POPULATION DYNAMICS OF THE RAGGEDTOOTH SHARK (*CARCHARIAS TAURUS*) ALONG THE EAST COAST OF SOUTH AFRICA

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Abstract

This thesis develops the first open population model for any shark species worldwide using the Cormack-Jolly-Seber (CJS) model. In conjunction with a tagging study, five auxiliary studies were conducted to investigate stock structure, post-release mortality, tag shedding, and tag-reporting rates. The results from each of the studies were used to correct for any violations of the models assumptions to provide the first unbiased estimates of survival and abundance for the raggedtooth shark (*Carcharias taurus*) in South Africa.

The *C. taurus* population exhibited complex stock structuring, by size and sex. Competitive shore anglers fished an estimated 37, 820 fishing days.year^{-1} (95% C.I. = 28, 281 - 47, 359 days.year^{-1}) for sharks, and caught 1764 (95% C.I. = 321 – 3207) *C. taurus*. Although released alive, post-release mortality ranged from 3.85% for young-of-the-year sharks to 18.46% for adult sharks. Between 1984 and 2004, a total of 3471 *C. taurus* were tagged. In all, 302-tagged sharks (8.7%) were recaptured. Both juvenile (< 1.8 m TL) and adult sharks (> 1.8 m TL) displayed philopatric behaviour for specific parts of their ranges, including gestating and parturition areas. Significant differences were observed in the percentage of recaptures between the different tag types, tagging programs, individual taggers and capture methods used to tag sharks. The annual tag retention rate for juvenile sharks, 94.19% (95% C.I. = 80.68% - 100.00%) was significantly higher than for adult sharks, estimated at 29.00% (95% C.I. = 6.76% - 64.39%). Tag reporting rates, from fishermen varied both spatially and temporally from

0.28 (95% C.I. = 0.00 – 0.63) to 0.77 (95% C.I. = 0.56 – 0.97). Associated tag wound damage and biofouling growth indicated that B-type tags were a suitable tag type for use on *C. taurus*, whereas C-type tags were not. The CJS bias-adjusted estimate for juvenile survival was 0.456 (95% C.I. = 0.367 – 0.516) and for adult sharks, 0.865 (95% C.I. = 0.795 – 0.915). From 1984 to 2004 the mean bias-adjusted population size for juvenile sharks was estimated at 3506 (95% C.I. = 2433 – 4350) and for adult sharks, 5899 (95% C.I. = 7216 – 11904). Trends in abundance over the 20-year study period indicated a stable, healthy population.

Acknowledgments

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Chapter 1
General introduction

1. 1. Overview of species

Carcharias taurus Rafinesque, 1810 is one of three species belonging to the family Odontaspididae (Compagno 2001). In South Africa, it is commonly known as the raggedtooth shark or raggie, but is also referred to as the sand tiger shark in America and as the grey nurse shark in Australia.

The global distribution of *C. taurus* has been extensively documented (Last and Stevens 1994, Compagno 2001). It is a wide-ranging coastal species found primarily in warm-temperate and tropical waters around the main continental landmasses, except in the eastern Pacific Ocean off North and South America. It inhabits the continental shelf down to 190 m, but is most commonly found at depths between 10 and 40 m in sandy-bottomed gutters or gullies, and in rocky caves in the vicinity of inshore reefs and islands (Otway and Parker 2000, Compagno 2001, Smale 2002). Raggedtooth sharks are able to maintain neutral buoyancy by swallowing air at the surface and holding it in their stomachs (Bass 1972), and are often found hovering motionless just above the seabed either alone or in groups of up to eighty individuals (Cliff 1989, unpub). *C. taurus* is an opportunistic feeder, consuming a wide variety of teleost fish as well as smaller elasmobranches. They occasionally consume invertebrates such as squid, crabs and lobsters (Bass *et al.* 1975, Compagno 2001, Smale 2005) and are considered to be ambush predators. Observations also suggest that this species feeds co-operatively by forming packs and concentrating prey prior to attack (Ireland 1984, Smale 2005).

Sexual dimorphism, in terms of length, is evident: females attain a maximum size of 320 cm total length (TL) and males 260 cm TL (Bass *et al.* 1975, Compagno 2001). Size at maturity also differs between sexes, as well as between geographic locations. In the northwestern and southwestern Atlantic, size at maturity has been reported to occur at between 220 and 230 cm *TL* for females, and between 190 and 195 cm *TL* for males (Gilmore *et al.* 1983, Branstetter and Musick 1994, Lucifora *et al.* 2002). In South Africa, however, females and males have been reported to mature between 230 and 260 cm *TL* and between 190 and 220 cm *TL*, respectively (Bass *et al.* 1975, Smale 2002). The equivalent ages to these lengths at maturity are nine to ten years for females, and six to seven years for males (Goldman 2002). Raggedtooth sharks are long-lived, with an estimated longevity of up to 40 years for females and 30 years for males (Goldman 2002).

The reproductive biology of *C. taurus* has been well-documented (Bass *et al.* 1975, Gilmore *et al.* 1983, Gilmore 1993, Branstetter and Musick 1994). It is an ovoviviparous and aplacental species, with the developing embryos obtaining nutrition through both oophagy and adelphophagy. Adelphophagy results in a maximum fecundity of two pups per litter after a gestation period of approximately 9 to 12 months (Bass *et al.* 1975, Gilmore *et al.* 1983). Pups are born at a total length between 95 and 120 cm (Cadenat 1956, Taniuchi 1970, Bass *et al.* 1975). Reproductive periodicity has been a source of some contention. Gilmore (1993) stated that *C. taurus* reproduces annually in the northwestern Atlantic, while Gordon (1993) proposed a similar hypothesis for Australian waters. Alternatively, Cliff (1989, unpub.) and Branstetter and Musick (1994) presented evidence supporting a two-year reproductive cycle with a resting stage in between for both the South African and northwestern Atlantic populations respectively. A biennial reproductive cycle has also been suggested for *C. taurus* in the southwestern Atlantic (Lucifora *et al.* 2002).

The broad-scale distribution and migratory habits of *C. taurus* in South Africa are known for only part of its range and have been inferred largely from beach meshing captures and tagging data collected by the Natal Sharks Board (Wallet 1973, *Bass et al.* 1975, Cliff 1989 unpub, Dudley 2002). In South Africa, *C. taurus* has been occasionally reported from the west coast, but is more commonly found along the east coast from Cape Town to northern KwaZulu-Natal (Bass *et al.* 1975, Smale 2002). Mature females are thought to reside primarily off KwaZulu-Natal; the whereabouts of mature males outside of the mating season are unknown. Juveniles reside in nursery areas in the Eastern Cape (Smale 2002).

Mating is thought to occur off the south coast of KwaZulu-Natal from October to the end of November (Cliff 1989, unpub). Pregnant females then move northward to spend the early part of their gestation in the warmer waters of northern KwaZulu-Natal and possibly southern Mozambique. During July and August the near–term pregnant females begin to move southwards towards the cooler waters of the Eastern Cape (Wallet 1973, Bass *et al.* 1975, Cliff 1989, unpub), where they give birth from September to November (Smale 2002). After parturition, many of the females then migrate back to Natal. An abrupt cessation of catches in the shark nets off KwaZulu-Natal at the end of December has been used to infer that the reproductive migration has terminated (Wallet 1973, Bass *et al.* 1975).

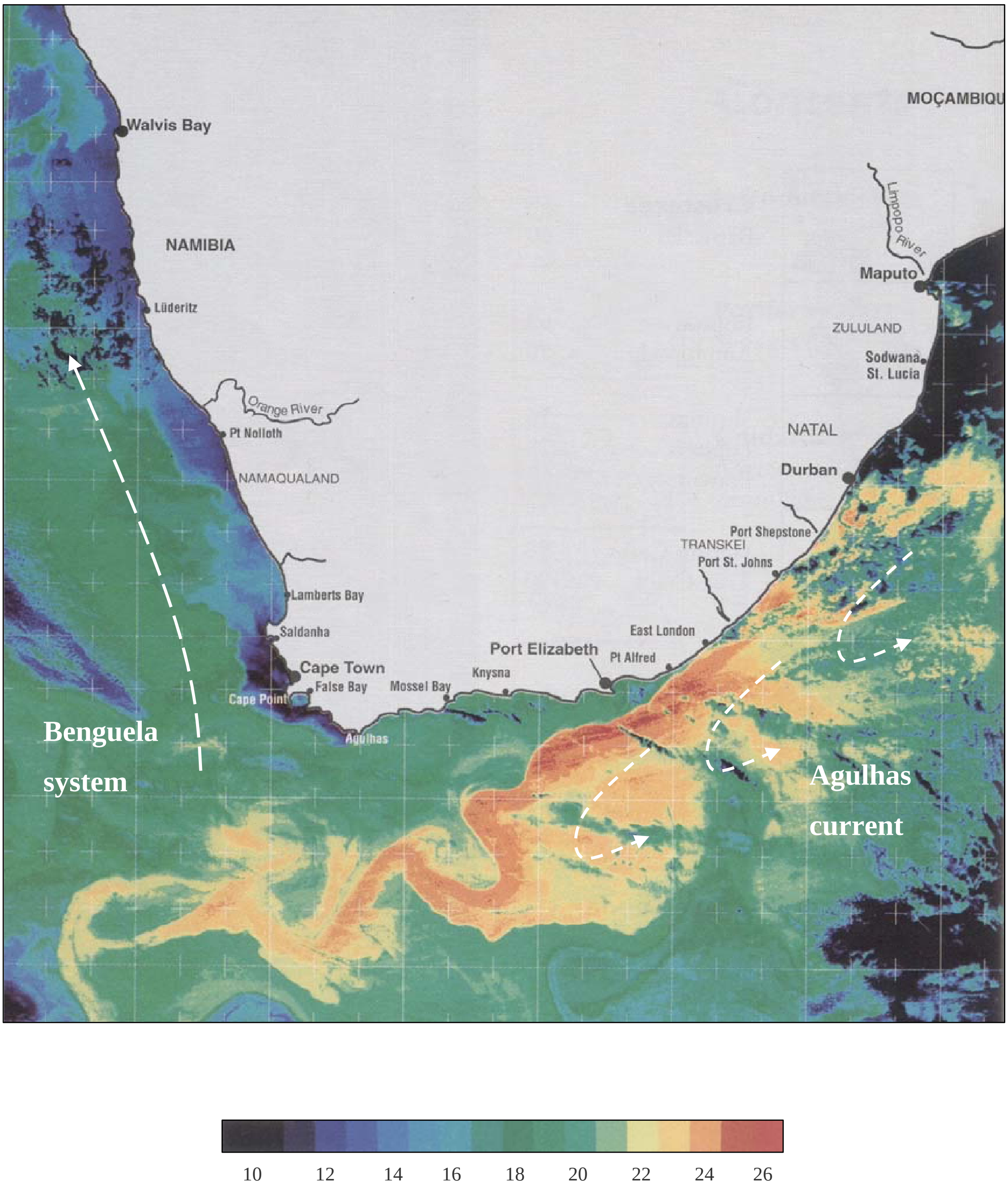
1. 2. Study area

South Africa has a coastline of almost 3000 km, extending from the mouth of the Orange River on the southern African west coast, to Ponta do Ouro on the Mozambique border on the East African coast (Fig. 1.1). The coastline extends southwards to a relatively low latitude (35˚S), and is bordered by three ocean systems: the Atlantic, Indian and Southern Ocean (Schumann 1998). Although these geographical boundaries are accepted to be somewhat arbitrary (Shannon 1989), the interactions between them can extend over distances of thousands of kilometres.

The coast is bordered by two major ocean currents, the Agulhas Current, flowing southwards past the east and southeast coasts, and the Benguela Current, flowing northwards up the West coast. The Agulhas Current is the principal oceanographic feature of the South African marine environment and is responsible for transporting warm water from the tropics southwards along the east coast. The current is up to 160 km wide and at its core can have a sea surface temperature of up to 26˚ C (Schumann 1998). As it moves southward, the current hugs the shallow continental shelf, which can vary from only a few kilometres in width in the vicinity of Port St Johns, to over

250 km on the Agulhas bank (Schumann 1987). At this point, the main part of the current retroflects eastwards into the interior of the Indian Ocean and the marine environment begins to become influenced by the cooler waters of the Benguela Current.

The Benguela Current is not a strongly identifiable current in the sense of the Agulhas Current, and is a broad, cooler and rather sluggish system in the eastern South Atlantic (Shannon 1989). As the Benguela Current flows northwards up the West coast, it plays an important role in upwelling processes, during which times the water temperature can drop to below 13˚ C (Brink 1983). As a consequence of these two major oceanic currents, three biogeographical zones can be broadly recognised along the South African coastline based on water temperature: a cool temperate west coast zone extending from Cape Town northwards, a warm temperate south coast zone and a subtropical east coast zone from approximately East London northward (Turpie *et al.* 2000). One notable environmental feature of the south coast zone is intermittent coastal upwelling, which results in the emergence of cold nutrient rich water (Brink 1983). Upwelling is common between October and April, reaching a maximum during the summer months of November to February (Schumann *et al.* 1982, Beckley 1983). The upwelling is caused by northeasterly winds or easterly winds, which increase in frequency and intensity during the summer (Schumann and Martin 1991).



Sea surface temperature in degrees Celsius

Fig. 1.1. Satellite image of South Africa illustrating the major ocean currents and associated water temperatures

1. 3. Conservation and protection

C. taurus have been fished throughout their global range, but are of variable importance internationally (Compagno 2001). They are primarily caught with line fishing gear, but are also taken in bottom-set gill-nets and in pelagic and bottom trawls. They are rarely targeted specifically, and are more often caught as a bycatch in multi-species fisheries directed at more productive and highly valued teleost or other chondrichthyan species. Their meat has little commercial value, but is utilised for human consumption in some regions, as are its fins in the oriental sharkfin trade (Compagno 2001). Because this species typically inhabits shallow inshore areas, it is rarely, if ever, caught by the large-scale industrial fisheries operating on the high seas. Its near-shore distribution, however, makes it susceptible to small-scale multi-species and artisanal fisheries as well as recreational fishermen, spearfishers and shark control programs. As bycatch in other fisheries, it is often reported as unidentified shark, or not reported at all. As a result, the extent these fisheries have impacted on global populations is uncertain. This species could, therefore, be at a high risk of depletion in many countries without the fact being recognised.

In the northwestern Atlantic, the population of *C. taurus* has declined by an estimated 80-90% since the 1970's (Musick *et al.* 1993, Musick *et al.* 2000). On the east coast of Australia, there are estimated to be less than 500 and possibly less than 300 individuals remaining. There are concerns that the population has fallen to such critically low numbers that individual animals may be failing to find mates, critically impacting on reproduction (Otway and Parker 2000). It has been estimated that the time to quasi-extinction[1] for this population may be as short as 45 to 53 years (Otway *et al.* 2004). Dramatic declines have also been reported in the southwestern Atlantic (Lucifora *et al.* 2002). The life history characteristics of *C. taurus* make it particularly vulnerable to over-exploitation (Pollard *et al.* 1996, Compagno 2001). Due to declining population trends worldwide, it is listed as a 'Vulnerable' species by the IUCN in its Red List of Threatened Animals (Hilton-Taylor 2000). An overview of

[1] Time to quasi-extinction (years elapsed for the population to consist of ≤ 50 females)

the population status for *C. taurus* for its known global distribution range according to the IUCN Red List Assessments (2003) is given in Fig. 1.2.

Despite its ‘Vulnerable’ listing, the degree of protection afforded to *C. taurus* around the world is limited. In the northwestern Atlantic, they were placed on the protected species list, amended to the NMFS Fishery Management Plan for Atlantic sharks in 1997. They are also fully protected from all recreational and commercial fishing in Australia since they were listed as ‘Vulnerable’ on Schedule 1 part 2 of the Endangered Species Protection act 1992 (ESP Act) in October 1997. In South Africa, this species was decommercialised through the Marine Living Resources Act in 1998. Although currently protected from commercial fishing in South Africa, bycatch in any fishery potentially poses a realistic threat to their survival. As a result, this species in South Africa was listed in 2003 as ‘Near Threatened’ on the IUCN Red list of Threatened Animals (Dicken *et al.* in prep).

1. 4. South African fisheries

1. 4. 1. Commercial fisheries

In South Africa, *C. taurus* has never been specifically targeted by any fishery and the limited data available indicates that it is rarely caught as a bycatch, with the exception of the commercial handline fishery (Table 1.1). This information may be misleading given the fact that sharks are often discarded at sea or simply recorded as “unspecified shark” and that there is a high level of non-reporting in these fisheries. Despite these limitations, this information is important in that it suggests that this species is probably absent or very rarely present in the deep offshore areas that are fished by the commercial trawl (Compagno *et al*. 1991 Smale *et al.* 1993) and long-line sectors (Penny and Punt 1993, Kroese *et al.* 1995, Japp *et al.* 1995). Two fisheries in which *C. taurus* are regularly caught are the bather protection nets of the Natal Sharks Board (NSB), (Wallet 1983, Dudley and Cliff 1993, Dudley 2002) and the recreational line fishery (Coetzee *et al.*1989, Smale 2002, Pradervand and Govender 2003).

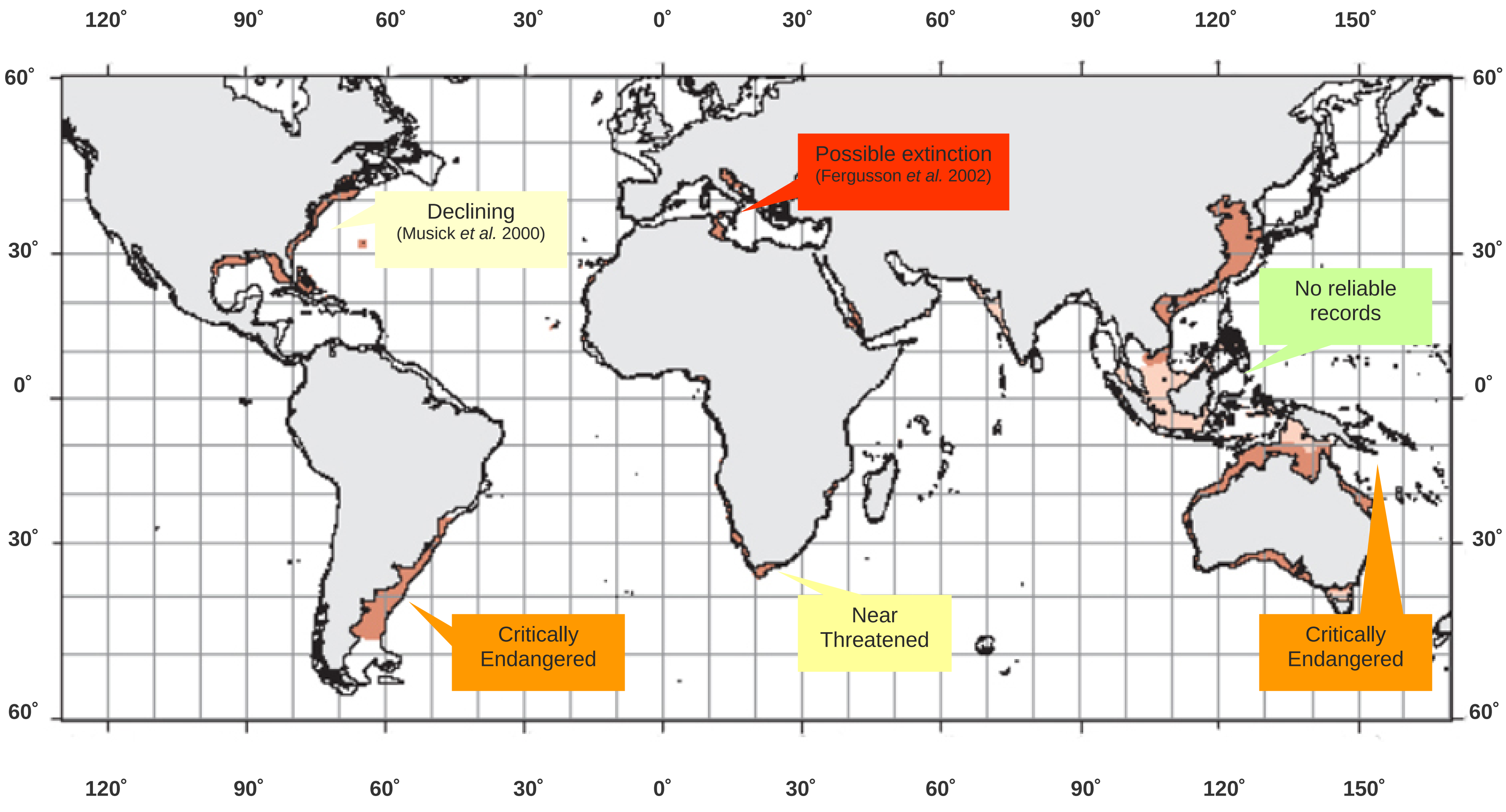


Fig. 1.2. Global distribution pattern for *Carcharias taurus* and population status according to the IUCN Red List Assessments (2003). In regions where assessments have yet to be conducted, existing fisheries data have been used to infer population status

Table 1.1. All fisheries in South Africa that have a shark component and key references to catches of *Carcharias taurus* from past scientific studies

Fishery	Area	Target species	Catch *C. taurus*	Key references
St. Joseph net	Inshore on West Coast	*Callorhinchus capensis*	No	Freer and Griffiths (1993)
Domestic tuna longline	Offshore to EEZ	*Thunnus* spp. and *Xiphias gladius*	No	Penny and Punt (1993), Kroese *et al.* (1995)
Foreign tuna longline	Offshore to beyond EEZ	*Thunnus* spp. and elasmobranchs	No	Penny and Punt (1993), Kroese *et al.* (1995)
Hake long line	West and South Coast to 500m	*Merluccius* spp.	No	Japp *et al.* (1995)
Off shore trawl	West Coast to 600m	*Merluccius* spp.	No	Compagno *et al.* (1991), Japp *et al.* (1994)
Inshore trawl	South and East Coast to 200m	*Austroglossus pectoralis* and *Merluccius* spp.	No	Smale *et al.* (1993), Kroese *et al.* (1995)
Prawn trawl	Natal East Coast to 200m	Crustaceans	No	Fennessy (1994)
Gill-net	Inshore on West Coast	*Liza richardsonii*	No	Kroese *et al.* (1995), Hutchings and Lamberth (2002)
Beach seine	Inshore West and South Coast	Teleosts	No	Lamberth *et al.* (1994), Hutchings and Lamberth (2002)
Shark longline offshore	West and South Coast >100m	Elasmobranchs	No	Penny and Punt (1993), Kroese *et al.* (1995)
Shark longline inshore	West and South Coast < 100m	Elasmobranchs	No	Penny and Punt (1993), Kroese *et al.* (1995)
Commercial handline	Inshore to 200m	Teleosts and elasmobranchs	Yes	Kroese *et al.* (1995)
Recreational line	Inshore to 200m	Teleosts and elasmobranchs	Yes	Coetzee *et al.* (1989), Smale (2002) Pradervand (2004)
Protective nets	East coast	Elasmobranchs	Yes	Wallet (1983), Dudley and Cliff (1993), Dudley (2002)
Aquarium trade	East Cape	Elasmobranchs	Yes	Smale (1997)

1. 4. 2. Bather protection nets

Bather protection nets were first installed on the Natal coast in 1952; this was followed by the formation of the Natal Anti-Shark Measures Board, now the Natal Sharks Board, in 1964. This is a statutory body responsible for protecting bathers against shark attack. Most nets are 212 m long and 6 m deep, with a stretched mesh of 50 cm. They are deployed in two rows parallel to the coast, roughly 500 m offshore in a water depth of 10 to 14 m. They are anchored in fixed positions throughout the year and are serviced an average of 20 times per month, sea and weather conditions permitting (Wallet 1983, Davies *et al.* 1989). The mean annual catch of *C. taurus* in the nets is 214, of which approximately 40% survives (Dudley 2002). Since the 1980's the majority of released sharks have been tagged as part of the Oceanographic Research Institute (ORI) cooperative tagging program. In the last 5 years, there has been an extensive net reduction from 39 km in 1999 to 27 km in 2004 (Cliff, NSB, pers. comm.). The nets are deployed over a coastline of 326 km between Richards Bay and Port Edward (Dudley 2002).

1. 4. 3. Recreational fisheries

The recreational line fishery comprises four components; shore anglers, ski boat anglers, light tackle boat anglers (LTB) and spearfishers. Shore anglers, however, are the only component to actively target sharks and catch *C. taurus.* Catch data from the line fishery are voluntarily submitted to the National Marine Linefish System (NMLS) for collation and analyses. Unfortunately, due to high levels of non-reporting, only 466 *C. taurus* have been recorded over the last 20 years (Smale 2002). The existing catch records therefore vastly underestimate the total catch of this species along the coast and provide no information on effort. Additional catch information is available from the ORI and the Port Elizabeth Museum (PEM) cooperative tagging programs.

The other components of the recreational fishery rarely target sharks and invariably regard them as a nuisance and return them to the water either alive or dead. As a result, this catch is not reported and remains unidentified. In past surveys of these fisheries, few *C. taurus* have been recorded (Smale and Buxton 1985, Hecht and Tilney 1989, Brouwer and Buxton 2002 and Fennessy *et al.* 2003). These incidental captures, however, including those of the commercial handline fishery are important. They provide invaluable information on the seasonal and spatial distribution of *C. taurus* in waters that are not fished by the shore angling sector. These catches also provide additional information on sources of fishing mortality.

1. 5. South African stock assessment and data deficiencies

At present, there is no information on the population size of *C. taurus* in South Africa. This information is required to assess the validity and effectiveness of the current protective legislature. An estimation of the size of the population and trends in abundance are needed to document its population status. This information will enable appropriate management actions to be implemented to ensure that the South African population does not decline to the extent that are evident elsewhere in the world. The information currently available in the NMLS, while possibly better than that available for many other species of sharks, still has large gaps in terms of what is required for an appropriate stock assessment. To successfully model a population, it is essential to have a thorough understanding of the geographical range of the species, its temporal and spatial distribution and population structure (Springer 1967). Despite previous research by Wallet (1973), Bass *et al.* (1975), Cliff (1989, unpub.) and Smale (2002), this information is still not available.

1. 6. Modelling approach

Long-term time series of catch and effort data are seldom available for shark species, particularly for those that are not exploited commercially, such as *C. taurus*. In the absence of fishery dependent data, Anderson (1990) in discussing fishery models as applied to elasmobranchs, suggested alternative methods such as mark-recapture as a means to obtain estimates of absolute abundance. In studies such as these, marked fish are released and then recaptured alive on multiple occasions. Mark-recapture studies can be broadly categorised into open or closed population models. Closed population models assume that the population size does not change over the study period (Williams *et al.* 2001). In contrast, open population models do not assume that population size is constant and allow for births, deaths, emigration, or immigration (Pollock *et al.* 1990, Williams *et al.* 2001). These models, however, have seldom been applied to shark species because of a lack of appropriate biological or fisheries input data. They have been limited to only a few studies, all of which have assumed that the population is “closed” (Cliff *et al.* 1996 and Strong *et al.* 1996 for white sharks *Carcharodon carcharias*, Campana *et al.* 1999 for porbeagles *Lamna nasus*).

There are several approaches to modeling “open” populations. The Jolly-Seber (JS) model (Jolly 1965, Seber 1965) is a fully open population model that incorporates estimates of recruitment of new animals to the population to estimate population size. The JS model requires that all captured individuals be marked on release. This requirement can rarely be satisfied in any mark-recapture experiments that rely on cooperative tagging programs. An alternative, yet more restricted model, is the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Lebreton *et al.* 1992, Pollock *et al.* 1990, Williams *et al.* 2001). This model follows only marked animals over time allowing only survival and probability of capture (and not recruitment) estimation. While less general, these model estimates can subsequently be used to estimate abundance.

The CJS model is dependent on the following assumptions (Pollock *et al.* 1990): (1) all animals present at sample time i have the same probability of being captured; (2) all animals immediately after sampling have the same probability of surviving to sample time $i + 1$; (3) no tags are lost or over-looked; (4) all animals are released immediately after the sample and all sample periods have a short duration (relative to time intervals between tagging periods); (5) all emigration from the sample area is permanent and indistinguishable from death, and (6) the survival and capture of an individual is independent of the survival and capture of all other animals.

1. 7. Outline of thesis

This thesis focuses on the development of a CJS model to provide initial estimates of survival and abundance for *C. taurus* in South Africa. A simple overview of the thesis structure and design is represented by a flow diagram in Fig. 1.3. The appropriate fisheries input data required for the construction of the model was obtained through a series of fishery surveys and experiments that are described in the following Chapters. Each Chapter deals with a specific piece of the “puzzle” and contributes information necessary to correct for any violations of the models assumptions. A review of the literature suggests that this is the first application of an open population model to any shark species worldwide. The survey designs implemented in this thesis will help to provide information on the suitability and application of mark-recapture experiments to other shark cooperative tagging programs.

Based on the present knowledge of the life history of *C. taurus* in South Africa four size classes were identified:

- Young-of-the-year (YOY) (size class 1). Sharks that were less than the recorded maximum size at birth 1.2 m (TL), (Cadenat 1956 and Taniuchi 1970).
- Juveniles (size class 2). Sharks between 1.2 and 1.8 m (TL). Post neonatal individuals larger than the maximum length at birth, but smaller than the size at maturity for either males or females.
- Sub-adults (size class 3). Sharks between 1.8 and 2.4 m (TL). These individuals consisted of a mixture of maturing females and maturing and mature males.
- Adults (size class 4). All sharks greater than 2.4 m (TL). The sexually mature component of the population.

These size-classes were used throughout the thesis, to compare spatial and temporal distribution patterns between the different life history stages. The approximate ages that corresponds to each of these size classes based on the age/length relationship of Goldman (2002) is given in Table 1.2.

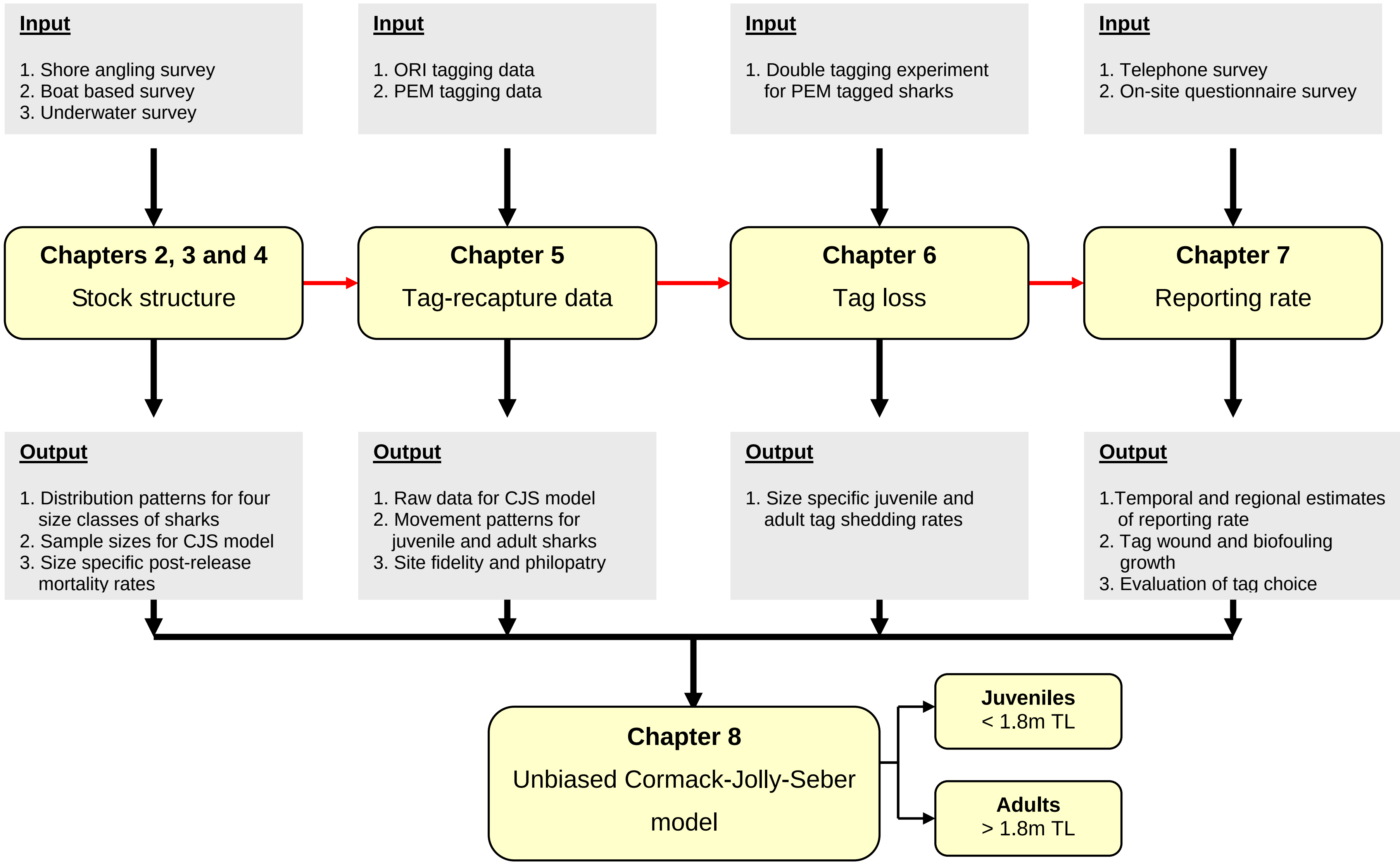


Fig. 1.3. Flow chart illustrating thesis design and development

Table 1.2. Size classes and corresponding ages of *Carcharias taurus* (based on parameters from the northwest Atlantic) used for a comparison in spatial and seasonal distribution patterns along the South African coast

Size Class	Category	Total length (cm)	Age (years)	
			Male	Female
1	YOY	< 120	0 to 1	0 to 1
2	Juveniles	120 to 180	1 to 5	1 to 5
3	Sub adults	180 to 240	5 to 10	5 to 14
4	Adults	> 240	> 10	> 14

1. 7. 1. Chapters 2, 3 and 4

The first intuitive step in the development of the CJS model, in the absence of appropriate data, is the collection of additional data from the fishery sectors that actively exploit *C. taurus* (section 1.4). This was achieved by conducting a comprehensive survey of the competitive shore-angling fishery (Chapter 2). Additional information was also collected from the inshore boat-based line fishery (Chapter 3) and spearfishers and SCUBA divers (Chapter 4). Data from all three surveys provided vital information on the complex stock structure and spatial segregation of the population by size and sex. If the different life history stages of the population are spatially distinct, they may be subject to varying fishing pressures and have different capture probabilities (assumption 1). Violation of the equal catchability assumption will lead to a negative bias in population size (Pollock *et al.* 1990). Under these circumstances it would be appropriate to model each life history stage separately.

Catch and effort data from the competitive shore-angling fishery were used to estimate capture sample sizes for each sampling period in the CJS model. Negative bias in the estimated survival rate occurs when post-release survival is affected by factors such as capture method and handling times prior to release (assumption 2) (Arnason and Mills 1981, Brownie and Robson 1983). Information on post-release mortality was collected in the survey to adjust model estimates accordingly.

1. 7. 2. Chapter 5

Data collected from the ORI and PEM cooperative tagging programs were used to provide information on the delineation of nursery and pupping areas, the migration patterns of breeding females and aspects of site fidelity and philopatry. These data were used to “fine tune” the basic temporal-spatial patterns of the different life history stages described in Chapters 2, 3 and 4. The performance of various tag types and tagging methods, used in the tagging programs were evaluated through a comparison of tag recovery rates. Tag recaptures from both programs were used as the raw input data in the construction of the CJS model.

1. 7. 3. Chapter 6

Tag loss has been known to occur in many shark-tagging studies (Davies and Joubert 1966, Francis 1989, Xiao 1996, Govender and Birnie 1997, Xiao *et al.* 1999). If tagged sharks loose their tags, then survival rates are underestimated (Arnason and Mills 1981) and the population size overestimated (McDonald *et al.* 2003). To adjust for a possible violation of assumption 3 (no tag loss), a double tagging experiment was conducted to estimate the tag shedding rate of B-type tags inserted by PEM taggers. Size-specific tag shedding rates for different life history stages were investigated.

1. 7. 4. Chapter 7

The models third assumption, in addition to that of no tag loss, is that all tags are recovered. Insuring the reporting of recovered tags in a voluntary tagging program, however, is difficult. Non-reporting can lead to an underestimate of capture probability and an overestimate of the population size. Data collected from the shore angling survey in Chapter 2 was used to estimate the non-reporting rate of recaptured sharks. Tag-reporting levels were used to adjust the CJS estimates accordingly. Information on the condition of the tag (biofouling growth) and any associated tag wound damage to the shark were also collected on recapture. This information was used to evaluate the performance and suitability of the different tag types used in the cooperative tagging programs.

1. 7. 5. Chapter 8

Information from Chapters 2 to 7 were integrated in the construction of a CJS model to provide estimates of survival, capture probability and abundance for *C. taurus* in South Africa. The model was fitted to 20-years of data from 1984 to 2004 to examine temporal trends in abundance. The model was applied to juvenile sharks (< 1.8m TL), adult sharks (> 1.8 m TL) as well as to a combined dataset.

Chapter 2

A survey of the elasmobranch specific component of the competitive shore angling fishery in South Africa

2. 1. Introduction

There are an estimated 412,000 shore-based anglers in South Africa (McGrath *et al.* 1997). Many fisheries managers assume that these anglers constitute a homogenous group, and as such, design and implement surveys accordingly (Bryan 1977). However, there is no such thing as the average angler (Shafer 1969). As a result, anglers must be grouped according to their level of specialisation and target species (Fisher 1997). Recreational shore anglers on the basis of this concept can be separated into two main components; club anglers who are registered to the South African Shore Angling Association (SASAA) and actively target sharks in competitions to earn club points, and social anglers who fish exclusively for teleosts for recreation and for consumption (van der Elst 1989, Taylor 1993, Brouwer and Buxton 2002, Pradervand and Govender 2003, Pradervand 2004). Understanding this diversity in catch preference identifies the competitive club anglers as the target population from which to obtain information on the catch and effort of *C. taurus*, or indeed, any other shark species within the recreational shore fishery in South Africa.

SASAA is composed of 11 regional fishing provinces (rather than current political provinces) and has a current membership of 2,699 anglers (Table 2.1). Anglers affiliated to these provinces fish in a variety of competitions with the intention to score maximum points. The scoring system is based on total catch weight such that two points are awarded for every kilogram of “edible” (teleost) fish caught and one point for every kilogram of “inedible” (cartilaginous) fish caught. Because of the scoring system employed by SASAA, anglers in most competitions tend to target the larger and heavier elasmobranch species in preference to teleost species (Clark and Buxton 1989, Coetzee *et al.* 1989). Prior to 1985, all elasmobranchs once caught and weighed in competitions were then killed and buried on the beach. With an increasing environmental awareness and concern for declining shark populations, most sharks and rays are now released alive.

Table 2.1. SASAA provincial club membership 2003/2004 (E. Holmes, SASAA secretary)

Coastal provinces	Membership	Inland provinces	Membership
Zululand and Natal	979	Orange Free State	113
Border	162	Southern Transvaal	153
Eastern Province	530	Gauteng	115
Southern Cape	123	Northern Gauteng	185
Boland	117	Mpumalanga	50
Western Province	172		

There are essentially five different formats that SASAA competitions can take: (1) national and (2) inter-provincial competitions, which are held between competing countries or provinces, respectively; (3) fixed venue or common venue competitions which are fished by teams of six anglers submitted from all clubs within the particular province; (4) postal competitions (Zululand and Natal only) in which teams of six to eight anglers are permitted to fish for a consecutive six-hour period over weekends anywhere from Kosi Bay, in northern KwaZulu-Natal to the Mbashe River in the Transkei; and lastly, (5) individual club competitions which are only open to members of the particular club. The sites and dates for all of these competitions are determined *a priori* at the onset of each fishing year and are fished irrespective of weather conditions. With the exception of Zululand and Natal, who fish competitively all year round, the other provinces hold competitions on average once a month from September to May. There is little fishing activity in the winter months outside of this period due to unfavourable weather conditions and poor catches. All competitions, with the exception of postal competitions, are fished for a fixed eight-hour period usually from 7.00 am to 3.00 pm. No restrictions are placed on choice of terminal tackle or the type of bait used (natural or artificial). Leaders, including traces however, are restricted to a maximum length of 9 m of any material of any breaking strain (Pradervand 2004).

Club anglers rarely fish for sharks outside of competitions (Taylor 1993), and consequently, roving creel surveys, which are traditionally used to obtain catch and effort data over wide areas, are ineffective in collecting data for *C. taurus*. This is particularly evident from past surveys of the South African shore based fishery by Joubert (1981), Clarke and Buxton (1989) and Brouwer *et al.* (1997) which, failed to record a single catch of *C. taurus*. Because of its distinctive dentition, this species is rarely recorded as a misidentified shark. Given the high frequency of club competitions, catch records from organised angling provide an ideal source from which to obtain information on catches of *C. taurus.* Previous studies that have used competition data to assess various aspects of the South African shore fishery have all recorded catches of *C. taurus* (Coetzee and Baird 1981, Coetzee *et al.* 1989, Smale 2002, Pradervand and Govender 2003, Pradervand 2004). These surveys, however, have been limited to only small sections of the coast and provided no detailed information on either stock structure or relative abundance.

The primary objective of this Chapter was to collect catch and effort data on *C. taurus* from club affiliated anglers. This was achieved through a telephone survey, an on-site questionnaire survey, and the collection of historical club catch records. Data collected in the telephone survey was used to provide the first estimates of total catch and effort for *C. taurus*, or indeed any species of shark in the South African shore angling fishery. These data, together with historical club catch records, were used to quantify its spatial distribution patterns along the entire South African coast. The data collected in the questionnaire survey included information on post-release mortality and non-reporting rates. Only anglers affiliated to the six coastal provinces were surveyed, as an initial pilot survey of the inland provinces indicated that they rarely fished at the coast outside of one or two competitions a year, and caught few *C. taurus.*

2. 2. Shore angling study area

For the purposes of this component of the thesis, the South African coastline was subdivided into 28, 100-km coastal areas (Fig 2.1). This scale of division was considered sufficient to identify the major trends and patterns in the spatial distribution of *C. taurus*, together with any regional variations in fishing effort. Coastal areas were shaded different colours to provide a basic idea of the regions fished by each of the six coastal fishing provinces. Area 14 encompasses the Tsitsikamma Marine Protected Area and, consequently, is not fished by any of the fishing provinces.

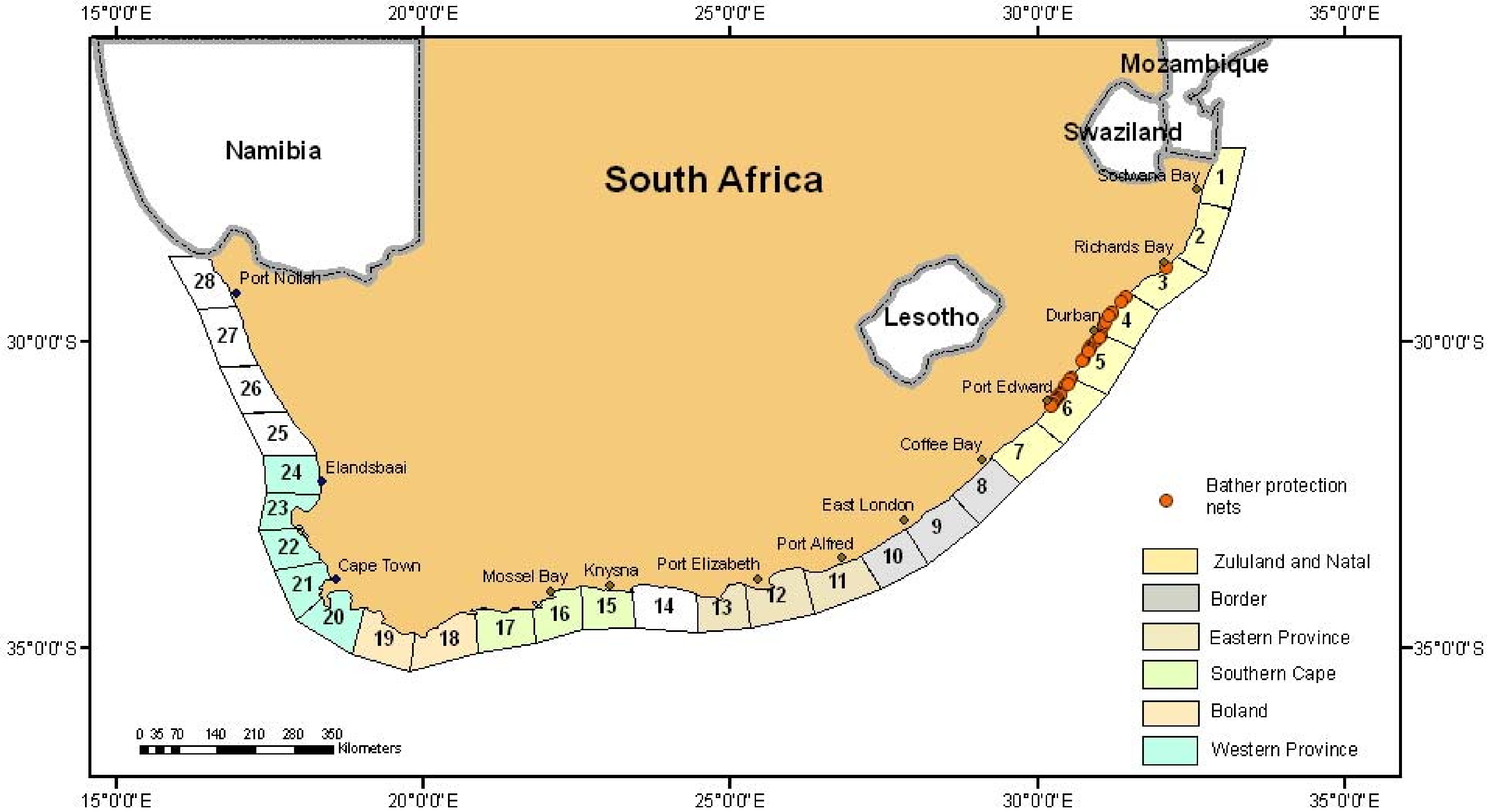


Fig. 2.1. Map of South Africa showing the location of the 28 100-km coastal areas used in the spatial analysis of catch and effort data. Also shown are the approximate areas that anglers within each of the 6 coastal provinces fish, as well as the location of the bather protection nets

2. 3. Material and methods

2. 3. 1. Telephone survey to obtain information on catch and effort

A telephone survey of fishermen, randomly selected from club telephone directories from each of the six coastal fishing provinces, was conducted during the 2002/2003 fishing season from September 2002 to August 2003. Since there were more fishermen registered to some provinces than others, the sampling frame was stratified prior to the survey with the number of anglers surveyed allocated proportionally to each province. Anglers that were selected were asked if they would be willing to participate in the survey. If they agreed, they were contacted every three months and asked to recall the number of days they had fished for sharks (both competitively and socially), where they had fished (which 100 km area), and the number and sizes (either length or weight) of any *C. taurus* they had caught each month within the recall period.

C. taurus can be caught on a variety of heavy tackle types whilst fishing for a range of shark species. As a result, fishermen were asked to recall the number of days they had fished for sharks in general, rather than for *C. taurus* specifically to provide a comparable estimate of fishing effort along the entire coast. The survey recall period was chosen based on a study of recall bias by Westat (1989) who concluded that the recall period should be less than six months. Calls were made primarily from 9.00 am to 5.00 pm on weekdays and call back times were arranged at the angler’s convenience.

When the target population is known, which it is in this case, telephone surveys are an appropriate surveying technique for collecting catch and effort data (Essig and Holliday 1991). Telephone surveys have been applied to fishing club members and tournament participants (Weiss-Glanz and Stanley 1984), as well as to licensed anglers (Weitham 1991). Telephone surveys are cost effective, flexible and have the ability to cover a large geographic area without the problems of interviewer access (Brown 1991, Weithman 1991). Telephone surveys are also particularly useful for collecting data on easily identifiable, highly desirable or rare species such as *C. taurus* because biases in angler's ability to recall the number of fish they have caught are reduced (Essig and Holliday 1991, Weithman 1991). Nevertheless, the survey is subject to some bias caused by the unreliable memories of respondents (Essig and Holliday 1991). This recall bias can involve omission, where respondents forget earlier events, or telescoping where respondents report events later than they occurred.

2. 3. 2. Catch and effort calculation

Catch and effort estimates were calculated for each 100 km coastal area using a modified version of the method developed by Pollock *et al.* (1994). A distinction was made between club-registered anglers who, although affiliated to a fishing province, do not fish in a club team, and competitively active club members who do. An estimate of the number of competitively active anglers within each province was obtained from the relevant provincial angling secretary. Competitive fishing effort was classed as any fishing for sharks within a competition framework in which a catch would score competition points for the angler. Social fishing was classified as any other fishing effort.

Total annual social, $\hat{E}_{i,\,social}$, and competitive fishing effort, $\hat{E}_{i,\,comp}$, for the *i*th 100 km coastal area were calculated as:

$$\hat{E}_{i,\,social} = \sum_{j=1}^{6} N_{j,\,social}\ \bar{e}_{ij,\,social} \quad (2.1) \quad \text{and} \quad \hat{E}_{i,\,comp} = \sum_{j=1}^{6} N_{j,\,comp}\ \bar{e}_{ij,\,comp} \quad (2.2)$$

Where

$N_{j,\,social}$ is the number of club anglers registered in each of the six coastal fishing provinces

$N_{j,\,comp}$ is the number of competitively active club anglers in each of the six coastal fishing provinces

$\bar{e}_{ij,\,social}$ is the mean social fishing effort claimed by anglers from the *j*th fishing province in the *i*th 100 km coastal area

$\bar{e}_{ij,\,comp}$ is the mean competitive fishing effort claimed by anglers from the *j*th fishing province in the *i*th 100 km coastal area.

Total annual fishing effort for the *i*th 100 km coastal area, $\hat{E}_{i,\,total}$, was calculated as:

$$\hat{E}_{i,\,total} = \hat{E}_{i,\,social} + \hat{E}_{i,\,comp} \tag{2.3}$$

The total social and competitive annual fishing effort variance for each 100 km coastal area was calculated as:

$$Var\left(\hat{E}_{i,\,social}\right) = \sum_{j=1}^{6} N_{j,\,social}{}^{2}\ Var\left(\bar{e}_{ij,\,social}\right) \tag{2.4}$$

$$Var\left(\hat{E}_{i,\,comp}\right) = \sum_{j=1}^{6} N_{j,\,comp}{}^{2}\ Var\left(\bar{e}_{ij,\,comp}\right) \tag{2.5}$$

where

$$Var\left(\bar{e}_{ij,\,social}\right) = \left(\frac{N_{j,\,social} - n_j}{N_{j,\,social}}\right)\frac{s^2_{ij,\,social}}{n_j} \tag{2.6}$$

$$Var\left(\bar{e}_{ij,\,comp}\right) = \left(\frac{N_{j,\,comp} - n_j}{N_{j,\,comp}}\right)\frac{s^2_{ij,\,comp}}{n_j} \tag{2.7}$$

and n_j is the number of registered club anglers interviewed in the *j*th coastal province, and $s^2_{ij,\,social}$ and $s^2_{ij,\,comp}$ are the sample effort variances for social and competitive fishing respectively, in the *i*th 100 km coastal area by anglers in the *j*th coastal province.

Total annual fishing effort variance for each 100 km coastal area, $Var\left(\hat{E}_{i,\,total}\right)$, was calculated as:

$$Var\left(\hat{E}_{i,\,total}\right) = Var\left(\hat{E}_{i,\,social}\right) + Var\left(\hat{E}_{i,\,comp}\right) \tag{2.8}$$

The mean sample catch per unit effort (CPUE) for social, $CPUE_{i,\,social}$, and competitive fishing, $CPUE_{i,\,comp}$, in each 100 km coastal area were calculated as:

$$CPUE_{i,\,social} = \frac{\sum_{i=1}^{n} c_{i,\,social}}{n_{i,\,social}} \quad (2.9) \qquad \text{and} \qquad CPUE_{i,\,comp} = \frac{\sum_{i=1}^{n} c_{i,\,comp}}{n_{i,\,comp}} \quad (2.10)$$

Where, $c_{i,\,social}$, and, $c_{i,\,comp}$, are the number of *C. taurus* caught socially and competitively by all anglers sampled within each 100 km coastal area and, $n_{i,\,social}$ and, $n_{i,\,comp}$, are the total number of days fished socially and competitively by all anglers interviewed within each 100 km coastal area.

Catch rate variance was calculated as the variance of the average catches claimed by anglers interviewed using the standard formula for sample variance (Zar 1996).

$$Var\left(CPUE_{i,\,social}\right) = \frac{\sum_{i=1}^{n} c_{i,\,social}^{2} - \left(\dfrac{\sum_{i=1}^{n} c_{i,\,social}}{n_{i,\,social}}\right)^{2}}{n_{i,\,social} - 1} \tag{2.11}$$

$$Var\left(CPUE_{i,\,comp}\right) = \frac{\sum_{i=1}^{n} c_{i,\,comp}^{2} - \left(\frac{\sum_{i=1}^{n} c_{i,\,comp}}{n_{i,\,comp}}\right)^{2}}{n_{i,\,comp} - 1} \tag{2.12}$$

Total social, $C_{i,\,social}$, and competitive catch, $C_{i,\,comp}$, for the entire shore angling fishery for each 100 km coastal area was estimated by multiplying the total estimated social and competitive effort by the social and competitive CPUE respectively:

$$C_{i\ social} = CPUE_{i\ social} \cdot \hat{E}_{i\ social} \quad (2.13) \qquad \text{and} \qquad C_{i\ comp} = CPUE_{i\ comp} \cdot \hat{E}_{i\ comp} \quad (2.14)$$

The total annual catch, $C_{i,\,total}$ for each 100 km coastal area was calculated as

$$C_{i,\,total} = C_{i,\,social} + C_{i,\,comp} \tag{2.15}$$

Total social, $Var\left(C_{i,\,social}\right)$, and competitive catch variances, $Var\left(C_{i,\,comp}\right)$, were calculated as the product of the social and competitive CPUE and effort variances respectively.

$$Var\left(C_{i,\,social}\right) = Var\left(CPUE_{i,\,social}\right) \cdot Var\left(E_{i,\,social}\right) \tag{2.16}$$

$$Var\left(C_{i,\,comp}\right) = Var\left(CPUE_{i,\,comp}\right) \cdot Var\left(E_{i,\,comp}\right) \tag{2.17}$$

The total annual catch variance for the *i*th 100 km coastal area was calculated as

$$Var\left(C_{i,\,total}\right) = Var\left(C_{i,\,social}\right) + Var\left(C_{i,\,comp}\right) \tag{2.18}$$

2. 3. 3. On-site angler questionnaire survey

Anglers, who had been randomly selected for the telephone survey, were also asked to complete a questionnaire (Appendix 2.1) to obtain information on the following five categories: (1) participation; (2) catchability; (3) post-release mortality rates; (4) non-reporting rates (discussed in Chapter 7); and (5) temporal catch and effort trends. The last category was developed to gauge the reduction in catch and effort (if any) due to the implementation in December 2001 of Schedule 44 of the National Environmental Management Act (Act No. 107 of 1998), which prohibited the use of vehicles on beaches.

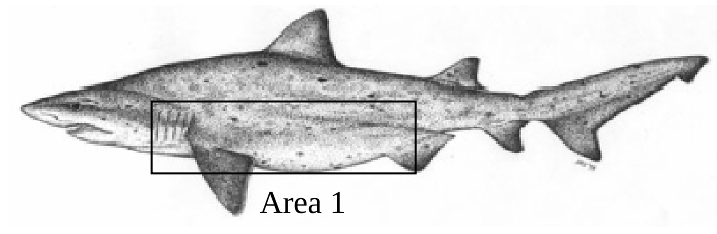
The questionnaire was developed in collaboration with members of the target population. The design and wording of the questionnaire was pre-tested by giving it to 20 random anglers and their responses evaluated. Pre-testing of the survey design indicated that the questionnaire took about ten minutes to complete. The questionnaire was too lengthy to conduct by phone and a high non-response rate was anticipated in a mail survey. As result, the survey was conducted where possible by an on-site face-to-face interview. Face-to-face interviews have the added advantage in developing a rapport with the respondent and creating an interest in the survey (Brown 1991).

The most effective method to conduct on-site interviews is in areas where there is a high density of anglers (Essig and Holliday 1991). Fixed venue competitions, which are set at a predetermined location, date and time, provided a suitable venue at which to interview a large congregation of the target population. Anglers were interviewed at these competitions during the 2001/2002 and 2002/2003 fishing seasons. From a preliminary analysis of competition catch records, it was evident that *C. taurus* were caught more regularly in some fishing provinces than others. It is reasonable to assume that anglers in the provinces where *C. taurus* were rarely, if ever caught, would have little information that would be relevant to the questionnaire. Using this prior knowledge, it was decided not to attend any competitions in either Zululand or Natal. Many anglers registered to these provinces, however, were surveyed face-to-face at inter-provincial and National competitions held within the other fishing provinces. Anglers in these, and other, provinces that were not interviewed on-site, were interviewed over the phone or sent a copy of the questionnaire by post. If the questionnaire hadn't been retuned within a month, follow up calls were made once a month for a four-month period. A mail survey, in conjunction with the on-site and telephone survey, had the added benefit of an increased response rate due to the rapport that had been developed in the personnel interview.

2. 3. 3. 1. Post-release mortality

Mortality rates are influenced by factors such as size (Nuhfer and Alexander 1992, Muoneke and Childress 1994, Schisler and Bergersen 1996), stress, anoxia and prolonged handling times (Muoneke and Childress 1994) as well as tackle type and hooking location (Nuhfer and Alexander 1992, Diodati and Richards 1996). Based on field observations of post-release mortality, a points system was developed, in which the angler's treatment of the shark and its condition prior to release were assessed by asking a series of questions relating to the "last shark" the angler had caught. Each question was scored from 0 to 100. Points from each of the questions were then tallied and if the total score summed to 100 or more then the shark was deemed to have suffered post-release mortality (Table 2.2).

Table 2.2. Post-release mortality scoring system based on a series of questions related to the "last *Carcharias taurus*" the angler had caught

Question	Category	Score
Weighed shark	Guessed weight	0
	Hammock	0
	Scale hooked in dorsal fin	10
	Scale hooked in gills	50
Swallowed hook	Yes	20
	No	0
Blood from gills	Yes	20
	No	0
Out of water for more than 10 min	Yes	50
	No	0
Injuries on rocks	Yes	10
	No	0
Return to water	Yes	0
	No (Dead)	100
Swim away strongly	Yes	0
	No	20
Gaff and location	Area 1 (Gills, stomach)	50
	Elsewhere	10
		

2. 3. 4. Collection of historical club catch records

An introductory letter was sent to the Chairperson and Records Officer of each coastal fishing province asking for their co-operation and participation in the collection of national, inter-provincial, fixed venue and postal competition catch data for *C. taurus* for as far back as their records existed. Individual fishing clubs were contacted by phone and asked for catch records that their club possessed. Because there are so many clubs registered in Natal, it was not feasible to contact all of them and only 20 were selected at random. Club catch records, in most instances, consisted of the date, place of capture and the weight of the shark. In order to obtain historical catch data, as well as complete catch information for the 2002/2003 fishing season, the survey was conducted over a three-month period from May to July 2003. Additional information on the spatial distribution of catches was obtained from the ORI and PEM cooperative tagging programs. Many of these records provided information not only on the weight of the shark, but also its sex, precaudal length (PCL) and total length (TL).

2. 3. 5. Length weight conversion

The four life history stages outlined in Chapter 1 were categorised by total length. Catch records collected from the surveys, club records and the PEM and ORI tagging programs, however, were a mixture of weights, precaudal lengths and total lengths. To standardise units of measurement, all precaudal lengths and weights were converted to total length. Using length and weight measurements from the NSB (n = 100) and the PEM tagging program (n = 625), where total length was calculated with the tail bent down to the perpendicular following Compagno (2001), the following relationships were estimated:

The relationship between TL (mm) and PCL (mm):

Males: $TL = (PCL \text{ x } 1.333) + 68.555 \quad (n = 287, r^2 = 0.99)$

Females: $TL = (PCL \text{ x } 1.290) + 115.560 \quad (n = 438, r^2 = 0.99)$

Combined: $TL = (PCL \text{ x } 1.299) + 104.507 \quad (n = 725, r^2 = 0.99)$

The relationship between weight (kg) and TL (mm):

Males: $W(kg) = 3.349 \text{ x } 10^{-10} \left(TL^{3.394}\right) \left(n = 267, r^2 = 0.98\right)$

Females: $W(kg) = 2.337 \text{ x } 10^{-10} \left(TL^{3.445}\right) \left(n = 433, r^2 = 0.98\right)$

Combined: $W(kg) = 1.296 \text{ x } 10^{-9} \left(TL^{3.205}\right) \left(n = 700, r^2 = 0.98\right)$

Significant differences were observed between male and female PCL - TL (ANCOVA, $P \leq 0.001$; Fig. 2.2), and length - weight (ANCOVA, $P \leq 0.001$; Fig. 2.3) relationships. The increased sample size of this study (particularly for larger individuals) improves the accuracy and precision of the length - weight relationship, compared to the equation given by Smale (2002), whose equation underestimates the weight of individuals larger than 2500 mm TL.

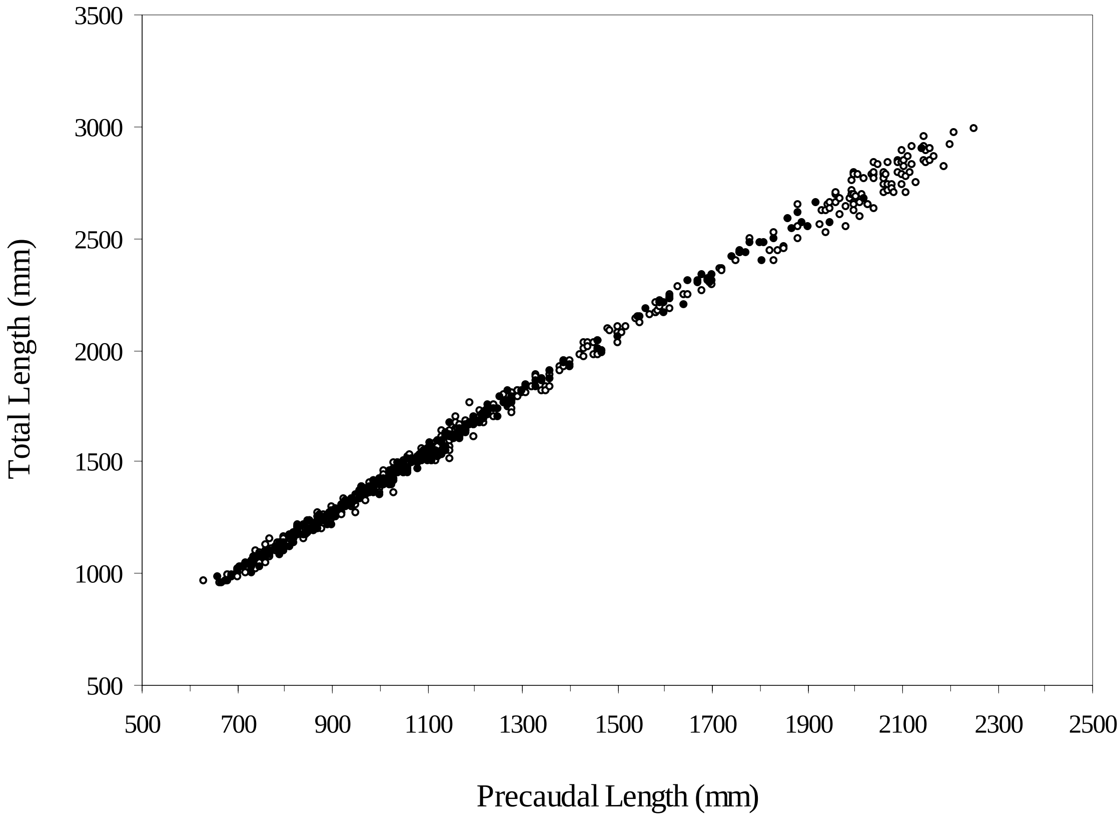


Fig. 2.2. Precaudal length to total length relationship for *Carcharias taurus*. Black dots are males (n = 287), empty circles are females (n = 438)

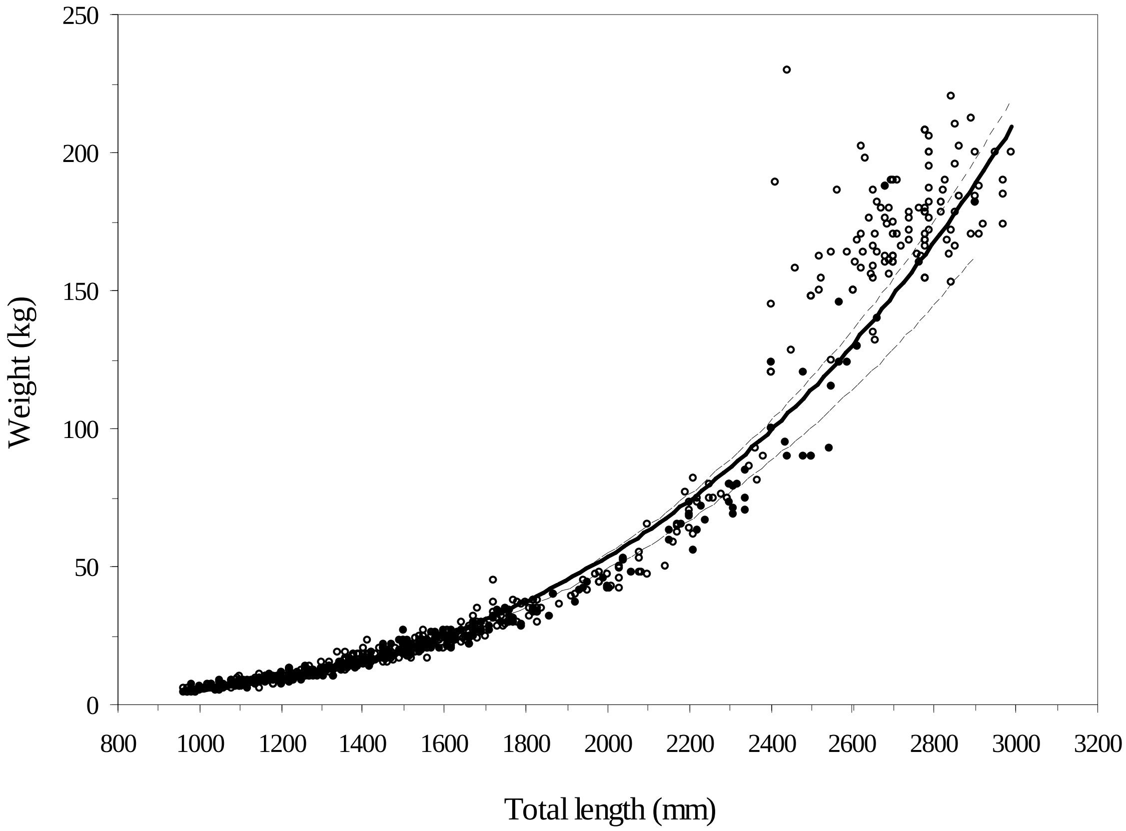


Fig. 2.3. Length - weight relationship for *Carcharias taurus*. Black dots are males (n = 267), empty circles are females (n = 433). The upper dashed trend line is for females, the lower dashed line is for males; the solid line in between them is for the sexes combined

2. 4. Results

2. 4. 1. Telephone survey

2. 4. 1. 1. Respondent catch and effort

A total of 477 coastal club registered anglers, 22.9% of the target population, were interviewed by telephone every three-months to solicit information on their fishing effort for sharks and the number and size of *C. taurus* they had caught within each month of the recall period. A summary of the telephone survey results is given in Table 2.3.

Anglers in Zululand and Natal have a competitive fishing calendar, which extends throughout the year. Unfavourable weather conditions, however, from June to August restrict the fishing season in the other coastal provinces to a nine-month period from September to May. Taking this into consideration, the annual shark fishing effort expended by anglers in each coastal province was similar, at about two to three days a month. Anglers in Border and the Eastern Province recorded the highest catches of *C. taurus*, 314 and 351 sharks, respectively. These catches were almost five times greater than the next highest catch (n = 74) reported by anglers in the Southern Cape. Catches of *C. taurus* were disproportionate amongst the anglers surveyed within each of the provinces. This trend was greatest in the Eastern Province and Border where 21.0% and 35.7% of anglers recorded 76.0% and 79.9% of the catch, respectively.

Table 2.3. A regional summary of the annual shark fishing effort and catch of *Carcharias taurus* by coastal club affiliated anglers interviewed by telephone every three months from September 2002 to August 2003

Province	Anglers interviewed	Club registered anglers	Competitively active members	Total effort days.year^{-1}	Average effort days.year^{-1} ± SE	Number of *C. taurus* caught
Zululand and Natal	128	979	400	3785	30 ± 1.36	51
Border	70	162	120	1711	24 ± 2.15	314
Eastern Province	124	530	150	2319	19 ± 1.41	351
Southern Cape	48	123	100	1196	25 ± 2.56	74
Boland	56	117	100	1084	20 ± 1.59	17
Western Province	51	172	150	1039	20 ± 1.69	8
Total	477	2083	1020	11134	23 (± 1)	815

2. 4. 1. 2. Total club angling effort

Total shark fishing effort for all coastal club affiliated anglers was estimated to be 37, 820 fishing days.year^{-1} (95% C.I. = 28, 281 - 47, 359 days.year^{-1}). The spatial distribution of effort was not uniform along the coast, with most effort occurring in Areas 4 (16.0%), 5 (12.5%), 6 (10.0%), 13 (7.0%) and 20 (7.5%), (Fig. 2.4). The lack of fishing effort in Area 14 is because this area encompasses the Tsitsikamma Marine Protected Area, within which fishing is prohibited. Competitive fishing contributed to 30% of all shark-fishing effort along the coast, with the highest relative contributions in Areas 13 (47.0%), 18 (50.0%) and 19 (41.0%). The monthly distribution of fishing effort from Areas 1 to 8 remained reasonably uniform, reflecting the year round competitive calendar of the Zululand and Natal Rock and Surf union. In Areas 9 to 24, the competitive fishing season runs from September to April, and consequently the majority of fishing is in these months. Little shark-directed fishing is conducted in the winter months from May to August due to unfavourable weather conditions and the targeting of non-cartilaginous species.

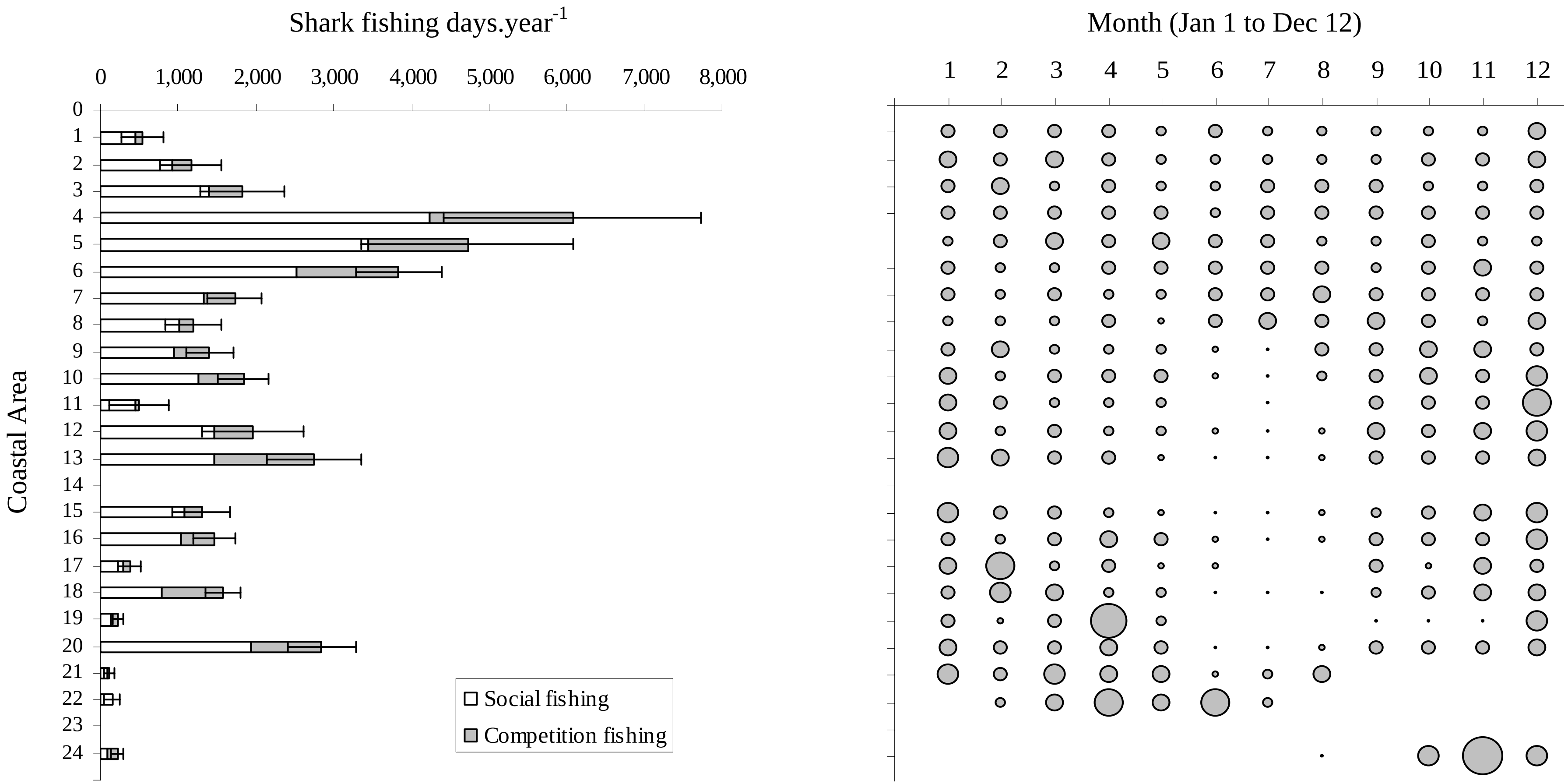


Fig. 2.4. Total annual shark fishing effort and 95% confidence intervals for each 100 km area along the South African east coast estimated from coastal club-registered anglers (left panel) and the corresponding monthly effort proportions (right panel), where monthly effort data are scaled to sum to unity for each coastal area

2. 4. 1. 3. Catch per unit of effort

Kolmolgorov-Smirnov and Bartlett's Chi squared tests indicated that monthly CPUE was both heteroscedastic ($P < 0.01$) and inhomogeneous ($P < 0.01$) for each of the 100 km coastal areas. As a result, non-parametric analyses were used to compare variations in CPUE between sites.

The mean CPUE for the whole coastline from Area 1 to 24 was 0.073 *C. taurus* fisher^{-1}.day^{-1} (95% C.I. = 0.068 – 0.078 fisher^{-1}.day^{-1}). CPUE varied significantly between sites (Kruskal-Wallis, $P < 0.05$) and ranged from a high of 0.260 *C. taurus* fisher^{-1}.day^{-1} in Area 10 to zero *C. taurus* fisher^{-1}.day^{-1} in Areas 21 to 24 (Fig. 2.5). CPUE tended to be higher in coastal Areas 10 to 13 and to decline progressively with increasing distance both up and down the coast. There was an abrupt reduction in CPUE between areas protected by the NSB bather protection nets (Areas 3 to 6) and adjacent non-netted areas. This reduction, however, was not significant (Kruskal-Wallis, $P > 0.05$). Competitive CPUE was greater than social CPUE for all coastal areas and significantly greater for Area 1 and Areas 7 to 12 (Mann-Whitney U-test, $P < 0.05$). Monthly CPUE showed distinct seasonality and with the exception of Area 8, was generally higher in the summer months from November to March, and lower in the winter months from May to August.

2. 4. 1. 4. Total club-angling catch

The total number of *C. taurus* caught annually by coastal club anglers from Areas 1 to 24 was estimated at 1764 (95% C.I. = 321 – 3207), with social and competitive fishing accounting for 54% and 46% of the total catch, respectively. Most *C. taurus* were caught in Areas 10, 12 and 13. The combined catch of these three areas accounted for 60% of the entire estimated catch (Fig. 2.6). The monthly distribution of catches reflects the trends in monthly CPUE, with the majority of catches in all areas, with the exception of Area 8, being made in the summer months from November to April.

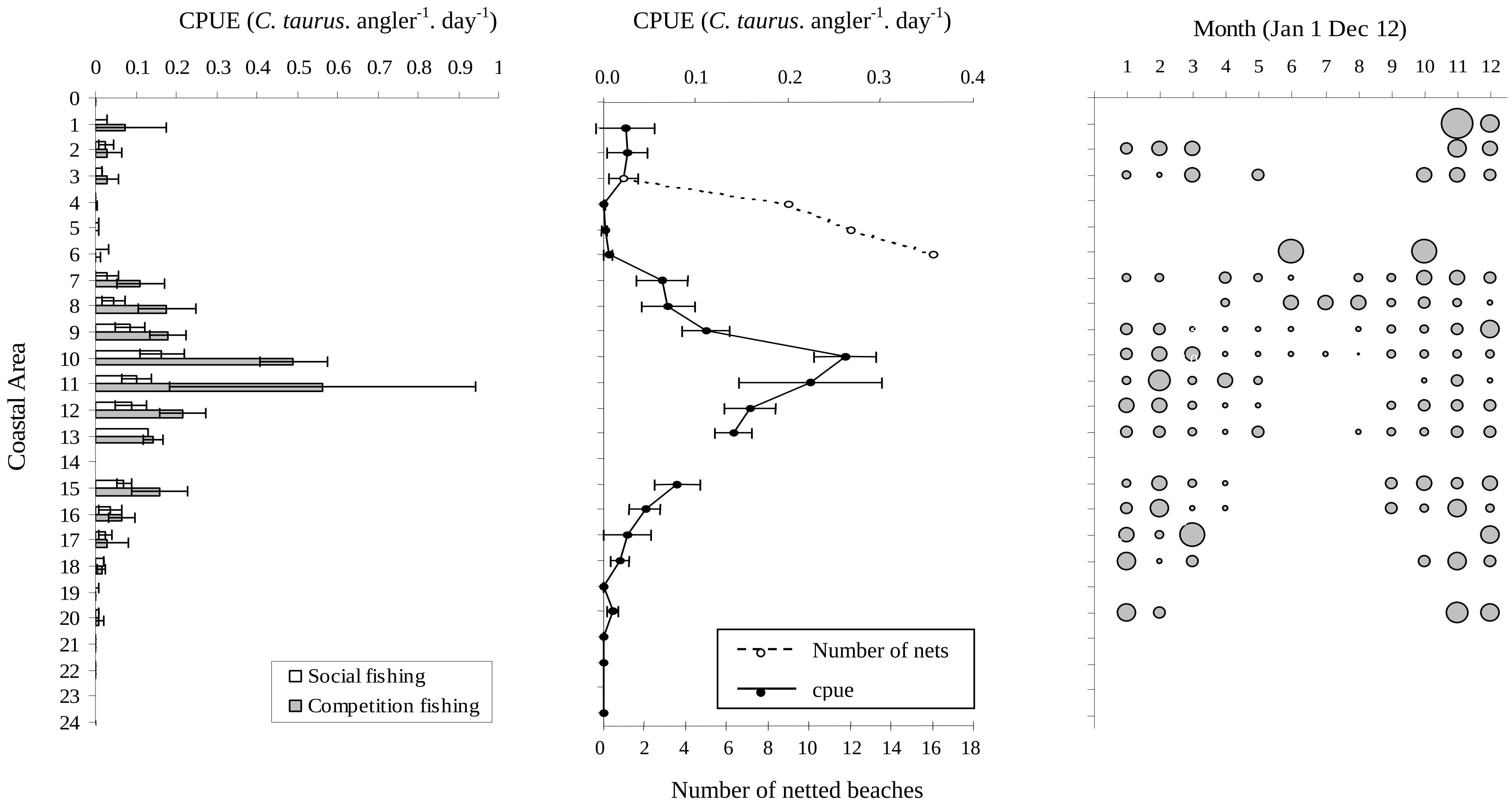


Fig. 2.5. Social and competitive CPUE and 95% confidence intervals for *Carcharias taurus* for each 100 km coastal area (left panel). Total CPUE and the number of netted beaches (middle panel), and the corresponding monthly total CPUE proportions (right panel), where monthly CPUE data are scaled to sum to unity for each coastal area

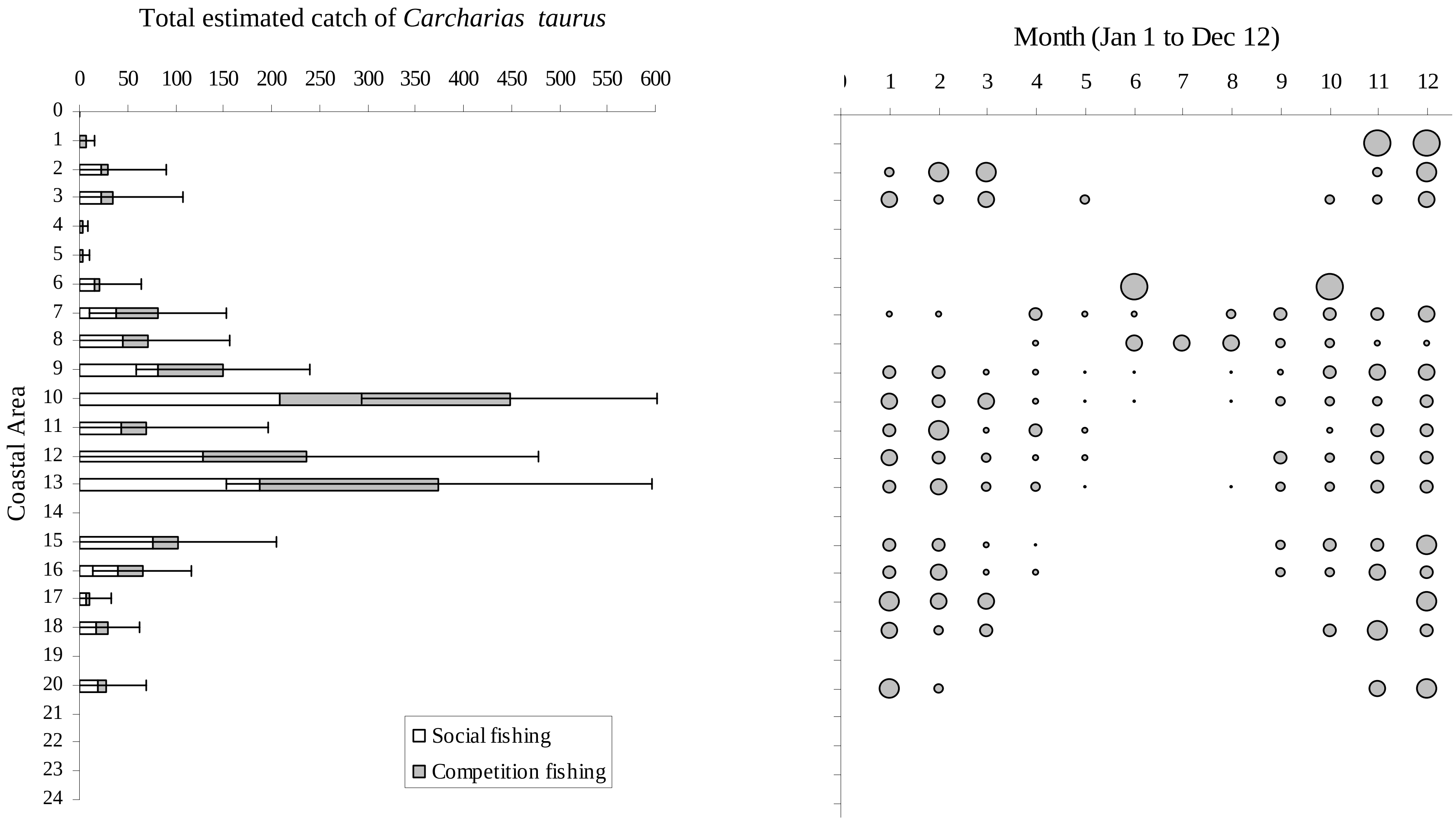


Fig. 2.6. Total estimated catch of *Carcharias taurus* and 95% confidence intervals for each 100km area along the South African coast (left panel) and the corresponding monthly catch proportions (right panel), where monthly catch is scaled to sum to unity for each coastal area

2. 4. 1. 5. Size composition of catch

The relative abundance and total estimated catch of the four size classes of *C. taurus*, previously identified in Chapter 1, are given in Fig. 2.7. Total catch was calculated by multiplying the social and competitive CPUE for each size class by the total estimated social and competitive fishing effort. The results indicate a distinct spatial segregation of the population based on size. YOY sharks were recorded from Areas 9 to 17, the majority (92.1%) between Areas 10 and 13. CPUE for YOY sharks was significantly greater in Area 10 compared to Areas 11 to 13 (Kruskal-Wallis, $P < 0.05$). Juvenile sharks were distributed over a greater range, from Areas 7 to 20, although a large proportion (89.2%) was recorded in Areas 9 to 15. Sub-adult sharks ranged as far north as Area 3, and adult sharks were recorded along the entire coast from Areas 1 to 20.

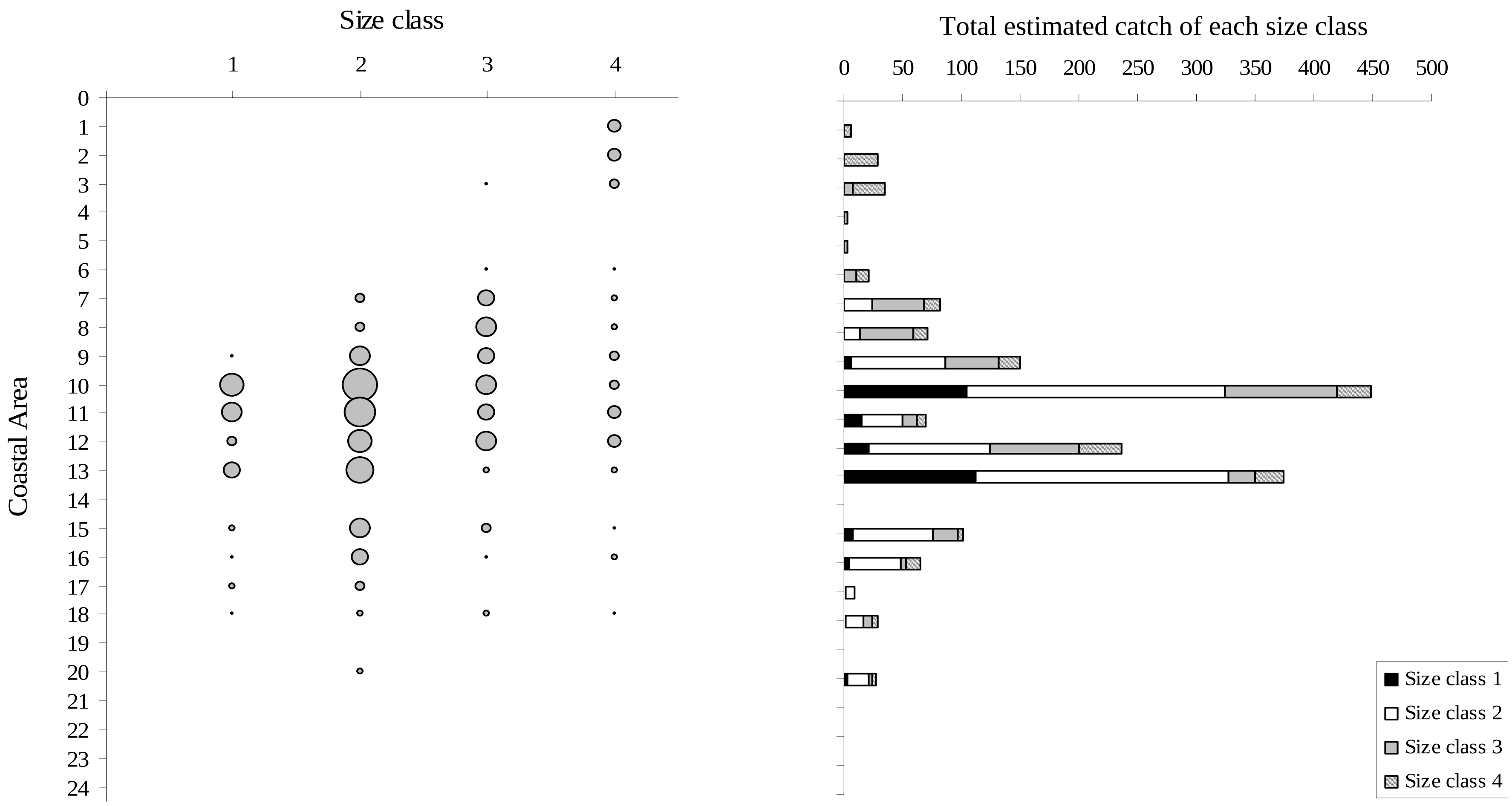


Fig. 2.7. Relative abundance (CPUE) of the four size classes of *Carcharias taurus* along the South African coast (left panel) and the total estimated catch of each size class (right panel)

2. 4. 2. On-site angler questionnaire survey

2. 4. 2. 1. Angler participation

Anglers who had participated in the telephone survey also completed a detailed questionnaire by either an on-site interview, by post or telephone (Table 2.4). All but two of the fishers interviewed were males, 97.7% were white, 1.9% were Indian, 0.4% Coloured, and none of fishers interviewed were black. The majority of interviewees were aged between 20 and 40 (47.2%), with less than 10% under the age of 20. Most fishers (66.5%) only fished for sharks in competitions, and 85.7% stated that they had never actively fished for sharks before they had joined a club. The majority of respondents in Zululand and Natal (56.2%), Boland (44.6%) and the Western Province (45.1%) had never caught *C. taurus* while 31.4% of anglers in Border and 39.5% in the Eastern Province had caught more than 50.

Table 2.4. Regional summary for the method of questionnaire interview

Province	On-site survey	Mail survey	Telephone survey
Zululand and Natal	34	37	57
Border	55	15	-
Eastern Province	112	12	-
Southern Cape	18	27	3
Boland	53	3	-
Western Province	50	1	-
Total	322	95	60

2. 4. 2. 2. Catchability

Of the 477 anglers interviewed, 326 (68.3%) stated that they had caught at least one *C. taurus*. The majority of anglers from all coastal provinces (70.8%), when asked about the "last *C. taurus*" they had caught, had been specifically targeting this species. Only 12.3% had been targeting other species of shark, 5.5% ray or skate species and 11.4% teleosts. A regional comparison in target preference is given in Fig. 2.8, and clearly indicates that *C. taurus* is actively targeted in Areas 2, 10 to 13 and 18, and caught predominantly as a bycatch for fishing for other species in Areas 5, 15, 16 and 20.

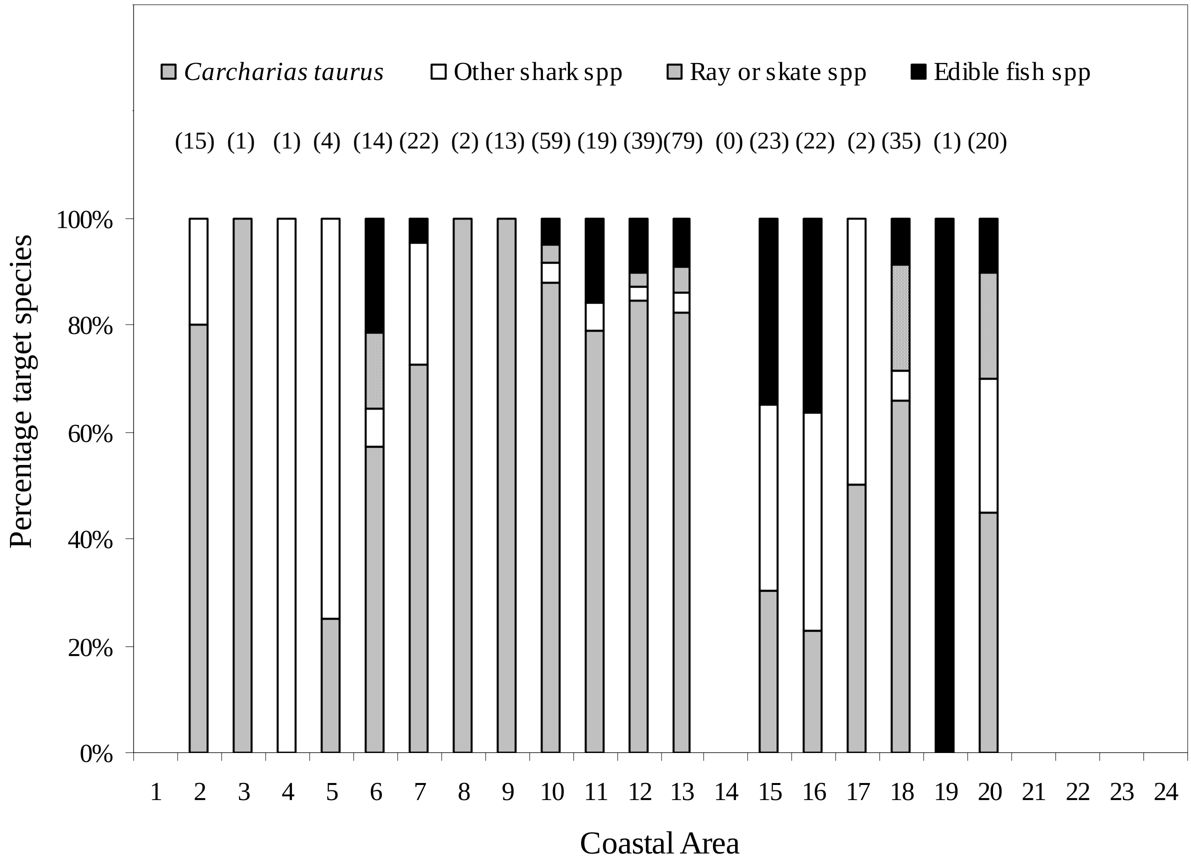


Fig. 2.8. A regional comparison in the species that were targeted by anglers interviewed in the questionnaire survey while fishing for the "last *Carcharias taurus*" they had caught. The numbers of anglers interviewed in each Area are given above each bar in brackets

Anglers reported using a variety of different bait types (n = 32) to catch their "last *C. taurus*". The most commonly used bait was mullet head (33.1%), probably *Mugil cephalus* or *Liza* spp., and mackerel head (*Scomber japonicus*) (17.5%). The majority (81.7%) of sharks had been caught during the day and the average number of hours anglers had spent fishing on the trip was seven. On the day they had caught their "last *C. taurus*", interviewed anglers were asked how many in total they had landed and how many they thought they had hooked, but lost. Anglers were able to assume that the lost sharks were *C. taurus* and not some other species based on previous catches during the day, and in the characteristic manner *C. taurus* takes a baited line and fights once hooked. The average success rate of the 326 anglers interviewed from all coastal provinces that had caught *C. taurus* was 57.0%.

Anglers were asked a series of environmental questions relating to the condition of the sea at the time they had caught their "last *C. taurus*". Almost all sharks (82.7%) had been caught in murky or dirty water, compared to clean water (17.3%), and 67.0% had been caught while the tide was rising, rather than dropping (33.0%). In each coastal area, with the exception of Areas 1 to 4 sharks were caught in water that was lower than the average temperature for that time of year (Fig. 2.9). For all coastal areas the majority of sharks (79.5%) were caught in a water temperature of between 15 and 20˚ C. For Areas 10 to 16, 14.3% were caught in water below 15˚ C.

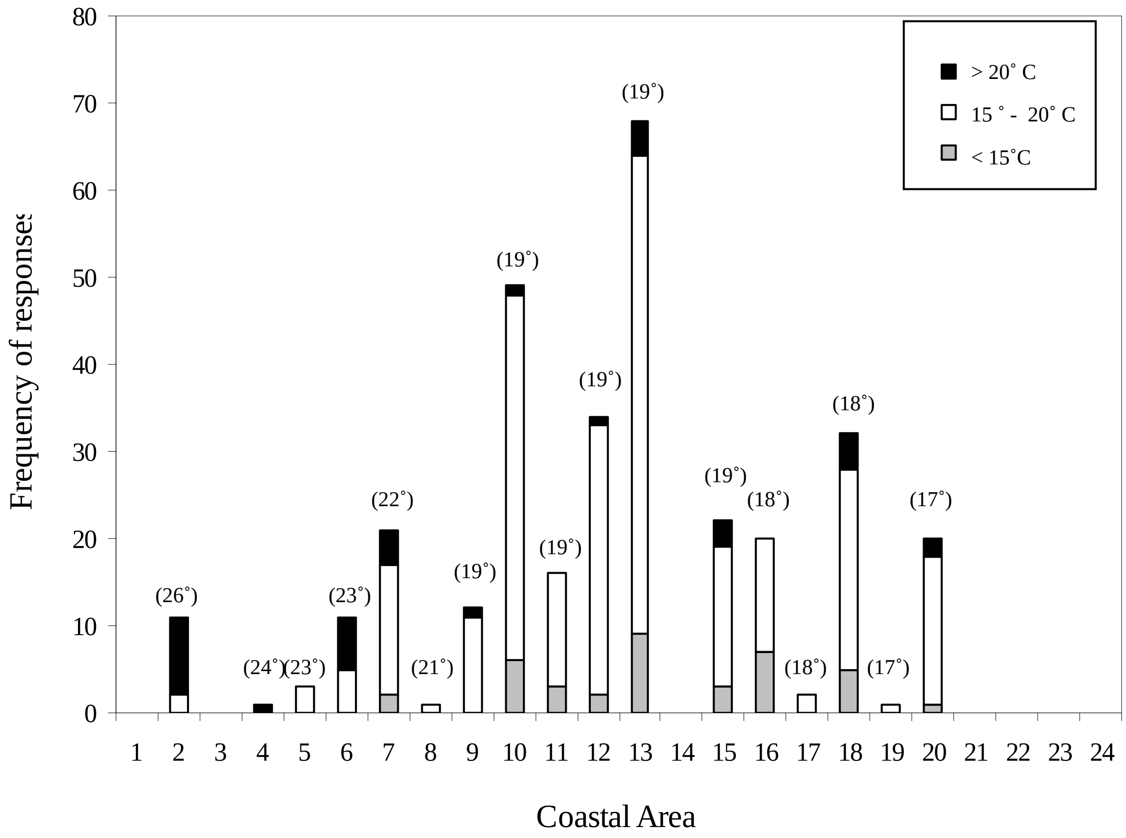


Fig. 2.9. A regional comparison in water temperature in which interviewed anglers caught their "last *Carcharias taurus*" as compared to the average summer water temperature for that coastal region (in brackets above each bar)

2. 4. 2. 3. Post-release mortality

Almost all (98.8%) of the 326 anglers surveyed who had caught *C. taurus* agreed that this species should be released alive after capture. However, angler's interview responses, particularly those related to gaffing and weighing, indicated that post-release mortality was likely for all size classes (Table 2.5).

Table 2.5. Post-release mortality estimates for the different size classes of *Carcharias taurus*

Size class	Number recorded in survey	Number that scored > 100	% Suffer post-release mortality
1	26	1	3.85%
2	160	7	4.38%
3	75	6	8.00%
4	65	12	18.46%

The higher mortality rates for the larger size classes were predominantly the result of the time it took to weigh the shark before it was returned to the water. The majority of adult sharks (76.9%) were out of the water for ten minutes or longer before they were returned, compared to only 11.5% of YOY sharks. Based on these post-release mortality calculations and the total catch of each size class (Section 2. 4. 1. 5) the total number of sharks expected to die after having been returned to the sea is given in Table 2.6. Another source of mortality within the shore-angling fishery is the capture and export of live *C. taurus* for the aquarium trade. At present a total of approximately 30 sharks are exported annually (J. Visser, International Marine Exhibits, pers. comm.).

Table 2.6. Summary of the number of each size class of *Carcharias taurus* that would be expected to die from post-release mortality based on the estimated annual shore angling catch

Size class	1	2	3	4
Estimated annual catch	278	842	406	237
Post-release mortality	11	37	32	44

2. 4. 2. 4. Temporal catch and effort trends

Anglers were asked their opinion on the relative abundance of *C. taurus* in the coastal areas that they regularly fished. Anglers who had been fishing for more than 20 years were also asked whether they thought this species had increased or decreased in abundance over the last two decades. Anglers in Border (25.9%) and the Eastern Province (21.4%) considered *C. taurus* to be very abundant in the areas that they commonly fished (Areas 9 and 10 and 11 to 13, respectively). The majority of anglers in the other four coastal provinces considered this species to be scarce, 17.5% of anglers in Zululand and Natal considered it to be very scarce (Areas 1 to 6). Anglers in Zululand and Natal (60.5%), the Eastern Province (46.3%), Boland (46.2%) and the Western Cape (60%) believed that the population size of *C. taurus* had remained relatively constant over the last 20 years. Anglers in the Southern Cape (62.5%) thought it had decreased and anglers in the Border region that it had increased (64.5%) or even greatly increased (22.6%).

Since the banning of vehicles on beaches in December 2001, 76.2% of interviewed anglers stated that they now spent less time fishing for sharks. The predominant reason (95.5%) cited for this decrease was the inability to access the best fishing spots and to carry the heavy equipment such as scales, slings and gaffs necessary to weigh the shark once it had been caught. Anglers in Zululand and Natal (24.2%) and the Western Cape (23.08%), however, also expressed concerns about vehicle security as a major reason for their reduction in effort. In response to a reduced effort in shark fishing, 49.2% of all interviewed anglers stated that they now fished more for non-cartilaginous species because it required less and lighter equipment. This trend was most pronounced in the Eastern Province (61.5%) and Border (63.8%). Due to a reduction in shark fishing effort and an increase in the targeting of non-cartilaginous species the majority of anglers (74.2%) stated that they now caught fewer *C. taurus* than before the vehicle ban.

The SASAA club membership has dropped by 30% in the last three years since the banning of vehicles on beaches (E. Holmes, SASAA secretary, pers. comm.).

Decreases have been greater in the coastal compared to the inland unions especially in the Eastern Province and Boland, which have lost 49.6% and 36.8% of their members respectively. Despite the decrease in affiliated SASAA membership the number of anglers attending provincial competitions has only decreased in Border from 150 to 120, (E. Clur, Border secretary, pers. comm.), and the Eastern Province from 250 to 150, (P. Van Zyl, Eastern Province secretary, pers. comm.).

2. 4. 3. Collection of historical club catch records

2. 4. 3. 1. Catch records

A total of 7,337 *C. taurus* catches were collected from competitive club records, the NMLS, as well as the ORI and PEM tagging databases. Part of the ORI database consisted of sharks that had been caught, tagged and released from the bather protection nets of the NSB (n = 972) between Areas 3 and 6. These records have been included in the following analyses due to the lack of shore angling catches in this region and the proximity of the nets to the coast.

The collected catch data, in the absence of information on effort does not accurately portray patterns of abundance. The data is biased by seasonal variations in fishing effort and regional variations in the quality of club and provincial records. Despite these limitations, the data collected in this survey were considered more appropriate than the CPUE obtained in the telephone survey (n = 815) to reflect spatial and seasonal distribution patterns because of the larger sample size. Catch records collected from the combined data sources also provided information, in many cases, on the sex of the shark allowing a comparison in distribution patterns between male and female sharks.

If the number of recorded catches for any coastal area was less than 10, they were omitted from the following figures (Fig. 2.10 to Fig. 2.13). This was done to reduce the size of the proportional monthly catch bubbles, to allow a more accurate representation of trends in the other coastal areas.

2. 4. 3. 2. YOY sharks

A total of 1,120 catch records of YOY sharks were collected from the combined data sets. The smallest individual reliably recorded was 3 kg, [750mm (TL)]. YOY sharks were recorded from costal Areas 7 to 20, but the vast majority (93.8%) were from Areas 10 to 13, suggesting this was the primary nursery area. YOY sharks were recorded in every month, but were most abundant from October to February (Fig. 2.10). Sexes were obtained from 193 sharks with females dominating the sample (60.1%).

2. 4. 3. 3. Juvenile sharks

A total of 2,995 catch records of juvenile sharks were collected from the combined data sets. Catches were recorded from Areas 6 to 20, but the vast majority (89.2%) were between Areas 10 and 13 (Fig. 2.11). In Areas 10 to 13, these sharks exhibited a seasonal distribution pattern similar to that observed for YOY sharks. In Areas 6 to 9 catches were also recorded in the winter months of July and August. A total of 589 sharks were sexed and females again dominated the sample (58.1%).

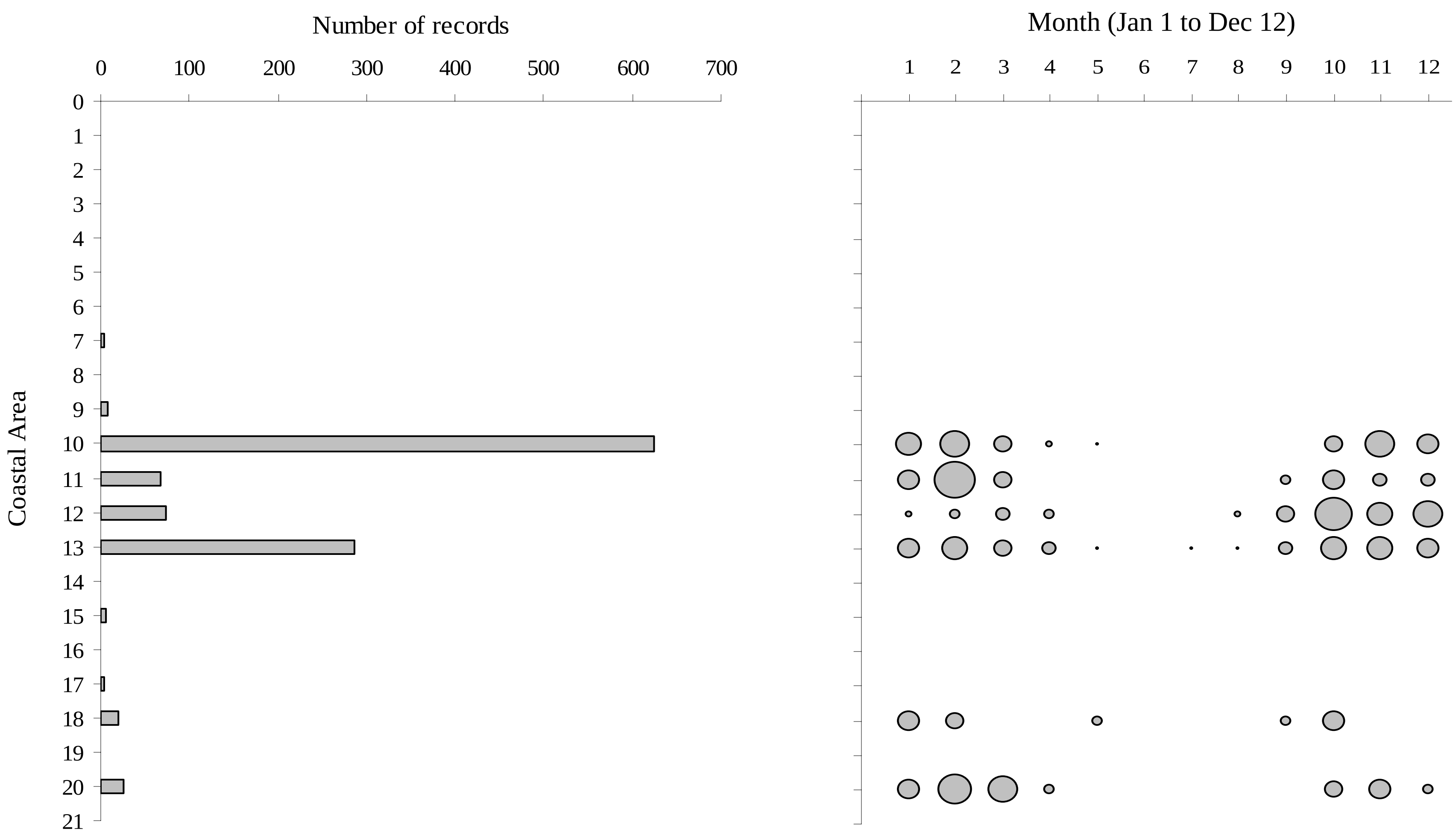


Fig. 2.10. Frequency of catch records of YOY *Carcharias taurus* collected from club records and the ORI and PEM tagging databases (left panel) and the corresponding monthly catch proportions (right panel), where monthly catch is scaled to sum to unity for each coastal area

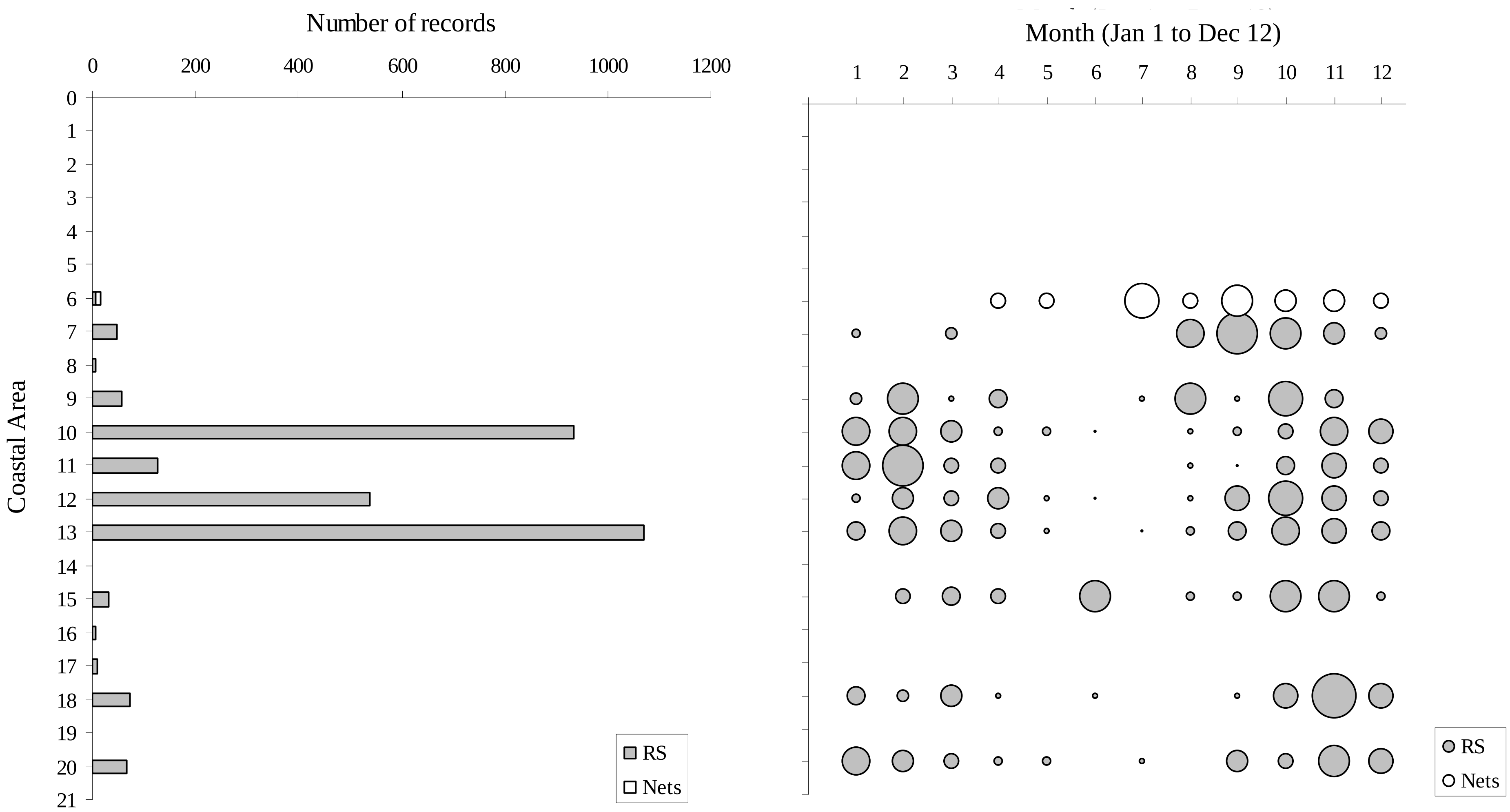


Fig. 2.11. Frequency of catch records of juvenile *Carcharias taurus* collected from club records and the ORI and PEM tagging databases (left panel) and the corresponding monthly catch proportions (right panel), where monthly catch is scaled to sum to unity for each area

2. 4. 3. 4. Sub-adult sharks

A total of 1,723 catch records of sub-adult sharks were recorded from the combined data sets between Areas 3 to 20. Although sub-adult sharks were recorded from the same coastal areas as YOY and juvenile sharks, 32.1% of catches were recorded from between Areas 3 and 9. Sharks were most commonly caught in Areas 9 to 13 from January to May, and in Areas 3 to 8 from June to November. These observations suggest a seasonal movement of sharks northward in the winter and southward in summer (Fig. 2.12). A spatial difference in the sex ratio of catches was evident between coastal areas. Male sharks (69.2%) dominated the catch in Area 8 (n = 13) and female sharks (80%) dominated the catch in Area 13 (n = 73).

2. 4. 3. 5. Adult sharks

A total of 1,499 catch records of adult sharks were collected in the survey. The largest shark that was reliably recorded was 3260mm (TL). Catch records were collected along the entire coast from Areas 1 to 20 (Fig. 2.13). Adults were the most prevalent size class recorded in Areas 1 to 6 and dominated the catch in the bather protection nets between Areas 3 to 6. Adult sharks exhibited a seasonal movement pattern similar to that observed for sub-adults. The catches in Areas 1 to 3 and Areas 10 to 13 were highest between the months of November and February. Catches in these areas were dominated by females, 92.2%, in Areas 1 to 3 (n = 226) and 79.3%, in Areas 10 to 13 (n = 53). Females caught in Areas 1 to 3 were predominantly pregnant (Cliff, NSB, pers. comm.) and in Areas 10 to 13, *post partum* (Smale 2002). These observations lend support to a biennial reproductive cycle as hypothesised by Cliff (1989, unpub.). Catches of adults in Areas 10 to 13 during the months of November to February coincide with an increase in catches of YOY sharks during the same period. Only 57 adult males were recorded in the survey and their pattern of distribution remains unclear. The majority of males (78.9%) were caught between the months of February and April in Areas 10 to 13.

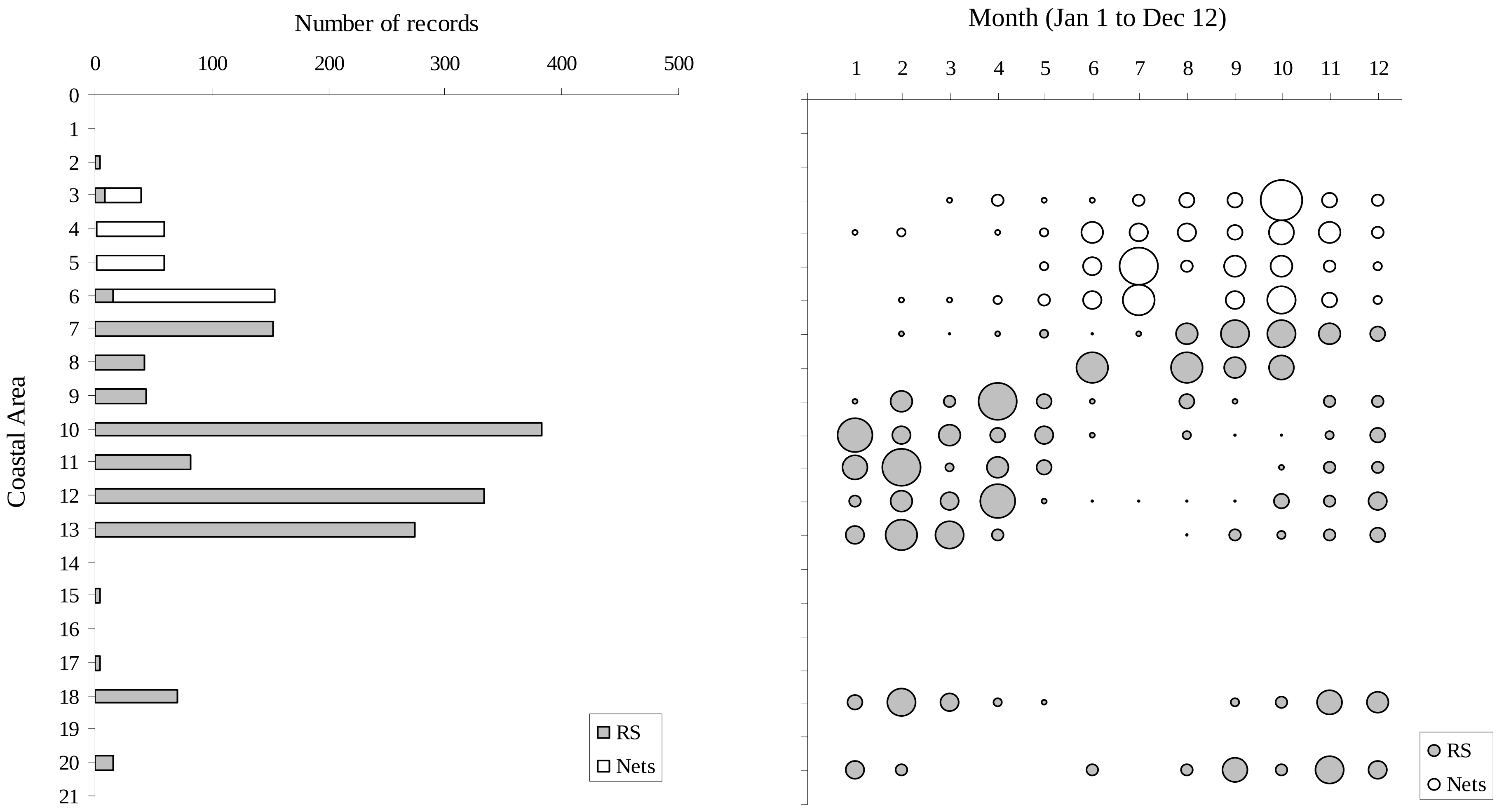


Fig. 2.12. Frequency of catch records of sub-adult *Carcharias taurus* collected from club records and the ORI and PEM tagging databases (left panel) and the corresponding monthly catch proportions (right panel), where monthly catch is scaled to sum to unity for each coastal area

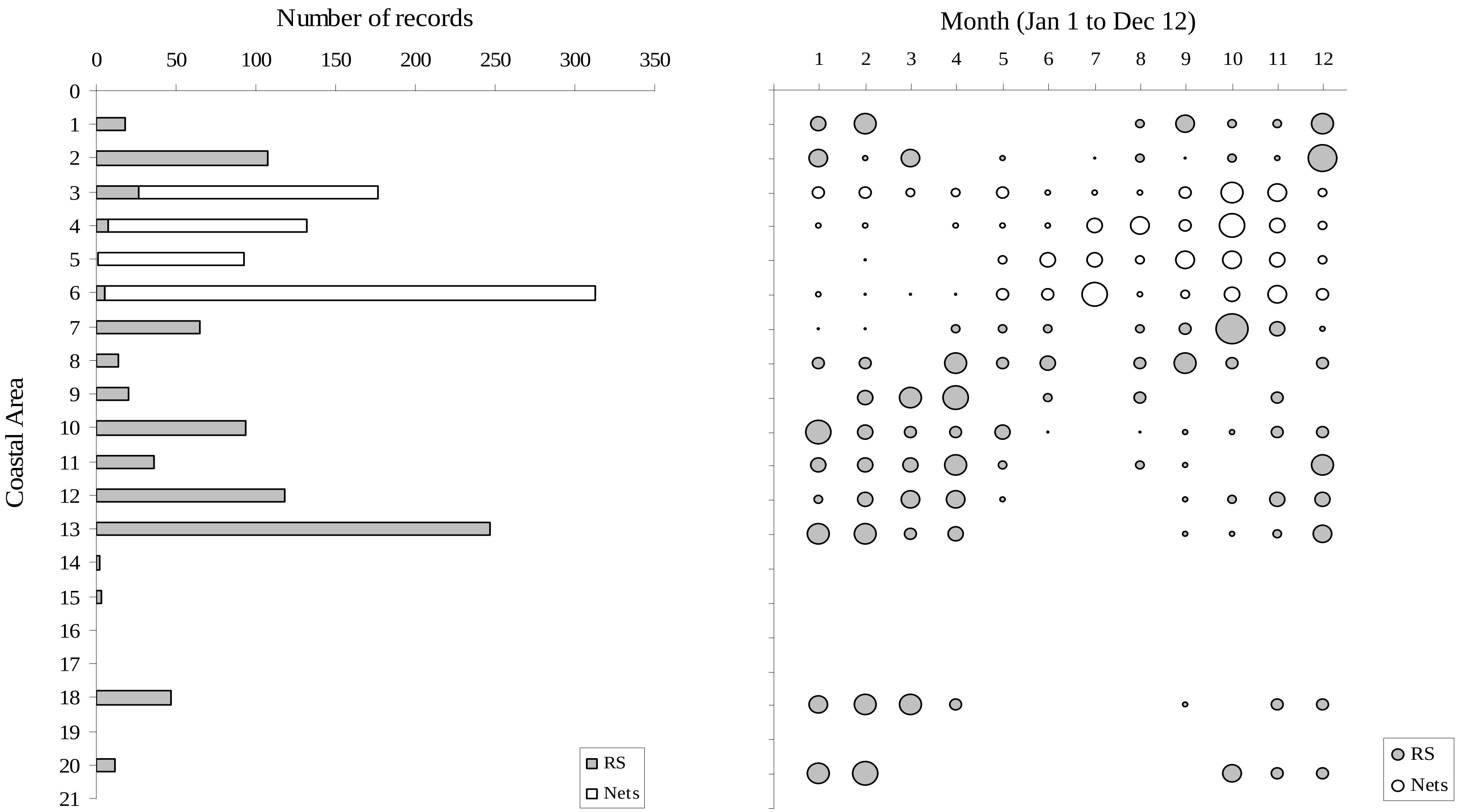


Fig. 2.13. Frequency of catch records of adult *Carcharias taurus* collected from club records and the ORI and PEM tagging databases (left panel) and the corresponding monthly catch proportions (right panel), where monthly catch is scaled to sum to unity for each coastal area

2. 4. 3. 6. Habitat utilisation

All size classes of sharks were caught within the primary nursery Areas 10 to 13. To investigate the possibility that size classes within the nursery area were segregated by habitat type, mean (TL) of catches between areas of sandy beach and rocky reef in Areas 12 and 13 were compared. Fig. 2.14 is an aerial photo of the typical rocky reef formation that is found extending from the shoreline. It is characterised by a system of long parallel reef structures separated by sandy gullies. The length frequency distribution of catches made in each habitat is given in Fig. 2.15. Sub-adult and adult sharks dominated the catch from areas of sandy beach (53.1%), whereas catches in areas of rocky reef were comprised predominantly of YOY and juvenile sharks (86.92%). The mean length of sharks caught from areas of beach (1915mm) was statistically larger from those caught in areas of reef (1536mm) (t-test, $P < 0.05$). A contingency table ($P < 0.001$) indicated a significant relationship between size class and habitat.

Fig. 2.14. Aerial photo of long reef at Aston Bay (Area 13) typical of the rocky reef habitat utilised by YOY and juvenile *Carcharias taurus*

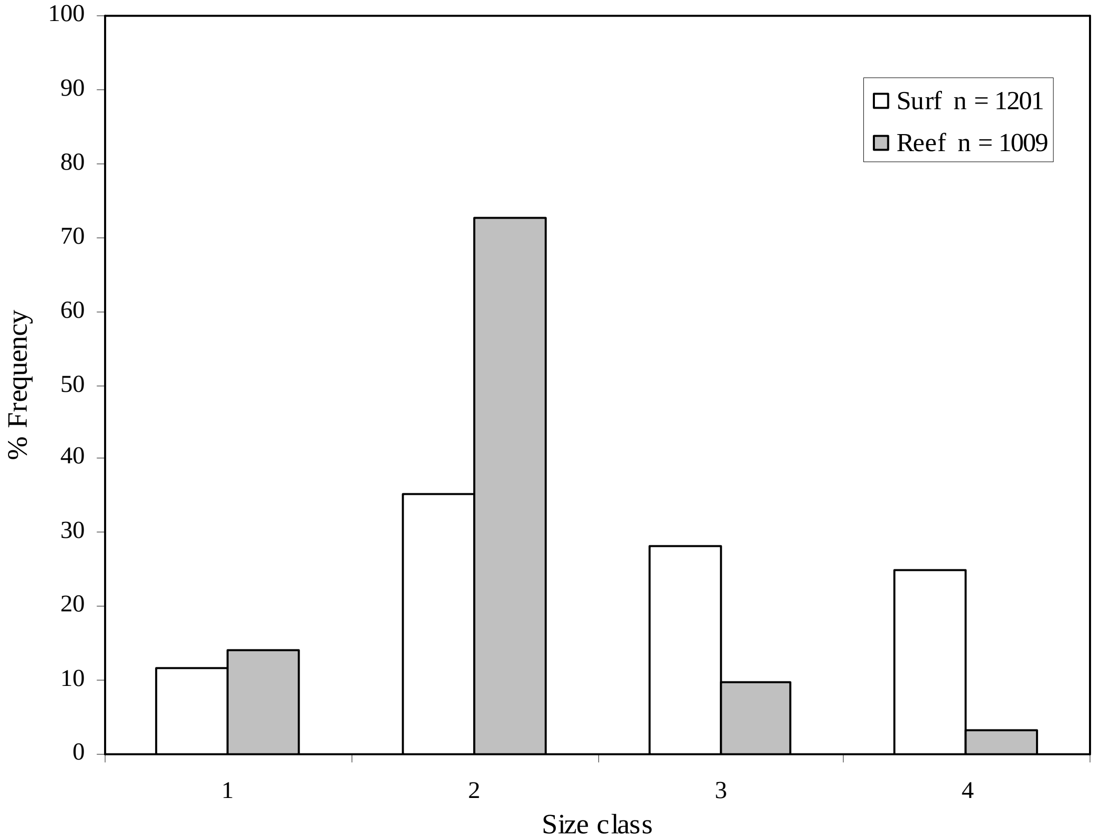


Fig. 2.15. A comparison in the size composition of *Carcharias taurus* caught from areas of sandy beach and rocky reef in Areas 12 and 13

2. 4. 3. 7. Temporal catch trends

The Border Rock and Surf Angling Association (BRSAA) was the only fishing province from which a comprehensive record of competitive catches of *C. taurus* were available. A regression analysis of the temporal trend in the number of *C. taurus* caught showed a significant increase (Slope $P < 0.05$) over the period 1982 to 2003 (Fig. 2.16). The temporal distribution of competition effort has remained relatively constant over this time period, as has the format of the competitions, the number of competing anglers and the target species preference for elasmobranchs (Pradervand and Govender 2003). As such, the catch records can be used as a general index of relative abundance.

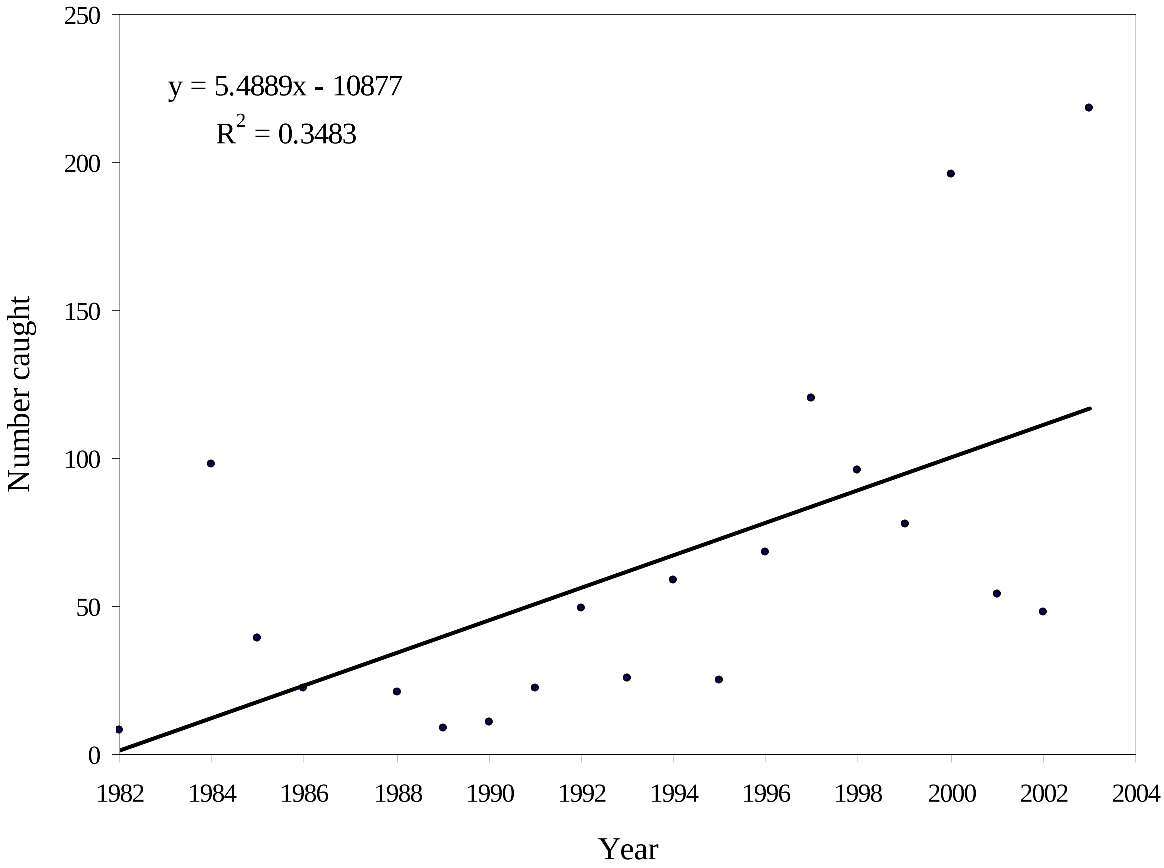


Fig. 2.16. Temporal trends in competition catches of *Carcharias taurus* from the Border Rock and Surf Angling Association (BRSAA) for the period 1982 to 2003

2. 5. Discussion

2. 5. 1. Telephone survey of competitive shore anglers

Estimates of total shark fishing effort and catch of *C. taurus* are dependent on a number of assumptions and biases. First, it was assumed that only club-anglers affiliated to coastal fishing provinces actively target sharks and catch *C. taurus*. Non-club anglers were excluded from the survey as previous studies (Van der Elst 1989, Taylor 1993, Brouwer and Buxton 2002, Pradervand and Govender 2003, Pradervand 2004) indicated that this component of the recreational fishery did not target sharks. On-site angler interviews in this study, however, indicated that 14% of club anglers had targeted shark species before they had joined a club. Unfortunately, there are no accurate figures available on the number of non-club recreational anglers in South Africa. Van der Elst (1989) suggested that were about 288,000 shore anglers in 1987. Bennett (1991) extrapolated these figures by assuming a 6% annual growth rate and estimated that the number had risen to 380,000 individuals by 1991, and would probably reach 1 million by 2010. Even if a small percentage of these non-club anglers actively target shark species, the total shark fishing effort and catch of *C. taurus* estimated in this study will be grossly underestimated. Club anglers registered to the five-inland provinces were excluded from the survey, as they rarely fish at the coast. These anglers did target sharks, however, in one or two coastal competitions every year. Their exclusion from the survey, together with non-club anglers, will also result in an underestimate of effort and catch.

Second, it must be assumed that anglers correctly recalled the number of days they had fished for sharks, where they had fished, and the number of *C. taurus* they had caught within each month of the three-month recall period. Despite the recall period being less than the six months recommended by Westat (1989), anglers may have incorrectly assigned trips to the wrong time interval or confused fishing trips for teleost species with those for elasmobranchs. Fishers are also more likely to remember the more memorable trips, when large catches were made, than trips when no fish were caught (Pollock *et al.* 1994). It is expected that this recall bias and possibly prestige bias (exaggeration of catch size or rate) would cause the anglers interviewed to overestimate their catch rate.

Third, CPUE was calculated as shark.angler^{-1}.day^{-1}. An angler day was defined as any outing that was specifically directed towards catching sharks. Consequently, no differentiation was made between a two-hour and a twelve-hour fishing trip. The average time anglers had spent fishing for their "*last C. taurus*", however, was seven hours. As a result, shark.angler^{-1}.day^{-1} was an appropriate unit of measurement and would have resulted in little bias as a result of large variances in the duration of fishing trips.

The fourth assumption was that *C. taurus* was only caught when anglers were specifically targeting it, or other elasmobranch species. The majority (71.0%) of anglers interviewed when asked about the "last *C. taurus*" they had caught had been fishing for sharks, however, 11.4% had been targeting teleost species. The fact that *C. taurus* can be caught accidentally when not fishing for sharks suggests that it will be caught by some non-club anglers. If this assumption fails, estimates of the total catch in this survey will be underestimated.

The total estimated annual shore fishing effort for sharks along the east coast of South Africa (37, 820 days.year^{-1}) was two orders of magnitude lower than the total effort for all species (3,204,172 days.year^{-1}) estimated from a roving creel survey of all recreational shore anglers by Brouwer *et al.* (1997) and Mann *et al.* (2003). Estimates from the surveys are not comparable, however, due to differences in sampling method, target species and sampling frame. This study provides the first estimates for recreational shark fishing effort in South Africa. Despite the biases, already outlined, these estimates provide an important reference against which future estimates can be compared.

Taylor (1993) stated that club anglers rarely fished for sharks outside of competitions. Club anglers interviewed in this survey, however, fished for sharks not only in club competitions for points, but also socially for practice and enjoyment. In fact, 70% of all shark fishing effort was outside of recognised club competitions. The spatial distribution of shark fishing effort varied along the coast. The greatest effort was generally recorded in the most populous areas, where the majority of clubs and competitions were located. Consequently, the greatest shark-fishing effort was recorded in KwaZulu-Natal (Areas 4 to 6), the Eastern Cape (Areas 10 and 13) and the Western Cape (Area 20). Club-anglers, particularly from KwaZulu-Natal, Border and the Eastern Cape, travelled to the Transkei coast (Areas 7 and 8) to specifically target shark species. As a result, shark-fishing effort in this region was surprisingly high, despite being relatively inaccessible and underdeveloped. Anglers in Zululand and KwaZulu-Natal (Areas 1 to 6) fished throughout the year. Fishing effort elsewhere along the coast (Areas 7 to 20) was limited to the summer months between September and May, due to unfavourable weather and sea conditions in the winter.

CPUE was higher in competitions when compared to social fishing. This result was not surprising since anglers fish much harder during competitions for points than socially for relaxation and entertainment. Comparisons in CPUE revealed distinct regional variations in abundance along the coast as well as clear evidence of size structuring. Abundance was highest between Areas 10 and 13 and decreased progressively both up and down the coast. This pattern reflected the high abundance of YOY and juvenile sharks in these areas. The spatial and seasonal distribution of the *C. taurus* population will be discussed in more detail in the following sections.

Accepting the assumptions already outlined the total annual catch of *C. taurus* was estimated to be 1764 (95% C.I. = 321 – 3207). The majority (60%) were caught between Areas 10 and 13, reflecting the high CPUE and fishing effort in these areas. The uncertainty in the estimate of total catch was due to the large variations in fishing effort and catch amongst individual anglers. Fishing effort ranged from 0 to 130 days.year^{-1}, whereas the number of *C. taurus* that interviewed anglers caught ranged from 0 to 33. Hilborn (1985) highlighted the large variation in fishing effort amongst anglers within the recreational sport fishery and that a few avid fishermen caught a disproportionate amount of the total catch. Similarly, Taylor (1993) stated that up to 80% of fish caught in competitions are by only a few top anglers. The results from this survey presented a similar picture, most notably in the Eastern Cape and Border where, 21% and 36% of the anglers interviewed caught 76% and 79% of all *C. taurus* recorded, respectively.

2. 5. 2. On-site survey of competitive shore anglers

Competitive club angling is a white-male dominated sport; only two of the 477 anglers interviewed were female and none were black. There were marked regional variations in the number of *C. taurus* caught. The majority of anglers (56.3%) from Zululand and Kwazulu-Natal had never caught a *C. taurus*, whereas many of the anglers from Border (31.5%) and the Eastern Cape (39.5%) had caught more than 50. Angler responses reflected the regional variations in CPUE and provide further evidence that the highest abundance of *C. taurus* is located within Areas 10 to 13.

Anglers that had caught at least one *C. taurus* were asked a series of questions relating to the "last *C. taurus*" they had caught. Most anglers from all fishing provinces, with the exception of the Southern Cape (Area 15 and 16) and Western Province (Area 20), had been specifically targeting this species when they had caught their last one. Anglers in the Southern Cape and Western province had been targeting other species. A possible explanation is that *C. taurus* is not commonly caught in these areas and, as a result, is not targeted. The fact that it is still caught as a bycatch using a variety of bait types (n = 32) reflects the opportunistic feeding behaviour of this species.

Almost all anglers (98.8%) agreed that *C. taurus* should be returned alive to the sea once it had been caught. Interview responses, however, to a series of questions related to the capture, handling and the condition of the shark on release, suggested that some of the sharks would suffer post-release mortality. The system of scoring that was developed in this survey, which assigned a certain number of "mortality points", to varying fishing and weighing practices was a subjective process. As a result, the post-release mortality rates may be subject to bias. Despite this fact, some interesting trends were observed. Post-release mortality rates increased progressively with the size of the shark. Larger adult sharks are "played" for longer periods than juvenile or YOY sharks. They may be "played" for up to two-hours. The longer a shark is "played", the greater are the effects of stress and fatigue (Skomal and Chase 2002). At some point, these effects reach a critical level after which the shark is unable to recover. In order to land a large shark quickly, it may be more efficient to use a gaff. It is important that the shark is gaffed away from its eyes, snout, gills and vital body organs. Unfortunately (20%) of the anglers interviewed had gaffed their "last *C. taurus*" within these sensitive areas, which could result in increased post-release mortality.

The time it took to return a shark to the water once it had been caught increased with the size of the shark. Most adult sharks (76.9%) were left on the beach for more than ten minutes, while scales, stretchers and other equipment were assembled to weigh the shark for competition points. What a tired fish requires most is oxygen and it is imperative that it be returned to the water as soon as possible. The SASAA has recently become aware of this issue and is currently in the process of changing the weight-based competition scoring system to a length-based system for any sharks over 5 kg.

Past studies of post-release mortality (Nuhfer and Alexander 1992, Matlock *et al.* 1993, Muoneke and Childress 1994) have shown that the single most important factor in catch and release survival is the location of the hook wound in the fish. Deep hooking in the stomach, throat, or gills causes the highest death rates, compared to hooking in the snout, upper jaw and cheek. The results from this survey indicated that only 12.3% of the “last *C. taurus*” that anglers had caught had swallowed the hook. Field observations suggested that most anglers, rather than trying to remove the hook, simply cut the trace leaving the hook in place. This practice has been shown to reduce the mortality rate by over 80% in rainbow trout (Klein 1965). Swallowed hooks may rust inside fish, leading to infection and poisoning, or tear the visceral tissue of the oesophagus and stomach (Steeger *et al.* 1994, Aalbers *et al.* 2004, Lindsay *et al.* 2004). J. Visser (International Marine Exhibits, pers. comm.), however, has observed up to 50 hooks on the bottom of tanks containing groups of 20 to 30 *C. taurus*. This suggests that swallowed hooks are often regurgitated and cause few long-term effects. Hook wound infection is markedly reduced in cooler water (Schramm *et al.* 1987). Most *C. taurus* (79.5 %) were caught in water less than 18˚ C and, consequently, hooking mortality from infections was expected to be minimal.

Anglers who actively targeted and caught large numbers of *C. taurus* possessed a remarkable degree of Local Ecological Knowledge (LEK) on the seasonal location, abundance and fishing conditions for *C. taurus*. This species was most commonly caught in dirty water, after a sudden drop in water temperature. These environmental conditions are typical of upwelling events common within the south coast zone (Brink

1983). It is possible that *C. taurus* is moving closer inshore during these periods to feed on non-cartilaginous fish species that may have become sluggish from a sudden drop in water temperature (Hanekom *et al.* 1989). The dirty water would also confer a competitive advantage for ambushing prey.

The majority of anglers (76.7%) believed that the population of *C. taurus* had remained relatively stable or had even increased over the last two decades. This opinion is supported by a significant increase in the number of *C. taurus* caught in angling competitions in the Border fishing province (Areas 9 and 10) from 1984 to 2004. Further evidence of a healthy resource is provided by the consistent CPUE and the mean size of *C. taurus* caught in the bather protection nets over the last twenty years (Dudley 2002, Dudley and Simpfendorfer in press). A small but significant decline in the mean size of female maturity and size at pregnancy, however, was observed from catches in the nets (Dudley 2002).

The major change in the shore angling fishery over the last two decades was the banning of vehicles on beaches in 2001. As a result of the ban, anglers were unable to access the best shark fishing spots, or carry the heavy tackle necessary to weigh sharks. In response, many of the anglers interviewed (49.0%) had switched from targeting sharks to smaller non-cartilaginous species. These species require lighter fishing tackle and can be fished from more readily accessible areas. This shift in target preference will place additional pressure on many of South Africa's non-cartilaginous reef fish species, which are already considered to be under pressure (Mann 2000).

2. 5. 3. Spatial distribution patterns inferred from competitive catch records

2. 5. 3. 1. Nursery areas

Catch records from the competitive shore angling fishery indicated that the Eastern and Western Capes were nursery areas for YOY and juvenile *C. taurus* and confirmed the findings of both Bass (1975) and Smale (2002). The distribution of sharks within the nursery areas was not homogenous, with 93% of YOY sharks and 89% of juvenile sharks caught between Areas 10 and 13. Variation in abundance is most probably the result of sea temperature, which is considered to be the most important factor governing the distribution of fish populations along the South African coast (van der Elst 1989, Turpie *et al.* 2000). Juvenile sharks ranged over a broader area than YOY sharks. This range extension may be as a result of a greater tolerance to temperature variations or an increased choice in habitat utilisation due to a reduced risk of predation.

Previous research has suggested that the primary characteristics of a nursery area are predator avoidance (Holland *et al.* 1993, Morrissey and Gruber 1993, Merson and Pratt 2001 and Heupel and Hueter 2002) and an abundant food source (Branstetter 1990, Castro 1993, Simpfendorfer and Milward 1993). Although there is no evidence of predation on smaller con-specifics, other elasmobranchs become increasingly important in the diet of larger *C. taurus* (Bass *et al.* 1975 and Gelsleichter *et al.* 1999, Smale 2005). Other potential predators that are known to inhabit the nursery region are the white shark (*Carcharodon carcharias*), bull shark (*Carcharhinus leucas*), dusky shark (*C. obscurus*), bronze whaler shark (*C. brachyurus*) and spotted sevengill cow shark (*Notorynchus cepedianus*). YOY and juvenile sharks were typically caught by anglers in areas of high profile reef. In contrast, sub-adult and adult sharks comprised less than 13% of shore angling catches in these areas. These results may be biased by the greater likelihood of losing larger sharks in areas of reef, but suggest that rocky reef areas may provide safety from larger sharks by access restriction (Springer 1967, Branstetter 1990, Castro 1993).

The sex ratio of YOY and juvenile sharks (77 males to 116 females) was similar to the sex ratio obtained by Smale (2002). In contrast to the results of this study, Merson and Pratt (2001) in a study of juvenile sandbar sharks (*C. plumbeus*) reported an almost equal male to female sex ratio. It is not uncommon while fishing for *C. taurus* to catch more than five in quick succession. This observation doesn’t explain whether the animals are moving together or are simply drawn to the bait in a relatively confined area. Aggregation behaviour, however, may have biased the sample sex ratio.

YOY sharks appeared in the nursery areas at the end of September, with the greatest numbers caught (76%) between November and February. The increase in the number of YOY sharks coincided with an increased catch of mature sharks, many of them females (76%). There were no apparent regional variations in the arrival of female sharks or the onset of pupping within the nursery areas. This was surprising, considering the differences in the distances migratory pregnant females had to travel from their gestation grounds in northern KwaZulu-Natal to pup in Areas 10 to 20. The earliest catches of juvenile sharks coincided with the appearance of YOY sharks, when the water temperature typically ranged between 18˚ C and 22˚ C. The latest both size classes were encountered was May, when the water temperature dropped to between 15˚ C and 18˚ C. These observations are consistent with other studies (Castro 1993, Merson and Pratt 2001) suggesting that water temperature is the cue to the onset and conclusion of the *C. taurus* pupping and summer nursery season.

In temperate zones, cold winter temperatures force YOY and juvenile sharks into deeper offshore or warmer water (Castro 1993). In the northwestern Atlantic juvenile *C. taurus* occupy summer nurseries from North Carolina to Cape Cod and winter nurseries in the warmer waters between North Carolina and northern Florida (Gilmore *et al.* 1983, Gilmore 1993). Anglers caught few YOY or juvenile sharks anywhere along the entire east coast of South Africa between May and August. The location of the winter nursery areas remains uncertain. During the winter it is possible that juvenile sharks move into deeper offshore water. Alternately, they may move northwards towards the Transkei coast situated between the Eastern Cape and KwaZulu-Natal. This area of coast, however, is rarely dived or fished, due to its inaccessibility and often-poor diving conditions.

2. 5. 3. 2. Adult population

Adult *C. taurus* were found along the entire east coast of South Africa from Kosi Bay (Area 1), in northern KwaZulu-Natal, to Bontkop (Area 21), on the west coast. Its distribution west of Cape Point, however, is a rare and anomalous occurrence, effectively signalling its most southern range. Sub-adult sharks had a slightly reduced geographical range, and were rarely recorded north of the Tugela River (Area 3). The seasonal occurrence of adult sharks along the coast is related to a breeding migration of predominantly female sharks (Bass *et al.* 1975, Cliff 1989, unpub.) This migration is well defined and can be traced through the spatially and seasonally distinct phases of mating, gestating and parturition.

Previous studies based on catches from the bather protection nets of the NSB (Bass *et al.* 1975, Cliff 1989, unpub.) postulated that mating takes place off the south coast of KwaZulu-Natal (Areas 4 and 6) between October and December. Aggregations of male and female *C. taurus* are commonly observed by divers at Aliwal shoal (Area 5) from July to October. Most of the sharks are mature or maturing males (57%), and many of the females display mating scars (Allen and Peddemors 2000). The predominance of male sharks (64%) in shore angling catches suggested male aggregations during the same time periods in Areas 7 and 8. Anglers reported catching mature female sharks with characteristic pre-copulatory scarring on their flanks as far south as Coffee Bay (Area 8). These observations suggest that mating takes place not only earlier in the year than previously believed, but also over a broader geographical range. The seasonal timing of mating is similar to that observed in the northwestern Atlantic (Gilmore 1993). In the southwestern Atlantic, however, mating has been reported to occur during the summer, in much cooler water between 12˚ C and 16˚ C (Lucifora *et al.* 2002). The male to female sex ratio during the mating season in the southwestern Atlantic was 2:1 (Lucifora *et al.* 2002). The lower sex ratio observed in this survey and that of Allen and Peddemors (2000) suggests a much lower level of male competition for females in South Africa.

Catch records confirm the findings of Wallet (1973) and Bass *et al.* (1975) that pregnant females move northwards after mating, into the warmer waters of northern KwaZulu-Natal to gestate. A similar movement northwards to gestate has been observed in the southwestern Atlantic (Lucifora *et al.* 2002). In the northwestern Atlantic, however, the mating and gestating areas coincide (Gilmore 1993). Cliff (NSB, pers. comm.) suggested that hydroid growth (*Amphisbetia operculata* and *Plumularia* spp.) on the teeth of gestating females was evidence that they were not feeding. Contrary evidence is provided, however, from 125 shore angling catch records, which clearly indicate many of the gestating sharks are feeding.

Catch records also indicate that gestating females begin to migrate southwards in March, towards the Eastern and Western Cape nursery areas to pup. Wallet (1973) and Bass *et al.* (1975) stated that during the months of June to August most of the female sharks that were caught in the bather protection nets were pregnant and carrying two full-term embryos. In the southwestern Atlantic, however parturition is believed to occur in the same warm subtropical waters as the gestation grounds in southern Brazil (Lucifora *et al*. 2002). The presence of pregnant females in Areas 1 and 2 between November and March and mature, but non-pregnant females at the same time of year in Areas 10 to 13 provides direct evidence of a biennial reproductive cycle as proposed by Cliff (1989, unpub.). A biennial cycle has also been proposed for *C. taurus* in the northwestern Atlantic (Branstetter and Musick 1994) and the southwestern Atlantic (Lucifora *et al.* 2002).

The whereabouts and movement patterns of mature males outside of the mating season remains uncertain. Wallet (1973) and Bass *et al.* (1975) believed that males reside in northern KwaZulu-Natal and southern Mozambique, but the results from this survey do not support this hypothesis. Gilmore (1993) suggested that male sharks, in the northwestern Atlantic inhabit deeper offshore water outside of the mating season. A similar hypothesis has been proposed for male sharks in the southwestern Atlantic (Lucifora *et al.* 2002) and in Australia (Otway and Parker 2000). Approximately half (51%) of the sub-adult and adult sharks caught by anglers in Areas 9 and 10, during the pupping season were males, compared to only 20% in Area 13. These catch records suggest that male sharks may move south after mating into the northern part of the juvenile nursery area. Mature male sharks have also been shown to occupy part of the nursery area off the East coast of America (Gilmore 1993).

Chapter 3

A survey of the inshore boat-based line fishery comprising of recreational light tackle boat, ski boat anglers and the commercial handline fishery

3. 1. Introduction

The South African inshore boat-based linefishery is comprised of commercial linefish, and recreational ski boat and light tackle boat components. Light tackle boats (LTB) are small, partly decked craft with one engine and as such are limited to a distance of 1 nm from the shore. These anglers typically operate in estuaries and rivers and fish with a 4 kg breaking strain line (van der Elst 1989). Recreational ski-boats are larger wet-deck craft, 4.5 to 8 m long, and are powered by twin outboard engines and operate anywhere from the surf line to a distance of 40 nm from the shore (Smale and Buxton 1985). Commercial line fishing, by comparison, is less simple to categorise because it is conducted from a wide variety of vessels and by a diverse spectrum of fishermen. Firstly, there are large company owned fully decked boats that operate at sea for 1 to 7 days and manned traditionally by a crew of 15 to 20 professional fishermen. Secondly, there are smaller privately owned ski boats used on a daily basis by fishermen who fish to supplement existing incomes (Smale and Buxton 1985).

These fishery sectors do not actively target shark species and have almost no catch records for *C. taurus*. Data from these boat-based fisheries are important, however, as they provide information on the spatial distribution of *C. taurus* in deeper offshore areas that are not fished by shore anglers. Although catches of *C. taurus* are rarely recorded, anglers within this fishery have a unique Local Ecological Knowledge (LEK) on the seasonal occurrence of this species in the areas they fish. This information has been accumulated over years, decades or even generations while fishing for other species of fish. The primary objectives of this survey were to; (1) provide additional information on the spatial and seasonal distribution pattern of *C.*

taurus and information on any tag recaptures in areas that are not fished by the shore-angling fishery and (2) to obtain an estimate of fishing mortality within these fisheries.

3. 2. Material and methods

Light tackle boat clubs are affiliated to the South African Light Tackle Boat Association (SALTBA) and 75% of recreational ski boat clubs to the South African Deep Sea Angling Association (SADSAA) (van der Elst 1989). All commercially licensed boats are registered with Marine and Coastal Management (MCM) and, in most cases, associated to a regional commercial forum. A list of affiliated clubs and commercial forums were obtained from each of the relevant organisations and used as the sampling frames for telephone surveys which were conducted from September 2002 to March 2003. This information was supplemented with additional data obtained through key informant interviews with fishermen who were deemed to be the most knowledgeable and willing to provide information.

The chairperson of each of the coastal clubs registered to SALTBA and SADSAA and the chairperson of each commercial linefish forum were sent an introductory letter describing the purpose of the survey and asking their co-operation in the collection of information related to the catch and distribution of *C. taurus*. Only coastal affiliated clubs were contacted as anglers within these clubs were considered to have a superior LEK compared to inland anglers who only occasionally fish at the coast. A follow-up phone call was made a few days after the letter had been posted, introducing myself, and assessing the willingness of the club to participate in the survey. Each chairperson was asked to discuss the survey at their next club or association meeting to obtain information on the areas that their anglers fished and any catches of *C. taurus*. If any *C. taurus* were caught, the club anglers were asked to provide information on the size and seasonal timing of the catches, the fate of the catch (released alive or dead) and whether or not any of the sharks that were caught had been tagged. Clubs that were willing to participate in the survey were contacted a month later to collect the information they had gathered from their members.

Key informant interviews were conducted with “local experts” previously identified by each of the clubs. These anglers were posted a South African Navy (SAN) chart of the area that they commonly fished and had knowledge of, and asked to mark on the chart, in detail, the areas that they fished together with any catch details of *C. taurus*. Interviews with these anglers were deliberately “open[1]” in an attempt to solicit as much information as possible.

3. 3. Results and discussion

3. 3. 1. Light tackle boat

Of the 34 LTB clubs contacted, *C. taurus* were only caught by clubs registered to Border and the Eastern Province. Anglers in these two fishing provinces operate in local estuaries and an area approximately 5 km north and south to a distance of 1 nm, from the East London and Port Elizabeth harbours, respectively. The estuaries were all small shallow systems open to the sea. *C. taurus* were only actively targeted by anglers during club competitions which are held three to four times a year. Outside of competitions, anglers stated they fished almost exclusively for non-cartilaginous species. Competition catch records for the last 10 years were unavailable for either fishing province. However, on average less than five *C. taurus* are caught in bay and estuarine competitions held by Border (M. Arentsen, chairperson LTB Border, pers. comm.) and less than ten in the Eastern Province (J. Beukes, chairperson LTB Eastern Province, pers. comm.). Although LTB anglers practice a catch and release ethic, it is common practice by the majority of anglers to “subdue” the sharks that they catch before they are brought aboard the boat to be weighed. As a result, the mortality rate of released sharks is probably high.

A list of all the estuaries fished by LTB anglers that were interviewed and those in which *C. taurus* had been recorded is given in Fig. 3.1. Anglers stated that *C. taurus* were most commonly caught in the Kariega and Kromme estuaries in the summer months from December to March, ranging in size from 5 to 30 kg. Catches in the other estuaries were infrequent. In all of the estuaries that were fished, anglers

[1] The term “open” refers to an informal interview, not structured by a standard list of questions.

reported catching the majority of sharks at the mouth, but catches were recorded as far as 3 km from the mouth of the Gonubie estuary and 4 km from the mouth of the Knysna estuary. Estuaries are known to be an important component of the nursery habitat for C. *taurus* off the east coast of America, due to the abundance of food and reduced predatory pressures (Gilmore 1993). Estuaries in South Africa, however, are typically smaller and shallower. Although *C. taurus* was caught by LTB anglers in 11 of the 30 estuarine rivers that they fished, they were only regularly caught in the Kariega and Kromme rivers. Paterson and Whitfield (2000) estimated that juvenile *C. taurus* comprised 2.3% of the channel ichthyofauna in the Kariega river, but was absent from the shallower eelgrass and creek areas of the estuary. Little research has been conducted on the role of estuarine systems as a refuge for juvenile sharks in South Africa. The results from this survey suggest that estuarine systems, although utilised by YOY and juvenile *C. taurus* do not form an important component of the nursery area habitat in South Africa.

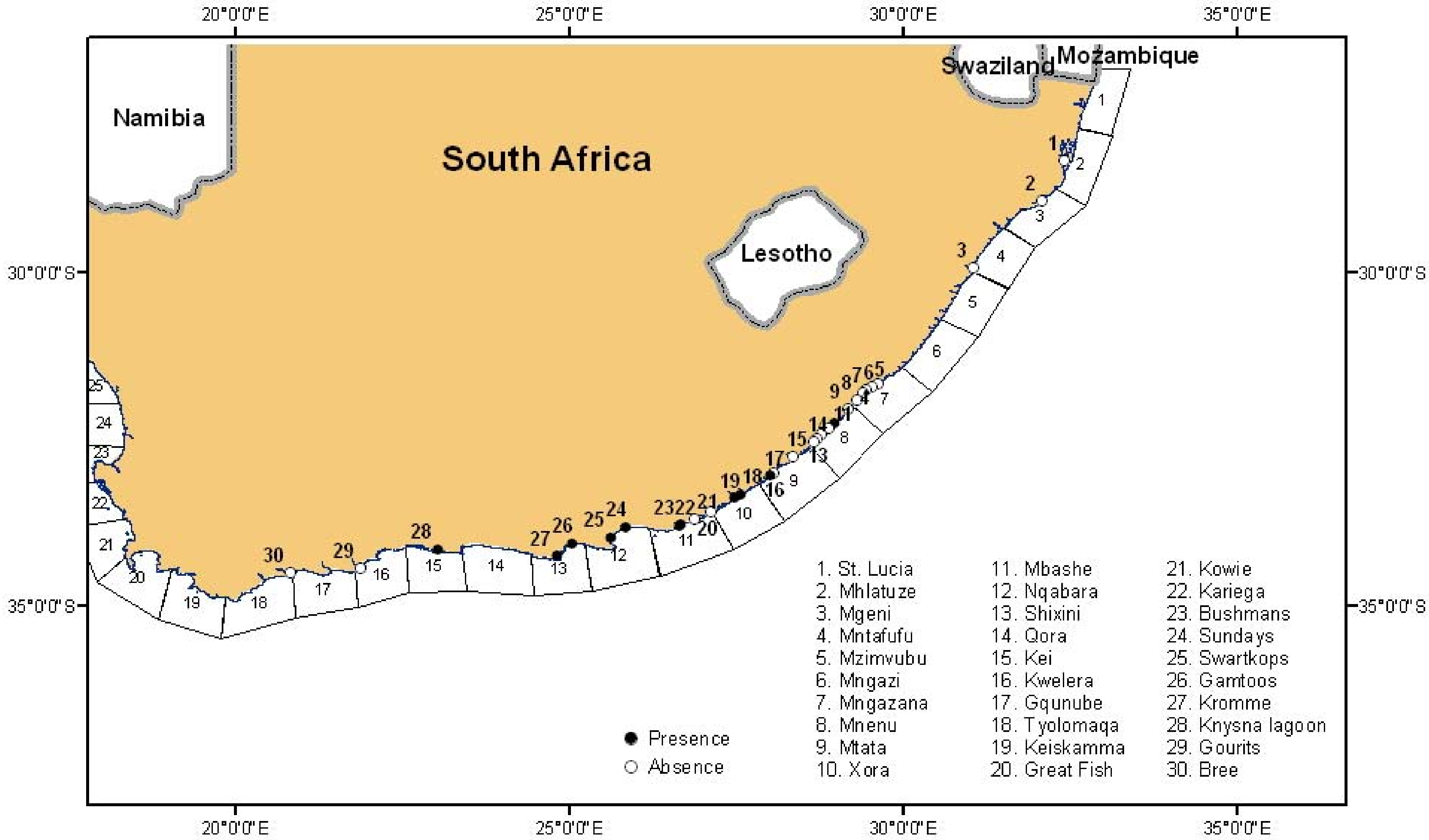


Fig. 3.1. Map of South Africa showing the location of the 30 estuarine rivers fished by light tackle boat anglers. Symbols indicate those rivers in which *Carcharias taurus* is caught

3. 3. 2. Ski Boat and commercial handline

A total of 75 coastal ski boat clubs and 25 commercial Linefish operators were contacted, of which only 33 and 15, respectively, were willing to supply a list of fishing co-ordinates and catch information. A possible explanation for this poor response rate may have been due to a combination of factors. Firstly, fishermen are often reluctant to reveal their “best kept” fishing spots. Secondly, since the banning of vehicles on beaches in December 2001, many boat-launching sites have been closed, which has resulted in a feeling of animosity to the scientific community. Thirdly, the widely held perception of many anglers that the catch information they supply will eventually be used as a tool against them to place further restrictions on catch quotas.

In all, 1095 fishing co-ordinates were collected in the survey from Areas 1 to 23. However, *C. taurus* was only recorded at 209 of the sites from Areas 2 to 18, and of these most catches were made at only a few specific reefs. *C. taurus* were most commonly caught at depths between 20 to 40 m, although catches were reported as deep as 80 m, while fishing for hake (*Merluccius capensis*) in Areas 15 and 16. None of the anglers interviewed specifically targeted shark species. Any *C. taurus* that were caught, were accidentally taken while targeting non-cartilaginous fish species, most notably geelbek (*Atractoscion aequidens*), in Areas 2 to 7, kob (*Argyrosomus* spp.) and yellowtail (*Seriola lalandi*) in Areas 8 to 13, and kob and hake in Areas 15 to 18. Prey density may be a cue for habitat choice, particularly for the sub-adult and adult life history stages. Silvester (1977) suggested that the northward movement of C. *taurus* in Australia might be linked to the migration of grey mullet (*Mugil cephalus*). In South Africa, geelbek, yellowtail and other predatory species migrate northwards from the Cape to KwaZulu-Natal in winter with the sardine run. The sardine run is an annual phenomenon that takes place between the months of June and August. Sardines (*Sardinops sagax*) extend their geographical distribution from the west coast up the east coast in response to decreasing water temperatures (Armstrong 1991). Anglers, particularly in Areas 6 to 9, reported increased catches of *C. taurus* associated with the sardine run. The breeding migration of *C. taurus* along the coast is not intrinsically associated with the movement of sardines, however, they are likely to affect spatial distribution patterns on a smaller scale.

YOY sharks were not recorded by boat anglers at any of the deeper reefs they fished. This suggests they are segregated from the rest of the population within their nursery areas by depth. The spatial and seasonal distributions of catches of the other three size classes were similar to those recorded by the shore-angling fishery (Fig. 3.2). Despite a similar seasonal catch pattern, these results may be biased by a greater fishing effort in the summer months, mainly due to more favourable weather conditions. There is also a seasonal change in target species by recreational anglers in Areas 3 to 6. In the summer months, anglers tend to use lures and target game fish species such as king mackerel (*Scomberomorus commerson*). In the winter, baited hooks are used to catch bottom feeding reef fish such as red steenbras (*Petrus rupestris*). Clearly, the bottom fishing techniques in winter have a much greater chance of catching *C. taurus* than mid-water trolling in the summer.

All of the recreational fishermen interviewed stated that they preferred to "cut the line" and release any *C. taurus* that had been accidentally caught rather than try to land them on the boat. In contrast, commercial fishermen admitted that *C. taurus* were regarded as an unwanted pest when fishing for more valuable non-cartilaginous fish species and on occasion would be killed rather than released alive. Despite the commercial ban on this species, and its poor market value (R2 - R3.kg^{-1}), interviewed anglers knew of fishers that actively targeted *C. taurus* to sell in order to supplement their income. The consensus among the interviewees was that this trend was increasing as a direct response to the reduction of allocated Linefish licences in 2004. There is no way to accurately calculate these aspects of fishing mortality, however, from key informant interviews the best estimates are presented in Table 3.1. These estimates are higher compared to the number killed in either the shore-angling fishery (n = 124, Chapter 2) or from captures in the bather protection nets of the NSB (n = 128), (Dudley 2002). Assuming that these estimates are correct, the boat based fishery, although not actively targeting *C. taurus*, represents the greatest source of fishing mortality to the population.

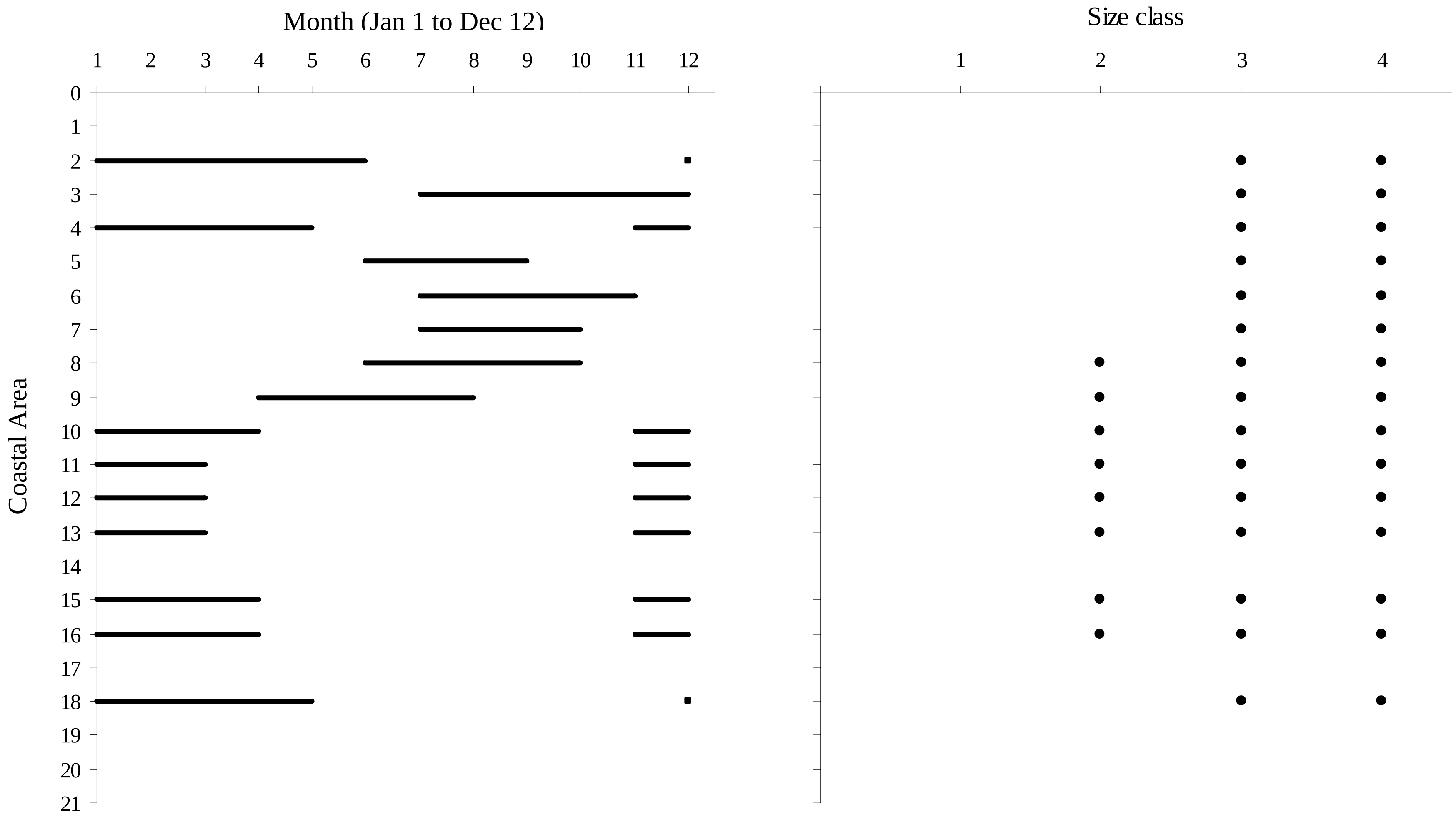


Fig. 3.2. Seasonal and spatial catch distribution of *Carcharias taurus* from the recreational ski boat and commercial linefish operators (left panel) and the size classes caught (right panel)

Table 3.1. The annual estimated numbers of *Carcharias taurus* that are killed by the commercial linefish industry

Area	Month	Number per month	Total
1 to 3	No information	-	-
4 to 6	June to September	15	180
7 to 11	No information	-	-
12 to 13	December to March	20	160
15 and 16	December to March	10	40
18	December to February	10	30

Interviewed anglers reported catching *C. taurus* at a number of reefs in Areas 4 to 6. This stretch of coast is protected by bather protection nets of the NSB and is an area in which shore anglers reported rarely catching *C. taurus*. Boat-based anglers reported incidental seasonal catches of *C. taurus* as high as two to three per day and up to 20 per night at some reefs in Algoa Bay (Area 12). Despite these high capture rates, only four anglers in Areas 3, 10 and 13 reported to have caught a tagged shark and none of them had been able to read the tag number or report the recapture to the relevant tagging organisation. One angler knew of a fisherman who had caught four tagged sharks in a day, in Area 13, and another who had caught three tagged sharks in Area 12, but again, none of these recaptures had been reported. Clearly, sharks that have been tagged by shore anglers, or released from the bather protection nets are moving into deeper waters that are fished by recreational and commercial ski boat fishermen. The high non-reporting rate evident in this fishery, however, hampers investigations into these offshore movement patterns. The development of educational and outreach programs has dramatically improved recovery percentages in other cooperative tagging programs (Pepperell 1990, Kohler *et al.* 1998). Such an approach might encourage the participation of anglers within the boat-based fishery in South Africa.

Chapter 4

A survey of spearfishers and scuba divers

4. 1. Introduction

There are estimated to be 7,000 participants in the spearfishing industry, of which approximately 900 are registered to clubs affiliated to the South African Spearfishing Federation (Mann *et al.* 1997). There are approximately 100 000 SCUBA divers in South Africa, and this number is increasing rapidly (Booth and Hecht 2000). In South Africa, SCUBA divers are qualified under three main bodies: (a) the National Association of Underwater Instructors (NAUI); (b) the Professional Association of Dive Instructors (PADI); and (c) the Confederation Mondial des Activites Subaquatiques (CMAS). Once qualified, most SCUBA divers dive with a local dive operator or club, which is affiliated to one of these organisational bodies. Some SCUBA diving and spearfishing clubs are also registered to the South African Underwater Union (SAUU), which was founded in 1964 to administer the network of spearfishing and diving clubs throughout the country.

Experience and knowledge of the marine environment is not equally distributed throughout the diving community. To fully utilise available knowledge, it is necessary to identify members of this community who are most well informed (Johnson 1990). It is reasonable to assume that SCUBA diving instructors working for a local club or operator and regularly dive throughout the year would have more knowledge than other less experienced divers who are only recently qualified, or only dive on rare occasions. It is perhaps more difficult to identify members of the spearfishing sector who would be the most knowledgeable. Spearfishing is physically much more challenging than SCUBA diving, requiring long breath holds, long swims and long periods of water exposure. Consequently, there is a marked difference in the skill and knowledge between the participants (Cook 1990). Using this divide in the spearfishing community, it is reasonably accurate to assume that spearfishers who are affiliated to a club are more active and hence fitter and better divers than non-club members. Based on these assumptions, it was concluded that to gain as much information as possible concerning sighting of *C. taurus*, qualified SCUBA diving instructors and club affiliated spearfishers would form the target population to be interviewed. Because members of this target population dive continually throughout the year, monthly shark sightings would not be greatly masked by differing seasonal diving activity. The central aim of this present survey was to obtain qualitative information on the location, frequency and seasonality of *C. taurus* in areas that are not fished by any sectors of the recreational or commercial fishery, and in areas they are not feeding. This is particularly true in regions such as northern KwaZulu-Natal, where it has been suggested, that pregnant females while gestating, stop eating and will not take a baited hook (Cliff 1989, unpub.).

4. 2. Material and methods

Between January and August 2003, 91 questionnaires (Appendix 4.1) were posted to all coastal SCUBA diving operators listed in the local “Divestyle” diving magazine (including 10 operators in Mozambique), together with a covering letter explaining the purpose of the study. Another 100 questionnaires were posted to SCUBA diving instructors and spearfishing clubs selected at random from lists supplied by PADI and the South African Spearfishing Federation, respectively. In the absence of postal addresses, an additional 231 questionnaires were also e-mailed to CMAS affiliated dive instructors. The questionnaire was designed to be easy to fill-out and to solicit information on the seasonal occurrence of *C. taurus* and sightings of any tagged sharks.

C. taurus is an easily identifiable shark and due to its docility, is highly sought after by many dive operators who advertise specific trips to dive with these sharks. As a result, divers regularly record their observations in logbooks, reducing the recall bias of sightings inherent in many surveys (Essig and Holliday 1991). In an attempt to improve the response rate of the mail survey, a telephone call was made to each of the dive clubs or divers before the questionnaire was posted, thanking them in advance for their co-operation and participation in the survey. Unfortunately, this protocol could not be followed for the CMAS divers, as the list of instructors that had been supplied didn't contain contact phone numbers. If the questionnaire hadn't been returned within a month, follow-up calls (or e-mails) were made once every month for a three-month period. The questionnaire was advertised on the South African Spearfishing website at www.spearfishingsa.co.za. A link to a more detailed questionnaire at http://fishwatch.tripod.com/raggie was also advertised at the top of each of the postal questionnaires.

Since spearfishers commonly cover large areas while diving, it was often impractical on the postal questionnaire for them to list specific dive sites, at which they had seen any *C. taurus*. To overcome this problem, and to obtain as much information as possible, South African Navy (SAN) charts were posted to spearfishers who were deemed to have the most knowledge. These experienced spearfishers were identified by members of their own club who had already filled out a postal questionnaire. Spearfishers were asked to mark on the charts the areas where they dived and to note *C. taurus* sighting. If any *C. taurus* had been observed, they were also asked to provide information on sizes and any tagged individuals. In some instances, respondents completed questionnaires containing information for the same reefs. Where the information differed slightly in the size or seasonality of shark sightings, an average of the recorded data was made and used as a single database entry.

4. 3. Results and discussion

A total of 124 (64.9%) of the 191 questionnaires that had been posted to SCUBA divers and spearfishers were returned. This response rate was markedly higher than the 16% obtained from a postal survey of KwaZulu-Natal spearfishers by Mann *et al.* (1997). The response rate, in this study, can be considered reasonable according to Brown (1991) who recommends a response rate of between 60% and 75% for surveys directed at a specific audience. Of the 231 questionnaires that were e-mailed to CMAS affiliated dive instructors, only 23 (10%) were returned. This poor response rate highlights the necessity and effectiveness of integrating the postal survey with a personal introduction and, if necessary, follow-up phone calls.

A total of 557 reef locations were recorded in the survey from Areas 1 to 28. Divers had observed C. *taurus* at 203 of the sites between Areas 1 and 20 (39.3%), and at only one site (Area 23) between Areas 21 and 28 (2.5%). These results provide further evidence that the distribution of *C. taurus* west of Cape Point is a rare and anomalous occurrence. Dive locations and sightings of *C. taurus* ranged in depth from 3 to 40 m. Divers sighted YOY sharks within Areas 10 to 20, inhabiting the same reefs as larger sub-adult and adult sharks. The YOY sharks were typically observed swimming at depths of between 5 and 10 m within protective rocky gullies and the larger sharks in deeper water on the outskirts of the reef. These observations suggest that depth may play an important role in the distribution of the different life history stages. As previously discussed in Chapter 2, YOY and juvenile sharks may be utilising shallow water reefs as a refuge from larger species of sharks. YOY and juvenile sharks are known to feed on species such as kob (Arg*yrosomus spp.*) and guitarfish (*Rhinobatus annulatus*), which are commonly found over sandy bottom substrates. A large proportion of their prey, however, consists of shallow reef dwelling species such as white musselcracker (*Sparodon durbanensis*), blue hottentot (*Pachymetopon aenum*) and twotone fingerfin (*Chirodactylus brachydactylus*) (Smale 2005). The distribution, and habitat utilisation of reef areas by YOY and juvenile sharks may reflect the abundance of these prey items.

The seasonal distribution of shark sightings within each coastal area (Fig. 4. 1) was based on the reef that the majority of interviewed divers had observed the greatest number of sharks. The distributional patterns and size classes of sharks observed were very similar to those inferred from catch records in the shore angling (Chapter 2) and inshore-boat based surveys (Chapter 3). Because shore anglers caught few YOY or juvenile sharks during the winter (Chapter 2) it was suggested that these life history stages might move into deeper offshore water in response to declining water temperatures. Although spearfishers and SCUBA divers were active throughout the year, they observed few of these sharks at any of the reefs they dived. The whereabouts of the winter nursery areas remains unknown.

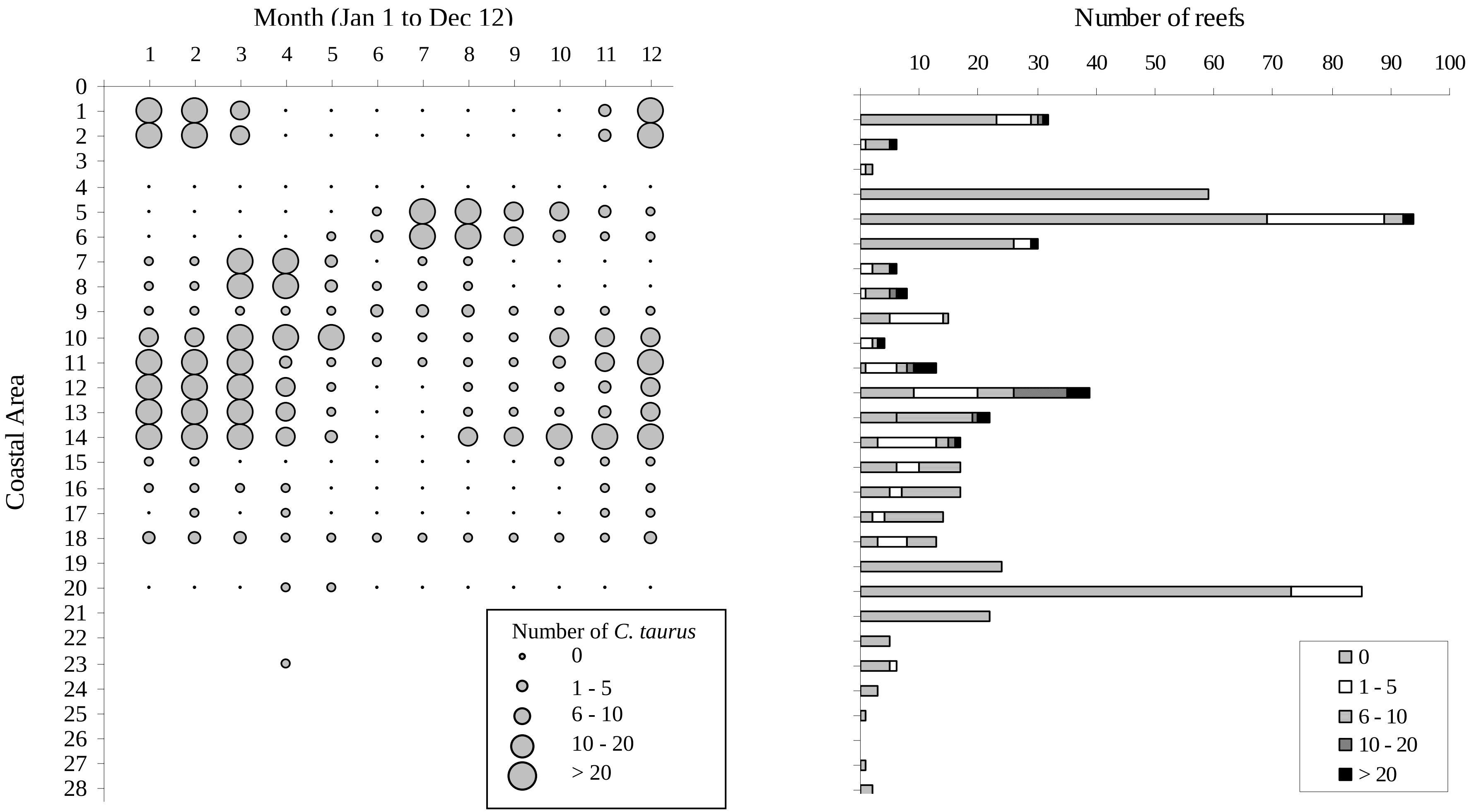


Fig. 4.1. Monthly sightings of *Carcharias taurus* at reefs in Areas 1 to 28 (left panel), and the maximum numbers of *Carcharias taurus* observed at all of the reefs recorded in the survey within each of the coastal areas (right panel)

Although *C. taurus* were observed at reefs from Areas 1 to 23, no more than five were ever sighted on reefs from Areas 19 to 23. In Areas 4 to 6, within which the bather protection nets of the NSB are deployed, *C. taurus* had never been observed at any of the 59 reefs dived in Area 4. They were seen at only 25 (26.6%) of the 94 reefs in Area 5 and at only 4 (13.3%) of the 30 reefs in Area 6. These observations suggest that the bather protection nets effectively prevent the utilization of inshore reefs. Sharks in these areas may be forced to utilise deeper offshore reefs such as Aliwal Shoal and Protea banks. Both these reefs are located more than 5 km offshore and were the only two sites in Areas 5 and 6 at which more than five sharks had been observed. These sites are thought to be important aggregation sites for breeding adults (Peddemors 1995, Allen and Peddemors 2000). Concern has been expressed in recent years, however, that aggregations at these sites are declining in response to increased diver pressure (Tienhoven, in prep). If this is the case, it may represent yet a further reduction in suitable habitat availability within Areas 4 to 6.

At 23 of the 32 (71.9%) reefs that interviewees had dived in Area 1 *C. taurus* was never seen, whereas at one site (Quatermile) over 20 sharks were commonly observed from December to March. Diver observations are biased by water clarity, the popularity of the dive site and seasonal effort. This pattern of reef preference, however, was evident at reefs along the entire coast. Why some reefs are chosen over others, despite similar physical characteristics, at this stage, remains unclear. The identification of aggregation sites, particularly those associated with the reproductive activities of mating, pupping and gestation are essential for effective fisheries management.

Tagged sharks were observed at only a few dive sites, and only the shape and colour, not the tag number were identifiable. As a result, these sightings provided little useful information on the identification of offshore movement patterns. This was not surprising as recreational divers are scientifically untrained, and concerned with matters other than data collection. Scientific monitoring of *C. taurus* over a wide geographical area and a long time period is financially and logistically unfeasible. The Local Ecological Knowledge (LEK) available from recreational SCUBA divers, although limited to simple observations, is a potentially valuable resource to marine science.

The survey results from dive operators in Mozambique were not included in the preceding sections because this thesis is concerned with the distribution of *C. taurus* along the South African coast, not the Southern African coast. For the sake of completeness and because South Africa and Mozambique share the same stock, a brief overview of the results are given in the following paragraph.

In Mozambique, divers had observed *C. taurus* at Ponta do Oura on the South African border and further North at Ponta Malogane, Inchaca Island, Inhambane and Bazaruto Island. *C. taurus* were observed infrequently and only in small groups comprising of one or two large individuals. These results were in stark contrast to observations made 30 years ago by Condon (1970) who reported seeing aggregations of up to 30 individuals in the vicinity of Inhaca Island. In the 1960's and 70's spearfishers were paid a bounty of 300 Escudos per shark and up to four sharks were shot every weekend around Inchaca Island alone (N. Gomez, ORI, pers. comm.). The results of this present survey suggest that the *C. taurus* population in Mozambique has been dramatically reduced over the last two to three decades. Wallet (1973) and Bass *et al.* (1975) believed that male sharks, outside of the mating season, reside in southern Mozambique. The results from this survey do not support this hypothesis.

Chapter 5

Movements, recapture patterns and the effect of tag type on the return rate of juvenile and adult *Carcharias taurus*

5. 1. Introduction

The first dedicated tagging programme of elasmobranchs off South Africa was initiated in 1964 by the Oceanographic Research Institute (ORI) to help devise protective measures against shark attack off the KwaZulu-Natal coast (Davies and Joubert 1966). In 1984, ORI initiated a cooperative tagging program reliant on the joint participation of scientists and volunteer recreational anglers. This program was designed to provide a logistically feasible means to obtain basic life history and population dynamics information on a variety of teleosts and elasmobranchs (van der Elst 1990). The program has been immensely popular, and by 2003 had a membership of 4,126 anglers (Bullen *et al.* 2004). In 1994, the Port Elizabeth Museum (PEM) initiated a considerably smaller cooperative tagging program consisting of between 10 and 20 volunteer anglers. This program focused on the collection of age and growth validation and movement patterns of sharks off the Eastern and Western Cape coasts.

Data collected from cooperative tagging programs can be used for a variety of purposes. It can be used to develop information on stock structure and movement patterns (van der Elst 1990, Pepperell 1990, Kohler *et al.* 1998) as well as providing information on abundance, survival and exploitation rates (Kohler and Turner 2001). This type of information is crucial in defining essential habitat and evaluating the effects of commercial and recreational exploitation and anthropogenic activities on endangered species. Despite the need for data derived from tagging studies, there have been few published results from the cooperative tagging programs in South Africa. Of the 46 species of sharks that have been tagged, recapture data has only been used to estimate the population size of the white shark *Carcharodon carcharias* (Cliff *et al.* 1996), movement patterns of the spotted seven gilled cow shark *Notorynchus* *cepedianus* (Ebert 1996) and mortality estimates for the dusky shark *Carcharhinus obscurus* (Govender and Birnie 1997).

Along with the benefits associated with a cooperative tagging program, there are also disadvantages (van der Elst 1990 and Kohler and Turner 2001). One of the problems inherent in the ORI program is the non-standardisation of tag use. Anglers have tagged *C. taurus* using a variety of different tag types, some of which are designed for use on fish < 3 kg. Another source of variability is in the different methods by which sharks are caught and tagged. In coastal Areas 1, 2 and 5, *C. taurus* are tagged predominantly underwater by scientific divers using Hawaiian slings. In Areas 3 to 6 they are caught and tagged in the bather protection nets of the NSB. While in the other areas along the coast, the majority are caught and tagged by shore anglers. Variability due to differences in tagger performance has also been identified as a potential source of error in which recreational fishers do the majority of tagging (van der Elst 1990).

This Chapter aims to assess the spatial and temporal movement patterns of C. *taurus* using tag recapture data from both the ORI and PEM collaborative tagging programs. Movement patterns were used to confirm the geographical extent and seasonal utilisation of nursery areas by juvenile sharks, inferred from catch records and observations collected in Chapters 2, 3 and 4. They were also used to investigate aspects of site fidelity, natal homing and the female reproductive migration. Recovery rates were used to compare the performance of the different tag types and capture methods used in the tagging programs as well as the variability in tagger performance.

5. 2. Materials and method

5. 2. 1. Tagging

Four different tag types, A, B, C and D-type tags have been used to tag *C. taurus* by members of the ORI cooperative tagging program (Fig. 5.1). Anglers in the PEM program, scientific divers and staff of the NSB have only tagged sharks with B-type tags. Some of these sharks were also injected with the antibiotic oxytetracycline as part of an age and growth validation experiment.

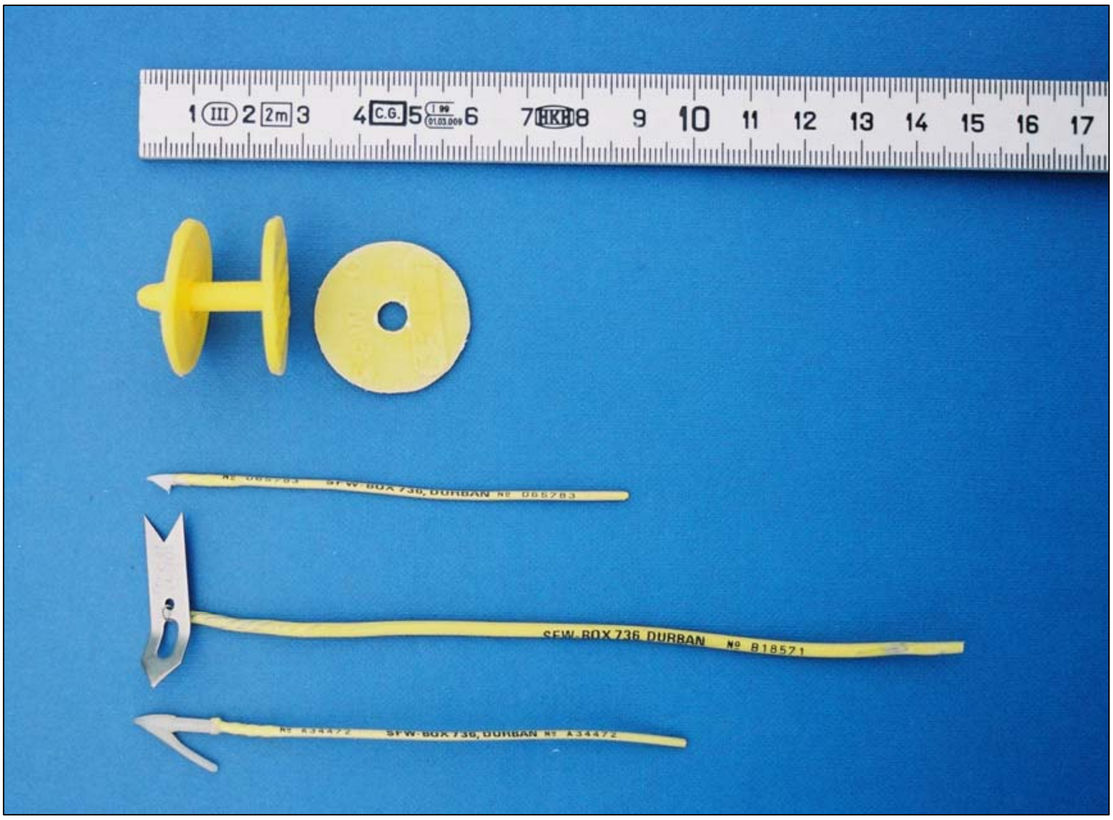


Fig. 5.1. From top to bottom, the four tag types, C, D, B and A used by members of the ORI and PEM cooperative tagging programs

A-type, B-type and D-type tags are Hallprint manufactured dart tags, and comprise of a monofilament vinyl streamer attached to either a plastic barb (type A and D) or stainless steel pointed head (type B). All pertinent tag information, including the tag number, return address and telephone number of the tagging program are printed on the streamer. Application of the tags is accomplished using a stainless steel tagging needle, which is used to drive the pointed head of the tag into the dorsal musculature at the base of the first dorsal fin. Once inserted, the tags are pulled gently to ensure that they are securely attached. If they have not been inserted correctly, they are reapplied. Taggers are instructed to apply the tag at an angle of approximately 45˚ so that the streamer lies alongside the shark while it swims in an attempt to minimise hydrostatic drag. Scientific divers tagged sharks underwater using a Hawaiian sling. C-type tags are locally manufactured plastic disk tags, similar in design to the Jumbo Rototag. The tag is applied with an applicator, through a hole towards the base of the first dorsal fin created by a leather punch. The tag is comprised of two plastic disks (a male and female component) that are placed on either side of the hole, and then clipped together. All tag information is printed on the outside of the disk. The issue of this tag type to anglers was curtailed in 2001 due to excessive biofouling growth and fin damage (Bullen and Mann 2004). Despite this fact, anglers who already possessed this tag type continued using it to tag sharks.

Anglers in both cooperative tagging programs were asked to record the following data when tagging a shark: tag number, date, locality, sex, weight, precaudal and total length and the taggers name and address. This data was then mailed on a pre-addressed data card back to the ORI program or e-mailed/faxed to the PEM program depending on which organisation the angler was affiliated to. Unfortunately, many of the anglers in the ORI program failed to report all of the requested information, which limited data analysis. To improve the reporting rate of tag recoveries, this study was advertised in newspaper articles, posters and radio interviews. It also featured in the "Tagging News" a tag and release information pamphlet distributed to members of the ORI tagging program. A series of workshops were also held at fishing clubs throughout the country encouraging fishermen to record and report any tag recaptures.

Catch data collected in Chapter 2 indicated the distinct spatial segregation of the juvenile (<1.8m TL) and adult (>1.8m TL) components of the *C. taurus* population. As a result of this segregation, only adult sharks are caught in the bather protection nets of the NSB and tagged underwater by scientific divers. Consequently, tag recapture data were analysed separately for juvenile and adult sharks. Data for both size classes were analysed on the basis of the 28-coastal areas previously described in Chapter 2 (Fig. 2.1).

5. 2. 2. Tag recovery percentages and tag type

To compare tagging performance, annual recovery rates were estimated for each tag type (A, B and C), tagging method (shore angling, nets and underwater) and cooperative tagging program (PEM and ORI). Comparisons between tagging method and tagging program were based on the recovery rates of B-type tags. D-type tags were excluded from analyses because only five sharks had been tagged with this tag type and the tag was designed for use on teleost fishes < 3 kg in mass. Annual recovery rates were calculated using the methods outlined in Oritz *et al.* (2003). Due to the annual variation in the number of sharks tagged, the type of tags used and tagging methods employed, recovery rates were standardised as a function of time at liberty for which at least 90% of recaptures were caught. As an example, if the specified time at liberty was two years, then the tag recovery rate for 2004 would ignore any recaptures that had been originally tagged after 2002.

If $R_{m,t,y}$ represents the number of releases from tag and release method *m*, using tag type *t* during year *y*; and $X_{m,t,y,i}$ is the number of recoveries from tag and release method *m*, using tag type *t* and year *y*, over the time period *i* when $i \geq y$ and $TL_{t,m}$ is the time at liberty for the specific tag type and tag and release method for which approximately 90% of all recoveries are made. Given this notation, two annual recovery rates were estimated and plotted against time:

1. The cumulative annual recovery rate of sharks tagged and released by the different tagging methods $\left(P_{m,y}\right)$ was calculated as the number of all recoveries of B-type tags, by all capture methods since the first year of release *m* to year *y* minus the time at liberty ($TL_{t,m}$), divided by the accumulated number of releases of "B-type" tags up to year *y*, by tag and release method *m*.

$$P_{m,y} = \left(\frac{\sum_{m} \sum_{i=m}^{y-TL_{t,m}} X_{m,t,y\,i}}{\sum_{i=m}^{y} R_{m,t,y}} \right) \text{x}\, 100 \qquad (5.1)$$

2. The cumulative annual recovery rate for the different tag types $\left(P_{t,y}\right)$ was calculated as the number of all recoveries of tag type *t* by all tag and release methods since the first year of release *m* to year *y* minus the time at liberty $TL_{t,m}$, divided by the accumulated number of releases of tag type *t* up to year *y*, by shore fishermen.

$$P_{t,y} = \left(\frac{\sum_{m} \sum_{i=m}^{y-TL_{t,m}} X_{m,t,y\,i}}{\sum_{i=m}^{y} R_{m,t,y}} \right) \text{x } 100 \qquad (5.2)$$

5. 2. 3. Movement patterns

Area of recapture, minimum travel distance (MTD), and the number of days at liberty were assessed for all shark recaptures. MTD was defined as the distance travelled between the tagging and recapture locality. Localities were defined as the distance in kilometres along the coast from the Tanzania/Mozambique border according to Bullen and Mann (2004). Because of the generally north-south orientation of the South African coastline, movements from the tagging site included strong northward or southward directional components. Northward movements greater than 20 km for juvenile sharks and 50 km for adult sharks were defined as positive displacements, and southward movements of the same magnitudes as negative displacements.

Few juvenile sharks were tagged or recaptured outside of the summer fishing season. As a result, the data was inadequate to investigate seasonal movement patterns. Survey results collected in Chapter 2, suggested that juvenile sharks exhibited site fidelity to summer aggregation sites. To test this hypothesis, a 90-day season was chosen, such that recaptures made within 0 to 45 days of tagging, or within ± 40 days of a tagging anniversary, were classed as “in season” and recaptures made outside these periods were classed as “out of season”. A two-sample t-test, assuming unequal variances, was then used to compare the distances travelled between the seasons. The test was repeated using a shorter 60-day season. A two-sample t-test was also used to compare the average MTD between juvenile male and female sharks.

To test the hypothesis that mature female sharks undergo a biennial breeding migration, a 360-day season was selected. Recaptures made within 0 to 180 days of tagging or within ± 180 days of a tagging anniversary were classed as "in season" and recaptures outside these periods as "out of season". Tests using shorter season lengths were not possible because of the small number of recaptures. It was not possible to compare the movement patterns between adult male and female sharks, because of the low number of male recaptures.

5. 3. Results

5. 3. 1. Juvenile sharks

5. 3. 1. 1. Tag recovery percentages and tag type

From 1984 to 2004 a total of 1,107 juvenile *C. taurus* were tagged and released using ORI A-type, B-type, C-type or PEM B-type tags (Table 5.1). All sharks were caught and tagged while fishing from the shore by either scientists or volunteer taggers. A total of 125 sharks were recaptured over the 20-year study period, representing an overall tag recovery rate of 11.3%. An additional eight sharks were tagged and released from the bather protection nets of the NSB using ORI B-type tags. These tag releases have been excluded from the following analyses, because it was suspected that these sharks had been measured incorrectly and were in fact adults. The number of sharks tagged, varied considerably not only between years, but also in the type of tags used. PEM taggers tagged the majority of sharks (58.8%) and most of these (89.3%) were tagged between 2001 and 2004. The number of sharks tagged with A-type tags by ORI taggers also increased over this time period, whereas the number of sharks tagged with ORI B and C-type tags decreased.

The time at liberty for recaptured sharks that had been tagged with either of the three tag types or by ORI or PEM taggers ranged from 1 day to 5.2 years, with an average of 372 days (95% C.I. = 350 – 394 days). The times at liberty, for which more than

90% of recaptures were made for ORI A-type and B-type tags, was three-years, and for ORI C-type tags and PEM tagged sharks two-years (Fig. 5.2). These times at liberty were used to standardise cumulative annual percent recovery rates (Fig. 5.3) using Equation 5.2. Some of the sharks tagged as juveniles (n = 14) were recaptured as adults. As a result, the time at liberty, for which the cumulative percentage recovery was 100%, represented the fact that tagged sharks were no longer caught, not a transition to the adult life history stage.

The trajectory of annual recovery rates, over the 20-year study period, for ORI B-type tags indicated a historical high in 1990, which gradually declined and stabilised near the end of the time series. The recovery rate for ORI C-type tags remained reasonably constant, whereas the recovery rate for ORI A-type and PEM tagged sharks increased. The annual recovery rates for ORI B and C-type tags were almost half of those associated with sharks tagged with ORI A-type tags and those tagged by PEM taggers. A chi-square test on the numbers released to the number recaptured indicated a significant difference ($P = 0.007$) in the recovery rates between the three different tag types and between sharks tagged by ORI and PEM taggers. These results suggest that ORI A-type tags and tags inserted by PEM taggers have higher tag retention, or lower tag induced mortality, than ORI B or C-type tags. There was no evidence to suggest that tag recovery rates were affected by a differential reporting rate between the different tag types or between tags inserted by ORI or PEM taggers.

Table 5.1. Number of juvenile *Carcharias taurus* tagged and recaptured by tag type and year, from 1984 to 2004

	Numbers tagged					Numbers recaptured				
Year	ORI A	ORI B	ORI C	PEM	Total	ORI A	ORI B	ORI C	PEM	Total
1984	1		4		5					0
1985	2		11		13			1		1
1986	4		26		30			1		1
1987		8	14		22		1	1		2
1988		6	22		28					0
1989	1	9	15		25		1	1		2
1990	1	20	19		40		1	2		3
1991	1	4	17		22			2		2
1992	1	4	16		21		2			2
1993			21		21					0
1994	3	6	32	3	44			5		5
1995	13	10	40	25	88	1		2		3
1996	2		34	5	41			2	1	3
1997	2	2	11		15	1	1	1	1	4
1998	2	4	14	4	24	1		2		3
1999		2	15	8	25	1		1	2	4
2000		2	10	19	31			2	3	5
2001	11	1	3	101	116		1	1	8	10
2002	25	4	6	176	211	2			19	21
2003	16	1	1	141	159	7			26	33
2004	6		1	119	126	1			20	21
Total	91	83	332	601	1107	14	7	24	80	125

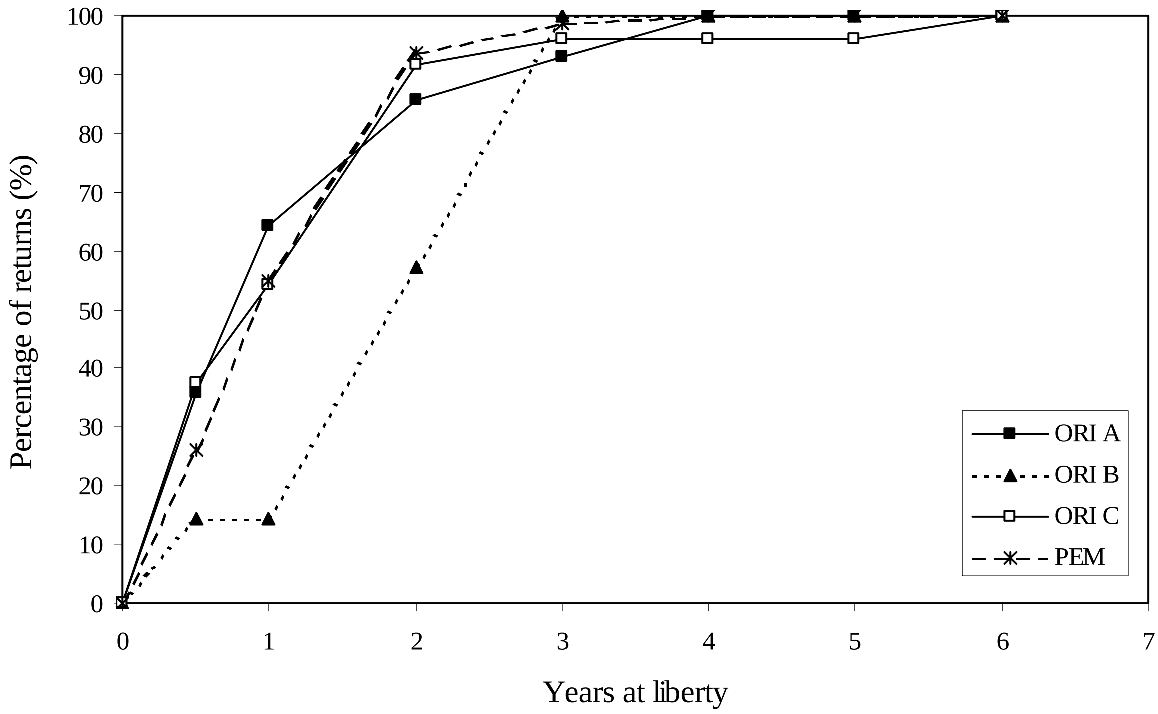


Fig. 5.2. The cumulative percentage of ORI A, B, C and PEM tag recoveries from juvenile *Carcharias taurus*

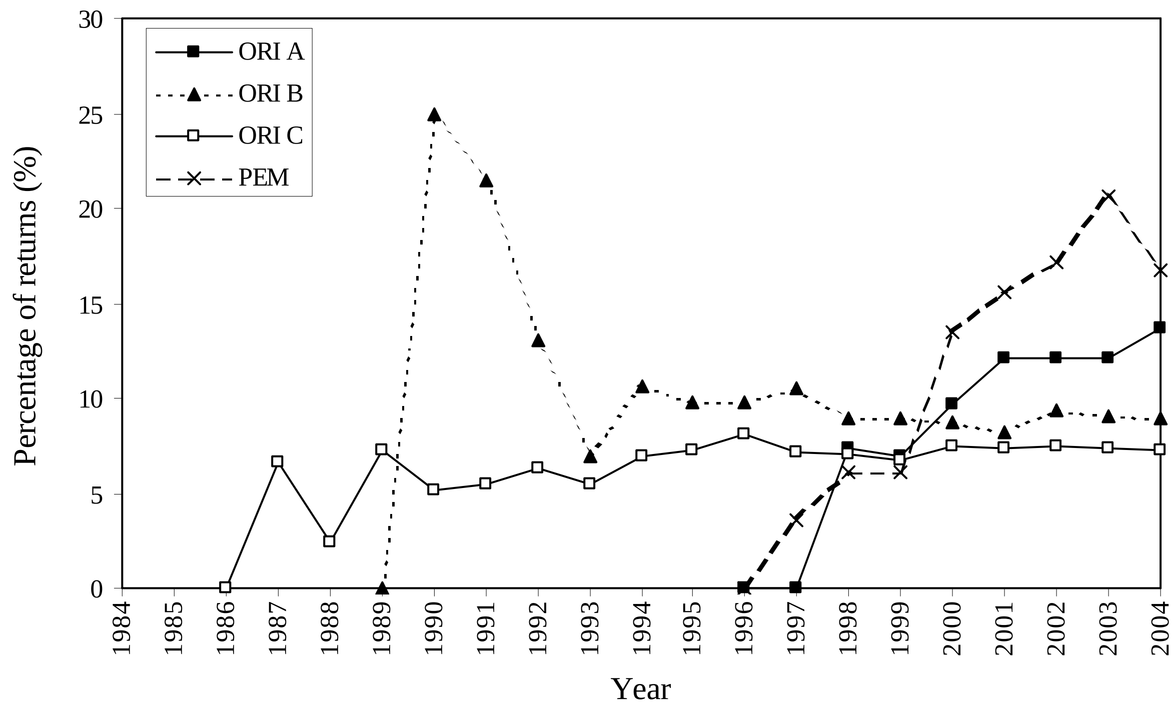


Fig. 5.3. Annual recovery percentage for ORI A, B, C and PEM tags from juvenile *Carcharias taurus*

5. 3. 1. 2. Movement patterns

Juvenile *C. taurus* were tagged and released in coastal Areas 6 to 20. The majority (86.0%) were tagged between Areas 10 and 13 (Table 5.2). ORI A, B and C-type tags were used throughout the range of tagging, whereas PEM taggers operated almost exclusively (99.3%) between Areas 10 to 13. The majority of tag recaptures, 98.4% (n = 173) were reported by shore anglers, whereas recreational ski boat anglers only reported 1.6% (n = 2). There were no recaptures reported from the commercial fishery. All movements greater than 20 km made by juvenile tagged sharks are shown in Fig. 5.4. Of the 125 sharks recaptured, 74 (59.0%) were re-caught within 5 km of the original tagging locality and 115 (92.0%) within 50 km. The average distance travelled was 18.7 km (95% C.I. = 10.8 – 26.6 km). Only eight-recaptured juvenile sharks had moved to a different coastal area involving a movement of over 100 km. Four of these recaptures were to the North of the original tagging locality, and four to the South. The greatest movement observed for a recaptured juvenile was 268 km. The shark had moved from the “Dredges” in Area 10 to Port St. Johns in Area 7 and was at liberty for 269 days. Because of the restricted movement patterns exhibited by juvenile sharks, the majority of recaptures (83%) were made between Areas 10 to 13. Surprisingly, no recaptures were reported in Areas 15 or 16, despite the fact that 24 juvenile sharks had been tagged and released within this 200 km stretch of coast.

The mean distances travelled by recaptured juvenile *C. taurus* classified by season and sex are given in Table 5.3. A two-sample t-test indicated there was no significant difference between the distance travelled “in season” and “out of season” for either a 60 (P = 0.80) or 90-day season (P = 0.85). There was also, no significant difference in the distance travelled between male and female sharks (P = 0.95). Despite these results, plots of MTD against days at liberty (Fig. 5.5) suggest that juvenile *C. taurus* may make cyclic annual movements to and from summer nursery areas and or exhibit some degree of seasonal site fidelity.

Table 5.2. Number of juvenile *Carcharias taurus* tagged and recaptured within each coastal area categorised by tag type

Area		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Tagged	A									4	41	7	4	11		4	2	1	10		7	
	B							2			49	2	8	6	1	2	2	1	3		7	
	C						1	7	1	16	103	23	30	68	1	10	3	10	36		23	
	PEM									3	198	70	95	234			1					
Total							1	9	1	23	391	102	137	319	2	16	8	12	49		37	
Recaptured	A										4	1		1					5		2	1
	B										2			3				1	1			
	C									2	7	3	1	4				1	4		2	
	PEM							1	1		18	10	3	47								
Total								1	1	2	31	14	4	55				2	10		4	1
Annual catch		0	0	0	0	0	0	25	13	86	324	49	125	327	0	76	49	10	17	0	21	

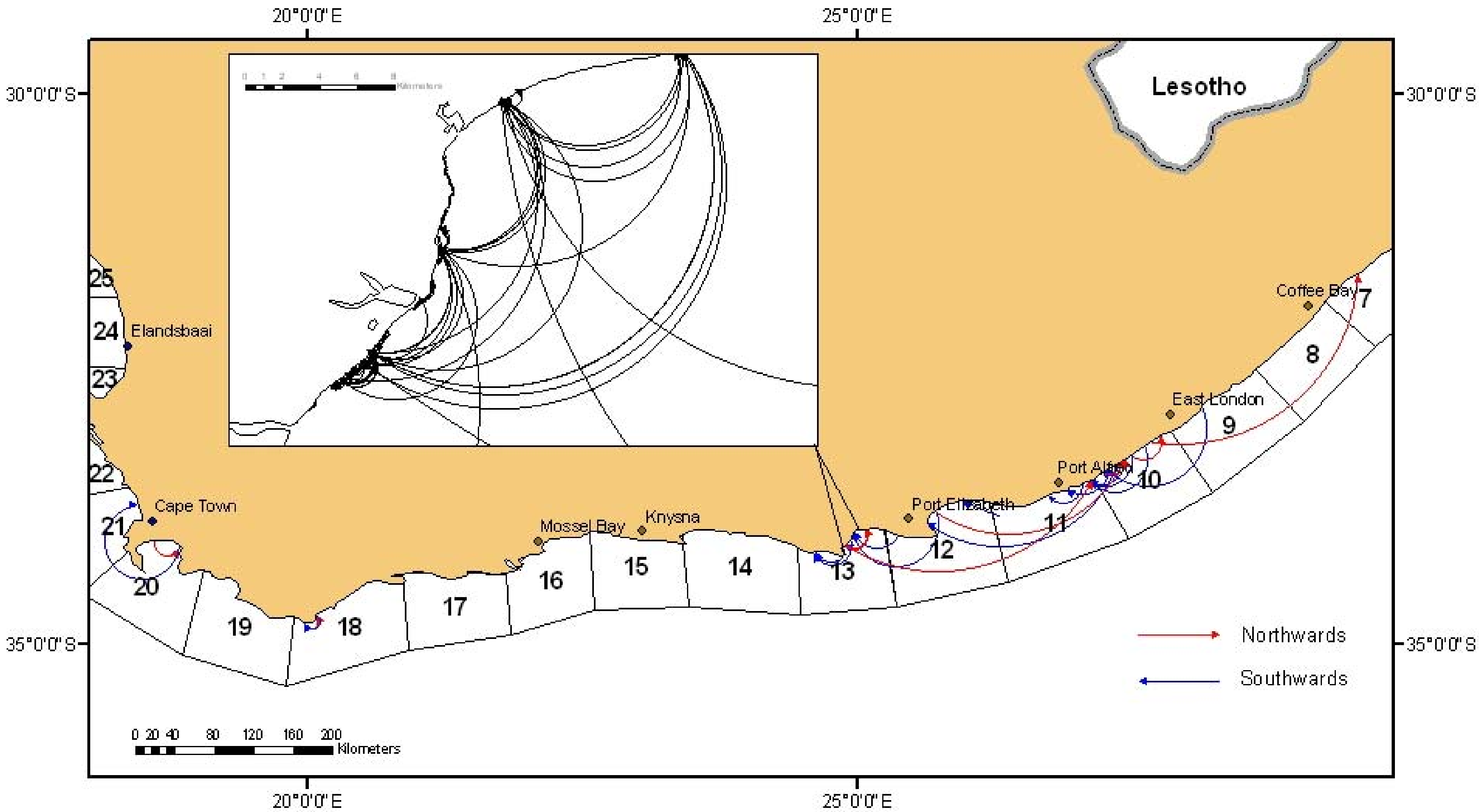


Fig. 5.4. Movements (>20 km) of juvenile *Carcharias taurus* from tag-recapture data 1984 to 2004. The insert, a 30 km section of Area 13, shows the fine scale movement of the majority of juvenile recaptures

Table 5.3. Minimum travel distance of recaptured juvenile *Carcharias taurus*, shown as mean ± SE classified by season and sex. Sample size is shown in parentheses

60-day season		90-day season		Sex	
In-season	Out-of-season	In-season	Out-of-season	Male	Female
19.9 ± 8.2 (41)	18.2 ± 4.5 (84)	17.6 ± 6.3 (54)	19.6 ± 5.2 (71)	18 ± 9.5 (30)	17.3 ± 6.4 (51)

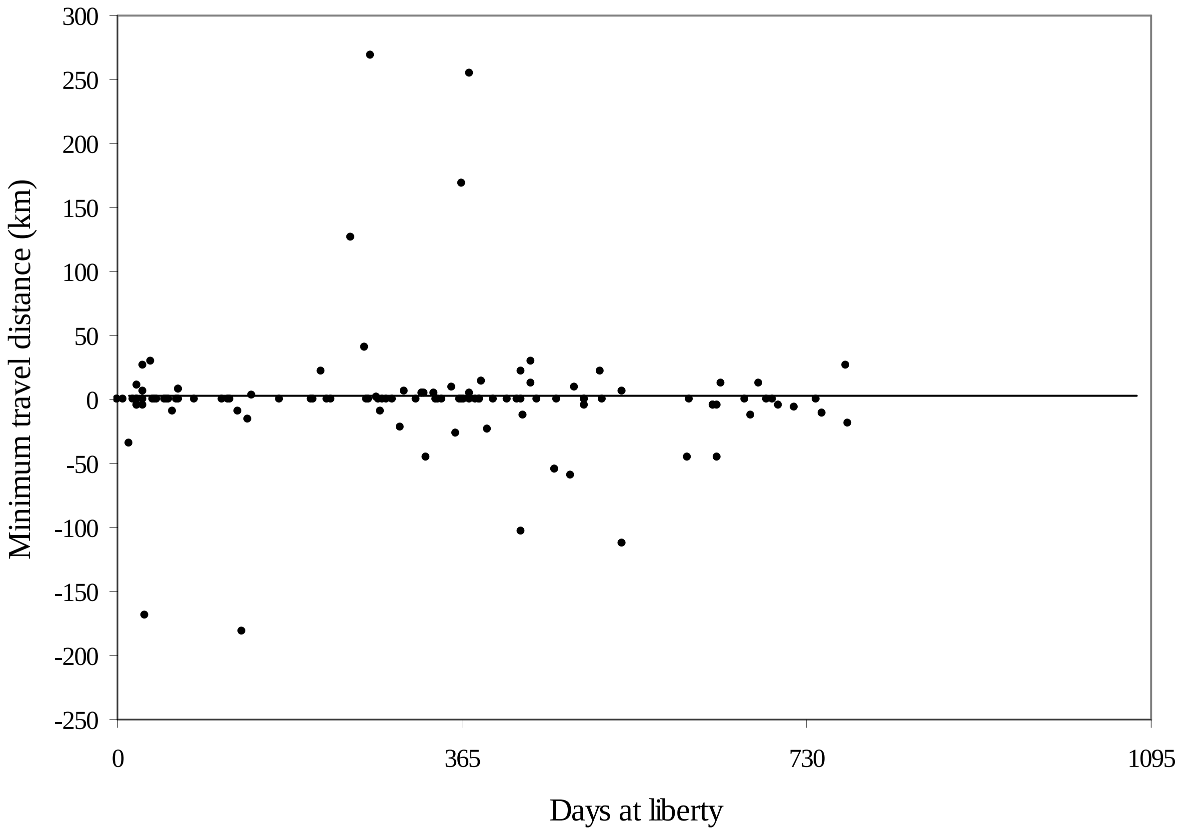


Fig. 5.5. Relationship between minimum travel distance and days at liberty for recaptured juvenile *Carcharias taurus*. Positive and negative values reflect a northward or southward movement, respectively

The maximum rate of travel recorded was 5.6 km.day^{-1} for an unsexed juvenile shark. The shark travelled 168 km in 30 days from the Strand in Area 20 to Bontkop in Area 21. This was the only *C. taurus* (tagged or untagged) to be caught on the west coast of South Africa and this exceptionally high displacement velocity should be viewed with caution. The next two fastest rates of travel were 2.7 km.day^{-1} and 1.4 km.day^{-1}. All other recaptures, 122 (96%) had travelled at a rate below 1.0 km.day^{-1}. Rates of travel are minima, since the juvenile sharks may have travelled further than the MTD between the tagging and recapture sites.

5. 3. 2. Adult sharks

5. 3. 2. 1. Tag recovery percentages and tag type

From 1984 to 2004 a total of 2,364 adult *C. taurus* were tagged and released using ORI A, B, C or PEM tags (Table 5.4). Sharks were tagged and recaptured by shore anglers, in the nets of the NSB and underwater by scientific divers (Table 5.5). A total of 177 sharks were recaptured over the 20-year study period, representing an overall tag recovery rate of 7.5%. The percentages of sharks tagged by shore anglers (31.0%), by divers (30.5%) and from catches in the bather protection nets (38.5%) were similar. The number of sharks tagged by each method, however, has varied considerably over the 20-year study period. The number of sharks tagged by divers and from catches in the bather protection nets has declined since 2001, whereas the number of sharks tagged by shore anglers has increased. The most commonly used tag by shore anglers is the ORI C-type tag, 341 (46.4%). The use of this tag type was curtailed in 2001, however, due to excessive fin damage. Since 2001, the majority of sharks have been tagged with ORI A-type tags, 79 (28.5%) and with B-type tags by PEM taggers, 161 (58.1%).

The time at liberty for recaptured adult sharks that had been tagged with either of the three tag types, or tagging methods ranged from 1 day to 10.8 years, with an average of 929 days (95% C.I. = 791 – 1067 days). The times at liberty for which more than 90% of recaptures were made for the different tag types and tagging methods are given in Table 5.6. These times at liberty were used to standardise cumulative annual percent recovery rates for the three different methods of capture and tagging (Fig. 5.6) using Equation 5.1. They were also used to standardise the cumulative annual percent recovery rates for sharks tagged by PEM and ORI shore anglers using A, B and C-type tags (Fig. 5.7) using Equation 5.2.

Table 5.4. Number of adult *Carcharias taurus* tagged, by specific tag type and capture method from 1984 to 2004

	Numbers tagged by shore angling				Numbers tagged with ORI B-type tags by divers and from catches in the NSB bather protection nets				Total
Year	ORI A	ORI B	ORI C	PEM		Diving	Nets		
1984		2	4			5			11
1985	2	1	16			30			49
1986	1	3	16			72	1		93
1987	2	6	9			10	89		116
1988	2	8	21			57	64		152
1989	2	2	15			2	86		107
1990	5	7	9			79	171		271
1991	1	6	13			82	45		147
1992	1	3	8			84	36		132
1993	1	4	25			29	113		172
1994	1	12	21	2		42	28		106
1995	2	20	23	4		36	59		144
1996	3	4	29	6		14	51		107
1997		4	9			28	38		79
1998	5	8	21			83	16		133
1999	1	8	29	2			45		85
2000	2	3	40	3			14		62
2001	11	1	21	7		10	14		64
2002	21	2	9	28			9		69
2003	29		3	51		21	31		135
2004	18	1		75		34	2		130
Total	110	105	341	178		718	912		2364

Table 5.5. Number of adult *Carcharias taurus* recaptured, by specific tag type and capture method from 1984 to 2004

	Numbers recaptured from those tagged and released by shore angling				Numbers recaptured from those tagged and released by divers and from catches in the NSB bather protection nets				Total
Year	ORI A	ORI B	ORI C	PEM		Diving	Nets		
1984									0
1985			1						1
1986						4			4
1987			1			3			4
1988			1			4	4		9
1989		1	1			4	3		9
1990							7		7
1991						3	1		4
1992		1				5	3		9
1993			1			5	4		10
1994		1				6	1		8
1995		2		1		5	3		11
1996		1	1			6	3		11
1997			1			11	3		15
1998		4	2			7	3		16
1999	1	3	2	1		5	5		17
2000		1	1	2		3	3		10
2001	1	1	1	1		3	1		8
2002	1		1	3		3			8
2003				4		2			6
2004	3	1		5		1			10
Total	6	16	14	17		80	44		177

Table 5.6. The time at liberty (years) for the different tag types and tagging methods that were used to standardise annual cumulative recovery percentages for tagged adult *Carcharias taurus*

	Tag type				Release method		
	ORI A	ORI B	ORI C	PEM	Shore angling	Nets	Diving
Time at liberty	6	7	5	6	6	6	8
% Returned	100.0	93.8	92.3	93.7	93.2	90.3	91.4

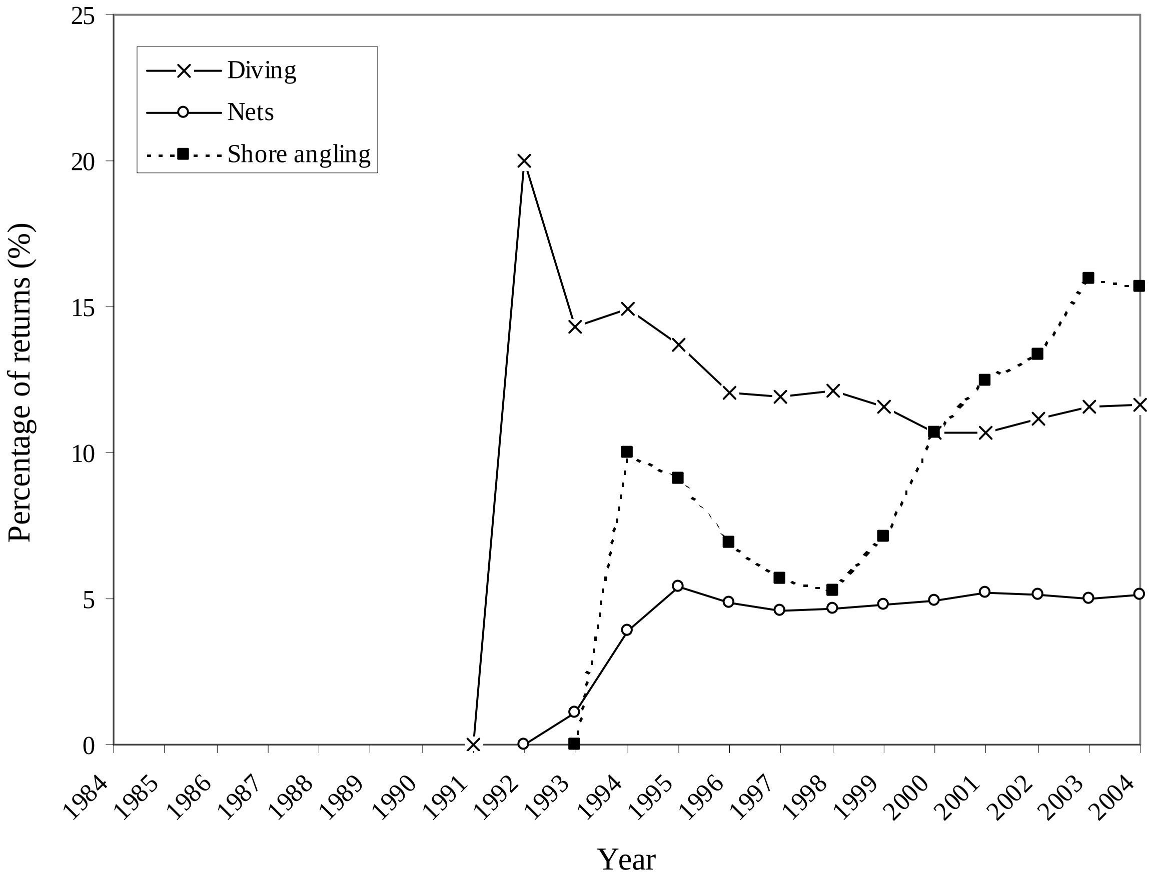


Fig. 5.6. Annual recovery percentage for tagged adult *Carcharias taurus* released by shore anglers, divers and from catches in the bather protection nets with B-type tags

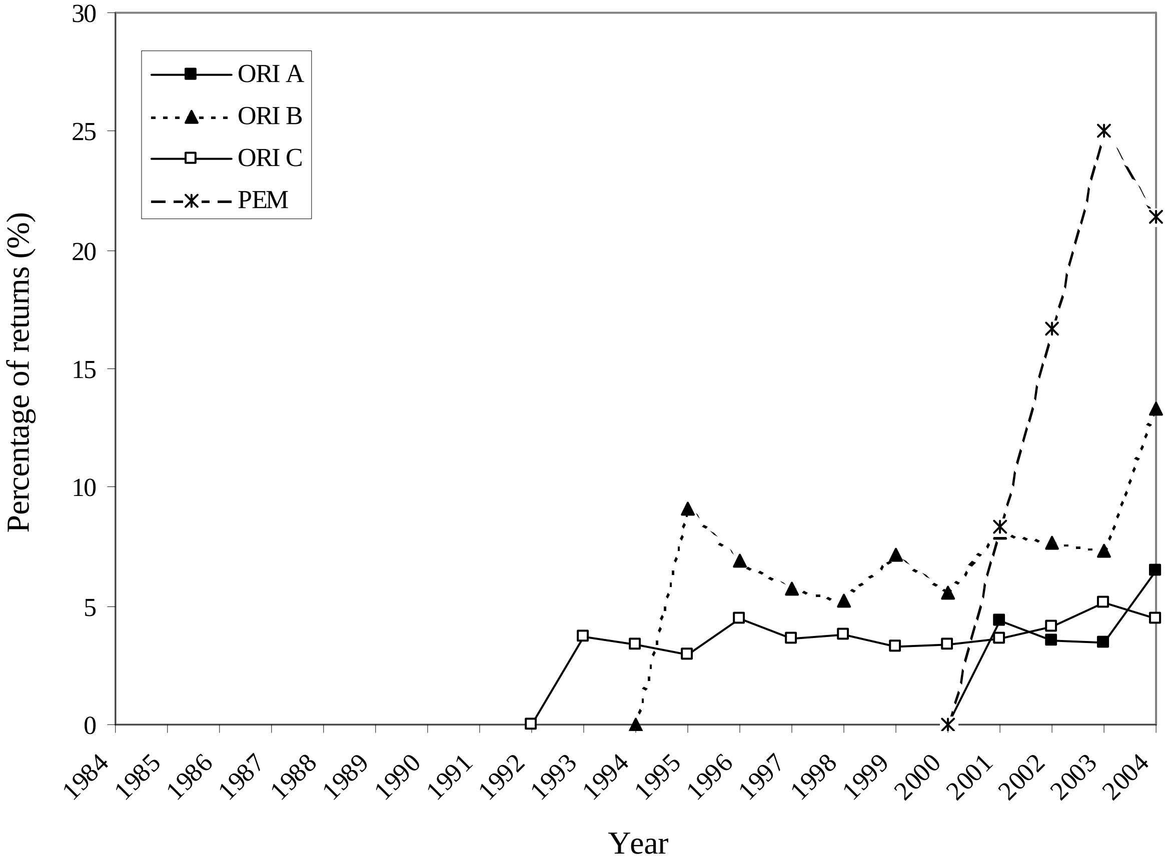


Fig. 5.7. Annual recovery percentage for adult *Carcharias taurus* tagged by shore anglers using ORI A, B, C and PEM tags

The trajectory of annual recovery rates, for sharks tagged and released by divers and from the bather protection nets of the NSB have remained reasonably constant over the 20-year study period. In contrast, the annual recovery rate for sharks tagged by shore anglers has steadily increased. The annual recovery rate for sharks that had been tagged and released from the bather protection nets was approximately half the rate of those that had been tagged by divers and almost a third less than those tagged by shore anglers. A chi-square test on the numbers released to the number recaptured, indicated that these recovery rates were significantly different ($P < 0.01$). Differences in annual recovery rates were also evident between the different tag types used by shore anglers. The highest recovery rates were for sharks that had been tagged by PEM taggers. The lowest recovery rates were for sharks that had been tagged with

ORI C-type tags. These results were similar to those obtained for juvenile tag recaptures. Only three PEM tagged sharks were recaptured in 2003 and 2004. As a result, the high annual recovery rates for these years should be viewed with caution. A chi-square test on the numbers released to the number recaptured indicated that the recovery rates for the different tag types used by shore anglers were significantly different ($P < 0.01$).

5. 3. 2. 2. Movement patterns

Adult *C. taurus* were tagged and released along the entire east coast of South Africa from Areas 1 to 20 (Table 5.7). The method by which sharks were tagged varied between coastal areas. In Areas 1 and 2, the majority of sharks were tagged by divers (90.1%). In Areas 3 to 6, the majority (90.4%) were tagged from catches in the bather protection nets. Shore anglers tagged all sharks in Areas 7 to 20. ORI A, B and C-type tags were used by shore anglers in all coastal areas, however, PEM taggers operated almost exclusively (97.2%) between Areas 10 and 13. The primary method of tag recapture was dependent on the coastal area within which the tagged shark was caught. In Areas 3 to 6, the majority of recaptures (80.8%) were made in the bather protection nets. In Areas 7 to 20, shore-anglers caught the majority (93.8%) of recaptures. Only seven recaptures (3.9%) were reported from recreational or commercial ski boat fishers.

All movements greater than 50 km made by adult tagged sharks are shown in Fig. 5.8. Of the 177 sharks recaptured, 72 (40.7%) were re-caught within 100 km of the original tagging locality, 136 (76.8%) within 500 km and 152 (85.9%) within 1000 km. The average distance travelled was 342 km (95% C.I. = 275 – 409 km). The greatest movement observed for a recaptured adult was 1,897 km. This was a female shark, that had moved from “raggy reef”” in Area 2, to the Strand in Area 20, and was at liberty for 1,377 days. Adult sharks, particular females, are highly migratory. Female sharks, move up the coast to breed and gestate and down the coast to pup. As a result, sharks recaptured after a time at liberty greater than 12-months may have travelled a greater distance than their recapture site.

Table 5.7. Number of adult *Carcharias taurus* tagged and recaptured, classified by coastal area, tag type and tag and release method, (S = shore angling, N = bather protection nets and D = divers)

Area		1		2		3		4		5			6		7	8	9	10	11	12	13	14	15	16	17	18	19	20
Method		S	D	S	D	S	N	S	N	S	N	D	S	N	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Tagged by tag type	A	4		7		3								2	8	3	5	29	16	4	10	1	1	1		16		2
	B	4	27	13	618	4	158	1	171	1	149	73	4	433	12		2	18	1	16	10			1		5		13
	C	5		38		8			1		1		3	2	34	4	3	41	26	43	79	1	6	4	4	35		7
	PEM															2	3	60	34	20	59							
Total		40		676		173		173		224			444		54	9	13	148	77	83	158	2	7	6	4	56		22

		1		2		3		4		5			6		7	8	9	10	11	12	13	14	15	16	17	18	19	20
Recapture method	Shore	3		12		4		5		3			2		1	2	2	12	4	14	25		2	1		8		3
	Nets					24		13		4			22															
	Diving			3																								
	Boat			1				1							1					2						2		
Total		3		16		28		19		7			24		2	2	2	12	4	16	25	0	2	1	0	10	0	3
Annual catch		6		29		35		3		3			22		57	58	63	125	20	113	48	0	26	16	0	12	0	6

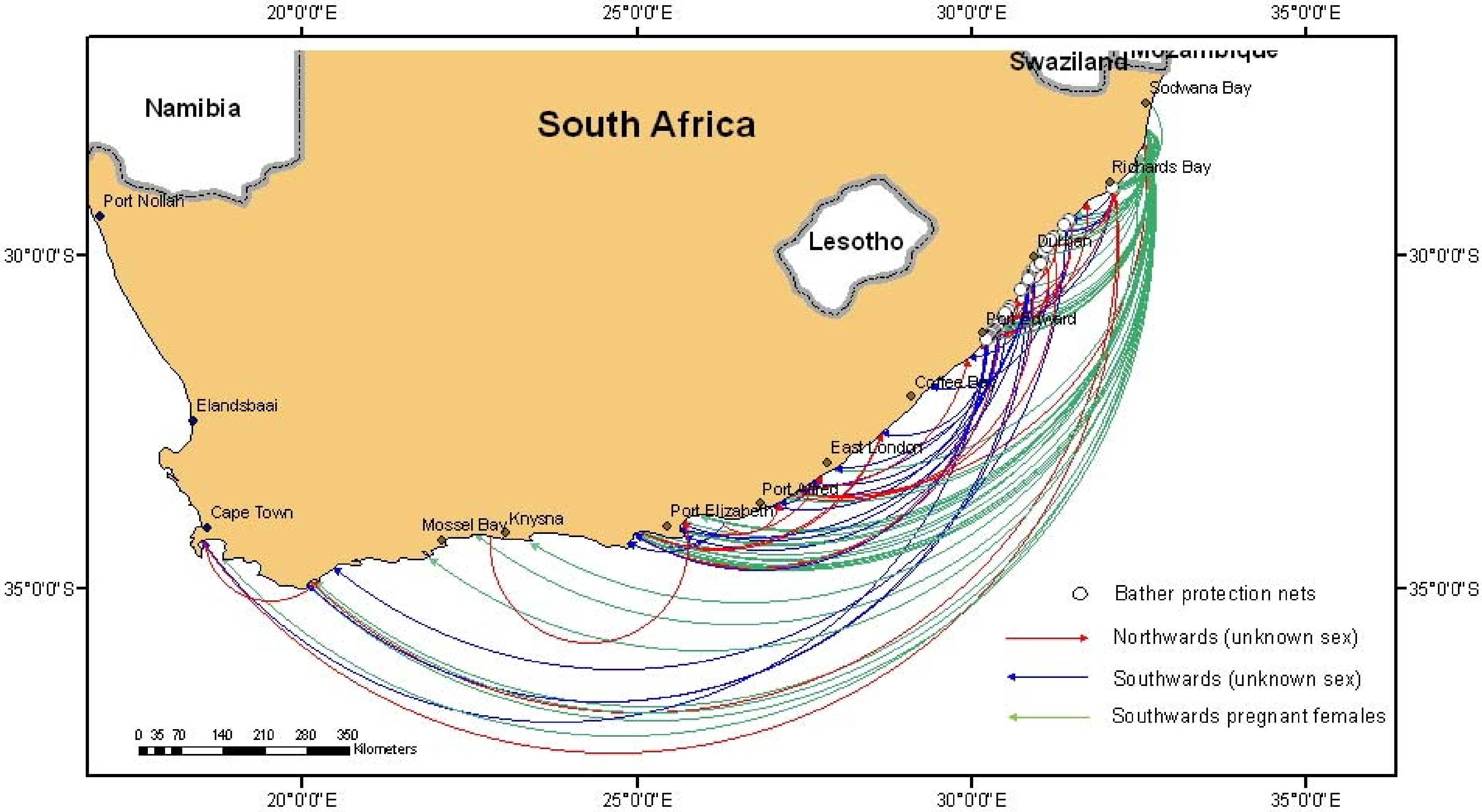


Fig. 5.8. Movements (>50 km) of adult *Carcharias taurus* from tag-recapture data 1984 to 2004

The majority of recaptured sharks were female, 56.5% (n = 100), while only four sharks were males (2.3%). All other recaptures by the fishermen, 41.3% (n = 73) were unsexed. The distances that recaptured adult sharks moved displayed no apparent cyclic movement pattern (Fig 5.9). A biennial movement pattern was observed, however, when distances were correlated with times at liberty for only recaptured female sharks (Fig. 5.10). The mean distance that female sharks were recaptured from their original tagging locality in-season and out-of-season for a 360-day season was 288.5 km (n = 54) and 487.6 km (n = 46) respectively. A two-sample t-test indicated that this seasonal difference was significant (P = 0.042).

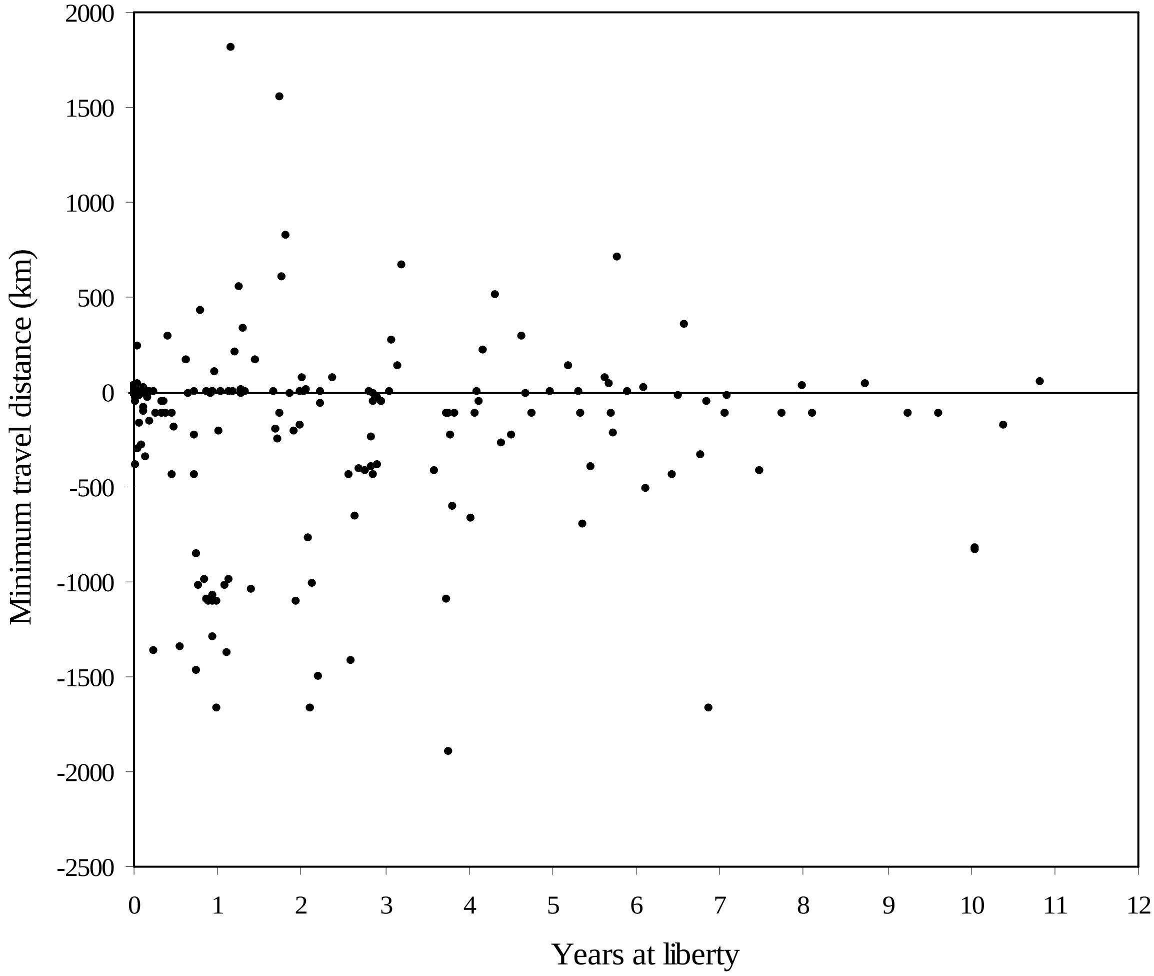


Fig. 5.9. Relationship between minimum travel distance and years at liberty for recaptured adult *Carcharias taurus*. Positive and negative values reflect a northward or southward movement, respectively

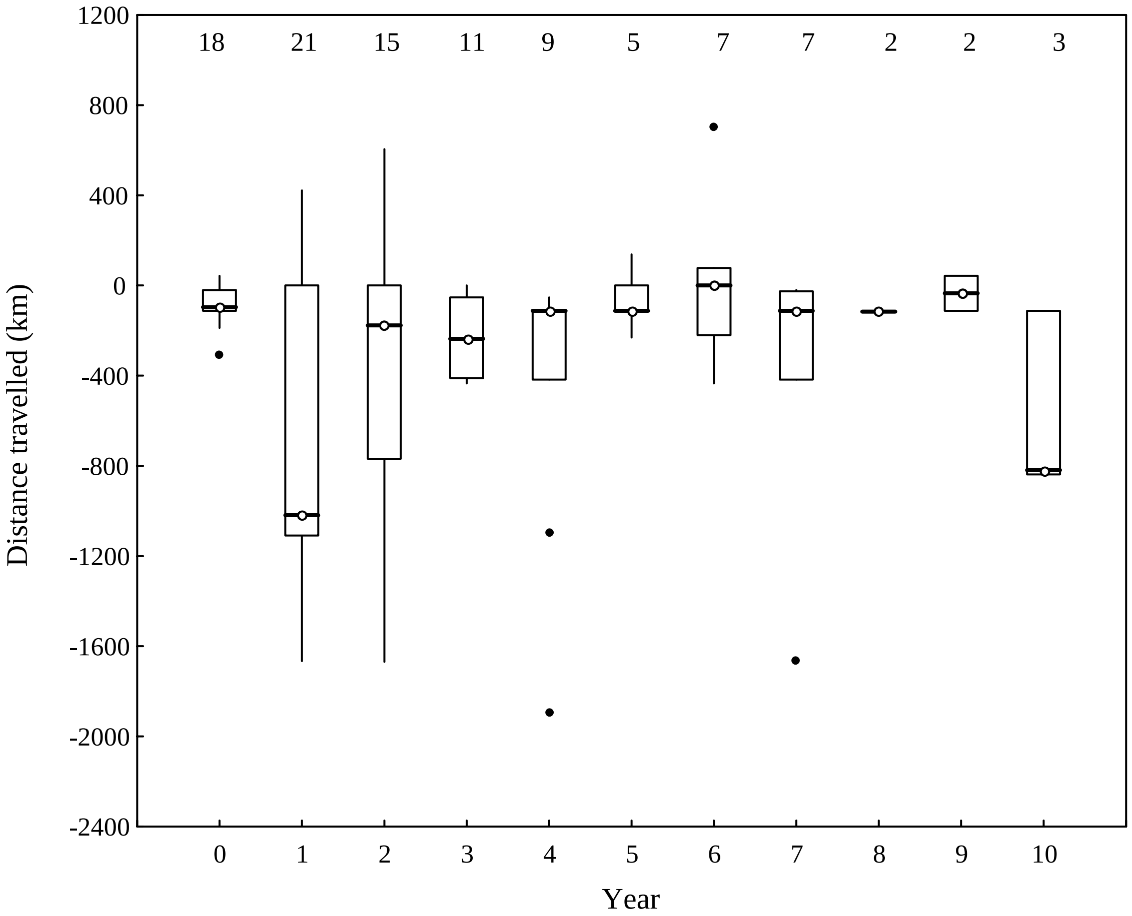


Fig. 5.10. Box plots of minimum travel distance against time at liberty for mature female *Carcharias taurus*. Boxes illustrate the interquartile range for minimum travel distance with the median distance represented by the solid bar and open circle. Whiskers are drawn to the shortest distance travelled, not beyond 1.5 times the interquartile range. Solid points indicate the maximum distance travelled. Numbers show sample sizes larger than 1

A total of 71 pregnant, gestating female sharks were tagged in Areas 1 and 2. Recaptures of these sharks, within a 12-month period, indicated their movement southwards to pup in the nursery Areas 9 to 20. The majority of these sharks were recaptured in Areas 10 to 13 (66.6%) compared to Areas 14 to 20 (30.4%). The average rate at which pregnant females moved south was 2.6 km.day^{-1} (95% C.I. = 2.04 – 3.16 km.day^{-1}). One recaptured female, however, travelled 383 km in 13-days from Cape Vidal in Area 2, to Uvongo in Area 6 at rate of 29.5 km.day^{-1}. A total of 37 recaptured sharks had moved northwards from their original tagging site. Only one female shark, however, was recaptured within a time at liberty of less than 12-months. This shark had moved 422 km from Gamtoos in Area 13, to Mazeppa Bay in Area 8 at rate of 1.45 km.day^{-1}.

5. 3. 3. Relative efficacy of individual taggers

A total of 262 taggers in the ORI tagging program had tagged at least one *C. taurus*, however, only 14-taggers had tagged more than ten. This compared to 9 of the 15 volunteer taggers in the PEM tagging program. The tag recovery rates from these anglers were used to compare the performance of individual taggers (Table 5.8). The recovery rate from sharks tagged by PEM scientists was 16.9%. In comparison, only three ORI taggers and four PEM taggers had a tag recovery rate greater than 10.0%. There were no recaptures, from a total of 122 sharks tagged, from six ORI taggers. In contrast, ORI tagger number one had a recovery rate of 18.5%. ORI taggers were not consistent in the tag type that they used, suggesting a haphazard approach to tagging.

It has already been shown that recapture rates are affected by tag type and the life history stage of the shark. Despite these factors, there is a clear variability in individual tagger performance, which could potentially bias tag-recapture data. As an example, ORI tagger number 10 has tagged the majority (76.7%) of all sharks in Area 7, but none of them have been recaptured. The lack of any tag recaptures, apart from providing no information on the movement patterns of sharks in this coastal area, may also lead to incorrect conclusions concerning the size of the population.

Table 5.8. A comparison in the tag recovery rates of *Carcharias taurus* tagged by individual ORI and PEM taggers

Tagger	Tagged (tag type)			Total recaptured	Recapture rate %
	A	B	C		
ORI 1	8		19	5	18.5
ORI 2	1	12	4	3	17.6
ORI 3			27	3	11.1
ORI 4	11	48	26	8	9.4
ORI 5	8		6	1	7.1
ORI 6	5	18	13	3	8.1
ORI 7			34	2	5.9
ORI 8		6	40	2	4.3
ORI 9		3	8	0	0.0
ORI 10		13	33	0	0.0
ORI 11	38		14	0	0.0
ORI 12	4		28	0	0.0
ORI 13	4		17	0	0.0
ORI 14			22	0	0.0
PEM scientist		242		41	16.9
PEM 1		12		2	16.7
PEM 2		83		13	15.7
PEM 3		32		5	15.6
PEM 4		44		5	11.4
PEM 5		153		11	7.2
PEM 6		18		1	5.6
PEM 7		37		0	0.0
PEM 8		29		0	0.0
PEM 9		14		0	0.0

5. 4. Discussion

5. 4. 1. Tag return rates

The overall recapture rate for *C. taurus* (8.7%) was higher than for the majority (55%) of the 52 shark tagging studies reviewed by Kohler and Turner (2001), which reported return rates of less than 5%. The return rate for *C. taurus* tagged in the Atlantic by the National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program

(CSTP) was only 5.5% (Kohler *et al.* 1998). Recapture rates, however, are influenced by a variety of factors, which can limit the validity of the inferences that may be drawn from these data. First, recapture rates are influenced by the life history characteristics of the species. *C. taurus*, is an inshore species of shark, that is readily caught by recreational anglers. Some species, occur farther offshore, in deeper waters and are not present in areas during the primary fishing season, or are not readily caught. Juvenile *C. taurus* remain in nursery areas for extensive periods of time. They are less migratory than adult sharks and consequently more prone to capture and recapture. This may be a possible explanation for their higher recapture rate (11.3%) opposed to adult sharks (7.5%).

Second, the recovery rate of sharks tagged with A, B, or C-type tags varied markedly suggesting that tag choice was an important variable in recapture rates. The recapture rate of sharks tagged with C-type tags (disk tags) was lower for both juvenile and adult sharks compared to the other two types of dart tag. Disk tags are susceptible to entanglement and fouling in capture gear and vegetation (Olsen 1953, van der Elst 1990). Davies and Joubert (1966) estimated that 4% of C-type tagged dusky sharks (*Carcharias obscurus*) lost their tags as a result of fouling in the bather protection nets of the NSB. This type of tag can lead to splitting and deterioration of the fin, especially in juvenile sharks (Kato and Carvallo 1967, Carrier 1985) whose cartilaginous dorsal rays are softer (Olsen 1953). For these reasons, the use of C-type tags was curtailed in 2001. Dart tags were retained for longer periods than the C-type tag. Carrier (1985) observed a similar result in a study of the comparative success of external tags on nurse sharks (*Ginglymostoma cirratum*). The recovery rate of A-type tags was generally greater than B-type tags for juvenile sharks and vice versa for adults. A-type tags are smaller than B-type tags and have nylon, compared to stainless steel, pointed tag heads. B-type tags were designed for use on sharks > 25 kg and may have caused tag induced mortality in juvenile sharks resulting in a lower recapture rate. Results from other studies on shark species have shown that return rates were similar for nylon and stainless steel dart tags (Lenarz *et al.* 1973, Baglin *et al.* 1980) or higher for the stainless steel dart (Pepperell 1990). Recapture rates, however, are affected by the species of shark (Davies and Joubert 1966, Pepperell 1990, Kohler and Turner 1998) and the method of tagging (Bayliff and Holland 1986).

Third, an inherent problem associated with collaborative tagging programs is the variability in individual tagger performance (Hearn *et al.* 1987, van der Elst 1990). Incorrect tag application can result in tag loss and tag induced mortality, resulting in reduced recapture rates (Begg *et al.* 1997, Kohler and Turner 1998). The recovery rate of sharks tagged by PEM taggers was significantly higher than that of ORI taggers. This suggests that sharks tagged by ORI taggers have a higher incidence of tag loss or tag induced mortality. There are over 4,000 participants in the ORI tagging program (Bullen *et al.* 2004), compared to only 15 voluntary taggers in the PEM tagging program. PEM taggers were carefully selected and trained in tagging techniques before they were inducted into the tagging program. Many of the ORI taggers, in comparison, are poorly trained and tag less than one shark a year. Less than a third of its members are currently active. These taggers are inexperienced and likely to tag, and handle the shark incorrectly leading to low recovery rates. ORI taggers used a variety of different tag types, including D-type tags, to tag sharks. D-type tags are similar in design to A-type tags, but designed for use on fish < 3 kg. These results suggest a haphazard approach to tagging and a lack of training in tag application by many ORI taggers. ORI has recently become aware of these problems and has begun to restrict the number of new members to its tagging program.

Fourth, the three different capture methods that were used to obtain sharks for tagging (shore angling, diving and bather protection nets) had a significant impact on their recapture rates. The recapture rate for adult sharks that had been released after capture in the bather protection nets was less than a third of those that had been released after shore angling. One explanation is that many of the sharks that were tagged and released from the nets were in a poor state of health and suffered post-release mortality. Increased mortality as a result of gear type has been reported in several studies. Francis (1989) observed that the recapture rate of trawl caught rig (*M. lenticulatus*) were less than those caught in set nets. Similarly, the recapture rate of various carcharhinid shark species caught in gill-nets was one-half to two-thirds that of sharks that had been released after hand-lining (Stevens *et al*. 2000). Tagging underwater, using a Hawaiian sling, is probably the least stressful of the three tagging methods employed. Underwater observations of the nurse shark, *G. cirratum* (Pratt and Carrier 2001) and the Pacific angel shark, *S. californica* (Pittenger 1984) tagged in situ have indicated that few of the sharks leave the tagging area and that there is no marked change in behaviour. This tagging method, however, is less precise than if a tag is inserted once the shark has been landed. Tags inserted into landed sharks, can be gently pulled to ensure that they are securely attached and re-applied if necessary. It is rarely possible to do this underwater and may be a possible explanation for the lower recapture rate of sharks tagged underwater compared to those tagged by shore anglers.

There were marked variations in the number of sharks tagged each year, in the type of tags used, and the methods to obtain sharks for tagging. As a result, the trends in the number of sharks tagged and recaptured must be interpreted with caution. A pre-requisite to the success of any tagging program is publicizing the program to as many fishing sectors as possible. Outreach and educational activities have been key in improving recovery percentages. This has included working with volunteer taggers in the PEM tagging program to plan and promote all aspects of tagging and data collection. Since 2001, increased collaboration between scientists and anglers has resulted in a dramatic increase not only in the number of sharks tagged, but also in the percentage of tags recovered. Commercial and recreational ski boat fishers are known to catch *C. taurus*, however, few tag recaptures are reported from this sector. This may be due to the resentment of scientific research or fisheries management, or the belief that the tagging study may in some way result in reduced catch quotas. Whatever the reasons, participation in the tagging programs should be encouraged within this fishery sector to redress the potentially high non-reporting rate.

5. 4. 2. Movement patterns

5. 4. 2. 1. Juvenile Carcharias taurus

Recapture information indicated that the movements of juvenile *C. taurus* were limited. Few sharks, less than 8%, had moved more than 50 km suggesting that little mixing may occur between juvenile sharks inhabiting different areas within the nursery grounds. Recreational shore anglers target *C. taurus* throughout the geographical range of its nursery area (Chapter 2). Fishing effort is not constant throughout the year, however, and is limited to the summer months (September to May) due to unfavourable weather conditions in the winter. This, combined with few offshore releases by recreational and commercial ski-boat fishers, severely restricts the analysis of movement patterns. As a result, the observed movements of recaptured juveniles may not be true, but a reflection of variable fishing effort.

Annual recaptures of juvenile sharks provided evidence of a cyclic annual movement to and from summer nursery areas. The proximity of recaptures to the original release site in the same months, one year, two year, or three years after tagging suggests that juvenile sharks may exhibit natal nursery homing. This behaviour has also been observed for juvenile sandbar sharks, *Carcharhinus plumbeus*, (Merson and Pratt 2001), juvenile blacktip sharks, *Carcharhinus limbatus* and juvenile blacknose sharks, *Carcharhinus acronotus* (Hueter *et al.* 2004). If juvenile sharks are strongly philopatric for regions of the nursery area, then density-dependent factors may curtail population growth (Springer 1967). Similarly, over-fishing and environmental perturbations will have a more dramatic effect on individuals that depend on a specific locality compared to those that are part of a larger homogenous stock.

The movement of juvenile *C. taurus* out of the summer nursery areas during the winter months suggests that water temperature tolerances may play a role in habitat use. Similar movements in response to decreasing water temperatures have been observed for juvenile blacktip sharks (Castro 1996) and juvenile sandbar sharks (Merson and Pratt 2001). Preliminary data from these studies suggests that the juveniles are forced to move into deeper offshore, or warmer water. The location of juvenile *C. taurus* winter nursery areas, however, remains unknown.

5. 4. 2. 2. Adult Carcharias taurus

Movements of adult *C. taurus* were much more extensive than the juveniles. Movements were associated primarily with reproduction, with one pregnant female travelling 1,897 km from the gestating areas in northern KwaZulu-Natal to the parturition areas in the Eastern Cape to pup. The maximum distance travelled by *C. taurus* tagged in the Atlantic by the CSTP was 1,187 km (Kohler *et al.* 1998). The movement of pregnant females south along the coast to pup is rapid. The fastest movement observed was 29.5 $km.day^{-1}$. This shark had been at liberty for 13 days and had travelled 383 km. Stevens *et al.* (2000) recorded a similar maximum rate of travel (25 $km.day^{-1}$) for *Carcharhinus tilstoni*. Tagging studies in New Zealand have reported maximum rates of travel of 21 $km.day^{-1}$ for *Mustelus lenticulatus* (Francis 1988) and 23 $km.day^{-1}$ for *Galeorhinus galeus* (Hurst *et al.* 1999). In contrast the maximum rate of travel for *C. taurus* tagged in the Atlantic was only 5.4 $km.day^{-1}$ (Kohler *et al.* 1998).

The majority of pregnant, gestating female sharks (66.6%) tagged in Areas 1 and 2 were recaptured within the nursery Areas 9 to 13, compared to Areas 14 to 20. The fishing effort within these two regions was similar, 8477 and 7789 fishing $days.year^{-1}$, respectively (Chapter 2). Assuming that the non-reporting rate is the same in both regions then the observed movement patterns are true and not a reflection of variable fishing effort. This spatial recapture pattern was not surprising, given that the majority (94.2%) of YOY sharks were recorded within Areas 10 to 13 (Chapter 2).

Recaptures of female sharks closer to their original tagging site in alternate years, provided evidence of a biennial reproductive cycle, as indicated from catch records in Chapter 2. Evidence for a two-year reproductive cycle with a resting stage in between has also been observed for *C. taurus* populations in the North Atlantic (Branstetter and Musick 1994) and the South Atlantic (Lucifora *et al.* 2002). Successful reproduction in captivity over the last ten years also supports a two-year reproductive cycle hypothesis (Henningsen *et al.* 2004). Few adult male sharks were recaptured. As a result, their movement patterns in relation to the female breeding migration and their whereabouts outside of the breeding season remains unknown.

Recaptures of gestating females in the same areas that they were originally tagged, in the same months, every other year suggests that female sharks may be philopatric to their gestating areas. There were an insufficient number of recaptures to investigate the possibility of philopatry to the mating or pupping areas. A female shark tagged as a juvenile in Area 10 was recaptured 8 years later, as an adult, only 34 km from the originally tagging site. Unfortunately, there was no data on the reproductive state of the female, but it is possible that this shark had returned to its natal nursery area to pup. In other shark species, nuclear and mitochondrial DNA markers have been used to indicate strong to moderate signals of natal philopatry for the lemon shark, *N. brevirostris* (Feldheim *et al.* 2002), and the blacktip shark (Keeney *et al.* 2003).

For sharks with natal philopatry, the specific areas they return to must confer some form of competitive advantage, indicating that the nursery areas do not provide a homogenous habitat. Focused studies on shark nursery areas (Branstetter 1990, Castro 1993, Merson and Pratt 2001, Heupel and Hueter 2002) suggest that predator avoidance and prey abundance are the critical factors influencing habitat choice. The greater number of pregnant female recaptures and the higher abundance of juvenile sharks in the nursery Areas 10 to 13 compared to 14 to 20, suggests that temperature also plays an important role.

Chapter 6

Estimation of juvenile and adult *Carcharias taurus* tag shedding rates

6. 1. Introduction

Tag loss is perhaps the most critical issue that must be considered in any population assessment based on tag release and recapture data (McFarlane *et al.* 1990, Adam and Kirkwood 2001). In many studies, tags are assumed to be retained permanently by tagged animals. If they are lost or shed (which often happens), estimates of important parameters such as mortality and migration rates can be biased (Xiao 1996, Fabrizio *et al.* 1999, Adam and Kirkwood 2001). Consequently, numerous attempts have been made to estimate tag-shedding rates (Wetherall 1982, Francis 1989, Lenarz and Shaw 1997, Xiao *et al.* 1999). The most common technique is that of double tagging, a technique developed by Beverton and Holt (1957), in which two tags are inserted into the same individual. Many models and estimation procedures have since been developed, which have been extensively reviewed by Wetherall (1982). More recent models have been reparameterized, to allow for the inclusion of additional parameters such as exact, rather than pooled times at liberty (Kirkwood and Walker 1984, Xiao 1996), tag type (Barrowman and Myers 1996), tagging operator (Hearn *et al.* 1991) as well as permanence of tags (Fabrizio *et al.* 1996).

There are two types of tag shedding (Beverton and Holt 1957, Wetherall 1982). Type I shedding is a once off event, occurs immediately after tagging, and is usually the result of poor tag insertion and placement. Type II shedding is the continual loss of tags over time once the tagged animal has been released. For long-lived species, this may not be constant and has been observed to increase with time at liberty as tags deteriorate or fail with age (Baglin *et al.* 1980). In addition, poorly secured tags are shed earlier in the experiment while others become more firmly embedded due to tissue growth (Kirkwood 1981, Hampton and Kirkwood 1990).

The purpose of this Chapter was to estimate Type I and Type II shedding rates of B-type tags from *C. taurus* inserted by PEM taggers. Tag shedding rates were estimated from a double tagging experiment carried out in conjunction with the PEM tag and release cooperative tagging program outlined in Chapter 5. Differences in shedding rates between juvenile (<1.8m TL) and adult (>1.8m TL) size classes were evaluated.

6. 2. Material and methods

6. 2. 1. Tagging

The technique for double tagging was exactly the same as for single PEM tagged sharks, outlined in detail in Chapter 5. The only difference was that a second tag was inserted 3 to 4 cm posterior to the first tag (Fig. 6.1). This placing was deemed sufficient to ensure that the interaction between the two tags was negligible. Consecutively numbered pairs of tags were used for each double-tagged shark. The musculature at the base of the first dorsal fin in juvenile sharks is thin. As a result, tags were not inserted on opposite sides of the fin in case the insertion of the second tag adversely affected the attachment of the first tag.

6. 2. 2. Data analysis

The model used to estimate tag shedding was the maximum likelihood approach that was initially developed by Kirkwood and Walker (1984) but later extended by Hampton (1997) and Adam and Kirkwood (2001). The model was designed for use with small data sets, in which the number of recaptured fish and the number of fish that have shed a tag are low. The model assumes a constant Type II shedding rate and requires that the exact dates of recovery are known.

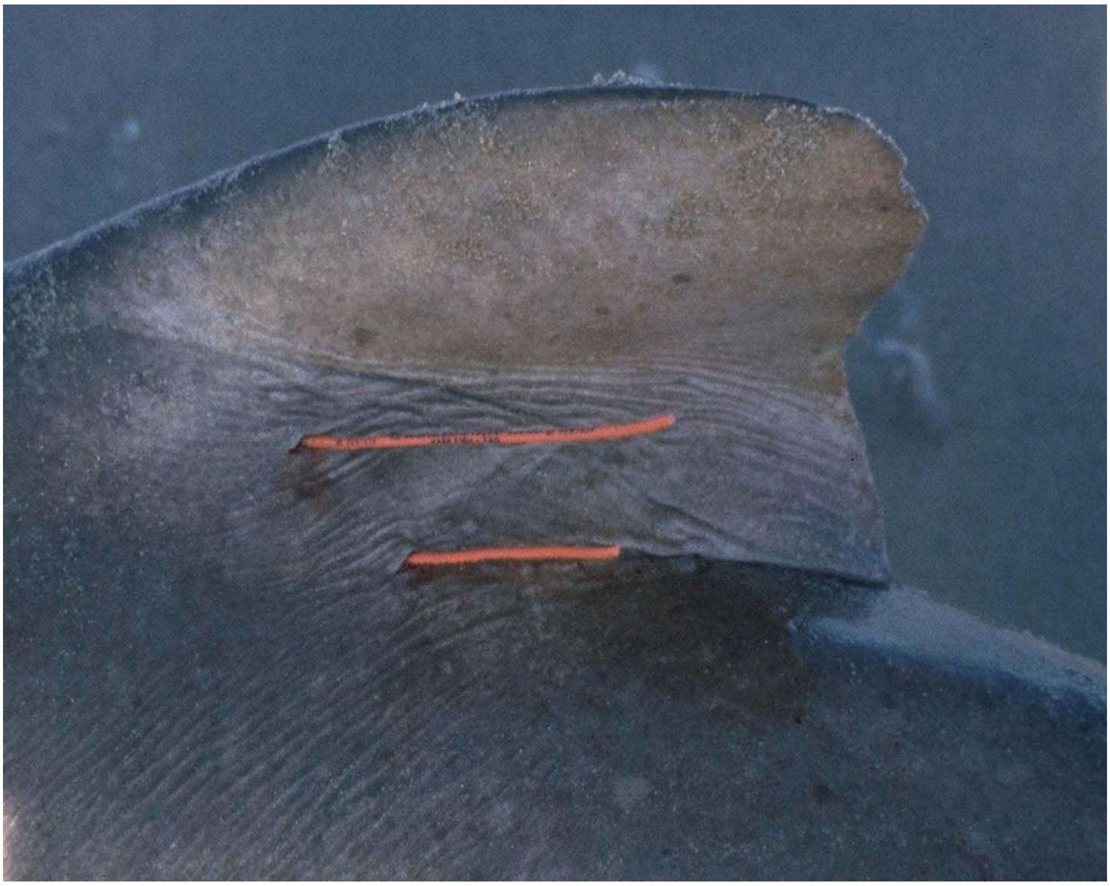


Fig. 6.1. Placement of tags at the base of the first dorsal fin, in a double tagging experiment on *Carcharias taurus*

Following Hampton (1997) and Adam and Kirkwood (2001), the probability of a tag being retained at time t is given by:

$$Q(t) = \alpha \exp(-\lambda t) \quad (6.1)$$

where α is the immediate Type I retention probability (1 - Type I shedding probability) and λ the continuous Type II shedding rate. Under the assumption that both tags after immediate shedding have an identical (and independent) Type II shedding rate then the probability of a fish, after release retaining 0, 1, or 2 tags respectively, at time t is given by:

$$P_0(t) = [1 - Q(t)]^2$$

$$P_1(t) = 2\,Q(t)\,[1 - Q(t)]$$

$$P_2(t) = Q(t)^2 \qquad (6.2)$$

In reality, observed recoveries will only consist of sharks retaining either one or two tags. The probability of an originally double-tagged shark at time t_i retaining either one or two tags, conditional on the retention of at least one tag are:

$$P_1'(t_i) = \frac{P_1(t_i)}{1 - P_0(t_i)} \qquad (6.3)$$

$$P_2'(t_i) = \frac{P_2(t_i)}{1 - P_0(t_i)} \qquad (6.4)$$

If n fish are recaptured and reported to have retained at least one tag, indicator variables for the recovery of either 1 or 2 tags are given by $N_i^{(2)}$ = 0, $N_i^{(1)}$ = 1 and $N_i^{(2)}$= 1, $N_i^{(1)}$ = 0, respectively.

The Log-likelihood (LL) of the data, conditional on recapture times $\{t_i, i = 1, 2,..., n\}$ and the model parameters α and λ, is given by:

$$LL = (t_1, t_2 \mid \alpha, \lambda) = \sum_{i=1}^{n} \left(N_i^{(2)} \ln\left[P_2'(t_i)\right] + N_i^{(1)} \ln\left[P_1'(t_i)\right] \right) \qquad (6.5)$$

Maximum likelihood estimates of α and λ were obtained by non-linear maximisation of the LL.

The model was applied to both juvenile and adult sharks separately, as well as to a pooled dataset. A likelihood-ratio test was used to assess the statistical significance of improvements in the fit of the models that included size specific shedding parameters. As an indication to the annual tag loss for each data set, the proportion of tags retained each year, $Q_{1\,yr}$, was calculated from Equation 6.1 by using the estimated parameters.

Equation 6.1 was also used to estimate the overall tag loss for juvenile and adult sharks as well as for the pooled dataset after a time at liberty for which the majority (approximately 90%) of all tags had been recovered $\{Q(t)\}$. This equated to a time at liberty of two years for juvenile sharks, six years for adult sharks, and three years for the pooled dataset (Chapter 5, section 5. 3.). Approximate 95% confidence intervals for α, λ, $Q_{1\,yr}$ and $Q(t)$ were obtained by the percentile method (Efron 1982) applied to distributions of the parameters generated from 1000 nonparametric bootstrap (or Monte Carlo) samples of each data set.

6. 3. Results

In all, 108 *C. taurus* (84 juvenile and 24 adult) were double tagged between 2002 and 2004, of which 17 were recaptured (Table 6.1). Only one of the 11 juvenile sharks that were recaptured had shed a tag, compared to five of the six adult sharks. In all of these recoveries, only the rear tag had been retained. Although few, these recaptures indicate a clear difference in shedding rates not only between size classes, but also in tag positions.

The parameters of the tag-shedding model fitted to both size classes as well as the pooled dataset are given in Table 6.2. Bootstrap estimates of the averages for the parameters α, λ, $Q_{1\,yr}$ and $Q(t)$, were similar to the maximum likelihood estimates. Likelihood ratio tests (Hilborn and Mangel 1997) indicated that the size specific models provided a significantly better fit to the data (P = 0.017) when compared to the pooled model (Table 6.3), suggesting that tag loss for juvenile and adult sharks should be modelled separately.

Table 6.1. Numbers of recoveries and times at liberty of originally double tagged *Carcharias taurus* retaining one (indicating which tag, front or rear) or two tags on recapture

Days at liberty	1 tag	2 tags
	Juvenile sharks	
28	0	1
81	0	1
226	0	1
277	0	1
285	0	1
327	0	1
337	1 (R)	0
364	0	1
439	0	1
631	0	1
636	0	1
	Adult sharks	
242	0	1
400	1 (R)	0
481	1 (R)	0
647	1 (R)	0
669	1 (R)	0
744	1 (R)	0

Table 6.2. Maximum likelihood estimates of rates of immediate tag retention α, continuous tag loss λ and the estimated proportion of tags retained after $Q_{1\,yr}$ and

$Q(t)$ for *Carcharias taurus*: (A) the pooled data set, (B) juvenile sharks and (C) adult sharks. Also shown are estimates of the average, bias and upper and lower 95% confidence intervals derived from 1000 nonparametric bootstrap replicates

(A) Pooled data set

	α	λ (per year)	$Q_{1\ yr}$	$Q_{3\ yr}$
Maximum likelihood estimate	0.999	0.241	0.786	0.485
Bootstrap average	0.998	0.251	0.776	0.495
Bias (%)	100.17	96.110	101.220	97.910
Lower 95% confidence interval	1.000	0.073	0.587	0.206
Upper 95% confidence interval	1.000	0.526	0.920	0.792

(B) Juvenile sharks

	α	λ (per year)	$Q_{1\ yr}$	$Q_{2\ yr}$
Maximum likelihood estimate	1.000	0.055	0.947	0.896
Bootstrap average	0.979	0.041	0.942	0.907
Bias	102.160	131.670	100.500	98.860
Lower 95% confidence interval	0.898	0.000	0.807	0.635
Upper 95% confidence interval	1.000	0.229	1.000	1.000

(C) Adult sharks

	α	λ (per year)	$Q_{1\ yr}$	$Q_{6\ yr}$
Maximum likelihood estimate	1.000	1.141	0.319	0.001
Bootstrap average	0.827	1.326	0.290	0.007
Bias	120.850	86.060	110.120	14.810
Lower 95% confidence interval	0.500	0.443	0.068	0.000
Upper 95% confidence interval	1.000	2.000	0.644	0.070

Table 6.3. Likelihood ratio test of the pooled tag-shedding model versus the size specific tag-shedding models

Model	No. of parameters	LL	χ^2	df	P
Pooled data	2	-9.068	5.991	2	0.017
Size categories	4	-5.016			

The mean probability of Type I tag retention for both size classes was high, at almost 100%. The major difference between the two size classes was in the rate of continuous Type II tag loss rate. Juvenile sharks had a low Type II tag loss rate (0.041 per year) whereas adult sharks had a high loss rate of 1.326 per year. According to the size specific tag-shedding models, these parameter values would result in a much higher proportion of juvenile sharks retaining their tags every year 94.19% (95% C.I. = 80.68% - 100.00%) compared to adult sharks 29.00% (95% C.I. = 6.76% - 64.39%). The values for $Q(t)$ at which 90% of all sharks were recaptured (two years for juveniles and six years for adults) indicated that the majority of tags for juvenile sharks 90.66% (95% C.I. = 63.52% - 100.00%) would still be retained compared to less than 1% of tags attached to adult sharks 0.70% (95% C.I. = 0.00% - 6.98%). It must be noted, however, that the confidence in the estimation of Type II tag loss for adult sharks was considerably lower than for juveniles.

6. 4. Discussion

The application of the double tagging model is based on several implicit assumptions that are outlined in detail by Beverton and Holt (1957), Kirkwood (1981) and Hearn *et al.* (1991); four assumptions warrant discussion.

First, and perhaps most importantly, it is assumed that the shedding rates of the two tags are similar. For each of the six sharks recovered that had retained a single tag only the front tag had been shed. This provides clear evidence of differing tag shedding rates. Because only the first tag was shed there was no information with which to estimate the shedding rate of the second tag, and therefore to utilise an alternative model that incorporates different tag shedding rates. Differences in shedding rates between the tags were unexpected, as the tags were of the same type, attached by the same tagger and inserted in almost identical areas. Francis (1989) observed a similar disproportionate shedding of front compared to rear tags in rig (*Mustelus lenticulatus*) and proposed that the front tag was more exposed to greater water flow rate, and therefore subjected to a higher drag than the rear tag. This is perhaps a valid assumption for the large types of Rototag that were used by Francis (1989), but it is doubtful whether this tag placement configuration confers such an advantage for the more streamlined dart tags used in this experiment

Second, it is assumed that both tags are lost independently. It is possible that the front tags are more susceptible to biofouling than rear tags, or in some way reduce the amount of biofouling on rear tags, possibly through the disruption of water flow. Increased biofouling on the front tag may increase the drag to a point, which eventually is sufficient to tear it free. The recapture of a bio-fouled tag weighing 41.3g (dry mass, Chapter 7), suggests that encrusting tag growth can be extreme enough to possibly cause tag breakage or shedding as a result of increased drag. Because of the few recoveries of sharks still retaining both tags, there are insufficient observations at present to test this hypothesis. The possibility that the attachment of the front tag may confer some form of advantage to the retention of the rear tag would be a violation of the model's second assumption. If this assumption fails, there will be fewer observations of fish retaining one tag, and consequently shedding rates will be underestimated.

Third, it must be assumed that the shedding rates of PEM tags applied in the double tagging experiment are the same as those for sharks tagged with a single PEM tag. In the single tagging experiment scientists and volunteer anglers both tagged sharks, whereas only scientists double tagged sharks. The similarity in the return rates of single tagged fish, tagged by volunteer anglers in the PEM tagging program and scientists (Chapter 5) suggests that this assumption had not been grossly violated.

Because all double tagged sharks in the experiment were tagged by scientists, there was little bias in the estimation of shedding rates as a result of the different tagging proficiencies of the operators attaching the tags as suggested by Hearn *et al.* (1987).

The fourth assumption was that double tag recoveries were reported or not reported as a pair, and that the probability of reporting a tag pair was similar to that of reporting a single tag. All 11 double-tag recoveries were reported as a pair, and there was no evidence to suggest that single and double-tagged sharks were reported with a different probability. Under this assumption reporting rates have no influence on the estimation of either Type I or Type II shedding parameters (Hampton 1997).

The vast majority of adult sharks that were recaptured retained only a single tag (five out of six) compared to only one of 11-juvenile sharks. Adult sharks are regularly caught in the bather protection nets off the coast of KwaZulu-Natal and tag shedding as a result of entanglement in the nets has been documented for dusky sharks (*Carcharhinus obscurus*) by Davies and Joubert (1966) and Govender and Birnie (1997). The musculature at the base of the first dorsal fin is thicker in larger sharks. There is the possibility that in adult sharks the tag may not have been inserted deep enough to become attached behind the cartilaginous dorsal rays and as a result, were less securely attached than in smaller juvenile sharks. Xiao *et al.* (1999) found that the shedding rate of dart tags anchored in the basal cartilage of the dorsal fin was about half that of tags anchored in the dorsal musculature for both the school shark (*Galeorhinus galeus*) and gummy shark (*Mustelus antarcticus*).

The tag-shedding model fitted to the data assumes a constant Type II shedding rate. Under this assumption, the model suggests that after a time at liberty of six years the probability of an adult shark retaining a tag is less than 1%, i.e. all tags had effectively been shed. Tag recaptures up to 11 years after initial tagging (Chapter 5) are clear evidence that this is not the case. Kirkwood (1981) and Hampton and Kirkwood (1990) found evidence in bluefin tuna (*Thunnus maccoyii*) that Type II shedding may decrease over time as the tag becomes more securely fixed as tissue is built up around the tag shaft. Due to the low number of tag recoveries, it was not possible to fit the data to a model that allowed the probability of shedding to decrease over time. The tag recovery data available, however, suggests that such a model would be applicable. Faster tissue growth in young sharks may also explain the increased tag retention in juvenile compared to adult sharks.

Immediate Type I tag retention was extremely high for both juvenile and adult sharks. This was not surprising since all double-tagged sharks were carefully tagged once shore anglers had landed them. Once a tag had been inserted, the tag was carefully examined to ensure that it was securely attached. In cases where the tag appeared to be attached poorly, it was removed and another tag inserted. This method of tag application has clear advantages over the use of methods such as Hawaiian slings or long tagging poles where tag application is less precise.

Given the low number of tag recoveries and the lack of compliance with some of the model assumptions, the parameter estimates should be viewed with caution. The estimated annual tag losses for juvenile and adult sharks were 5.8% and 71.0% respectively. In comparison, Xiao *et al*. (1999) estimated an annual dart tag loss of 41% for school sharks and 63% for gummy sharks. Simpfendorfer (1999b) reported a dart tag-shedding rate of 0.346 yr^{-1} for dusky sharks (*C. obscurus*). These values are much higher than those calculated for juvenile sharks in this study, but the gummy shark estimates are comparable to those calculated for adult sharks. Comparisons in shedding rates estimated from other experiments were complicated due to differences in species (Pepperell 1990), method of capture (Hurst *et al.* 1999), type of tag (Xiao *et al.* 1999), tag position (Davies and Joubert 1966, Xiao *et al.* 1999), as well as differences in the mathematical construction of the tag shedding model (Xiao 1996).

Chapter 7

Estimates of tag-reporting rates for *Carcharias taurus* and a preliminary investigation into the effect of tag type on tag wounds and biofouling growth

7. 1. Introduction

Tag release-recapture experiments must consider the proportion of recaptured fish not reported to reduce bias and improve their precision in the estimation of survival rates and abundance (Paulik 1963, Pollock *et. al* 1991, Hampton 1997, Xiao *et al.* 1999, Denson *et al.* 2002). If the non-reporting rate is unknown and assumed to be negligible, as is the case in some tagging studies (Cliff *et al*. 1996 for white sharks *Carcharodon carcharias*), the probability of capture can be under-estimated and population size over-estimated.

A variety of techniques have been used to estimate tag-reporting rates. For example, some tagging programs have compared the return rate of standard tags to those with a high-value reward (Rawstron 1971, Murphy and Taylor 1991, Denson *et al.* 2002). Alternatively, other programs have used seeding experiments, in which fish are secretly implanted with tags in the unprocessed catch on board fishing vessels, or in anglers catches (Green *et al.* 1983, Campbell *et al.* 1992). Hearn *et al.* (1999) compared tag return rates from a fishery, with those of a control group (such as vessels carrying fisheries observers) in which all tags recoveries were reported. Hilborn (1988) estimated tag-reporting rates from tag-recovery observations at different stages of catch handling and processing. Hearn *et al.* (1998) estimated reporting rates by comparing tag recoveries before and after a fishing season, in which fishing intensity was highly variable. Finally, Pollock *et al.* (1991) compared the number of tag recoveries reported voluntarily to the total number recovered by anglers estimated from a creel or port survey.

In South Africa, *C. taurus* is targeted recreationally rather than commercially. It is caught in relatively low numbers and by a specialised sector of anglers. As a result, many of the methods previously described to estimate reporting rates are not applicable. The technique developed in this study is based on the creel survey design of Pollock *et al.* (1991) and utilises information on tag reporting obtained as part of the competitive shore angling survey outlined in Chapter 2.

The objective of this Chapter is to provide reliable estimates of regional tag reporting rates from competitive shore anglers along the South African coast. Estimates of reporting rates were followed up with angler interviews to assess attitudes to tag reporting. This was used to identify areas in the tagging programs that could be improved upon in the future. Information on the effects of tag type on the extent of bio-fouling and tag wound damage were also collected to assess the effectiveness and suitability of the various tag types used in the cooperative PEM and ORI tagging programs. This information is important in curtailing the use of unsuitable tag types.

7. 2. Material and methods

7. 2. 1. Angler survey

The design and implementation of the integrated telephone and on-site survey of randomly selected club affiliated anglers has already been fully described in Chapter 2. A section of the questionnaire was designed specifically to solicit information on tag recoveries by asking a series of questions related to the “last tagged shark” the interviewed angler had caught. The questions included, but were not limited to, information on tag type, tag wounds and biofouling growth (Appendix 2.1). The questionnaire also included a series of questions determining the reasons for non-reporting and the angler’s knowledge of the PEM and ORI cooperative tagging programs. Between May and August 2004, all of the anglers who had participated in the original survey were contacted again in a telephone survey. The anglers were asked identical questions to the previous on-site survey, but related instead to catches of tagged sharks and tag reporting for the 2002/2003 and 2003/2004 fishing seasons.

7. 2. 2. Estimation of non-reporting rate

Tag reporting rates were estimated using the procedure outlined in Pollock *et al.* (1991). This approach incorporates differences in reporting rates between scientists or other survey agents, and fishermen. It is assumed that scientists, and anglers who are members of either the PEM or ORI tagging programs, report a tag recapture with a probability of one. In contrast, anglers who are not involved in any recognised tagging program will report a recapture with variable probability λ (for $0 \leq \lambda \leq 1$).

The estimate of λ is given by
$$\hat{\lambda} = \frac{R_v}{\left(\hat{R}_{total} + R_v\right) - R_r} \tag{7.1}$$

where:

R_v - the number of tags recovered by fishermen who are not members of a cooperative tagging program and are reported voluntarily.

R_r - the number of tags recovered by scientists or fishermen who are members of a cooperative tagging program.

$\hat{R}_{total}$ - an estimate of the total number of tags recovered by fishermen who are not affiliated to a tagging program. These tags are either reported or not.

$\left(\hat{R}_{total} + R_v\right) - R_r$ - the estimated number of tags recovered by anglers that are available to be reported with probability λ.

The variance of $\hat{\lambda}$ is given by:

$$\operatorname{Var} \hat{\lambda} = \frac{\hat{\lambda}\left(1-\hat{\lambda}\right)}{\hat{R}_{total} - R_r} + \frac{\hat{\lambda}\left(1-\hat{\lambda}\right)\operatorname{Var}\left(\hat{R}_{total}\right)}{\left(\hat{R}_{total} - R_r\right)^3} \tag{7.2}$$

The total number of tags estimated to have been recovered by fishermen who are not part of any tagging program, $\hat{R}_{total}$, was estimated from the telephone survey. A distinction was made between tag recoveries caught during competitions and those that were caught while fishing socially. The number of tagged sharks that anglers in the survey stated they had not reported was expanded to the number that would have been found if the entire target population (all coastal club affiliated anglers) had been sampled, a list of which was obtained from SASAA (Table 7.1). Estimation of $\hat{R}_{total}$ and its variance was calculated using the method outlined in Pollock *et al*. (1994). This method was previously used in Chapter 2, Equations 2.1 to 2.18 to estimate the total catch and effort and their associated variances for *C. taurus* in the competitive shore-angling fishery. The only difference in this present study was in the estimation of s_i^2, which was calculated assuming a Binomial distribution to reflect the fact that tag recaptures are either “reported” or “not reported”.

Because of the low numbers of tag recoveries made each year it was not possible to calculate the levels of tag reporting for each of the 28, 100 km long coastal areas. Reporting rates were estimated instead for six larger coastal regions (Table 7.2). These regions were chosen based on regional differences in the methods by which tagged sharks were recaptured (diving, nets or anglers) and the general areas fished by each of the six coastal fishing provinces described in Chapter 2.

Table 7.1. SASAA provincial club membership from 2001 to 2004 (E. Holmes, SASAA secretary) and the number of anglers sampled from each province. The figures in parentheses are the number of competitively active members in each province, which remained the same over the three-year study period

Coastal provinces	Sample size	Membership 2001/2002	Membership 2002/2003	Membership 2003/2004
Zululand and Natal	128	1319 (400)	1509	979
Border	70	224 (120)	191	162
Eastern Province	124	1052 (150)	874	530
Southern Cape	48	152 (100)	154	123
Boland	56	185 (100)	188	117
Western Province	51	245 (150)	193	172

Table 7.2 Division of the South African coastline to estimate regional variations in tag-reporting levels

Coastal region	100 km area	Primary tag recapture method	Fishing province
1	1 and 2	Scientific divers	Natal and Zululand
2	3 to 6	NSB nets	Natal and Zululand
3	7 to 9	Shore angling	Border
4	10 to 13	Shore angling	Eastern Province
5	14 to 18	Shore angling	Southern Cape and Boland
6	19 to 21	Shore angling	Western Province

7. 3. Results

7. 3. 1. Angler survey

Angler responses to the questionnaire survey soliciting information on the reporting levels of tagged *C. taurus* are given in Table 7.3. The proportion of anglers who had caught a tagged *C. taurus* was highest in the Eastern Cape (36.8%) and Border (26.7%) fishing provinces and lowest in Zululand and Natal (3.5%). None of the anglers in the Western province had ever caught a tagged *C. taurus*. These results are not surprising and reflect the regional variation in the relative abundance and tagging effort of *C. taurus* along the coast (Chapter 2 and Chapter 5). The majority of anglers in Zululand and Natal (100.0%), Border (75.0%) and Eastern Province (59.0%) stated that they voluntarily reported their tag recoveries to either the ORI or PEM tagging organisations, whereas anglers from the Southern Cape (66.7%) and Boland (50.0%) did not.

Table 7.3. Angler survey responses to the capture and reporting of tagged *Carcharias taurus*

Fishing province	Caught *C. taurus*	Caught a tagged *C. taurus*	Reported recapture	Knew what to do with tag recovery
Zululand and Natal	57	2	2	2
Border	60	16	12	14
Eastern Province	106	39	23	34
Southern Cape	44	3	1	1
Boland	32	4	2	3
Western Province	28	0	0	0

Most anglers, with the exception of those in the Southern Cape, stated that they knew what to do when they caught a tagged shark and who to report the recovery to. Anglers were asked a series of questions to assess the major reasons for non-reporting. The majority of anglers, 59.3% (n = 16) who had not reported a tag recapture stated they had simply forgotten to record the tag number and contact the relevant tagging organisation, 22.2% (n = 6) stated they couldn't read the tag number as a result of excessive biofouling, 14.8% (n = 4) stated they didn't know who to contact and only 3.7% (n = 1) stated that the tag had broken off.

Anglers who had caught a tagged shark were questioned about the type of tag and whether or not the tag had damaged the shark in any way (Table 7.4). Of the 93 tag recaptures reported in the survey, the majority (68.4%) were PEM B-type tags. Tag inflicted damage to the shark varied with tag type and was greatest for ORI C-type tags (disk tags) (77.8%) and lowest for PEM B-type tags (23.7%). Open wounds at the site of insertion (Fig. 7.1) were observed in 31.2% of ORI B-type tags and 23.7% of PEM B-type tags. From observations in the field these wounds occasionally appeared to be necrotic and infected (n = 12). In 61.1% of disk tag recoveries, anglers stated that the disk had become embedded in the fin causing splitting and fin deterioration (Fig. 7.2).

Table 7.4. A summary of the number of different tag types recovered by anglers and associated tag-inflicted injury and biofouling

Tag type	Number	Wound around insertion point	Tag biofouling	Fin grown over tag
ORI C-type tag	18	3	15	11
ORI B-type tag	16	5	12	0
PEM B-type tag	59	14	43	0

Fig. 7.1. PEM B-type tag insertion wound at the base of the first dorsal fin in a juvenile female (1.5 m TL) *Carcharias taurus*

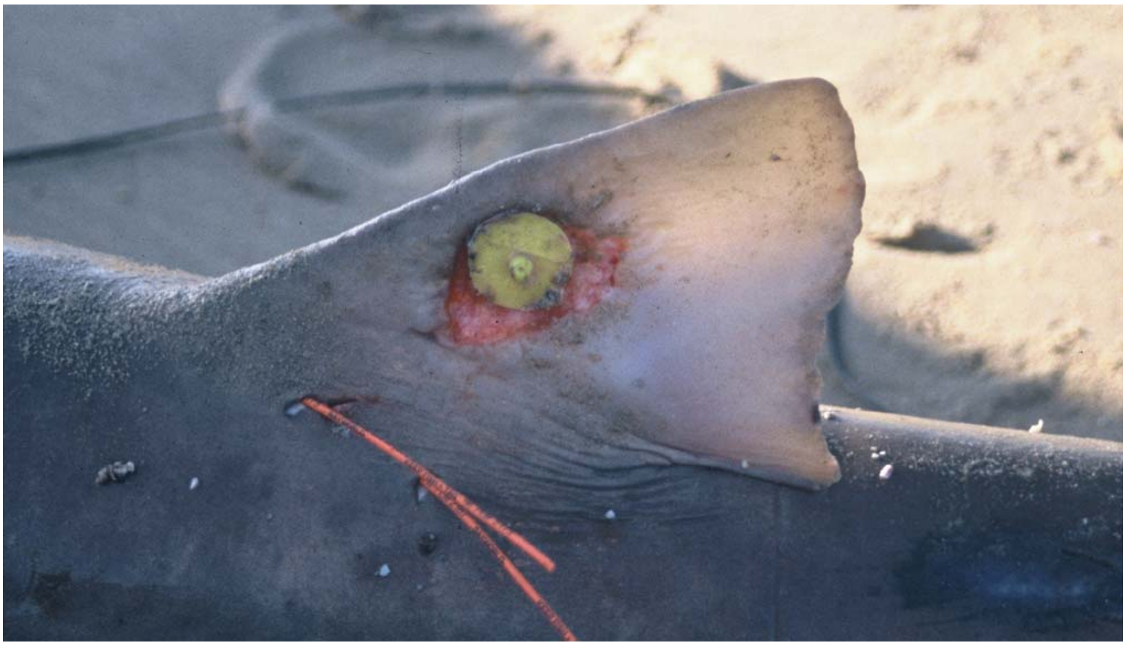


Fig. 7.2. Gross effects of an ORI C-type tag (disk tag) attached to the first dorsal fin of a sub-adult female (2.2 m TL) *Carcharias taurus.* Note the placement of two PEM B-type tags used for the double tagging study in Chapter 6

In almost all tag recoveries (75.3%) and for all tag types, anglers noted some form of tag biofouling. Fig. 7.3 illustrates the type and amount of encrusting growth that can form on a B-type tag. The growth was so excessive as to cause abrasion to the fin surface and wound irritation. The white-disk shaped object at the base of the tag was composed of a calcium compound and appeared to form a protective plug covering the wound site. This particular tag had been at liberty for 859 days and the encrusting growth weighed 41.3g (dry mass). A total of 14 different taxa of biofouling organisms were recorded growing on the tag (Table 7.5). In contrast to B-type tags, the predominant type of biofouling growth observed on disk tags (n = 3) were cirripeds (Fig.7.4).

Fig. 7.3. Biofouling growth on a PEM tag inserted into the base of the first dorsal fin of a sub-adult (2.3 m TL) *Carcharias taurus* after a time at liberty of 859 days

Table 7.5. A list of biofouling organisms that were recorded on one PEM B-type tag recovered from a sub-adult (2.3 m TL) *Carcharias taurus*, that was at liberty for a period of 859 days

Species	Number
Algae	3
Ascidians	2 (colonial), 2 (solitary)
Bivalve mollusc	1
Cirripedia	1
Echinoidea	1
Hydrozoa	2
Polychaeta	1
Ophiuroidea	1

Fig. 7.4. Encrusting barnacle growth on an ORI C-type tag (disk tag) attached to the first dorsal fin of an adult (2.4 m TL) *Carcharias taurus*. The material on the fin and flank had been scraped off from the tag to reveal its number

7. 3. 2. Tag-reporting rates

Estimation of tag-reporting levels was limited due to the low number of tag recaptures in all regions (Table 7.6). This was particularly evident in Regions 1, 3 and 6 where no recaptures were reported in either the 2001/2002 or 2002/2003 fishing seasons. These shortcomings are primarily the result of logistical problems associated with the capture, tagging and release of a sufficient numbers of sharks in a recreational fishery. In regions for which there was no information on the non-reporting of tag recoveries, but recaptures had been made voluntarily, or by scientists, the reporting rate was assigned a probability of one.

Estimation of the regional tag-reporting rates was influenced by the method of recapture and the number of tag recoveries. In Regions 1 and 2, only nine tag recaptures were recorded over the three-year study period. The majority of these recaptures (78.0%) were made either underwater or from captures in the bather protection nets of the NSB by scientists. Only two recaptures were made voluntarily by shore-anglers. As a result, the probability of reporting a tag in these regions was one. In the other regions the tag-reporting rate was lower. This was not surprising given the fact that many more tagged sharks were recaptured by shore-anglers (n = 43) who were not affiliated to either the PEM or ORI tagging programs. These anglers, unlike scientists, report tag recaptures with a probability of between zero and one.

In Regions 3 to 6, the highest tag-reporting rates were estimated in Region 4 and the lowest in Region 5. However, the number of tag recoveries was too low to compare statistically. In Region 4, tag-reporting rates increased progressively over the three fishing seasons from 0.28 in 2001/2002 to 0.77 in 2003/2004. A similar trend was observed in the tag-reporting levels in Region 5, which increased from 0.27 in 2002/2003 to 0.41 in 2003/2004. Unfortunately, there were insufficient tag recoveries to support a meaningful statistical comparison in the reporting levels between the different tag types.

Table 7.6. Mean tag reporting levels and 95% confidence intervals for *Carcharias taurus* estimated for the 2001/02, 2002/03 and 2003/04 fishing seasons from an integrated tagging study and telephone survey of club affiliated coastal anglers

Season	Region	Recoveries not reported (social fishing)	Recoveries not reported (comp fishing)	R_v	R_r	R_{total}	$SE\left(\hat{R}_{total}\right)$	λ (95% CI)
2001/02	1	-	-	-	-	-	-	-
	2	-	-	-	2	2	-	1.00 (-)
	3	-	-	-	-	-	-	-
	4	2	1	4	8	22	15.81	0.28 (0.00* – 0.63)
	5	-	-	1	-	1	-	1.00 (-)
	6	-	-	-	-	-	-	-
2002/03	1	-	-	-	-	-	-	-
	2	-	-	-	2	2	-	1.00 (-)
	3	-	-	-	-	-	-	-
	4	5	6	14	22	56	26.67	0.41(0.20 - 0.61)
	5	1	1	2	0	7	3.02	0.27 (0.00* - 0.62)
	6	-	-	-	-	-	-	-
2003/04	1	-	-	1	2	3	-	1.00 (-)
	2	-	-	1	1	2	-	1.00 (-)
	3	-	1	4	0	6	1.73	0.63 (0.12 - 1.00*)
	4	4	5	14	16	34	6.82	0.77 (0.56 - 0.97)
	5	1	1	3	0	7	2.32	0.41 (0.03 - 0.78)
	6	-	-	1	1	2	-	1.00 (-)

Note: λ must be a value between 0 and 1. Cases in which the 95% CI of λ exceeded these boundaries are marked by *

7. 4. Discussion

7. 4. 1. Suitability of tag

The high incidence of fin damage and tag wounds observed from the recaptures of sharks tagged with ORI disk tags supports the decision by ORI to curtail their use in 2001. This tag inhibits the lateral expansion of the fin causing it to split as it grows around the side of the tag, resulting in severe erosion of the fin tissue. Similar wounds caused by other types of disk tags have been reported on carcharhinids (Davies and Joubert 1966, Stevens *et al.* 2000) and on juvenile nurse sharks, *Ginglymostoma cirratum* (Carrier 1985). The percentage of sharks that exhibited some form of tag damage associated with B-type dart tags was less than a third of those tagged with ORI C-type tags. The tag wound associated with B-type tags consisted of an open wound, which appeared to be irritated by the continual movement of the tag streamer at the point of tag insertion. Davies and Joubert (1966) and Manire and Gruber (1991) both recommended that dart tags, similar to the B-type tags used in this study, not be used on sharks smaller than 1 m TL due to bacterial infections at the site of insertion. In contrast, Heupel and Bennett (1997) concluded that dart tagging caused only localised tissue disruption and that wounds were free of infection, even in sharks whose tags were heavily fouled with algae. As a result, this tag type was considered an acceptable method of tagging. It should be noted, however, that Heupel and Bennett (1997) used plastic, not metal tag heads.

A larger percentage of sharks that were tagged with B-type tags by members of the ORI tagging program exhibited tag wounds when compared to those tagged by members of the PEM tagging program. When tagging an animal it is imperative to use a clean applicator and tags to avoid introducing foreign matter into the tissue that can cause infection. Approximately 34% of all PEM tagged sharks were injected with the antibiotic oxytetracycline as part of an age validation experiment. The use of an antibiotic may have reduced wound infection in these sharks. Another possibility is that anglers in the ORI tagging program are not as careful in their tagging procedure as those registered with the PEM program. This would not be surprising given the much larger membership of the ORI program and the fact that many of its taggers are inexperienced and tag less than one fish a year. Many of these anglers tag purely because there is a certain status attached to tag-and-release. As a result, they do not take the time required to tag correctly. These results highlight the damage that can be inflicted if the shark is handled or tagged in an incorrect manner. Clearly there is a need to ensure that anglers are properly trained and educated before they are allowed to participate in a cooperative tagging program.

Tag damage associated with both tag types was exacerbated by the presence of biofouling growth, which resulted in the continual irritation and abrasion of the wound. The vast majority of recoveries of both tag types (75.3%) displayed some form of fouling. This compared to only 16.0% of recoveries of dusky sharks (*Carcharhinus obscurus*) tagged with rototags (Davies and Joubert 1966). However, it should be noted that the mean time of liberty of the sharks recaptured by Davies and Joubert (1966) was less than 40 days. Dusky sharks are active mid-water swimmers, whereas *C. taurus* are typically found hovering, almost stationary, within shallow rocky reef gullies and overhangs. This sedentary lifestyle is possibly more conducive to the fouling of tags than that of dusky sharks.

A variety of encrusting organisms, such as filamentous algae, barnacles, sponges and ascidians have been found growing on recaptured tags (Heupel *et al.* 1998, Joubert and Davies 1966, and Heupel and Bennet 1997). None of these studies, however, investigated the composition and magnitude of tag biofouling. An extensive search of the literature, suggests that this is the first study to do so, and provides preliminary information on the community structure of biofouling growth. This data is important, as biofouling growth could possibly increase the effects of drag to a point causing shedding (Chapter 6).

7. 4. 2. Tag reporting rates

The tag-reporting model used in this study depends on two important assumptions. First, it must be assumed that all tag recoveries made by scientists, or anglers registered to the PEM and ORI tagging programs, are reported with a probability of one. It is unlikely that scientists would fail to report a tag recapture. The results from the survey, however, indicated that anglers would on occasion simply forget to record the tag number or forget to contact the relevant tagging authority. Anglers also failed to report tag recaptures if they couldn't read the tag number due to excessive biofouling growth. A violation of this assumption would result in an underestimation of reporting rates.

Second, it is necessary to assume that the survey design is correct such that the total number of tags estimated from expansion of those solicited from the telephone survey ($\hat{R}_{total}$) does not suffer from model bias. The survey design used in this study, assumed that *C. taurus* were only caught by competitive anglers registered to clubs affiliated to the six coastal fishing provinces. The basis of this assumption has already been fully outlined in Chapter 2. In reality, however, a small number of *C. taurus* will also be caught by club anglers registered to inland fishing provinces, as well as accidentally by non-club affiliated anglers while fishing for non-cartilaginous species. If anglers who are not part of the sampling frame catch many tagged fish then the reporting rate will be over estimated.

Reporting rates varied markedly both between regions and fishing seasons, from 100.0% in Regions 1 and 2, to only 27.4% in Region 5. These estimates, however, were imprecise as a result of the low number of tag recaptures. Low rates of encountering tags, with the exception of Region 4, also limited the identification of spatial and temporal trends in reporting rates. Regional variations in reporting rate were expected due to differences in the number of tag recoveries and the method of capture. In Regions 1 and 2, tagged sharks were predominantly caught in the bather protection nets of the NSB or sighted underwater by scientific divers. As a result, these sharks were reported with a probability of one. In the other regions recaptures were made by shore anglers, many of who were not members of any recognised tagging program. As a result, only a fraction of recaptures were reported.

Fundamental to the success of any tagging program is publicising the program to as many fishermen as possible (Oritz *et al.* 2003). All of the anglers that were interviewed in this survey were aware of the ORI cooperative tagging program. Interview responses to the questionnaire survey, however, indicated a marked difference in the reporting levels by anglers registered to the different coastal fishing provinces. In Zululand and Natal, 100% of anglers who had caught a tagged shark stated they had reported the recapture, compared to only 43% of anglers in the Southern Cape. The high tag return levels from anglers in Zululand and Natal, in this study, were similar to those obtained by van der Elst (1990), who estimated that on average only 3% of recreational anglers in Natal did not return tags.

Matlock (1981) concluded that public information programs cannot assure high reporting rates and that other factors play an important role. The reason most often given by anglers (59%) for not reporting a tag recapture was that they had simply forgotten to record the tag number and contact the relevant tagging authority. This reflects a general disinterest and apathy concerning the tagging programs. Van der Elst (1990) concluded that this was also the primary reason for recreational anglers in Natal for not returning a tag. At a regional level, reasons for non-reporting varied between the fishing provinces. In the Southern Cape, a lack of education was the overriding factor. Two of the three anglers in this province, who had caught a tagged shark, did not know what to do with the tag or who to contact. This is an important observation, which highlights the shortcomings at present in the South African tagging programs. Educational outreach programs have been a key factor in improving the recovery percentages for many collaborative tagging programs (Pepperell 1990, Kohler *et al.* 1998). Angler interview responses in this survey clearly indicate that a similar approach would be beneficial in South Africa, particularly in regions such as the Southern Cape.

Tag reporting levels in Region 4 were consistently higher in all fishing seasons compared to Regions 3, 5 and 6. In Region 4 there was a greater collaborative effort between scientists and volunteer anglers than in the other regions. Collaboration was particularly close in the 2002/2003 and 2003/2004 fishing seasons with the formation of a small group of specialised PEM volunteer shark taggers. During this period, reporting levels in Region 4 increased almost three-fold from 28.2% in 2001/2002 to

76.8% in 2003/2004. Over this three-year period, three anglers reported 25.6% of all tag recaptures. Two important observations can be made from these results. First, reporting rates can be significantly improved through increased collaboration. Positive effects have already been observed in other constituent-based tagging programs worldwide (Scott *et al.* 1990, Kohler *et al.* 1998 and Hunter and Holts 1999). Second, these results demonstrate the impact a few skilled anglers can have on tag reporting rates. This fact highlights the importance of evaluating angler behaviour and interaction with the tagging program.

Chapter 8

Estimates of juvenile and adult *Carcharias taurus* abundance along the east coast of South Africa

8. 1. Introduction

Raggedtooth sharks (*Carcharias taurus*) have life history characteristics that render them particularly susceptible to over-exploitation. This is evident from dramatic worldwide population declines as a result of both directed harvesting and indirect impacts such as by-catch (Musick *et al.* 2000, Otway and Parker 2000, Lucifora *et al.* 2002, Otway *et al.* 2004). In response to declining global population trends, this species has been listed as Vulnerable globally by the IUCN (Hilton-Taylor 2000). Population declines have been particularly severe along the east coast of Australia, where the time to quasi-extinction has been estimated at less than 40 years (Otway *et al.* 2004).

In South Africa, *C. taurus* has never been specifically targeted by any commercial fishery and the limited data available indicates that it is rarely caught as bycatch. Despite this fact, the lack of any information on the status of the stock and severe population declines in other parts of the world led to its decommercilisation through the Marine Living Resources Act of 1998. Information on the population size of *C. taurus* in South Africa is essential in determining its protected status and the validity and effectiveness of the current protective legislature. An estimation of the size of the population and trends in abundance are required to document its population status. This information is crucial for effective fisheries management to ensure that the South African population does not suffer the dramatic declines that are evident in almost all other areas of its global distribution.

The few attempts at assessing shark stocks have produced questionable results because of insufficient data or the use of statistical models that incorporate invalid assumptions (Anderson 1990). Long-term time series of catch and effort data are seldom available for shark species, particularly for those that are not exploited commercially, such as *C. taurus*. As a result, traditional yield per recruit models (Grant *et al.* 1979 for the school shark *Galeorhinus galeus*, Smith and Abramson 1990 for the leopard shark, *Triakis semifasciata*) or age and size structured approaches (Wood *et al.* 1979 for spiny dogfish, *Squalus acanthias*, Punt and Walker 1998, and Punt *et al.* 2000 for the school shark *Galeorhinus galeus*) are not applicable.

In the absence of fishery dependent data, demographic models such as life history or stage-based models have been used to investigate the potential response of shark populations to anthropogenic perturbations (Cortés 1995, Smith *et al.* 1998, Brewster-Geisz and Miller 2000, Mollet and Cailliet 2002, Otway *et al.* 2004). These models do not, however, incorporate the effects of emigration or recruitment, and rely on indirect estimates of natural mortality. Anderson (1990), in discussing fishery models as applied to elasmobranchs, suggested alternative methods such as mark-recapture as a means to obtain estimates of absolute abundance. Mark-recapture models can be broadly defined as either “open” or “closed”. Closed population models, assume that the population is “closed” to any additions or removals, such as births, deaths, emigration, or immigration, whereas open models allow for these changes (Williams *et al.* 2001, Pine *et al.* 2003). These models, however, have seldom been applied to shark species because of a lack of appropriate biological or fisheries input data. They have been limited to only a few studies, all of which have assumed that the population is “closed” (Cliff *et al*. 1996 and Strong *et al.* 1996 for white sharks *Carcharodon carcharias*, Campana *et al.* 1999 for porbeagles *Lamna nasus*).

There are several approaches to modeling open populations. The Jolly-Seber (JS) model (Jolly 1965, Seber 1965) is a fully open population model that incorporates estimates of recruitment of new animals to the population to estimate population size. This model is not applicable to this study, however, since not all captured sharks were tagged. An alternative, yet more restricted model is the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Lebreton *et al.* 1992, Pollock *et al.* 1990, Williams *et al.* 2001). This model follows only marked animals over time allowing only survival and probability of capture (and not recruitment) estimation. While less general, this model facilitates an adjustment (for model violations) to apparent capture and survival rates, which can then be used to estimate abundance. The objective of this Chapter was to use the CJS model incorporating the tagging data from the ORI and PEM cooperative tagging programs to estimate the population size of juvenile and adult *C. taurus* along the South African east coast. A review of the literature suggests that this is possibly the first application of an open population model to any shark species worldwide.

8. 2. Model assumptions and data requirements

The CJS model has the following assumptions (Pollock *et al.* 1990): (1) all animals present at sample time *i* have the same probability of being captured; (2) all animals immediately after sampling have the same probability of surviving to sample time *i* + 1; (3) no tags are lost or over-looked; (4) all animals are released immediately after the sample and all sample periods have a short duration (relative to time intervals between tagging periods); (5) all emigration from the sample area is permanent and indistinguishable from death, and (6) the survival and capture of an individual is independent of the survival and capture of all other animals.

Estimating the abundance of *C. taurus* is problematic because its complex stock structure and the various methods in which sharks were tagged and released result in a violation of some of the model assumptions. These violations need to be accounted for in the development of the CJS model to avoid bias in the estimates of survival, probability of capture and abundance. First, the *C. taurus* population is distinctly segregated according to size with a well-defined nursery area. It was shown in Chapter 5 that pups and juvenile sharks < 1.8m TL within the nursery areas display moderate to high site fidelity and do not mix throughout the adult population. As a result, this component of the population is not subject to catches within the bather protection nets of the NSB, as are the adult sharks, yet have a higher probability of capture by shore anglers. These factors lead to heterogeneity in capture probabilities and a violation of the models first assumption. Second, it has been illustrated in Chapter 2 that a proportion of the sharks that are caught and subsequently released alive suffer size-class specific post-release mortality violating assumption 2. Third, results of the double tagging experiment in Chapter 6 indicated a clear violation of assumption 3, that of no tag loss. The tag loss experiment also suggested that tag loss was significantly higher for the adult compared to the juvenile component of the population. Differences in the percentage of tag recaptures also suggested that tag loss varied significantly between the seven different tag-types and capture methods used to tag sharks in this study (Chapter 5). Fourth, unlike most mark-recapture experiments, this study revolves around a cooperative tagging program. As a result, sharks are tagged randomly throughout the year and not during well-defined sampling periods as stated in assumption 4. Furthermore, the majority of tag recaptures are made not by the investigator, but by volunteer anglers. This factor introduces an element of non-reporting, which was estimated from an independent study in Chapter 7.

Powerful software (*SURGE* by Pradel and Lebreton 1991, *MARK* by White and Burnham 1999) has been developed to assist in CJS model fitting and selection. Unfortunately the unique features of this study, most notably, post-release mortality (PRM), tag specific tag-type/capture method tag loss (TL^j) and the non-reporting of tag recaptures (NR), make a simple model fit using these models inappropriate. As a result, a raggedtooth shark-specific CJS model was developed in order to incorporate the complexities specific to this study.

8. 3. Model development

The design protocol follows that of traditional CJS studies, in which capture histories are summarized into an m_{hi} array (Lebreton *et al*.1992, Williams *et al*. 2001).

8. 3. 1. Notation

The notation for the CJS model has been relatively well standardised (Cormack 1964, Lebreton *et al.*1992, Williams *et al.* 2001). Additional notations have been added as a result of the development of the model in this study.

8. 3. 1. 1. Statistics

s - number of sample occasions.

m_{hi} - number of marked animals caught in *i*th sample last caught in sample h

n_i - total number of animals captured at sample time i (estimated from the angler survey in Chapter 2 and from captures in the shark nets)

u_i - total number of unmarked animals captured at sample time i

m_i - total number of marked animals captured at sample time i

mm_i - number of u_i subsequently newly marked at sample time i . Not all sharks captured are marked, therefore $mm_i < u_i$

tm_i - number of marked animals released ($m_i + mm_i$) at sample time i

R_i - number of marked animals released after the *i*th sample ($R_i = tm_i - d_i$)

r_i - number of marked animals from the release of R_i animals, which are recaptured later in the experiment

z_i - number of marked animals caught before sample i not captured in sample i and captured after sample i

γ - percentage of sharks that suffer post-release mortality (Chapter 2)

d_i - number of tm_i that suffer post-release mortality ($d_i = tm_i \times \gamma$)

8. 3. 1. 2. Parameters

p_i - probability of capture at sample time i

ϕ_i - apparent survival (1 – mortality minus permanent emigration) from t_i to t_{i+1}

χ_i - probability of a release not being recaptured after period i. A recursive relationship exists for calculating the probability χ_i , where

$q_i = 1 - p_i$

$$\chi_i = \begin{cases} 1 & i = s \\ 1 - \phi_i \left(1 - q_{i+1}\, \chi_{i+1}\right) & i < s \end{cases} \tag{8.1}$$

8. 3. 1. 3. Functions of parameters

$\hat{M}_i$ - estimated number of marks in the population

such that $$\hat{M}_i = \frac{m_i + z_i}{1 - \hat{q}_i \hat{\chi}_i} \tag{8.2}$$

$\hat{N}_i$ - estimated size of the total population prior to sample *i*

such that $$\hat{N}_i = \frac{\hat{M}_i n_i}{m_i} \tag{8.3}$$

8. 3. 2. Likelihood

The likelihood component for marked recaptures can be expressed in terms of the statistics (r_i, m_i, z_i), calculated from the recapture matrix (m_{hi}). Following Cormack (1964), Seber (1982) and Schwarz and Arnason (1996), the likelihood can be written as:

$$L = \prod_{i=1}^{s-1} \binom{R_i}{r_i} (1 - \chi_i)^{r_i}\, \chi_i^{R_i - r_i} \prod_{i=2}^{s-1} \binom{m_i + z_i}{m_i} \left(\frac{p_i}{1 - q_i \chi_i}\right)^{m_i} \left(1 - \frac{p_i}{1 - q_i \chi_i}\right)^{z_i} \tag{8.4}$$

Initial model estimates for the parameters β were selected and the Log-likelihood minimised using the non-linear routine "Solver" in MS-Excel. A sin-link transformation was then used to back-transform them to the quantity of interest:

$$\theta_i = \frac{\sin(\beta_i) + 1}{2} \qquad \text{where } \theta = (p, \phi) \tag{8.5}$$

8. 3. 3. Incorporation of non-reporting rate, tag loss and post-release mortality

The CJS model does not distinguish how "deaths" accrue to marked animals in the population. If animals loose their tags then the observed recaptures will be smaller than expected and estimates of survival will be underestimated (Arnason and Mills 1981, McDonald *et al.* 2003). Pollock *et al.* (1990) extrapolated this conclusion to tag induced mortality, which reduces the number of marked sharks being returned to the population. Similarly, the capture probability will be underestimated if not all tag recaptures are reported to the relevant tagging authority. The effects of all of these problems lead to too few tagged fish being recovered with a positive bias on the estimation of population size. These effects are most pronounced, when capture probabilities are low, and fewer tags are available for recapture (McDonald *et al.* 2003).

8. 3. 3. 1. Non-reporting

As non-reporting affects "tag" capture probability, then the probability of capture, p_i, in year *i* of tag type *j* becomes $p_i^j \Psi^j$, where $\Psi^j = \frac{1}{RR}$ and *RR* is the reporting rate of tag type *j*. In other words, if the *RR* is 50%, then there should be twice as more tags reported and the probability of capture should theoretically double. Given a single "type" of tag *j*, then an annual time-dependent non-reporting rate can be modelled as:

$$\tilde{p}_i^j = p_i^j \Psi^j . \tag{8.6}$$

8. 3. 3. 2. Tag loss

Tag loss has two components; immediate Type I retention and continuous Type II tag retention. Each time a fish is tagged (this can happen more than once if the tagger replaces a tag because of biofouling or because the tagger notes a 'loose' tag inserted from a previous tagging period) then there will be immediate Type I retention, denoted as α. Then, over subsequent years, fish will retain their tags over a time interval *t*, known as Type II tag retention, and denoted as $\exp(-\lambda t)$.

All fish, when tagged first will have an initial Type I tag retention probability. Fortunately, in the case of *C. taurus*, Type I tag loss is negligible such that tags are retained at a rate of almost 100%. As tag retention affects the "tag" survival probability, it is necessary to correct for tag loss using the shedding rates estimated from a double tagging experiment in Chapter 6. The survival probability in each recapture period becomes:

$$\phi_i \Lambda \quad \text{where} \quad \Lambda = \frac{1}{\exp(-\lambda)} \tag{8.7}$$

For instance if 82% of the tags are retained, and $\lambda = 0.2$, then tag survival should be adjusted upwards by a factor of $\frac{1}{0.82} = 1.22$

In this study a variety of different tag-types and capture methods were used to tag sharks. Tag loss, however, was only estimated for sharks tagged with type B-tags by PEM taggers (Chapter 6). Tag-specific and time-dependent adjusted Type II survival probability can be calculated as:

$$\phi_i^j = \phi_i \Lambda_i^j, \tag{8.8}$$

where *j* is the tag-type (and/or capture method) and *i* the year. Λ_i^j for each tag-type/capture method was estimated by scaling λ based on the ratio of the tag specific recaptures to PEM tag recaptures estimated in Chapter 5. The Type II tag retention rate can be further simplified through assuming that it is temporally-invariant but still dependent on tag-type *j*. In this parameterisation, tags will be retained at an equal rate of $\exp(-\lambda)$ per year.

8. 3. 3. 3. Post-release mortality

Although *C. taurus* are invariably returned alive to the sea once caught, a small proportion will suffer post-release mortality due to the stressful effects of capture and tagging (Chapter 2). Post-release mortality in effect will reduce the number of marked fish being returned to the population (R_i). Accordingly, the number of marked animals released after the *i*th sample (tm_i) was reduced by subtracting the fraction of animals estimated to suffer post-release mortality (d_i):

$$R_i = tm_i - d_i \quad \text{where } d_i = tm_i \times \gamma \tag{8.9}$$

8. 3. 3. 4. Bias adjustment for abundance

The Maximum Likelihood Estimates (MLEs) are composite parameters of the different tag-types/capture methods. The following steps are taken to remove this bias:

1. Calculate the MLEs from the pooled data (no differentiation between tag-type).
2. Separate the capture history data into the different tag-type/capture methods. Calculate an m_{hi} array and the associated statistics for each tag-type/capture method-specific m_{hi} array.
3. For each tag-type/capture method, remove the bias from the parameter, $\tilde{\theta}_i$, automatically via:

$$\hat{\theta}_i^j = \frac{\left(\Phi^j \sin\left(\tilde{\theta}_i\right) + \Phi^j\right)}{2} \qquad \text{where } \Phi^j = \left\{\Psi^j, \Lambda_i^j\right\}. \tag{8.10}$$

4. Calculate tag-type/capture method specific q_i^j and χ_i^j.

5. Estimate the number of marks for each tag-type/capture method, $\hat{M}_i^j = \frac{\left(z_i^j + m_i^j\right)}{1 - q_i^j \chi_i^j}$, based on the tag-type/capture method specific summary and sufficient statistics. The population size from all tag-types is then calculated as:

$$\hat{N}_i = \frac{\left(\sum_{j=1}^{J} \hat{M}_i^j \, n_i\right)}{\left(\sum_{j=1}^{J} m_i^j\right)} \tag{8.11}$$

In the case of zero tag-loss and zero non-reporting, $\hat{N}_i$ is equal to the tag-disaggregated and non-disaggregated approaches.

8. 4. Estimation of parameter variance

Variance estimates for the model parameters were obtained using a hybrid parametric/nonparametric bootstrap. A total of 500 bootstraps were performed and approximate 95% confidence intervals were calculated using the percentile method (Efron 1982). At each iteration, the observed tag-specific capture histories were randomly re-sampled with replacement and a new m_{hi} array and associated summary and sufficient statistics calculated. At the same time, a random tag loss rate obtained from the double tagging experiment in Chapter 6 was selected.

The number of sharks caught at each sampling period (n_i) is a product of known captures in the bather protection nets of the NSB (Table 8.1) and an estimated number caught by shore anglers. The uncertainty in the numbers of sharks caught by shore anglers was accounted for by replicating capture sample sizes from the normal distribution, using the estimated number of sharks caught and its standard deviation obtained from the survey of shore anglers in Chapter 2. It is important not to misinterpret the catch trends in Table 8.1. The NSB has gradually reduced the number of netted beaches, particularly in recent years from 39 km in 1999 to 27 km in 2004.

As a result, catches in the nets, given net reduction have in fact remained relatively constant and should not be interpreted as a sign of a decreasing abundance.

Table 8.1. Annual catch of *Carcharias taurus* in the Natal Sharks Board bather protection nets between 1984 and 2003

Year	Number sharks caught in nets	Year	Number sharks caught in nets
1984	210	1994	100
1985	440	1995	170
1986	350	1996	220
1987	330	1997	180
1988	290	1998	90
1989	340	1999	160
1990	340	2000	96
1991	160	2001	91
1992	70	2002	86
1993	300	2003	90

8. 5. Model selection

Various model configurations were chosen to represent a suite of choices for capture probability (p_i) and survival (ϕ_i) (Table 8.2). For brevity, they will be referred by model number in the text as given in Table 8.2. The full model in which p_i and ϕ_i are both time dependent has 40 parameters to estimate. 'Nested' submodels of the full model were specified by estimating common parameters for both p_i and ϕ_i (Hilborn and Mangel 1997). Models 2 and 3, in which $p(t)$ and $\phi(t)$ were set to values pre-2001 and post-2001 respectively, reflected the change in shore angling fishing effort with the implementation of the vehicle beach ban in 2001. To reflect a reduction in the number of sharks killed in the nets and the beginning of a catch and release ethic amongst shore anglers in the early 1990's, $\phi(t)$ was varied before and after 1990 in Models 4 and 7. Akaike Information Criteria (AIC) were used as a model comparison statistic to determine the most parsimonious model (Burnham and Anderson 2002).

Table 8.2. Hierarchical model configurations and the number of parameters (Parms) to estimate

Model	Parameter configuration	Parms
1	$p(\cdot)\,\phi(\cdot)$	2
2	$p(1984-2000, 2001-2004)\phi(\cdot)$	3
3	$p(1984-2000, 2001-2004)\phi(1984-2000, 2001-2004)$	4
4	$p(1984-2000, 2001-2004)\phi(1984-1990, 1991-2004)$	4
5	$p(\cdot)\,\phi(t)$	21
6	$p(t)\,\phi(\cdot)$	21
7	$p(t)\,\phi(1984-1990, 1991-2004)$	22
8	$p(t)\,\phi(t)$	40

The (t) and $(.)$ notation signify time dependence and independence respectively

8. 6. Model application

The data analysed in this study consists of released and recaptured *C. taurus* collected between 1984 and 2005. Tag releases and recoveries were analysed over 12-month periods from the onset of pupping in September each year to the following year. The complexities of the tag recapture information (e.g. tag-types and capture - recapture methods) as well as tagging methodology have been described in Chapter 5. Mark-recapture data for juvenile sharks are given in Table 8.3 and for adult sharks in Table 8.4. If a shark was tagged as a juvenile, but recaptured as an adult, it was included in the adult dataset. Because of the distinct spatial segregation of juvenile and adult *C.*

taurus (Chapter 2 and Chapter 5) only adult sharks are susceptible to catches within the bather protection nets of the NSB. There are also differences in post-release mortality (Chapter 2) and tag shedding rates (Chapter 6) between the two size classes. For these reasons the CJS model was fitted to both datasets separately as well as to a combined dataset. Only 14 sharks were tagged as juveniles, but recaptured as adults over the 20-year study period. Due to a lack of information on the transition between life history stages, it was not possible to model juvenile and adult captures simultaneously using a multi-state model.

A summary of the input data, estimated from previous Chapters, which were utilised in the construction of the CJS models is given in Table 8.5. A non-reporting rate of 0.33 was used to adjust CJS estimates for the sampling occasions 03/04 and 04/05 (Chapter 7). A reporting rate of 0.5, however, was used for all sampling occasions prior to this period because of the paucity of data used in the estimation of reporting rates. This value is commonly used in tagging studies as a realistic estimate of reporting rate (Denson *et al.* 2002) and was considered appropriate in this study. Given the low number of tag recoveries, in the double tagging experiment in Chapter 6, the tag retention rate (29.0%) estimated for adult sharks was considered an overestimate of tag loss. As a result, the combined tag retention estimate for both juvenile and adult sharks was used instead. This value was considered a more reasonable approximation based on a greater number of tag recaptures.

Table 8.3. Mark-recapture data for juvenile (<1.8m TL) *Carcharias taurus* from 1984 to 2005

Year tagged	Year of recapture																					R_i - r_i
	84/85	85/86	86/87	87/88	88/89	89/90	90/91	91/92	92/93	93/94	94/95	95/96	96/97	97/98	98/99	99/00	00/01	01/02	02/03	03/04	04/05	
84/85		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
85/86			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22
86/87				2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24
87/88					1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32
88/89						0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20
89/90							1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	49
90/91								1	1	0	0	0	0	0	0	0	0	0	0	0	0	18
91/92									1	2	0	0	0	0	0	0	0	0	0	0	0	29
92/93										1	2	0	0	0	0	0	0	0	0	0	0	17
93/94											2	2	0	0	0	0	0	0	0	0	0	33
94/95												4	3	0	1	0	0	0	0	0	0	93
95/96													0	0	0	0	0	0	0	0	0	53
96/97														2	0	0	0	0	0	0	0	26
97/98															2	2	0	0	0	0	0	19
98/99																3	3	0	0	0	0	24
99/00																	2	1	1	0	0	31
00/01																		2	1	0	0	36
01/02																			19	7	3	150
02/03																				19	4	218
03/04																					7	194
m_i		0	0	2	1	2	2	3	2	3	4	6	3	2	3	5	5	3	21	26	14	
mm_i	9	22	26	33	20	50	18	28	18	34	97	47	25	21	27	30	34	176	220	175		
u_i	1120	1120	1120	1118	1119	1118	1118	1117	1118	1117	1116	1114	1117	1118	1117	1115	1115	1117	1099	1094	1106	
n_i	1120	1120	1120	1120	1120	1120	1120	1120	1120	1120	1120	1120	1120	1120	1120	1120	1120	1120	1120	1120	1120	
R_i	9	22	26	35	21	52	20	32	20	37	101	53	28	23	30	35	39	179	241	201		

Table 8.4. Mark-recapture data for sub-adult and adult (>1.8m TL) *Carcharias taurus* from 1984 to 2005

Year tagged	Year of recapture																					R_i - r_i
	84/ 85	85/ 86	86/ 87	87/ 88	88/ 89	89/ 90	90/ 91	91/ 92	92/ 93	93/ 94	94/ 95	95/ 96	96/ 97	97/ 98	98/ 99	99/ 00	00/ 01	01/ 02	02/ 03	03/ 04	04/ 05	
84/85		0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20
85/86			4	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	59
86/87				3	1	3	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	95
87/88					4	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	187
88/89						2	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	100
89/90							7	1	2	1	0	1	2	0	0	0	0	0	0	0	0	236
90/91								4	0	1	1	0	1	1	0	0	1	0	0	0	0	143
91/92									4	2	2	2	0	0	1	2	0	1	0	0	0	147
92/93										4	0	1	2	0	0	0	0	0	0	0	0	118
93/94											7	1	0	4	0	0	0	0	0	0	0	175
94/95												6	2	2	1	0	3	0	0	0	0	102
95/96													6	0	2	1	1	0	2	0	0	160
96/97														2	1	0	0	0	1	0	0	80
97/98															8	2	2	2	0	2	0	132
98/99																5	1	0	0	0	1	80
99/00																	0	0	1	0	0	78
00/01																		1	1	0	0	65
01/02																			2	5	1	72
02/03																				2	4	87
03/04																					3	203
m_i		0	6	4	7	6	8	7	8	11	11	11	14	11	13	10	8	4	7	9	9	
mm_i	22	66	105	193	99	244	144	154	117	178	105	161	70	137	74	69	59	76	86	197		
u_i	853	1018	987	969	926	977	975	796	705	932	732	802	849	812	720	793	731	730	722	724	724	
n_i	853	1083	993	973	933	983	983	803	713	943	743	813	863	823	733	803	739	734	729	733	733	
R_i	22	66	105	197	106	250	152	161	125	187	116	172	84	148	87	79	67	80	93	206		

Table 8.5. Estimates of shore angling catch (SC), post-release mortality (PRM) tag specific tag-type/capture method tag loss (TL^{j}) and non-reporting of tag recaptures (NR) used in the development of unbiased juvenile and adult *Carcharias taurus* CJS models

Bias adjustment	Juvenile model	Adult model
SC	1120	643
PRM	0.043	0.224
$TL^{Double\ tag}$	0.00	0.00
$TL^{PEM\ tag}$	0.053	0.214
$TL^{A\ tag}$	0.061	0.268
$TL^{B\ tag}$	0.104	0.268
$TL^{C\ tag}$	0.123	0.357
TL^{Nets}		0.357
TL^{Dive}		0.306
NR	0.5 (pre-03/04) 0.33 (post-03/04)	

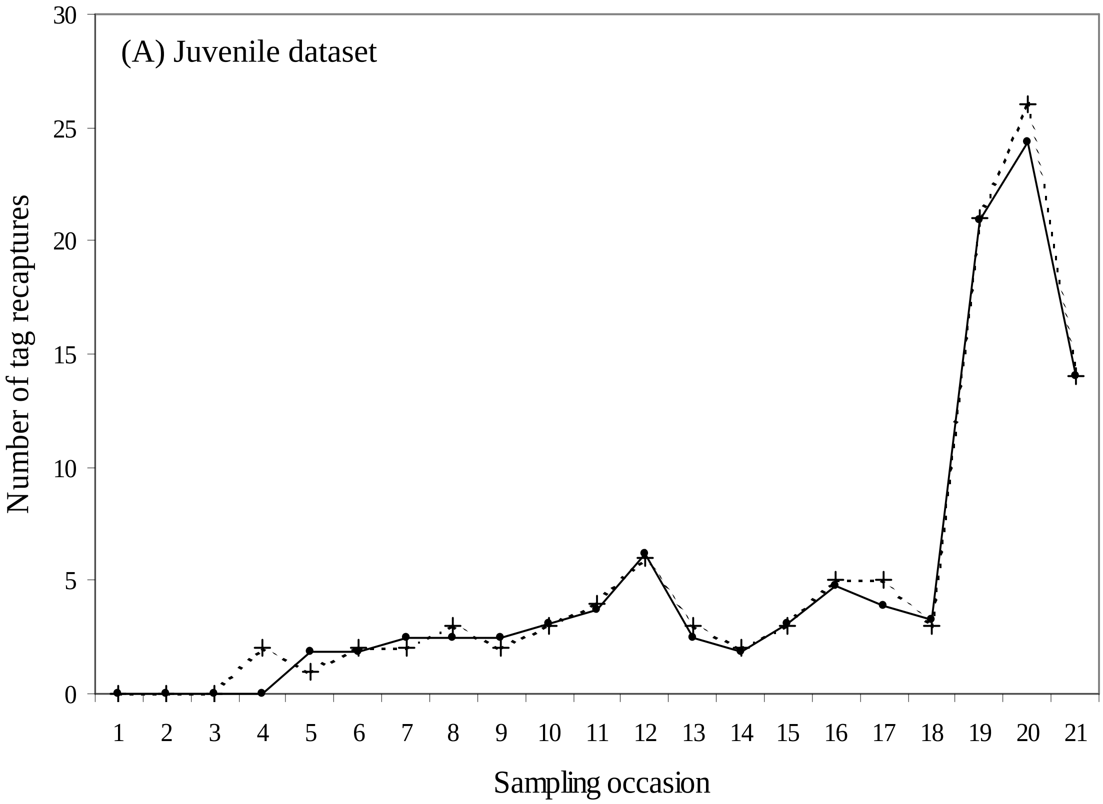
8. 7. Results

8. 7. 1. Model selection

The model comparison statistics for juvenile and adult datasets are given in Table 8.6. The most parsimonious for both life history stages was Model 2 $p(1984-2000,2001-2004)\phi(\cdot)$. The AIC statistic was used to indicate the strength of evidence for modelling the juvenile and adult datasets separately rather than as a combined dataset. The AIC for the aggregated model (Model 2 juvenile + Model 2 adult) was 2660.50, compared to 2694.99 for Model 2 of a combined dataset. This indicates that the two life history stages should be modelled separately, rather than together. Parameter estimates in the following sections are provided only for the selected best model (Model 2) for the juvenile and adult datasets. The predicted number of tag recaptures showed excellent agreement with the observed number for juvenile sharks and a reasonable approximation for the adult dataset (Fig. 8.1).

Table 8.6. Model fits for juvenile and adult CJS estimators, based on probability of capture and survival. κ indicates the number of estimated parameters; -ln L is the log likelihood; AIC is the Akaike Information Criterion measuring model fit; Δ is the difference between AIC and the lowest AIC; w_r are Akaike weights

Dataset	Model	κ	-ln L	AIC	Δ	w_r
Juvenile	1	2	443.04	890.08	1.00	0.24
	2	3	441.54	889.08	0.00	0.39
	3	4	441.19	890.39	1.32	0.20
	4	4	441.41	890.82	1.75	0.16
	5	21	428.02	898.04	9.72	0.00
	6	21	431.87	905.73	17.42	0.00
	7	22	431.85	907.70	19.46	0.00
	8	40	423.68	927.35	41.07	0.00
Adult	1	2	884.72	1773.43	1.98	0.14
	2	3	882.72	1771.45	0.00	0.37
	3	4	881.92	1771.84	0.40	0.30
	4	4	882.36	1772.71	1.27	0.19
	5	21	874.14	1790.29	19.20	0.00
	6	21	877.02	1796.03	24.95	0.00
	7	22	877.01	1798.02	26.97	0.00
	8	40	867.34	1814.69	44.56	0.00



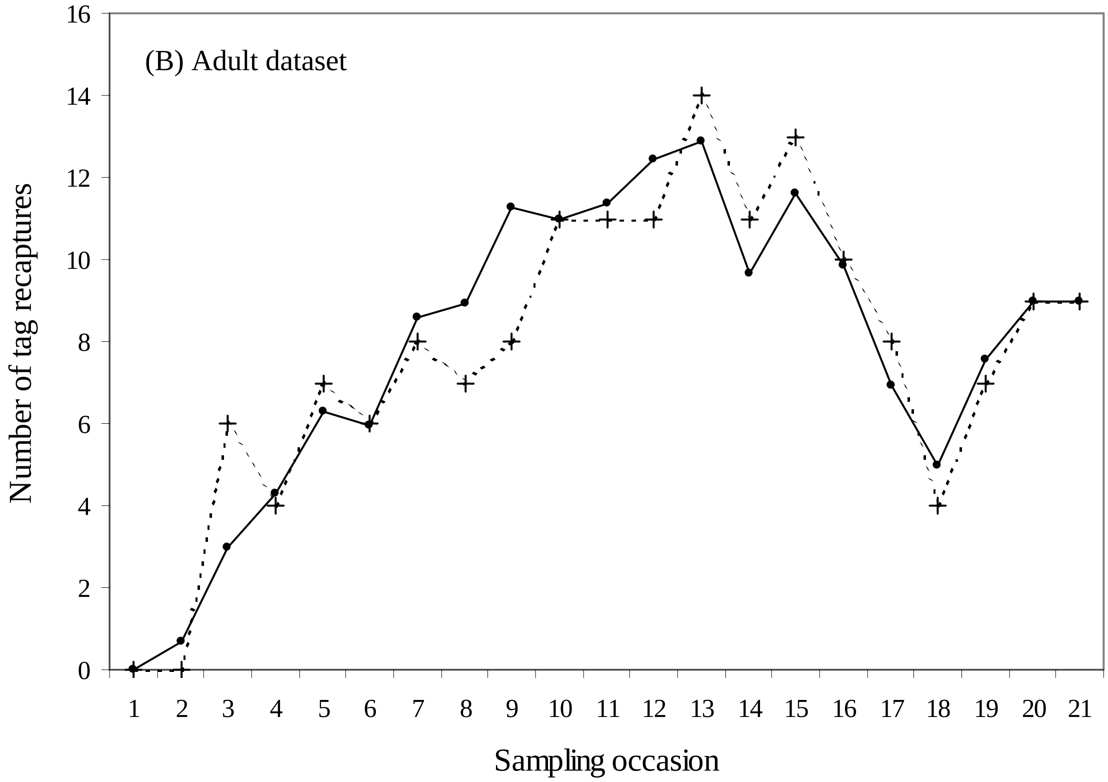


Fig. 8.1. The observed (dashed line) and the predicted number of tag recaptures (solid line) for each sampling occasion for (A) juvenile and (B) adult data sets

8. 7. 2. Survival and probability of capture

The estimates of parameters for the juvenile and adult models are given in Table 8.7. Mean bootstrap estimates for both p_i and ϕ_i were close to the maximum likelihood estimates, indicating that the estimation procedure was relatively unbiased. The estimate of p_i for juvenile sharks increased markedly post-2001, from 0.119 to 0.169. In contrast, p_i for adult sharks remained relatively constant. The estimates of p_{84-00} and p_{01-04} for juvenile sharks were 3.5 and 5 times greater, respectively than for adult sharks. The higher estimate of ϕ_i for adult (0.695), compared to juvenile sharks (0.429) was not surprising. Estimates of survival, however, are "apparent" not "true" survival; for apparent survival to be true survival emigration must not occur (Pollock *et al.* 1990). In this study, juvenile sharks effectively emigrate from the juvenile population when they reach a total length of 1.8 m and become part of the adult population. As a result, the juvenile estimate of survival is an underestimate of true survival. Apart from a possible movement into Mozambique waters, emigration of adult sharks from the South African population is negligible. Consequently, the survival estimate for adult sharks is a reasonable approximation of true survival.

Ad hoc adjustments were made to estimates of both p_i and ϕ_i to correct for bias resulting from PRM, TL^j and NR. PRM increased estimates of both p_i and ϕ_i upwards. The effects were greater for p_i than for ϕ_i. Adult sharks suffered greater post-release mortality than juvenile sharks. As a result, bias adjustments for the parameter estimates were greater for adult compared to juvenile sharks. Tag shedding also resulted in positive adjustments to estimates of ϕ_i, yet had no effect on p_i. Bias adjustments were greatest for C-type tags and for sharks that had been captured in the bather protection nets. A 50% and 33% time dependent tag non-reporting rate increased estimates of p_i, by 100% and 30% respectively, but had no effects on estimates of ϕ_i.

Table 8.7. Maximum likelihood estimates (MLEs) for capture probabilities (p_i) and survival rates (ϕ_i) for (A) juvenile and (B) adult *Carcharias taurus* from Model 2, $p(1984-2000,2001-2004)\phi(\cdot)$. Also shown are estimates of the average, upper and lower 95% confidence intervals and the coefficient of variation (CV) derived from 500 nonparametric bootstrap replicates. Bias corrected estimates to account for post-release mortality (PRM); tag specific tag-type/capture method tag loss (TL^j) and the non-reporting of tag recaptures (NR) are presented

(A) Juvenile *Carcharias taurus*

	Original unadjusted estimates			
	p_{84-00}	p_{01-04}	ϕ_i	
MLE	0.119	0.169	0.429	
Bootstrap average	0.122	0.172	0.428	
Lower 95% C. I	0.078	0.123	0.348	
Upper 95% C. I	0.172	0.250	0.490	
CV	19.73%	18.00%	8.90%	
	Bias-adjusted estimates			
	PRM	TL^j	NR	
			0.50%	0.33%
p_{84-00}	0.124	0.124	0.248	
p_{01-04}	0.175	0.175	0.351	0.228
ϕ_i	0.432			
$\phi_i^{Double\,tag}$		0.432	0.432	
$\phi_i^{A\,tag}$		0.459	0.459	
$\phi_i^{B\,tag}$		0.480	0.480	
$\phi_i^{C\,tag}$		0.489	0.489	
$\phi_i^{PEM\,tag}$		0.456	0.456	

(B) Adult *Carcharias taurus*

	Original unadjusted estimates		
	p_{84-00}	p_{01-04}	ϕ_i
MLE	0.035	0.034	0.695
Bootstrap average	0.035	0.034	0.694
Lower 95% C. I	0.027	0.020	0.642
Upper 95% C. I	0.044	0.050	0.740
CV	12.57%	23.68%	3.65%

	Bias-adjusted estimates			
	PRM	TL^j	*NR*	
			0.50%	0.33%
p_{84-00}	0.040	0.040	0.079	
p_{01-04}	0.039	0.039	0.078	0.051
ϕ_i	0.698			
$\phi_i^{Double tag}$		0.698	0.698	
$\phi_i^{A tag}$		0.912	0.912	
$\phi_i^{B tag}$		0.912	0.912	
$\phi_i^{C tag}$		0.997	0.997	
$\phi_i^{PEM tag}$		0.865	0.865	
ϕ_i^{Diving}		0.948	0.948	
ϕ_i^{Nets}		0.997	0.997	

Due to the difficulties in directly estimating natural mortality rates in sharks, a number of indirect methods have been developed. Five methods were chosen: Hoenig (1983); Peterson and Wroblewski (1984); Chen and Watanabe (1989); Jenson (1996); and Cortés (2000) to obtain comparative estimates of survivorship $\left(S = e^{-M}\right)$ (Table

8.8). Von Bertalanffy parameters from Goldman (2002) were used in each of the five methods, as was the value of t_{max} (40 years). For the Peterson and Wroblewski (1984) method, weights-at-age were assessed by calculating total length at age from the von Bertalanffy growth function and then converting these values into weight using the length-weight regression relationship in Chapter 2 (section 2. 3. 5). Two methods that give age dependent values are those of Peterson and Wroblewski (1984) and Chen and Watanabe (1989). Juvenile estimates of survival were calculated using an age of 2 and adult survival using an age of 20. These ages were used to represent an approximate mid-point for each size class. In the absence of commercial exploitation total mortality (Z) estimated in the Hoenig (1983) calculation can be viewed as an estimation of natural mortality (M).

Table 8.8. Indirect estimates of natural mortality (M) and survivorship (S) for juvenile (J) and adult (A) *Carcharias taurus*. W = body weight, K, t_0 = von Bertalanffy growth parameters and t_{max} = maximum age

Citation	Method	M	S (%)
Hoenig (1983)	$\ln(Z) = 1.44 - 0.982x\ln(t_{max})$	0.11	89.34
Peterson and Wroblewski (1984)	$M = 1.92\,W^{-0.25}$	(J) 0.17 (A) 0.11	(J) 84.54 (A) 89.75
Chen and Watanabe (1989)	$M_{(t)} = \dfrac{K}{1 - e^{-k(t-t_0)}}$	(J) 0.23 (A) 0.12	(J) 79.61 (A) 88.38
Jenson (1996)	$M = 1.6\,K$	0.19	83.06
Cortés (2000)	$M = \dfrac{\log_e(0.01)}{t_{max}}$	0.12	89.13

8. 7. 3. Abundance

Biased and bias-adjusted juvenile and adult population abundances for the 20-year study period are given in Figs. 8.2 and 8.3, respectively. The original, unadjusted annual population estimate for juvenile sharks ranged from 5436 (2001/2002) to 8767 (1988/1989). The overall estimate for the 20-year study period was 6794[1] (95% C.I. = 5031 - 9724). The unadjusted, annual estimate for the abundance of adult sharks was almost three times greater than that of juvenile sharks and ranged from 12126 (1986/1987) to 27029 (1990/1991). The overall estimate for the 20-year study period was 21790[1] (95% C.I. = 17158 – 30745). The greater number of adult compared to juvenile sharks was expected, considering juvenile sharks consisted only of the age classes 0 to 4, while adult sharks incorporated all subsequent age classes to the life expectancy of 40 years. Confidence intervals for estimates of both juvenile and adult abundance were fairly wide, which results from the small number of tag recaptures, particularly in the first half of the study period.

PRM, TL^j and NR all adjusted estimates of abundance negatively. NR was the biggest source of bias for estimates of juvenile abundance. In contrast, TL^j was the primary source of error in the bias adjustment of adult abundance. TL^j had a greater effect on estimates of adult compared to juvenile abundance for two reasons. Firstly, tags are shed at a greater rate for adult sharks, particular from sharks that had been tagged after capture in the bather protection nets. Secondly, the effect of tag loss on estimates of abundance is more pronounced when capture probabilities are low (McDonald *et al.* 2003). The number of adult sharks tagged with C-type tags and from captures in the bather protection nets progressively declined over the course of the study period, particularly in the last 5 years. Tag loss from this tag-type and tagging method were greater than from the other tag-types and capture methods used. As a result, the effects of tag loss on the estimates of adult abundance were more pronounced in the first half of the study period.

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[1] Overall juvenile and adult abundance estimates were calculated by dividing the sum of the annual estimates for each year, by the number of years in the study period. 95% confidence intervals were calculated from 500 bootstrap iterations.

The accumulated effect of PRM, TL^j and NR were to reduce the overall estimate of juvenile and adult abundance for the 20-year study period by approximately 50%. Because of the effects of bias on the estimates of abundance, it is perhaps more insightful to examine trends in abundance, rather than the absolute estimates themselves. Trends in abundance were analysed for only the last 10 years, due to the low number of tag recaptures in the first half of the study. Bias-adjusted (PRM, TL^j and NR) estimates for juvenile abundance remained relatively constant over the 10-year period (test of regression slope, P = 0.49). In contrast, bias-adjusted estimates of adult abundance significantly increased (test of regression slope, P = 0.019).

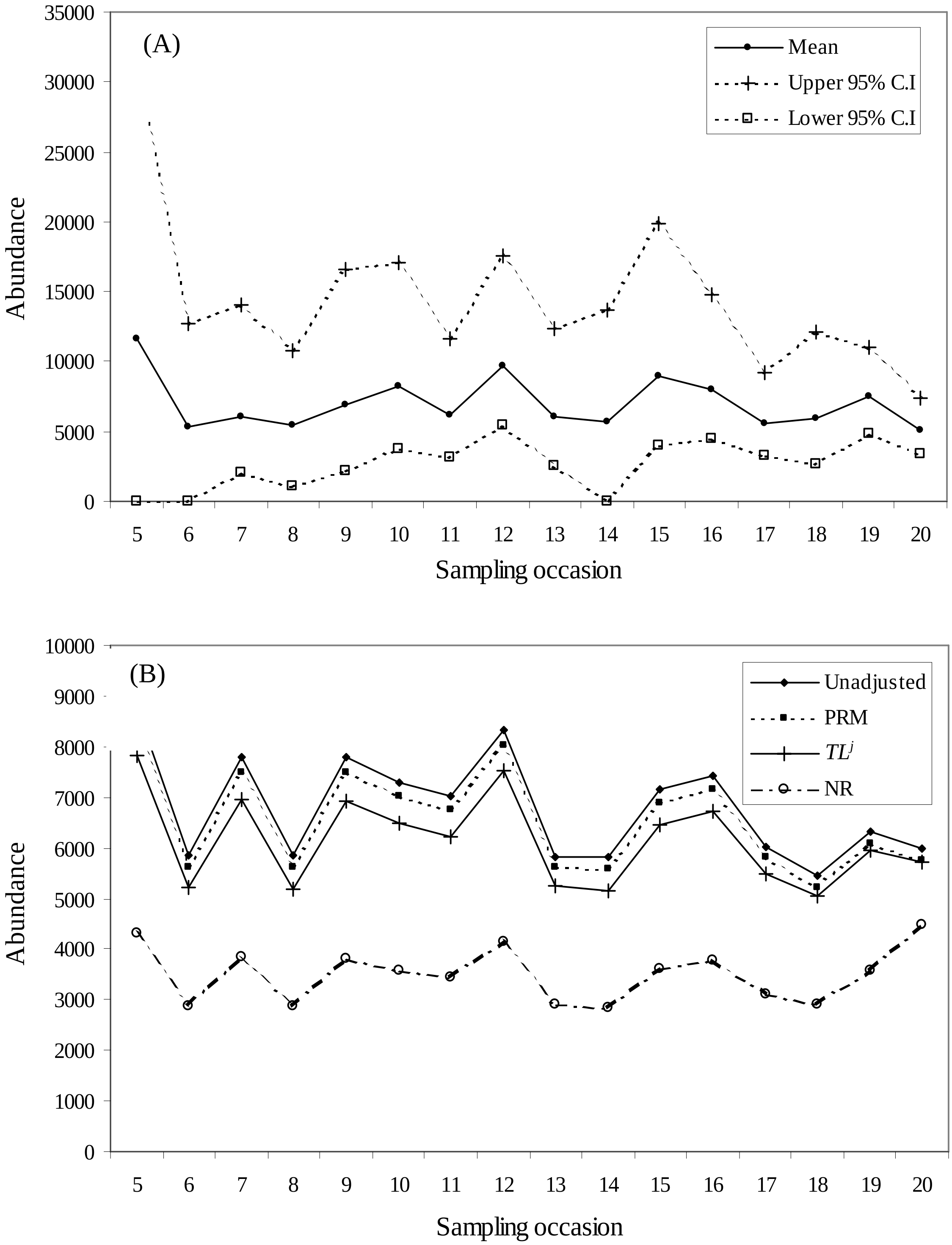
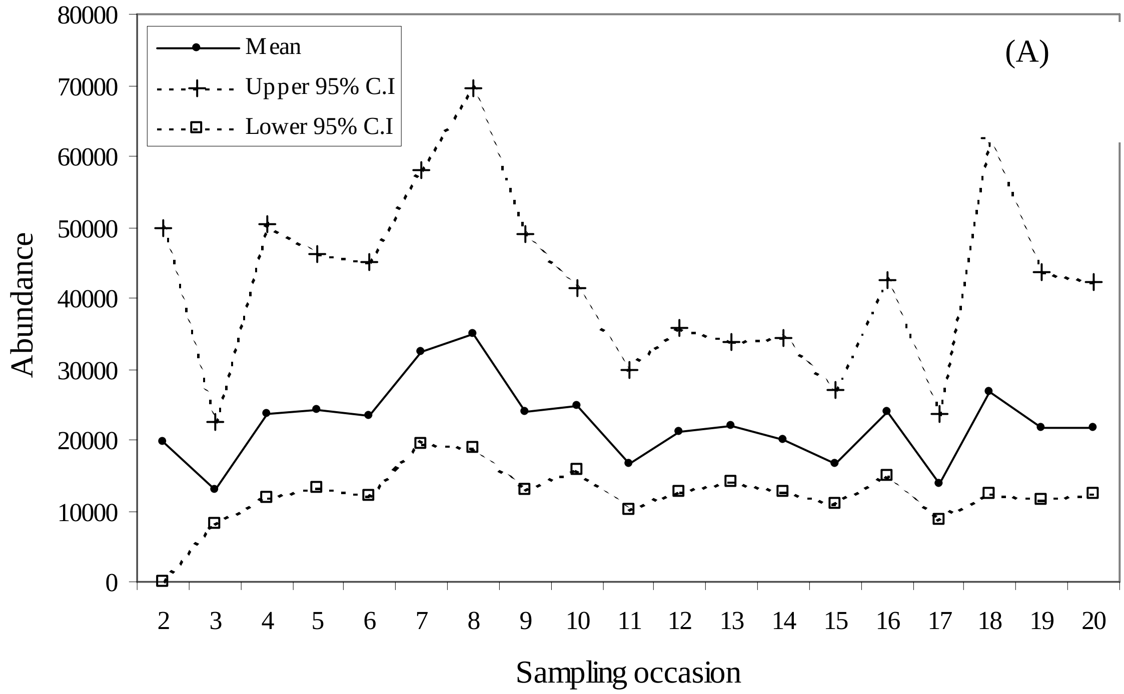


Fig. 8.2. (A) Unadjusted estimates of mean abundance (500 bootstraps) and 95% confidence intervals for juvenile *Carcharias taurus* from 1988/1989 to 2003/2004. (B) Unadjusted and bias-adjusted maximum likelihood estimates of abundance to account for post-release mortality (PRM); tag specific tag-type/capture method tag loss (TL^j) and the non-reporting of tag recaptures (NR)



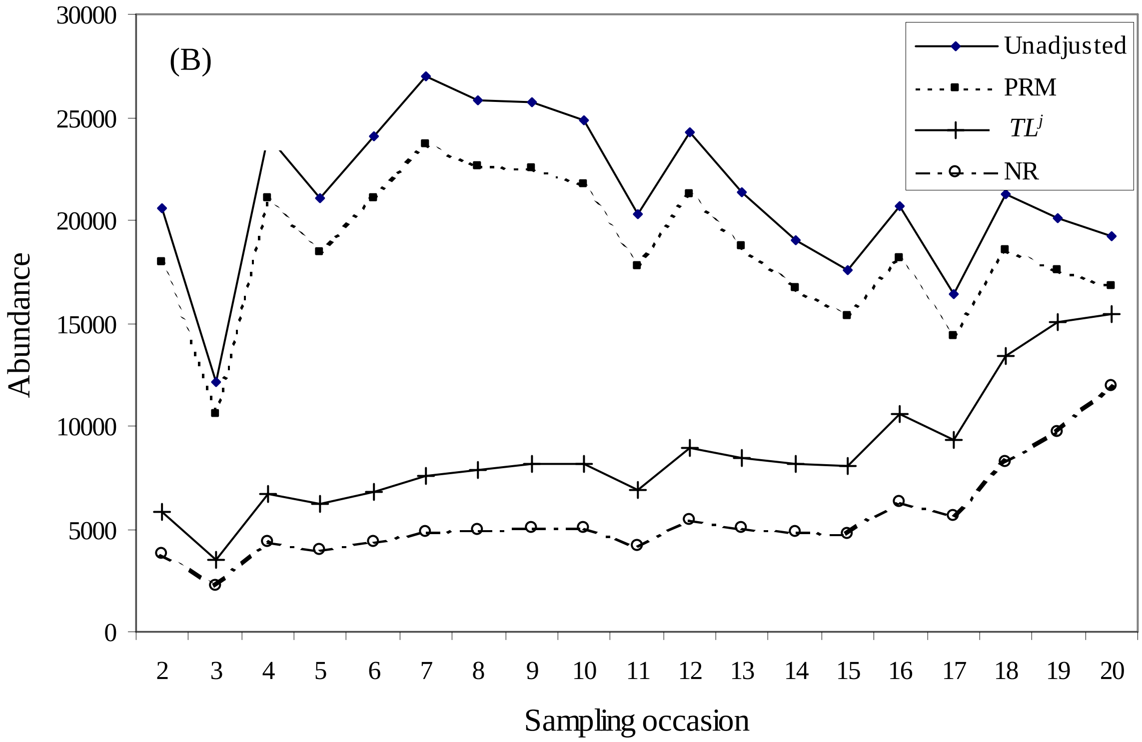


Fig. 8.3. (A) Unadjusted estimates of mean abundance (500 bootstraps) and 95% confidence intervals for adult *Carcharias taurus* from 1985/1986 to 2003/2004. (B) Unadjusted and bias-adjusted maximum likelihood estimates of abundance to account for post-release mortality (PRM); tag specific tag-type/capture method tag loss (TL^j) and the non-reporting of tag recaptures (NR)

8. 8. Discussion

The analysis presented in this Chapter represents the first application of an “open population” mark-recapture model to any species of shark population worldwide. The model provides estimates of survival and abundance, which will provide the first scientific data to support management decisions on a species that is threatened throughout much of its geographical range. The CJS model incorporates information obtained from auxiliary studies on; catches, stock structure, post-release mortality rates, non-reporting rates and tag specific tag type/capture method tag loss to adjust for violation of some of the models assumptions.

The first assumption of the CJS model is that every animal present in the population at sampling time *i* has an equal probability of capture. Catch data and tag recapture information, from Chapters 2 and 5, respectively have illustrated the distinct spatial segregation of the juvenile and adult population. Each component of the population is subject to regional variations in fishing pressure, as well as different methods of capture. For instance, juvenile sharks are only caught by shore-anglers, whereas adult sharks are also caught in the bather protection nets of the NSB. As a result, it was necessary to model juvenile and adult components of the population separately to avoid bias of the equal catchability assumption. A violation of this assumption would result in a negative bias in the estimation of abundance (Pollock *et al.* 1990).

The CJS model that best explained the data for both the juvenile and adult populations was Model 2, in which capture probability varied before and after 2001/2002 and survival was constant. In December 2001, the use of vehicles on beaches was prohibited. As a result of the ban, anglers stated that they fished less for sharks and caught fewer *C. taurus* (Chapter 2). A slight decline in p_{84-00} (0.035) to p_{01-04} (0.034) was evident for adult sharks. In contrast, the p_i for juvenile sharks rather than decreasing, increased from p_{84-00} (0.119) to p_{01-04} (0.169). Rather than detecting a change, as a result of the beach vehicle ban, the increase in juvenile p_i was probably a reflection of the greater number of juvenile sharks tagged by PEM taggers post-2001

(Chapter 5). The more parameterised models (Models 5 to 8), which attempted to reflect changes in the attitudes of fishermen from one of catch-and-kill to a catch-and-release ethic, and a gradual reduction in the number of bather protection nets, performed poorly. A possible explanation is that these sources of mortality have had little effect on the survivorship of either the juvenile or adult *C. taurus* populations. Alternatively (and possibly more likely), the effects of these changes in fishing pressures have been masked by the relatively small tag-recapture datasets used in this study.

The AIC statistic indicated a significant difference in the parameter estimates of $\hat{p}_i$ and $\hat{\phi}_i$ between the juvenile and adult datasets. Juvenile sharks tended to concentrate within rocky reef habitats within the nursery areas and exhibit a high degree of site fidelity. In comparison, adult sharks had a more dispersed distribution pattern extending along the entire coastline, possibly reflecting their wider ranging movements along the coast. Shore anglers had a greater probability of landing juvenile compared to adult sharks, which because of their size and strength allowed them to break tackle and be lost once hooked. As a result of these factors, it was not surprising that the bias-corrected estimates of p_i for juvenile sharks were three to four times greater than for adult sharks.

The juvenile bias-corrected estimate of $\phi_i^{PEM\,tag}$[2] (0.456), appears too low for a species that is born at $1\mathrm{m}\,TL$ in apparently well protected shallow–water areas. Simpfendorfer (1999) obtained similarly low survivorship values for male (0.466) and female (0.571) Australian sharpnose sharks (*Rhizoprionodon taylori*) using a catch curve analysis. Manire and Gruber (1993) estimated survival for an unexploited population of young of the year lemon sharks (*Negaprion brevirostris*) of 0.475. This estimate, however, as in the current study, is probably an underestimate as a result of emigration of juvenile sharks into the adult population when they reach maturity. The survival estimated here is therefore apparent survival (1-mortality minus emigration)

[2] Tag loss in Chapter 6 was estimated for sharks tagged by PEM taggers. As a result, bias-corrected estimates of $\phi_i^{PEM\,tag}$ are considered the appropriate value to compare with estimates of ϕ_i from other studies.

rather than true survival. Unfortunately, the data required to assess the juvenile-adult transition at present is unavailable and as a result, it is not possible to estimate true survival and emigration separately.

In a demographic analysis of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*), Cortés (1995) found that the population would only remain in equilibrium if first year survivorship was 51%. Juvenile survivorship values much lower than 50% are thus unlikely, especially for a larger species of shark such as *C. taurus*, which is less susceptible to predation. Indirect estimates of juvenile survival using the methods of Peterson and Wroblewski (1984) and Chen and Watanabe (1989), gave much more realistic estimates for true survival of 84.54% and 79.61% respectively. Grant *et al.* (1979) obtained similar direct estimates of survival (0.87) for the School shark (*Galeorhinus australis*). This is a small species of shark that would perhaps be expected to have a natural mortality rate comparable to that of juvenile *C. taurus,* because of its similar size and susceptibility to predation.

Ignoring a negligible movement into southern Mozambique, the adult population of *C. taurus* is closed to emigration. As such, the bias corrected estimate for adult survival, $\left(\phi_i^{PEM\ tag}\ \ 0.865\right)$ in contrast to that for juveniles reflects true, rather than apparent survival. This estimate is in good agreement with all five of the indirect estimates that ranged from 0.836 to 0.897. Aasen (1963) obtained a similar direct estimate of survival (0.852) for the Porbeagle shark (*Lamna nasus*) a species of similar size and life history characteristics to *C. taurus*.

Due to the uncertainty in the extent and effect of non-reporting rate and tag loss on the CJS estimates of abundance, it is perhaps prudent to discuss trends in population sizes rather than absolute estimates. Trends in juvenile abundance for both unadjusted and bias-adjusted estimates remained relatively constant over the course of the study period. Similar trends were evident for the adult population, however, bias-adjusted estimates of abundance indicated a significant (P = 0.019) increase in population growth over the last 10-years. Indications of a healthy population are supported by catch-rate, size and population trends evident from catches in the bather protection nets of the NSB (Dudley 2002, Dudley and Simpfendorfer in press). This information indicates that neither component of the population is being subjected to excessive fishing pressures. The ban on beach driving in 2001, which restricts the ability of the majority of fishermen to catch sharks, combined with a catch and release ethic and a continued reduction in the number of bather protection nets along the coast are all positive indicators that the minimal fishing pressure this species is subjected to will continue to decrease in the future. Nonetheless, the life history characteristics of this species make it particularly susceptible to any form of overexploitation. Additional mortality, even at low levels for a slow growing, late maturing species such as *C. taurus* could reduce the population growth rate to values of $\lambda < 1.0$ resulting in severe population declines in a very short time period (Baum *et al.* 2003). As a result, the current protective legislature prohibiting the commercial exploitation of this species should remain in place.

Despite a steady increase in the abundance of sharks in the adult component of the population, there was no corresponding increase in the juvenile component. This was surprising given the strong relationship between adult stock size and births in shark populations. The juvenile population consisted of sharks less than four years old, whereas the adult component incorporated all subsequent age classes to the life expectancy of 40 years. The lack of correlation in the population trends between the two life history stages may simply be a product of this crude division of the population into two unequal age brackets. Greater information on the transition of individuals between the life history stages would enable the development of a multi-state model in which the two components of the population could be modelled simultaneously.

Like many other studies on shark populations, the results reported in this Chapter must be considered preliminary because of the uncertainty in many of the models input values. Firstly, there is uncertainty in the capture sample sizes. The crude capture sample sizes estimated in Chapter 2 from a survey of shore anglers had wide 95% confidence limits and was only calculated for the 2002/2003 fishing season, yet applied to the entire study period. This uncertainty was accounted for by replicating capture sample sizes from a normal distribution, using the mean and standard deviation of the numbers caught. Despite the vehicle beach ban in 2001, there was no evidence of a marked reduction in the number of sharks caught compared to previous years. This was as a result of a small core of dedicated competitive anglers who catch the majority of sharks (Chapter 2). A gross miscalculation in sample size, or marked variations in the annual number of sharks caught could result in either an over or underestimate in the calculation of the CJS parameters. Secondly, there is uncertainty in the number of sharks that die from post-release mortality estimated in Chapter 2. However, because the numbers that are expected to die are minimal, this uncertainty will have little effect on the estimates of either $\hat{p}_i$ or $\hat{\phi}_i$. The fraction of fish that are expected to suffer post-release mortality is constant over all tagging episodes so there is no effect on the trends in abundance.

In addition to these uncertainties, the CJS estimates of p_i and ϕ_i^j were bias corrected for non-reporting and tag specific tag-type/capture method tag loss using simple *ad hoc* procedures. Not only are *ad hoc* procedures an unsatisfactory method for extending estimates in either direction, but there were also uncertainties in the accuracy of the estimation for both tag loss in Chapter 6 and reporting rate in Chapter 7. An additional problem with respect to tag loss was that it was only estimated directly for PEM tagged sharks. Tag shedding rates for the other tag-types and capture methods used in the study, were adjusted using a scaling factor based on a comparison in the percentage of tag recaptures between the specific tag-type and PEM tagged sharks (Chapter 5). Adjusted tag shedding rates, particularly for adult sharks tagged with type C-type tags and from captures in the bather protection nets resulted in very high bias-adjusted estimates of survival. As a result, it would be more appropriate in future studies to conduct a series of double tagging studies for each specific tag-type and capture method used.

Chapter 9

Conclusions and Future work

9. 1. Summary

In the absence of fishery dependent data, capture-recapture methods are commonly used to provide reliable estimates on population size and survival. This information, which is critical in making management decisions concerning endangered species, however, is lacking for almost all shark populations owing to insufficient data on catches and stock structure. This thesis focused on the development of a Cormack-Jolly-Seber (CJS) model. In conjunction with a tagging study, five auxiliary studies were conducted to investigate stock structure, post-release mortality, tag shedding, and tag-reporting rate. The results from each of the studies were used to correct for any violations of the models assumptions to provide the first minimally biased estimates of survival and abundance for *C. taurus* in South Africa.

In Chapters 2, 3 and 4, the underlying stock structure of *C. taurus* was investigated through a series of fishery surveys. The surveys were designed to obtain information on the spatial and seasonal distribution patterns of *C. taurus* for its full geographical range along the South African coast. The juvenile component of the population (< 1.8 m TL) inhabited a geographically distinct nursery area between Kei River and Cape Town. The distribution of the adult component of the population (> 1.8 m TL) was less restricted and ranged along the entire east coast from Kosi Bay on the South African/Mozambique border to Cape Town. Fishing effort and capture methods were heterogeneous over the geographical range of *C. taurus*. As a result, the juvenile component of the population is subjected to capture primarily by shore anglers, whereas the adult component is also vulnerable to capture in the bather protection nets of the NSB. The CJS model assumes that every animal in the population has the same probability of capture. To avoid a violation of the equal catchability assumption, the juvenile and adult components of the population were modeled separately to avoid a negative bias in the estimates of abundance.

Capture sample sizes for each time period in the CJS model were estimated from a survey of coastal club-affiliated shore anglers and catches in the bather protection nets. Other components of the recreational fishery were excluded from the sampling-frame, based on the assumption that they caught few *C. taurus*. Capture sample sizes were estimated under the conditions existing when the study was conducted. Due to annual variations in fishing effort, particularly with respect to the vehicle beach ban in 2001, catches have undoubtedly varied over the course of the 20-year study period. This uncertainty was accounted for by replicating capture sample sizes from the normal distribution using the estimated catch in 2002/2003 and its standard deviation.

The CJS model assumes that all animals have the same probability of surviving between sampling periods. Although *C. taurus* is released alive after capture, angling practices result in stress from the effects of capture, fatigue and prolonged handling times. As a result, not all of the sharks released survive, and a fraction suffers post-release mortality. Post-release mortality will negatively bias estimates of survival and positively bias estimates of abundance because of a reduction in the number of tagged sharks available for recapture. Based on a series of questions related to the "last *C. taurus*" the angler had caught, estimates of post-release mortality were markedly lower for juvenile compared to adult sharks. Differences between these life history stages provided further evidence that they should be modelled separately.

In Chapter 5, the movement patterns of the different life history stages were investigated from an analysis of tag-recapture data from the ORI and PEM collaborative tagging programs. Significant differences were observed in the percentage of recaptures between the different tag types, tagging programs and capture methods to tag sharks. Temporal and spatial movement patterns as well as the percentage of tag recaptures differed markedly between juvenile and adult sharks. These results strengthened the suggested proposal to model the two-size classes separately. Individuals from both the juvenile and adult populations displayed philopatric behaviour for specific parts of their ranges, including gestating and nursery areas. This has important implications for the conservation and management of *C. taurus*, because anthropogenic perturbations have a more dramatic effect on species within a localised area.

The CJS model assumes that all tagged individuals retain their tags. A double tagging experiment in Chapter 6 was conducted to assess the possibility that this assumption had been violated. Tag loss was estimated separately for juvenile and adult sharks and found to be significantly different. Tag-shedding biases survival estimates downwards, because the observed number of recaptures is lower than the actual number of recaptures expected, assuming all tags are retained. Estimates of survival for both juveniles and adults were corrected for tag-type/capture method specific tag loss using the *ad hoc* method of Arnason and Mills (1981). These bias adjusted estimates were then used to estimate abundance.

In Chapter 7, a telephone survey was conducted to estimate regional tag-reporting rates. The survey was conducted in conjunction with an on-site questionnaire survey to obtain important additional information on the reasons for non-reporting and the performance of the different tag types used in the study. Annual time-dependent non-reporting rates were used to adjust CJS model estimates of probability of capture and abundance. The multimethod approach used in this study was designed to solicit the maximum amount of data for the minimal expenditure of effort and money. Reporting rates were highest in regions where anglers worked in close association with scientists and increased in response to aggressive outreach and educational programs.

In the absence of appropriate fisheries data, demographic models have typically been used to obtain management related information for shark stocks. Previous demographic analyses that have estimated vital rates for *C. taurus* are Smith *et al.* (1998), Goldman (2002), Mollet and Cailliet (2002), Cortés (2002) and Otway *et al.* (2004). A limiting factor to the use of these models, however, is a reliable estimate of natural mortality, which has been based on indirect rather than direct methods. Indirect estimates of natural mortality ranged from 0.104 to 0.185, corresponding to a survival probability ranging from 0.901 to 0.831. Mortality is a key parameter in understanding the dynamics of any population. Incorrect estimates can drastically effect a model's predictions concerning the response of the population to various anthropogenic perturbations. The similarity between the direct estimate for adult survival obtained in this study (0.865) and the indirect estimates, suggest that management strategies based on the predictions of the demographic models would be reasonably accurate.

Although the estimates of abundance have been bias-corrected for the effects of post-release mortality, tag shedding and tag-reporting rate, they should still be viewed with caution, due to the uncertainties in capture sample sizes and the *ad hoc* methods used to adjust estimates of survival and probability of capture. Despite these facts, they still provide an important insight into the order of magnitude and population trends over the 20-year study period. Firstly, they indicate that the population in South Africa consists of tens of thousands and not hundreds of individuals, as is the case in eastern Australia. Secondly, they provide evidence that the population has remained relatively constant, or potentially has even increased in recent years, rather than declined, as result of excessive fishing or other threatening processes.

The model predictions were supported by angler interviews, which indicated that the majority of anglers believed that *C. taurus* was an abundant species and that its population had remained the same, if not increased, over the last two decades. Further evidence of a healthy stock was evident from a significant increase over the last 20 years in the number of *C. taurus* caught in competitions and a constant CPUE and mean size of *C. taurus* caught in the bather protection nets of the NSB.

Few *C. taurus* were caught in either the commercial or recreational fishery. The number of *C. taurus* caught in the bather protection nets has been dramatically reduced in recent years with a reduction in the number of netted beaches and their removal during the annual sardine migration. Fishing mortality has also decreased in the competitive shore fishery with the advent, in the last decade, of a catch and release ethic by the majority of anglers. A reduction in fishing effort and associated mortality was also evident in response to the vehicle beach ban in 2001. As a result of the ban not only did the number of registered club anglers dramatically drop, but the majority of those remaining stated that they now fished more for non-cartilaginous species. These trends are all positive indications that the minimal fisheries related mortality this species is currently subjected to, will only continue to decrease rather than increase in the future. The only worrying trend was the increased targeting of sharks by commercial ski boat anglers, in response to a reduction in the number of allotted linefish licences. Despite all these factors, the life history characteristics of *C. taurus* make it particularly susceptible to any form of exploitation. As a result, the current protective legislature, prohibiting the commercial exploitation of this species should remain in place.

Collaborative tagging programs are the only cost effective method for studying a species that is not exploited commercially and is only caught recreationally in relatively low numbers. Nevertheless, there are some significant data quality issues inherent in programs where volunteer anglers do the majority of tagging. In this study variability in the percentage of tag recaptures due to differences in tagger performance; the use of a variety of different tag types, different capture methods used to obtain sharks for tagging, and regional variations in reporting rate, were identified as potential sources of error. These limitations can be improved over time through increased outreach activities, a greater collaboration between anglers and scientists in the development of the tagging programs, the use of correct tag types, and the elimination of taggers who perform poorly.

Insightful information concerning the catchability of *C. taurus* and its spatial and temporal distribution patterns were obtained from anglers and divers Local Ecological Knowledge (LEK). This information is complimentary to that obtained from conventional scientific approaches, which are often hampered by a lack of suitable fisheries data. Although limited to simple observations LEK is a potentially valuable resource to marine science. Limitations in the data obtained from both systems of data collection underscore the need for achieving some form of synthesis between them.

9. 2. Future work

Information collected from the fishery surveys in Chapters 2, 3 and 4 provide the most complete description of the spatial and seasonal distribution patterns for *C. taurus* for its full geographic range along the South African coast. There are still large gaps in our knowledge, however, of the migratory pathways, in both time and space, for mature male sharks, the location of winter nursery areas and offshore movement patterns. Future surveys should concentrate on obtaining additional catch data from the boat-based fishery sectors and data deficient regions, such as the Transkei (Areas 7 and 8), to help answer these remaining questions.

The system of scoring that was developed in Chapter 2 to estimate post-release mortality rates was a subjective process. Ideally, a sample of competitively caught fish should be collected at the release site, held in pens, and observed for a few days to estimate mortality that released fish might be expected to suffer. This method, however, would be impractical for a large species of shark such as *C. taurus*. Future studies could possibly involve tracking released sharks using telemetry to provide a more accurate estimation of delayed mortality.

An analysis of tag recapture data in Chapter 5 provided evidence that adult female and juvenile sharks are philopatric to the same pupping areas. The movement patterns of juvenile sharks are limited and there was little mixing between adjacent populations. As a result of these movement patterns, the juvenile population possibly constitutes a metapopulation of heterogeneous components. In the present study the juvenile population was modelled as one homogenous stock, due to the low number of tag recaptures. Future studies, however, with additional data should take into consideration the spatial distribution of catch on a finer level. Rather than modelling the juvenile population as a single stock, regional populations could be modelled individually. Management actions could then be spatially structured based on a concept of “geographic neighbourhood”. Genetic samples could be taken from mature female and juvenile sharks to investigate the extent of site fidelity in natal philopatric behaviour, and test for genetic divergence among sharks from different nursery areas.

Unfortunately only a small number of sharks were tagged as juveniles, but later recaptured as adults. As a result, the juvenile and adult components of the *C. taurus* population were modelled separately. Additional information on the transition between life history stages, in the future, will possibly facilitate the development of more complex multi-state models.

One of the critical assumptions of the CJS model is that animals do not loose their tags. A variety of different tag types and capture methods were used in the study, however, tag loss was only directly estimated from a double tagging experiment for PEM B-type tags. Tag loss for the alternative tag types and capture methods were crudely estimated using a scaling factor, which was based on the percentage of tag recaptures compared to the percentage of PEM B-type tag recaptures. A simple *ad hoc* method was then used to bias correct estimates of tag type/capture method specific survival. There are two problems to this approach that should be improved upon in future models. Firstly, *ad hoc* methods are unsatisfactory and tag loss should be modeled along with other population parameters in the model. Secondly tag loss should be estimated directly for each of the tag types and capture methods used in the study.

Results from the on-site questionnaire survey suggested that tag wounds and biofouling growth were more prominent for some tags than others. Future research into tag wounds will help evaluate tag performance and the suitability of tag choice. Extensive tag biofouling may lead to an increased shedding rate due to the effects of drag. Methods to reduce biofouling should be investigated. An interesting avenue of research would be an analysis of the community structure of biofouling growth to explore the possibility of its use as “biological marker”.

Reporting rate is often assumed to be constant over time and geographic area (Hoenig *et al.* 1998). Reporting rates in this study suggested that both these assumptions are incorrect. An improvement to the CJS model used in this study would be to incorporate regional differences in reporting rates. This could be achieved in conjunction with the modelling of separate sub-stocks of the juvenile population according to the degree of philopatry. Non-reporting was the biggest source of bias in the estimation of abundance. Future work should focus on reducing non-reporting rates, particularly within the recreational and commercial boat-based fishery. This could be achieved by regular visits to the fishing ports and ski-boat clubs to speak to skippers and crews. The implementation of a well-publicised tag reward system may provide more accurate estimates of reporting rates compared to the creel survey used in Chapter 7.

Finally, this thesis represents the first attempt at estimating survival and abundance for any shark population worldwide utilising an open population model. The integrated, multimethod study provided information on stock structure, catches, post-release mortality rates, tag shedding and non-reporting rates in a manner that provided a greater understanding of the population dynamics of *C. taurus* in South Africa. Information from each of the studies was used to identify and adjust for possible violations of the CJS model. Cooperative tagging programs have typically been limited to a simple descriptive analysis of movement patterns. The multimethod approach used in this thesis could be applied to other tagging programs to estimate critical population parameters for other recreationally exploited species elsewhere in the world.

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Appendix 2. 1

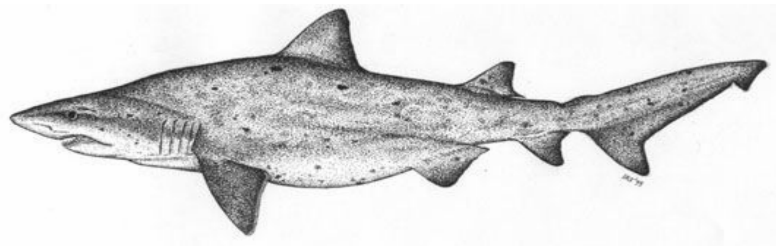
Competitive shore angling questionnaire

Date	Site	QN

RAGGEDTOOTH SHARK QUESTIONNAIRE

(For *ALL* rock-and-surf fishermen)

Matt Dicken Research Scientist Bayworld Port Elizabeth South Africa
+27 41 5840650 Ext 228 OR +27 72 2146215



South Africa is one of only a few places left on earth where a healthy, sustainable population of raggedtooth sharks remains.

- **Please take a couple of minutes to fill out this questionnaire**
- **The information gained from this questionnaire will provide invaluable data, which will be used to estimate the population size of the raggedtooth Shark ("raggie") in South Africa**

Return **the questionnaire by:**

- **Giving it personally to Matt Dicken**
- **Giving to club officials**
- **Posting it to: Matt Dicken**

  Port Elizabeth Museum

  P.O. Box 13147

  Humewood 6013

Please fill in your contact details				
Name		**Age**		
Contact no.		**Club**		
Do you fish fixed venues?	**Yes 1**		**No 2**	
Number of years club fishing?				
Fish for sharks prior to joining a club?	**Yes 1**		**No 2**	

Please tick (✔) the appropriate boxes

	Yes 1	No 2
1. Have you EVER caught a raggedtooth shark?		

If YES, please fill in the following questions…

	Yes 1	No 2
2. Do you actively fish for raggedtooth sharks?		
3. If YES, why?		

	Less than 10 1	10 - 50 2	More than 50 3
4. How many raggies have you caught?			

Think of the *<u>LAST</u>* raggedtooth shark that you caught

5. WHERE did you catch it? ___________________________________				
6. WHEN did you catch it? (mm/yy)_________________	Day time 1		Night time 2	
7. How many rods were you using?				

	Hook in mouth 1	Foul Hook (where on shark) 2
8. How did you catch your LAST Raggie?		
	Yes 1	**No 2**
9. Were you fishing for a raggie		
10. If NO, what were you fishing for?		
11. What strength was your main line?		
	Yes 1	**No 2**
12. Were you fishing with a leader line?		
13. If YES, what was the strength of the leader line?		

	Yes 1	No 2
14. Did you catch your LAST raggie on a wire trace?		

15. If YES, was it…	1	Plastic coated Breaking strain 60		5	Piano wire 2 strand	
	2	Plastic coated Breaking strain 70		6	Piano wire 3 strand	
	3	Plastic coated Breaking strain 90		7	Piano wire 4 strand	
	4	Plastic coated Breaking strain 120		8	Piano wire 5 strand	

16. How many hooks did you catch your LAST raggie on?	1		2	

17. If you used two hooks, how were they arranged?	Hooks tied back to back		1
	One fixed hook, one sliding		2
	Two fixed hooks, one behind the other.		3
	Other_____________________		4

18. What size hook or hooks, did you catch your LAST raggie on? Please indicate which size hook was first if using two hooks.	6º		1
	7º		2
	8º		3
	9º		4
	Other _______		5

19. What bait did you catch your LAST raggie on?	
20. At what time did you start fishing and how long (hours) did you fish for?	

	Yes 1	No 2
21. Did you catch more than one raggie on THAT day?		
22. If YES, how many?		

	Yes 1	No 2
23. Did you hook, but not land any raggies?		
24. If yes, how many?		

25. How do you know that these lost fish were raggies?			
26. How did you *weigh* the LAST raggie you caught?	Scale (hook in gills)		1
	Scale (hook in dorsal fin)		2
	Hammock / stretcher		3
	Other		4
	Guessed weight		5
27. How much did the LAST raggie you caught weigh? (Honestly!)	0 - 10kg		1
	10 - 20kg		2
	20 - 50kg		3
	50 - 100kg		4
	100+ kg		5

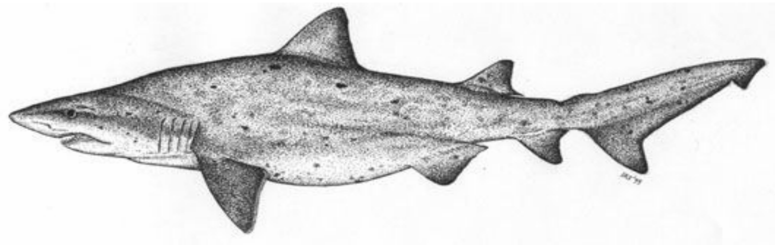
	Male 1	Female 2	Unknown 3
28. What sex was the LAST raggie you caught?			

	Return to water 1	Other 2
29. What did you do with the LAST raggie you caught?		

	Yes 1	No 2
30. Did it swallow the hook?		
31. Was there blood coming from its gills?		
32. Was it out of the water for more than 10 minutes?		
33. Had it sustained any injuries from capture i.e. cut by rocks?		
34. Did you gaff it?		
35. Did it die on the beach?		
36. Do you think that you did everything you could to make sure it survived if you returned it to the water?		
37. Did it swim away strongly?		
38. Were you fishing in a competition?		

	Fixed venue 1	Club 2	Other 3
39. If YES, what type of competition was it?			

40. If you gaffed the LAST raggie you caught, please indicate on the diagram below *where* you gaffed it.



41. Why did you gaff it where you did?	

	Strongly agree 1	Agree 2	Disagree 3	Strongly disagree 4
42. At the moment, it is accepted practice to return raggies to the water unharmed straight after capture. What is your opinion?				

43. On the day that you caught your LAST raggie, what was the water temperature?	0-15ºC		1
	15-20ºC		2
	20ºC+		3
44. On the day that you caught your LAST raggie, what was the colour of the water?	Dirty (chocolate)		1
	Murky (off-colour)		2
	Clean		3
45. On the day that you caught your LAST raggie, what were the water conditions?	Flat		1
	Choppy		2
	Big swell		3

46. When you caught your LAST raggie what was the tide status i.e. low, high, mid, pushing, falling etc.?	

	Very abundant 1	Abundant 2	Scarce 3	Very scarce 4
47. How would you rate the population of raggies in your province?				

	Population greatly increased 1	Population increased 2	Population the same 3	Population declined 4	Population greatly declined 5
48. If you have been fishing for more than 20 years, compare the population of raggies then to now in your province.					

				Yes 1	No 2
49. If you have been fishing for more than 20 years, do you think people still fish in the same areas for raggies?					
50. If NO, please state which areas are not fished anymore, or new areas that have become popular and why?					
	Fish a lot less 1	Fish less 2	Has not affected fishing 3	Fish more 4	Fish a lot more 5
51. How has the banning of 4x4s on the beach affected the number of HOURS you fish for sharks?					
	Catch a lot less 1	Catch less 2	Catch the same 3	Catch more 4	Catch a lot more 5
52. How has the banning of 4x4s on the beach affected the NUMBER of raggies you have caught?					
53. Why has the banning of 4 x 4 vehicles affected your fishing for raggies?		Access 1		Security 2	
		Yes 1		No 2	
54. Will you now fish more for edibles?					
55. If YES, why?					

		Fish often 1	Fish rarely 2	Do not fish 3
56. Do you fish for raggies in these months? Please tick the appropriate boxes.	Jan			
	Feb			
	March			
	April			
	May			
	June			
	July			
	August			
	Sept			
	Oct			
	Nov			
	Dec			
57. Why do you spend more time fishing for raggies in some months than other months?				

58. Please state, what you think are ideal conditions for catching a raggie		
	Yes 1	**No 2**
59. In the months you have indicated that you rarely, or do not fish for raggies do you fish for other species e.g. edibles using live bait / heads / fillets?		
	Yes 1	**No 2**
60. If YES, have you ever accidentally caught a raggie in these months?		
61. If YES how many have you caught?		
62. Where is the best place to catch SMALL raggies (less than 10kg)?		
63. What time of the year?		
64. Where is the best place to catch LARGE raggies (more than 115kg)?		
65. What time of the year?		
	Yes 1	**No 2**
66. Have you EVER caught a TAGGED raggedtooth shark?		
If YES, did you…		
67. Record and report the number?		
68. If NO, why didn't you report the number?		
69. Return tagged shark to the water?		
70. Leave tag in shark?		
71. Know what to do with the tag?		

	Yellow disc tag 1	**Yellow spaghetti Tag 2**	**Red spaghetti Tag 3**
72. What type of tag was it?			

	Yes 1	**No 2**
73. Biofouling on tag?		

74. Had the tag damaged the shark in any way? Describe	

Appendix 4. 1

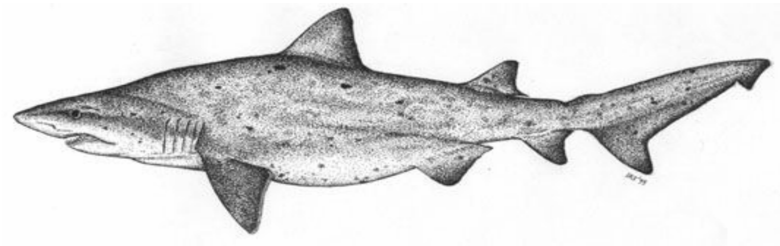
SCUBA diving and spearfisher questionnaire

Date	Site	QN

RAGGEDTOOTH SHARK QUESTIONNAIRE

(For *all SCUBA Divers and spearfishers)*

Matt Dicken Research Scientist Bayworld Port Elizabeth South Africa
+27 41 5840650 Ext 228 OR +27 72 2146215



Please help to record the sharks in our area. This research aims to record the occurrence of raggedtooth sharks off the South African coast. Please visit the Web address http://fishwatch.tripod.com/raggie to complete a more detailed questionnaire.

***Return* the questionnaire by:**

- **E-mail: raggedtoothshark@bayworld.co.za**
- **Post to Matt Dicken, Bayworld PO Box 13147, Humewood 6013, PE**
- **Fax to (041) 584 0661**

Please fill in your contact details			
Name		**Contact no.**	
Dive Club (if applicable)			
Address			

1. Please list ALL the dive sites that you have dived, and mark with a tick each site at which you have seen a raggie. List the dive spot where you see the most raggies as 1, the next best as 2 and so on in decreasing order.

1			9			17		
2			10			18		
3			11			19		
4			12			20		
5			13			21		
6			14			22		
7			16			23		
8			16			24		

For the dive spot you indicated in Q1 as the best place to see raggies, please answer the following questions.

2. Name of Reef		**3. Closest Town**	
4. Latitude		**5. Longitude**	
6. Distance from shore		**7.Depth raggies seen**	
8. Briefly describe the dive site features, ie Wreck, cave's, gullies, pinnacles etc and where raggies are commonly observed.			

9. For the dive spot you indicated in Q1 as the best place to see raggies, please tick the appropriate box on how many raggies you see in each month relative to the others. If you do not dive in a certain month please leave that month blank.

	Do not see 1	See 1-5 2	See 6-10 3	See10-20 4	See > 20 5
Jan					
Feb					
March					
April					
May					
June					
July					
August					
Sept					
Oct					
Nov					
Dec					

10. What size classes of raggies do you see? Please asterisk the commonest size class	0-1m 1	1-2m 2	2-3m 3	3m+ 4
11. Have you ever seen a tagged raggie?				
12 If yes please give details, on the shape and colour of the tag, where tag was located on the shark and where and when you saw the tagged shark?				

*** If you have any additional information on raggie sightings, please use the back of this sheet to list them.**