlier (after plotting residuals) and excluded. Data for the remaining 29 specimens generated the power equation:

$$TW = (2.166 \times 10^{-6})TL^{3.189};\ R^2 = 0.993$$

(Fig. 5).

Total length values were available for 33 females (108–450 cm TL), 23 males (107–344 cm TL), and 12 unsexed individuals. Using the length-weight relationship (above), estimated total lengths were assigned to a further 18 specimens with accurate total weights. The length distribution was essentially bimodal (Fig. 6) with 42% of the sample consisting of juveniles smaller than 200 cm TL, and a second mode (275–375 cm TL) comprising mature males and maturing/mature females (see below).

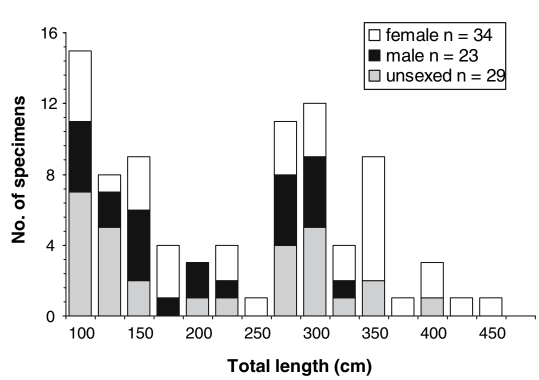


**Fig. 6** Length frequency distribution of *O. ferox*

## *Maturity and reproduction*

*Males* Table 5 summarises male reproductive data for 11 males between 107 and 344 cm TL. Five males between 107 and 168 cm TL were classed as immature with small, uncalcified claspers about 2% of TL. Six specimens larger than 200 cm were mature. All had large, swollen or calcified claspers, with clasper lengths from three specimens measuring between 6.6 and 10.2% of TL. The *ca.* 200 cm male from the Gulf of California had notably large, swollen and reddened claspers possibly indicating recent mating (P. Klimley, personal communication). Further signs of maturity were observed in the 225 and 344 cm males from NSW and the Azores when sperm was readily discharged after their pelvic areas were depressed (Ken J. Graham data; P. N. Duarte, personal communication).

*Females* Observations of female maturity were available for 14 specimens ranging in size from 109 to 410 cm TL (Table 6). Eight females between 109 and 280 cm TL were recorded as immature, and six larger than 350 cm TL showed evidence of maturity. Three immature specimens (114–267 cm TL) from NSW were examined internally (by Ken J. Graham) and none showed any sign of ovarian or uterine development. A 231 cm female from New Zealand was also considered immature: although only jaws were preserved, the collector reported that, although appearing bulky, no foetus or eggs were found internally (Garrick 1974). Mature females were 350 cm TL or greater. Villavicencio-Garayzar (1996) described the right ovary of his 364 cm specimen as enlarged and functional, and containing "hundreds of ova (modal diameter = 3 mm)". The 368 cm specimen from NSW showed the characteristics of being recently pregnant: the uteri were expanded and flaccid, and although the ovary was relatively large (1.8 kg) and mature, it contained no developing eggs. No pregnant females were reported and size at birth is unknown but, as several specimens between 107 and 110 cm TL were caught, birth size is probably around 100 cm TL. Although mature-sized sharks were caught across the whole depth range (15–880 m), all juveniles smaller than 150 cm TL came from depths greater than 200 m, suggesting parturition occurs in relatively deepwater (see Fig. 4).

**Table 5** Summary of male reproductive data

| TL (cm) | CLO (mm) | Clasper appearance | Observed maturity | Locality | Reference/source |
|---|---|---|---|---|---|
| 107 | – | – | Immature | South Africa | Bass et al. (1975) |
| 110 | – | – | Immature | South Africa | Leonard J. V. Compagno data |
| 111 | – | – | Immature | South Africa | Bass et al. (1975) |
| 155 | 33 | Small, uncalcified | Immature | NSW, Australia | Ken J. Graham data; AMS I.18775–002 |
| 168 | 30 | Small, uncalcified | Immature | NSW, Australia | Whitley (1950); AMS IB.1859 |
| 200[a] | – | Large, swollen | Mature | Gulf of California | A. P. Klimley, personal communication |
| 225 | 230 | Large, calcified | Mature | NSW, Australia | Ken J. Graham data |
| 275 | 180 | Large, calcified | Mature | California | Seigel and Compagno (1986) |
| 280 | 215 | Large, calcified | Mature | NSW, Australia | Ken J. Graham data; AMS I.43367–001 |
| 290 | – | Large, calcified | Mature | New Caledonia | B. Seret, personal communication |
| 344 | – | Large, calcified | Mature | Azores | P. Duarte, personal communication |

[a] approximate

**Table 6** Summary of female reproductive data

| TL (cm) | Ovary state | Uteri state | Maturity | Locality | Reference/source |
|---|---|---|---|---|---|
| 108 | Immature | Immature | Immature | NSW | Ken J. Graham data; AMS I.38629–004 |
| 109 | – | – | Immature | South Africa | Bass et al. (1975) |
| 114 | Immature | Immature | Immature | NSW | Ken J. Graham data; AMS I.18775–002 |
| 122 | Immature | Immature | Immature | NSW | Ken J. Graham data; AMS I.18775–002 |
| 136 | Immature | Immature | Immature | NSW | Ken J. Graham data; AMS I.18775–002 |
| 188 | – | – | Immature | New Zealand | Stewart (1997); NMNZ P.34344 |
| 199 | – | – | Immature | Hawaii | Clarke (1972); Leonard J. V. Compagno data |
| 231 | Immature | – | Immature | New Zealand | Garrick (1974) |
| 267 | Immature | Immature | Immature | NSW | Ken J. Graham data |
| 280 | No mature eggs | No pups | Immature | California | Seigel and Compagno (1986) |
| 360 | – | – | Mature | Japan | Abe et al. (1968) |
| 364 | 100s of small eggs | – | Mature | Gulf of California | Villavicencio-Garayzar (1996) |
| 366 | – | Distended | Mature | Gulf of Mexico | Bonfil (1995) |
| 367 | – | – | Mature | California | Seigel and Compagno (1986) |
| 368 | Spent, no yellow eggs | Flaccid | Mature | NSW | N. Otway personal communication |
| 410 | – | – | Mature | Mediterranean | Vacchi and Serena (1997) |

There were insufficient data to accurately determine size at maturity for either sex, but the information suggests that males mature between 200 and 250 cm TL, and females between 300 and 350 cm TL.

*Diet*

Feeding data for *O. ferox* are limited with few identified prey items identified. Seigel and Compagno (1986) recorded unidentified teleosts, rockfish *Sebastes* spp. and "pieces of an unidentified ray" from their Californian specimens. The juvenile *O. ferox* from South Africa contained teleost fish, squid and prawns, *Hymenopenaeus triarthrus* (Bass et al. 1975). The stomach contents of Whitley's (1950) *O. herbsti* holotype were "unidentifiable, apparently digested fish vertebrae and remains" and a "pillbug", presumably a marine isopod which may have been ingested as secondary prey. A 108 cm female from NSW, preserved in the Australian Museum, contained a "digested 40 cm squalid shark"

(M. McGrouther, personal communication). The 188 cm female from near New Plymouth, New Zealand, had "the tip of the spine of a small ghost shark (Chimaeridae) impaled in its lower jaw cartilage" (Stewart 1997). The only account of large prey is from B. Seret (personal communication) who advised that the 290 cm male *O. ferox* caught south of New Caledonia contained a 130 cm seal shark, *Dalatias licha*. Stomachs were empty in examined specimens from the Gulf of Mexico (Bonfil 1995), Malta (A. Buttigieg and J. Dalli, personal communication), the Azores (P. N. Duarte, personal communication), Canary Islands (A. Hernández, personal communication), and NSW (Ken J. Graham data, N. Otway, personal communication). Overall, identified prey comprised mainly demersal species of chondrichthyans, teleosts and prawns.

*Predators and parasites*

No literature was found reporting the occurrence of *O. ferox* in the stomach contents of other sharks. The only confirmed predator on adult *O. ferox* is the cookie-cutter shark *Isistius brasiliensis*, based upon a recent (March 2000) record of a female *O. ferox* from Fuerteventura, Canary Islands, bearing a single fresh cookie-cutter bite to the gills, on the right flank, just posterior to the 5th gill slit (A. Hernández, photograph). A female *O. ferox* photographed during a dive at Sharkland, Beirut (by W. Noshie, personal communication), bore a distinctive circular excision about the size of a tennis ball on the 1st dorsal fin. Although apparently healed, the wound extended completely through the fin tissue. We believe this injury could be a feeding scar inflicted by one of the larger "cookie-cutter"-type sharks such as *D. licha*.

Dailey (1971) reported the cestode *Litobothrium gracile* (Eucestoda: Litobothridea) from the spiral valve of an *O. ferox* caught off San Onofre, California. The pugnose eel *Simenchelys parasitica* Gill 1839 (family Synaphobranchidae), is also confirmed by a number of individuals found within the heart, body cavity and adjacent dorsal musculature of a 370 cm female *O. ferox* found drifting dead at the surface off south-eastern Fuerteventura, Canary Islands (Fig. 7). This shark was presumably adult but its ovaries were entirely missing, either having being consumed by the eels or having naturally degenerated. It is possible that the eels were contributory to the cause of death as no other obvious external or internal causal factors were found. This case is similar to that reported by Caira et al. (1997) for pugnose eels discovered in the carcass of a shortfin mako *Isurus oxyrinchus*.

**Fig. 7** Pugnose eel *Simenchelys parasitica* (*arrowed*), exposed within the heart of the Fuerteventura *O. ferox* (photo courtesy A. Hernandez)

## Discussion

### Areal distribution and status

Our data reinforced Bonfil's (1995) hypothesis that *O. ferox* has a cosmopolitan but disjunct distribution in warm-temperate and tropical waters of all oceans. Overall, the latitudinal range of *O. ferox* was between 46°N in the Bay of Biscay (Desbrosses 1930) to around 38–39°S in the Indian and Pacific Oceans, confirming its preference for warm temperate and tropical latitudes. The literature available to Bonfil (1995) reported about 40 *O. ferox* captures, and from those he concluded that the low incidence of deep-water fishing, coupled with the species' low abundance, probably accounted for the apparent disjunct or patchy distribution. Although we now have knowledge of about 160 *O. ferox* captures, and in situ observations by divers at eight shallow water sites, the overall picture of a patchy distribution has not greatly changed.

Historical and recent records are widespread in the Mediterranean Sea although some distributional maps of O. ferox (e.g. Compagno 1984; Bonfil 1995; Last and Stevens 1994) and some regional reviews (e.g. Quèro 1984) do not fully represent occurrences eastwards of the Ionian Sea. Repeated sightings of O. ferox by divers at the Shark Land two sites off Beirut may indicate that similar encounters are not unlikely at other sites on the (presently largely undeveloped) Lebanese coast and perhaps at other locations through the southern-central-eastern Mediterranean (e.g. Malta, Crete, Aegean Islands, Cyprus, Turkey and Syria).

There are now numerous records of smalltooth sandtigers from oceanic islands and deepsea ridges, as well the continental shelves and slopes of many larger landmasses. Bonfil (1995) noted that the only major oceanic areas where *O. ferox* remained unreported were the south-eastern Atlantic, south-western Atlantic and south-eastern Pacific Oceans. The Brazilian records of Menni et al. (1995) and Garla and Garcia Junior (2006) now eliminates the south-western Atlantic from that list. The south-eastern Atlantic and south-eastern Pacific Oceans are characterised by relatively cool waters (Benguela and Humboldt Currents, respectively) which may explain the absence of *O. ferox* in these areas. The Malpelo Island and (unconfirmed) Isla de Coco observations represent range extensions south from the Gulf of California. While the species may also be expected to inhabit the waters of the Galapagos Islands, the influence of prevailing cool currents around those islands may mitigate against this. Recent diver sightings of *O. ferox* at Pemba Island and the Cocos (Keeling) Islands in the Indian Ocean are further additions to the growing number of insular habitats now known to be occupied by the species.

New Zealand captures were from the east and west coasts of the North Island, but none from the South Island as shown in a number of distribution maps (e.g. Last and Stevens 1994; Bonfil 1995; Compagno 2001). The first recorded specimens were trawled (Garrick 1974), but several recent captures were from the steeply shelving depths close to White Island in the Bay of Plenty. The two juveniles taken by mesh net south of Port Taranaki were unusual in that their capture was in relatively shallow water (40 m) on the inner continental shelf, not contiguous to any deepwater. Their presence inshore maybe through an association with seasonal spawning runs of common warehou, *Seriolella brama* (A. Stewart, personal communication).

In contrast, all NSW captures were taken offshore by demersal trawling. The continental shelf along the NSW coast is ~15–25 n. miles wide with a gradual decline to the shelf edge at 200 m depth. Nowhere along the NSW coast does deepwater impinge closely inshore, in the manner of the insular and continental rocky, boulder-strewn or reef habitats frequented by *O. ferox* in the Mediterranean and other similar locations. However, considering the presence of *O. ferox* off NSW, on the Norfolk Ridge, and around the Kermadec Islands and New Zealand, it is surprising that there have been no records from the nearby Lord Howe or Norfolk Islands. These islands rise steeply from deepwater in the manner of many of the oceanic islands frequented by *O. ferox* (e.g. Canary Is., Azores, Madeira, Malpelo I., Hawaii). Lord Howe Island in particular is subject to extensive recreational line-fishing and diving, and several fish faunal surveys have been conducted around both of these islands (Allen et al. 1976; Francis 1991). However, no odontaspids of any species have been observed or recorded there (D. Pollard, personal communication).

The fairly wide continental shelf off NSW appears to have acted as a barrier to any movement of *O. ferox* into shallow near-shore locations. Despite intensive trawling over the past 60 years in shelf depths, there have only been five captures in depths less than 200 m, and all those were well offshore on the outer half of the shelf. The research data confirmed the preference by *O. ferox* for upper slope depths on the NSW coast with all 36 *Kapala* specimens, and 14 of the 16 captures by monitored commercial vessels, coming from depths between 300 and 850 m. The two specimens caught in 840–850 m were from twice the previous known maximum of 420 m which was recorded for a South African juvenile by Bass et al. (1975), and subsequently cited by other authors (e.g., Compagno 1984; Quèro 1984; Last and Stevens 1994; Bonfil 1995). Eastern Bass Strait appears to be the southern limit of distribution for *O. ferox* off south-eastern Australia. The recent capture off eastern Victoria extended the known range to south of Gabo Island and there were anecdotal reports of the species being caught as far south as the Bass Strait oil rigs (about 39°S). However, trawling grounds across Bass Strait and around southern Australia have been intensively surveyed and fished by research and commercial trawlers during the last 25 years but there have been no confirmed reports of specimens. *Kapala* caught two specimens of *O. ferox* off northern NSW.

However, because the continental slope is mostly of rough terrain, there is little deepwater trawling off northern NSW, or further north off Queensland. Consequently, there is no information on the distribution or status of the species along the north-eastern coast of Australia. Similarly, with no established offshore fisheries along most of Australia's west coast, there remains only the single record of *O. ferox* for Western Australia, and that from the North West Shelf.

We suspect that *O. ferox* might move over large oceanic distances by following submarine ridges and through associated island or seamount "hopping". For example, our data include records from the Kermadec Islands and White Island, at each end of the Kermadec Ridge. Further comparable records are from the Norfolk Ridge south of New Caledonia, from the Melville Bank/South West Indian Ridge off South Africa, and from the Ninety East Ridge and nearby Cocos (Keeling) Island in the Indian Ocean (Abe 1981; Gubanov 1985, this paper). It is noteworthy that all mid-oceanic captures of this species have been on or effectively proximal to deepsea ridges and peaks with minimum bottom depths along some ridges exceeding 2,000 m. Long-duration telemetry or PAT (pop-up archival tag) tracking of *O. ferox* accessed for study in shallow water sites, such as Malpelo or Lebanon, would be a particularly useful direction for further in situ research. Similarly, photographic evidence from Lebanon of readily identifiable *O. ferox* bearing conspicuous scars (via W. Noshie, personal communication) strongly indicates that individual sharks may perennially return to favoured sites; photo-identification and tagging work to establish the level of site fidelity exhibited by these sharks is another prospect for future in situ research.

Full knowledge of the distribution and abundance of such a widespread species as *O. ferox* is difficult to assess and relies on reporting. Compagno (2001) stated that the species is uncommon to rare, which accurately reflects the very small number of captures in most areas. However, as for many species described as rare, the term "rarely caught" is probably more appropriate for *O. ferox*. In many areas where it has been recorded, in particular the insular locations with steep and rough terrain descending quickly into deep water, its apparent scarcity probably more reflects the low level of fishing operations in such areas (Bonfil 1995). However, even where there have been multiple captures, as in the Mediterranean Sea, off southern Japan (Abe et al. 1968) and on the trawling grounds off south-eastern Australia, it remains an uncommon bycatch component of fishing activities. We can add that the absence of previous observations from diving, and probable misidentification as *C. taurus* (and other lamnoids), has further led to the belief that this species is less abundant than may actually prove to be the case for some select areas.

Although many captures have been brought to the attention of researchers by interested fishers, undoubtedly many more instances go unreported. Since the 1970s there has been a substantial increase in deepwater fishing effort worldwide. In particular, significant trawl fisheries have developed on the continental slopes and ocean ridges off Australia, New Zealand and southern Africa, and the now-known depths at which *O. ferox* commonly lives (300–700 m) are regularly trawled. Similarly, as shallow water fisheries become depleted, fishing gear such as mesh-nets, droplines and longlines are being deployed at increasingly greater depths. Most of our new records were derived from deepwater fishing, principally trawling, but include a number of recent Mediterranean and Atlantic captures by static fishing gear from depths greater than 100 m. Across all areas and fishing methods, the incidental catches of *O. ferox*, particularly juveniles, may be considerably greater than reported. Large sharks are more likely to be reported because of their novelty, conspicuous size, and low marketability. However, as instanced by the Croatian fishery where small *O. ferox* are marketed as an unrelated species (*Mustelus* spp.), juveniles are more easily landed and sold without attracting any attention.

While quantifying the effects of incidental fishing mortality is difficult, the results of the scientific fishery surveys off NSW have provided some quantitative data on the status of *O. ferox*. The 25 years dataset strongly suggested declining abundance, highlighting the vulnerability of the species to both accidental and directed fishing pressure. The recent captures off Eden and Bermagui in 2000–2004 indicate that small numbers of *O. ferox* still occur on the trawling grounds off southern NSW. However, the apparent decline in numbers of *O. ferox* is consistent with the very depleted state of most other demersal shark stocks on the central and southern

NSW upper slope (Graham et al. 2001). That study found that after 20 years of trawling, mean catch rates of elasmobranches had declined by about 80% and, in particular, catches of gulper sharks, *Centrophorus* spp., had been reduced to less than 1% of those recorded in 1976–1977. Although trawlers do not target *O. ferox*, it is likely that the original (albeit small) NSW population has been reduced to very low numbers. The scientific observer study of commercial catches reported by Liggins (1996, 1997) monitored between 5 and 9% of the estimated total trawl effort off Ulladulla for the years 1993–1997, with at least half of this fishing effort in slope depths between 250 and 600 m. The study reported an average of two *O. ferox* captures per year off Ulladulla which, by extrapolation to the total trawling effort, suggests that between 10 and 20 *O. ferox* may have been caught annually on the Ulladulla trawl-ground during the survey period. Trawling effort on grounds north of Ulladulla to about Newcastle is comparable, making it possible that during the 1990s, 20–40 *O. ferox* were caught annually on the trawl-grounds between Newcastle and Eden.

Overall, more than 50% of the continental slope area off NSW is untrawlable, consisting of ravines and rough bottom. It is therefore possible that the comparatively low-profile terrain of trawling grounds is not the favoured habitat of *O. ferox*, and those trawled specimens represent a relatively small proportion of the total population that have strayed onto the trawl grounds. However, the marked decrease in relative abundance off central and southern NSW suggests that trawling is having an adverse impact on the population. Whilst direct mortality through captures probably accounts for most of this decline, degradation of habitat through repeated bottom trawling and a decrease in favoured prey species (demersal teleosts) may also have a significant effect on *O. ferox* numbers. Combined with its likely very low fecundity, it is almost certainly susceptible to local extirpation even at seemingly low-capture rates. It is worth noting that during 1989–1996, *Kapala* completed several inshore trawl surveys with over 1,400 trawls in shelf depths (10–200 m). Only two juvenile specimens of *C. taurus* were captured (in 10–50 m), and no *O. ferox*.

Because the numbers of *C. taurus* along the NSW coast had been seriously depleted by indiscriminate killing by spear fishers, and by some commercial harvesting, that species was protected under government legislation in 1984 (Pollard et al. 1996). To avoid any mis-identification or claims of confusion with *O. ferox*, both species were included on the NSW protected species list. Despite this legal protection, compliance is difficult to enforce and carcasses of juvenile *O. ferox* are sometimes marketed simply as "shark". However, even if they or larger adults were returned to the sea intact, these sharks are unlikely to survive the trauma of trawl capture from deepwater. In a wider context, as exploitation of deepwater fishery resources increases worldwide, fishing mortality of such species as *O. ferox* will increase and may put the survival of the species at risk.

The Shark Specialist Group (SSG) of the World Conservation Union (IUCN) Species Survival Commission recently assessed the status of *O. ferox* as globally "vulnerable". A meeting of IUCN SSG's Mediterranean team (San Marino, September 2003) assessed the Mediterranean population of *O. ferox* as "endangered". Enacting adequate management of localities where these sharks are habitually within close range of humans and vulnerable to directed harassment or spot-fishery (i.e. notably Shark Land off Beirut, Malpelo Island and the Kermadec Islands) is an important step for the future.

### *Biology*

The weight-at-length relationship were highly correlated, justifying their use to generate the total lengths of specimens where only weights were recorded. However, despite the addition of estimated length data, the overall small sample and high number of unsexed individuals limited any detailed analyses. Much of the data were from widely dispersed, often single captures, and by a number of capture methods. As such, the distribution of the pooled length records should not be taken as representing the overall population structure of *O. ferox*. However, the data does show that many large specimens (>250 cm TL) were trawled, suggesting that all sizes were vulnerable to trawl gear.

Albeit the relationship between total length and depth was not strongly defined by regression, diver observations and catches at inshore and insular locations in depths less than 100 m were almost exclusively of large specimens (>200 cm TL), suggesting that only adults frequented shallow water. Conversely, almost all sharks smaller than about 150 cm TL were taken at depths greater than 300 m. However, the analysis was made somewhat equivocal by the recent New Zealand reports of diver sightings and mesh-net captures of four juveniles (150–200 cm TL) in depths less than 40 m; a Turkish 190 cm specimen taken artisanally at 30 m; and the several trawl records of relatively large specimens captured at depths between 400 and 880 m (Tables 1, 2, 3). However, all the neonates (<150 cm TL) and most small juveniles were taken by trawl on continental slope grounds well offshore. Similar depths at inshore locations with steeply shelving terrain cannot be trawled and fishing methods employed there, such as gillnetting and longlining, are usually confined to depths shallower than 200 m. That few juveniles were caught in gillnets or longlines at these insular locations further supports a hypothesis that juveniles seldom frequent depths less than 200 m, but additional capture records are needed to explore this further.

Because of the paucity of data, the size at maturity for both male and female *O. ferox* remains poorly defined. The lengths of both the smallest mature male (*ca.* 200 cm) and female (*ca.* 300 cm) were estimated rather than accurately measured. However, the confirmed mature male from NSW at 225 cm, and the mature Californian male at 275 cm, suggests that male maturation in the 200–250 cm TL range is likely. Females were immature to 280 cm, and all greater than 360 cm were mature. These data suggest that females probably mature between 300 and 350 cm TL. Our estimated sizes at maturity for *O. ferox* are somewhat larger than those reported for *C. taurus* (males 190–195 cm and females at 220–230 cm TL, Compagno 2001), but not unexpected as the maximum sizes of *O. ferox* (male 344 cm, female 450 cm TL) are appreciably greater than for *C. taurus* (male 257 cm, female 318 cm TL). That females mature at a significantly larger size than males is consistent for both species. Litter size, and size at birth are both unknown. A birth size between 100 and 110 cm TL is suggested by the sizes of the smallest specimens in our dataset (107-110 cm).

The areal and temporal reproductive characteristics of this species remain undescribed and evidence of nursery areas is effectively absent. We are not aware of any examples of *O. ferox* taken from the Mediterranean Sea measuring <140 cm TL; however A. Soldo (personal communication) observed small (*ca.* 140 cm) examples from Croatian fisheries, but no precise details are available. A few juveniles less than 200 cm TL have reportedly been caught by trawlers in the Sicilian Channel but again, no precise details are available and misidentification with other species is routinely problematic in these fisheries (Ian K. Fergusson, unpublished data).

The four juveniles between 107 and 111 cm TL described by Bass et al. (1975) were the smallest reported in the literature. Two of these specimens were from depths between 400 and 420 m, and all ten of our NSW juveniles smaller than 125 cm TL were caught at depths between 360 and 550 m. These combined records suggest that neonatal *O. ferox* are either born, or move soon after birth into deeper, offshore nursery depths on the upper slope and perhaps also around oceanic seamounts. By virtue of a benthopelagic existence at this early stage of their life-history, they may avoid predation by most potential predators that would otherwise threaten them in warm-temperate or tropical neritic areas (e.g. various large carcharhinid sharks such as *Carcharhinus leucas* or *C. obscurus*, large sphyrnids such as *Sphyrna mokkaran*, or the white shark *C. carcharias*). Further, based on stomach contents examined to-date, these young juveniles may well feed extensively and selectively upon small deepwater teleost fishes, crustaceans and cephalopods, and benefit from reduced competition with other similarly sized piscivorous sharks by occupying deeper offshore habitats.

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