Sexual segregation of pelagic sharks and the potential threat from fisheries

Gonzalo R. Mucientes[1], **Nuno Queiroz**[2,3],
Lara L. Sousa[2], **Pedro Tarroso**[2]
and David W. Sims[3,4,*]

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

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.spatialecology.com/htools/). 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.
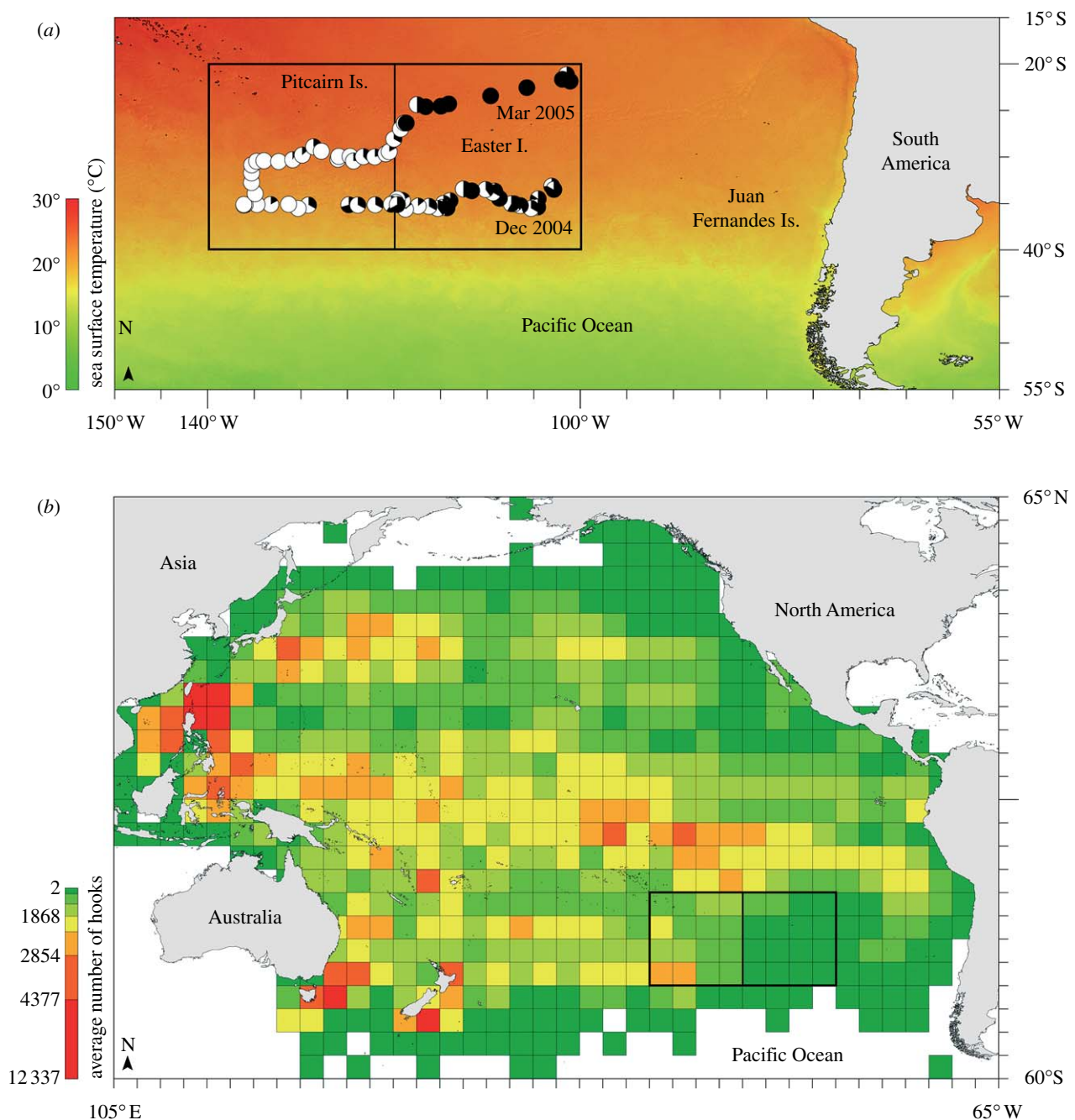
Figure 1. (*a*) Capture locations of male (white; $n=264$) and female (black; $n=132$) shortfin mako sharks in the southeast Pacific with respect to a false colour remote-sensing image of SST. (*b*) Longline effort data averaged by 5×5 degree squares for the Pacific from 1950 to 2004; class breaks were 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.

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 predominantly in the west and females mainly in the east (figure 1*a*; 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 2*a*). 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
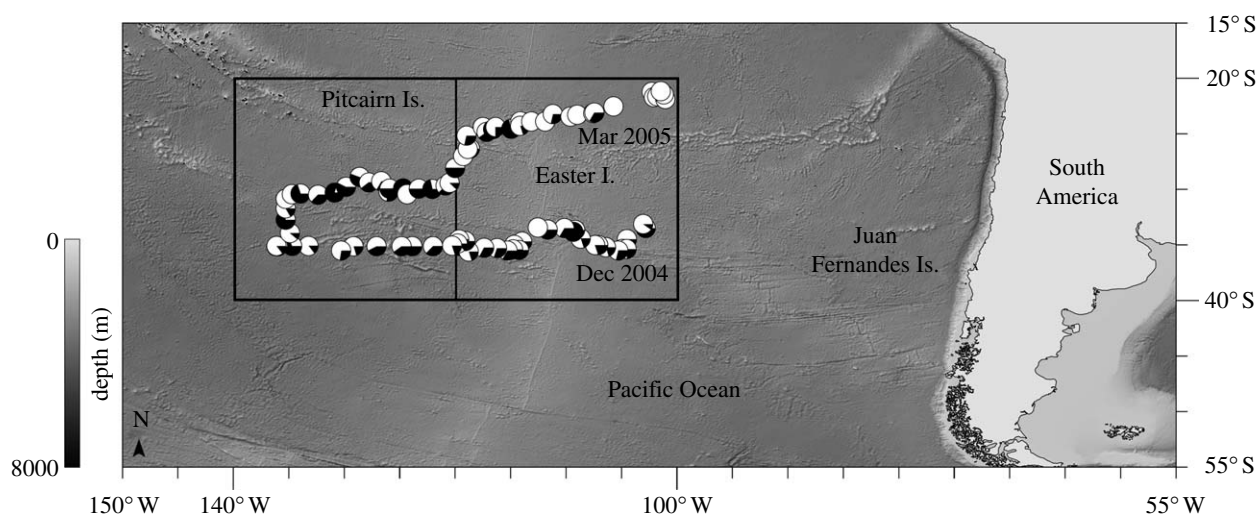
Figure 2. Capture locations of male (white; $n=445$) and female (black; $n=231$) blue shark in the southeast Pacific with respect to seabed bathymetry. Inset black boxes represent the survey area.

a 55-yr period), whereas females dominated in the area with lower historical effort (figure 1b); average number of 'historical' longline hooks set in each surveyed area was significantly different (*t*-test: $t=2.86$, $p=0.019$, $n=23$).

The pattern of the blue shark sex distribution from the same longline sets as shortfin mako indicated a general bias towards mature males across the entire area (figure 2; ratio, male : female, 1.00 : 0.34. Total mature individuals: male, 425; female, 64; total immature: male, 25; female, 167).

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 movements 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 segregation 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

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 *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 *Squalus acanthias* in the English Channel may have resulted in stock collapse in just a few years (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 (Stevens 1990). Nevertheless, even with sexual structuring at these scales, blue shark populations may also be affected by sex differential exploitation. For example, *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 (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.

Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J. & Doherty, P. A. 2003 Collapse and conservation of shark populations in the northwest Atlantic. *Science* **299**, 389–392. (doi:10.1126/science.1079777)

Casey, J. G. & Kohler, N. E. 1992 Tagging studies on the shortfin mako shark (*Isurus oxyrinchus*) in the western North Atlantic. *Aust. J. Mar. Freshwater Res.* **43**, 45–60. (doi:10.1071/MF9920045)

Compagno, L. J. V. 2002 *Sharks of the world*. FAO Fishery Synopsis, vol. 2. Rome, Italy: Food and Agriculture Organization of the United Nations.

Ford, E. 1921 A contribution to our knowledge of the life-histories of the dogfishes landed at Plymouth. *J. Mar. Biol. Ass. UK* **12**, 468–505.

Heist, E. J. 2008 Molecular markers and genetic population structure of pelagic sharks. In *Sharks of the open ocean: biology, fisheries and conservation* (eds M. D. Camhi, E. K. Pikitch & E. A. Babcock), pp. 323–333. Oxford, UK: Blackwell.

Klimley, A. P. 1987 The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environ. Biol. Fish.* **18**, 27–40. (doi:10.1007/BF00002325)

Magurran, A. E. & Macias Garcia, C. 2000 Sex differences in behaviour as an indirect consequence of mating system. *J. Fish. Biol.* **57**, 839–857. (doi:10.1111/j.1095-8649.2000.tb02196.x)

Magurran, A. E. & Seghers, B. H. 1994 A cost of sexual harassment in the guppy, *Poecilia reticulata*. *Proc. R. Soc. B* **258**, 89–92. (doi:10.1098/rspb.1994.0147)

Pardini, A. *et al.* 2001 Sex-biased dispersal in white sharks. *Nature* **412**, 139–140. (doi:10.1038/35084125)

Sibert, J., Hampton, J., Kleiber, P. & Maunder, M. 2006 Biomass, size, and trophic status of top predators in the Pacific Ocean. *Science* **314**, 1773–1776. (doi:10.1126/science.1135347)

Simpfendorfer, C. A., Hueter, R. E., Bergman, U. & Connett, S. M. H. 2002 Results of a fishery-independent survey for pelagic sharks in the western North Atlantic, 1977–1994. *Fish. Res.* **55**, 175–192. (doi:10.1016/S0165-7836(01)00288-0)

Sims, D. W. 2005 Differences in habitat selection and reproductive strategies of male and female sharks. In *Sexual segregation in vertebrates: ecology of the two sexes* (eds K. E. Ruckstuhl & P. Neuhaus), pp. 127–147. Cambridge, UK: Cambridge University Press.

Sims, D. W., Southall, E. J., Quayle, V. A. & Fox, A. M. 2000 Annual social behaviour of basking sharks associated with coastal front areas. *Proc. R. Soc. B* **267**, 1897–1904. (doi:10.1098/rspb.2000.1227)

Southall, E. J., Sims, D. W., Witt, M. J. & Metcalfe, J. D. 2006 Seasonal space-use estimates of basking sharks in relation to protection and political–economic zones in the NE Atlantic. *Biol. Conserv.* **132**, 33–39. (doi:10.1016/j.biocon.2006.03.011)

Stevens, J. D. 1974 The occurrence and significance of tooth cuts on the blue shark (*Prionace glauca* L.) from British waters. *J. Mar. Biol. Ass. UK* **54**, 373–378.

Stevens, J. D. 1990 Further results from a tagging study of pelagic sharks in the North-east Atlantic. *J. Mar. Biol. Ass. UK* **70**, 707–720.

Wearmouth, V. J. & Sims, D. W. 2008 Sexual segregation of marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Adv. Mar. Biol.* **54**, 107–170. (doi:10.1016/S0065-2881(08)00002-3)