Large-scale distribution of three deep-water squaloid sharks: Integrating data on sex, maturity and environment


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A B S T R A C T
Deep-water sharks exhibit species-specific reproductive strategies, which include segregation by sex, size and reproductive stage. However, due to the wide spatial distribution of most species, available information, usually collected at a regional scale, is usually not adequate to infer species reproductive spatial dynamics. This study draws together information on the distribution of reproductive stages of three species of squaliform sharks: Portuguese dogfish Centroscymnus coelolepis (Somniosidae), leafscale gulper shark Centrophorus squamosus (Centrophoridae) and birdbeak dogfish Deania calcea (Centrophoridae), gathering data from several geographical areas from the Atlantic, Indian and Pacific Oceans. For each species we analysed the sex ratio and the spatial patterns of reproductive stages within regions, considering the influence of geographical area, depth, season, temperature and salinity. The combination of statistical methods used in this study successfully identified a number of life history patterns which reflect different uses of habitat by sex and life cycle stage. Pregnant females of the three species are spatially segregated, inhabiting shallower and/or warmer waters. In the case of the leafscale gulper shark this segregation might be associated with large scale migrations. In contrast, in Portuguese dogfish all adult maturity stages occur in the same geographical area. Pregnant female birdbeak dogfish were rare in all samples. Larger immature specimens of all the three species distribute deeper than the remaining maturity stages in most of the regions analysed. Mature males of leafscale gulper shark and birdbeak dogfish were more broadly distributed than mature females, supporting the possibility of sex-biased dispersal. Neonates and small sized specimens were scarce in the Northeast Atlantic potentially explained by their concentration in nurseries, and/or by gear selectivity. Management measures will benefit from considering the geographic scale of demographic variation between species. However, standardized collaborative approaches will be needed for comprehensive assessment.

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1. Introduction

There is worldwide concern for the conservation of deep-water sharks due to low biological productivity and population declines (Kyne and Simpfendorfer, 2010). Life history characteristics typically include a slow growth rate, late age-at-maturity and low fecundity, indicating long generation times (Garcia et al., 2008; Graham and Daley, 2013). Consequently, populations that have declined will require decades or even centuries to recover (Pratt and Casey, 1990; Simpfendorfer and Kyne, 2009).

Effective management of these species requires precautionary approaches founded on an understanding of species-specific life histories (Simpfendorfer and Kyne, 2009). Life-history traits are quite diverse among deep-water sharks, but some strategies, including segregation patterns, are similar to other elasmobranch species (Wearmouth and Sims, 2008). Although less studied than shallow-water species, segregation within a population by sex, size and/or reproductive stage has been reported for a number of deep-water shark species (Muñoz-Chapuli, 1984; Yano and Tanaka, 1988; Wetherbee, 1996; Girard and Du Buit, 1999; Clarke et al., 2001; Jakobsdottir, 2001; McLaughlin and Morrissey, 2005). Segregation may be advantageous in a population to maximize reproductive success, minimize predation risk or potential aggressive interactions, and for size or sex-specific foraging requirements (Sims, 2005; Wearmouth and Sims, 2008). Segregation can occur at different scales, and is often linked to particular environmental or ecological features. The set of factors potentially influencing segregation may be complex. Therefore, demographic data from the full range of a population is fundamental to assessing status and particularly for predicting responses to exploitation.

Attempts to develop adequate quantitative stock assessments for deep-sea sharks have fallen short of expectations due to inadequate data, particularly in the Atlantic and southwestern Pacific. Information available on deep-water sharks is derived either from sampling of commercial catches or from scientific surveys. Fishery data are often restricted to those deep-sea sharks that are of greatest commercial importance, and have been limited historically by a lack of taxonomic and geographic precision. In contrast, fishery-independent surveys are often temporally irregular, and none have had sufficient geographic coverage to ensure that all demographic components of the populations are sampled. These deficiencies are exacerbated by the global distribution of some species that include waters under many jurisdictions, and also by their specific reproductive strategies where mating and pupping might be decoupled in space and time, due to sperm storage (Moura et al., 2011a). Major scientific investment is required to gain a full understanding of the spatial and temporal population dynamics of deep-water sharks, and enable estimates of sustainable exploitation levels to be derived.

The Portuguese dogfish (Centroscymnus coeleoplos, Somniosidae), the leaf scale gulper shark (Centrophorus squamosus, Centrophoridae) and the birdbeak dogfish (Deania calcea, Centrophoridae) are viviparous sharks widely distributed on the mid-continental slope at depths of 800–1600 m in the Atlantic, Indian and Pacific Oceans (Compagno et al., 2005). These species reach 120–160 cm total length and are frequently caught by deep-water trawl and bottom longline fleets (Stevens, 2003; Stevens and Correa, 2003; White, 2003). In the EU waters, a zero total allowable catch (TAC) was adopted in 2010 for a variety of deep-water sharks, including these species (Council Regulation (EU) no 1359/2008). In Australia, in addition to a TAC regime, there are spatial/death closures over some areas with important historical catches (Woodhams et al., 2012). In the northwest Atlantic Ocean, southwest Indian Ocean and in New Zealand, there are currently no management regulations for these species.

This study draws together regional knowledge of size distribution and reproductive stages of three species of squaliform sharks. For each species, we analysed and compared the spatial patterns within and among different regions of the Atlantic, Indian and Pacific Oceans, using commercial and survey data. Spatial variation of the defined maturity groups was studied considering the influence of depth, temperature, salinity, area and season. The key findings are presented in the context of regional management arrangements required to ensure sustainability of populations.

2. Material and methods

2.1. Data sources

Biological data were collected onboard commercial trawl and longline fishing vessels, and during research surveys conducted in six different ocean regions: northeastern (NE) Atlantic Ocean (including the mid-Atlantic ridge), centre-eastern (CE) Atlantic Ocean, southeastern (SE) Atlantic Ocean, northwestern (NW) Atlantic Ocean, southwestern (SW) Indian Ocean and southwestern (SW) Pacific Ocean (Fig. 1; Table A1). All specimens were caught within the bathymetric range of 200–3200 m.

2.2. Data collation and standardization

The spatial and temporal resolution of the data varied among geographic areas due to the logistical constraints associated with the different sampling methods (e.g. depth, gear, duration, year, season). In order to allow the comparison of datasets from different sampling years the distribution patterns of each species in each geographical area and region were assumed to be temporally consistent.

A number of data standardization steps were applied to produce a single database. As much of the data had been collected opportunistically, the geographic precision of the capture locations varied among sources. Therefore, the first key step was to standardize locations by ocean ‘region’. Data from NE Atlantic, SW Indian and SW Pacific regions were further classified by ‘geographic area’. The second step was to ensure that the biological attributes recorded were consistent among regions. Biological data provided for each specimen included the species total length (TL), sex and maturity stage. Maturity stage data were standardized by classifying each individual according to a maturity stage group. These groups are based on Stehmann (2002) modified after Figueiredo et al., (2008) and Irvine et al., (2012) (equivalent stages indicated in parentheses). For males, two groups were considered: immature (immature and maturing) and mature (mature and active). For females four groups were considered: immature (immature and maturing), mature (mature-non-pregnant, pre-ovulatory), pregnant (developing, differentiating and expecting) and post-natal (post-natal). Where regenerating females (maturity, not for the first time) had been observed, they were combined with post-natal stages. In the dataset from the SW Indian Ocean the information was not sufficient to discriminate between post-natal and mature females.

Published studies show that neonates of these three species are scarce or entirely absent from the NE Atlantic. This study examined a size-based subset of the data for immature specimens for the same pattern. The term “juvenile” was used for small immature individuals between length-at-birth and a pre-determined upper limit. These sizes were based on published values from the NE Atlantic (Girard and Du Buit, 1999; Clarke et al., 2002; Figueiredo et al., 2008) and were assumed to be applicable to other regions. Size-at-birth was taken as 25–31 cm for the Portuguese dogfish (Moura et al., 2011b), 38–44 cm for the leafscale gulper shark (Bañón et al., 2016).
Fig. 1. Worldwide sampling sites for the Portuguese dogfish, leafscale gulper shark and birdbeak dogfish. NW Atlantic, including (a) Gulf of Mexico; (b) U.S. east coast; and (c) Greenland. NE Atlantic including (d) Iceland; (e) Rockall and Hatton Banks; (f) Scotland; (g) north of the Charlie-Gibbs Fracture Zone; (h) Ireland; (i) north Azores; (j) Bay of Biscay; (k) Portugal; (l) south Azores; (m) Madeira Archipelago; and (n) Canarias Archipelago. CE Atlantic in particular (o) Mauritania. SE Atlantic in particular (p) Namibia. SW Indian including (q) Mozambique Plateau; and (r) Madagascar Plateau. SW Pacific including (s) New South Wales; (t) Tasmania (Australia); (u) Chatham Rise and North Island; and (v) South Island and Campbell Plateau (New Zealand).
2.3.3. and 28–33 cm for the birdbeak dogfish (Irvine et al., 2012). The upper limit sizes applied were <60 cm for the Portuguese dogfish and leafscale gulper shark and <55 cm for the birdbeak dogfish. Hereafter term “immature” will refer only to the fraction of immature stage specimens above the upper size limit for juveniles. Juvenile and immature specimens were only combined when estimating the proportion of maturity stages by geographical area.

Datasets lacking maturity stage, sex or size were only considered in some analysis or in assessing geographic distribution.

2.3. Statistical analysis

All data analyses were conducted in the R software environment (R Core Team, 2012). For each species-region combination, the relationship of maturity to depth was evaluated with boxplots constructed using the package Lattice (Sarkar, 2008).

The influence of gear type (trawl or longline) on length and maturity stage was also evaluated for the NE Atlantic region, where different types of gears were used for the collection of the specimens.

2.3.1. Sex ratio

The influence of depth on sex ratio was examined for each species–area combination by calculating the median and interquartile ranges of the proportion of females by depth strata (100 m). This analysis was restricted to geographical areas with 25 or more hauls of >1 individual. The depth intervals varied between species: 800–1700 m for the Portuguese dogfish, 500–1700 m for the leafscale gulper shark and 500–1400 m deep for the birdbeak dogfish. These intervals include the depths where each species were sampled more frequently.

2.3.2. Mapping and occurrence of maturity stages

For males and females, the proportion of individuals at each maturity stage was described and plotted for each geographical area and region where sufficient data were available (only datasets with maturity information for a total of 30 or more individuals were considered).

To characterize the spatial pattern of the different life stages, the occurrence of each maturity stage was mapped using ArcGIS v.9.0. The analysis was restricted to observations with precise geographic location. These data were overlaid on mapped coastline and bathymetry data extracted from the General Bathymetric Chart of the Oceans (GEBCO) [IOC, IHO and BODC, 2003].

2.3.3. Environmental variables and maturity

Temperature and salinity values were estimated for each haul, based on geographical position and depth, using the World Ocean Atlas 2009 database from U.S. National Oceanographic Data Center (Antonov et al., 2010; Locarnini et al., 2010) and the 3D estimation method implemented in Ocean Data View Software (Schlitzer, 2011). 3D point estimation is a fast weighted averaging procedure and combines the environmental information with user specified longitude, latitude and depth, assuming specific averaging length scales (Schlitzer, 2011). Scales were considered as 2.5% of the axis ranges for longitude and latitude and 100 m for depth. Yearly environmental values were used in calculations because a preview of the monthly data found only minor variation. Further, the monthly environmental data did not cover the full depth range of the catch data. Constrained correspondence analysis (CCA) was used to explore how the maturity stages of each species were influenced as a biological response to four environmental variables: temperature, salinity, depth and season. This analysis used the Vegan package for R software (Oksanen, 2011). This method combines a multivariate ordination presence/absence of maturity stage with a constrained regression maximizing the correlation between the maturity stages ordination axes and the selected environmental variables. It was assumed that the ecological range of each maturity stage analysis has been sampled and further assumed that each maturity stage presents a unimodal response to each independent variable (ter Braak, 1986; Borcard et al., 2011). It is pertinent to note that whilst the inertia (percentage of variation explained) is typically low (<10%) when CCA is applied to binary variables, the results can still be ecologically meaningful (ter Braak and Verdonschot, 1995; Oksanen, 2011). Two matrices were constructed for this analysis: one corresponding to the occurrence of maturity stages (presence/absence, dependent variable), and the other corresponding to the environmental variables mentioned above (independent variables). CCA were fitted conditioned to the geographical area, i.e. area was partially out from the analysis before constraints, and only to regions with representative data (>100 georeferenced hauls with maturity information). The final selection of independent variables for inclusion in the CCA model followed a stepwise process, based on the Aikake information criterion (AIC). The variance inflation factor (VIF) was used to avoid multicollinearity, i.e. inclusion of environmental variables strongly correlated with each other (ter Braak, 1986; Oksanen, 2011). VIFs > 10 should be examined and avoided (Borcard et al., 2011). In cases where VIF > 10, all the possible combination of variables were considered in the CCA. Variable selection considered the Spearman correlation coefficient estimated between variables and the most rational results for VIF, AIC and proportion of inertia explained. Results of the analysis were plotted and scaled to maturity stages. Monte Carlo permutation tests were used to assess the significance of the terms and axis of the model. In both cases a significance level of 5% was adopted.

The function “ordisurf”, from the vegan R package was used for weighted fitting and plotting of a smooth surface of the selected variables. This function fits the environmental surface using thin plate splines in a generalized additive model (GAM), and then uses the results to predict and plot the surface on an ordination diagram (Oksanen et al., 2012). This analysis allows curvilinear relationships, and tests the linearity hypothesis of the biplot method (Oksanen, 2011). It is important to note that this method enables the evaluation of trends for each variable independently and is based on the proportion of variance explained by the variables included in the model.

3. Results

3.1. Portuguese dogfish

3.1.1. Sampling details

Portuguese dogfish data were obtained for all six regions and represented eighteen geographical areas. A total of 9388 specimens were recorded, of which up to 5940 individuals were selected for more detailed analysis, based on precision of recorded location and maturity information. This number excluded individuals from SW Pacific, without geo-referenced data, which were used solely to determine the proportion of individuals by maturity stage. Depth and TL ranges by sex and maturity stage are reported in Fig. 2 and Table A2. Maximum length was sexually dimorphic in most regions and geographic areas, with females attaining larger sizes than males. Exceptions were the SW Indian regions, New Zealand (SW Pacific) and Tasmania (SW Pacific).

3.1.2. Sex ratio

Females outnumbered males in the NE Atlantic (with exception of the Bay of Biscay), in the CE Atlantic and in the SE Atlantic, whereas the opposite was observed for the SW Indian and SW
Pacific Oceans (Table 1). Sex ratios varied within and between depth strata for all geographical areas analysed (Fig. A1). In Scotland, Mauritania and Namibia the proportion of females increased with depth.

3.1.3. Mapping and occurrence of maturity stages

Population structure varied between regions and geographical areas. In the NE Atlantic and in the SW Pacific (Australia) all maturity stages were sampled (Table 1, Fig. 3), with length ranges being similar among fishing gears in the first region (Fig. A2). For females, the proportions by different maturity stages were similar in some NE Atlantic geographical areas (excluding Rockall and Hatton Banks, North Azores and Canarias) and in Tasmania. In these areas, mature females accounted for around 17–25% of the samples, with pregnant females making up 8–17%. In contrast, the proportion of mature and immature males varied widely within the NE Atlantic and SW Pacific regions. The pattern was different for other regions. In the CE and SE Atlantic regions, mature, pregnant and post-natal females and mature males were absent or seldom observed. In the NW Atlantic region, juveniles prevailed in the samples and only one mature female was recorded. Some areas in the SW Indian region provided contrast: off the Mozambique plateau, immature and mature females were most common, with some pregnant females also recorded; off the Madagascar plateau, mature males were more common and pregnant females made up nearly 30% of the female sample.

The number of juveniles caught varied among regions: zero or low numbers were recorded in the NE Atlantic (n = 7), SW Indian (n = 0) and SW Pacific, Australia (n = 8), whilst much higher numbers were reported for the NW Atlantic (n = 53), CE Atlantic (n = 796), with the highest numbers recorded in the SE Atlantic (n = 695). Some of these were potentially neonates since their sizes were close to the estimated length-at-birth. Most of the juvenile specimens were caught by trawlers, with the exceptions being one individual caught by longline in the NE Atlantic and a small portion of the NW Atlantic sample that was caught with traps.

3.1.4. Environmental variables and maturity

For the NE Atlantic data (excluding juveniles, that were recorded in low number), depth was the only factor selected in the CCA model. This model explained 10% of the total inertia (pCanonical relationship = 0.005; pAxis = 0.002). Depth was negatively correlated with axis 1. The ordination and surface model of the environmental variable selected showed that pregnant females
had the shallowest distribution, mature males were deeper and all other stages deeper still, and at closely located sites (deviance explained = 58%) (Fig. 4).

All the other datasets were inadequate to run the CCA, either due to the low representation of maturity groups (CE Atlantic and SE Atlantic datasets were composed mainly of juveniles and immature specimens) or to insufficient data (as the case of NW Atlantic and SW Indian Ocean). In the CE Atlantic, 68% of the juveniles caught occurred between 1300 and 1500 m deep. Juveniles and immature specimens were caught in the same hauls, although each haul was typically dominated by one group or the other. Those hauls clearly dominated by juveniles were mostly located at centre-south slope of Mauritania. In the NW Atlantic, juveniles were recorded from 670 to 2624 m but 88% of these catches were shallower than 1000 m. In the SW Indian Ocean, maturity stages were not correlated with depth.

3.2. Leafscale gulper shark

3.2.1. Sampling details

Data for the leafscale gulper shark were obtained for all regions of the Eastern Atlantic and for the SW Pacific. A total of 5480
Portuguese dogfish, NE Atlantic

Fig. 4. Constrained correspondence analysis of the Portuguese dogfish distribution by maturity stage. Ordination of the maturity stages (black circles) and hauls (grey circles) overlaid with the surface model fitted for depth (in metres) in the NE Atlantic (n = 2991; 509 hauls). Axes 1 accounted for 100% of the variance of the fitted values.

specimens were sampled, with up to 3483 meeting the criteria for inclusion in the statistical analyses. Depths and TL ranges by sex and maturity stage are reported on Fig. 2 and Table A3. Females attained larger sizes than males for most geographical areas.

3.2.2. Sex ratio

In the NE Atlantic, sex ratios varied between areas. Males predominated over females on the Rockall and Hatton Banks, off Ireland, Portugal, on the Mid Atlantic Ridge (Northern Azores) and in Madeira (Table 2). Females were more frequently caught in the remaining areas. In the northern areas of the NE Atlantic (Scotland and Ireland) the proportion of females increased with increasing depth although there was also high variability within each depth strata (Fig. A3). In the CE Atlantic, males and females were caught in equal numbers, but samples sizes were too low for more detailed analysis. In the SW Pacific (New Zealand), females were significantly more abundant than males in the two geographical areas and sex ratios were not influenced by depth.

3.2.3. Mapping and occurrence of maturity stages

The proportions of maturity stages varied considerably among regions and geographical areas (Table 2, Fig. 5). In the NE Atlantic, all the maturity stages were caught and size ranges did not differ among fishing gears (Fig. A4). In this region, apart from Iceland, mature males were more common than immature males, and were broadly distributed along the continental slopes. In contrast, mature females were far less common, with immature specimens dominating the catch, except around Iceland and further south around Madeira and Canaries. Pregnant females were only recorded in three regions: off Iceland (n = 5 out of 36 females sampled), Portugal (n = 3 out of 122 females sampled) and from the Madeira Archipelago (n = 30 out of 60 females sampled). Post-natal females were recorded from most of the geographical areas except the Canarias and Madeira Archipelagos and the mid-Atlantic ridge north to the Azores. Despite the large sample sizes in many areas, only 3 juveniles were caught from SW of the Portuguese mainland. These specimens, as well as all the other juvenile specimens recorded from other regions, were caught using trawl nets. In the CE Atlantic, immature specimens dominated the sample. Mature males were recorded all along the surveyed slope. No mature females were caught in this area. The few records of this species in the SE Atlantic included immature (including juveniles) and mature specimens from both sexes. Around New Zealand in the SW Pacific region, immature individuals were dominant for both males and females. Pregnant and post-natal females were rare (n = 12 and 4 out of 508 females sampled, respectively). Juveniles occurred mainly on the northern slopes of the Chatham Rise and also to the southwest of the South Island of New Zealand (Puysegur Bank).

3.2.4. Environmental variables and maturity

In the NE Atlantic, juveniles were excluded from the CCAs due to small sample sizes. In this region, depth and temperature were the environmental factors selected in the CCA model, explaining 16% of the total inertia ($p_{canonical\ relationship\ depth} = 0.005$; $p_{canonical\ relationship\ temperature} = 0.005$; $p_{axis1} = 0.002$; $p_{axis2} = 0.002$). These two environmental variables were highly correlated with axis 1, with depth being positively related and temperature being negatively related with this axis. Axis 2 was also negatively correlated with temperature. The surface model of the selected environmental variables indicated that the distribution of males was not related to depth or temperature, but post-natal and mature females tended to occur in relatively shallower sites (deviance explained = 76% and 53% for depth and temperature, respectively) (Fig. 6a and b). Pregnant females were distributed preferentially at warmer stations compared to the remaining maturity stages, particularly immature females, which were usually found at greater depths and lower temperatures.

In the SW Pacific data (excluding pregnant and post-natal females due to their low numbers in the samples), the best CCA model included only depth and salinity (6% of the total inertia explained; $p_{canonical\ relationship\ depth} = 0.002$; $p_{canonical\ relationship\ salinity} = 0.075$; $p_{axis1} = 0.002$; $p_{axis2} = 0.950$). Depth was positively correlated with axis 1 and salinity was positively correlated to axis 2, the latter explaining a small fraction of variation. The ordination and the surface models of the selected environmental variables showed that immature males, females and juveniles all co-occurred at relatively deeper and less saline waters (deviance explained = 96.5% and 100% for depth and salinity, respectively) (Fig. 6c and d). Mature males were associated with shallower, more saline waters. Nine of the twelve females were found in waters shallower than 900 m. The two post-natal females sampled in the South Island were collected from depths shallower than 650 m, whereas those sampled in the Chatham Rise and North Island were both collected in the 900 m stratum.

Sample sizes from the CE Atlantic and SE Atlantic were insufficient for CCA (n = 26 and 13 hauls, respectively), but differences in maturity stages occurrence were also found to be related with depth. In the CE Atlantic, 75% of the juveniles occurred $<$900 m deep, at similar depths to mature males, whereas immature specimens were found relatively deeper. In the SE Atlantic, juveniles (n = 4) were caught between 550 and 800 m deep, shallower than all other maturity stages.

3.3. Birdbeak dogfish

3.3.1. Sampling details

Data were obtained from the Atlantic and the SW Pacific. A total of 14468 specimens was collected, of which 12189 met the criteria for inclusion in the statistical analysis. Depth and TL ranges by sex are reported in Fig. 2 and Table A4. In all the areas sampled, females attained larger sizes than males.
Table 2
Leafscale gulper shark. Proportion of maturity stages, total numbers by sex (n) and sex-ratio (number of females for one male) by geographical area and by region (in bold). The immature groups include juveniles. F: females; M: males.

<table>
<thead>
<tr>
<th>Geographical area/region</th>
<th>Leafscale gulper shark</th>
<th>Sex ratio F:M</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td></td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>Immature</td>
</tr>
<tr>
<td>Iceland</td>
<td>10</td>
<td>0.80</td>
</tr>
<tr>
<td>Rockall and Hatton Banks</td>
<td>352</td>
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<tr>
<td>Scotland</td>
<td>308</td>
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</tr>
<tr>
<td>Ireland</td>
<td>322</td>
<td>0.39</td>
</tr>
<tr>
<td>Portugal</td>
<td>133</td>
<td>0.25</td>
</tr>
<tr>
<td>North Azores (MAR)</td>
<td>82</td>
<td>–</td>
</tr>
<tr>
<td>Madeira Archipelago</td>
<td>145</td>
<td>0.06</td>
</tr>
<tr>
<td>Canarias Archipelago</td>
<td>31</td>
<td>0.48</td>
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<tr>
<td>Total NE Atlantic</td>
<td>1383</td>
<td>0.27</td>
</tr>
<tr>
<td>CE Atlantic (Mauritania)</td>
<td>42</td>
<td>0.76</td>
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<tr>
<td>Chatham Rise and North Island</td>
<td>134</td>
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<tr>
<td>South Island, Campbell Plateau</td>
<td>182</td>
<td>0.58</td>
</tr>
<tr>
<td>Total SW Pacific</td>
<td>316</td>
<td>0.70</td>
</tr>
</tbody>
</table>

3.3.2. Sex ratio
Sex ratios varied between regions. For the NE Atlantic region, males predominated over females at most sampling locations, except in the Bay of Biscay, Portugal and Canarias Archipelago (Table 3). In this region, sex ratios were variable among depth strata, but with no discernable trend (Fig. A5). In the CE Atlantic, females predominated over males but in the SE Atlantic the contrary was observed. In these two regions, the proportion of females decreased.

Fig. 5. Leafscale gulper shark. Occurrences of (a) juveniles, (b) mature males and females; (c) pregnant and post-natal females in the NE Atlantic; of (d) juveniles, (e) mature males and females; (f) pregnant and post-natal females in the SW Pacific (New Zealand).
with depth. In the SW Pacific region (New Zealand), the numbers of males and females were similar off the South Island but on the Chatham Rise and around the North Island, females were more common than males. In this area, the proportion of females seemed to decrease with depth, despite the high variability observed (wide interquartile ranges).

3.3.3. Mapping and occurrence of maturity stages

The proportion of maturity stages observed varied considerably among geographical areas and regions (Table 3, Fig. 7). In the NE Atlantic, specimens of all maturity stages were caught and size ranges were similar among fishing gears (Fig. A6). In this region, mature males were widely distributed, but their proportion was variable among geographical areas. Immature females outnumbered mature females in almost all regions, except the Canarias Archipelago. The number of pregnant females was low or totally absent in most geographical areas. Post-natal females were mainly recorded in northern areas, often spatially separated from other stages. In this region, juveniles were caught both with trawls and longlines, and were recorded on Hatton Bank (n = 10), off Ireland (n = 2) and on the SW Portugal mainland (n = 5), but representing less than 1% of the total sample from these areas. In contrast, the
Table 3

Birdbeak dogfish. Proportion of maturity stages, total numbers by sex (n) and sex-ratio by geographical area and by region (in bold). The immature groups include juveniles. F: females; M: males.

<table>
<thead>
<tr>
<th>Geographical area/region</th>
<th>Birdbeak dogfish</th>
<th>Sex ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>Immature</td>
</tr>
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<td>Iceland</td>
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<td>Scotland</td>
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<td>Ireland</td>
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<td>0.48</td>
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<tr>
<td>Rockall and Hatton Banks</td>
<td>248</td>
<td>0.21</td>
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<tr>
<td>Bay of Biscay</td>
<td>66</td>
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<tr>
<td>Portugal</td>
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<td>–</td>
</tr>
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<td>Canarias Archipelago</td>
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<td>0.4</td>
</tr>
<tr>
<td>Total NE Atlantic</td>
<td>1589</td>
<td>0.40</td>
</tr>
<tr>
<td>CE Atlantic (Mauritania)</td>
<td>542</td>
<td>0.93</td>
</tr>
<tr>
<td>SE Atlantic (Namibia)</td>
<td>211</td>
<td>0.55</td>
</tr>
<tr>
<td>Chatham Rise and North Island</td>
<td>3548</td>
<td>0.37</td>
</tr>
<tr>
<td>South Island, Campbell Plateau</td>
<td>195</td>
<td>0.12</td>
</tr>
<tr>
<td>Total SW Pacific</td>
<td>3743</td>
<td>0.36</td>
</tr>
</tbody>
</table>

central and southern areas of the eastern Atlantic, off the coasts of Mauritania (CE Atlantic) and Namibia (SE Atlantic), much higher numbers of juveniles were caught, representing 38–41% of the samples (all caught with trawl nets). In the CE Atlantic, immature females and males (including juveniles) made up over 90% of the specimens caught. Further south, in the SE Atlantic region, immature specimens also accounted for a large percentage of the catches (~50%). Here, pregnant and post-natal females were entirely absent. In the SW Pacific around New Zealand, mature males made up nearly 90% of males caught from the Campbell Plateau, and 63% further north on the Chatham Rise and off the North Island., immature females (including juveniles) were more common, making up over 78% of females examined. Pregnant and post-natal females were common around North Island but were absent from the Campbell Plateau. Juveniles were caught by trawl nets in both areas for which data were available, and were far more common on the Chatham Rise and North Island shelf (23% of specimens caught) than around the Campbell Plateau further south (2.8%).

3.3.4. Environmental variables and maturity

In the NE Atlantic, depth was the leading environmental factor selected by the CCA model, explaining 12% of the total inertia (\(p_{\text{canonical relationship depth}} = 0.005; P_{\text{axis1}} = 0.002\)). Juveniles were excluded from this analysis due to low numbers. Depth was positively correlated with axis 1. The ordination of the maturity stages and the overlaid surface model for depth showed that mature males and both immature males and females tended to occur at greater depths, while pregnant, post-natal and mature females were associated with relatively shallower depths (deviance explained = 80%) (Fig. 8A).

In the SW Pacific New Zealand data, the CCA adjustment showed multicollinearity for temperature, depth and season. As a result the selected model just included salinity and temperature (10% of the total inertia explained; \(p_{\text{canonical relationship salinity}} = 0.005; p_{\text{axis1}} = 0.002\)). Temperature was highly negatively correlated with axis 1 whereas salinity was primarily correlated (negatively) with axis 2. The ordination of the maturity stages overlaid on the surface models of each selected variable showed that post-natal and pregnant females occurred in warmer and higher salinity waters (deviance explained = 99.5% and 96.1% for temperature and salinity, respectively) (Fig. 8B and c). Mature males were associated with deeper sites and juveniles with intermediate temperatures and salinity values.

The CE Atlantic and SE Atlantic datasets were not adequate for CCA because they were dominated by immature specimens. In the CE Atlantic 92% of the juveniles occurred shallower than 1000 m. Juveniles and immature specimens co-occurred in the same hauls but each instance either juveniles or immature specimens clearly dominated.

4. Discussion

Progress in understanding the population structure of the Portuguese dogfish, leavescale gulper shark and birdbeak dogfish has been impaired by the difficulty of compiling and comparing data from the many different geographical areas and jurisdictional waters where these species occur. This study combined available biological information from research surveys and sampling of commercial catch to understand the population dynamics of these species within each region. However, the likely effects of different fishing gears limited some analyses among areas and within regions to qualitative or semi-quantitative descriptions. Previously published finer-scale spatial resolution analysis identified that size frequencies and selectivity ogives for Portuguese dogfish and birdbeak dogfish from Ireland differed between trawls and longlines (Clarke et al., 2005). In this study, trawls and longlines adequately sampled all maturity stages and sizes, except for juveniles, which were primarily caught with trawls. It was hoped that the use of presence/absence of maturity stages in each haul minimized this gear effect.

4.1. Species distribution

The combined data for the Portuguese dogfish, leavescale gulper shark and birdbeak dogfish indicate that all three species are widely distributed at a global scale. Regional differences in bathymetric distributions were observed; the leavescale gulper shark specimens were mainly caught between 600 and 1500 m in the NE Atlantic, with occasional records in down to 3300 m. The depth range from the New Zealand region (SW Pacific) extended into shallower water (361 m) to at least 1250 m (with 1300 m the maximum depth sampled in this region). Its average range clearly overlaps that of the birdbeak dogfish, but is shallower than that of the Portuguese dogfish, which was regularly sampled as deep as 2000 m, with occasional records down to 2800 m. Spatial distribution patterns also differed among species, as discussed below.
4.2. Sex ratio and population segregation

Variations in sex ratio must be considered when assessing species population dynamics, particularly in those areas where fishing pressure is high. In all three species, sex ratio varied with geographical area and is likely to vary with depth. This variability might be associated with sex or maturity stage segregation and requires a more detailed data.
Fig. 8. Constrained correspondence analysis of birdbeak dogfish distribution by maturity stage. Ordination of the maturity stages (black circles) and hauls (grey circles) overlaid with the surface model fitted for (a) depth in the NE Atlantic (n = 2672; 310 hauls) for (b) depth (in metres) and (c) salinity (in PSU) in the SW Pacific (New Zealand, n = 7508; 445 hauls). In the NE Atlantic analysis axis 1 accounted for 100% of the variance of the fitted values whereas in the SW Pacific axis 1 and 2 accounted for 61% and 39% of the variance of the fitted values, respectively.

The three species share some similarity in patterns of distribution by sex and maturity stage. For example, pregnant females tended to be spatially segregated from the rest of the population, as well as mature and post-natal females of leafscale gulper shark and birdbeak dogfish. The distribution of the different reproductive stages has often been related to depth (e.g. Yano and Tanaka, 1988; Girard and Du Buit, 1999; Clarke et al., 2002), and depth was shown to be an important factor in the distribution of all three species in this analysis. Temperature and salinity were also important. Results suggest that habitat requirements change through the different life phases of these sharks. Season was not found to significantly affect the occurrence of maturity stages, which likely reflects the longer-than-annual reproductive cycle known to occur in squaliform sharks (Kyne and Simpfendorfer, 2010).

Despite relatively extensive sampling of research and commercial catches in the NE Atlantic, neonates and small immature specimens (juveniles) were scarce for all three species, as previously reported in a number of individual studies (Girard and Du Buit, 1999; Clarke et al., 2002; Bañón et al., 2006; Figueiredo et al., 2008; Severino et al., 2009). In contrast, high numbers of juveniles
were caught in other areas such as CE Atlantic, SE Atlantic, and SW Pacific. The data collected in these regions are not adequate to confidently infer the habitat preferences of neonates and smaller immature specimens in the NE Atlantic. However, the absence of these small fish in the NE Atlantic may be a consequence of their concentration in nurseries outside the sampling areas, movement to/occurrence in pelagic (Compagno et al., 1991) or deeper waters (Jakobsdóttir, 2001; Bañón et al., 2006) and/or by gear selectivity (Irvine et al., 2012).

The concentration of juvenile sharks in nurseries, defined by Heupel et al. (2007) as aggregations in spatially separated locations repeatedly used across years, is a relatively common phenomenon in elasmobranchs. Such areas are suggested to provide suitable habitats for somatic growth due to high prey abundance and low mortality rates, although this assumption might not always hold true (Heupel et al., 2007). In Japan, juveniles of the closely related Owston's dogfish (Centroscymnus owstonii, Somniosidae) were found outside Suruga Bay, in around 300–800 m water depth, shallower than the adult population (Yano and Tanaka, 1988). Spiny dogfish (Squalus acanthias, Squalidae) neonates, poorly documented off the US east coast, were recently found in a particular area, in shallower and colder waters than the adults, and also associated with a different type of substrate (Sulikowski et al., 2013). The existence of nursery areas seems a plausible explanation for the high numbers of neonates and smaller immature fish observed in particular locations comparative to other areas of the overall distribution range for the species in this study.

Another possible explanation for these early life stages being poorly documented in the NE Atlantic region is gear selectivity. Trawl nets using comparatively smaller mesh codends were used in CE Atlantic, SE Atlantic, and SW Pacific, and could have resulted in a higher retention of juveniles, as has been previously reported for the birdbeak dogfish in the SW Pacific (Irvine et al., 2012). However, it is unlikely that differences in size composition could only be ascribed to gear selectivity since small-sized species, such as the lantern sharks (Etmopterus spinax and Etmopterus pulsillus, Etmopteridae; maximum TL = 60 cm and 50 cm, respectively, Compagno et al., 2005) are frequently caught by the longline fisheries (e.g. Armstrong, 2010), and in research trawl surveys. It should be noted that data from the SW Pacific (New Zealand) for the leafscale gulper shark and for the birdbeak dogfish indicated that juvenile specimens co-occurred with other maturity stages in some areas, e.g., the northern slopes of the Chatham Rise and on Puysegur Bank south of New Zealand. In the CE Atlantic, where a significant concentration of juveniles was also observed, an experimental longline haul fished approximately 15 m off the sea floor and captured only large specimens which were seldom recorded in the trawl samples (P. Pascual, personal communication). These observations suggest that juveniles and adults of the three species might co-occur in the same area or potential nurseries, but have different habitat and/or prey choices, with juveniles being more benthic than adults. In fact, ontogenetic differences in the diet are usually reported for elasmobranchs with modifications from a benthic to a pelagic feeding strategy in some species (Farias et al., 2006; Hallett and Daly, 2011).

Given the results presented here, it is likely that a combination of factors could be hampering the detection of juveniles in the NE Atlantic. Further investigations in the NE Atlantic should include experiments to test habitat hypotheses, such as sampling greater depths, “untrawlable” hard substrates and the use of vertical longlines to assess the relative position of the different life stages in the water column.

The probability of occurrence of larger immature specimens (>55 or 60 cm) of all three species increased with depth (particularly for females), with the exception of the birdbeak dogfish in SW Pacific. In addition, immature specimens of both sexes of Portuguese dogfish and birdbeak dogfish may aggregate according to age or size, as suggested by the CCA models.

Mature males of leafscale gulper shark and birdbeak dogfish were more broadly distributed than mature females, supporting the possibility of sex-biased dispersal in these species. A genetic population study has shown that male leafscale gulper sharks have higher levels of male-mediated gene flow in comparison to females, which were found to have more limited dispersal (Verissimo et al., 2012). Sex-biased dispersal has been documented for other shark species (Pardini et al., 2001; Portnoy et al., 2010; Daly-Engel et al., 2012) and has been related to the reproductive philopatry of females that, in some elasmobranchs species, return to specific areas to give birth (Huetter et al., 2005).

The aggregation of pregnant females of all the three species preferentially occurred at relatively warmer and/or shallower depths. These conditions are favourable to embryonic development as physiological processes are accelerated (Economakis and Lobel, 1998; Robbins, 2007). Another possible trigger for segregation might be related to specific nutritional requirements of pregnant females that could necessitate their migration to particular grounds. In the case of the birdbeak dogfish, matrotrophy appears to occur (Paiva et al., 2012), whilst the Portuguese dogfish and leafscale gulper shark are assumed to be lecithotrophic (Moura et al., 2011b; Figueiredo et al., 2008), although the existence of supplemental maternal nourishment (e.g. histotrophy) has never been studied in the latter.

4.3. Portuguese dogfish

The Portuguese dogfish was the only species where mature and pregnant females were regularly caught in multiple regions, with mature fish often comprising over 50% of all females sampled (e.g. NE Atlantic and Australia, SW Pacific). The occurrence of all adult reproductive stages within the same geographical area and, in many cases in similar proportions, suggests that this species is able to complete its life cycle within these areas. However, this is not incompatible with a widespread mixing across the continuous distribution of the species. Indeed, an apparent lack of genetic structure was found for the NE and CE Atlantic, and a large scale migration of the NE specimens to the CE Atlantic waters to give birth has been proposed (Verissimo et al., 2011). However, the capture of even low numbers of small specimens, post-natal and pregnant females with near-term embryos in a number of areas of the NE Atlantic (Girard and Du Buit, 1999; Clarke et al., 2001; Bañón et al., 2006; Figueiredo et al., 2008), suggests that the existence of undiscovered concentration areas of juveniles in the NE Atlantic may also be hypothesized.

The only other published studies for this species outside the NE Atlantic are from Suruga Bay (Japan), and are in agreement with those presented here: all maturity stages except juveniles were commonly found, and sexual segregation was evident, with pregnant and mature females commonly found shallower than the remaining specimens (Yano and Tanaka, 1984, 1988).

4.4. Leafscale gulper shark

In most regions, immature females of leafscale gulper shark predominated over mature females, and pregnant individuals were rare. The distribution pattern formerly assumed for this species in the NE Atlantic is based on the proposed existence of a large scale migration, where females would give birth off the Madeira Archipelago, from which there are reports of pregnant females (Severino et al., 2009). In the combined dataset presented here, pregnant females were also found off Iceland, indicating another potentially important reproductive area in the northern part of the NE Atlantic. Occasional captures of pregnant females off Portugal.
and off Galicia have also been reported (Ba˜non et al., 2006). The existence of migratory patterns for this species is proposed for the SW Pacific too, where all the maturity stages were present (although with pregnant females being rare), but were associated with specific geographical areas at a certain time in their life cycle. Our data also suggest the existence of at least two nursery grounds along western Africa, in Mauritania and Namibia, but no genetic differentiation between Eastern Atlantic and South Africa has been detected yet (Verissimo et al., 2012).

4.5. Birdbeak dogfish

All life stages of the birdbeak dogfish were recorded in most of the regions analysed, although with some differences in the proportions of maturity stages (or lack of some) among geographical areas. Based upon the minimal size overlap between specimens caught off Ireland and those caught off Portugal, Clarke et al. (2002) suggested that the birdbeak dogfish undergoes a migration along continental slopes between Irish and Portuguese waters, similar to that has been postulated for New Zealand populations, where extensive migrations associated with reproduction are thought to occur (Clark and King, 1989). Our data support breeding migrations. However, in the NE Atlantic, all maturity stages, including pregnant and post-natal females, were present in almost all areas, and at least 50% of males were mature. Juveniles were caught in small numbers on Hatton Bank and off the SW of Portugal, suggesting the existence of more than one nursery area, likely at shallower depths. In the CE and SE Atlantic, despite the dominance of immature specimens, mature fish were also relatively common (more evident in the SE Atlantic), but pregnant and post-natal females were scarce or lacking. In New Zealand waters, juvenile fish were abundant, particularly on the Chatham Rise and off the eastern coast of the North Island, but the proportions of mature fish varied by geographical area. Pregnant females were encountered in low numbers, and only on Chatham Rise and around the North Island. The results suggest the existence of population partitioning according to life stage, particularly for pregnant stages, despite their rarity. Similarly, the occurrence of pregnant females was rare on the Australian continental slope (Irvine et al., 2012). Here, juveniles (30–60 cm) were the major component of the catch in shallower depth strata (700–900 m) reflecting possible regional differences compared to the New Zealand population, where juveniles were found at intermediate depths, in relation to other maturity stages.

4.6. Management implications

The successful management of deepwater sharks relies on an understanding of the spatial and temporal distribution of the demographic components of their populations (Wearmouth and Sims, 2008). This knowledge is required for the development of management measures that ensure the stability of their demographic structure (Simpfendorfer and Heupel, 2004), especially in cases where exploitation impacts differ at regional scales. The identification of the life stages most critical and vulnerable to exploitation is also essential, and if adequate information is made available, it will be possible to establish specific regulations, probably spatially/depth structured, to preserve those stages as well as their essential habitats (Simpfendorfer and Heupel, 2004). The present study contributes to these management goals by compiling many different data sources to make progress in elucidating the likely population structure, habitats and migration patterns of deepwater sharks. The resulting hypotheses need to be tested in future studies, particularly to elucidate migrations, and further investigate spatial distribution and preferential habitats for these three species.

Despite some similarities in the distribution patterns of the three species studied, there are differences in habitat usage by sex and by life history stage. Given their scarcity in our data, it is likely that neonates and small immature sharks, and pregnant female leafscale gulper shark and birdbeak dogfish (in some regions), are not directly impacted by current fishing pressure. However, it is important to note that the protection of nursery areas alone may not be sufficient to conserve a shark population (Kinney and Simpfendorfer, 2009). The available data also suggests that these fisheries have impacted only portions of the whole population and distribution area of these three species: the spatial extent of commercial fishing is limited and is therefore unlikely to overlap with their full distribution.

This study was innovative in collating worldwide information for these wide-ranging species. The continuation of such collaborative data pooling is essential to update life-history data, spatial and temporal information. It is also necessary to implement standardized, long-term and broader-scale monitoring programs that will enable the determination of the stock status (Ward-Paige et al., 2012). There is currently no standardized sampling at a global scale, but coordinated efforts are required for adequate stock assessments as well as monitoring the impacts of fishing on these species. Future studies should also focus on other ecological factors influencing the demographic-specific distributions of each population, such as oceanographic conditions, substrate characterization and prey interactions. Such factors are important for understanding the response of populations to either anthropogenic-induced changes or environmental variations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2014.03.019.

References


