Sexual segregation of pelagic sharks and the potential threat from fisheries

Gonzalo R. Mucientes1, Nuno Queiroz2,3, Lara L. Sousa2, Pedro Tarroso2 and David W. Sims3,4,*

1Instituto de Investigaciones Marinas, CSIC, Eduardo Cabello 6, 36208 Vigo, Spain
2CIBIO—Universidade de Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-668 Vairão, Portugal
3Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK
4School of Biological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

*Author for correspondence (dws@mba.ac.uk).

Large pelagic sharks are declining in abundance in many oceans owing to fisheries exploitation. What is not known however is whether within-species geographical segregation of the sexes exacerbates this as a consequence of differential exploitation by spatially focused fisheries. Here we show striking sexual segregation in the fastest swimming shark, the shortfin mako Isurus oxyrinchus, across the South Pacific Ocean. The novel finding of a sexual ‘line in the sea’ spans a historical longline-fishing intensity gradient, suggesting that differential exploitation of the sexes is possible, a phenomenon which may underlie changes in the shark populations observed elsewhere.

Keywords: distribution; behaviour; sex ratio; sexual harassment; overfishing; conservation

1. INTRODUCTION

Pelagic sharks are facing widespread declines owing to fisheries expansion into the open ocean within the past few decades (Baum et al. 2003). Recent studies have suggested that reductions in relative abundance of up to 80 per cent have occurred in as little as 15 years for some species (Baum et al. 2003), although lack of accurate harvest data hampers quantitative stock assessments. Despite some fisheries assessments showing less pronounced declines for large sharks (Sibert et al. 2006), they are undoubtedly particularly susceptible to over-harvesting because of slow growth rates, a late age at maturity and low fecundity (Compagno 2002).

Management of pelagic shark populations is poorly developed and takes little account of behavioural characteristics such as spatial and temporal movements and distributions. Recent studies have shown that large sharks cross national boundaries, exhibit sex-biased dispersal and often return to favoured areas (Sims et al. 2000; Pardini et al. 2001; Southall et al. 2006).


Therefore, if high fishing activity occurs in key areas where, for example, the majority of a population aggregate for feeding or mating opportunities, or where important components of a population (e.g. pregnant females, juveniles) choose to remain, there is a potential for increased rates of decline. A potential factor exacerbating declines may be the sex-biased exploitation as a consequence of within-species sex differences in habitat use (Sims 2005).

Sexual segregation is a widespread behaviour in the animal kingdom and can arise within a species owing to, among other factors, sex differences in body size, activity, behaviour, nutritional requirements and/or habitat selection (Magurran & Macias Garcia 2000; Wearmouth & Sims 2008). Habitat segregation by sex appears common among sharks (Klimley 1987; Wearmouth & Sims 2008), where adult males and females within a species use different habitats either within the same or different areas (Sims 2005). Habitats may be selected differentially by the sexes for social, thermal or forage-related reasons, for example (Wearmouth & Sims 2008). However, the potential role of sexual segregation in the over-exploitation of shark populations remains an open question because distinct boundaries in the ocean between male and female sharks have not been documented in detail, or in relation to fisheries activity.

To investigate whether (i) sexual segregation in open-ocean sharks is evident over medium time scales (weeks to months) and (ii) population structuring by sex may lead to differential availability of shark sexes to the fishery, we made detailed observer records of shortfin mako Isurus oxyrinchus and blue shark Prionace glauca catches during commercial longlining in the South Pacific Ocean.

2. MATERIAL AND METHODS

Shortfin mako and blue sharks (see the electronic supplementary material for species biological information) were caught by a Spanish commercial surface-longline vessel targeting swordfish Xiphias gladius in the southeast Pacific Ocean between 20–40°S and 100–140°W, from 9 December 2004 to 9 March 2005 (summer season, December–February). A total of 89 longline sets were deployed during the night at different depths, ranging from 20.1 to 27.4 m. Hooks (n=172 878) were fixed to monofilament lines and baited with mackerel Scomber scombrus. All sharks were sexed on-board and the fork length was measured.

Capture locations were plotted as sex ratios with locations geo-referenced using tools in ArcGIS v. 9.2 (http://www.spatial ecology.com/itools/). Sea surface temperature (SST) data were obtained through the online Ocean ESIP Tool (POET; http://poet.jpl.nasa.gov/). As an estimate of primary productivity, chlorophyll ‘a’ images were derived from the Sea-viewing Wide Field of view Scanner (http://oceancolor.gsfc.nasa.gov/). Pearson’s correlation coefficients were estimated between sexes (number of sharks caught per individual longline set) and SST or chlorophyll a. Stomach contents (n=396 sharks) were analysed in situ during evisceration. Items were identified to the lowest taxa possible and only the presence/absence was recorded. A multivariate randomization procedure (ANOSIM) was performed to test for diet differences between the sexes.

Longline catch and yearly effort data aggregated by 5°×5° degree squares covering the whole Pacific Ocean between 1950 and 2004 were provided by the Secretariat of the Pacific Community (http://www.spc.int/). Longlining data were used since purse-seine fishery data for the western Pacific indicates low mako catches (less than 2% of total by-catch; see the electronic supplementary material). Effort data (number of hooks) for every visited square were averaged and a t-test performed between the two main surveyed areas.

Received 11 December 2008
Accepted 12 January 2009

This journal is © 2009 The Royal Society
3. RESULTS

A total of 264 male and 132 female *I. oxyrinchus* were captured. Data showed clear sexual segregation over the four-month period with males occurring predominately in the west and females mainly in the east (figure 1; electronic supplementary material, figure 1; regression analysis: proportion female versus longitude; $r^2=0.56$, $F=88.34$, $p<0.0001$). Based on length measurements at sexual maturity (Compagno 2002), 84 per cent of males were considered adult, compared with only 13 per cent of females, indicating size, in addition to sexual, segregation (electronic supplementary material, figure 2a). To examine this striking separation, we mapped the capture locations of the sexes on remote-sensing images of environmental variables. These showed no significant correlation between males and SST ($r=0.550$, $p=0.670$; figure 1) or between male or female occurrence and chlorophyll a (males: $r=-0.165$, $p=0.201$; females: $r=-0.060$, $p=0.674$; electronic supplementary material, figure 3) and the negative correlation of female occurrence with SST was inconclusive (see Results in the electronic supplementary material). Examination of prey items in stomach contents showed no difference in diet between the sexes ($R=0.017$, $p=0.195$; electronic supplementary material, table 1). Males were predominant in the area where longline fishing intensity was historically higher (averaged over

**Figure 1.** (a) Capture locations of male (white; $n=264$) and female (black; $n=132$) shortfin mako sharks in the southeast Pacific with respect to a false colour remote-sensing image of SST. (b) Longline effort data averaged by $5 \times 5$ degree squares for the Pacific from 1950 to 2004; class breaks were determined statistically by finding adjacent feature pairs between which there was a relatively large difference in data value — natural breaks. Inset black boxes represent the survey area.
70 km h

swimming shark (clocking speeds up to approx.
intriguing because this species is the world's fastest
observed between male and female shortfin mako is
previously reported. The sexual ‘line in the sea’ we
sharks at this scale is striking and has not been
Clear population structuring in large, open-ocean
4. DISCUSSION

Clear population structuring in large, open-ocean
sharks at this scale is striking and has not been
previously reported. The sexual ‘line in the sea’ we
observed between male and female shortfin mako is
intriguing because this species is the world’s fastest
swimming shark (clocking speeds up to approx.
70 km h$^{-1}$) and capable of long-distance movements.
Tagging shows trans-Atlantic migrations are rare
however (Casey & Kohler 1992), but with sufficient
genetic exchange among stocks for a single species
worldwide (Heist 2008). Nonetheless, this exploited
shark displays pronounced sex and size segregation at
the regional scale, which does not appear to closely
reflect prey, SST or primary productivity, at least over
the time scale of this study. Furthermore, the
observed pattern appeared to be principally the result
of spatial rather than temporal effects because the
large changes in sex ratio were too abrupt (occurring
over 8 and 24 days) within the core summer months
to be consistent with large-scale, synchronous move-
ments of the sexes as the survey progressed, which
would be expected if segregation were wholly
temporally driven (see Discussion in the electronic
supplementary material).

Numerous hypotheses have been proposed to
explain sexual segregation in animals, but how and
why it occurs remains controversial and largely
unresolved for many taxa (Wearmouth & Sims 2008).
For the sexually size dimorphic scalloped hammerhead
shark Sphyrna lewini (females grow larger), Klimley
(1987) proposed that females segregated from males
by moving to offshore habitat to feed on different, more
energy-rich prey that conferred increased growth rates,
such that maturity was reached at a larger body size
than similar aged males; a larger female body size is
necessary to support large, well-developed embryos.
It was suggested that this strategy would act to match
the reproductive lifetime of females with that of males
within the same cohort. Shortfin mako exhibit
sexual body size dimorphism with females growing up
to 4 m in length, some 30 per cent larger than
males, and giving birth to a few large young (embryo
at-birth length, approx. 0.7 m; frequency, 4–16 per
female; Compagno 2002). Although the present
study could not conclusively identify behavioural
mechanisms, our results indicate that mako sex segre-
gation is probably unrelated to different nutritional
requirements, because male and female diets were
not different and basal productivity between male
and female habitats was a poor predictor of the
observed pattern.

Sexual segregation in mako shark in this study was
observable at the large spatial scale but was not
absolute because some mixing was evident. Males
and females were captured on the same longline sets
at a number of locations, principally around the line
separating western from eastern sectors, but also
along the thermal front boundary zone in the south
(figure 1a). Thermal fronts are often prey rich and
act to aggregate predators with greater apparent
mixing of the sexes owing to feeding or courtship
opportunities (Sims et al. 2000). Although we are
unable to provide an explanation for why shortfin
mako segregate sexually, it is possible that it occurs
owing to social factors. Courtship and mating in
sharks are highly aggressive during which (often
multiple) males inflict serious bite wounds on females
(Stevens 1974). It is possible that mako shark sexual
harassment (by males) results in fitness consequences
for females (Magurran & Seghers 1994), interactions
that manifest at the large geographical scale as sexual

![Figure 2. Capture locations of male (white; n=445) and female (black; n=231) blue shark in the southeast Pacific with respect to seabed bathymetry. Inset black boxes represent the survey area.](image-url)
segregation. That mature females were not captured in large numbers \( n=15 \) suggests that they were absent from the study area, which may also reflect avoidance behaviour.

The finding of marked sexual segregation in a fast-swimming, highly mobile pelagic shark at the broad scale has implications for assessing fisheries effects on shark populations. Complex structuring coupled with region-specific fishing activities may have disproportionate effects on different components of shark populations. In support of this, we found sex differences in potential exposure to fishing effort for \textit{I. oxyrinchus} owing to geographical separation of the sexes (see Discussion in the electronic supplementary material). For shortfin mako in this study, we hypothesize that more intense longlining in the west, if it occurs over the shorter, seasonal term, has the potential for higher relative catch rates of males but lower catches of females. Exploitation of sharks exhibiting seasonal sexual segregation could be a major contributor to population declines. For example, the seasonal capture of sex-specific schools of mature female spurdog \textit{Squalus acanthias} in the English Channel may have resulted in stock collapse in just a few years (\textit{Ford} 1921).

We also found evidence for sexual segregation of blue shark in the southeast Pacific region, since catches were dominated by mature males, suggesting that segregation occurs at a larger spatial scale than the area studied here. Our findings are consistent with tagging and surveys showing that blue shark sexually segregated over very large, perhaps even ocean-basin scales (\textit{Stevens} 1990). Nevertheless, even with sexual structuring at these scales, blue shark populations may also be affected by sex differential exploitation. For example, \textit{P. glauca} in the western Atlantic are thought to segregate sexually and our proposal of sex-biased exploitation seems supported because male relative abundance declined by 80 per cent between 1977 and 1994 but no change was discernible for females over the same period (\textit{Simpfendorfer et al.} 2002).

What these and the current study indicate is the need for wide-scale, spatially referenced recording of shark sexes by global high-seas fisheries. However, given the lack of even the most basic shark catch data for most fisheries, the potential problem we highlight may already have impacted populations. There is an urgent need for proper reporting by high-seas fisheries of shark catches by species, number of individuals and biomass, together with their sex.

The authors thank the captain and crew for scientific access to commercially caught sharks and V. Wearmouth for manuscript comments. N.Q. was supported by Fundação para a Ciência e a Tecnologia (FCT) grant SFRH/BD/21354/2005 and D.W.S. by the UK Natural Environment Research Council (NERC) Oceans 2025 Strategic Research Programme.


