

Distribution and trend in abundance of the porbeagle (*Lamna nasus*) in the southern hemisphere

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Abstract. Knowledge of a species' distribution is an important element in its effective management and conservation. The porbeagle (*Lamna nasus*) is a common by-catch shark in the tuna longline fishery in the southern hemisphere, but its distribution and abundance are largely unknown. The investigation of observer data from the tuna longline fishery and other fishery survey data has revealed that (1) porbeagles are distributed in the pelagic waters across the oceans of the southern hemisphere, (2) juveniles and adults are distributed in cooler environments than are neonates, (3) pregnant females occur in the pelagic waters of the Indian Ocean and the Tasman Sea, most being frequently recorded around the Cape of Good Hope between June and July and (4) the standardised catch per unit effort (CPUE) based on tuna longline fishery (1994–2011) and driftnet survey (1982–1990) data indicate no continuous decreasing trend in the abundance of the southern porbeagle, contrary to the declining trend reported in a limited region in the South Atlantic. Considering its circumglobal distribution, stock status of this population should be assessed using information from the areas of its major distribution, including pelagic waters, and international coordination across oceans is necessary for the effective management of this population.

Additional keywords: distribution pattern, pelagic ocean, relative abundance, segregation.

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Introduction

Knowledge of the geographic range and core habitat area of a certain species is essential for the evaluation of the impact of exploitation on a population. In the case of fisheries, the available information on the distribution of by-catch species is limited by the spatiotemporal distribution of the fishing effort, which follows the distribution of the target species, so this information does not always pertain to the core habitat area of the by-catch species. Therefore, the integration of information from various sources is necessary to determine these distribution patterns comprehensively, especially for by-catch species with wide geographic ranges.

The porbeagle (*Lamna nasus*) is a lamnid shark that inhabits temperate, subarctic and subantarctic waters. This species is distributed in the North Atlantic Ocean and is thought to occur in a circumglobal band in the southern Pacific, Atlantic and Indian Oceans (Yatsu 1995; Compagno 2001; Last and Stevens 2009). Among the Lamnidae, porbeagles prefer cooler temperatures than do the species of *Isurus* and *Carcharodon*, and are frequently caught at temperatures of 5–10°C (Campana and Joyce 2004). They are a common littoral and epipelagic shark, most abundant on continental offshore fishing banks, but also found far from land (Compagno 2001). Although recent satellite tagging research has revealed that they undertake large-scale migrations

to off-shelf or oceanic regions in the North Atlantic (Pade *et al.* 2009; Saunders *et al.* 2011), their detailed distribution pattern in the pelagic ocean is largely unknown in both hemispheres.

In common with other Lamnidae species, the reproductive system of this species is aplacental viviparity with oophagy. The litter size is reported to be four or fewer and the gestation period is estimated to be 8–9 months in both the North Atlantic and the south-west Pacific (Francis and Stevens 2000; Jensen *et al.* 2002), with a 1-year reproductive cycle reported for the northern population. With their late maturity (age at 50% maturity is 8–11 years for males and 13–18 years for females; Jensen *et al.* 2002; Francis *et al.* 2007) and slow growth rate (Natanson *et al.* 2002; Francis *et al.* 2007), the productivity of this species is estimated to be low (Dulvy *et al.* 2008; Cortés *et al.* 2010). In their interactions with humans, porbeagles in the North Atlantic have a history of being intensely exploited and have suffered population collapse. The target fishery for the porbeagle first began in the north-eastern Atlantic as early as the 1920s (Gauld 1989; Francis *et al.* 2008), but collapsed in the 1960s after intense and unregulated fishing. Much of the effort in the east shifted to the western area in 1961, followed by the collapse of the population there in the 1960s and again in the 1990s (Camhi 2008; Campana *et al.* 2008). Consequently, strict management restrictions on the catch of porbeagles have been introduced by relevant fishing

countries on both sides of the North Atlantic. As a result of the implementation of catch limits and the conservation of mating grounds, signs of recovery have been reported for the north-western population, despite the low stock status (ICCAT 2009).

Concerns about the deterioration of the porbeagle stock status have also arisen for the southern population, on the basis of its similar life-history traits (Francis and Stevens 2000; Francis *et al.* 2007), and the decline in the population that has been suggested in a limited area (south-western Atlantic; Pons and Domingo 2009). However, there are significant differences between the situations of the populations in the North Atlantic and the southern hemisphere. First, the range of the southern population is thought to be wider than that of the northern population, judging from the fragmental record, although the distribution pattern in the pelagic area has not been fully investigated across the oceans. Second, the porbeagles in the southern hemisphere have not been targeted but are caught mainly as a by-catch of the longline fisheries that target southern bluefin tuna (*Thunnus maccoyii*), as well as of various fisheries targeting different species in temperate waters (Francis *et al.* 2008; Pons and Domingo 2009). Therefore, the impact of fisheries on this stock could differ from that on the northern population. Our knowledge of the biology of this species in the southern hemisphere and any quantitative evaluation of the impact of fisheries on the stock are limited compared with those for the northern population. Although some local studies have been performed in the south-western Pacific (Francis and Stevens 2000; Francis *et al.* 2001; Francis and Duffy 2005), the research throughout its range is insufficiently comprehensive.

The longline fishery for southern bluefin tuna ('SBT') has developed extensively in the temperate areas of the southern hemisphere, except areas of west longitude in the South Pacific (Shingu 1978; CCSBT 2012). Considering the interaction between the porbeagle and different fisheries, information from the SBT fishery and various fishery surveys conducted in the South Pacific should be a useful source of data on the distribution and abundance of the southern porbeagle.

The aims of the present study were (1) to describe the geographic range and distribution pattern of the porbeagle in the southern hemisphere and (2) to estimate the trend in its abundance on the basis of the Japanese pelagic longline fishery data for SBT and fishery survey data for other pelagic species.

Materials and methods

Data

In the present study, both commercial fishery data and survey data were used. The fishery data consist of on-board observer data for the SBT longline fishery (hereafter, the 'SBT observer data') and logbook data from the Japanese tuna longline fishery (referred to hereafter as the 'logbook data'). The survey data derive from longline research and driftnet research conducted by the Japan Marine Fisheries Resources Research Center (JAMARC; presently the Marine Fisheries Research and Development Center, Fisheries Research Agency). A brief summary of each data source is given in Table 1.

SBT observer data

The SBT observer data were obtained from the scientific observer program of the Commission for the Conservation of

Table 1. Summary of the data used in the present study
JAMARC DN, Japan Marine Fisheries Resources Research Center longline survey; PCL, precaudal length; SBT, southern bluefin tuna; SST, sea-surface temperature; -, not available

Type	Source	Fishery	Target	Period	Month	Research area	Effort (no. of hooks or length (km) of driftnet)	No. of porbeagles	Observed size range	General distribution	Ontogenetic distribution	Sex ratio	Relationship between SST at capture and ontogenetic stage	Abundance
Commercial Survey	SBT observer	Longline	<i>Thunnus maccoyii</i>	1992–2010	Year round	Southern hemisphere	34 779 825	12 084	48–226 cm PCL	+	+	+	+	–
Commercial Survey	JAMARC LL	Longline	<i>Gasterochisma melampus</i>	1987–1994	Year round	South Pacific	1 949 554	494	8–149 kg	+	–	–	–	–
Commercial Survey	JAMARC DN	Driftnet	<i>Allothunnus fallai</i>	1982–1990	September–March	South Pacific	15 680 338	3 645	5–125 kg	+	–	–	–	+
Commercial	Logbook data	Driftnet	Braminae spp.	1984–1986	July–April	South Pacific	7 770 043	3 345	3–112 kg	–	–	–	–	+
Commercial	Logbook data	Longline	<i>Thunnus</i> spp.	1994–2011	Year round	Southern hemisphere	177 842 293 [^]	24 163 [^]	–	–	–	–	–	+

[^]Amount after filtering.

Southern Bluefin Tuna (CCSBT) for the Japanese pelagic longline fishery. The data for 1992–2010 were available for the present study. The main fishing ground observed included temperate areas in waters off the Cape of Good Hope (hereafter, referred to as ‘off the Cape’), the south-eastern Indian Ocean and the Tasman Sea (Fig. 1a). The gear configurations of the longline fishery observed were as follows: the number of branch lines between floats was 6–11; the mean number of hooks per set was ~3100; and the shallowest and deepest depths of the gear were ~50–100 m and 120–180 m, respectively. Gear setting was estimated to commence at 0640 hours and gear retrieval was estimated to commence at 1600 hours. The sea surface temperature (‘SST’) ranged from 6.2°C to 30.0°C (mean \pm s.d. $14.0 \pm 4.3^\circ\text{C}$).

The observers collected the following information on the longline operation: date, location, and time of gear setting and retrieval, number of branch lines between floats, total hook number, SST (at noon) and biological data (body length, weight, sex, maturity status and the number of embryos for pregnant females). In the present program, precaudal length (PCL, cm) was used as the standard body length for the porbeagle. Body length was measured to the nearest centimetre.

Logbook data

The catch number of porbeagles and the operational data (date, location, number of branch lines between floats, total hook number) per set were available from the logbook data of the Japanese tuna longline fishery in the southern hemisphere for the period between 1994 and 2011. Although logbook data

are available for before 1994, the reporting of species-specific catches commenced in 1994. To estimate the porbeagle population abundance, the logbook data were filtered to obtain the data to be used in the CPUE analysis by extracting the cruise data for which the reporting rate (number of sets with any shark catch/total number of sets in each cruise) was $\geq 80\%$ (Matsunaga 2009).

JAMARC longline survey data (referred to as ‘JAMARC LL data’)

JAMARC conducted longline surveys for the butterfly kingfish (*Gasterochisma melampus*) between 1987 and 1994 (JAMARC 1987–1994). These surveys were conducted exclusively from the subtropical to subantarctic areas in the South Pacific Ocean (Fig. 1a). The gear configuration in the JAMARC LL survey was as follows: number of branch lines between floats was 6–8, except for three surveys in 1994 (11 or 14 lines), 1996 and 1997 (10 lines for both years); the mean number of hooks per set was ~2400; and the shallowest and deepest depths of the gear were 50–120 m and 150–225 m, respectively. Gear setting was estimated to commence at 0300 hours and gear retrieval was estimated to commence at 1230 hours. SST ranged from 3.0°C to 24.0°C (mean \pm s.d., $15.7 \pm 3.5^\circ\text{C}$).

The JAMARC LL data consist of operational data, which are the same as the SBT observer data, and the catches in numbers and weights (whole and processed) of porbeagle per set. However, the data for body length and sex were not included, so these data are not included in the ontogenetic analysis and shown in the corresponding figures.

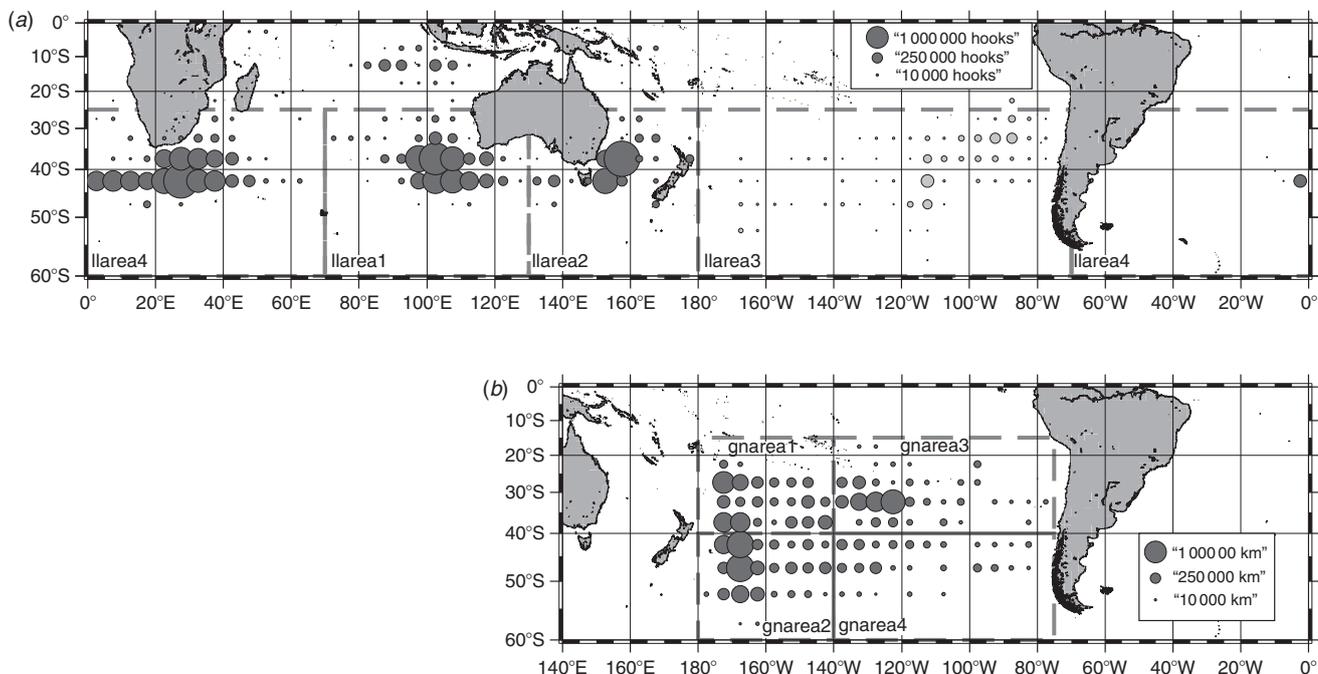


Fig. 1. Distribution of effort in the (a) longline research (southern bluefin tuna (SBT) observer and Japan Marine Fisheries Resources Research Center longline (JAMARC LL) survey data) and (b) driftnet surveys (for *Allothunnus fallai* and *Braminae* spp.). The subareas for catch per unit effort (CPUE) standardisation for the longline data and the driftnet data are shown. Of the longline research, the effort for the JAMARC LL survey is indicated by the sky-blue circles. The effort for two driftnet surveys was combined.

JAMARC driftnet survey data (referred to as 'JAMARC DN data')

JAMARC conducted a large-mesh driftnet surveys targeting *Allothenus fallai* between 1982 and 1990 (JAMARC 1982~1989) and targeting pomfret (Braminae spp.) between 1984 and 1986 (JAMARC 1984~1987). Both surveys were combined for our analysis because the gear configurations were almost the same. A series of surveys was conducted exclusively in the South Pacific Ocean (Fig. 1b), mainly between July and April. The nets were set before sunset and retrieved 4–8 h after setting. Mesh sizes of 150 mm, 160 mm and 180 mm were used most frequently and the net depth was ~10 m from the sea surface. The mean number of nets per set was 690 and the mean length of the nets was 33.8 m.

The JAMARC DN data consist of the details of the operations (date, location, time of setting and retrieval, number of nets, mesh size, length and depth of the nets, SST at setting) and the catches in numbers and weights (whole and processed weight) of porbeagle. SST ranged from 5°C to 26.6°C (mean \pm s.d., 15.5 \pm 3.9°C).

Analysis of the distribution

For an overview of the spatial distribution of the population, the catch number and effort data (hook number and net length) from the SBT observer program, the JAMARC LL data, and the JAMARC DN data were compiled separately by 5-degree squares and the catch per unit effort (CPUE) was calculated (referred to hereafter as the 'overall CPUE'). In this process, the year and month were combined. The definition of CPUE was the catch in numbers of porbeagle per 1000 hooks for the longline gear and the catch in numbers of porbeagle per 1000 m for the driftnet gear. To establish an overview of the ontogenetic distribution pattern, the size data collected in the SBT observer program were classified into three ontogenetic stages (neonates, juveniles and adults), based on the criteria described below. The definition of 'neonate' included individuals between the birth length and the size at 1-year old, estimated using the growth equations of Morinobu (1996) for porbeagle collected in the SBT fishery ground. The von Bertalanffy growth curves estimated by Morinobu (1996) are intermediate between those in the North Atlantic (Aasen 1963; Natanson *et al.* 2002) and those in the South Pacific (Francis *et al.* 2007), and the estimated asymptotic length (L_{∞}), growth coefficient (K) and theoretical age at zero length (t_0) are as follows: male, $L_{\infty} = 250$, $K = 0.066$, $t_0 = -4.64$; female, $L_{\infty} = 214$, $K = 0.082$, $t_0 = -4.43$. For males, juveniles and adults were separated on the basis of the length at maturity (mid-point of the range) estimated by Francis and Duffy (2005). For females, individuals smaller than the minimum size of the pregnant females observed (153 cm) were treated as juveniles and those larger than 153 cm were treated as adults because the estimated length at maturity (mid-point of the range: 156 cm PCL) reported by Francis and Duffy (2005) was larger than the observed minimum length of the pregnant females. The length at maturity, reported in fork length (FL), was converted to PCL as follows: $PCL = 0.90 \times FL - 1.42$ (Morinobu 1996; $n = 421$, $R^2 = 0.99$). Therefore,

neonate: <78 cm for both sexes;

juvenile: 78 cm \leq PCL <129 cm for males, 78 cm \leq PCL <153 cm for females; and

adult: \geq 129 cm for males, \geq 153 cm for females.

For individuals lacking information on their sex, individuals smaller than 78 cm were treated as neonates. Individuals smaller than 129 cm and larger than 153 cm were treated as juveniles and adults, respectively. Individuals between 129 cm and 153 cm (12.4% of data used) were removed from the ontogenetic analysis.

After the assignment of categories for each individual, the catch in numbers by category was calculated per set. Thus, the catch (in numbers for each category) and effort data were compiled by 5-degree squares, with year and month aggregated, and the CPUE for each category was calculated.

To evaluate the ontogenetic distribution pattern, focusing on environmental factors, SST at capture was compared among the ontogenetic stages with the Tukey–Kramer test, taking into consideration the unequal sample sizes among stages (Sokal and Rohlf 1995). Individual data with body size, sex and SST at capture taken from the SBT observer data were used for the analysis. Because SST is affected by month, the statistical analysis was conducted by month (between April and December) for months with a positive number of observations for each stage. The year and area (indicated in Fig. 1a) were combined because there were frequently missing observations, depending on the year and area.

For the analysis of the sex ratios, individual data with body size, sex, date and location at capture taken from the SBT observer data were divided into strata, consisting of ontogenetic stage, month and area (indicated in Fig. 1a). Because the amount of data for the central and eastern South Pacific (Iarea3) was small and the data were collected exclusively in the western South Pacific (Iarea2), only the sex ratio in Iarea2 was analysed in the South Pacific. Because the amount of unsexed data within this area was large, the data for Iarea2 were divided into western (hereafter referred to as 'Tasman Sea') and eastern subareas (hereafter referred to as 'NZ'), with the border at 160°E. Before the analysis, the strata containing unsexed individuals were removed, to obviate their effect on the results of the statistical analysis. The sex ratios were tested for the strata with positive observations for both sexes, using a binomial test. The occurrence of single sex was described for the strata with more than two individuals.

Differences were considered statistically significant at $P = 0.05$.

Relative abundance

The standardised CPUE for the porbeagle was estimated using a generalised linear model (GLM) approach with the GENMOD procedure of SAS (version 9.2). The numbers of observations used for the analysis are available in Table S1, available as Accessory Material to this paper.

In the GLM analysis of the tuna longline logbook data, a delta-lognormal model (Lo *et al.* 1992) was applied because the proportion of sets with a zero catch of porbeagles was high (~90%). This model consists of the following two separate steps: the ratio of the zero catch is estimated using logistic regression (binomial distribution) in the first step and the CPUE in the positive sets is estimated using a lognormal distribution in

the second step. The following form was assumed for the full model in each step:

(1st step)

$$\log \frac{p}{1-p} = \text{intercept} + \text{year} + \text{area} + \text{quarter} + \text{gear} \\ + \text{interactions},$$

$$E[X] = p, X \sim \text{Bin}(\theta), X = 1 \text{ (if catch number} > 0), \\ 0 \text{ (otherwise), and}$$

(2nd step)

$$\log(\text{CPUE}) = \text{intercept} + \text{year} + \text{area} + \text{quarter} + \text{gear} \\ + \text{interactions} + \text{error} \\ \text{error} \sim N(\mu, \sigma^2),$$

where \log is the natural logarithm, $\log(p/(1-p))$ is the logit link function, p is the ratio of sets with zero catch, year is the effect of the year (1994–2011), quarter is the effect of the season (1–4), area is the effect of the area (1–4), gear is the effect of the gear depth (1–2), and ‘*interactions*’ refer to the two-way interactions of all explanatory variables. All explanatory variables were treated as categorical. For the quarter effect, the year was divided into four equal seasons, including spring (October–December), summer (January–March), fall (April–June) and winter (July–September). For the area effect, the southern hemisphere was divided into four subareas on the basis of the distribution of the fishery data (Fig. 1a). For the gear effect, the depth of the gear was classified by the number of branch lines between the floats (numbers in parentheses), as Gear 1 (6–10) and Gear 2 (11–15). The standardised CPUE is calculated as the product of the estimated values for the least-squares mean derived from the two models: non-zero catch ratio \times CPUE for positive catches.

In the GLM analysis of the driftnet survey data, a log-normal error distribution was assumed because of the relatively small number of zero catches and the much smaller Akaike’s information criterion (AIC) than that in the model that assumed a negative binomial error distribution. The following model was assumed for the standardisation:

$$\log(\text{CPUE} + \text{constant}) = \text{intercept} + \text{year} + \text{area} + \text{SST} \\ + \text{error} \\ \text{error} \sim N(\mu, \sigma^2),$$

where year is the effect of the year (1982–1990), area is the effect of the area, and SST is the effect of SST, consisting of nine categories (5–7.9°C, 8–9.9°C, 10–11.9°C, 12–13.9°C, 14–15.9°C, 16–17.9°C, 18–19.9°C, 20–21.9°C and 22–23.9°C). SST was included instead of quarter because the effect of SST is suggested to be large on driftnet gear (Yatsu 1995) and the much smaller AIC was observed than in the model with quarter. The survey ground was divided into four subareas (Fig. 1b), on the basis of the oceanographic characteristics described by Yatsu (1995). The mesh size was not included in the main effects because the mesh size was almost constant among the surveys. To overcome the problem of zero catch, one-tenth of the mean CPUE was uniformly added to each value of the nominal CPUE as a constant

term (ICCAT 1997). Two-way interactions were not included in the model because of the missing data for each interaction.

With these standardisation methods, model selection was conducted using a stepwise χ^2 test for the delta-lognormal model and an F -test for the lognormal model, and the variables with statistical significance at 0.05 were included in the final model. The least-squares mean were calculated on the basis of the final model, and the yearly trend in the standardised CPUE was computed. The confidence interval for the delta-lognormal model was estimated according to Shono (2008). The diagnostic plots are presented separately for the 2nd step of the delta-lognormal model (longline data analysis) and the lognormal model (driftnet data analysis).

Results

General distribution

The overall CPUE calculated from the SBT observer data and JAMARC LL survey data indicates that porbeagles are widely distributed longitudinally in the pelagic waters of the southern hemisphere (Fig. 2a). The northern and southern limits of occurrence were recorded at 28°30’S and 53°39’S, respectively, in the SBT observer data and at 22°18’S and 60°00’S, respectively, in the JAMARC LL data. A continuous distribution was indicated, at least between the South Pacific and the south-eastern Indian Oceans and between the south-western Indian Ocean and the south-eastern Atlantic Ocean. The gap between the south-eastern and south-western Indian Ocean reflects the fact that there was no effort in the corresponding area. The CPUE in the area south of 40°S was larger than that north of 40°S, except in the south-eastern Indian Ocean. The CPUE south of 50°S was markedly larger than that in the northern area of the South Pacific. In relation to SST, porbeagles were caught at temperatures of 6.5–20.9°C according to the SBT observer data and at 3.0–24.0°C according to the JAMARC LL survey data. The highest CPUE (in parentheses) was recorded at 9.3°C (11.9) in the former and at 10.5°C (21.9) in the latter (see Fig. S1, available as Accessory Material for this paper).

The CPUE in the JAMARC DN survey indicated that porbeagles are widely distributed in the pelagic waters across the South Pacific and that their occurrence pattern clearly differs latitudinally at 35°S (Fig. 2b). The northern and southern limits of occurrence were 28°16’S and 56°44.3’S, respectively. Between 25°S and 35°S, the CPUE was very small compared with that south of 35°S. In the area south of 35°S, porbeagles were constantly recorded across the South Pacific, whereas the CPUE between the dateline and 140°W was higher than that in the more eastern area. The continuous CPUE within the South Pacific supports the results of the JAMARC LL survey. In relation to SST, porbeagles were caught at temperatures of 5.0–19.6°C and the highest CPUE (in parentheses) was recorded at 13.3°C (7.1) (see Fig. S1).

Ontogenetic distribution pattern

The CPUE by ontogenetic stage is shown in Fig. 3. Generally, the CPUE of neonates was high in the area north of 40°S, except off the Cape. In contrast, juveniles occurred in the southern area at higher densities than did the neonates. In the area south of 45°S off the Cape, the CPUE for juveniles was much higher than

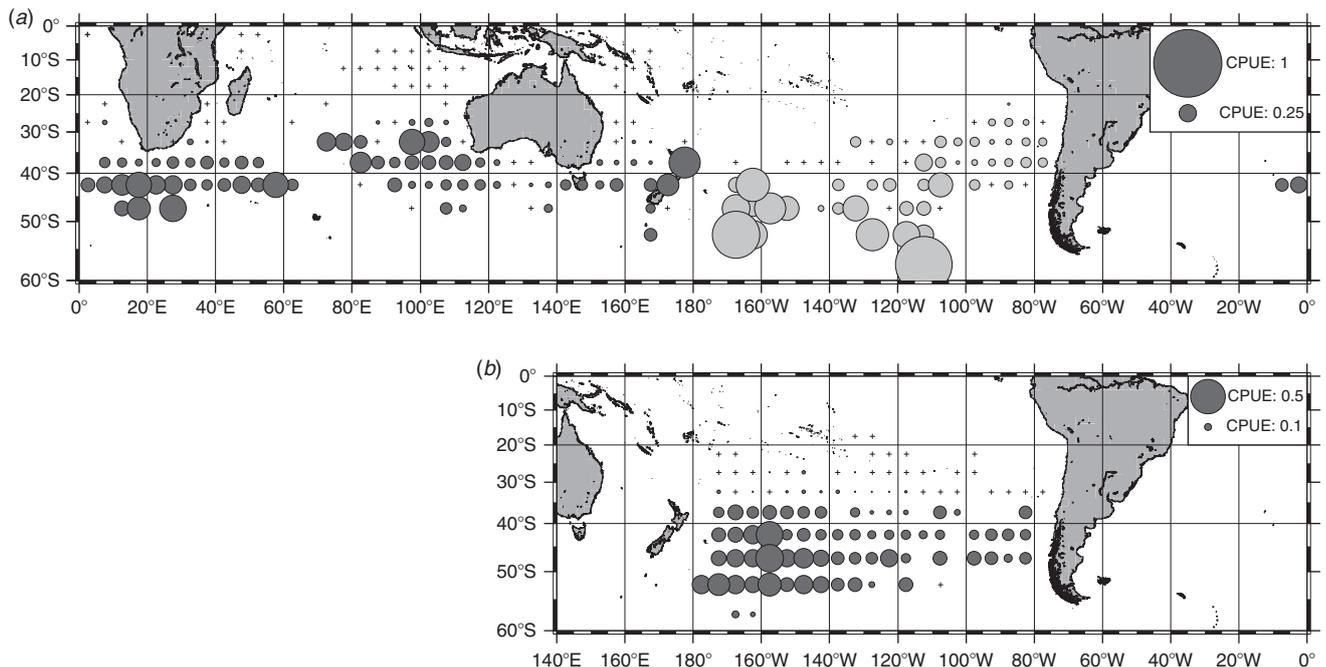


Fig. 2. Overall catch per unit effort (CPUE) by 5-degree squares for the (a) longline (southern bluefin tuna (SBT) observer and Japan Marine Fisheries Resources Research Center longline (JAMARC LL) survey data) and (b) driftnet surveys (for *Allothunnus fallai* and *Braminae* spp.). Year and month are combined for both CPUEs. For the longline survey, the CPUE in JAMARC LL survey is indicated in sky-blue. Crosses denote no catch.

that for neonates. For adults, both the amount of data and CPUE were too small to detect clear differences in the distributions of the stages, but little overlap was observed between the distributions of the neonates and the adults.

A multiple-comparison analysis indicated that the SST at capture for the neonates was significantly higher than those for the juveniles and adults in every month analysed ($P < 0.05$), except April, when there was no significant difference between the neonates and the adults. No statistically significant difference was detected in SST at capture for the juveniles and adults in any month analysed, except July and November, whereas SST at capture was significantly ($P < 0.05$) higher for the juveniles than for the adults. The relationship between ontogenetic stage and SST at capture is shown with all the years and months combined (Fig. 4).

The sex ratios for the neonates, juveniles and adults were analysed statistically. As a result of the exclusion of the strata containing unsexed individuals, the data for nine strata of neonates, seven strata of juveniles and nine strata of adults were tested. For the neonates, the sex ratio was equal in five strata (April and November in the waters off the Cape, January and July in the south-eastern Indian Ocean, August in the Tasman Sea), whereas females dominated in four strata (May ($P = 0.015$, $n = 50$) and June ($P < 0.01$, $n = 59$) in the south-eastern Indian Ocean and May ($P < 0.01$, $n = 15$) and July ($P < 0.01$, $n = 20$) in NZ). Only females ($n = 2$) were caught in April in NZ. For the juveniles, the sex ratios in all strata were equal (April and October in the waters off the Cape; June and July in the south-eastern Indian Ocean; and April, May and July in NZ), whereas only females were recorded in August in NZ ($n = 2$) and the Tasman Sea ($n = 2$). However, for the adults, the sex ratios were biased towards the males ($P < 0.05$) in six strata (July in the waters off

the Cape ($n = 51$), August ($n = 15$), September ($n = 53$), October ($n = 28$), and November ($n = 21$) in the south-eastern Indian Ocean, and June in the Tasman Sea ($n = 12$) and were equal in the other three strata (May in the Tasman Sea, July in the south-eastern Indian Ocean and the Tasman Sea). Only males ($n = 4$) were recorded in December in the south-eastern Indian Ocean.

The pregnant females were recorded in the waters off the Cape, the south-eastern Indian Ocean and the Tasman Sea, but were most frequently observed in the waters off the Cape (Fig. 3). In the area off the Cape, 28 pregnant females were recorded from May to September, and predominantly in June and July almost every year. The records for the Indian Ocean and the Tasman Sea were obtained for one individual in August and July, respectively.

Relative abundance

The final GLM adopted for the standardisation of the longline CPUE was:

$$\log \frac{p}{1-p} = \text{intercept} + \text{year} + \text{area} + \text{quarter} \\ + \text{gear} + \text{area} * \text{gear} + \text{quarter} * \text{gear} \quad (1\text{st step})$$

$$E[X] = p, X \sim \text{Bin}(\theta), X = 1 \text{ (if catch number} > 0), \\ 0 \text{ (otherwise), and}$$

$$\log(\text{CPUE}) = \text{intercept} + \text{year} + \text{area} + \text{quarter} \\ + \text{gear} + \text{quarter} * \text{gear} + \text{error} \\ \text{error} \sim N(\mu, \sigma^2). \quad (2\text{nd step})$$

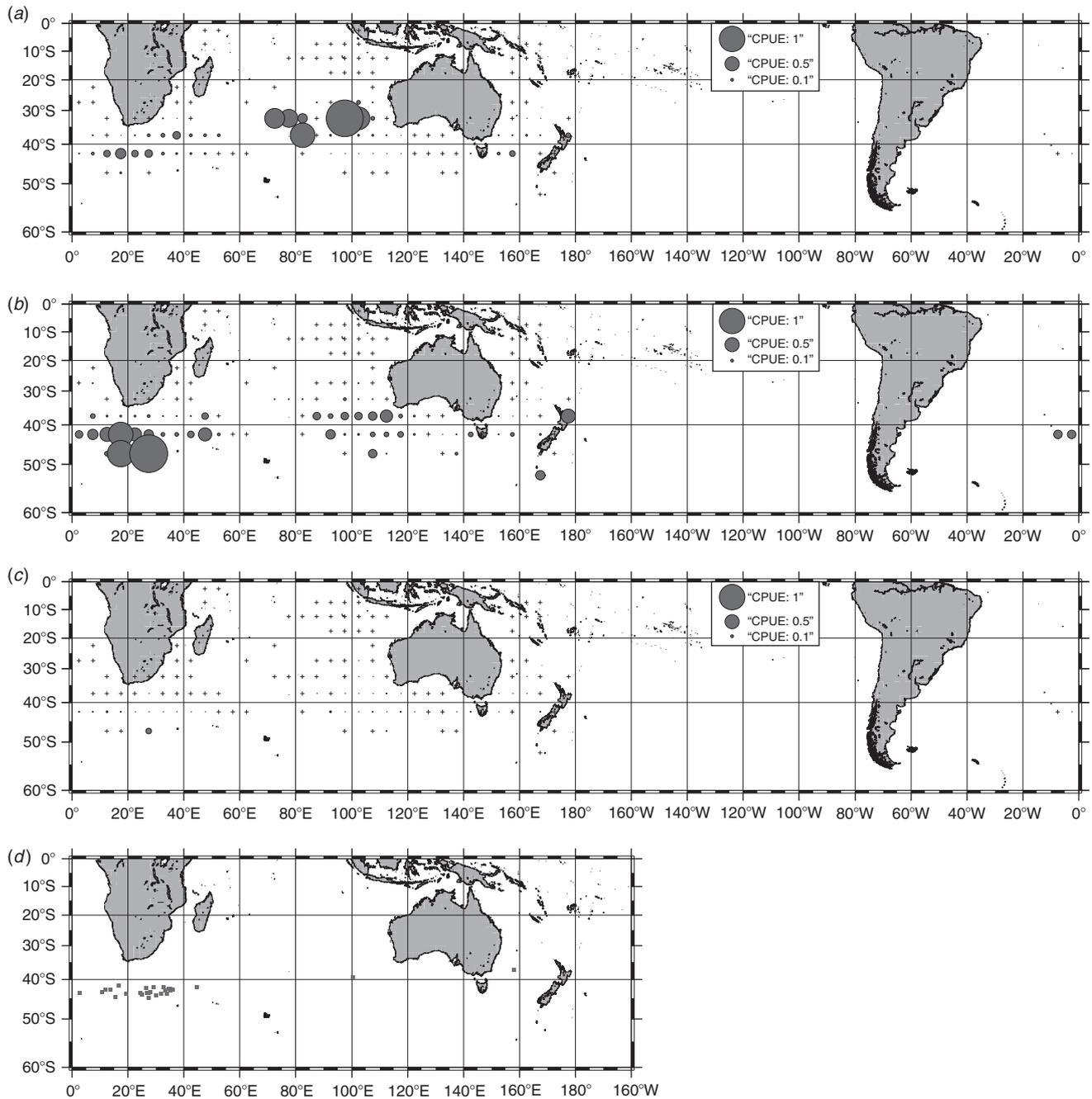


Fig. 3. Overall catch per unit effort (CPUE) for each ontogenetic stage for (a) neonates, (b) juveniles, and (c) adults, and (d) the localities at which pregnant females were recorded. Crosses in (a), (b), and (c) denote no catch.

The standardised residual plot and Q–Q plot for the 2nd step in the final model indicated that the shape of residual plot was close to a normal distribution and the assumed error structures were satisfactory (see Figs S2 and S3, available as Accessory Material for this paper). The selection of variables, on the basis of the aforementioned criteria, allowed the inclusion of the interactions between ‘area and gear’ and ‘quarter and gear’ for the 1st step and between ‘quarter and gear’ for the 2nd step, as indicated (Table 2). The overall trend in the standardised CPUE

for the porbeagles caught by the Japanese tuna longline fishery in the southern hemisphere was relatively stable, with a low estimate in 2004 and a high estimate in 2008. The fluctuation in the standardised CPUE between 2007 and 2009 was larger than that in the preceding years (Fig. 5).

The annual trend in CPUE estimated from the JAMARC DN survey was stable, ranging between ~ 0.08 and 0.12 during the period analysed (Fig. 6). The standardised residual plot and the Q–Q plot for the final model indicated that the shape of the

residual plot was close to a normal distribution and the assumed error structures were satisfactory (see Figs S4 and S5, available as Accessory Material for this paper). The effect of SST was large compared with other effects (Table 2).

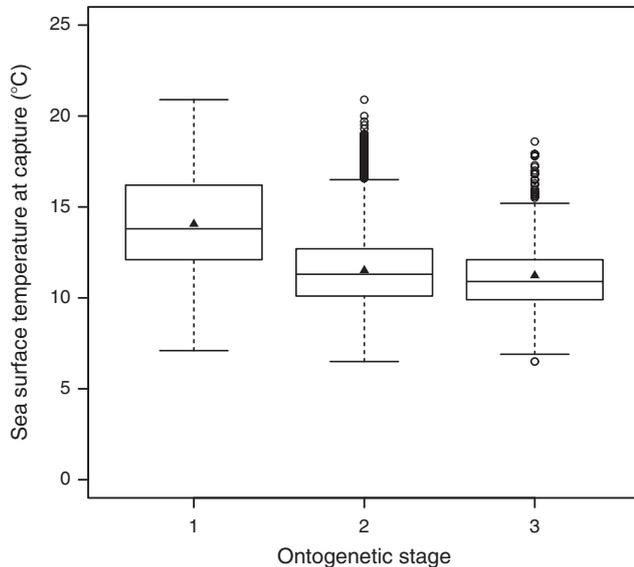


Fig. 4. Relationship between ontogenetic stage and sea-surface temperature at capture (*x*-axis, ontogenetic stage; *y*-axis, temperature at capture: 1, neonate; 2, juvenile; 3, adult). For each stage, the solid horizontal line represents the median, the triangles the mean value, the boxes mark the 25th and 75th percentiles, and the whiskers mark each percentile $\pm 1.5 \times$ inter-quartile range (IQR).

Discussion

Geographic range

The present study has demonstrated the continuous distribution of the porbeagle between the South Pacific and the south-eastern Indian Oceans, and between the south-western Indian Ocean and the south-eastern Atlantic Ocean. Their common occurrence in the pelagic ocean is also indicated in a wide area of the southern hemisphere.

When we combined the existing records on the occurrence of the porbeagle in this area (Compagno 2001), the distribution of the southern population appeared to be continuous, at least between the South Pacific and the south-eastern Atlantic, although the occurrence of the porbeagle in the central South Indian Ocean was not confirmed in the present study because of the lack of fishing effort in this area. A genetic study has suggested that the populations in the South Atlantic and the South Indian Oceans are not genetically separated (Kitamura and Matsunaga 2009). Considering the wide distribution and possible connectivity among the oceans, the geographic range of the southern population is likely to be much wider than that of the northern population. A tendency to exhibit limited movement and a lower abundance in the pelagic ocean, which are indicated in the North Atlantic (Kohler *et al.* 2002; ICCAT 2009; Pade *et al.* 2009), are unlikely in the southern porbeagle.

The present study has provided a new record of the southern limit ($60^{\circ}00'S$) of the porbeagle in the South Pacific (JAMARC LL data). Yatsu (1995) noted that the porbeagle is the third-most dominant species in the subantarctic region of the South Pacific (from $\sim 40^{\circ}S$ to $57^{\circ}S$, with seasonal fluctuations in the northern boundary), at least in the summer and early fall. However, the

Table 2. Results of Type III SS in each generalised linear model for catch per unit effort (CPUE) standardisation of longline data (upper) and driftnet data (lower) SST, sea-surface temperature

Longline data Binomial model (1st step)					
Explanatory variable	d.f.	χ^2	<i>P</i>		
Year	17	721.48	<0.0001		
Area	3	251.43	<0.0001		
Quarter	3	150.52	<0.0001		
Gear	1	332.28	<0.0001		
Area \times Gear	3	180.28	<0.0001		
Quarter \times Gear	3	11.28	0.0103		
Longline data Lognormal model (2nd step)					
Explanatory variable	d.f.	Type III SS	Mean square	<i>F</i>	<i>P</i>
Year	17	204.71	12.04	17.04	<0.0001
Area	3	98.08	32.69	46.26	<0.0001
Quarter	3	53.97	17.99	25.46	<0.0001
Gear	1	5.38	5.38	7.61	0.0058
Quarter \times Gear	3	6.99	2.33	3.29	0.0197
Driftnet data Lognormal model					
Explanatory variable	d.f.	<i>F</i>	<i>P</i>		
Year	8	18.66	0.0168		
Area	3	121.01	<0.0001		
SST	8	399.79	<0.0001		

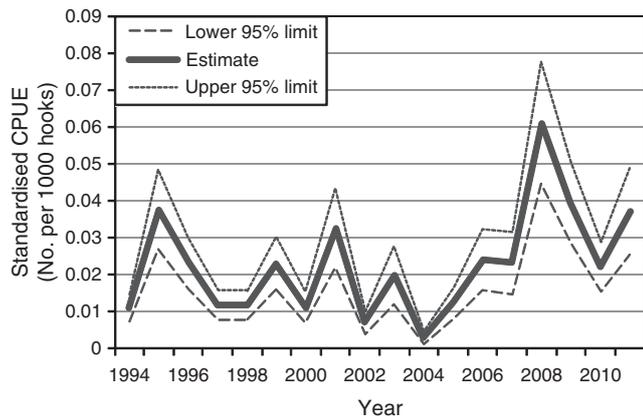


Fig. 5. Standardised catch per unit effort (CPUE) for the porbeagle, on the basis of the logbook data from the Japanese tuna longline fishery from 1994 to 2011.

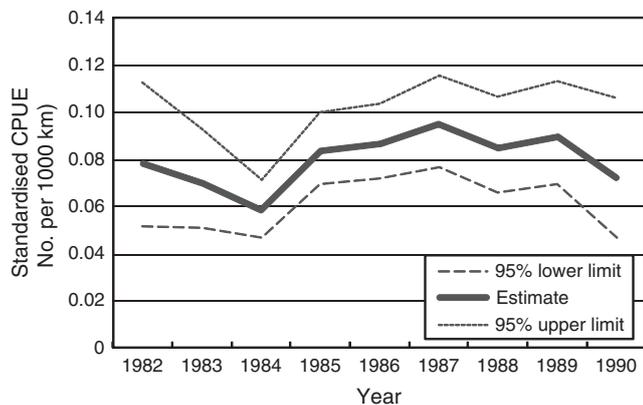


Fig. 6. Standardised catch per unit effort (CPUE) for the porbeagle, on the basis of driftnet survey data from 1982 to 1990.

southern limit recorded in the SBT observer data ($53^{\circ}39'S$) was north of that region in the South Pacific. Does this record reflect the real southern limit of the porbeagle in the SBT fishery ground? According to Campana and Joyce (2004), the SST in the porbeagle fishery ground in the North Atlantic ranges from $7.0^{\circ}C$ to $11.0^{\circ}C$, whereas more than 80% of longline operations in the SBT observer data were conducted in areas with SSTs above $11^{\circ}C$, in accordance with the preferred ambient temperatures of the SBT of over $10^{\circ}C$ (Davis and Stanley 2002; Patterson *et al.* 2008), which is higher than that of the porbeagle (5 – $10^{\circ}C$; Campana and Joyce 2004). Regarding the distribution of the CPUE, the JAMARC LL survey covered a wider area in both the southern direction and the SST range than did the SBT observer data. As a result, a relatively high CPUE was recorded in locations at the latitudes ($53^{\circ}39'$ – $60^{\circ}00'S$) and SSTs (3 – $11^{\circ}C$) that were not fully covered by the SBT observer data. Because the observation in the area south of $50^{\circ}S$ was relatively small, further effort should clarify the distribution pattern in this area. These records suggest that the main area of the SBT fishery grounds is located on the warmer (i.e. northern) edge of the

porbeagle habitat and that the southern porbeagle occurs in more colder (i.e. southern) areas, outside the SBT fishery grounds.

Ontogenetic distribution pattern

As reported for many sharks (Springer 1967), porbeagles display a segregation of habitat by size (Yatsu 1995) and by sex (Aasen 1963; O'Boyle *et al.* 1998). The present study indicated that the distribution of the neonates barely overlaps that of the juveniles and adults and that the juveniles and adults tend to occur in the area south of the neonatal habitat. The latitudinal shift in the distribution of the neonates in the lower latitudes to that of the juveniles and adults in the higher latitudes is also supported by the negative relationship between the ontogenetic stage and SST at capture.

The number of records of adults was small compared with those of the neonates and juveniles in the SBT observer data. The discordance between the gear depth and the vertical habitat of the porbeagle and the differences in gear selectivity (including the preference for the bait and the suitability of the hook size among ontogenetic stages) are unlikely to explain the rare occurrence of adults in the SBT observer data, when we consider our existing knowledge on longline fishery and porbeagles (Løkkeborg and Bjordal 1992; Joyce *et al.* 2002; Pade *et al.* 2009). Instead, the mismatch between the SBT fishing ground (i.e. its southern limit) and the main habitat of the adult porbeagle seems a more plausible explanation. However, information on the distribution of the adult in higher latitudes and colder environments is limited in the southern hemisphere. Other than the record of Svetlov (1978) of the occurrence of a postpartum female in Antarctic waters ($54^{\circ}28'S$, $35^{\circ}29'W$) at an SST of $3.2^{\circ}C$, Yatsu (1995) indicated a clear trend in which the mean bodyweight of the porbeagle increases as the SST decreases (range, 5 – $20^{\circ}C$) in the South Pacific. According to the investigator on the JAMARC LL survey, the aggregation of pregnant females occurred at a high latitude, $\sim 60^{\circ}S$ (S. Sawadaishi, pers. comm.). In relation to the water temperature, the records for the porbeagle in the North Atlantic suggested that larger individuals tend to occur in colder environments, such as Grand Banks and the Gulf of St Lawrence (Aasen 1963; O'Boyle *et al.* 1998), where the influence of the cold Labrador current is dominant (Carruthers 1961). According to O'Boyle *et al.* (1998), not only the mean body size but also the proportion of mature females in the Grand Banks (60.4–83.9%) is higher than that on the Scotian Shelf (15.4–26.6%), especially in June, October and November, when the SST in Grand Banks is below $10^{\circ}C$ (Mason *et al.* 1999). Considering the fact that most commercial longline fisheries targeting SBT are developed in areas with SSTs above $10^{\circ}C$, the available information suggests that adult porbeagles are potentially distributed at higher latitudes with low temperatures, outside the SBT fishery grounds.

Occurrence of pregnant females

We have provided new information on the frequent occurrence of pregnant females in the pelagic waters off the Cape and one record each from the south-eastern Indian Ocean and the Tasman Sea. Off the Cape, 89% of pregnant females were recorded in June and July, which overlaps the peak of parturition (June–July) in the south-western Pacific Ocean (Francis and Stevens 2000). Moreover, small neonates between 50 cm (PCL)

and 60 cm (PCL) were recorded in the same area from May to November, with the largest number in August (Y. Semba, unpubl. data). Although the peak of parturition and the pupping ground were not clarified in the present study, the environment in the area off the Cape seems to be preferred by pregnant females, as is the south-western Pacific. In the southern hemisphere, the occurrence of pregnant females had been previously recorded almost exclusively in the exclusive economic zone (EEZ) of New Zealand and the Tasman Sea near New Zealand (Francis and Stevens 2000). The information presented here suggests that pregnant females are not exclusively concentrated in coastal areas, but are also distributed in pelagic areas.

In the south-eastern Indian Ocean, only one record of a pregnant female was available, whereas a high CPUE for neonates was observed. Neonates occurred in this area from May to January but most of them were recorded from August to December, which is after the known peak of parturition. Because the effort was also concentrated between August and December, the disproportionate occurrence of neonates and pregnant females might be attributable to the seasonal bias in the observations, given that females leave the pupping ground soon after the birth.

To explain the limited occurrence of pregnant females in the SBT fishery grounds, the present study suggests that adult females, including pregnant females, segregate from not only neonates and juveniles but also adult males, on the basis of the ontogenetic shifts in both the habitat and the sex ratio (from even to male dominance), which was also indicated in a past study (Francis and Stevens 2000). The temporal change in the adult sex ratio from male dominance between August and November to an even sex ratio in May and July (mid-fall and early winter) may be related to the mating event, if mating peaks in the fall as it does in the North Atlantic (Aasen 1963; Jensen *et al.* 2002).

Relative abundance

In the present study, the trend in the population abundance of the porbeagle was estimated on the basis of commercial tuna longline-fishery data (logbook data) and driftnet survey data, which covered a wide range of the southern hemisphere. The amount of zero-catch data limited the inclusion of some interaction terms in the GLM. We suggest that the extremely low (in 2004) and high (in 2008) CPUEs were caused by a biased distribution of effort (i.e. interaction between year and area), which could not be considered in the model, and so do not reflect the actual trend in abundance. Except for these estimates, the trend in abundance showed no decline throughout the period analysed, although there were some fluctuations. When we combined the fact that most porbeagles caught by tuna longline fisheries are juveniles (Francis *et al.* 2007) with the results of the present study, we inferred that the abundance of juveniles in the SBT fishery ground did not show a declining trend during the period analysed. Because the adults are segregated outside the SBT fishery ground (i.e. small interaction between the SBT fishery and adults) and no large-scale fisheries interact with the adult porbeagle in the pelagic area south of the SBT fishery grounds (CCAMLR 2012), the impact of fishing on the adult abundance of the southern population is suggested to be small.

The standardised CPUE estimated from the JAMARC DN survey data also showed a stable trend in abundance in the South Pacific between 1982 and 1990. Because no further surveys have

been conducted since 1990, subsequent trends in the population abundance of the porbeagle in the South Pacific are unknown. However, the impact of large-scale fisheries is suggested to be small because the effort of the SBT fishery developed in this area (e.g. south of 20°S) is quite small (CCSBT 2012) and the overlap between the ranges of the porbeagle and the fishery grounds of the purse seine fishery developed in the eastern Pacific is small (Román-Verdesoto and Orozco-Zöllner 2005).

Conclusion

The present study has shown new aspects of the distribution of the porbeagle in the southern hemisphere on various scales, together with estimates of the trend in abundance, as follows: (1) on the population scale, porbeagles are extensively distributed in the pelagic waters across the oceans; (2) on the intrapopulation scale, large individuals, especially adult individuals including mature females, penetrate into higher latitudes with colder environments; (3) the pelagic ocean is clearly a more important habitat for the southern population of porbeagles than was previously thought; and (4) the trend in the standardised CPUE, showing no significant declines, indicated that the levels of abundance of porbeagles (mostly juveniles) caught in the SBT fishery ground have not changed greatly during the period analysed.

Considering that the SBT fishery grounds may constitute the northern part of the southern porbeagle distribution, where neonates and juveniles dominate, further investigation of the biological aspects of the sharks, including the distribution of the adults, and a stock assessment based on fishery statistics from both coastal and pelagic areas, are required for the sustainable management and conservation of this population.

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References

- Aasen, O. (1963). Length and growth of the porbeagle (*Lamna nasus*, Bonnaterre) in the North West Atlantic. *Fiskeridirektoratet. Skrifter. Serie Havundersøkelser* **13**, 20–37.
- Camhi, M. D. (2008). Conservation status of pelagic elasmobranchs. In 'Sharks of the Open Ocean'. (Eds M. D. Camhi, E. K. Pikitch and E. A. Babcock.) pp. 396–417. (Blackwell Publishing: Oxford, UK.)
- Campana, S. E., and Joyce, W. N. (2004). Temperature and depth associations of porbeagle shark (*Lamna nasus*) in the northwest Atlantic. *Fisheries Oceanography* **13**, 52–64. doi:10.1111/J.1365-2419.2004.00236.X
- Campana, S. E., Joyce, W., Marks, L., Hurley, P., Natanson, L. J., Kohler, N. E., Jensen, C. F., Mello, J. J., Pratt, H. L., Jr, Myklevoll, S., and Harley, S. (2008). The rise and fall (again) of the porbeagle sharks

- population in the Northwest Atlantic. In 'Sharks of the Open Ocean'. (Eds M. D. Camhi, E. K. Pikitch and E. A. Babcock.) pp. 445–461. (Blackwell Publishing: Oxford, UK.)
- Carruthers, J. N. (1961). The Atlantic Ocean—North and South. In 'Atlantic Ocean Fisheries'. (Eds G. Borgstrom and A. J. Heighway.) pp. 1–17. (Fishing News (Books): London, UK.)
- Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (2012) *Statistical Bulletin* **24**, 2002–2011 Available at: <http://www.ccamlr.org/en/data/statistical-bulletin> [accessed 5 February 2013]
- Commission for the Conservation of Southern Bluefin Tuna (CCSBT) (2012). 'Catch and Effort Data.' Available at: http://www.ccsbt.org/site/sbt_data.php [accessed 5 February 2013].
- Compagno, L. J. V. (2001). 'Sharks of the World: an Annotated and Illustrated Catalogue of Shark Species Known to Date. Species Catalogue for Fishery Purposes No. 1. Vol. 2.' (FAO: Rome.)
- Cortés, E., Arocha, F., Beerkircher, L., Carvalho, F., Domingo, A., Heupel, M., Holtzhausen, H., Santos, M. N., Ribera, M., and Simpfendorfer, C. (2010). Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. *Aquatic Living Resources* **23**, 25–34. doi:10.1051/ALR/2009044
- Davis, T. L. O., and Stanley, C. A. (2002). Vertical and horizontal movements of southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight observed with ultrasonic telemetry. *Fishery Bulletin* **100**, 448–465.
- Dulvy, N. K., Baum, J. K., Clarke, S., Compagno, L. J. V., Cortés, E., Domingo, A., Fordham, S., Fowler, S., Francis, M. P., Gibson, C., Martínez, J., Musick, J. A., Soldo, A., Stevens, J. D., and Valenti, S. (2008). You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems* **18**, 459–482. doi:10.1002/AQC.975
- Francis, M. P., and Duffy, C. (2005). Length at maturity in three pelagic sharks (*Lamna nasus*, *Isurus oxyrinchus*, and *Prionace glauca*) from New Zealand. *Fishery Bulletin* **103**, 489–500.
- Francis, M. P., and Stevens, J. D. (2000). Reproduction, embryonic development, and growth of the porbeagle shark, *Lamna nasus*, in the southwest Pacific Ocean. *Fishery Bulletin* **98**, 41–63.
- Francis, M. P., Griggs, L. H., and Baird, S. J. (2001). Pelagic shark bycatch in the New Zealand tuna longline fishery. *Marine and Freshwater Research* **52**, 165–178. doi:10.1071/MF00086
- Francis, M. P., Campana, S. E., and Jones, C. M. (2007). Age underestimation in New Zealand porbeagle sharks (*Lamna nasus*): is there an upper limit to ages that can be determined from shark vertebrae? *Marine and Freshwater Research* **58**, 10–23. doi:10.1071/MF06069
- Francis, M. P., Natanson, L. J., and Campana, S. E. (2008). The biology and ecology of the porbeagle shark, *Lamna nasus*. In 'Sharks of the Open Ocean'. (Eds M. D. Camhi, E. K. Pikitch and E. A. Babcock.) pp. 105–113. (Blackwell Publishing: Oxford, UK.)
- Gauld, J. A. (1989). Records of porbeagles landed in Scotland, with observations on the biology, distribution and exploration of the species. Report No. 45. Fisheries Research Services, Aberdeen, Scotland.
- International Commission for the Conservation of Atlantic Tunas (ICCAT) (1997). Report of the bluefin tuna methodology session. International Commission for the Conservation of Atlantic Tunas SCRS/1996/014. Available at http://www.iccat.es/Documents/CVSP/CV046_1997/no_1/CV046010187.pdf [accessed June 2012].
- International Commission for the Conservation of Atlantic Tunas (ICCAT) (2009). Report of the 2009 porbeagle stock assessments meeting. International Commission for the Conservation of Atlantic Tunas SCRS/2009/014. Available at http://www.iccat.es/Documents/Meetings/Docs/2009_POR_ASSESS_ENG.pdf [accessed June 2012].
- Japan Marine Fisheries Resources Research Center (JAMARC) (1987~1994). Report on the studies for the development of new fishery resources for Gastero. Present Marine Fisheries Research and Development Center, JAMARC, FRA, Yokohama, Japan.
- Japan Marine Fisheries Resources Research Center (JAMARC) (1982~1989). Report on the studies for the development of new fishery resources for Allothunnus. Present Marine Fisheries Research and Development Center, JAMARC, FRA, Yokohama, Japan.
- Japan Marine Fisheries Resources Research Center (JAMARC) (1984~1987). Report on the studies for the development of new fishery resources for Pomfret. Present Marine Fisheries Research and Development Center, JAMARC, FRA, Yokohama, Japan.
- Jensen, C. F., Natanson, L. J., Pratt, H. L., Jr, Kohler, N. E., and Campana, S. E. (2002). The reproductive biology of the porbeagle (*Lamna nasus*) in the western North Atlantic Ocean. *Fishery Bulletin* **100**, 727–738.
- Joyce, W. N., Campana, S. E., Natanson, L. J., Kohler, N. E., Pratt, H. L., Jr, and Jensen, C. F. (2002). Analysis of stomach contents of the porbeagle shark (*Lamna nasus* Bonnaterre) in the northwest Atlantic. *ICES Journal of Marine Science* **59**, 1263–1269. doi:10.1006/JMSC.2002.1286
- Kitamura, T., and Matsunaga, H. (2009). Population structure of porbeagle (*Lamna nasus*) in the North Atlantic Ocean and SBT fishery found as inferred from mitochondrial DNA control region sequences. CCBST-ERS/0909/08. 8 p. Available at http://www.ccsbt.org/site/contact_details.php? [accessed June 2012].
- Kohler, N. E., Turner, P. A., Hoey, J. J., Natanson, L. J., and Briggs, R. (2002). Tag and recapture data for three pelagic shark species: blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and porbeagle (*Lamna nasus*) in the North Atlantic Ocean. International Commission for the Conservation of Atlantic Tunas SCRS/2001/064. Available at http://www.iccat.int/Documents/CVSP/CV054_2002/no_4/CV054041231.pdf [accessed June, 2012].
- Last, P. R., and Stevens, J. D. (2009). 'Sharks and Rays of Australia.' 2nd edn. (CSIRO Publishing: Melbourne.)
- Lo, N. C., Jacobson, L. D., and Squire, J. (1992). Indices of relative abundance from fish spotter data based on delta-lognormal models. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2515–2526. doi:10.1139/F92-278
- Løkkeborg, S., and Bjørndal, Å. (1992). Species and size selectivity in longline fishing: a review. *Fisheries Research* **13**, 311–322. doi:10.1016/0165-7836(92)90084-7
- Mason, C. S., Petrie, B., and Topliss, B. J. (1999). Satellite measurements of sea-surface temperature: an application to regional ocean climate. *NAFO Scientific Council Studies* **32**, 45–54.
- Matsunaga, H. (2009). Standardized CPUE for blue shark and shortfin mako caught by the Japanese tuna longline fishery in the Atlantic Ocean. International Commission for the Conservation of Atlantic Tunas SCRS/2008/149. Available at http://www.iccat.int/Documents/CVSP/CV064_2009/no_5/CV0640501677.pdf [accessed June, 2012].
- Morinobu, S. (1996). Study on the distribution and age and growth of the two Lamnidae species in the southern bluefin tuna fishery ground (in Japanese). M.Sc. Thesis, Tokai University, Shizuoka.
- Natanson, L. J., Mello, J. J., and Campana, S. E. (2002). Validated age and growth of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean. *Fishery Bulletin* **100**, 266–278.
- O'Boyle, R. N., Fowler, G. M., Hurley, P. C. F., Joyce, W., and Showell, M. A. (1998). Update on the status of NAFO SA 3–6 porbeagle shark (*Lamna nasus*). Document No. 98/41. Canadian Science Advisory Secretariat, Fisheries and Oceans, Ottawa, Ontario, Canada.
- Pade, N. G., Queiroz, N., Humphries, N. E., Witt, M. J., Jones, C. S., Noble, L. R., and Sims, D. W. (2009). First results from satellite-linked archival tagging of porbeagle shark, *Lamna nasus*: area fidelity, wider-scale movements and plasticity in diel depth changes. *Journal of Experimental Marine Biology and Ecology* **370**, 64–74. doi:10.1016/J.JEMBE.2008.12.002
- Patterson, T. A., Evans, K., Carter, T. I., and Gunn, J. S. (2008). Movement and behaviour of large southern bluefin tuna (*Thunnus maccoyii*) in the Australian region determined using pop-up satellite archival tags. *Fisheries Oceanography* **17**, 352–367. doi:10.1111/J.1365-2419.2008.00483.X

- Pons, M., and Domingo, A. (2009). Standardized CPUE of porbeagle shark (*Lamna nasus*) caught by Uruguayan pelagic longline fleet (1982–2008). International Commission for the Conservation of Atlantic Tunas SCRS/2009/093. Available at http://www.iccat.int/Documents/CVSP/CV065_2010/no_6/CV065062098.pdf [accessed June 2012].
- Román-Verdesoto, M., and Orozco-Zöller, M. (2005). Bycatches of sharks in the tuna purse-seine fishery of the eastern Pacific Ocean reported by observers of the Inter-American Tropical Tuna Commission, 1993–2004. Inter-American Tropical Tuna Commission Data Report 11, La Jolla, CA.
- SAS (2009). 'SAS/STAT® 9.2 User's Guide, Second Edition.' (SAS Institute Inc.: Cary, NC, USA.)
- Saunders, R. A., Royer, F., and Clarke, M. W. (2011). Winter migration and diving behaviour of porbeagle shark, *Lamna nasus*, in the Northeast Atlantic. *ICES Journal of Marine Science* **68**, 166–174. doi:10.1093/ICESJMS/FSQ145
- Shingu, C. (1978). 'Ecology and stock of southern bluefin tuna [In Japanese; English translation in CSIRO, Division of Fisheries and Oceanography, 1981].' (Japan Fisheries Resources Conservation Association: Tokyo.)
- Shono, H. (2008). Confidence interval estimation of CPUE year trend in delta-type two-step model. *Fisheries Science* **74**, 712–717. doi:10.1111/J.1444-2906.2008.01581.X
- Sokal, R. R., and Rohlf, F. J. (1995). 'Biometry. The Principles and Practice of Statistics in Biological Research.' 3rd edn. (W. H. Freeman: New York.)
- Springer, S. (1967). Social organization of shark populations. In 'Sharks, Skates, and Rays'. (Eds P. W. Gilbert, R. F. Mathewson and D. P. Rall.) pp. 149–174. (The Johns Hopkins Press: Baltimore, MD.)
- Svetlov, M. F. (1978). The porbeagle, *Lamna nasus*, in Antarctic waters. *Journal of Ichthyology* **18**, 850–851.
- Yatsu, A. (1995). Zoogeography of the epipelagic fishes in the South Pacific Ocean and the Pacific sector of the subantarctic, with special reference to the ecological role of slender tuna, *Allothunnus fallai*. *Bulletin of the National Research Institute of Far Seas Fisheries* **No. 32**.