Insights into the reproductive biology and fisheries of two commercially exploited species, shortfin mako (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*), in the south-east Pacific Ocean.

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ABSTRACT

In 2005 and 2010; 1,241 *Isurus oxyrinchus* and 1,153 *Prionace glauca* were collected from 178 longline sets in a ship-board observer program in coastal waters off Caldera, Chile (27°S). Catch composition was significantly biased towards *I. oxyrinchus* in 2005, but both species were caught in the same proportion in 2010. The sex ratio for *I. oxyrinchus* and for *P. glauca* did not differ significantly from unity within or between years. Sharks matured (L_{50}) at a total length of 190.3 cm for male and 199.2 cm for female for *P. glauca*; and 180.2 cm for male *I. oxyrinchus*. Size-at-maturity for female *I. oxyrinchus* was not determined due to the near absence of mature specimens examined. Generalised additive models (GAMs) were used to examine catch per unit effort (CPUE) in relation to sea surface temperature, wind speed, time of day, hook depth and soak time. The GAMs revealed a significant effect of depth on *P. glauca* CPUE, and depth and wind speed for *I. oxyrinchus* CPUE. The predominance of small, immature sharks caught in the coastal, artisanal fishery indicates that both species may use the area as a pupping, and possibly a nursery zone during spring and summer. National data on catch composition and annual landings provide evidence of an increasing trend to land *P. glauca*, possibly to satisfy the international shark fin trade. Conservation measures, such as the introduction of a minimum capture size for sharks to protect the recruitment into the population, conservative fishing quotas and delimitation of fishing areas are necessary to ensure the sustainability of both species in the region.

Additional keywords: reproductive biology; fishery management; CPUE; environmental preferences; Chile.

1. INTRODUCTION

There is global concern about the impact of depletion and possible loss of apex predator fishes in marine ecosystems (Dulvy et al., 2003; Myers et al., 2007; Ferretti et al., 2010). This concern is of particular relevance in relation to sharks as their biological characteristics make them particularly vulnerable to over-exploitation (Stevens et al., 2000; Caillet et al., 2005). Downward trends in pelagic shark catches have been documented in many oceanic fisheries, for example, in the north-east Atlantic (Pawson and Vince, 1999; Baum et al., 2003, Dulvy et al., 2008), off southern Africa (Petersen et al., 2009), Japan (Nakano, 1999) and in the Mediterranean Sea (Ferretti et al., 2008).

The shortfin mako shark, *Isurus oxyrinchus* Rafinesque, 1810, is an important component of pelagic shark community, ranging through most tropical and temperate oceans of the world (Compagno et al., 2005). In the south-east Pacific, *I. oxyrinchus* is caught in commercial oceanic longline and gill-net fisheries that target swordfish (*Xiphias gladius* Linnaeus, 1758), as well as being caught in the coastal, artisanal longline fishery that operates in northern Chile and southern Peru (Acuña et al., 2001; Gilman et al., 2007). The latter is the only Chilean artisanal fishery that target sharks. In addition to *I. oxyrinchus*, this fishery has a bycatch of blue shark, *Prionace glauca* (Linnaeus, 1758) and to a lesser extent, porbeagle, *Lamna nasus* (Bonnaterre, 1788) (Lamilla et al. 2010).

In Chilean waters (and outside of the Exclusive Economic Zone) the directed shark fishery, and the associated shark bycatch, has grown substantially in recent years due primarily to a declining abundance of valuable teleost species and management restrictions placed on these teleost fisheries (Cerna and Licandeo, 2009). In contrast to the oceanic fishery, the coastal artisanal fishery has discrete operational boundaries; these are mainly related to the limited autonomy of vessels that restricts the length of trips and hence, fishing areas. This 'subsistence fishery', that started in 1979, is focused on the coastal zone from southern Peru (Gilman et al., 2007) to 35°S in Chile where boats of 9–18 m length explore coastal temperate water-masses of about 18°–21° C which are associated with a relatively large abundance of sharks (Acuña et al., 2001).

While there are legal minimum sizes for pelagic sharks (which includes *I. oxyrinchus* and *P. glauca*) caught in Peruvian waters, the only regulation of shark fishing in Chilean waters is in the types of gear allowed to be used (Lamilla et al., 2010), despite the fact that Chile has a National Plan of Action to promote the conservation and management of sharks. While *I. oxyrinchus* is retained by both oceanic and coastal fisheries, *P. glauca* is generally discarded after finning which has resulted in under reporting of the latter species in official landings records (Lamilla et al., 2008). Commercial shark landings in the decade 1999 to 2009 increased four-fold for *I. oxyrinchus*, from 237 to 950 tonnes and almost sixty-fold for *P. glauca*, from 7 to 408 tonnes (SERNAP, 2009).

Isurus oxyrinchus reproduces by oophagic viviparity (Lamniform oophagy), with an average of 12 pups per litter and a 15–18 month gestation period (Gilmore, 1990; Snelson et al., 2008). There is a large sexual difference in the size and age at maturity, with males maturing at about 195 cm total length (L_T) at 6 years of age, and females at 265–280

cm L_T at 16 years of age (Stevens, 2008; Semba et al., 2009). While segregation among the developmental stages (Nakano and Nagasawa, 1996) and geographical sexual segregation (Mucientes et al., 2009) have been reported, little is known about stock structure or genetic diversity (Heist et al., 1996) due to the species' large, diffuse, and highly dispersive populations (Schrey et al., 2003).

Prionace glauca reproduces by placental viviparity, gives birth to an average of 30 pups after a 9–12 month gestation period (Henderson et al., 2001), and females may breed every year (Stevens, 1984; Hazin et al., 1994). Birth usually occurs in spring and summer, with pupping and nursery areas seemingly located in intermediate-latitude oceanic convergences with high prey availability (Nakano and Stevens, 2008). Growth is relatively rapid, with males maturing at 4–6 years and females at 5–7 years of age (Lessa et al., 2004; Manning and Francis, 2005). Distinct sex and size segregation is evident, with size generally decreasing with increasing latitude (Henderson et al., 2001). Blue sharks are a major bycatch of longline and gill-net oceanic fisheries, but because of poor reporting the magnitude of the catch and mortality is not reflected by official statistics (Nakano and Stevens, 2008). Additionally, recent population assessments indicate a moderate to large declining trend in both abundance and size of blue sharks in north-west Atlantic (Baum et al., 2003), central Pacific (Ward and Myers, 2005) and the Mediterranean (Ferretti et al., 2008).

To properly manage and conserve pelagic shark species it is necessary to have adequate information on their life-histories in order to understand the ecology and susceptibility to overexploitation (FAO, 2003; Garcia and Cochrane, 2005). Various analyses suggest that both sharks *I. oxyrinchus* and *P. glauca* may have undergone significant declines in abundance over parts of its distribution (Nakano, 1999; Pawson and Vince, 1999; Baum et al., 2003, Ward and Myers, 2005; Dulvy et al., 2008; Ferretti et al., 2008; Cailliet et al., 2009). Due to estimated and inferred declines, probable increases in fishing pressure, and considering the life history characteristics of *I. oxyrinchus*, the Indo-west Pacific and Atlantic subpopulations have recently been classified as Vulnerable on the IUCN Red List of threatened species; the north eastern Pacific subpopulation as Near Threatened; while the south Pacific population remains without conservation assessment (Cailliet et al., 2009). *Prionace glauca* is listed as Near Threatened globally (Stevens, 2009)

In the south-east Pacific, age and growth (Cerna and Licandeo, 2009) and habitat use (Abascal et al., 2011) of *I. oxyrinchus*, and the reproductive cycle of *I. oxyrinchus* and *P. glauca* (Acuña et al., 2001) have been examined, although information of the species' reproductive biology in the region is incomplete. The aims of the present study are to estimate life-history traits, including size-at-maturity, sex ratios and catch composition, as well as to describe the species' environmental preferences in Chilean waters. Annual landings and shark fin exports are discussed in relation to fishing practices and factors involved in the commercial fishery of pelagic sharks in Chile.

2. METHODS

Specimens of *I. oxyrinchus* and *P. glauca* were collected during on-board observer surveys in the artisanal longline fishery targeting *I. oxyrinchus* based in Caldera, Chile (27°04′ S, 70°51′ W) in the Southern Hemisphere summer fishing season (January and February) in two different years (2005 and 2010). Sharks were collected from 78 fishing trips made by 18 vessels of 12–17 m length using 5.5 km monofilament longline gear with wire traces and M/K No. 2 hooks. Sets comprised 200−350 hooks, each suspended from surface buoy spaced every 180−200 m. Hooks were baited using fresh and/or dry-salted chub mackerel (*Scomber japonicus* Houttuyn, 1782) or Chilean jack mackerel (*Trachurus murphyi* Nichols, 1920). Maximum soak time was 240 min, with sharks hooked during the longline deployment removed, the hook rebaited, and the capture time recorded.

2.1. *Biological data*

Data recorded at the time of collection included sex, maturity and total length (L_T). Measurements were made to the nearest centimetre (cm) in a straight line with the shark lying on its ventral surface (Francis & Duffy, 2005). Left clasper post-cloacal length (L_C) was also recorded.

Three reproductive-stage classifications were determined for each sex as juvenile, adolescent and adult. Changes in the reproductive organs were used to further assess the onset of maturity (Mollet et al., 2000). Males were considered to be adult when the claspers were elongated and the terminal cartilage elements were calcified. Adolescent individuals were those whose claspers extended beyond the posterior edge of the pelvic fins, but lacked calcification of the terminal cartilage elements. Juveniles had short, flexible claspers that did not extend beyond the posterior edge of the pelvic fins. Internally, coiling of the epididymides and testes development were also indicators of maturation (Stevens, 1983). Females were determined to be mature if they demonstrated one or more of the following characters: presence of pups *in utero*; large vitellogenic ova; and an oviducal gland distinctly differentiated from the uterus. Adolescent individuals had smaller ovaries, with some differentiation and no mature ova; undeveloped oviducal gland and uteri strap-like in appearance. Juveniles lacked any differentiation of the ovaries, and the oviducal gland was not differentiated from the uterus (Mollet et al., 2000).

Chi-square Goodness-of-Fit (χ^2) (Sokal and Rohlf, 1987), was used to test for significant sex bias between males and females proportion of each species within each year and between the two years sampled. Binomial maturity data (immature 0, mature 1) were determined by sex using 10 cm size class intervals. Size at 50% maturity was calculated by fitting the following logistic curve (by minimization of the least squares), to the relationship between the fraction of mature males or females and L_T, as a function of

$$L_T, Y = [1 + e^{-(a + bX)}]^{-1}$$

where Y is the fraction of mature individuals in length class X, and a and b are the model coefficients. The ratio $a{:}b$ represents the size at which 50% of the sharks were mature (Mollet et al., 2000). In addition, the relationship between L_T and L_C were used to further

assess the onset of first maturity (Restrepo and Watson, 1991). Comparisons of median L_T for males and females for each species were performed using the Mann-Whitney U test with significance accepted at $P < 0.05$.

2.2. Fishery data

Observer-monitored size and catch composition in each set and the final destination of each shark, as target species (whole-body landed), or as bycatch (incidentally caught shark, landed whole), discard (whole shark returned to the sea) or finned (removal of fins from a shark and discard of the body at sea, Hernández et al., 2008). For each longline set five environmental factors were recorded: sea surface temperature (SST) (^{o}C), wind speed (Beaufort scale), soak time (min), depth of hooks (m) and local time for each longline set deployed. Duration of each set was calculated as the length of time from when the first hook entered the water to when the last hook was retrieved. Set duration was multiplied by the number of hooks to give fishing effort in hook-hours. A total of 55,758 hooks were included in the data set. The number of sharks caught in each set was divided by the fishing effort to give the CPUE as sharks per 1000 hook hours. CPUE was log-transformed (log (CPUE+1)), in order to assess the departure of original data from normality and were calculated separately for each species. To explore the environmental parameters as predictors of the CPUE, generalised additive models (GAMs) were fitted for each species using a Quasi-Poisson error structure and a log link function to fit the response (Hastie and Tibshirani, 1990; Bigelow et al., 1999):

$$\log(\text{CPUE}+1) = b_0 + f_1(b_1\text{SST}) + f_2(b_2\text{Bathymetry}) + f_3(b_3\text{Soak time}) + f_4(b_4\text{Time-of-Day}) + f_5(b_5\text{Wind speed})$$

Where b_i are regression coefficients and f_i is a smoothing function applied to each continuous variable. Analyses were performed using R (R Core Team, 2012), with significance accepted at $P < 0.05$.

2.3. Landings

Information on annual commercial landings for the period 1979–2008 was extracted from the Chilean landings database of the Fishery National Service (SERNAP). Data were organised by the three landing categories recognised by the fishing Authority: artisanal (vessels under 18 m length), industrial vessels inside EEZ (exclusive economic zone) and industrial vessels in international waters. Also, shortfin mako and blue shark fin exports were extracted from National Customs Service (Servicio Nacional de Aduanas) Foreign Trade Statistics Database for the period 2000–2008.

Intentionality of the fishery will be tested considering artisanal and industrial landing records as well on-board observed catches. Target (*I. oxyrinchus*) and bycatch (*P. glauca*) species will be contrasted with an expected 50:50 ratio, as both species shares the same food resources and habitat preferences and seasonal distribution in the region (Acuña et al., 2001).

3. RESULTS

3.1. Catch composition

A total of 1,241 *Isurus oxyrinchus* and 1,153 *Prionace glauca* were caught and examined, and represents the total catch of sharks from 178 longline sets made in two separate years; 2005 and 2010 (Fig. 1). Catch composition (blue and shortfin mako shark proportion) had a significant bias towards shortfin mako sharks in 2005 (1:0.82; χ^2 = 5.634; d.f. = 1; *P* = 0.0178) but no differences were observed in 2010 (0.95:1; χ^2 = 0.30; d.f. = 1; *P* = 0.584).

In 2005, shortfin mako sharks under 80 cm L_T were discarded (dead or alive) due to market restrictions; blue sharks under 100 cm L_T were always discarded (dead or alive), while larger specimens could be retained either whole or as fins only. A 5% discard of shortfin mako over 80 cm L_T was observed during 2005, whereas there was no discard during 2010 of *I. oxyrinchus* of any size. An increase in the proportion of blue sharks landed rose from 18% in 2005, to 44% in 2010, and there was a related fall in the proportion being finned, which decreased from 60% in 2005 to 38% in 2010. The proportion of blue sharks discarded without use was similar in both years (22% and 18%, respectively).

3.1.1. Isurus oxyrinchus

A total of 640 females and 601 male shortfin mako sharks were examined. The male to female sex ratio was similar between years (1:1.16 in 2005; 1:1.03 in 2010) and no differences were observed within years: for 2005 χ^2 = 1.786; d.f. = 1; *P* = 0.181 and for 2010 χ^2 = 0.068; d.f. = 1; *P* = 0.794. Body size of females caught in 2005 ranged from 76 to 213 cm L_T (mean and standard deviation, 121.9 ± 23.7 cm) while males ranged from 75.5 to 240 cm L_T (122.4 ± 25.4 cm). Body size of females in 2010 ranged from 80 to 338 cm L_T (138.7 ± 24.2 cm) and males from 66 to 267 cm L_T (136.3 ± 124.5 cm) (Fig. 2a).

No significant differences were found between median sizes by sex and year (2005: W = 779.5; *P* = 0.741; and 2010: W = -2569.0; *P* = 0.220); but significant differences were found in size structure between years (W = 70954; *P* < 0.0001) as the modal size increased, but the smallest size-class (70–90 cm L_T) was largely absent in 2010. The smallest free-swimming specimen examined was a 66.1 cm L_T male and there was no sign of an umbilical scar on any specimen in the smallest size class

For male sharks; juveniles ranged from 66 cm to 148 cm L_T, adolescents from 96 cm to 184 cm L_T and adults from 180 cm to 267 cm L_T. Coiled epididymides were present in specimens over 174 cm L_T and correlated with elongated, partially calcified claspers. There was a sigmoid relationship between clasper and total length (Fig. 3a), with clasper growth in relation to L_T most rapid in adolescent sharks. In female juvenile and adolescent sharks, the oviducal glands were indistinct from the uteri. Juvenile females ranged from 80 cm to 144 cm L_T, adolescents from 164 to 250 cm L_T. Vitellogenic, mature ova were found in a single 338 cm L_T specimen. No gravid females were observed. Using binomial maturity data, the size where 50% of *I. oxyrinchus* males were mature (L_{50}) was 180.2 cm

L_T (Fig. 4a), and the equivalent L_{50} for females was not conclusive as no mature females were obtained during surveys.

3.1.2. *Prionace glauca*

The male to female sex ratio of blue sharks, based on the examination of 1,153 individuals (576 female, 577 male), was similar between the two years of the study (1:1.12 in 2005; 1:0.94 in 2010) and no differences were observed within 2005 ($\chi^2 = 0.618$; d.f. = 1; $P = 0.431$) and 2010 ($\chi^2 = 0.348$; d.f. = 1; $P = 0.556$). In 2005, the body size ranged from 56 to 249 cm L_T (133.1 ± 35.4 cm) for females, and 52 to 310 cm L_T (152.7 ± 48.6 cm) for males (Fig. 3b). In 2010, body size ranged from 75.5 to 249 cm L_T (139.0 ± 27.5 cm) for females and 77 to 310 cm L_T (151.3 ± 43.3 cm) for males (Fig. 2b).

Significant differences were found between median body size (L_T) by sex in both study years (W = 3959.5; $P < 0.05$ for 2005 and W = 3204.0; $P < 0.05$ for 2010), with smaller female (133 cm and 135.5 cm L_T in 2005 and 2010, respectively) than that male (143 cm and 140 cm L_T) despite having similar size structure (W = 3020; $P = 0.398$). Juvenile male sharks ranged from 52 to 146 cm L_T, adolescent sharks from 115 cm to 219 cm L_T, and adult sharks from 181 cm to 310 cm L_T. Males over 200 cm L_T had coiled epididymides and well-developed testes, which was consistent with the observation that fully-calcified claspers were found in individuals over 195 cm L_T (Fig. 3b). The size of juvenile female sharks ranged from 56 and 145 cm L_T; adolescents from 110 to 180 cm L_T, and mature females from 171 to 249 cm L_T. Using binomial maturity data, the size where 50% of *P. glauca* females were mature (L_{50}) was 199.2 cm L_T (Fig. 4c). Size of 50% of maturity for males was 190.3 cm L_T (Fig. 4d). No gravid females were observed and mature ova were found in 8.4% of the mature female sharks caught.

3.2. *Environmental preferences and CPUE*

Values of CPUE for individual sets ranged from 0 to 230 sharks/1000 hook-hours for shortfin mako sharks and 0 to 662 sharks/1000 hook-hours for blue sharks. In total, there were 14 sets (9%) where *I. oxyrinchus* was not caught and 35 sets (23%) where *P. glauca* was not caught. For shortfin mako, the GAM indicated depth ($P = 0.019$) and wind speed ($P = 0.038$) have significant interaction with catch rate; but time of day, soak time and SST did not (Table 1, Fig. 5). For blue shark, the GAM indicated that environmental variables analysed were not significant with the exception of depth ($P = 0.030$). The relationship between *I. oxyrinchus* and *P. glauca* populations' catch rates and environmental variables are shown in Fig. 5.

3.3. *National landings*

Shark fishing records in Chile began in 1978, when 33 tonnes of *I. oxyrinchus* were landed. Since then, only with the exception of 1981 in which 32 tonnes were landed, annual landings of *I. oxyrinchus* and *P. glauca* increased exponentially to 1991 when 1,118 tonnes

were landed (Fig. 6a). After 1990, the bycatch of the industrial fleet was recorded separately to the artisanal fishery landings. Post-1990 the artisanal landings have fluctuated markedly, but with an overall downward trend. From 2000, artisanal and industrial landings have followed a similar pattern, peaking at 1,354 tonnes in 2001, followed by a dramatic decrease to 448 tonnes in 2003; and since then industrial landings have been almost twice that of the artisanal fishery.

The export of shark fin has been recorded since 2001, but the identity of the sharks involved is not known and is likely to include over ten species of cartilaginous fishes (Hernández et al., 2008). In the period from 2001 to 2008, over 190,000 kg of dry shark fins were exported to Asian markets, but since then the average export of dry fin has decreased to 2,600 kg per annum (Fig. 6b).

Overall, the annual effect evidences a decline after the peak landing during 2000, with low landings levels in subsequent years despite increased fishing effort. Moreover, the blue shark to shortfin mako shark landing ratio has increased 30-fold in the artisanal fishery and about 15–30-fold in the industrial landings over the 1998–2009 period (Fig. 6c).

4. DISCUSSION

Bycatch and target fisheries are the major source of mortality for oceanic sharks (Dulvy et al., 2008). Information on life-history traits and the constraints these impose on the species' ability to withstand exploitation are required for proper fishing mortality assessments (Stevens, 2008). The attainment of sexual maturity is a major milestone, in an elasmobranch's life-history which governs distribution, behaviour, and biology of pelagic sharks (Francis and Duffy, 2005).

There are many examples of sex-specific traits, such as sex-biased dispersal (Pardini et al., 2001) and sex-specific differences in resource use (Klimley, 1987) and habitat selection (Sims et al., 2001). Various hypotheses have been proposed to explain the phenomenon, such as sexual differences in reproductive strategies (Sims, 2005) and physiological requirements (Wearmouth and Sims, 2008); that are related to sexual maturity. Moreover, reproductive events of mating, gestation and parturition directly influence the physiological condition (King, 1984), migration (Bansemer and Bennett, 2009) and habitat use (Castro, 1993; Heupel et al., 2007) at seasonal or annual scales. Therefore, both the size-at-maturity and the seasonality of reproductive events must be known to understand the spatio–temporal pattern of distribution and behaviour of sharks throughout their lifetime.

The absence of differences in sexual structure for *I. oxyrinchus* and *P. glauca* in the South Pacific Ocean, are in accordance with previous studies for both species in coastal fishing grounds of Mexico (Conde-Moreno and Galván-Magaña, 2006), Brazil (Carvalho et al., 2011), Canada (Campana et al., 2005), Portugal (Maia et al., 2007), USA (Simpfendorfer et al., 2002) and New Zealand (Bishop et al., 2006).

Size-at-maturity (L_{50}) in both species appears consistent with previous results despite the relatively absence of mature females in the current study. In both years, the lack of gravid females or those in which the uteri were developed suggest that mature sharks were absent from the fishing grounds during the fishing season (or were not feeding or catchable).

Size-at-birth of *I. oxyrinchus* in the South Pacific Ocean appears to be consistent with reports from other geographical regions, with L_T at birth generally around 65–70 cm (Casey and Kohler, 1992; Duffy and Francis, 2001; Costa et al. 2002; Maia et al. 2007). Habitat use and selection influence population dynamics, intraspecific and interspecific interaction, ecosystem structure and biodiversity (Grubbs, 2010). The predominance of the smaller size-classes (between 70 and 100 cm L_T) in both years of sampling suggests that *I. oxyrinchus* females use the coastal area where the fishery is conducted as a pupping ground and possibly, a nursery zone during spring and summer on an annual basis. If a juvenile growth rate of about 50 to 61 cm year^{-1} for the first year of life (Pratt and Casey, 1983; Maia et al. 2007) is considered, two major trends can be recognized in the catch size distribution: sharks between 60 and 70 cm L_T are likely to be young-of-the-month (YOM); while sharks between 100 and 120 cm L_T represent the young-of-the-year (YOY). The variation in size of the YOY captured during the January/February period of 2005 and 2010 suggests that parturition at the population level may occur over a period of some months, and generally prior to summer with the last recruits of the pupping season represented by the smallest individuals. Assuming an average growth rate for the first year of life of 61.1 cm year^{-1} (Maia et al., 2007), the main cohort, 52% of the catch, relates to those sharks born in the pupping season (winter to early-summer) just prior to the sampling effort.

A marked decrease in the fraction of YOM and YOY in *I. oxyrinchus* is apparent when the 2005 and 2010 total lengths are compared, which may reflect an additive effect of the capture of juveniles in this fishery or a delayed pupping season in 2010. In both years, thermal anomalies were experienced in ocean surface temperatures due to the effect of the El Niño Southern Oscillation (Sielfeld et al., 2010, Sarachik and Cane, 2010). This natural phenomenon is documented to alter the 'normal' structure of marine ecosystems in South Pacific Ocean (Zhang et al., 2008); but by conducting the fishery surveys in similar oceanographic conditions, the environmental effects might be excluded as an explanation of the differences of the pupping season. There was a shift from a relatively high proportion (25.5%) of YOM sharks in the 2005 catch to a low proportion (9.1%) in 2010, and although it is not possible to be certain of the reason(s) for this observation it would be consistent with a decrease in the number of mature females returning to the nursery area to pup in 2010 compared to in 2005.

The lack of large-bodied *I. oxyrinchus* in the catch might be explained by different habitat use of mature sharks. In the current study the shortfin mako catch is dominated by relatively small individuals (< 160 cm L_T), which may be explained by an ontogenetic and seasonal spatial segregation in the study area. Spatial segregation between sexes and among ontogenetic stages has been reported for many shark species (Springer, 1967, Klimley, 1987, Cailliet et al., 2005, Dulvy et al., 2008, Bansemer and Bennett, 2009,

Mucientes et al., 2009, Abascal et al., 2011); and for example, large adult female sharks are rarely observed in the same, generally inshore locations as conspecific juvenile and immature sharks (Grubbs, 2010). Gilmore (1990) and Compagno (2001) report that *I. oxyrinchus* occupies a depth range from the surface to at least 500 m, and prefers water temperatures around 18°C; while juveniles may spend 90% of their time in the upper mixed layer of the water column without diel activity patterns in horizontal or vertical movements (Holts and Bedford, 1993, Sepulveda et al., 2004, Abascal et al., 2011). Given the preference of juvenile *I. oxyrinchus* for the upper mixed layer (80% of their time was spent in the upper 12 m, based on animals tracked in California (Sepulveda et al., 2004) and taking into account that larger *I. oxyrinchus* dive deeper (Gilmore, 1990; Compagno, 2001), juvenile shark are likely to be a common component of the catch in a fishery based on surface/shallow set longlines, as in the current study.

Our observations are consistent with those made on eastern North Atlantic (Maia et al., 2007) and eastern North Pacific (Sepulveda et al., 2004) populations, where immature shortfin mako sharks tended to occupy the upper 20 m of the water column, with larger individuals occurring with increasing depth. The upper 30 m of the epipelagic zone in the north of Chile is rich in small scombrid and carangid fishes (Alegría, 1995, Zuleta, 2005), that are a major component of the diets of smaller-sized *I. oxyrinchus* (López et al., 2009) and *P. glauca* (López et al., 2010). Sharks over 180 cm L_T prefer deeper habitat in the mixed layer, located at 30 to 150 m depth (Abascal et al., 2011), and spend most of their time at environmental temperatures of between 17°C and 24°C. This zone is inhabited and preferred by tunas and related fishes (Block et al., 1997), and thus provides a relative abundance of larger prey for larger sharks (Brill et al., 1999). Cerna and Licandeo (2009) report a large population *I. oxyrinchus* close to our study area in the bycatch of *Xiphias gladius* longline fishery at 40–60 m depth, with mature specimens up to 330 cm L_T. Similar observations have been made in oceanic fisheries bycatch targeting tunas and swordfishes (Gilman et al., 2007).

The GAM output of the environmental factors may not explain the CPUE trend in our results, mainly due to the high heterogeneity of the epipelagic water mass. Depth and wind speed have a significance correlation ($P > 0.05$) in CPUE and this might explain habitat preferences of the smaller size-class in *I. oxyrinchus* although the results are inconclusive for *P. glauca*.

The key factor for habitat selection of juvenile *I. oxyrinchus* appears to be related to a warm SST (Maia et al., 2007). Waters off Caldera had a mean SST of 15.7°C over the last ten years (SHOA, 2012), with the lowest mean monthly SST of about 14°C in July and the highest SST of about 18°C in January. During our study, SST varied from 17.7°C to 21.9°C following similar conditions described by Maia et al. (2007) and despite the lack of significant correlation between SST and CPUE in our study, our interpretation of habitat preferences takes the short, seasonal nature of the fishery into consideration. During the Austral summer, movement of warm water masses due to the position of South Pacific gyre (Ahumada et al., 2000), are coupled with primary production and a small pelagic faunal bloom off north-central Chile (off Caldera) as a consequence of post-upwelling phases during late winter and spring (Vásquez et al., 1998; Camus and Andrade, 1999).

This type of ecosystem association has been reported for *I. oxyrinchus* nursery areas in the southern California Bight (Holts and Bedford, 1993, Sepulveda et al., 2004) and Baja California (Conde-Moreno and Galván-Magaña, 2006, Vélez–Marín and Márquez-Farías, 2009).

Habitat occupancy by *I. oxyrinchus* is likely to be a result of broad-scale ecosystemic factors that were outside the scope of the present study that lead to a combination of suitable prey and prey abundance, water temperatures within a preferred range and regions of high primary production as these factors benefit the development and growth of juvenile sharks and their prey (Sepulveda et al., 2004, Heupel et al., 2007, Maia et al., 2007, Abascal et al., 2011). It may be, however, that other factors are also important, as Murcientes et al. (2009), suggest that habitat selection for pelagic sharks "does not appear to closely reflect prey, SST or primary productivity" at least over the time scale of their study.

The historic landing records for *I. oxyrinchus* and *P. glauca* show evidence of cycles of increased exploitation followed by collapse, as has occurred in many other fishing areas around the world; *e.g.* Japan (Nakano, 1999), Portugal (Maia et al., 2007), Brazil (Costa et al., 2002), New Zealand (Duffy et al., 2003, Bishop et al., 2006), Mediterranean Sea (Boero and Carli, 1979), northeast Pacific (Pawson and Vince, 1999), northwest Atlantic coast of USA (Baum et al. 2003) and Canada (Campana et al., 2005). A major difference between our study area and these other regions is in the measures taken to regulate the catch and landing of sharks. While strong measures have been adopted in many regions of the world, there are no fishing quotas for any shark species in Chilean waters, although annual landings tend to auto-regulate due to the strong seasonal nature of the artisanal fishery.

In Chile, of the few fisheries that record *I. oxyrinchus* and *P. glauca* in their landings, the artisanal longline fishery and industrial longline fishery directed to catch swordfish are the largest; and both share a common fishing area in the Chilean EEZ (Lamilla et al., 2010). The blue shark, caught as bycatch in both fisheries, is the most frequent species (59% of total catch) in the swordfish fishery (Acuña et al., 2001), while it comprises 45−55% of the catch in the artisanal fishery. However, the proportion of blue sharks landed in comparison to shortfin mako sharks has increased markedly in the period spanning 1997–2003, and 1998–2001 in the artisanal and industrial fisheries respectively. The reason for this shift towards landing blue sharks is unknown as there were no changes in relevant fishery regulations, the national market is very limited and there is no export market for blue shark meat. One possibility is that the increase on *P. glauca* landings is related directly to the dried shark fin market. Blue shark is the main species (83.9%) found in the Chilean shark fin market (Hernández et al., 2008), and there has been an upward trend in price and therefore availability of this relatively high revenue commodity in recent years.

As gear selectivity, encounterability of the gear, given the species' vertical catch distributions, and species' catchability appear similar, our results suggest that *I. oxyrinchus* and *P. glauca* have similar susceptibilities within the artisanal fishery. Considering the official landings records however, the temporal trend of the *P. glauca: I. oxyrinchus* catch

ratio suggests that the target species (*I. oxyrinchus*) may have declined in importance relative to the increasing bycatch of *P. glauca*; which is the opposite of our observations. The reported dry fin export (Fig. 6b) indicates that a decline started in about 2003, which may relate to the reported decline in the reported landings in industrial vessels (Fig 6a), for which reporting is mandatory. The continued and increasing trend to land blue sharks in both artisanal and industrial fisheries (Fig. 6c) may indicate a change of intentionality of the fisheries and a decline in the availability of shortfin mako shark.

As industrial vessels fish over a broad latitudinal range and across seasons, in contrast to the artisanal fishery for which we present detailed data, it is likely that the annual recruitment of *I. oxyrinchus* may be confronting a significant and ongoing threat. The current absence of management measures in Chile, may be a reflection of the relative paucity of research on highly migratory species (Barría, 2010), but conservation measures in Chile need to address both the artisanal fishery and the bycatch in industrial fisheries. Fishing practices that include minimum catch-sizes for sharks, conservative fishing quotas and delimitation of fishing areas to prevent the continued removal of immature *I. oxyrinchus* should be considered in order to ensure sustainability.

Acknowledgments

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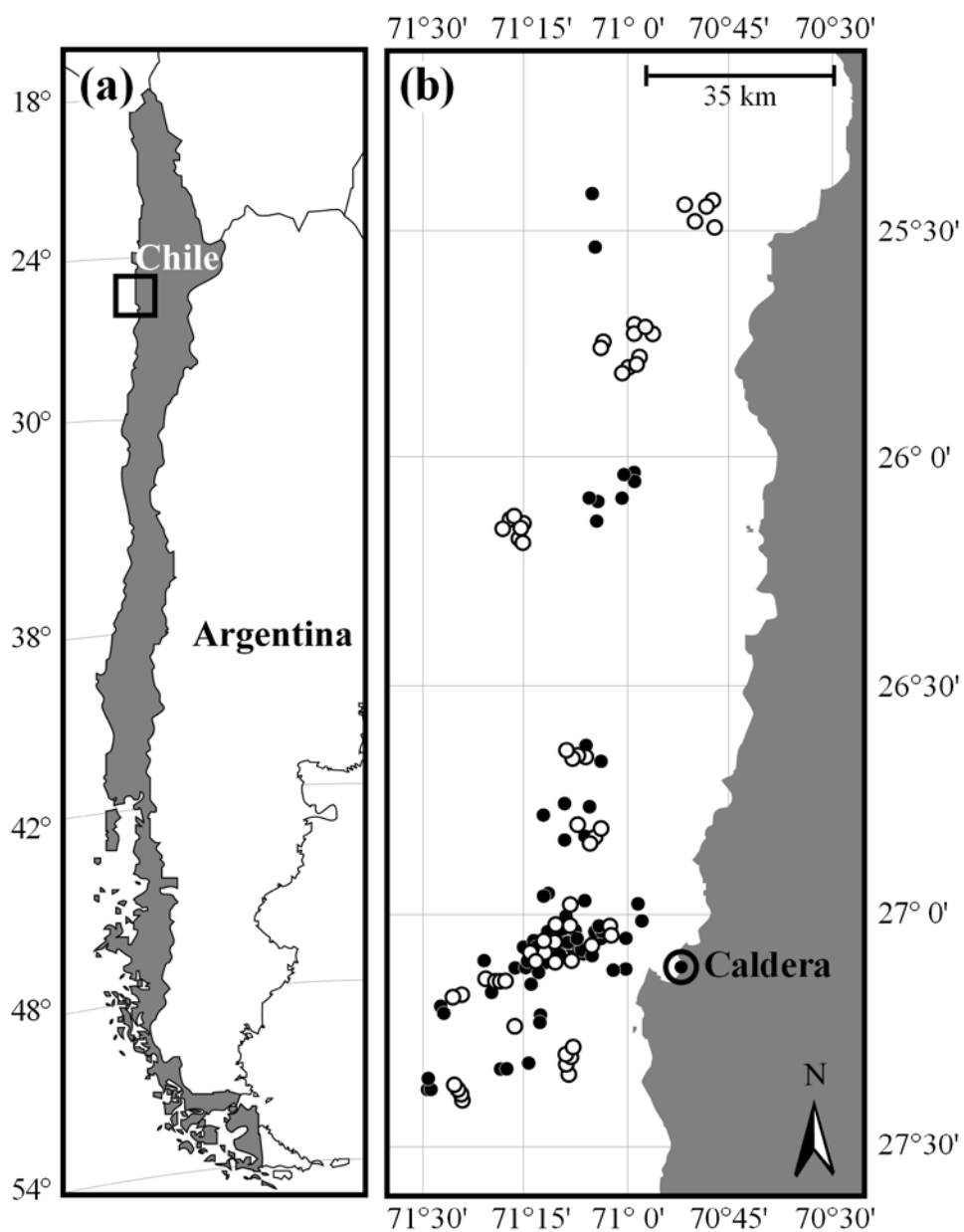
Figure 1 Map of (a) Chile showing location of study area (inset box), and (b) position of longline sets sampled in 2005 (white circles) and 2010 (black circles).
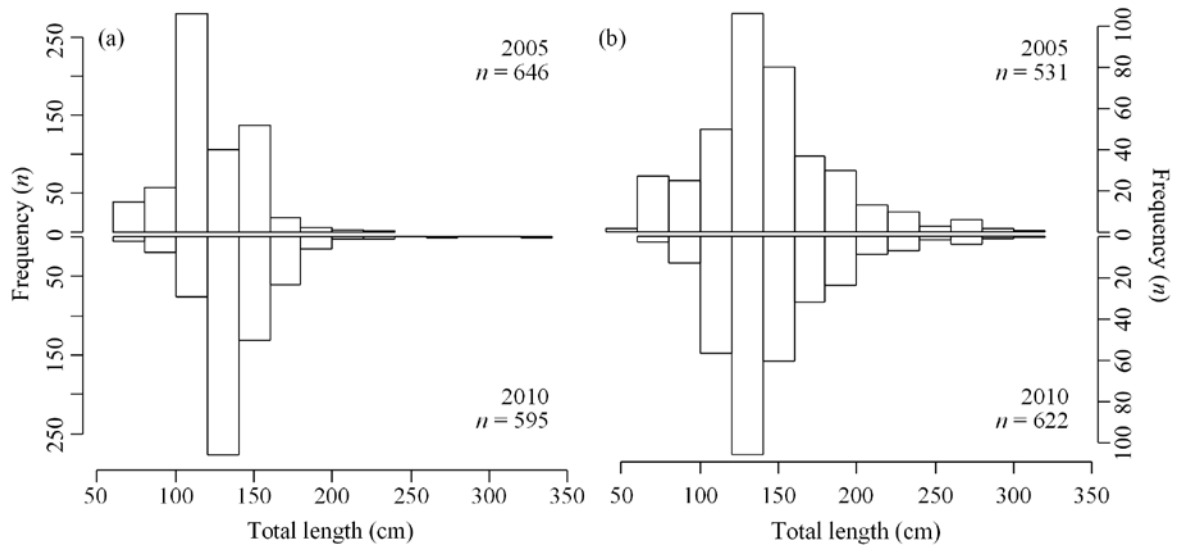
Figure 2 Length frequency distribution of *Isurus oxyrinchus* (a) and *Prionace glauca* (b) in 2005 and in 2010.
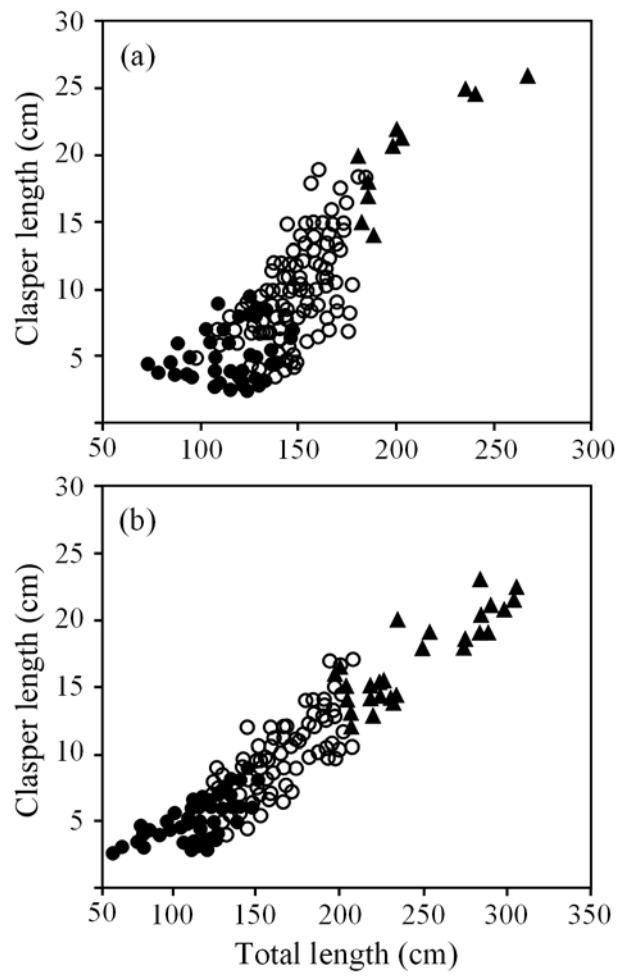
Figure 3 Relationships between inner clasper length and total length based on reproductive classifications of *Isurus oxyrinchus* (a) and *Prionace glauca* (b). Maturity condition is indicated as juveniles (●); adolescents (○) and adults (▲).
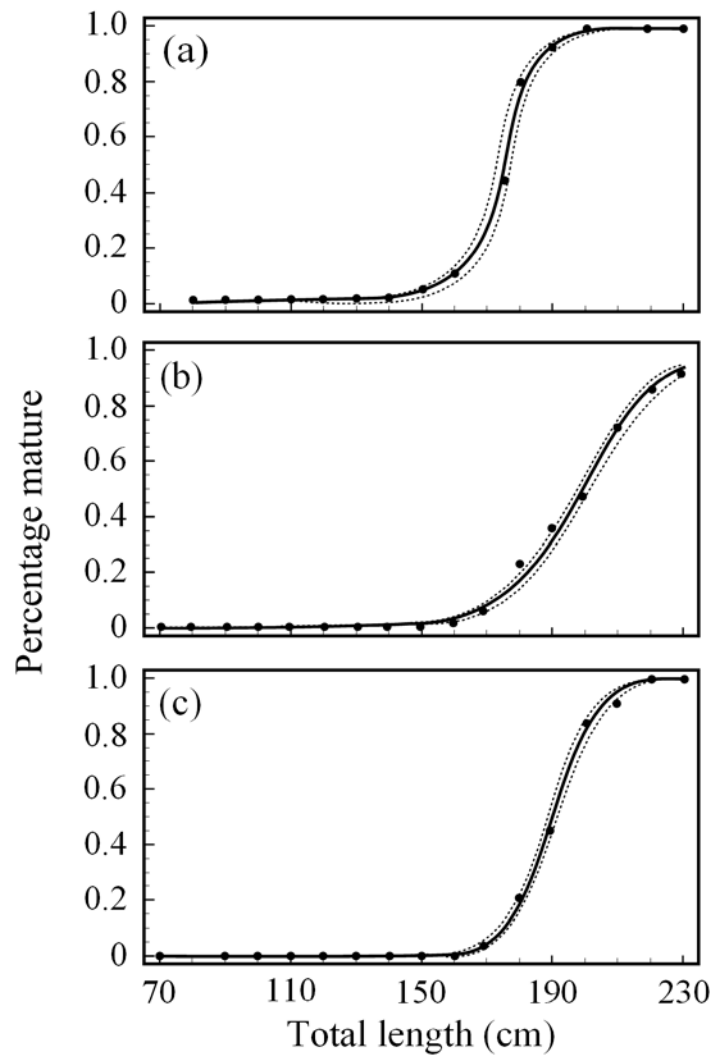
Figure 4 Logistic model (line) fitted for the relationship between total length and percentage of mature *Isurus oxyrinchus* (a) male; and *Prionace glauca* (b) female and (c) male. Circles indicate the observed percentage of mature individual in each size interval. Dashed line indicated 95% confidence interval for the logistic model.
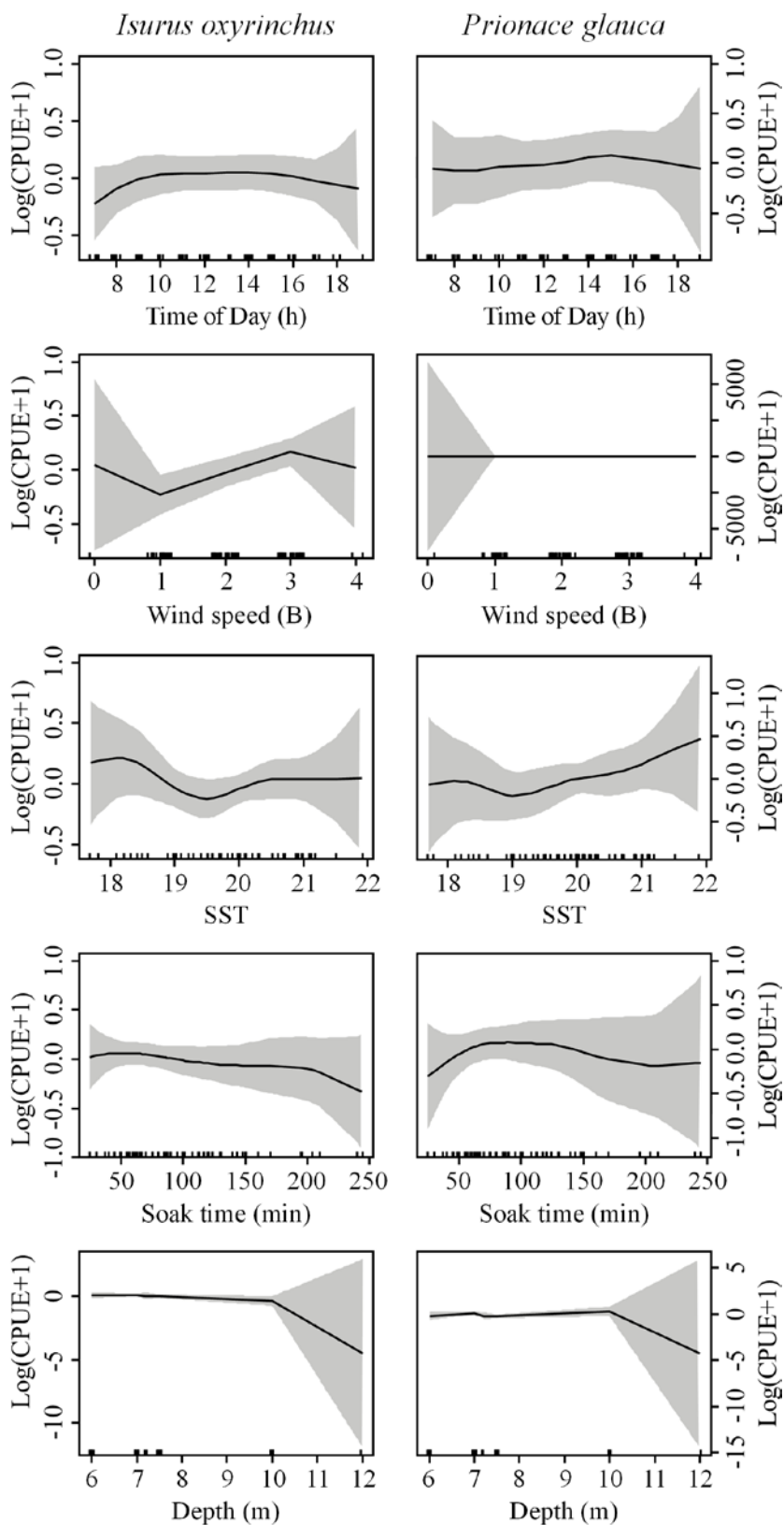
Figure 5 Generalised Additive Model (GAM) output for *Isurus oxyrinchus* and *Prionace glauca*; and the influence of the each environmental variable on the CPUE. Grey areas represent 95% confidence intervals.
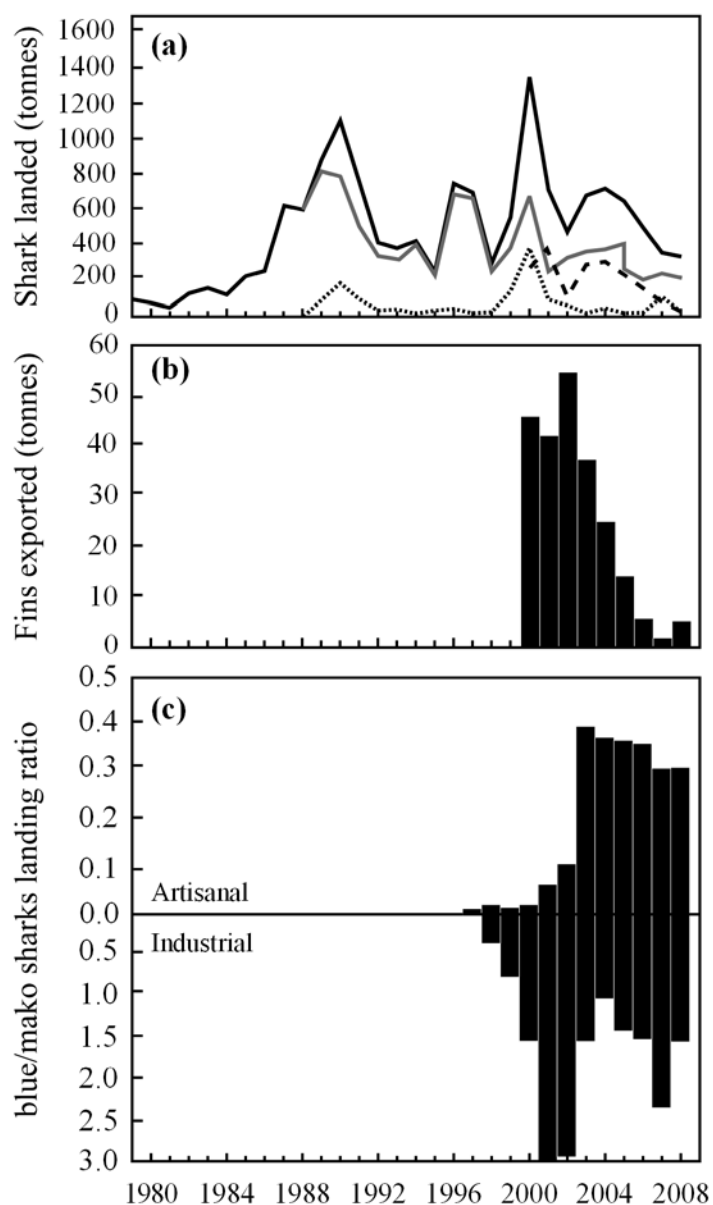
Figure 6 Landings of *Isurus oxyrinchus* and *Prionace glauca* in Chile (a) by fishery type, (b) export of dried shark fins and (c) fishery landing proportion from Chile between 1979 and 2009. Lines in (a) indicates tonnes of sharks landed at overall national (black line), artisanal (grey line), economic exclusive zone industrial (dashed line) and international waters (IW) industrial (dotted line) fisheries.