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***Seasonal and lunar trends in catch rates of sharks caught in
the protective gill nets off KwaZulu-Natal, South Africa***

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TABLE OF CONTENTS

Declaration	i
Abstract	ii
Introduction	
Biological rhythms	1
Natal Sharks Board and netting	4
Literature review	6
Key questions	7
Materials & Methods	
Catch data	9
Lunar information	9
Tools	10
Statistical analysis	11
Results	
All species combined	13
<i>Carcharhinus obscurus</i> (dusky shark)	16
<i>Carcharias taurus</i> (spotted ragged tooth shark)	18
<i>Sphyrna lewini</i> (scalloped hammerhead shark)	20
<i>Carcharhinus brevipinna</i> (spinner shark)	22
<i>Carcharhinus limbatus</i> (blacktip shark)	24
<i>Carcharhinus brachyurus</i> (copper shark)	26
<i>Sphyrna zygaena</i> (smooth hammerhead shark)	28
<i>Galeocerdo cuvier</i> (tiger shark)	30
<i>Carcharhinus leucas</i> (bull shark)	32
<i>Carcharodon carcharias</i> (white shark)	34
<i>Carcharhinus plumbeus</i> (sandbar shark)	36
<i>Carcharhinus amboinensis</i> (java shark)	38
<i>Isurus oxyrinchus</i> (mako shark)	40
Discussion	42
Conclusion	48
Acknowledgements	50
Literature cited	51

DECLARATION

I declare that the research produced in this thesis is my own original work except where otherwise acknowledged. I am the senior author and principal contributor to all aspects of the thesis. The catch data used for the analyses are property of the Natal Sharks Board.

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ABSTRACT

A retrospective statistical analysis of catch and effort data for sharks captured in protective gill nets along the KwaZulu-Natal coastline was carried out with the objective to establish if the frequency of shark catches is related to different phases of the moon and secondly to season. All of the most commonly netted shark species (*Carcharhinus obscurus*, *Carcharias taurus*, *Sphyrna lewini*, *Carcharhinus brevipinna*, *Carcharhinus limbatus*, *Carcharhinus brachyurus*, *Sphyrna zygaena*, *Galeocerdo cuvier*, *Carcharhinus leucas*, *Carcharodon carcharias*, *Carcharhinus plumbeus*, *Carcharhinus amboinensis*, *Isurus oxyrinchus*) displayed seasonal trends. When the numbers of sharks captured were pooled peak numbers were caught during the months of May – July and October – February. For all species, significant changes in catch rate, in relation to shifting phases of the moon, were found with the highest catch rate being recorded in the last quarter and the lowest during full moon. However, when separated by sex, males had the highest catch rate in the first quarter and lowest in full moon while females displayed the same pattern as the combined sexes. This difference is possibly a result of more females being captured in the nets. Findings nevertheless show that certain shark species have high catch rates under specific moon phases. The changes in catch rates are likely explained by the biology of each species. Known visual predators show high catch rates during full moon, while new moon is related to higher catch rate of species more associated with turbid habitats.

INTRODUCTION

Biological rhythms

Periodical or cyclical occurrences in nature are common and form the basis of several biological responses, such as timing of physiological processes, migrations and changes in behavior. The year, month and day are examples of periodic occurrences caused by relative positions of the earth, moon and sun to each other. These astronomically induced periodicities ultimately govern biological rhythms. Seasonal periodicity is the recurring time interval between seasonal events taking place, such as a particular meteorological condition (*e.g.* precipitation and temperature) or the migration of certain species. Seasonal events vary in rhythmicity on a greater scale than the coinciding positioning of the sun and earth, sometimes more than a month, occasionally affecting the time and extent of seasonal behavior (Alcock 1993) such as migrations. The relative position of the sun and the moon also produce gravitational tidal forces on the earth, causing a cyclic rise and fall of the surface of bodies of water such as lakes and the ocean as the earth rotates. These in turn, lead to changes in the water level and consequentially produce water currents, the source of many ecological and behavioral responses. Although high tides and low tides occur roughly twice per day, the periodicity of these is more than half of a day length and hence progressively shifts out of phase with the day and night-cycle. Extremes in water surface levels caused by tides also vary with the phase of the moon, being maximal when the sun, moon and earth form a line, *i.e.* around full moon and new moon. These are near-monthly events, which in turn initiate interrelated cyclical responses in the marine environment, *e.g.* at spring tides and neap tides (Cowley 2001). Tidal currents present favorable conditions for the transport of for instance larvae, which are carried away from the high-risk areas of the intertidal zone and shallow waters where predation is substantial, to the safer waters offshore (Gonçalves *et al.* 2003, Stevens 2003). This is often correlated with a specific moon phase and/or season, and

increases the chances of evading predators. At the same time, prey availability is likely increased at high tides, thereby escalating the presence of predators at this time. Thus it is a matter of optimizing the timing of either event by both predator and prey.

Favorable light conditions will assist a visual predator in locating prey, whereas low-light conditions will logically benefit the prey species.

The circadian rhythm is a well-known endogenously controlled rhythm in organisms linked to physiological processes such as hormonal production and brain activity, as well as behavior. This rhythm is based on a day-night period and is endogenously maintained in the organism unless isolated over an extended period of time from external stimuli, *e.g.* the light - dark cycle, to synchronize the internal rhythm. In an ecological context, an interesting question in this regard is whether the behavior of a particular organism reacts directly to the stimuli, or is primarily controlled by the internal “clock” (Tarling *et al.* 1999). A means of testing this is to isolate the organism from the external stimuli over a time in a controlled setting, which is often done in aquaculture research by manipulating the particular stimuli to optimize growth (Dalley 1979 as cited in Naylor, 1999), but regardless of establishing the determining factor it is clear that the specific associated behavior has a selective advantage. Migrations in the marine environment take place in the forms of anything from small-scale daily vertical locomotion of plankton in the water column to long inter-oceanic seasonal migrations. Seasonal migrations are usually associated with breeding and feeding, whereas short-cycled daily migrations typically involve foraging and prey avoidance, taking advantage of changing light conditions or tides. Phototactic movement is a direct response to a light source such as solar or lunar light and aids visually adapted marine organisms in many aspects. Whether for instance tidal currents play a primary role in spatial movement of fish in the photic zone, the direct influence from light is also likely very important for its adapted behavior. It is useful to

distinguish between the lunar or solar influence by either *direct* (i.e. light) or *indirect* (i.e. tides) control on organisms whenever possible. As the sun presents more frequent and stronger periods of light than of the reflection from the moon, the solar variable is a stronger rhythm than the lunar variable. Even so, examples of species with a lunar component are common in the marine environment and play an important role not only in an ecological aspect, but also in marine resource exploitation and management.

One of the best known examples of the behavior of an organism synchronized with multiple rhythmic components is the spawning of the Palolo worm (*Palola viridis*), a polychaete worm which has annual, lunar, daily and tidal rhythm components (Bentley *et al.* 1999). The event is very predictable as it takes place largely during three days around the times of the third quarter of the moon that occur over a six to seven week period in October and November (Caspers 1984). Another common example of predictable time of spawning with a lunar component is that of some species of corals (Twan *et al.* 2003). Coral mass spawning forms the basis for immense ecological responses, as the behavior and distribution of organisms on higher trophic levels are altered during the period of gamete release. Among crustaceans there are several species of crabs that show a lunar pattern of synchronized reproduction (Adamczewska and Morris 2001, Stevens 2003, Skov *et al.* 2004), polychaets (Levinton 1982) and prawns (Griffiths 1999). Example of prawns with a lunar distribution pattern (Jerling and Wooldridge 1992) and green algae (Togashi and Cox 2001) also exists. Among fishes there are also instances of species with a lunar component (Rooker *et al.* 1996, Masterson *et al.* 1997, Okamura *et al.* 2003, Rahman *et al.* 2003, 2004, Miller and Skilleter 2006, Vinagre *et al.* 2006).

As some predators, such as sharks, typically constitute the highest trophic level in an ecosystem, an interesting question is whether their response to environmental cues is direct or

a consequence of changes in behavior of their prey species. Prey migration, as would be expected, has a strong influence on the distribution and movements of its predatory species (Horning and Trillmich 1999) and subsequently the predator will often show a correlation with the same environmental cue. The understanding of these relationships form fundamental tools in fisheries management strategies and for dictating conservation efforts (Naylor 2005). By enumerating the abundance of an organism at various phases of the moon (Gaudreau and Boisclair 2000) one can attempt to establish a correlation. Alternatively, manipulating organisms with an artificial light during various phases of the moon (Nabli *et al.* 1999) can be used to gain knowledge of whether the light characteristic itself exerts a direct influence, separate from other physical effects the moon has.

Natal Sharks Board and netting

The coast of KwaZulu-Natal, South Africa, has for many years been subjected to shark attacks on people, and as a consequence the Natal Sharks Board (NSB) was founded in 1964 with the objective of reducing the frequency of attacks. By implementing protective gill nets along the most visited beaches (Fig. 1) the organization has since proven very effective in protecting people from sharks, and as such is regarded as a successful initiative. Shark nets are deployed approximately 400 m off the beach in water depth around 10-15 m in two rows parallel to the shore. Each net is typically 214 m long and has a stretched mesh of 51 cm, thereby targeting the larger and potentially dangerous sharks. The ecological cost is, however high because the number of sharks and other marine species not considered dangerous are also caught in the nets. Several alternative methods of protecting beach patrons have been tested (Smit and Peddemors 2003), but netting remains the most effective, and is therefore still in use. The most efficient means of preventing non-targeted species being caught is by removing the nets altogether. This is done during the annual “sardine run”, an event where

pilchard (*Sardinops sagax*) shift their distribution to the eastern part of the coast and congregate off the coast of KwaZulu-Natal (Armstrong *et al.* 1991). With this mass-congregation of pilchard follows also the intensified presence of predators, such as dolphins and sharks, and the protective gill nets are temporarily removed and beach patrons notified.

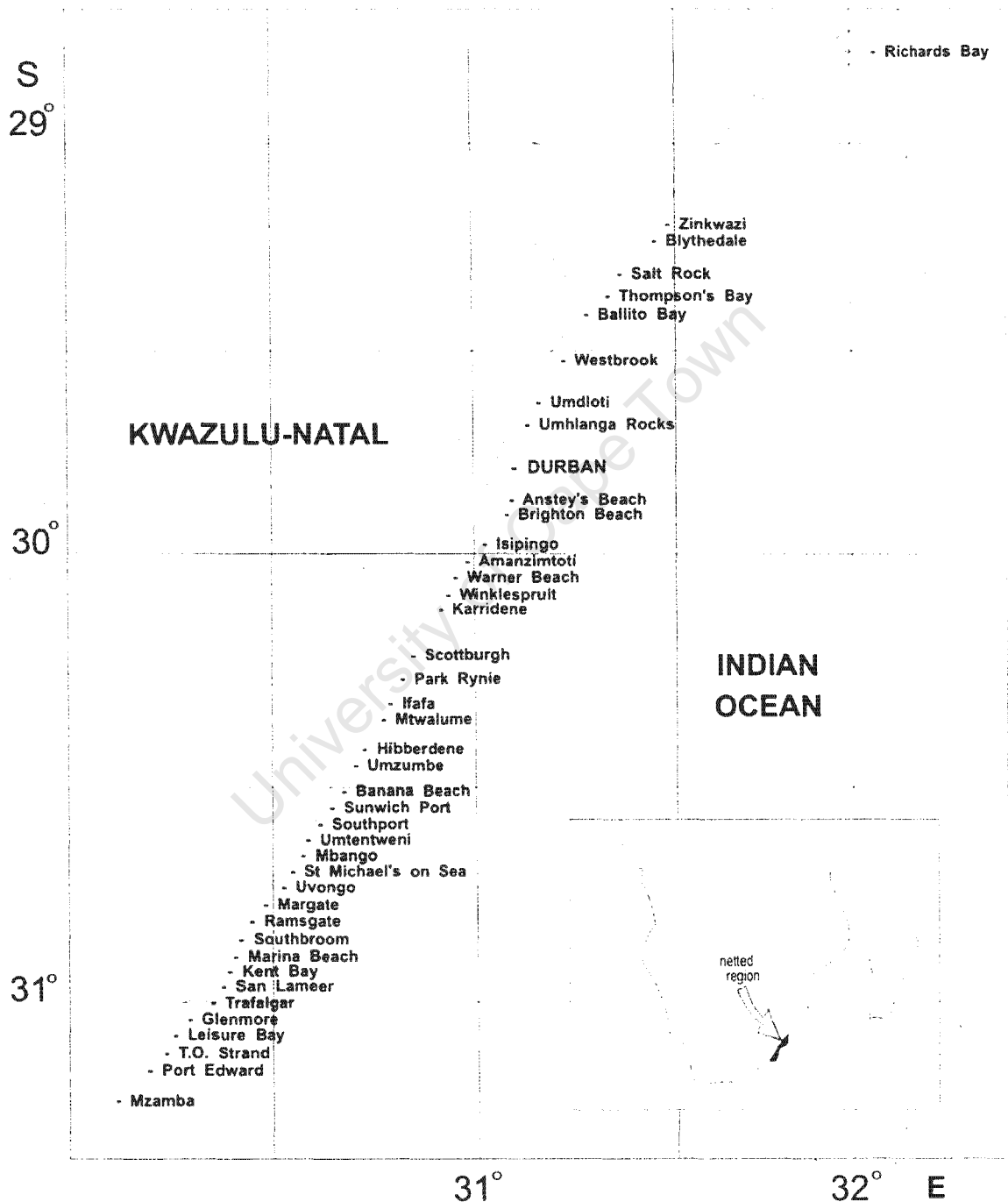


Fig. 1: Beaches in KwaZulu-Natal with protective gill nets employed and serviced (Source: Natal Sharks Board).

Literature review

An initial search for published work on marine organisms' responses to moon light revealed that the majority of papers were written on bony fish. The electronic search engines used were Web SPIRS, SilverPlatter's Biological Abstracts, Biological Abstracts Agriculture, Zoological Records, Bio One, Science Direct, Google, Yahoo, Scirus and ScienceMag. Queries were done with two or several combinations of the following key words: *lunar*, *moon*, *cycle*, *phase*, *marine*, *shark* and *elasmobranch*, and yielded a total of 546 articles. When subdivided into categories most of the research appears to have been conducted on bony fish (43%), while invertebrates (39%), plankton (7%), and other research (11%) such as on socio-economics, birds, mammals, and fishery accounts for the rest. In many studies the lunar variable is included as only one of several environmental parameters investigated.

Relatively little published literature specifically on sharks and environmental variables affecting their distribution and behavior was found. Davies (1963) compared shark attacks in Natal in relations to number of people utilizing the beaches, the seasonal influx of dangerous shark species and sea temperature. He found that elevated sea temperature drew more bathers to the beaches concurrently with the frequency of attacks increasing. However, no account of the moon phase in relation to shark attacks was investigated.

Pyle *et al.* (1996) compared the light intensity of the moon with frequency of great white shark sightings and attacks on pinnipeds at the Farallon Islands off California, by direct visual observations of attacks, applying a score from 1 to 100 as an estimated measure of light intensity reflected from the moon. Linear multiple regression in multivariate models were used to assess the effect of the moon, as well as other environmental variables, on sightings

and attack frequency. It was found that the number of sightings increased with decreased moonlight. However, questions were raised of whether the shark activity generally increased with reduced visibility, or if the prey had less ability of detecting the shark during these conditions. The great white shark is assumed to be mainly a diurnal hunter from previous observations and anatomical studies of retinal structure (Gruber and Cohen 1985).

In 2001 a presentation was given by Noggle at the annual meeting of the American Elasmobranch Society titled "The Influence of Tidal Stage and Lunar Phase on the Frequency of Shark Attacks". No publication has resulted from this study (Burgess, personal communication, Sep. 2004).

Cliff *et al.* (1996) compared environmental parameters such as El Nino – Southern Oscillation (ENSO) with shark net catches of great white sharks in KwaZulu-Natal, by applying an index of ENSO to quantify this parameter. The resulting Southern Oscillation Index (SOI), and in addition sea surface temperature, average rainfall and fishing effort were then analyzed in relation to shark catches. A relationship between the annual catch rates and the annual SOI values were evident, at least for most of the time period, with El Niños being followed by low catches.

The changing distribution of sharks in response to a particular lunar phase, in addition to other environmental factors, is valuable for the NSB when planning shark net deployment strategies. The objective of the project is to investigate any association between moon phases and the catch frequency of sharks experienced by the NSB.

Key questions

In this study the key questions asked are:

- Is there a relationship between moon phases and catch rates?
- Are some shark species significantly more frequently represented in the catches during a particular moon phase?
- Is there a significant difference between male and female sharks caught at a particular phase of the moon?

An attempt is made to answer these by statistically analyzing historical catch data in relation to the particular phase of the moon at the time of capture. An updated review of seasonality is also included to assist in determining in what months catches were highest.

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MATERIALS & METHODS

Catch Data

Data on sharks caught in the protective gill nets off the KwaZulu-Natal coast were obtained from the NSB. The catch data covered 26 years of fishing effort (1978 - 2003) and included all individual sharks recovered by meshing personnel (staff tending to the shark nets) of the NSB during this time. Records on date of capture, location of catch, species, sex and shark length, as well as the state of the shark, were registered. The database consisted of one record for each individual shark catch, totalling 30540 records. With such a number of reliable records this is one of the best shark catch datasets available worldwide. Although the database included 23 different shark species caught, some rare species were caught in too low numbers to make any reliable statistical inference for our study. For present purposes only the 13 most commonly caught species are therefore included (Table 1) where the total number of each species caught exceed 1% of all sharks netted by the NSB.

Species	n	% of total caught	Male	Female	Unknown
Dusky shark (<i>Carcharhinus obscurus</i>)	6030	19,8	2072	3575	383
Sand tiger shark (<i>Carcharias taurus</i>)	5052	16,6	1818	3136	98
Scalloped hammerhead shark (<i>Sphyrna lewini</i>)	3704	12,1	2436	1052	216
Spinner shark (<i>Carcharhinus brevipinna</i>)	3200	10,5	1499	1620	81
Blacktip shark (<i>Carcharhinus limbatus</i>)	2697	8,8	1230	1428	39
Copper shark (<i>Carcharhinus brachyurus</i>)	2676	8,8	1417	1192	67
Smooth hammerhead shark (<i>Sphyrna zygaena</i>)	1943	6,4	815	1050	78
Tiger shark (<i>Galeocerdo cuvier</i>)	1267	4,1	375	845	47
Bull shark (<i>Carcharhinus leucas</i>)	1172	3,8	514	621	37
White shark (<i>Carcharodon carcharias</i>)	934	3,1	399	498	37
Sandbar shark (<i>Carcharhinus plumbeus</i>)	556	1,8	188	364	4
Java shark (<i>Carcharhinus amboinensis</i>)	357	1,2	181	170	6
Mako shark (<i>Isurus oxyrinchus</i>)	348	1,1	228	109	11

Table 1. Shark species caught in shark nets 1978 – 2003 included in this study.

Lunar Information

Historical data on moon phases were downloaded from the NASA/Goddard Space Flight Center online Sun-Earth Connection Education Forum, Maryland 20771 USA, 20 Sep. 2004.

(<http://sunearth.gsfc.nasa.gov/eclipse/phase/phases.1901-2000.html>). The dataset contained date and time of day (UTC) for each of the four major moon phases. As the data used here stem from catches made in KwaZulu-Natal, with Durban as the centre of the area, this is regarded as one system for the purpose of this study (D. Laney - South African Astronomical Observatory. Personal communication, 21 Oct. 2004) and the dataset was consequently adjusted to Durban time by adding two hours to UTC.

The moon phases were given with an exactness of hour and minute at the height of the phase. However, such precision is superfluous to requirements as only the date of servicing the nets is available. It was assumed that the illumination by the moon would differ little from the apex for that particular phase on one day to the previous, or next, or even two or three days at each end. Hence one moon phase is assumed to end only when the next supersedes it and the time of the transition to the next was interpolated for each one. A lunar cycle is the time between one specific phase of the moon until the same phase appears again, which on average is approximately 29.5 days later. For the analysis this time was divided into quarters, each quarter representing a particular phase of the moon to compare with the catch frequency at the time.

Tools

Microsoft Excel 2000 was used for initial dataset management and manipulation. Microsoft Visual Basic 6.3 was then applied for coding the sub-routine necessary to re-generate samples for the bootstrap technique and Statistica 7.0 was used for the statistical analyses and tests for significant differences in the dataset.

Non-meshing days (i.e. rough weather at sea, days when personnel were not working) are counted as zero catch in the dataset. Sharks that were found after non-meshing days were not

included in the lunar analysis as the time of actual catch could not be established with any certainty.

Changes in catch rate over time were determined from the data and tested for significant variations by assessing the correlation between fishing effort and actual catch number. Seasonal patterns for each species and potential differences in sex ratio were examined, indicating sexual migration and segregation changing with season.

The dataset uses a rating system for the condition of the shark when found in the nets. This ranges from (1) alive at capture, (2) fresh dead, (3) starting to rot, (4) rotten, (5) skeleton to (6) scavenged remains. From these we may estimate an approximate time of capture when given the date at which the nets were serviced. Since the nets are only attended to during weekdays and days when sea conditions permit, the time a shark remains in a net may occasionally extend to several days. In order to reduce the margin of error for the time actually captured, only sharks found in condition 1 or 2 were included in the lunar analysis.

Statistical analysis

Significance in discrepancy of the average catch rates between the four general moon phases were determined by applying one-way ANOVA. Analysis of variance was used to test for significant differences between means of multiple independent samples. Due to the high number of days with zero captures, the catch frequencies were not normally distributed, but showed a bimodal negatively skewed distribution, and hence did not fulfill the assumptions required for applying ANOVA. This necessitated using a bootstrapping technique (Efron & Tibshirani 1993, Quinn & Keough 2002) by randomly re-sampling the available dataset many times (i.e. at least 1000), with replacement, using the original sample size. The computed values for the statistic form an estimate of the sampling distribution of the dataset. Averages

of the re-sampled distributions then formed the basis for using ANOVA and the results were compared using the Tukey's HSD test.

In order to establish patterns for sharks caught by the shark nets in general, all species were initially combined for the analysis. Subsequently, analyses for each species and each sex were carried out and tested for significant patterns between species.

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RESULTS

All species combined

A total of 30540 sharks were caught in the nets from 1978 – 2003. Mean annual catch for the species included in this study was 1173.6 individuals (range 513-2267). The number of live sharks at time of meshing varied notably between species (range 2.6 - 38.0%) and the survival rate for each species is specified in subsequent sections of the results. Long-term trends in annual catch patterns for the 13 species used in this study are described in Dudley *et al.* 2006.

Fig. 2 shows the seasonal patterns of catches. Most sharks were caught in July ($n=4035$) while April yielded the lowest number of shark catches ($n=1795$). August presented the most significant change in number of sharks netted with a 55% drop from the preceding month. The sharpest increase in catches took place from April to July. Males constituted 44%, females 52% and unknown sex 4% of the catch. Females dominated catches to a varying degree during all months except January and February, where males dominated.

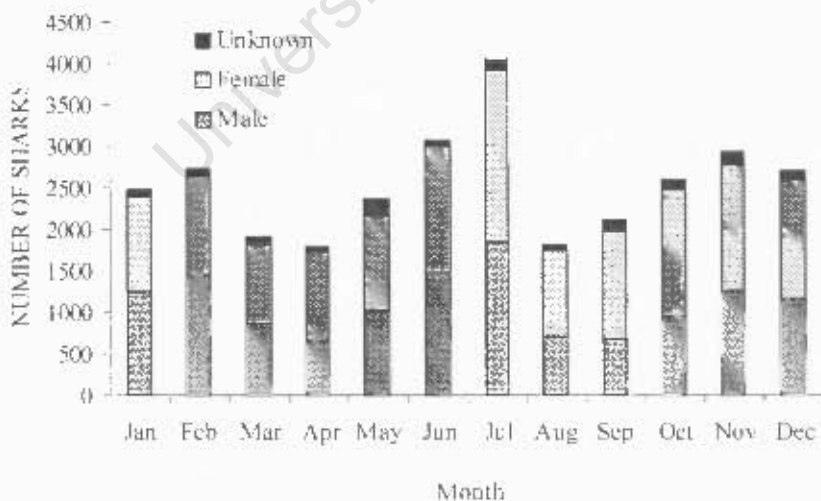


Fig. 2: Monthly catch pattern of sharks netted (1978-2003)

The catch rates for all species combined relative to the lunar cycle are shown in Fig 3.

Sharks were caught most frequently ($p < 0.05$, $F = 596.92$, $d.f. = 3$) during the last quarter of the moon. This was also the case for female sharks ($p < 0.05$, $F = 1060.85$, $d.f. = 3$), whereas males showed a higher catch rate during the first quarter ($p < 0.05$, $F = 316.10$, $d.f. = 3$). Shark catches were markedly lowest during full moon regardless of sex, although this was most notable for females, which showed the highest deviation from the average catch rate during this particular phase of the moon. The first quarter and last quarter of the moon presented the biggest spread in catch rate. For the combined sexes there was little difference in catch rates between the first and the last quarter.

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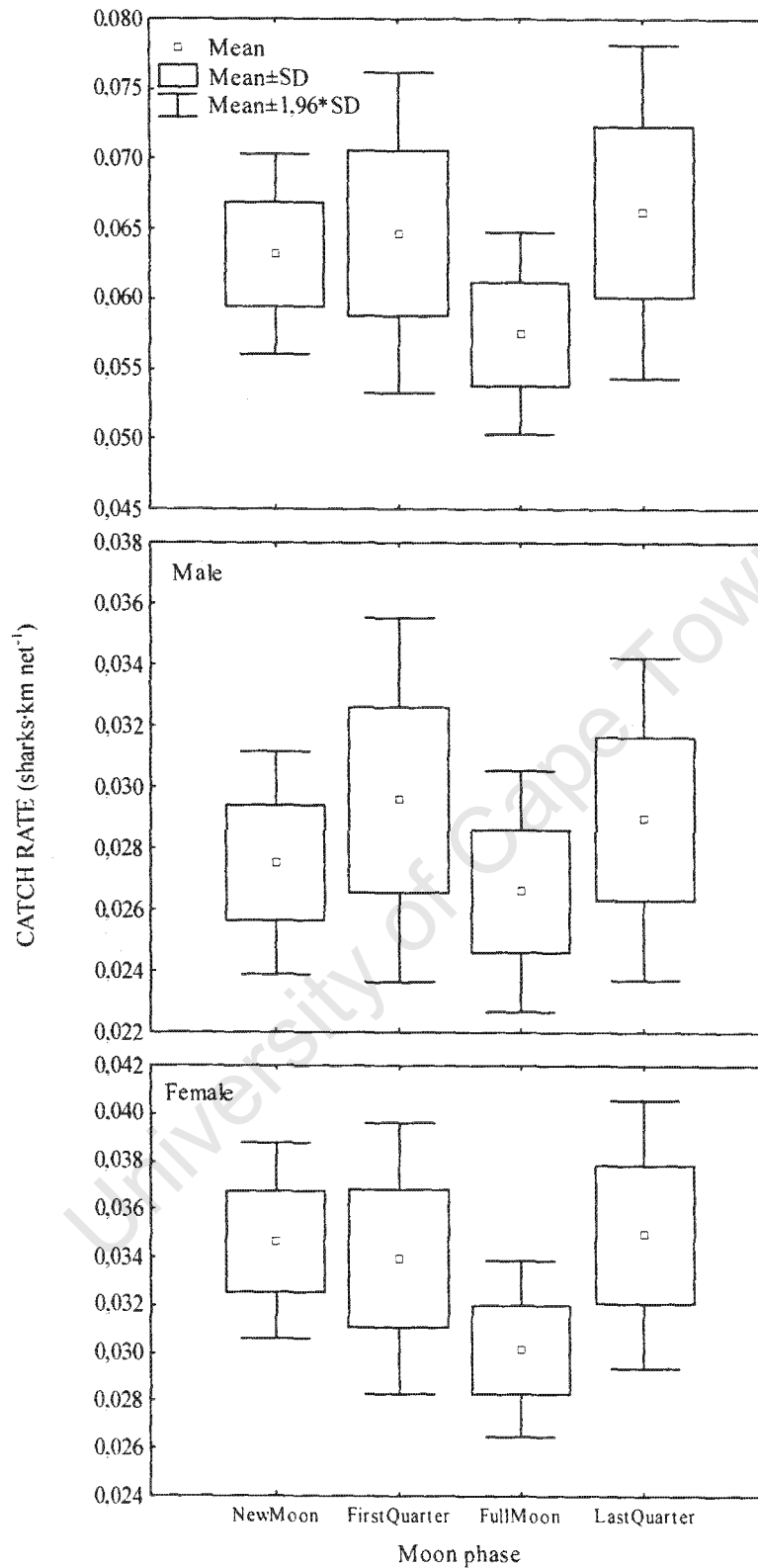


Fig. 3: Average catch rate per moon phase for all shark species combined and for males and females separately.

In the following sections the data are analysed on a species to species basis.

Carcharhinus obscurus (dusky shark)

A total of 6030 dusky sharks were caught in the nets from 1978 – 2003, making it the most commonly caught shark species. The survival rate for the dusky shark netted was 12.3% (n=748) and 4510 sharks were used for the lunar phase analysis. Most dusky sharks were caught in the months of June and July (Fig. 4), with an additional peak in December – January. July catches (n=952) were followed by a dramatic 70% decrease to the very low catches in August (n=285). February had the lowest catches of the year (n=277). Females were consistently most prevalent throughout the year and made up almost 60% of the catches, with males constituting 34% and non-determined sex 6%.

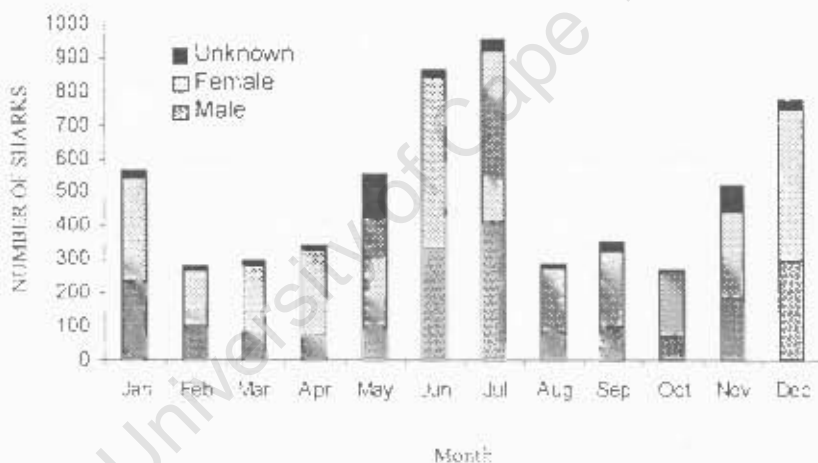


Fig. 4: Monthly catch pattern of *Carcharhinus obscurus* (1978-2003).

The dusky shark showed a significantly higher ($p < 0.05$, $F = 1403.99$, d.f.=3) average catch rate in the last quarter of the moon cycle (Fig. 5). When the two sexes are separated, however, female dusky sharks had the highest catch rates during new moon ($p < 0.05$, $F = 1058.07$, d.f.=3) as opposed to males, which were mostly caught during the last quarter ($p < 0.05$, $F = 1494.81$, d.f.=3). Full moon gave the lowest catches for dusky sharks regardless of sex, although there was little difference in catch rate from the first quarter of the moon.

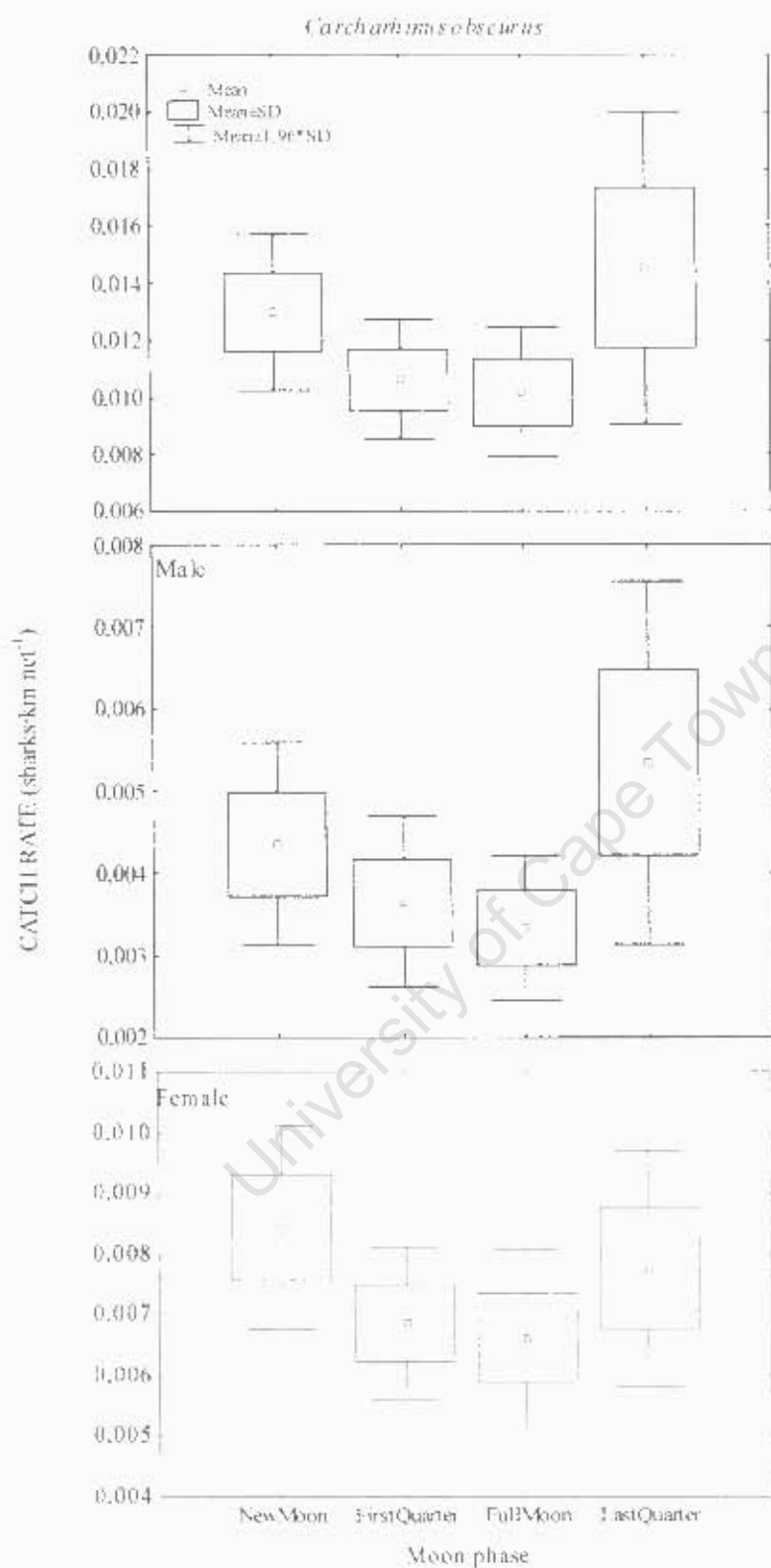


Fig. 5: Average catch rate per moon phase for *Carcharhinus obscurus* combined and for males and females separately.

Carcharias taurus (spotted ragged-tooth shark)

A total of 5052 sand tiger sharks were caught in the anti shark nets from 1978 – 2003. Mean annual catch was 194 individuals (range 70 – 438). The sand tiger shark had a relatively high survival rate of 35.9% ($n=1816$) and so 4181 sharks were used for the lunar analysis.

As shown in Fig. 6 most sand tiger sharks were caught during October ($n=1115$) and November with December showing a 63% decrease from November. January – April had very low catches with February the month with the least catches ($n=72$). Catches contained on average 62% females, 36% males and 2% non-sexed. Females were in the greatest number in all months except for May – July, where males dominated.

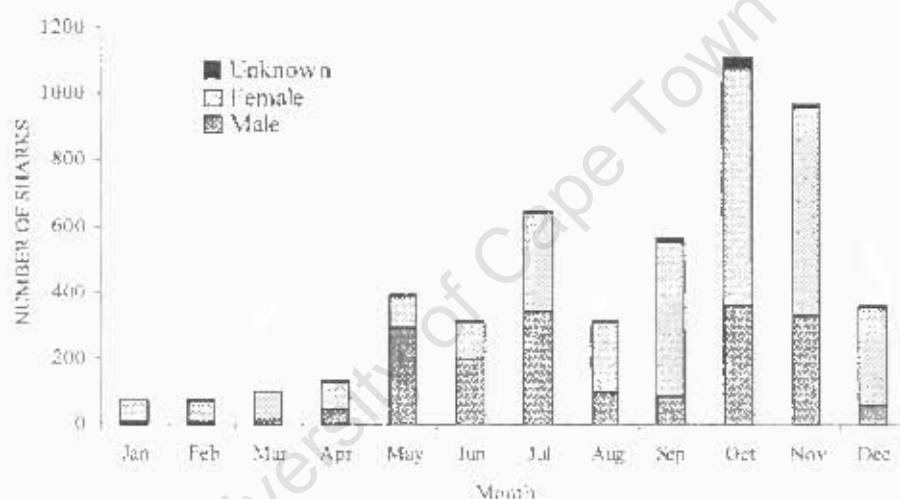


Fig. 6: Monthly catch pattern of *Carcharias taurus* (1978-2003).

The sand tiger shark showed a significantly higher ($p<0.05$, $F=549.67$, $d.f.=3$) average catch rate during the first quarter of the moon (Fig. 7). The lowest catches took place during the third quarter of the moon. When split by sex, males had a higher ($p<0.05$, $F=1024.00$, $d.f.=3$) average catch rate during the same phase of the moon, as did also females ($p<0.05$, $F=528.65$, $d.f.=3$). However, males were netted least during the third quarter in contrast to females, which were netted in lowest numbers during full moon.

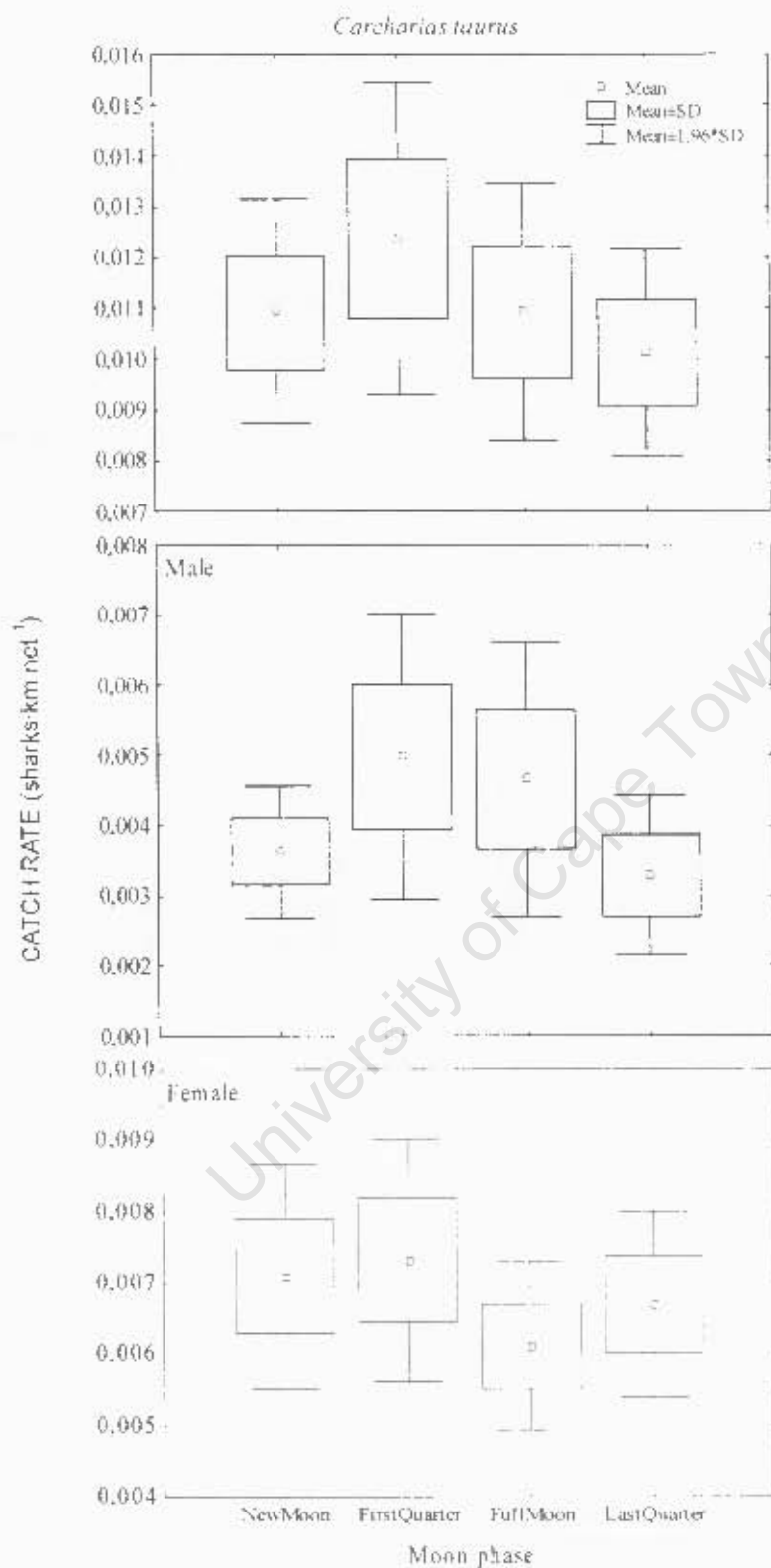


Fig. 7: Average catch rate per moon phase for *Carcharias taurus* combined and for males and females separately.

Sphyrna lewini (scalloped hammerhead shark)

A total of 3704 scalloped hammerhead sharks were netted from 1978 – 2003. Mean annual catch was 142 individuals (range 49 – 278). Scalloped hammerhead sharks had a survival rate of only 4% (n=147) and 2411 were used for the lunar analysis. Scalloped hammerhead sharks showed a clear seasonal trend throughout the year (Fig. 8) with the highest catches in January (n=642), declining gradually until June (n=125) and then increasing steadily again until December. Males made up 66%, females 28% and unknown sex 6% of the catches on average. Males dominated the catches in all months.

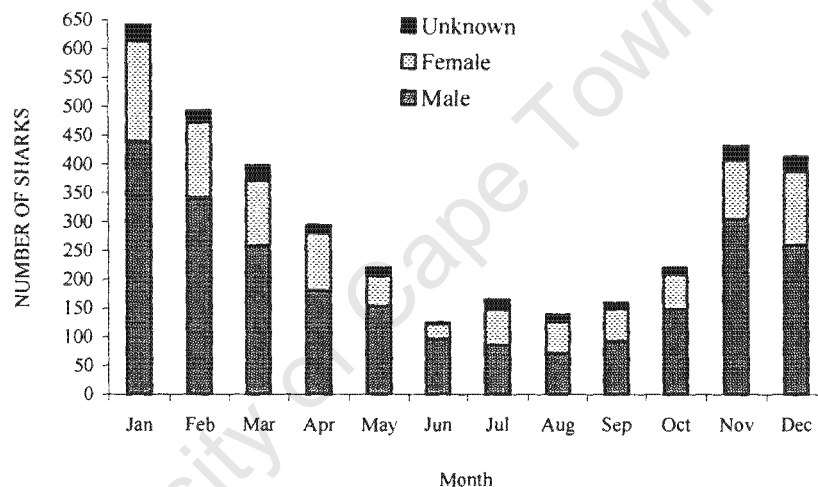


Fig. 8: Monthly catch pattern of *Sphyrna lewini* (1978 – 2003).

Scalloped hammerhead sharks were caught much more frequently ($p < 0.05$, $F = 1363.46$, $d.f. = 3$) during the new moon (Fig. 9). This was true for both pooled data and males ($p < 0.05$, $F = 1272.16$, $d.f. = 3$) and females ($p < 0.05$, $F = 1272.16$, $d.f. = 3$) were on average netted mostly during the new moon. Differences in catch rates between other phases were minor and inconsistent between males and females.

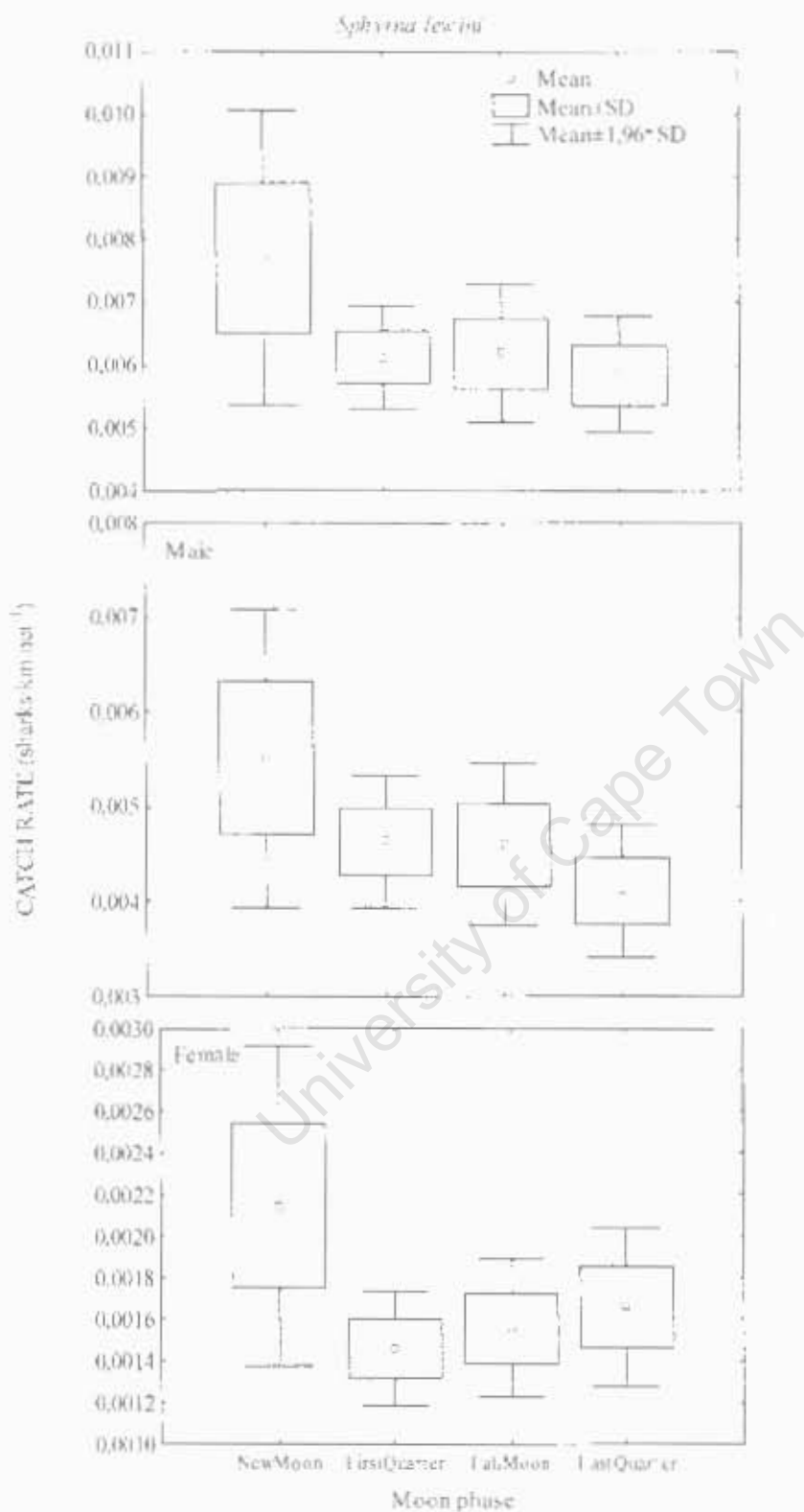


Fig. 9: Average catch rate per moon phase for *Sphyrna lewini* combined and for males and females separately.

Carcharhinus brevipinna (spinner shark)

A total of 3200 spinner sharks were caught in the nets from 1978 - 2003. Mean annual catch was 123 individuals (range 35 - 234). The spinner shark had a survival rate of 12.3% (n=395) and 2381 were used for the analysis. The spinner shark was netted most often during February (n=1069) when catches were more than double those in any other month (Fig. 10) and where an influx of males outnumbered females. From August (n=45) to December catches were generally low. On average the catches consisted of 51% female, 47% male and 2% unknown sex.

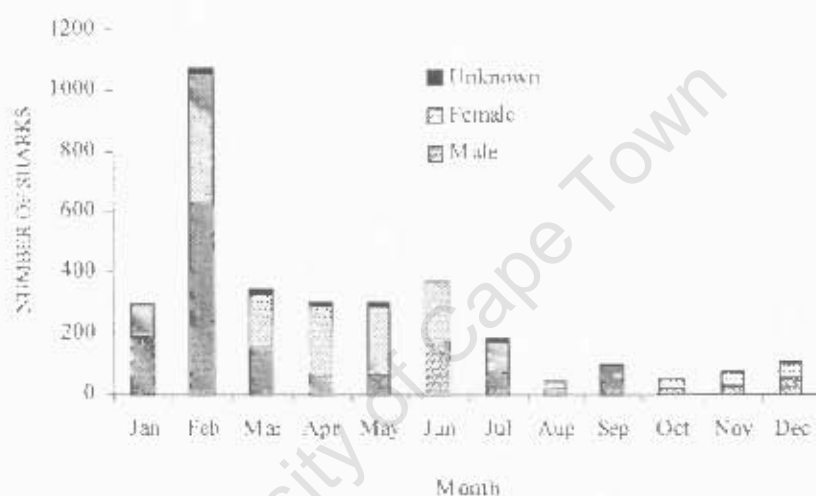


Fig. 10: Monthly catch pattern of *Carcharhinus brevipinna* (1978-2003).

The spinner shark showed a significantly higher ($p < 0.05$, $F = 1290.45$, $d.f. = 3$) average catch rate during the last quarter of the moon (Fig. 11). This was the case also for males ($p < 0.05$, $F = 1290.45$, $d.f. = 3$) and females separately ($p < 0.05$, $F = 1264.60$, $d.f. = 3$). Males showed the lowest catches during new moon and females during full moon. The biggest variance in catches was found during the last quarter moon.

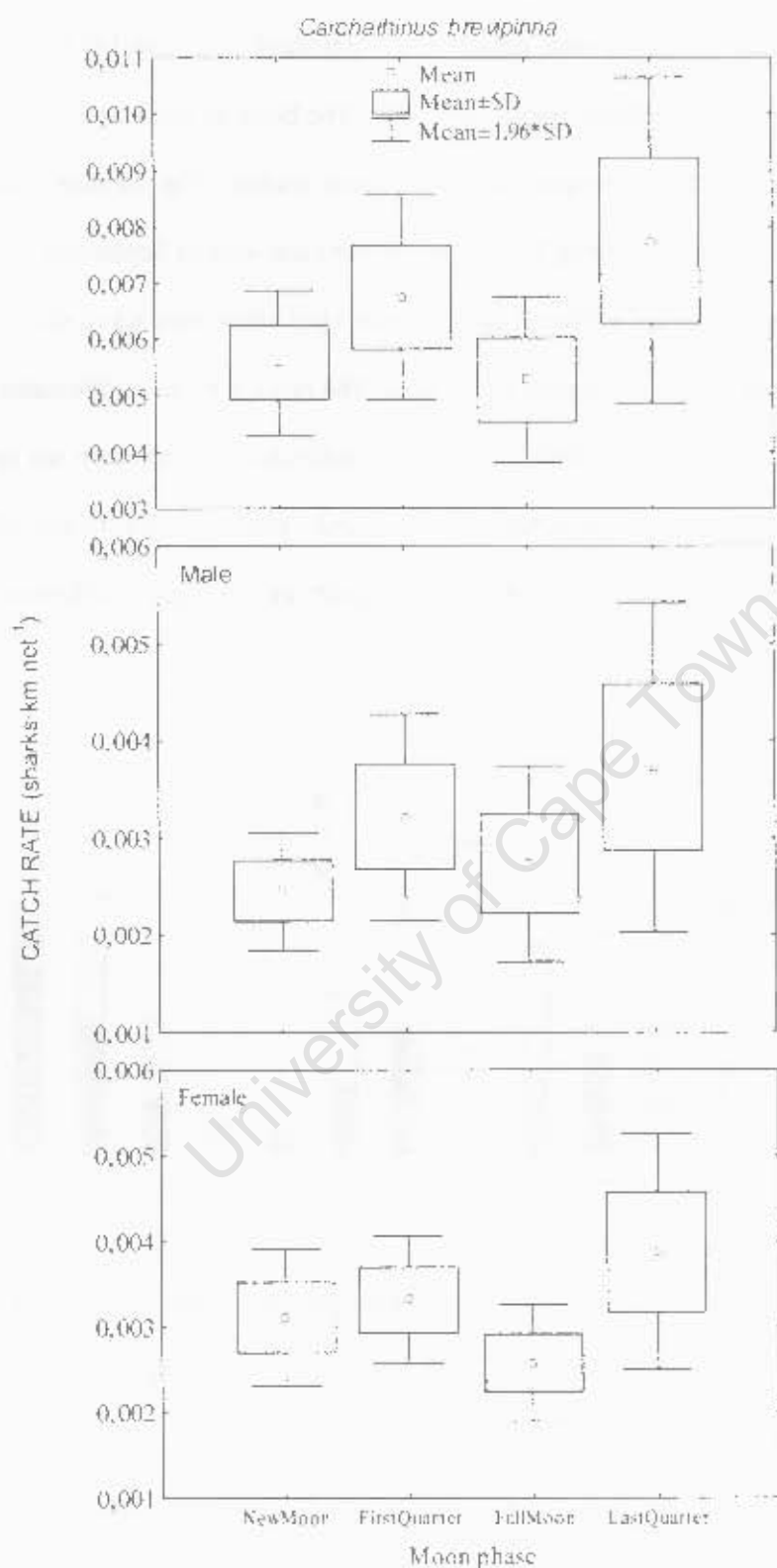


Fig. 11: Average catch rate per moon phase for *Carcharhinus brevipinna* combined and for males and females separately.

showed a higher average catch rate during new moon ($p<0.05$, $F=1063.66$, d.f.=3) with declining average catch rates for the first quarter, and full moon gave the lowest number.

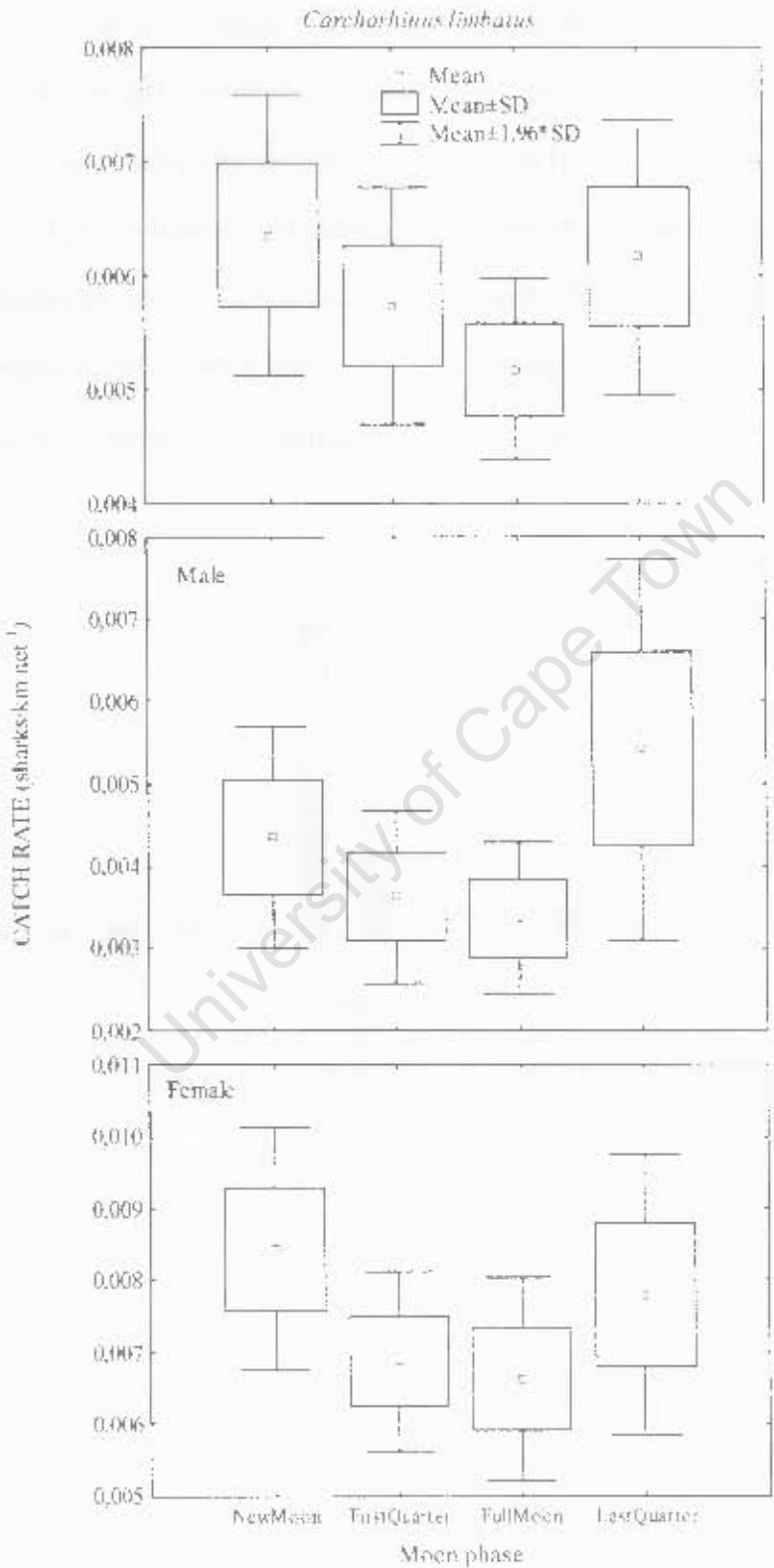


Fig. 13: Average catch rate per moon phase for *Carcharhinus limbatus* combined and for males and females separately.

Carcharhinus brachyurus (copper shark)

A total of 2676 copper sharks were caught in the anti shark nets from 1978 – 2003. Mean annual catch was 103 individuals (range 10 – 420). The copper shark had a survival rate of 15.5% ($n=416$) and 2154 sharks were used for the lunar analysis. The copper shark had a distinctive seasonal distribution (Fig. 14) with a strong seasonal peak in June and especially July ($n=1148$). November and December each saw the lowest number caught ($n=32$). On average catches consisted of 53% males, 45% females and non-sexed individuals 2%, although the ratio changed with season as October to June had a higher occurrence of males (4.2:1) whereas during the months of July and September more females were netted (1.2:1).

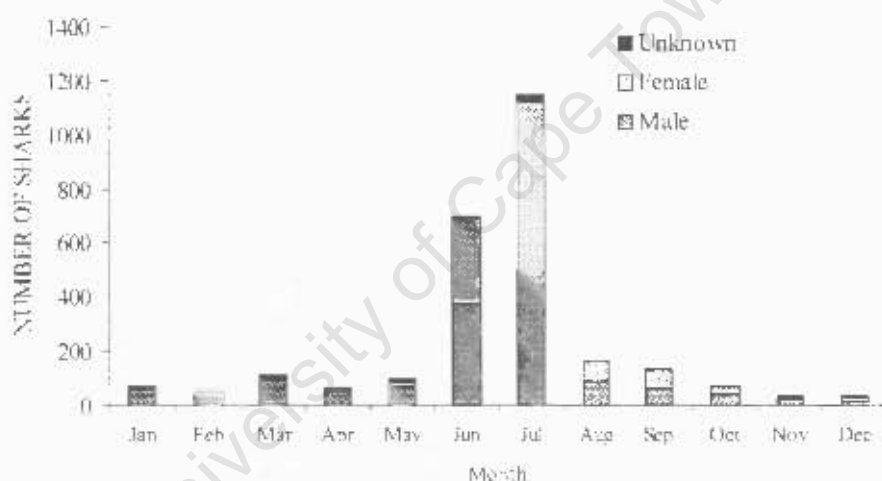


Fig. 14: Monthly catch pattern of *Carcharhinus brachyurus* (1978-2003).

Copper sharks showed a significantly higher ($p<0.05$, $F=441.04$, $d.f.=3$) average catch rate during the first quarter of the moon (Fig. 15). This was also the case for males ($p<0.05$, $F=478.38$, $d.f.=3$) and females ($p<0.05$, $F=477.95$, $d.f.=3$). New moon and full moon had virtually the same average catch rates, with new moon giving the lowest catches of males, and full moon showing the lowest catches of females. First quarter moon had the largest variation in catch rate.

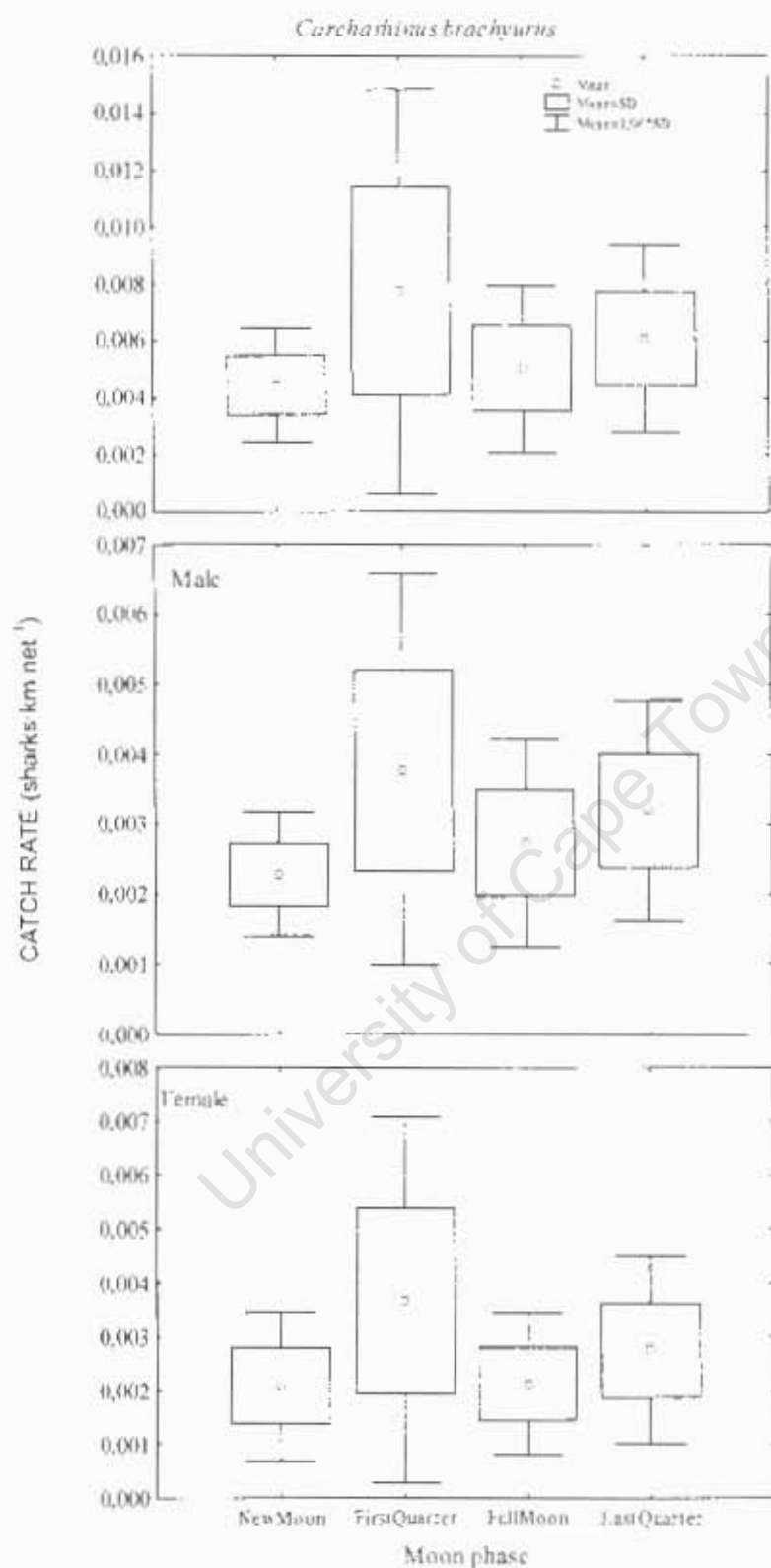


Fig. 15: Average catch rate per moon phase for *Carcharhinus brachyurus* combined and for males and females separately.

Sphyrna zygaena (smooth hammerhead shark)

A total of 1943 smooth hammerhead sharks were caught in the anti shark nets from 1978 – 2003. Mean annual catch was 75 individuals (range 9 – 271). The smooth hammerhead shark had a survival rate of only 2.6% ($n=51$), but since there were many recently-dead individuals found in the nets, 1525 sharks were used for the lunar analysis. Smooth hammerhead sharks showed a strong seasonal pattern (Fig. 16) peaking in July ($n=423$) and declining to a minimum in February ($n=9$). Males constituted on average 42% of the catches, females 54% and unknown sex 4%. Sex ratio remained fairly constant throughout the year with a slight majority of females netted in all months except December.

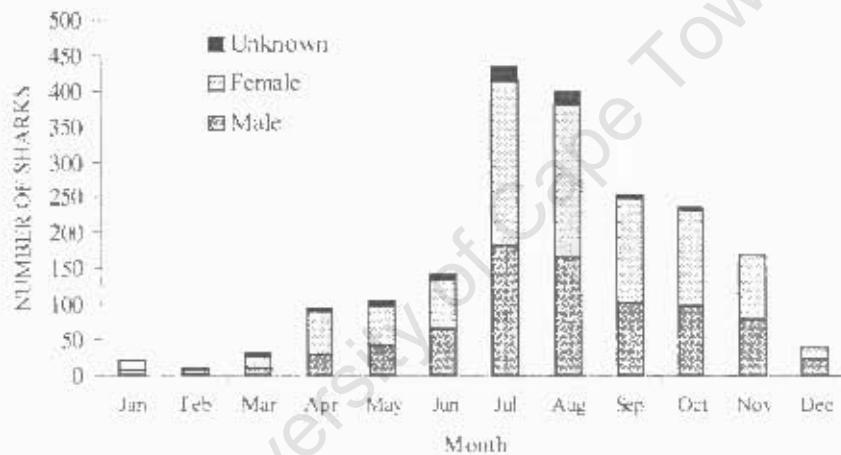


Fig. 16: Monthly catch pattern of *Sphyrna zygaena* (1978-2003).

Smooth hammerhead sharks were on average caught most often ($p<0.05$, $F=426.76$, $d.f.=3$) during full moon (Fig. 17). This was the case also for males ($p<0.05$, $F=404.54$, $d.f.=3$) and females ($p<0.05$, $F=470.23$, $d.f.=3$). New moon had the lowest catch rates and the catch pattern for all the phases of moon was very similar for both sexes.

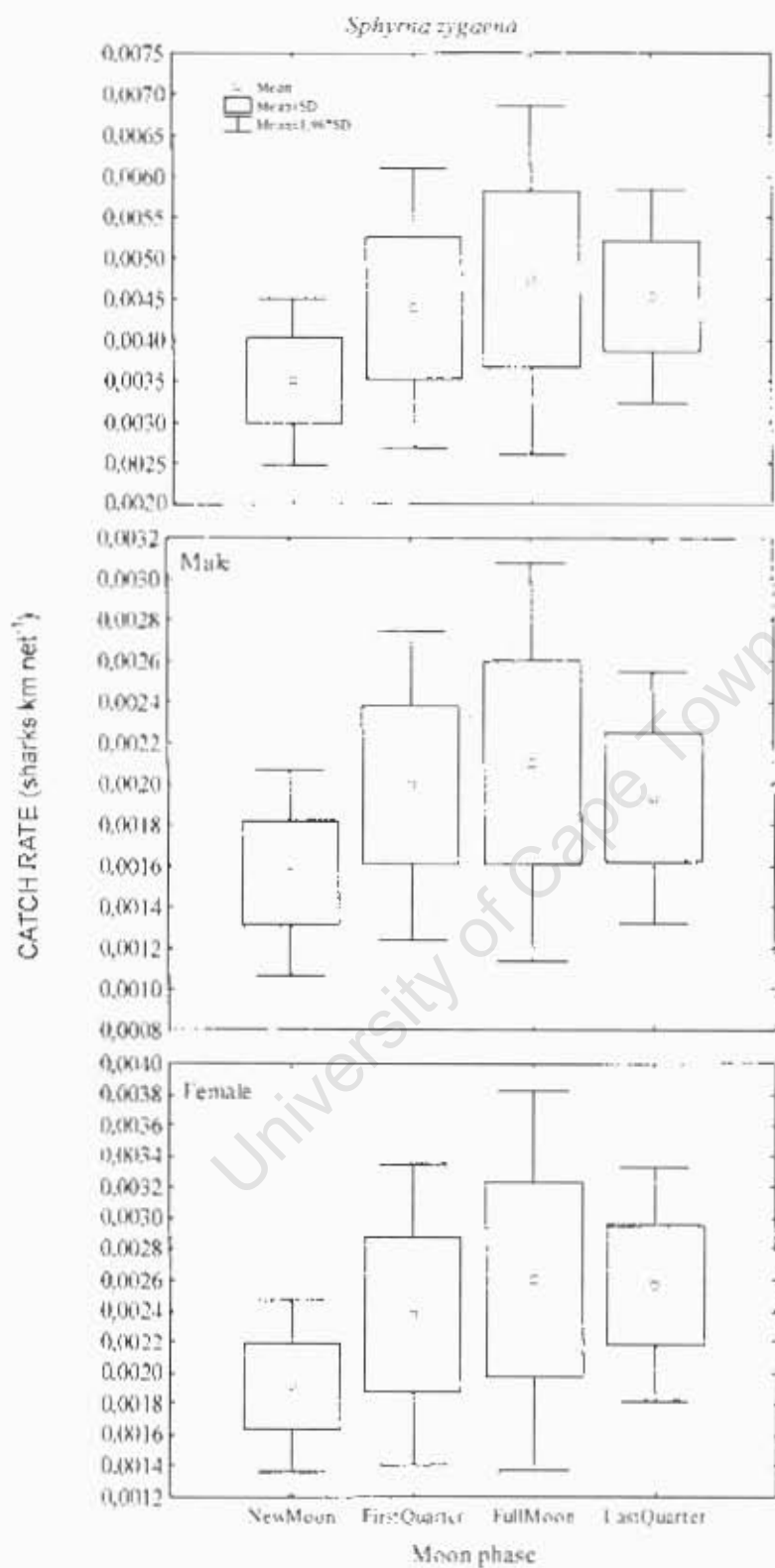


Fig. 17: Average catch rate per moon phase for *Sphyrna zygaena* combined and for males and females separately.

Galeocerdo cuvier (tiger shark)

A total of 1267 tiger sharks were caught in the anti shark nets from 1978 – 2003. Mean annual catch was 49 individuals (range 25 – 75). The tiger shark had a survival rate of 38% ($n=481$) the highest recorded for shark species caught by the Natal Sharks Board. With a high incidence of freshly dead tiger sharks found in the nets, a total of 1060 individuals were used for the lunar analysis. The tiger shark was netted all through the year (Fig. 18), with most sharks caught in October ($n=137$) to December, and least during June ($n=73$). There was less variation in catches throughout the year compared to other shark species netted. On average, 67% of the tiger sharks caught in the nets were female, whereas males made up for 30% and unknown sex 3%. For all months female tiger sharks outnumbered males by an average ratio of 2.4:1.

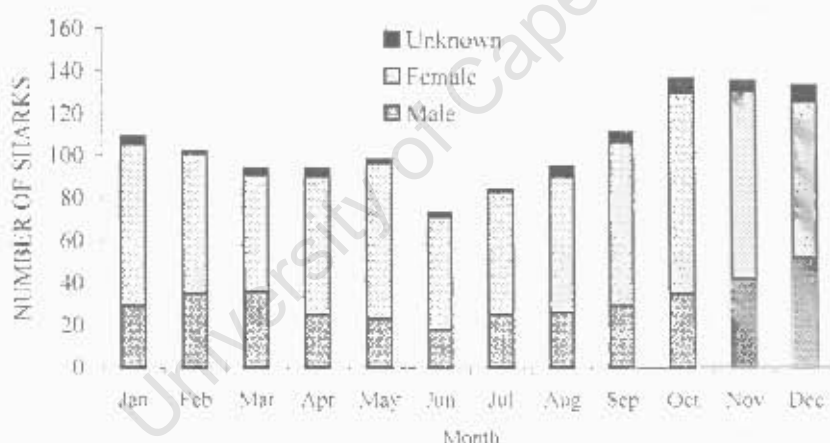


Fig. 18: Monthly catch pattern of *Galeocerdo cuvier* (1978-2003).

Tiger sharks were on average caught most often ($p<0.05$, $F=2906.35$, $d.f.=3$) during the last quarter of the moon cycle (Fig. 19) with a very sharp decline during the full moon phase, which had the lowest average catch rate. When split by gender, males were on average also caught most often ($p<0.05$, $F=2969.13$, $d.f.=3$) during the last quarter moon and least during full moon. The catch pattern changed distinctly for each transition to a new moon. Females

were netted most often during new moon ($p<0.05$, $F=1966.37$, d.f.=3) with a decline during first quarter moon and the lowest catch rate at full moon.

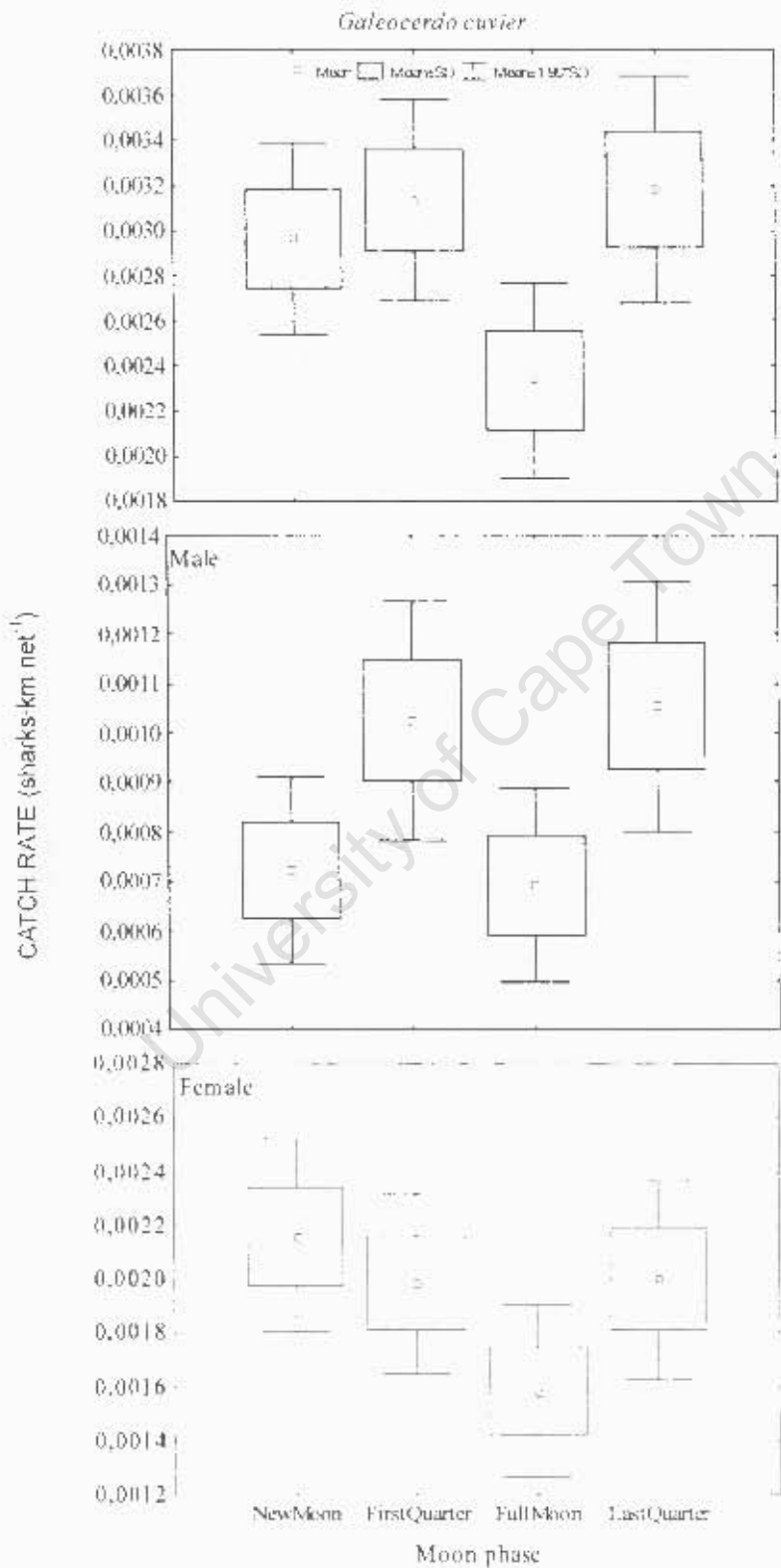


Fig. 19: Average catch rate per moon phase for *Galeocerdo cuvier* combined and for males and females separately.

Carcharhinus leucas (bull shark)

A total of 1172 bull sharks were caught in the protective gill nets from 1978 – 2003. Mean annual catch was 45 individuals (range 12 – 89). The bull shark had a survival rate of 22.1% ($n=259$) and a total of 913 individuals were used for the lunar analysis. Catches of bull sharks (Fig. 20) showed a smooth annual pattern with August giving the lowest catches ($n=37$) and December the highest ($n=217$). Between November and December an influx of bull sharks took place as an 84% increase in catches could be seen. Sex ratio was fairly even throughout the year, males contributing 44%, females 53% and unknown sex 3% to the catches, with only January and July having a higher ratio of males. Average ratio of females to males was 1.3:1 throughout the year.

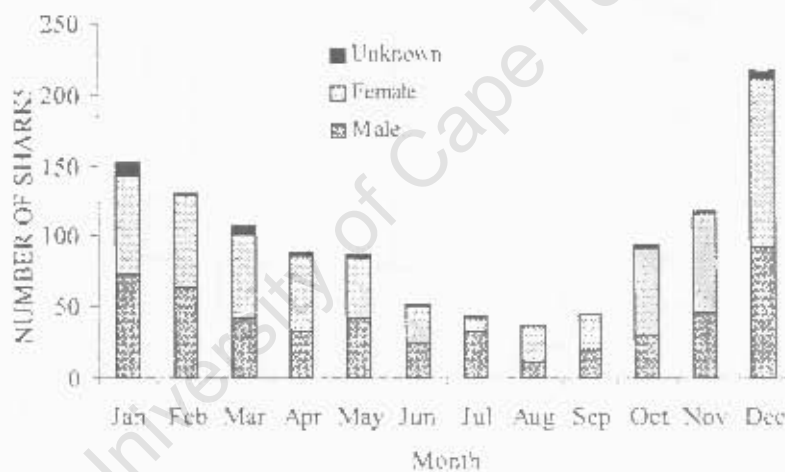


Fig. 20: Monthly catch pattern of *Carcharhinus leucas* (1978-2003).

Bull sharks were on average caught much most often ($p<0.05$, $F=5873.69$, $d.f.=3$) during the new moon. During full moon catches were lowest, about half of those during new moon. There was a strong decrease in catches from new moon (Fig. 21) followed by an increase in the last quarter. The same pattern applies to male ($p<0.05$, $F=4423.44$, $d.f.=3$) and female ($p<0.05$, $F=2988.45$, $d.f.=3$).

Carcharhinus leucas

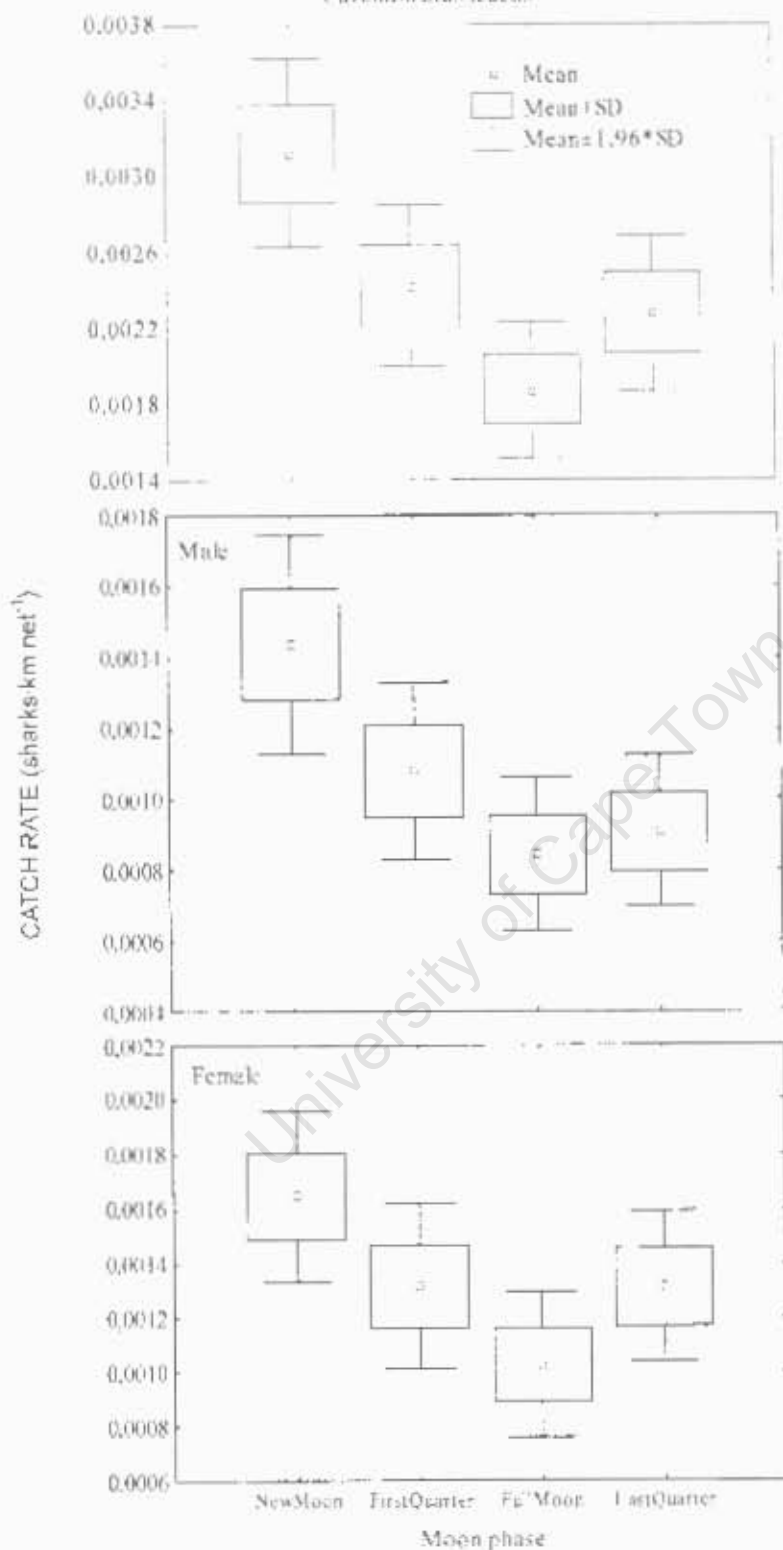


Fig. 21: Average catch rate per moon phase for *Carcharhinus leucas* combined and for males and females separately.

Carcharodon carcharias (white shark)

A total of 934 white sharks were caught in the nets from 1978 – 2003. Mean annual catch was 36 individuals (range 7 – 60). White sharks had a survival rate of 15.6% ($n=145$). A total of 707 white sharks were used for the lunar phase analysis. Sharks were caught most often during the second half of the year (66%), from July to December (Fig. 22). The lowest catches were seen during February ($n=35$) to April. August had the highest catches ($n=148$). A general negative slope followed August, lasting until February where catches started to rise again. On average, 43% of the catches consisted of males, 53% were females and undetermined sex represented 4% of sharks caught. Overall female to male average sex ratio was 1.4:1.

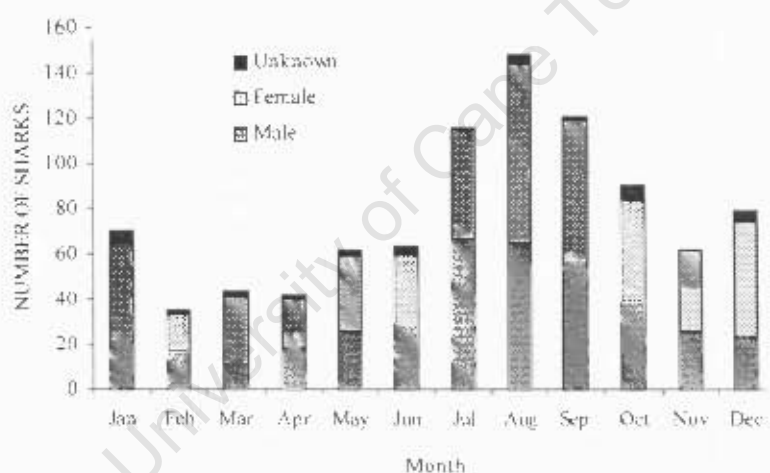


Fig. 22: Monthly catch pattern of *Carcharodon carcharias* (1978-2003).

The white sharks were on average caught most often ($p<0.05$, $F=467.45$, d.f.-3) during the full moon phase (Fig. 23) and least at new moon. Last quarter moon had the largest spread in catch rate. When split by sex, males were on average caught most often during the last quarter ($p<0.05$, $F=225.99$, d.f.-3) although the difference from full moon was negligible. The catch pattern showed a positive trend starting at new moon with the spread in catch rates being similar except for the last quarter, which had a larger spread. Females were represented most in catches at full moon ($p<0.05$, $F=625.44$, d.f.-3) and least during first quarter moon. The

spread in catch rates were similar for all phases of moon and the change in catch rate most distinct between first quarter and full moon.

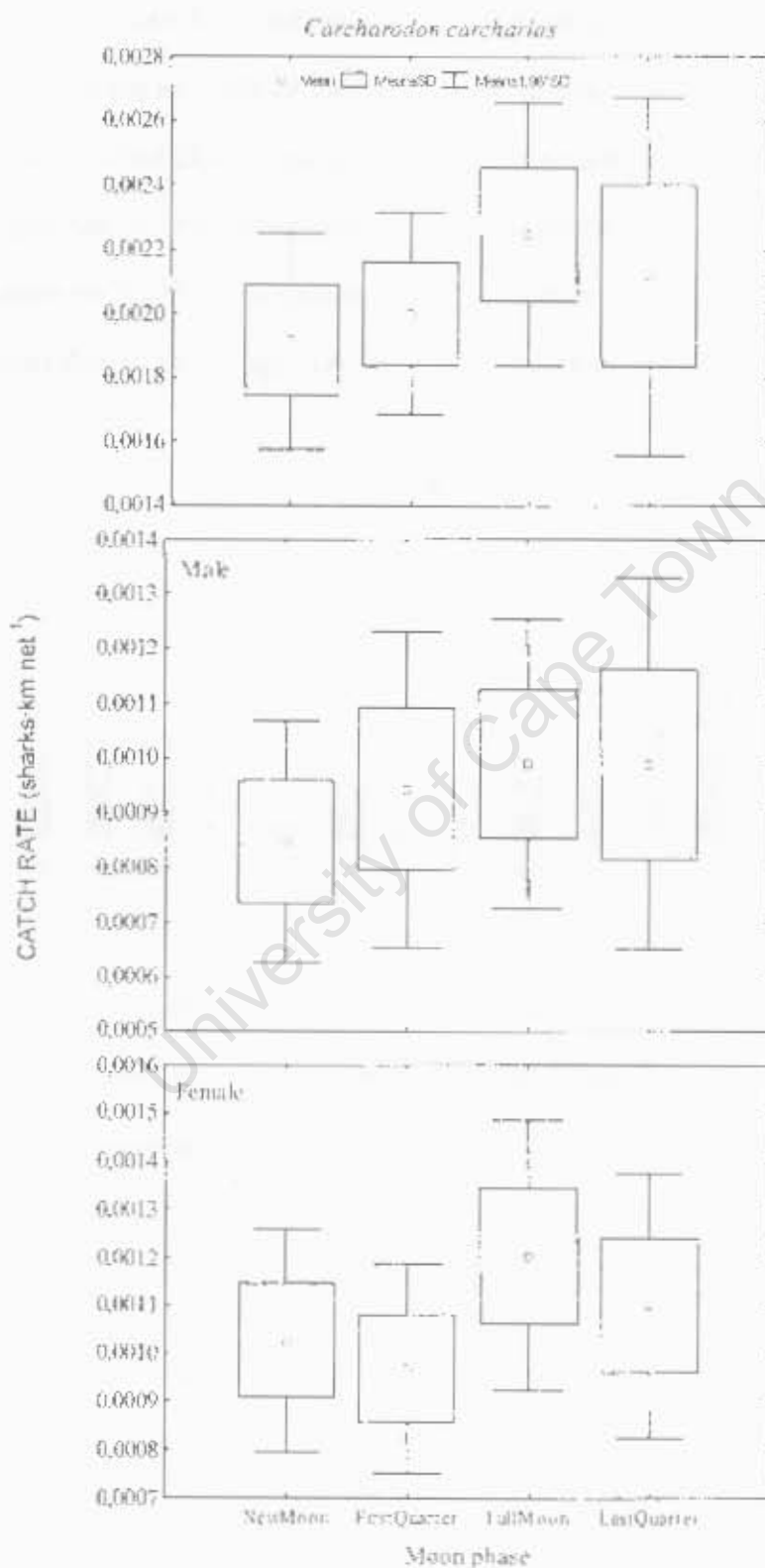


Fig. 23: Average catch rate per moon phase for *Carcharodon carcharias* combined and for males and females separately.

Carcharhinus plumbeus (sandbar shark)

A total of 556 sandbar sharks were caught in the anti shark nets from 1978 – 2003. Mean annual catch was 21 individuals (range 5 – 57). The sandbar shark had a survival rate of 13.1% (n=73). A total of 483 sandbar sharks were used for the lunar phase analysis. Sandbar sharks displayed a clear seasonal distribution pattern (Fig. 24) with high catches in summer and low ones in winter. February presented the highest catches (n=119) and August the lowest (n=4). Females dominated the catches, on average making up to 65% of the sharks netted, while males contributed 34% and unknown sex 1%. Average female to male ratio was 3.6:1.

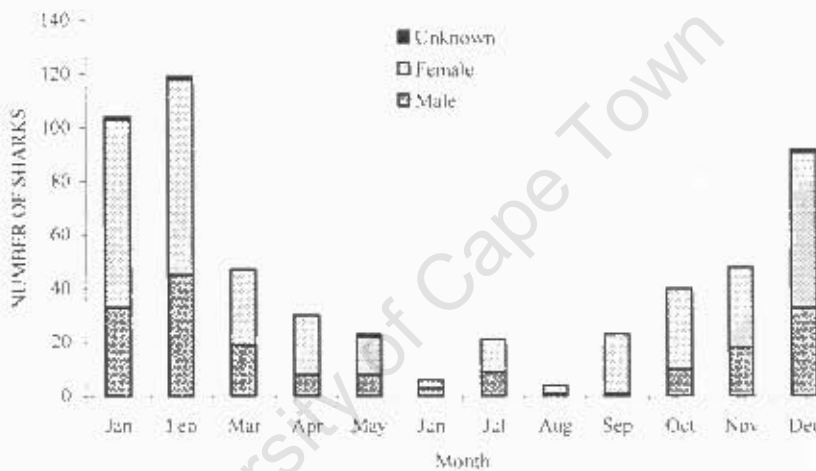


Fig. 24: Monthly catch pattern of *Carcharhinus plumbeus* (1978-2003).

Sandbar sharks were on average caught most often ($p < 0.05$, $F = 2302.76$, d.f.=3) during the full moon phase (Fig. 25), followed by a marked drop in the following moon phase. When split by sex, the same moon phase showed the highest catch rate for both males ($p < 0.05$, $F = 2577.86$, d.f.=3) and females ($p < 0.05$, $F = 2030.84$, d.f.=3). First quarter moon had the lowest average catch rate regardless of sex.

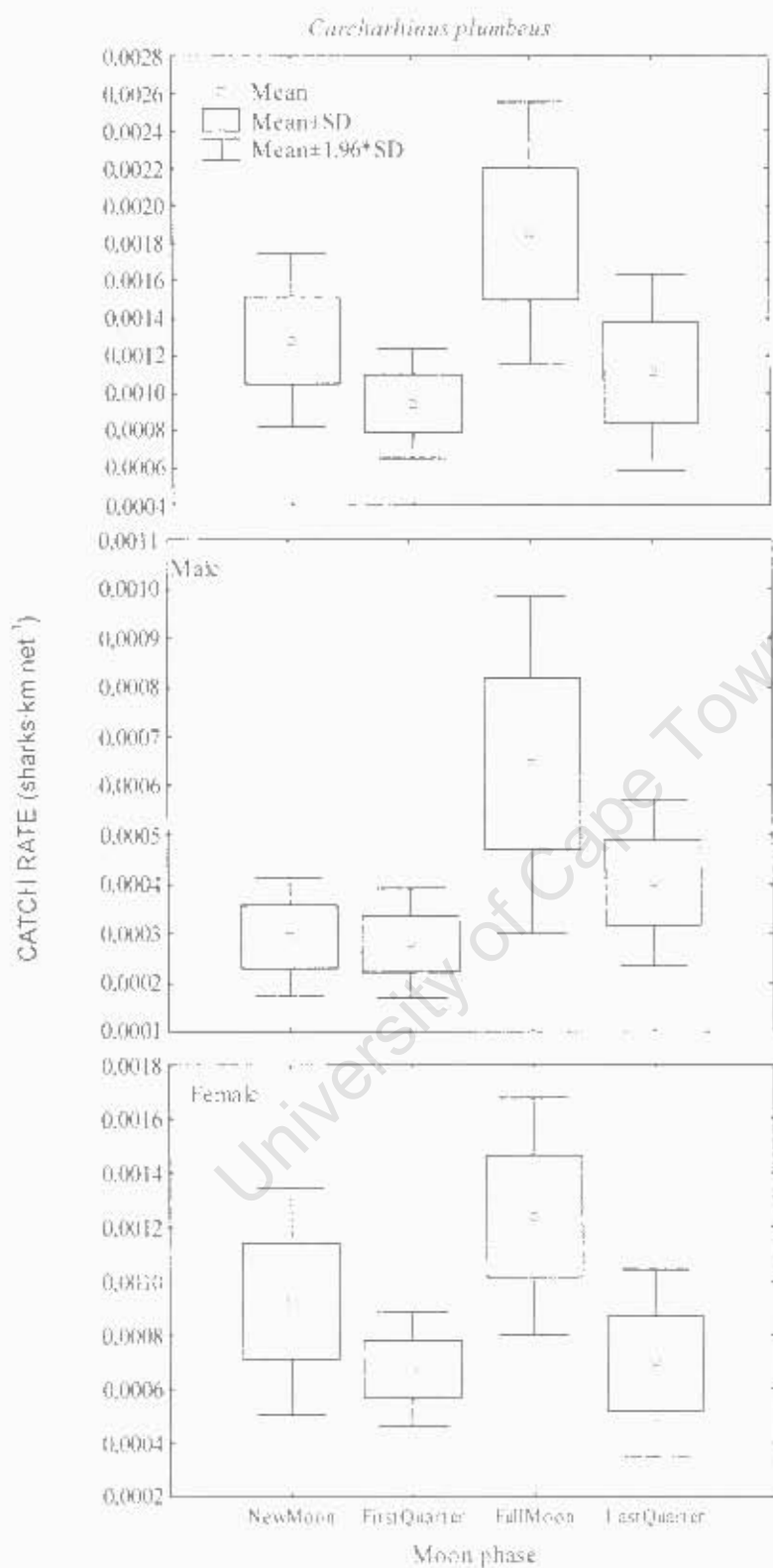


Fig. 25: Average catch rate per moon phase for *Carcharhinus plumbeus* combined and for males and females separately.

Carcharhinus amboinensis (Java shark)

A total of 357 Java sharks were caught in the anti shark nets from 1978 – 2003. Mean annual catch was 14 individuals (range 2 – 46). The Java shark had a survival rate of 21% (n=75). A total of 310 Java sharks were used for the lunar phase analysis. Java sharks displayed a seasonal distribution pattern (Fig. 26) with peak catches in January (n=55) declining until July (n=9), followed by an increase again during the second half of the year. The sex ratio was very even, males on average amounting to 50% of the total Java sharks netted, females 48% and unknown sex 2%, with a switch in sex ratio mid-year, males slightly more abundant during the first half.

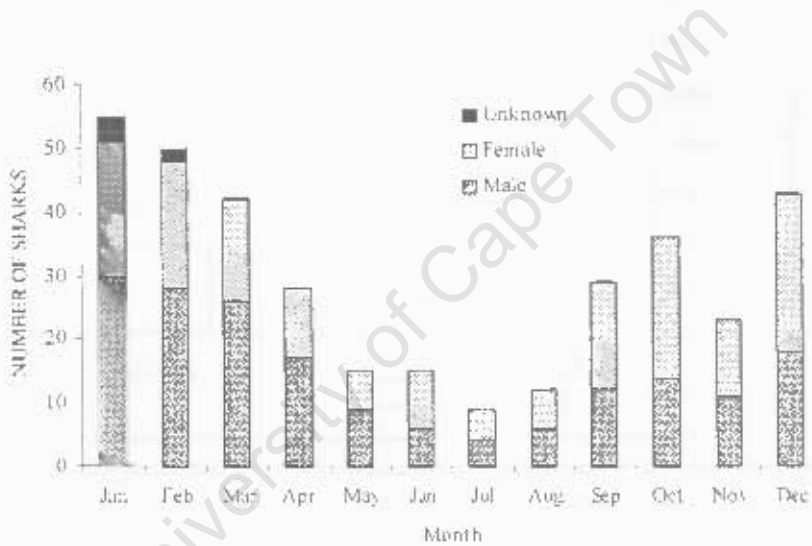


Fig. 26: Monthly catch pattern of *Carcharhinus amboinensis* (1978-2003).

Catches of the Java sharks showed a strong lunar pattern (Fig. 27) with highest catches ($p<0.05$, $F=1547.52$, d.f.=3) during the new moon and least during full moon. The new moon presented more than double the average catch rate than the full moon did. A similar pattern was found for both males ($p<0.05$, $F=1522.29$, d.f.=3) and females ($p<0.05$, $F=2026.62$, d.f.=3).

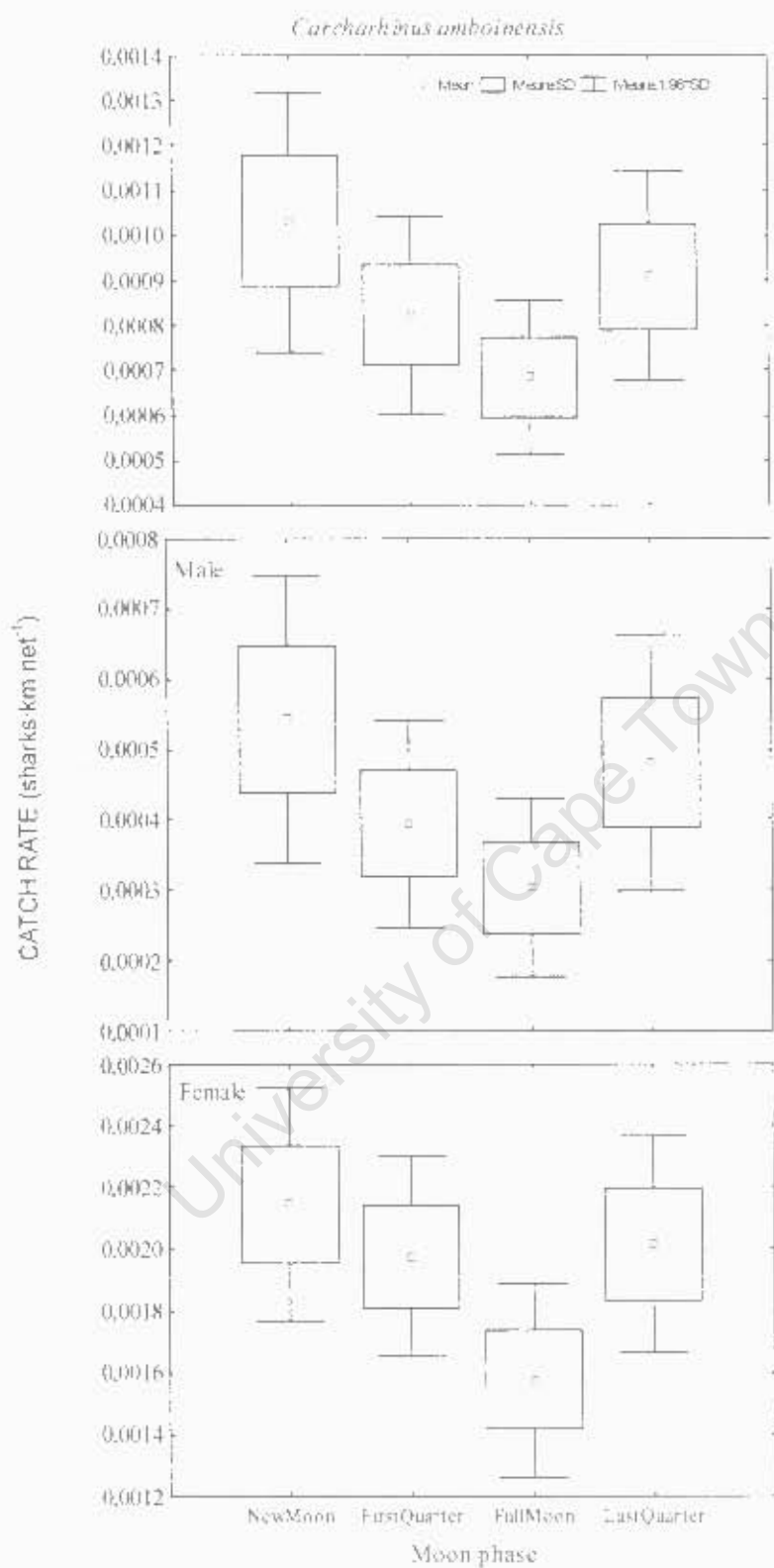


Fig. 27: Average catch rate per moon phase for *Carcharhinus amboinensis* combined and for males and females separately.

Isurus oxyrinchus (mako shark)

A total of 348 mako sharks were caught in the anti shark nets from 1978 – 2003. Mean annual catch was 14 individuals (range 7 – 30). The mako shark had a survival rate of no more than 7.2% ($n=25$). A total of 275 mako sharks were used for the lunar phase analysis. Mako sharks showed a clear seasonal peak in abundance (Fig. 28), with September giving the highest ($n=26$) and January the lowest ($n=6$) catches. Of the mako sharks 74% were netted during the second half of the year. Males were more abundant than females throughout the year, making on average up 66% of the catches compared to females 31% and non-sexed mako sharks 3%. Male mako sharks outnumbered females by a ratio of 3.6:1.

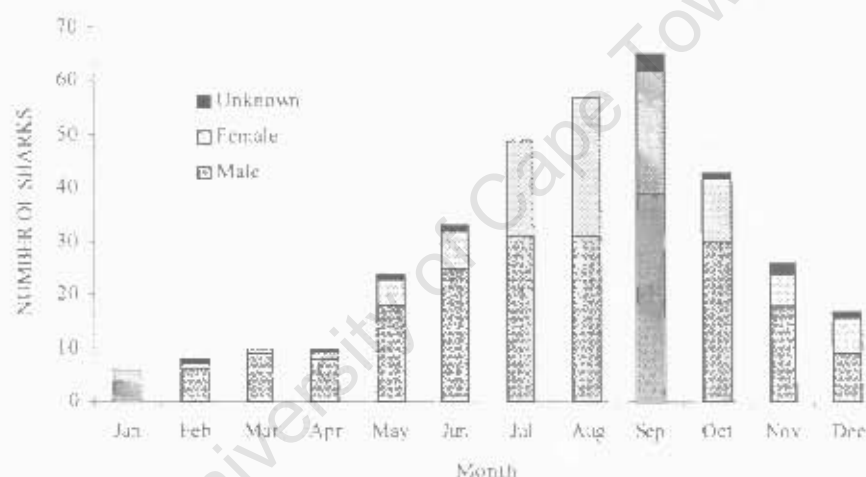


Fig. 28: Monthly catch pattern of *Isurus oxyrinchus* (1978-2003).

Mako sharks were on average caught most often ($p<0.05$, $F=794.04$, $d.f.=3$) during the first quarter of the moon cycle and least during new moon (Fig. 29). This was also the case for males ($p<0.05$, $F=221.68$, $d.f.=3$) and females ($p<0.05$, $F=842.83$, $d.f.=3$). However, the variance in catch rates were similar for all moon phases, especially for males.

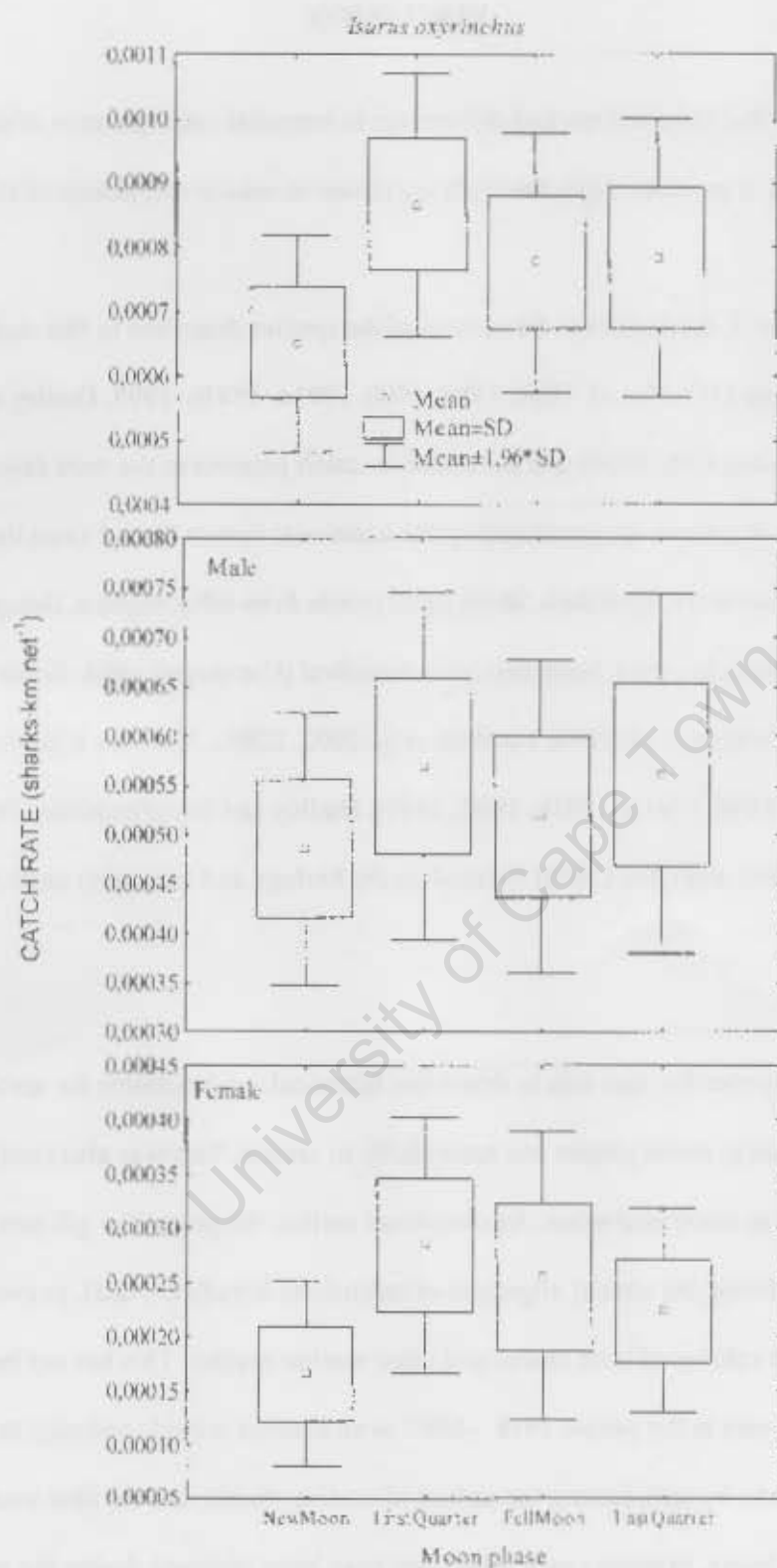


Fig. 29: Average catch rate per moon phase for *Isurus oxyrinchus* combined and for males and females separately.

DISCUSSION

Results indicate that there are marked differences in temporal catch patterns of different shark species captured in protective gill nets both in relation to season and phases of the moon.

Seasonal patterns in shark catches for several of the species described in this study has been previously recorded (Cliff *et al.* 1988, 1989, 1990, 1991a, 1991b, 1999, Dudley and Cliff 1993, and Allen and Cliff 2000) and show similar catch patterns to the ones described here. Any differences in pattern are explained by the additional data collected since the time each of the earlier analyses were published. Shark catch trends from other regions, though not directly applicable to KwaZulu-Natal, have also been described (Compagno 1984, Smale 1991, van Der Elst 1993, Ferreira *et al.* 1996, Lucifora *et al.* 2002, 2005). Previous work by Cliff *et al.* (1988, 1989, 1990, 1991a, 1991b, 1992, 1999), Dudley and Simpfendorfer (2006), Dudley *et al.* (1993), Allen and Cliff (2000) focused on the biology and long-term catch rate of sharks netted.

In this study, however the aim was to determine historical catch patterns for specific shark species in relation to moon phases and secondarily to season. This was also considered for separate as well as combined sexes. As mentioned earlier, the protective gill nets are removed from the water during the annual migration of sardines to KwaZulu-Natal, to avoid excessively high catches of both sharks and other marine species. This has not been constant practice for all years in the period 1978 – 2003 as an attempt is made annually to reduce the catch rate of sharks by anticipating the arrival of sardine shoals, and the data used thus reflects catches that are lower, in some years, when nets have been removed during the sardine run. The detailed dataset analysed here gives very good indications of seasonal patterns for a

number of species e.g. increased shark catch rates may be attributed to interactions with other organisms, either conspecifics or their prey.

It was observed that sex ratio switched between months for a number of shark species (*Carcharias taurus*, *Carcharhinus brevipinna*, *Carcharhinus limbatus*, *Carcharhinus brachyurus*). It is likely that the monthly influx of either males or females, depending on the species, is linked to sexually segregated movement (either within local waters (inshore-offshore movement) or to adjacent areas). Seasonal fish migrations are commonly related to either the cue to reproduce, response to shifting environmental conditions (typically temperature when fish generally move to warmer waters), or the movement of predators following their prey (Moyle and Cech 1988).

The lunar analysis revealed that last quarter moon had the highest catch rate for all shark species with sex combined (Fig. 3), while full moon had the lowest catch rate. When analysed for each separate species, however, the results varied greatly but showed significant relationships between moon phase and catch rates. Table 2 summarises the phase of the moon in relation to the highest and lowest catch rates for each shark species, sexes combined. There was little difference in the number of species with maximum catch rate in each of the moon phases. The greatest difference in catch rates between male and female sharks occurred at new moon, where females dominated.

Phase	New Moon	First Quarter	Full Moon	Last Quarter
Max catch rate	<i>Sphyrna lewini</i> <i>Carcharhinus limbatus</i> <i>Carcharhinus leucas</i> <i>Carcharhinus amboinensis</i>	<i>Carcharias. taurus</i> <i>Carcharhinus brachyurus</i> <i>Isurus. oxyrinchus</i>	<i>Sphyrna zygaena</i> <i>Carcharodon carcharias</i> <i>Carcharhinus plumbeus</i>	<i>Carcharhinus obscurus</i> <i>Carcharhinus brevipinna</i> <i>Galeocerdo cuvier</i>
Min catch rate	<i>Carcharhinus brachyurus</i> <i>Sphyrna zygaena</i> <i>Carcharodon carcharias</i> <i>Isurus oxyrinchus</i>	<i>Carcharhinus plumbeus</i>	<i>Carcharhinus obscurus</i> <i>Carcharhinus brevipinna</i> <i>Carcharhinus limbatus</i> <i>Galeocerdo cuvier</i> <i>Carcharhinus leucas</i> <i>Carcharhinus amboinensis</i>	<i>Carcharias taurus</i> <i>Sphyrna lewini</i>

Table 2: Lunar phases with maximum and minimum catch rates for shark species netted.

The reason for this lack of consistent pattern may be diverse and one has to look into the biology of each shark species, perhaps with an emphasis on hunting and preference of prey species, in order to hypothesise why this might be the case.

Sharks assumed to be visual predators would likely intensify activity at full moon, as the generally increased light levels are likely to benefit hunting. On the contrary one might argue that at the same time they would have an increased chance of avoiding the nets, which six (*Carcharhinus obscurus*, *Carcharhinus brevipinna*, *Carcharhinus limbatus*, *Carcharhinus amboinensis*, *Carcharhinus leucas* and *Galeocerdo cuvier*) of the thirteen species in the analysis in fact seem to do. Whilst it is not clear whether these species are visual predators they seem to avoid being caught on a full moon.

Whether the changing light intensity at different lunar phases directly affects shark movement need further attention. One factor is turbidity of the water, caused by suspended particles, which in essence determines the ability to visually interpret the shape and appearance of objects. The NSB estimates the transparency, or visibility, of the water at the time of meshing as standard procedure, though these data were deemed less reliable and therefore not used in this investigation. Regardless of this, some shark species, such as *Carcharhinus leucas*, are known to commonly frequent areas with high turbidity, and are often found feeding in fresh and estuarine bodies of water and close to river mouths (Compagno 1984b). This points to the fact that high turbidity may benefit some shark species in optimising foraging, as they are able to seize prey when the visibility of the water is low. Sharks have a complex array of sensory mechanisms to detect prey and vision may not be as important to many sharks in detecting prey as hearing or smell (Springer *et al.* 1989), both stimuli independent of the amount of light available. Even so, vision is important as a detection mechanism for a number of shark

species, and even in dim light most sharks may see with enough acuity to perceive prey and their surroundings. Although most of the experiments on visual systems in sharks have been anatomical studies of how the eyes work, rather than on how vision is used in a behavioural context, it is thought that *Carcharodon carcharias* is a diurnal hunter (Gruber *et al.* 1985) and therefore mainly a visual predator. For this species the average catch rate pattern showed a maximum at full moon. In contrast new moon displayed a maximum for *Carcharhinus leucas*, which mainly hunts in low visibility. *Sphyrna lewini* is another shark species frequently entering bays and estuaries (Compagno 1984b) where turbidity is often increased and density of prey species high, and the lunar analysis showed a maximum catch rate during new moon. Low-light conditions are likely to benefit shark species capable of hunting without vision. Subsequently *Carcharhinus amboinensis* displayed a maximum catch rate during new moon and a minimum during full moon, a species with an inshore habitat similar to *Carcharhinus leucas* (Compagno 1984b).

Sphyrna zygaena is a shark species recorded from coastal to oceanic habitats and is often observed near the surface (Compagno 1984b, van der Elst 1993) and the analysis showed the highest catch rates for this species occurred during full moon and lowest during new moon, possibly indicating that the species avoids low-light conditions. It is possible that species caught during the full moon are visual predators. *Carcharhinus plumbeus* also had a maximum catch rate at full moon, which at least for males showed a marked increase in catches during this part of the lunar cycle. *Galeocerdo cuvier* has a wide range of habitats from estuarine to offshore-pelagic (Compagno 1984b, van der Elst 1993) and full moon saw the least number netted indicating that this species is not a visual predator.

Isurus oxyrinchus, an epi-pelagic shark that frequents the coastal region (Compagno 1984a) and seems to avoid water with high turbidity (Cliff *et al.* 1990) possibly indicating that this species is also a visual predator, with new moon yielding the lowest catches. It is possible that some visual predators avoid water with low visibility and low-light conditions. Both *Carcharodon carcharias* and *Isurus oxyrinchus* were caught least during new moon, as were *Sphyrna zygaena* and *Carcharhinus brachyurus*, although it is unclear why this is the case for the latter two species.

A habitat versus catch rate matrix did not provide any conclusive relationship between the shark species' frequented habitats and corresponding catch rate for a particular moon phase. Several of the shark species analysed have wide-ranging habitats and to establish a simple link was not possible. Neither did a comparison of shark genera versus catch rate for particular lunar phases show any relationship, although it should be stressed that the biology varies greatly between shark species within the same genus. Probably a closer investigation into the behavioural biology of each shark species would provide hypotheses for why particular moon phases correspond to changing catch rates.

An interesting question at this stage is whether the changing light conditions associated with different phase of the moon influence a) the capability of sharks to detect prey or b) the ability to visually detect the nets and avoid being caught. Full moon increases both the chances of visually detecting prey and the protective gill nets, while the prey may likely have an increased probability of avoiding predators. New moon presents lower light intensities in the sea and thus a shark that is dependent on visual cues probably faces a greater risk of being caught in the nets.

The time at which a particular moon phase reached its peak was not confined to night-time only and thus sunlight and moonlight would sometimes appear at the same time, but would not likely influence the light intensity available during daytime. Meteorological conditions at the time of meshing were not taken into consideration in the analysis, as this was deemed not viable and if the historical data exists they are in all likelihood not reliable. Cloudy conditions obviously contribute to less intensity of light available at depth and could probably be an important factor to consider. As mentioned in the introduction, Pyle *et al.* (1996) were able to observe activity of sharks *in situ* and also included a variable on weather conditions and light intensity of the moon at the time of direct observation, an exactness not possible in this study.

ANOVA, as used in this investigation, is probably the most common method used when comparing only four moon phases (John Field, UCT, personal communication, 2004). For *Carcharhinus plumbeus*, *Carcharhinus amboinensis* and *Isurus oxyrinchus* the number caught were, however, relatively low, yielding on average less than two individuals caught per month, which presents a weaker precision than desired. For species such as *Isurus oxyrinchus*, a mainly offshore and oceanic species, it is probable that only a small portion of the population are caught as the protective gill nets are located very close to shore (Cliff *et al.* 1990). Seasonal migration of sharks, as well as sexual segregation, should be viewed in concordance with the catch rate for different moon phases to obtain a suggestion as to during which month and which moon phase one sex for a particular species has been recorded most frequently caught. For nine of the species analysed, males and females both showed the maximum catch rate at the same moon phase, while the remaining four differed, perhaps the most notable difference seen for *G. cuvier*.

Conclusion

Seasonality: Seasonal variation in catches and fluctuating sex ratio was found for all sharks possibly as a result of migratory behaviour, although a significant pattern was not apparent for all species such as *Galeocerdo cuvier*, which was netted relatively constantly throughout the year. Five species (*Sphyrna lewini*, *Carcharhinus leucas*, *Carcharhinus plumbeus*, *Carcharhinus amboinensis* and *Isurus oxyrinchus*) had an apparent seasonal catch pattern, while *Carcharhinus obscurus*, *Carcharhinus brachyurus* and to some extent *Sphyrna zygaena* displayed a marked peak in catches for two particular months (June and July), coinciding with the annually occurring migration of sardines. *Carcharhinus brevipinna* had a very distinct peak in February. Several species were netted with the one sex dominating throughout, while the species switching sex ratios at different times during the year may point towards sexually segregated migrations.

Lunar trends: While individual species, and sex, showed significant differences in catch rates between various phases of the moon, there was no evident pattern of a increase in number of species represented in the catches during a particular moon phase. This was not expected, as the behavioural biology of sharks vary even within genera and between species sharing habitats. Nonetheless, the findings are interesting, and the lack of a conclusive pattern should not be dismissed as entirely anecdotal without a closer look at the behaviour and ecology of each species. The fact that there are significant differences in catch rates between moon phases within species, and sex, begs the question as to why this is so.

Catch data are accumulated over time at the NSB and so the accuracy in continued trends will improve as the dataset grows. The models for the lunar analysis and seasonality used in this

study are designed generically, so that adding more data will increase the precision of the trends. Future inclusion of additional variables to the model, such as size classes of sharks, environmental factors and reliable data on turbidity would provide even more informative trends and merits further attention. In particular intraspecific size distribution in relation to different lunar phases is an interesting hypothesis to entertain.

The expertise on seasonality of sharks caught in the protective gill nets, together with lunar trends in catch rates, is a valuable tool in reducing catches, and continued focus on this warranted.

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