

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

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Abstract:

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 use of habitats 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.

Keywords: Commercial fishery data ; Deep-sea ; Life stage ; Population structure ; Survey data

1 **1. Introduction**

2

3 There is worldwide concern for the conservation of deep-water sharks due to low
4 biological productivity and population declines (Kyne and Simpfendorfer, 2010). Life history
5 characteristics typically include a slow growth rate, late age-at-maturity and low fecundity,
6 indicating long generation times (Garcia et al., 2008; Graham and Daley, 2011). Consequently,
7 populations that have declined will require decades or even centuries to recover (Pratt and
8 Casey, 1990; Simpfendorfer and Kyne, 2009).

9 Effective management of these species requires precautionary approaches founded on
10 an understanding of species-specific life histories (Simpfendorfer and Kyne, 2009). Life-history
11 traits are quite diverse among deep-water sharks, but some strategies, including segregation
12 patterns, are similar to other elasmobranch species (Wearmouth and Sims, 2008). Although
13 less studied than shallow-water species, segregation within a population by sex, size and/or
14 reproductive stage has been reported for a number of deep-water shark species (Muñoz-
15 Chapuli, 1984; Yano and Tanaka, 1988; Wetherbee, 1996; Girard and Du Buit, 1999; Clarke et
16 al., 2001; Jakobsdóttir, 2001; McLaughlin and Morrissey, 2005). Segregation may be
17 advantageous in a population to maximize reproductive success, minimize predation risk or
18 potential aggressive interactions, and for size or sex-specific foraging requirements (Sims,
19 2005; Wearmouth and Sims, 2008). Segregation can occur at different scales, and is often
20 linked to particular environmental or ecological features. The set of factors potentially
21 influencing segregation may be complex. Therefore, demographic data from the full range of a
22 population is fundamental to assessing status and particularly for predicting responses to
23 exploitation.

24 Attempts to develop adequate quantitative stock assessments for deep-sea sharks
25 have fallen short of expectations due to inadequate data, particularly in the Atlantic and
26 Southwestern Pacific. Information available on deep-water sharks is derived either from

1 sampling of commercial catches or from scientific surveys. Fishery data are often restricted to
2 those deep-sea sharks that are of greatest commercial importance, and have been limited
3 historically by a lack of taxonomic and geographic precision. In contrast, fishery-independent
4 surveys are often temporally irregular, and none have had sufficient geographic coverage to
5 ensure that all demographic components of the populations are sampled. These deficiencies
6 are exacerbated by the global distribution of some species that include waters under many
7 jurisdictions, and also by their specific reproductive strategies where mating and pupping
8 might be decoupled in space and time, due to sperm storage (Moura et al., 2011a). Major
9 scientific investment is required to gain a full understanding of the spatial and temporal
10 population dynamics of deep-water sharks, and enable estimates of sustainable exploitation
11 levels to be derived.

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

23 This study draws together regional knowledge of size distribution and reproductive
24 stages of three species of squaliform sharks. For each species, we analysed and compared the
25 spatial patterns within and among different regions of the Atlantic, Indian and Pacific Oceans,
26 using commercial and survey data. Spatial variation of the defined maturity groups was studied

1 considering the influence of depth, temperature, salinity, area and season. The key findings are
2 presented in the context of regional management arrangements required to ensure
3 sustainability of populations.

4

5 **2. Material and methods**

6

7 *2.1. Data sources*

8

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

15

16 *2.2. Data collation and standardization*

17

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

23

24 A number of data standardization steps were applied to produce a single database. As
25 much of the data had been collected opportunistically, the geographic precision of the capture
26 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

1 by 'geographic area'. The second step was to ensure that the biological attributes recorded
2 were consistent among regions. Biological data provided for each specimen included the
3 species total length (TL), sex and maturity stage. Maturity stage data were standardized by
4 classifying each individual according to a maturity stage group. These groups are based on
5 Stehmann (2002) modified after by Figueiredo et al. (2008) and Irvine et al. (2012) (equivalent
6 stages indicated in parentheses). For males, two groups were considered: immature (immature
7 and maturing) and mature (mature and active). For females four groups were considered:
8 immature (immature and maturing), mature (mature – non-pregnant, pre-ovulatory), pregnant
9 (developing, differentiating and expecting) and post-natal (post-natal). Where regenerating
10 females (maturing, not for the first time) had been observed, they were combined with post-
11 natal stages. In the dataset from the SW Indian Ocean the information was not sufficient to
12 discriminate between post-natal and mature females.

13 Published studies show that neonates of these three species are scarce or entirely
14 absent from the NE Atlantic. This study examined a size-based subset of the data for immature
15 specimens for the same pattern. The term "juvenile" was used for small immature individuals
16 between length-at-birth and a pre-determined upper limit. These sizes were based on
17 published values from the NE Atlantic (Girard and Du Buit, 1999; Clarke et al., 2002; Figueiredo
18 et al., 2008) and were assumed to be applicable to other regions. Size-at-birth was taken as 25-
19 31 cm for the Portuguese dogfish (Moura et al., 2011b), 38-44 cm for the leafscale gulper shark
20 (Bañon et al., 2006; Figueiredo et al., 2008) and 28-33 cm for the birdbeak dogfish (Irvine et al.,
21 2012). The upper limit sizes applied were < 60 cm for the Portuguese dogfish and leafscale
22 gulper shark and <55 cm for the birdbeak dogfish. Hereafter term "immature" will refer only to
23 the fraction of immature stage specimens above the upper size limit for juveniles. Juvenile and
24 immature specimens were only combined when estimating the proportion of maturity stages
25 by geographical area.

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

4 *2.3. Statistical analysis*

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

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

13 *2.3.1. Sex ratio*

14 The influence of depth on sex ratio was examined for each species-area combination
15 by calculating the median and interquartile ranges of the proportion of females by depth strata
16 (100 m). This analysis was restricted to geographical areas with 25 or more hauls of >1
17 individual. The depth intervals varied between species: 800 -1700 m for the Portuguese
18 dogfish, 500 -1700 m for the leafscale gulper shark and 500-1400 m deep for the birdbeak
19 dogfish. These intervals include the depths where each species were sampled more frequently.

21 *2.3.2. Mapping and occurrence of maturity stages*

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

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

6 7 *2.3.3. Environmental variables and maturity*

8 Temperature and salinity values were estimated for each haul, based on geographical
9 position and depth, using the World Ocean Atlas 2009 database from U.S. National
10 Oceanographic Data Center (Antonov et al., 2010; Locarnini et al., 2010) and the 3D estimation
11 method implemented in Ocean Data View Software (Schlitzer, 2011). 3D point estimation is a
12 fast weighted averaging procedure and combines the environmental information with user
13 specified longitude, latitude and depth, assuming specific averaging length scales (Schlitzer,
14 2011). Scales were considered as 2.5% of the axis ranges for longitude and latitude and 100 m
15 for depth. Yearly environmental values were used in calculations because a preview of the
16 monthly data found only minor variation. Further, the monthly environmental data did not
17 cover the full depth range of the catch data.

18 Constrained correspondence analysis (CCA) was used to explore how the maturity
19 stages of each species were influenced as a biological response to four environmental
20 variables: temperature, salinity, depth and season. This analysis used the Vegan package for R
21 software (Oksanen, 2011). This method combines a multivariate ordination presence/absence
22 of maturity stage with a constrained regression maximizing the correlation between the
23 maturity stages ordination axes and the selected environmental variables. It was assumed that
24 the ecological range of each maturity stage analysed has been sampled and further assumed
25 that each maturity stage presents a unimodal response to each independent variable (ter
26 Braak, 1986; Borcard et al., 2011). It is pertinent to note that whilst the inertia (percentage of

1 variation explained) is typically low (< 10%) when CCA is applied to binary variables, the results
2 can still be ecologically meaningful (ter Braak and Verdonschot, 1995; Oksanen, 2011). Two
3 matrices were constructed for this analysis: one corresponding to the occurrence of maturity
4 stages (presence/absence, dependent variable), and the other corresponding to the
5 environmental variables mentioned above (independent variables). CCA were fitted
6 conditioned to the geographical area, i.e. area was partially out from the analysis before
7 constraints, and only to regions with representative data (> 100 georeferenced hauls with
8 maturity information). The final selection of independent variables for inclusion in the CCA
9 model followed a stepwise process, based on the Aikake information criterion (AIC). The
10 variance inflation factor (VIF) was used to avoid multicollinearity, i.e. inclusion of
11 environmental variables strongly correlated with each other (ter Braak, 1986; Oksanen, 2011).
12 VIFs >10 should be examined and avoided (Borcard et al., 2011). In cases where VIF>10, all the
13 possible combination of variables were considered in the CCAs. Variable selection considered
14 the Spearman correlation coefficient estimated between variables and the most rational
15 results for VIF, AIC and proportion of inertia explained. Results of the analysis were plotted and
16 scaled to maturity stages. Monte Carlo permutation tests were used to assess the significance
17 of the terms and axis of the model. In both cases a significance level of 5% was adopted.

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

26

1 **3. Results**

2

3 *3.1. Portuguese dogfish*

4

5 *3.1.1. Sampling details*

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

15

16 *3.1.2. Sex ratio*

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

22

23 *3.1.3 Mapping and occurrence of maturity stages*

24 Population structure varied between regions and geographical areas. In the NE Atlantic
25 and in the SW Pacific (Australia) all maturity stages were sampled (Table 1, Fig. 3), with length
26 ranges being similar among fishing gears in the first region (Fig. A2). For females, the

1 proportions by different maturity stages were similar in some NE Atlantic geographical areas
2 (excluding Rockall and Hatton Banks, North Azores and Canarias) and in Tasmania. In these
3 areas, mature females accounted for around 17–25% of the samples, with pregnant females
4 making up 8–17%. In contrast, the proportion of mature and immature males varied widely
5 within the NE Atlantic and SW Pacific regions. The pattern was different for other regions. In
6 the CE and SE Atlantic regions, mature, pregnant and post-natal females and mature males
7 were absent or seldom observed. In the NW Atlantic region, juveniles prevailed in the samples
8 and only one mature female was recorded. Some areas in the SW Indian region provided
9 contrast: off the Mozambique plateau, immature and mature females were most common,
10 with some pregnant females also recorded; off the Madagascar plateau, mature males were
11 more common and pregnant females made up nearly 30% of the female sample.

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

20

21 *3.1.4. Environmental variables and maturity*

22 For the NE Atlantic data (excluding juveniles, that were recorded in low number),
23 depth was the only factor selected in the CCA model. This model explained 10% of the total
24 inertia ($p_{\text{canonical relationship}} = 0.005$; $p_{\text{axis}} = 0.002$). Depth was negatively correlated with axis 1. The
25 ordination and surface model of the environmental variable selected showed that pregnant

1 females had the shallowest distribution, mature males were deeper and all other stages
2 deeper still, and at closely located sites (deviance explained = 58%) (Fig. 4).

3 All the other datasets were inadequate to run the CCA, either due to the low
4 representation of maturity groups (CE Atlantic and SE Atlantic datasets were composed mainly
5 of juveniles and immature specimens) or to insufficient data (as the case of NW Atlantic and
6 SW Indian Ocean). In the CE Atlantic, 68% of the juveniles caught occurred between 1300 and
7 1500 m deep. Juveniles and immature specimens were caught in the same hauls, although
8 each haul was typically dominated by one group or the other. Those hauls clearly dominated
9 by juveniles were mostly located at centre-south slope of Mauritania. In the NW Atlantic,
10 juveniles were recorded from 670 to 2624 m but 88% of these catches were shallower than
11 1000 m. In the SW Indian Ocean, maturity stages were not correlated with depth.

12

13 *3.2. Leafscale gulper shark*

14

15 *3.2.1. Sampling details*

16 Data for the leafscale gulper shark were obtained for all regions of the Eastern Atlantic
17 and for the SW Pacific. A total of 5480 specimens were sampled, with up to 3483 meeting the
18 criteria for inclusion in the statistical analyses. Depths and TL ranges by sex and maturity stage
19 are reported on Figure 2 and Table A3. Females attained larger sizes than males for most
20 geographical areas.

21

22 *3.2.2. Sex ratio*

23 In the NE Atlantic, sex ratios varied between areas. Males predominated over females
24 on the Rockall and Hatton Banks, off Ireland, Portugal, on the Mid Atlantic Ridge (Northern
25 Azores) and in Madeira (Table 2). Females were more frequently caught in the remaining
26 areas. In the northern areas of the NE Atlantic (Scotland and Ireland) the proportion of females

1 increased with increasing depth although there was also high variability within each depth
2 strata (Fig. A3). In the CE Atlantic, males and females were caught in equal numbers, but
3 samples sizes were too low for more detailed analysis. In the SW Pacific (New Zealand),
4 females were significantly more abundant than males in the two geographical areas and sex
5 ratios were not influenced by depth.

6

7 *3.2.3. Mapping and occurrence of maturity stages*

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

1 females sampled, respectively). Juveniles occurred mainly on the northern slopes of the
2 Chatham Rise and also to the southwest of the South Island of New Zealand (Puysegur Bank).

3

4 *3.2.4. Environmental variables and maturity*

5 In the NE Atlantic, juveniles were excluded from the CCAs due to small sample sizes. In
6 this region, depth and temperature were the environmental factors selected in the CCA model,
7 explaining 16% of the total inertia ($p_{\text{canonical relationship depth}}=0.005$; $p_{\text{canonical relationship temperature}}=0.005$;
8 $p_{\text{axis1}}=0.002$; $p_{\text{axis2}}=0.002$). These two environmental variables were highly correlated with axis
9 1, with depth being positively related and temperature being negatively related with this axis.
10 Axis 2 was also negatively correlated with temperature. The surface model of the selected
11 environmental variables indicated that the distribution of males was not related to depth or
12 temperature, but post-natal and mature females tended to occur in relatively shallower sites
13 (deviance explained = 76% and 53% for depth and temperature, respectively) (Fig. 6a and b).
14 Pregnant females were distributed preferentially at warmer stations compared to the
15 remaining maturity stages, particularly immature females, which were usually found at greater
16 depths and lower temperatures.

17 In the SW Pacific data (excluding pregnant and post-natal females due to their low
18 numbers in the samples), the best CCA model included only depth and salinity (6% of the total
19 inertia explained; $p_{\text{canonical relationship depth}}=0.002$; $p_{\text{canonical relationship salinity}}=0.075$; $p_{\text{axis1}}=0.002$; $p_{\text{axis2}}=$
20 0.950). Depth was positively correlated with axis 1 and salinity was positively correlated to axis
21 2, the latter explaining a small fraction of variation. The ordination and the surface models of
22 the selected environmental variables showed that immature males, females and juveniles all
23 co-occurred at relatively deeper and less saline waters (deviance explained= 96.5% and 100%
24 for depth and salinity, respectively) (Fig. 6c and d). Mature males were associated with
25 shallower, more saline waters. Nine of the twelve females were found in waters shallower
26 than 900m. The two post-natal females sampled in the South Island were collected from

1 depths shallower than 650m, whereas those sampled in the Chatham Rise and North Island
2 were both collected in the 900m stratum.

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

9

10 3.3. *Birdbeak dogfish*

11

12 3.3.1. *Sampling details*

13 Data were obtained from the Atlantic and the SW Pacific. A total of 14 468 specimens
14 was collected, of which 12 189 met the criteria for inclusion in the statistical analysis. Depth
15 and TL ranges by sex are reported in Figure 2 and Table A4. In all the areas sampled, females
16 attained larger sizes than males.

17

18 3.3.2. *Sex ratio*

19 Sex ratios varied between regions. For the NE Atlantic region, males predominated
20 over females at most sampling locations, except in the Bay of Biscay, Portugal and Canarias
21 Archipelago (Table 3). In this region sex ratios were variable among depth strata, but with no
22 discernable trend (Fig. A5). In the CE Atlantic, females predominated over males but in the SE
23 Atlantic the contrary was observed. In these two regions the proportion of females decreased
24 with depth. In the SW Pacific region (New Zealand), the numbers of males and females were
25 similar off the South Island but on the Chatham Rise and around the North Island, females

1 were more common than males. In this area, the proportion of females seemed to decrease
2 with depth, despite the high variability observed (wide interquartile ranges).

3 4 *3.3.3. Mapping and occurrence of maturity stages*

5 The proportion of maturity stages observed varied considerably among geographical
6 areas and regions (Table 3, Fig. 7). In the NE Atlantic, specimens of all maturity stages were
7 caught and size ranges were similar among fishing gears (Fig. A6). In this region, mature males
8 were widely distributed, but their proportion was variable among geographical areas.

9 Immature females outnumbered mature females in almost all regions, except the Canarias
10 Archipelago. The number of pregnant females was low or totally absent in most geographical
11 areas. Post-natal females were mainly recorded in northern areas, often spatially separated
12 from other stages. In this region, juveniles were caught both with trawls and longlines, and
13 were recorded on Hatton Bank (n=10), off Ireland (n= 2) and on the SW Portugal mainland (n=
14 5), but representing less than 1% of the total sample from these areas. In contrast, the central
15 and southern areas of the eastern Atlantic, off the coasts of Mauritania (CE Atlantic) and
16 Namibia (SE Atlantic), much higher numbers of juveniles were caught, representing 38 - 41% of
17 the samples (all caught with trawl nets). In the CE Atlantic, immature females and males
18 (including juveniles) made up over 90% of the specimens caught. Further south, in the SE
19 Atlantic region, immature specimens also accounted for a large percentage of the catches
20 (~50%). Here, pregnant and post-natal females were entirely absent. In the SW Pacific around
21 New Zealand, mature males made up nearly 90% of males caught from the Campbell Plateau,
22 and 63% further north on the Chatham Rise and off the North Island., immature females
23 (including juveniles) were more common, making up over 78% of females examined. Pregnant
24 and post-natal females were common around North Island but were absent from the Campbell
25 Plateau. Juveniles were caught by trawl nets in both areas for which data were available, and

1 were far more common on the Chatham Rise and North Island shelf (23% of specimens caught)
2 than around the Campbell Plateau further south (2.8%).

3

4 *3.3.4. Environmental variables and maturity*

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

12 In the SW Pacific New Zealand data, the CCA adjustment showed multicollinearity for
13 temperature, depth and season. As a result the selected model just included salinity and
14 temperature (10% of the total inertia explained; $p_{\text{canonical relationship temperature}}= 0.005$; $p_{\text{canonical}}$
15 $\text{relationship salinity}= 0.005$; $p_{\text{axis1}}= 0.002$; $p_{\text{axis2}}= 0.002$). Temperature was highly negatively correlated
16 with axis 1 whereas salinity was primarily correlated (negatively) with axis 2. The ordination of
17 the maturity stages overlaid on the surface models of each selected variable showed that post-
18 natal and pregnant females occurred in warmer and higher salinity waters (deviance
19 explained= 99.5% and 96.1% for temperature and salinity, respectively) (Fig. 8b,c). Mature
20 males were associated with deeper sites and juveniles with intermediate temperatures and
21 salinity values.

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

26

1 **4. Discussion**

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

15

16 *4.1. Species distribution*

17

18 The combined data for the Portuguese dogfish, leafscale gulper shark and birdbeak
19 dogfish indicate that all three species are widely distributed at a global scale. Regional
20 differences in bathymetric distributions were observed; the leafscale gulper shark specimens
21 were mainly caught between 600 and 1500 m in the NE Atlantic, with occasional records in
22 down to 3300 m. The depth range from the New Zealand region (SW Pacific) extended into
23 shallower water (361 m) to at least 1250 m (with 1300 m the maximum depth sampled in this
24 region). Its average range clearly overlaps that of the birdbeak dogfish, but is shallower than
25 that of the Portuguese dogfish, which was regularly sampled as deep as 2000 m, with

1 occasional records down to 2800 m. Spatial distribution patterns also differed among species,
2 as discussed below.

3

4 *4.2. Sex ratio and population segregation*

5

6 Variations in sex ratio must be considered when assessing species population
7 dynamics, particularly in those areas where fishing pressure is high. In all three species, sex
8 ratio varied with, geographical area and is likely to vary with depth. This variability might be
9 associated with sex or maturity stage segregation and requires a more detailed data.

10 The three species share some similarity in patterns of distribution by sex and maturity
11 stage. For example, pregnant females tended to be spatially segregated from the rest of the
12 population, as well as mature and post-natal females of leafscale gulper shark and birdbeak
13 dogfish. The distribution of the different reproductive stages has often been related to depth
14 (e.g. Yano and Tanaka, 1988; Girard and Du Buit, 1999; Clarke et al., 2002), and depth was
15 shown to be an important factor in the distribution of all three species in this analysis.

16 Temperature and salinity were also important. Results suggest that habitat requirements
17 change through the different life phases of these sharks. Season was not found to significantly
18 affect the occurrence of maturity stages, which likely reflects the longer-than-annual
19 reproductive cycle known to occur in squaliform sharks (Kyne and Simpfendorfer, 2010).

20 Despite relatively extensive sampling of research and commercial catches in the NE
21 Atlantic, neonates and small immature specimens (juveniles) were scarce for all three species,
22 as previously reported in a number of individual studies (Girard and Du Buit, 1999; Clarke et
23 al., 2002; Bañon et al., 2006; Figueiredo et al., 2008; Severino et al., 2009). In contrast, high
24 numbers of juveniles were caught in other areas such as CE Atlantic, SE Atlantic, and SW
25 Pacific. The data collected in these regions are not adequate to confidently infer the habitat
26 preferences of neonates and smaller immature specimens in the NE Atlantic. However, the

1 absence of these small fish in the NE Atlantic may be a consequence of their concentration in
2 nurseries outside the sampling areas, movement to/ occurrence in pelagic (Compagno et al.,
3 1991) or deeper waters (Jakobsdóttir, 2001; Bañon et al., 2006) and/or by gear selectivity
4 (Irvine et al., 2012).

5 The concentration of juvenile sharks in nurseries, defined by Heupel et al. (2007) as
6 aggregations in spatially separated locations repeatedly used across years, is a relatively
7 common phenomenon in elasmobranchs. Such areas are suggested to provide suitable
8 habitats for somatic growth due to high prey abundance and low mortality rates, although this
9 assumption might not always hold true (Heupel et al., 2007). In Japan, juveniles of the closely
10 related Owston's dogfish (*Centroscymnus owstonii*, Somniosidae) were found outside Suruga
11 Bay, in around 300–800 m water depth, shallower than the adult population (Yano and Tanaka
12 1988). Spiny dogfish (*Squalus acanthias*, Squalidae) neonates, poorly documented off the US
13 east coast, were recently found in a particular area, in shallower and colder waters than the
14 adults, and also associated with a different type of substrate (Sulikowski et al., 2013). The
15 existence of nursery areas seems a plausible explanation for the high numbers of neonates and
16 smaller immature fish observed in particular locations comparative to other areas of the
17 overall distribution range for the species in this study.

18 Another possible explanation for these early life stages being poorly documented in
19 the NE Atlantic region is gear selectivity. Trawl nets using comparatively smaller mesh codends
20 were used in CE Atlantic, SE Atlantic, and SW Pacific, and could have resulted in a higher
21 retention of juveniles, as has been previously reported for the birdbeak dogfish in the SW
22 Pacific (Irvine et al., 2012). However, it is unlikely that differences in size composition could
23 only be ascribed to gear selectivity since small-sized species, such as the lantern sharks
24 (*Etmopterus spinax* and *Etmopterus pusillus*, Etmopteridae; maximum TL = 60 cm and 50 cm,
25 respectively, Compagno et al., 2005), are frequently caught by the longline fisheries (e.g.
26 Armstrong, 2010), and in research trawl surveys. It should be noted that data from the SW

1 Pacific (New Zealand) for the leafscale gulper shark and for the birdbeak dogfish indicated that
2 juvenile specimens co-occurred with other maturity stages in some areas, e.g., the northern
3 slopes of the Chatham Rise and on Puysegur Bank south of New Zealand. In the CE Atlantic,
4 where a significant concentration of juveniles was also observed, an experimental longline
5 haul fished approximately 15 m off the sea floor and captured only large specimens which
6 were seldom recorded in the trawl samples (P. Pascual, personal communication). These
7 observations suggest that juveniles and adults of the three species might co-occur in the same
8 area or potential nurseries, but have different habitat and / or prey choices, with juveniles
9 being more benthic than adults. In fact, ontogenetic differences in the diet are usually
10 reported for elasmobranchs with modifications from a benthic to a pelagic feeding strategy in
11 some species (Farias et al., 2006; Hallett and Daley, 2011).

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

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

21 Mature males of leafscale gulper shark and birdbeak dogfish were more broadly
22 distributed than mature females, supporting the possibility of sex-biased dispersal in these
23 species. A genetic population study has shown that male leafscale gulper sharks have higher
24 levels of male-mediated gene flow in comparison to females, which were found to have more
25 limited dispersal (Verissimo et al., 2012). Sex-biased dispersal has been documented for other
26 shark species (Pardini et al., 2001; Portnoy et al., 2010; Daly-Engel et al., 2012) and has been

1 related to the reproductive philopatry of females that, in some elasmobranchs species, return
2 to specific areas to give birth (Hueter et al., 2005).

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

12

13 *4.3. Portuguese dogfish*

14

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

1 suggests that the existence of undiscovered concentration areas of juveniles in the NE Atlantic
2 may also be hypothesized.

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

8

9 *4.4. Leafscale gulper shark*

10

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

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26 *4.5. Birdbeak dogfish*

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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, Clark 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

1 The successful management of deepwater sharks relies on an understanding of the
2 spatial and temporal distribution of the demographic components of their populations
3 (Wearmouth and Sims, 2008). This knowledge is required for the development of management
4 measures that ensure the stability of their demographic structure (Simpfendorfer and Heupel,
5 2004), especially in cases where exploitation impacts differ at regional scales. The
6 identification of the life stages most critical and vulnerable to exploitation is also essential, and
7 if adequate information is made available, it will be possible to establish specific regulations,
8 probably spatially/depth structured, to preserve those stages as well as their essential habitats
9 (Simpfendorfer and Heupel, 2004). The present study contributes to these management goals
10 by compiling many different data sources to make progress in elucidating the likely population
11 structure, habitats and migration patterns of deep-water sharks. The resulting hypotheses
12 need to be tested in future studies, particularly to elucidate migrations, and further investigate
13 spatial distribution and preferential habitats for these three species.

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

23 This study was innovative in collating worldwide information for these wide-ranging
24 species. The continuation of such collaborative data pooling is essential to update life-history
25 data, spatial and temporal information. It is also necessary to implement standardized, long-
26 term and broader-scale monitoring programs that will enable the determination of the stock

1 status (Ward-Paige et al., 2012). There is currently no standardized sampling at a global scale,
2 but coordinated efforts are required for adequate stock assessments as well as monitoring the
3 impacts of fishing on these species. Future studies should also focus on other ecological factors
4 influencing the demographic-specific distributions of each population, such as oceanographic
5 conditions, substrate characterization and prey interactions. Such factors are important for
6 understanding the response of populations to either anthropogenic-induced changes or
7 environmental variations.

8

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10

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23

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9 **Supplementary material**

10 Appendix A. Supplementary material (Tables A1, A2, A3 and A4 and Figures A1, A2, A3, A4, A5
11 and A6)

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3 **Table 1**

4 Portuguese 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
5 juveniles. F: females; M: males.

Portuguese dogfish Geographical area/region	Males			Females					Sex ratio
	n	Immature	Mature	n	Immature	Mature	Pregnant	Post-natal	F:M
Iceland	45	0.87	0.13	262	0.40	0.23	0.17	0.20	5.82
Rockall & Hatton Banks	104	0.44	0.56	669	0.42	0.23	0.00	0.34	6.43
Scotland	136	0.51	0.49	272	0.52	0.19	0.08	0.21	2.00
Ireland	255	0.33	0.67	538	0.43	0.25	0.08	0.24	2.09
Bay of Biscay	39	0.10	0.90	26	0.58	0.19	0.12	0.12	0.67
Portugal	114	0.32	0.62	253	0.37	0.23	0.17	0.23	2.22
North Azores (MAR)	19	0.21	0.79	30	0.20	0.80	---	---	1.58
Canarias Archipelago	88	0.27	0.73	181	0.35	0.63	0.02	---	2.06
TOTAL NE ATLANTIC	800	0.39	0.61	2231	0.42	0.27	0.07	0.24	2.80
CE ATLANTIC (Mauritania)	616	1.00	0.00	765	0.98	0.01	0.01	---	1.24
SE ATLANTIC (Namibia)	391	0.98	0.02	553	0.99	0.01	---	---	1.41
NW ATLANTIC (U.S. East Coast)	21	1.00	---	21	0.95	0.05	---	---	1.00
Mozambique Plateau	229	0.60	0.40	207	0.34	0.57	0.09	---	0.90
Madagascar Plateau	72	0.39	0.61	34	0.32	0.38	0.29	---	0.47
TOTAL SW INDIAN	301	0.55	0.45	241	0.34	0.54	0.12	---	0.80
New South Wales	62	0.68	0.32	23	0.65	0.09	0.09	0.17	0.37
Tasmania	171	0.09	0.71	70	0.51	0.17	0.16	0.16	0.41
TOTAL SW PACIFIC	233	0.25	0.75	93	0.55	0.15	0.14	0.16	0.40

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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.

Leafscale gulper shark Geographical area/region	Males			Females					Sex ratio
	n	Immature	Mature	n	Immature	Mature	Pregnant	Post-natal	F:M
Iceland	10	0.80	0.20	36	0.22	0.28	0.14	0.36	3.60
Rockall & Hatton Banks	352	0.28	0.72	275	0.90	0.04	---	0.06	0.78
Scotland	308	0.25	0.75	405	0.82	0.10	---	0.08	1.31
Ireland	322	0.39	0.61	248	0.95	0.04	---	0.01	0.77
Portugal	133	0.25	0.75	122	0.81	0.09	0.02	0.07	0.92
North Azores (MAR)	82	---	1.00	1	1.00	---	---	---	0.01
Madeira Archipelago	145	0.06	0.94	60	0.42	0.08	0.50	---	0.41
Canarias Archipelago	31	0.48	0.52	43	0.42	0.58	---	---	1.39
TOTAL NE ATLANTIC	1383	0.27	0.73	1190	0.81	0.09	0.03	0.06	0.86
CE ATLANTIC (Mauritania)	42	0.76	0.19	44	1.00	---	---	---	1.04
Chatham Rise & North Island	134	0.87	0.13	273	0.81	0.16	0.03	0.01	2.04
South Island, Campbell Plateau	182	0.58	0.42	235	0.74	0.23	0.02	0.01	1.29
TOTAL SW PACIFIC	316	0.70	0.30	508	0.78	0.19	0.02	0.01	1.61

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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.

Birdbeak dogfish Geographical area/Region	Males			Females					Sex ratio
	n	Immature	Mature	n	Immature	Mature	Pregnant	Post-natal	F:M
Iceland	151	0.19	0.81	100	0.55	0.24	0.04	0.17	0.66
Scotland	218	0.51	0.49	112	0.79	0.06	0.01	0.13	0.51
Ireland	901	0.48	0.52	602	0.83	0.10	0.02	0.05	0.67
Rockall & Hatton Banks	248	0.21	0.79	129	0.76	0.10	---	0.14	0.52
Bay of Biscay	66	0.12	0.88	100	0.85	0.14	0.01	---	1.52
Portugal	0	---	---	33	0.76	0.18	0.06	---	---
Canarias Archipelago	5	0.4	0.6	46	0.28	0.72	---	---	9.20
TOTAL NE ATLANTIC	1589	0.40	0.60	1122	0.77	0.14	0.02	0.07	0.71
CE ATLANTIC (Mauritania)	542	0.93	0.07	722	0.90	0.06	0.02	0.00	1.33
SE ATLANTIC (Namibia)	211	0.55	0.45	113	0.53	0.47	---	---	0.53
Chatham Rise & North Island	3548	0.37	0.63	3960	0.78	0.05	0.02	0.16	1.12
South Island, Campbell Plateau	195	0.12	0.88	187	0.83	0.17	---	---	0.96
TOTAL SW PACIFIC	3743	0.36	0.64	4147	0.78	0.05	0.02	0.15	1.11

Figure legends

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).

Fig. 2. Relationship between the sampling depth and maturity stage by region for the Portuguese dogfish, leafscale gulper shark and birdbeak dogfish (n= 16042). In the box-and-whisker plots, the box represents the 25th and 75th quantiles. The whiskers represent 1.5 times the interquartile range. The points beyond the whiskers are potential outliers. The black dots represent the medians. JV: juveniles; IM: immatures; MM: mature males; MF: mature females; PG: pregnant females; PN: post-natal females. Empty cells represent a lack of sampling data for the respective species and not necessarily that the species doesn't occur.

Fig. 3. Portuguese dogfish. Occurrences of (a) juveniles, (b) mature males and females, and (c) pregnant and post-natal females in the NE Atlantic.

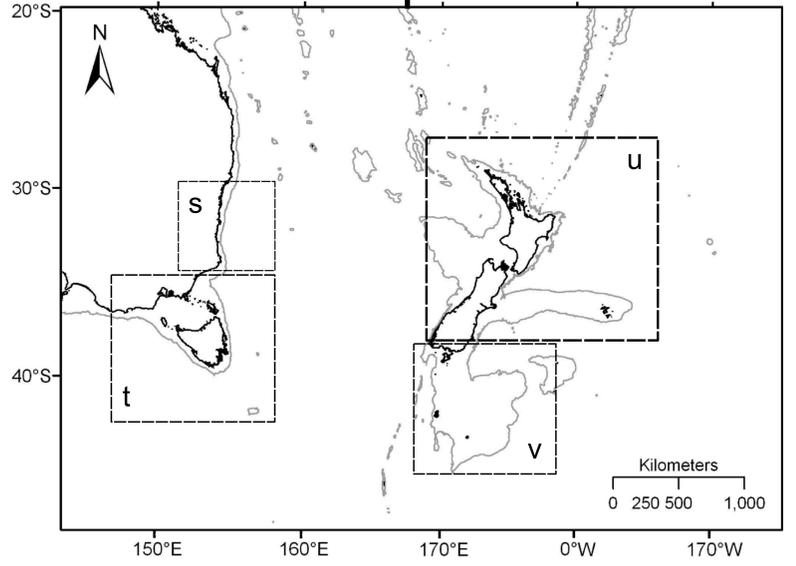
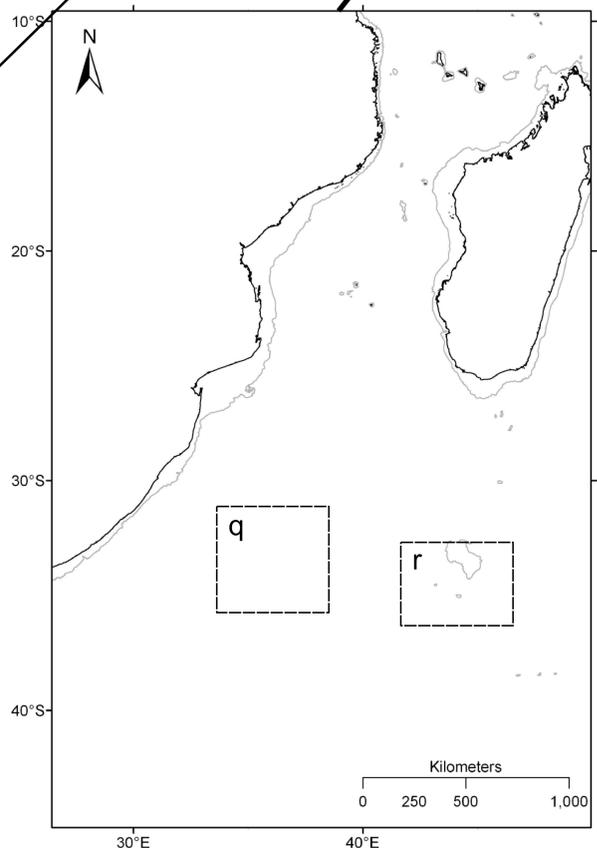
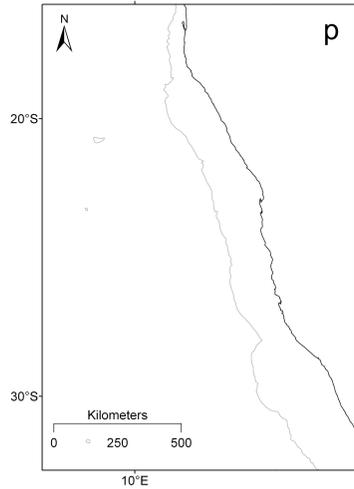
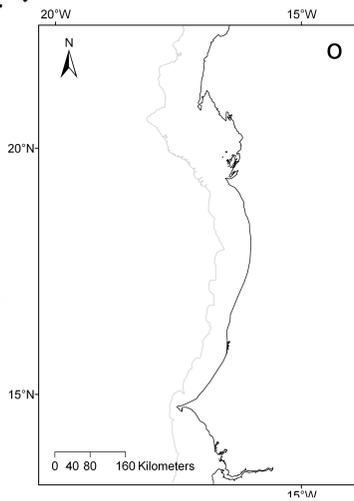
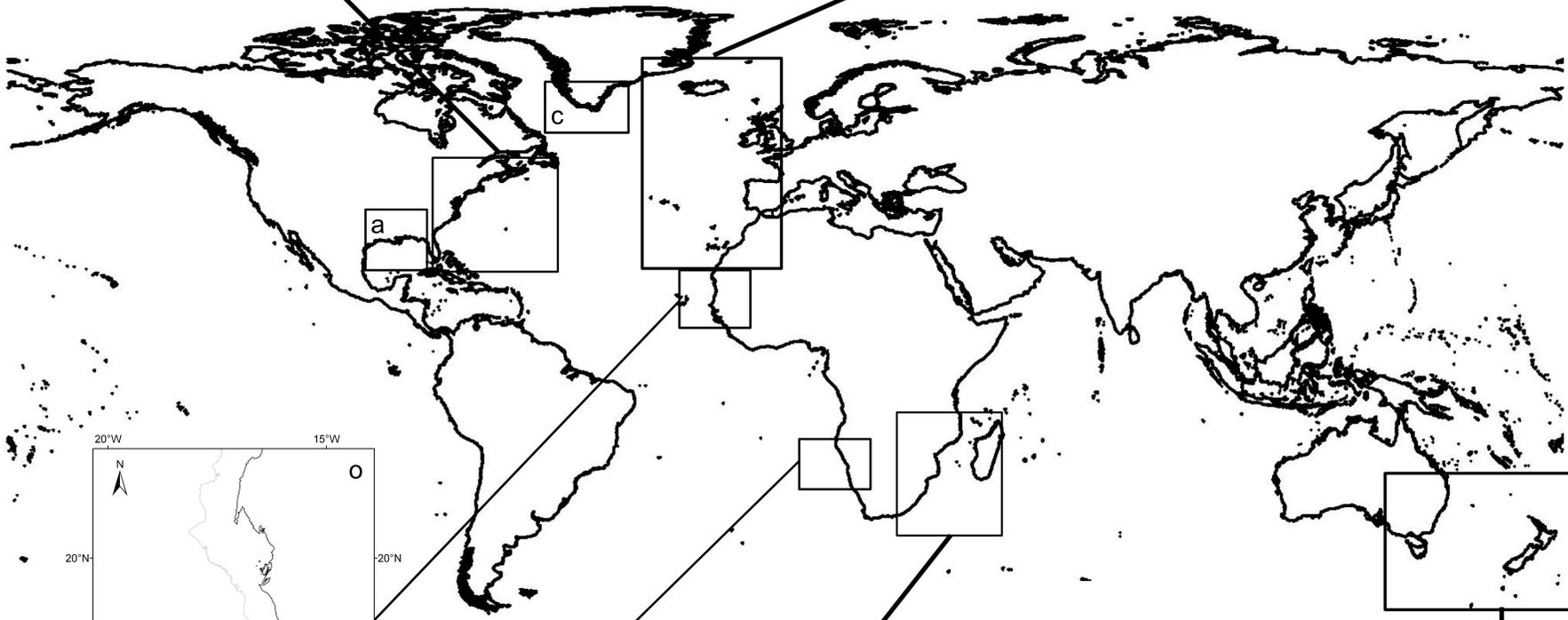
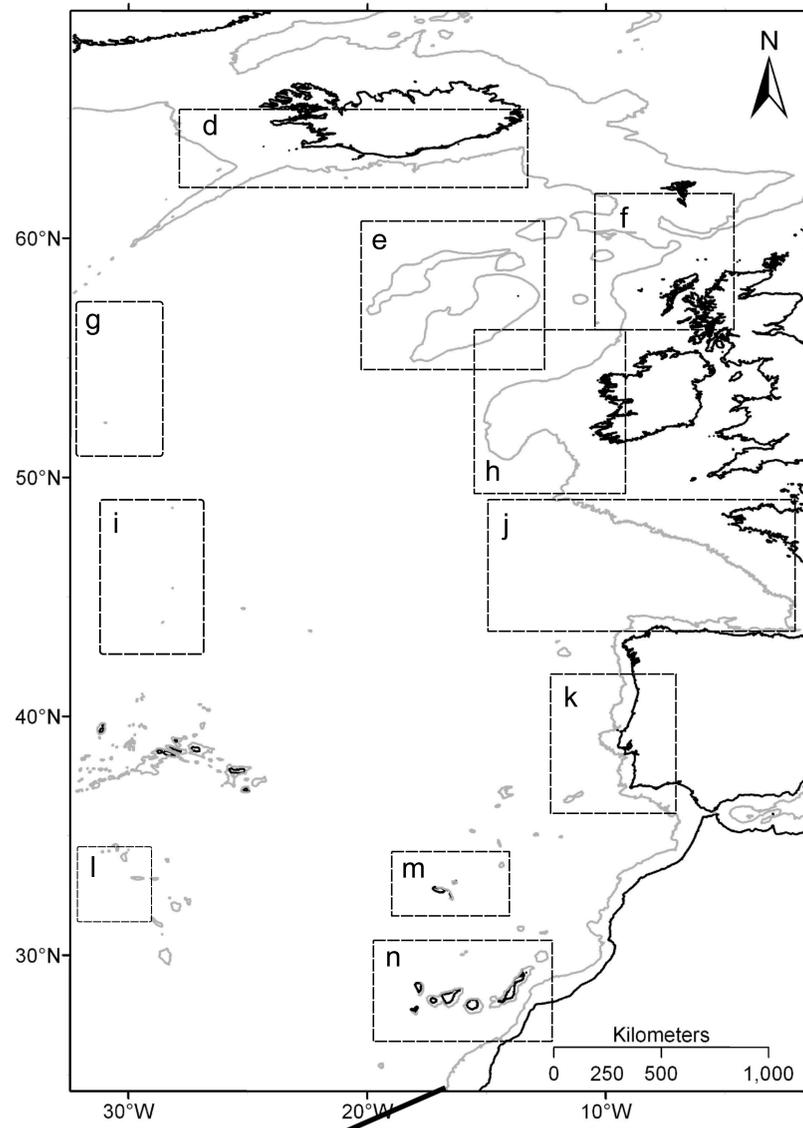
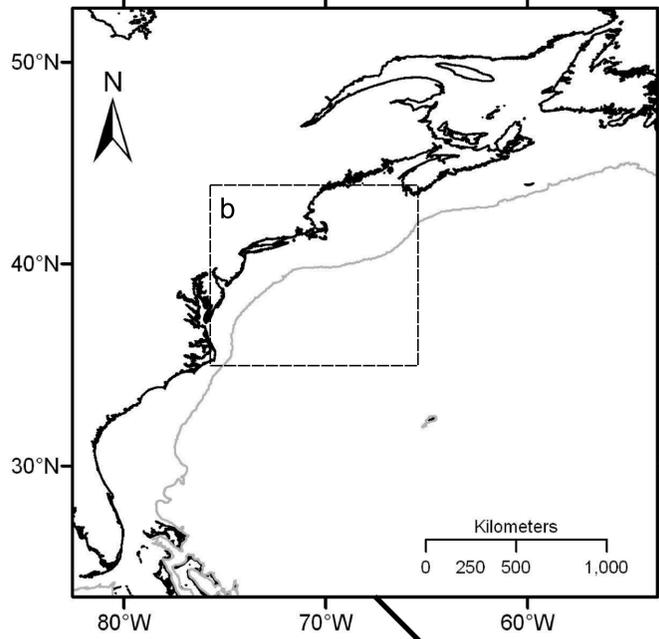
Fig. 4. Constrained correspondence analysis of the Portuguese dogfish distribution by maturity stage. Ordination of the maturity stages (black circles) and hauls (grey circles) overlaid with the surface model fitted for depth (in metres) in the NE Atlantic (n= 2991; 509 hauls). Axes 1 accounted for 100%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

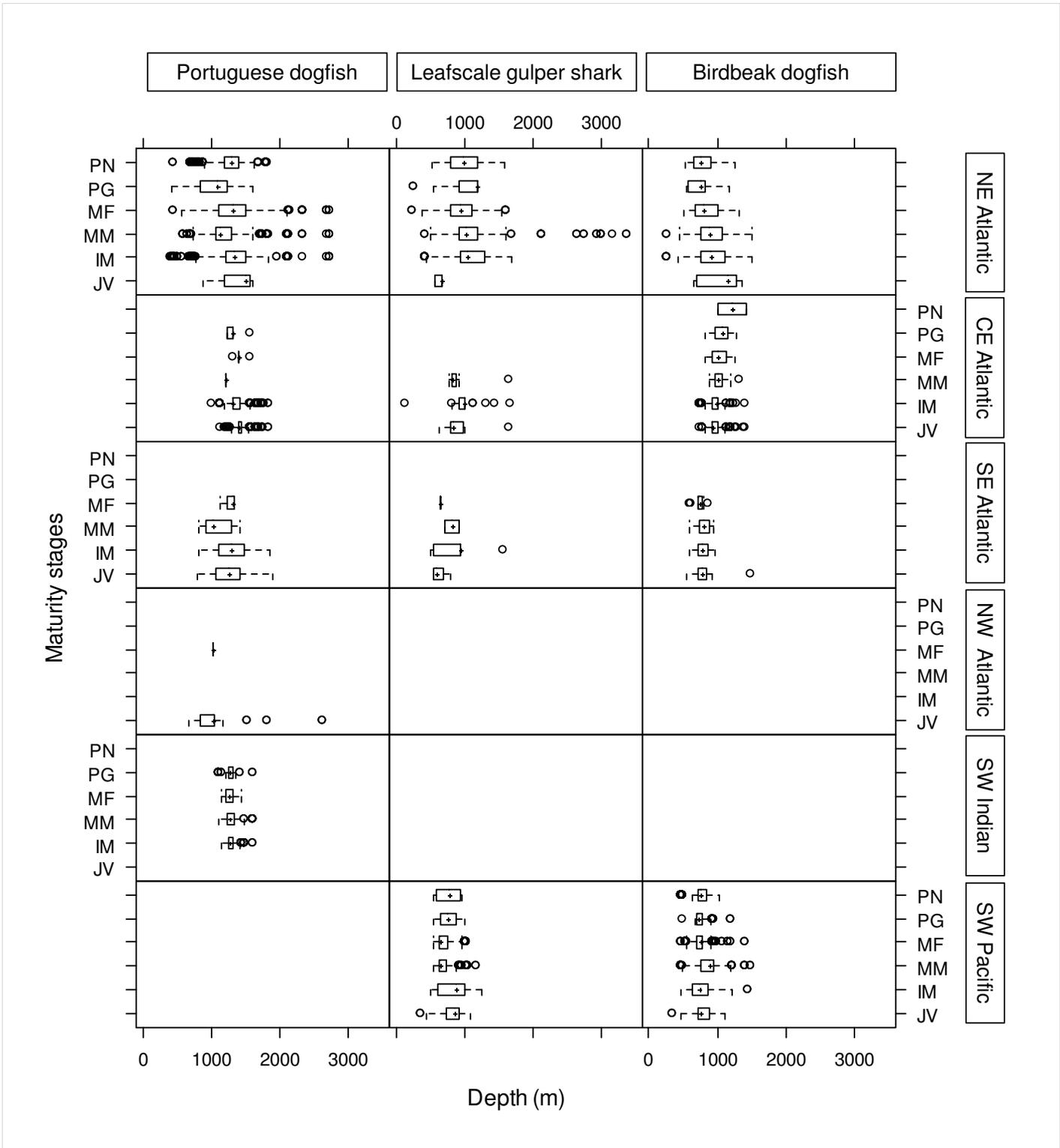
Fig. 5. Leafscale gulper shark. Occurrences of (a) juveniles, (b) mature males and females; (c) pregnant and post-natal females in the NE Atlantic; of (d) juveniles, (e) mature males and females; (f) pregnant and post-natal females in the SW Pacific (New Zealand).

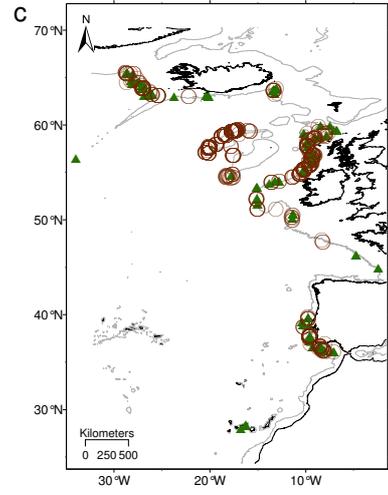
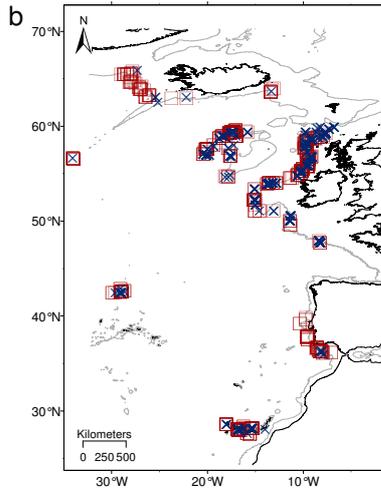
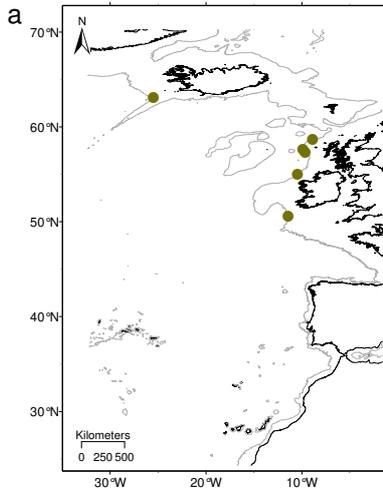
Fig. 6. Constrained correspondence analysis of leafscale gulper shark distribution by maturity stage. Ordination of the maturity stages (black circles) and hauls (grey circles) overlaid with the surface model fitted for (a) depth (in metres) and (b) temperature (in °C) in the NE Atlantic (n= 2435; 374 hauls) and for (c), depth and (d), salinity in the SW Pacific (New Zealand; n= 808; 241 hauls). In the NE Atlantic data axes 1 and 2 accounted for 63% and 37% of the variance of the fitted values, respectively whereas in the SW Pacific axes 1 and 2 accounted for 97% and 3% of the variance of the fitted values, respectively.

Fig. 7. Birdbeak dogfish. 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 CE Atlantic (Mauritania); of (g) juveniles, (h) mature males and females; (i) pregnant and post-natal females in the SW Pacific (New Zealand).

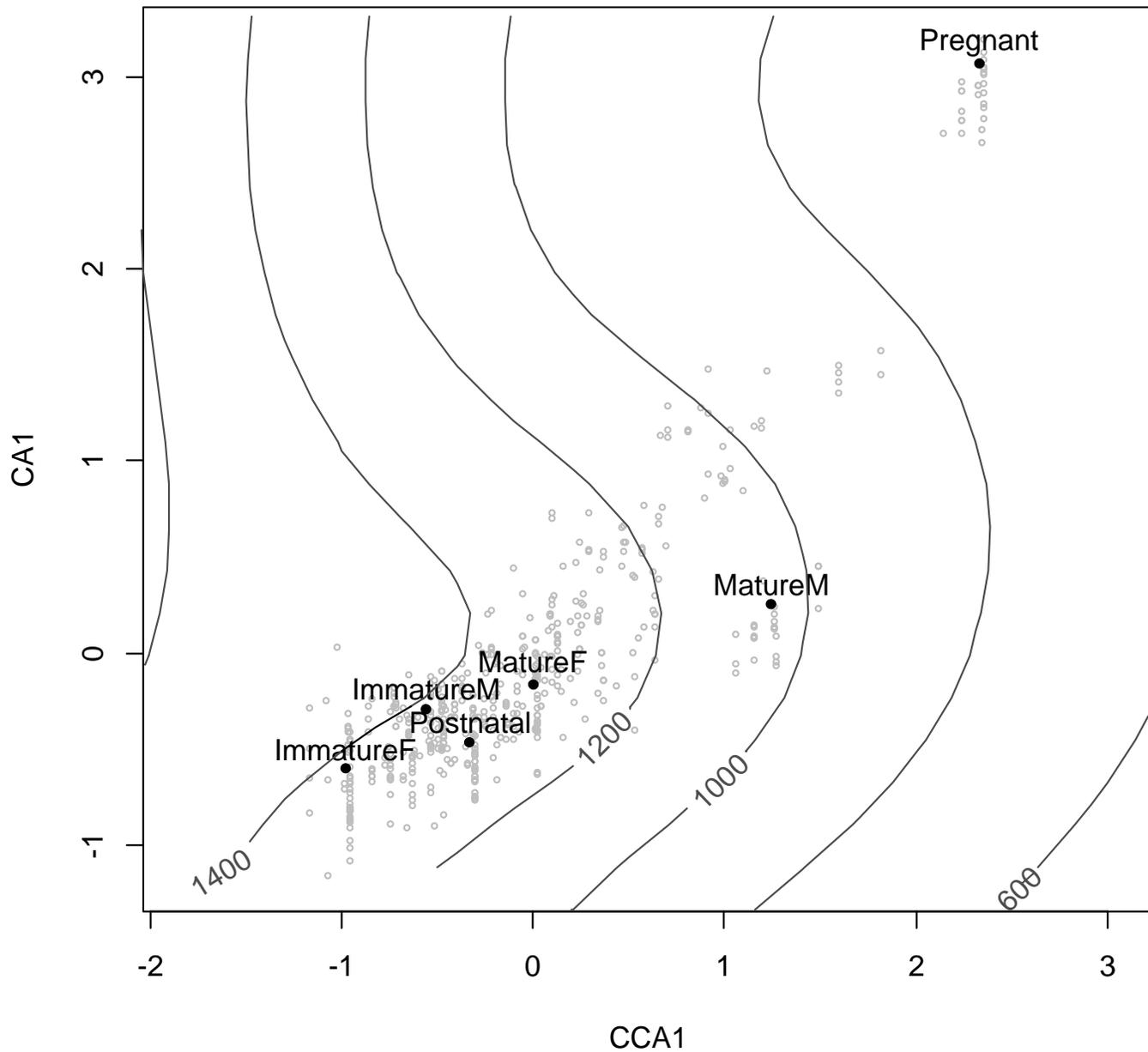
Fig. 8. Constrained correspondence analysis of birdbeak dogfish distribution by maturity stage. Ordination of the maturity stages (black circles) and hauls (grey circles) overlaid with the surface model fitted for (a) depth in the NE Atlantic (n= 2672; 310 hauls) for (b) depth (in metres) and (c) salinity (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.

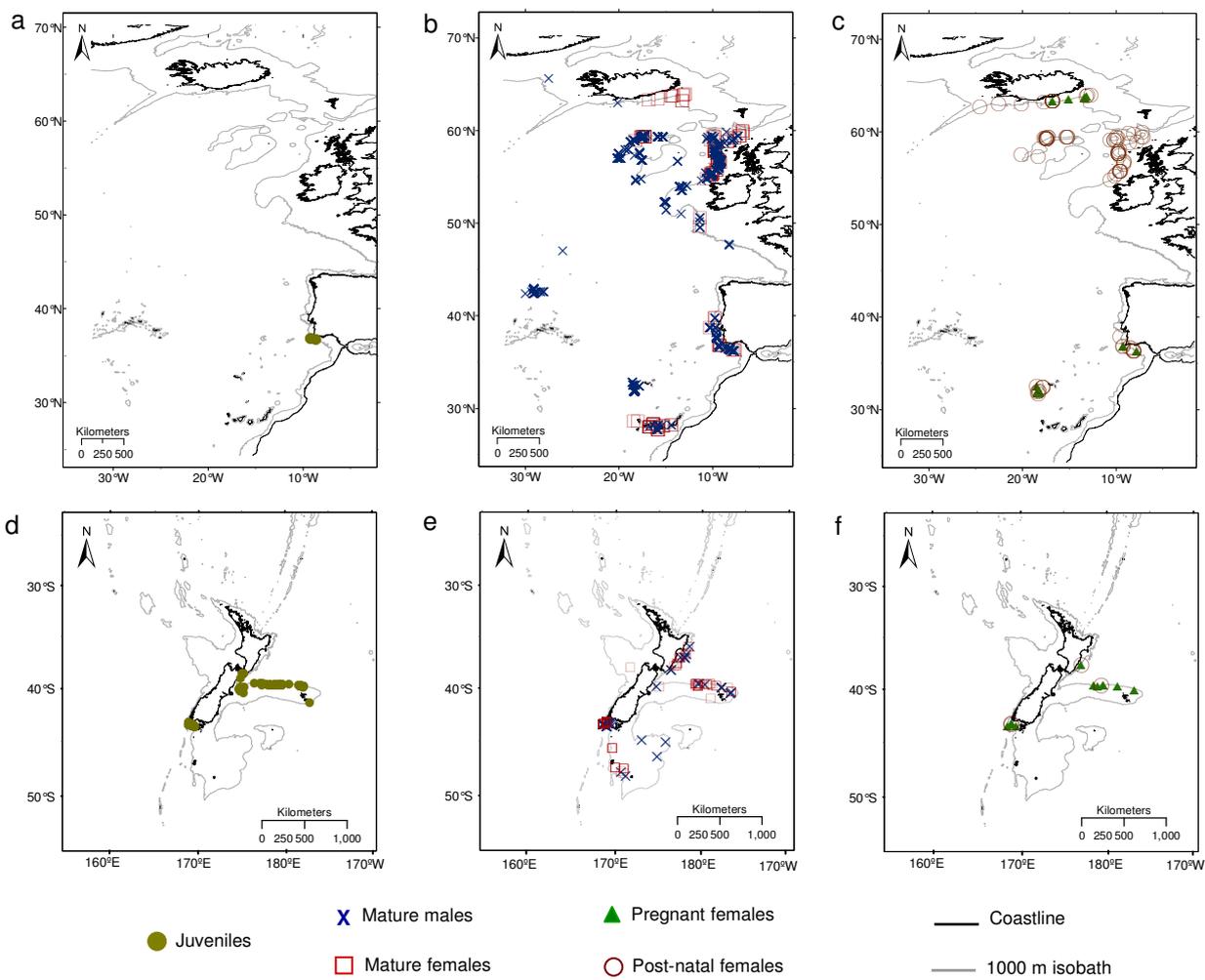


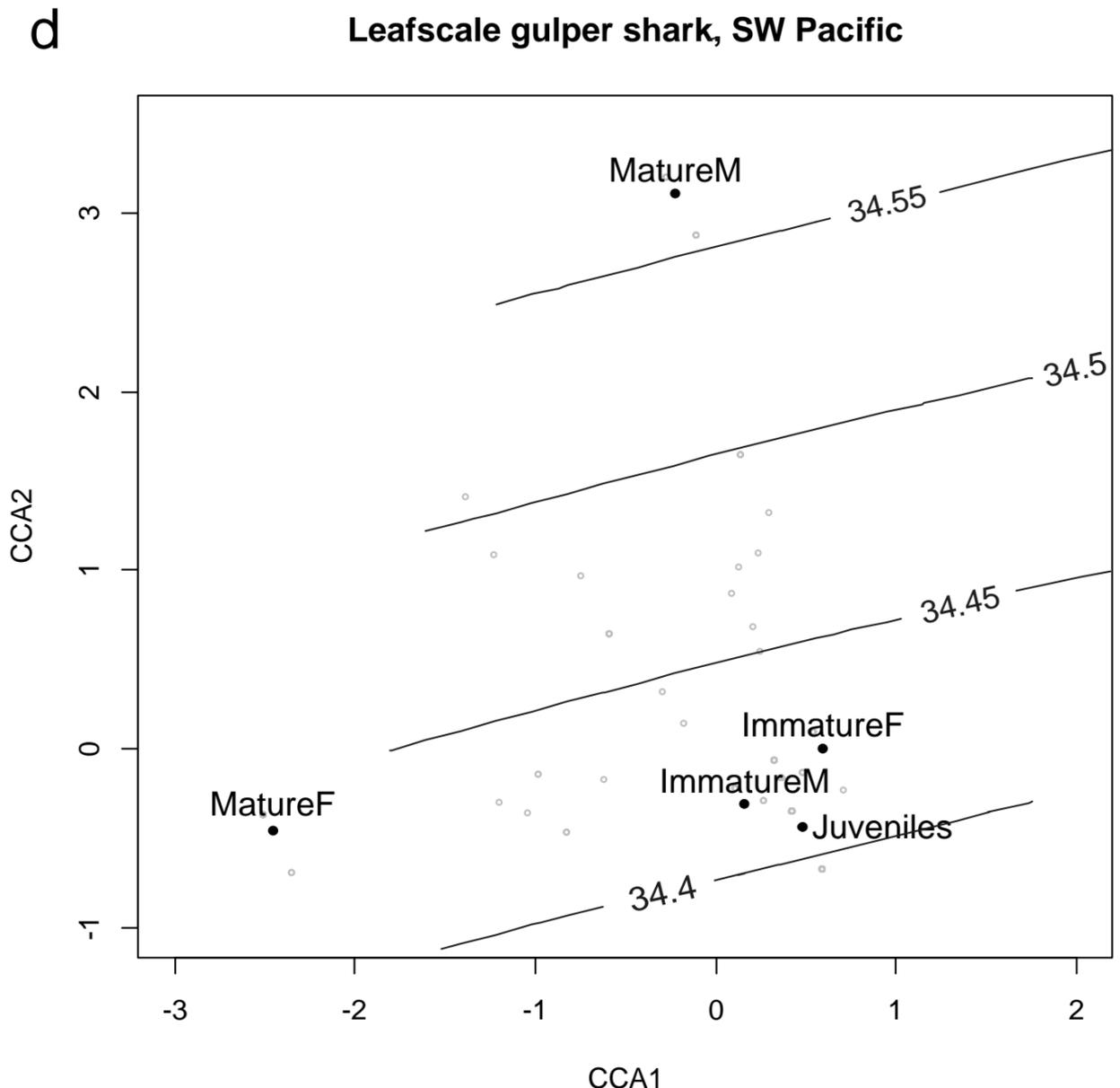
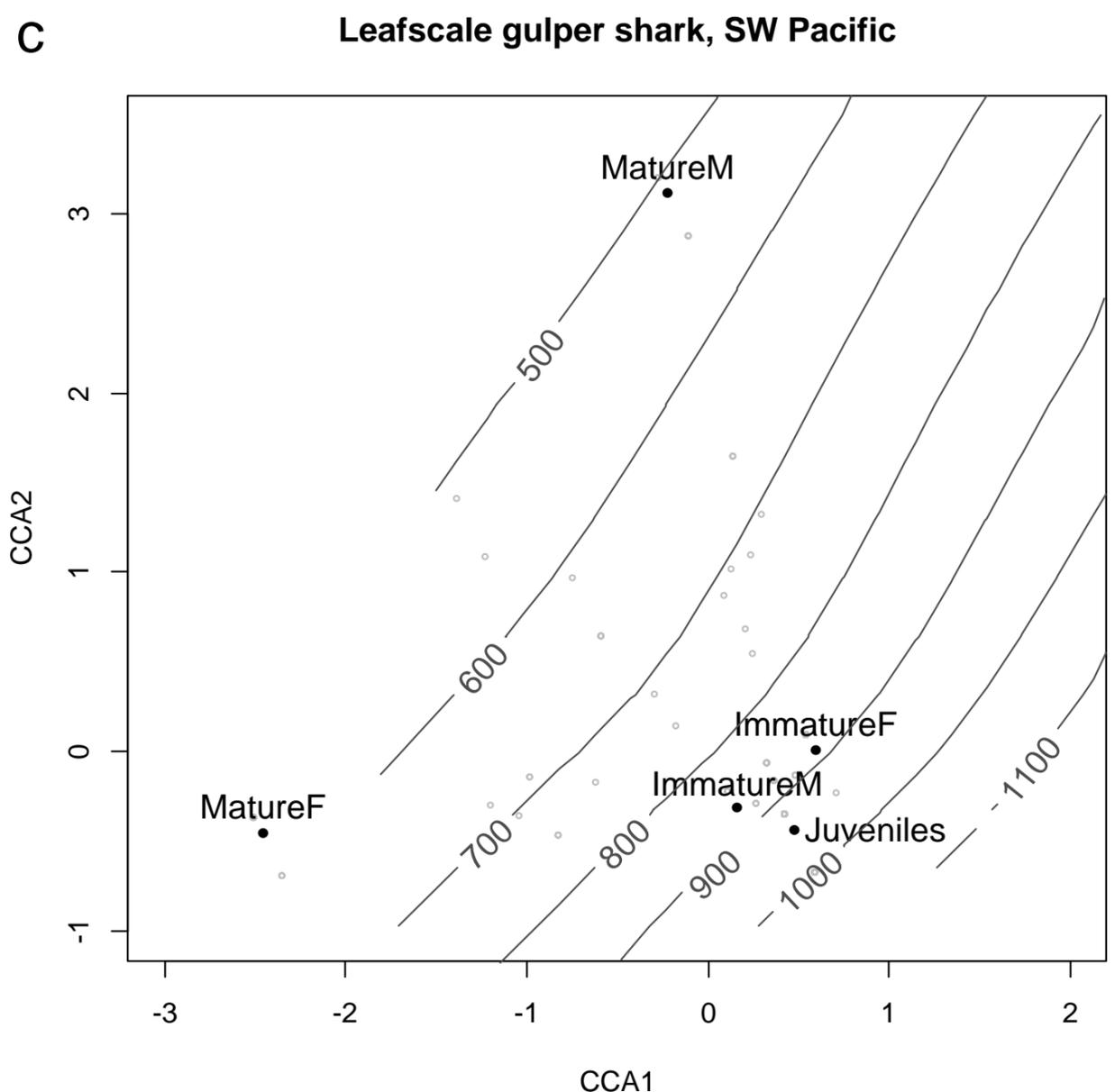
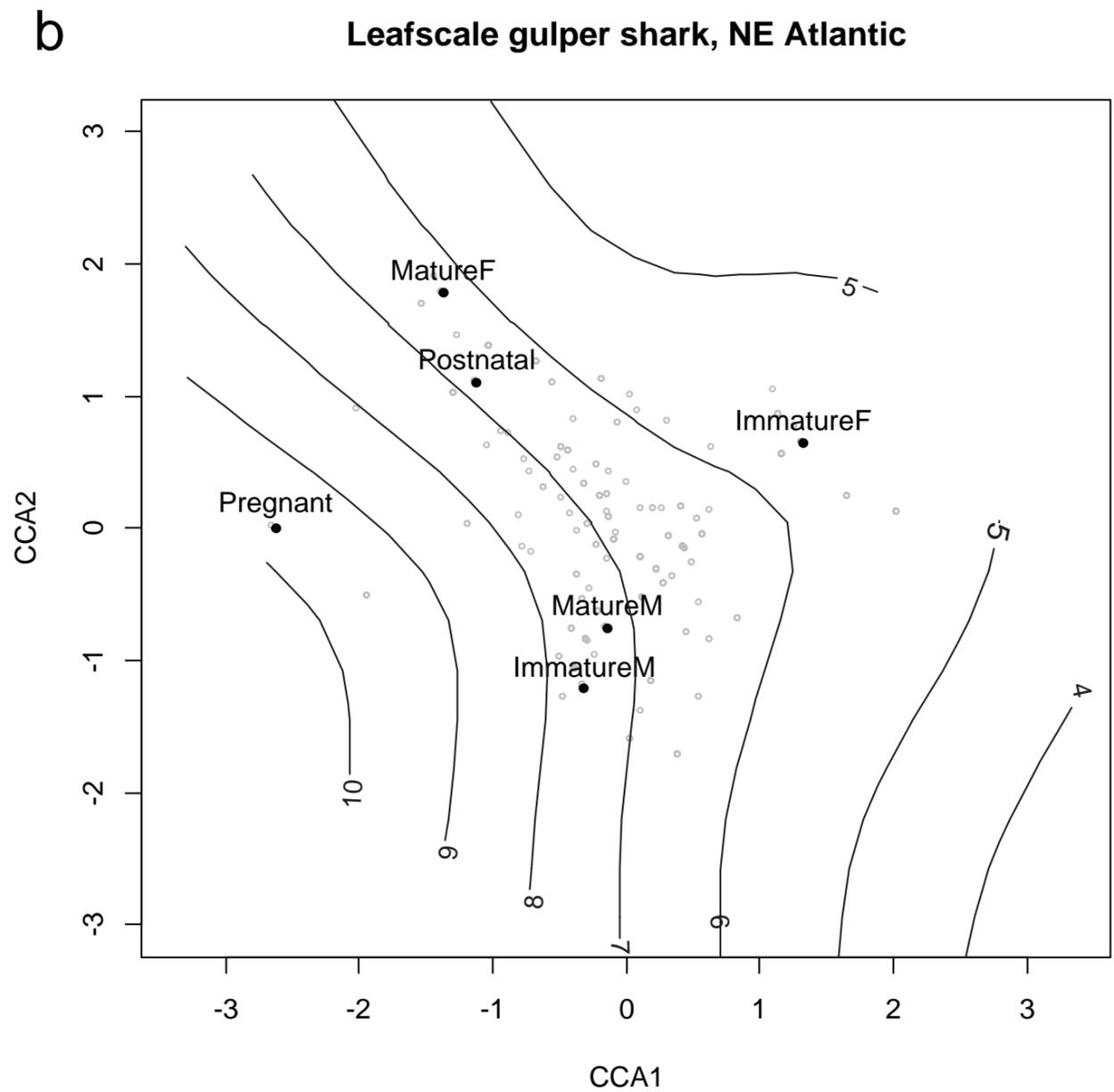
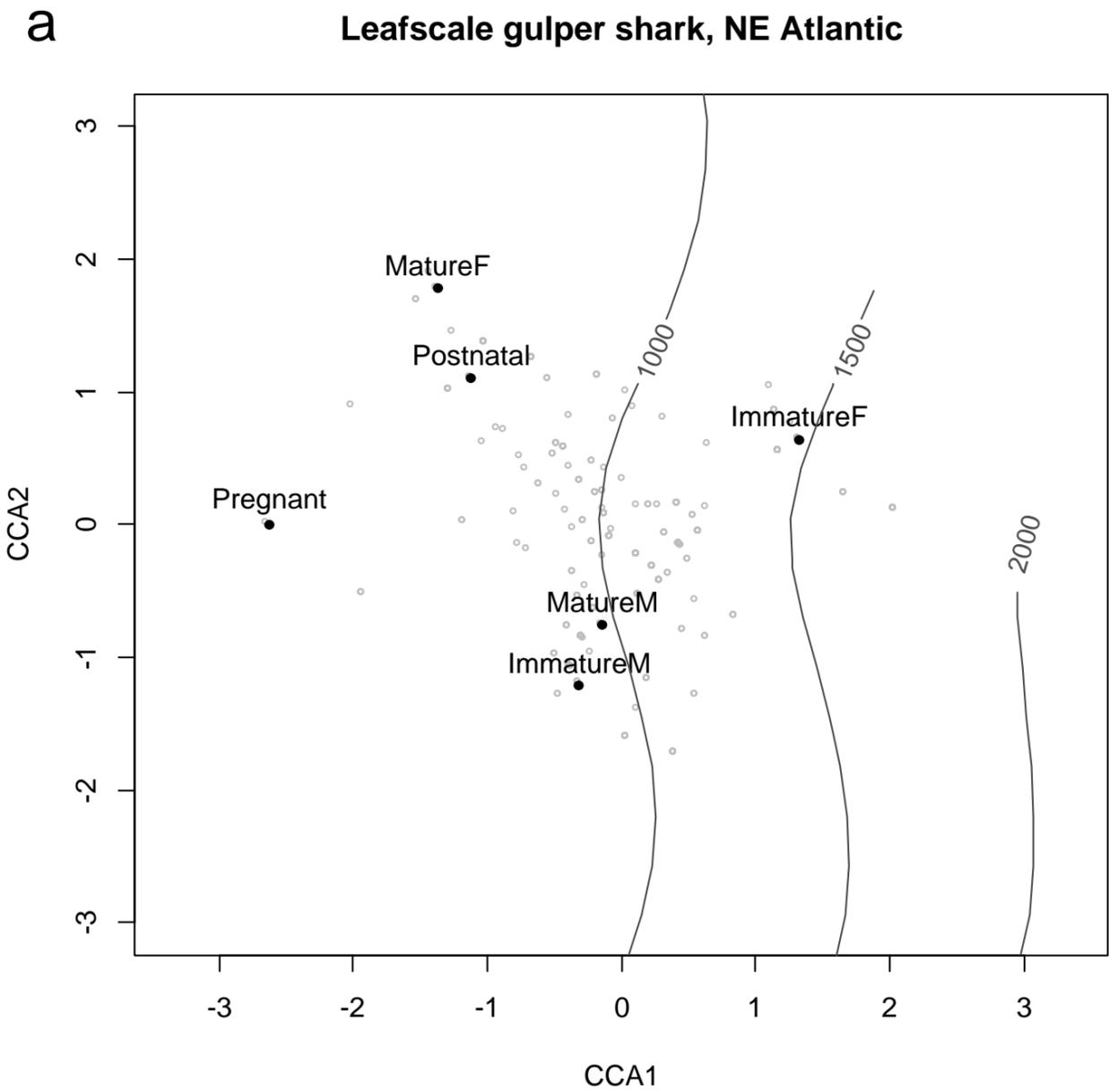


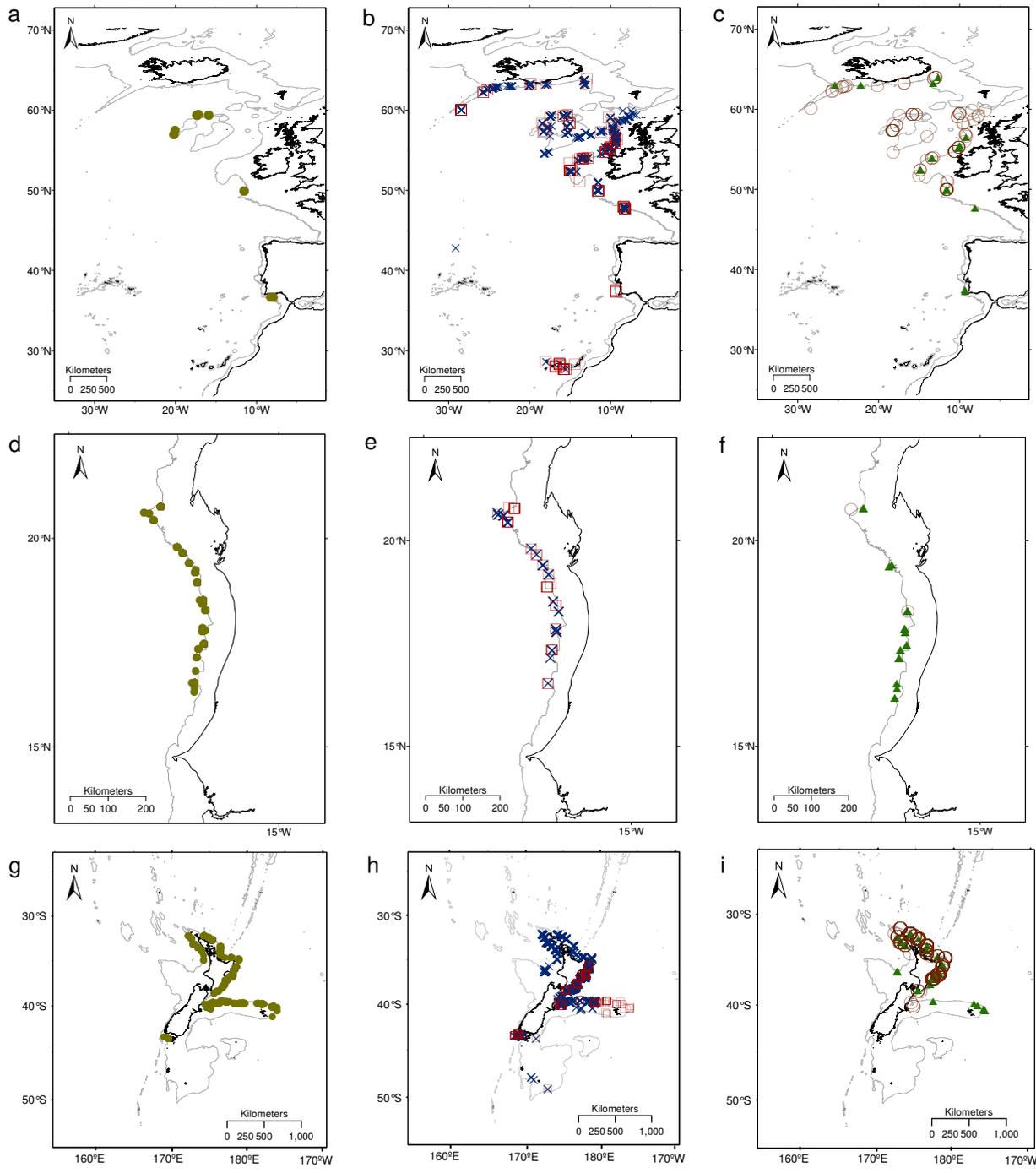


Portuguese dogfish, NE Atlantic









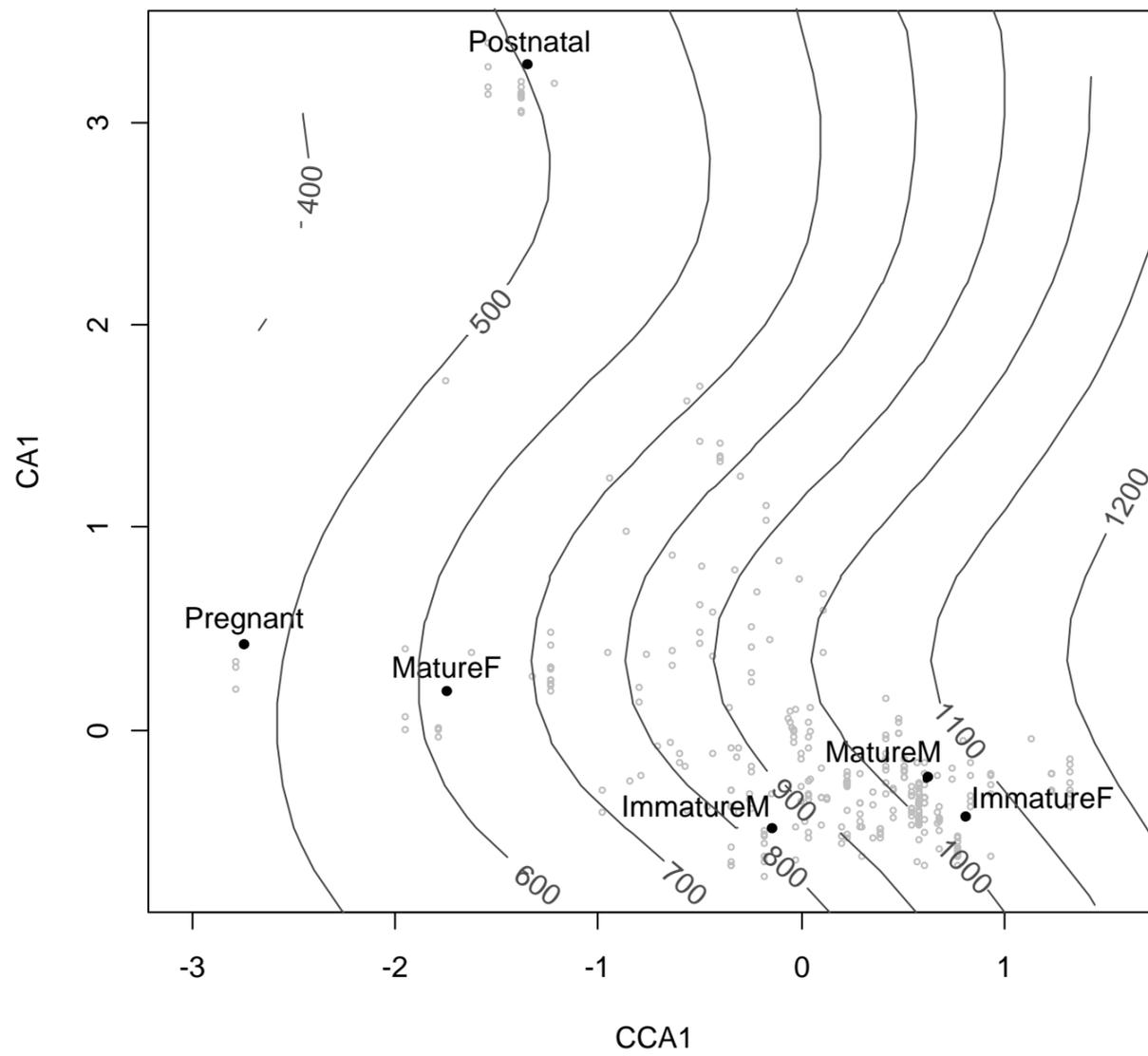
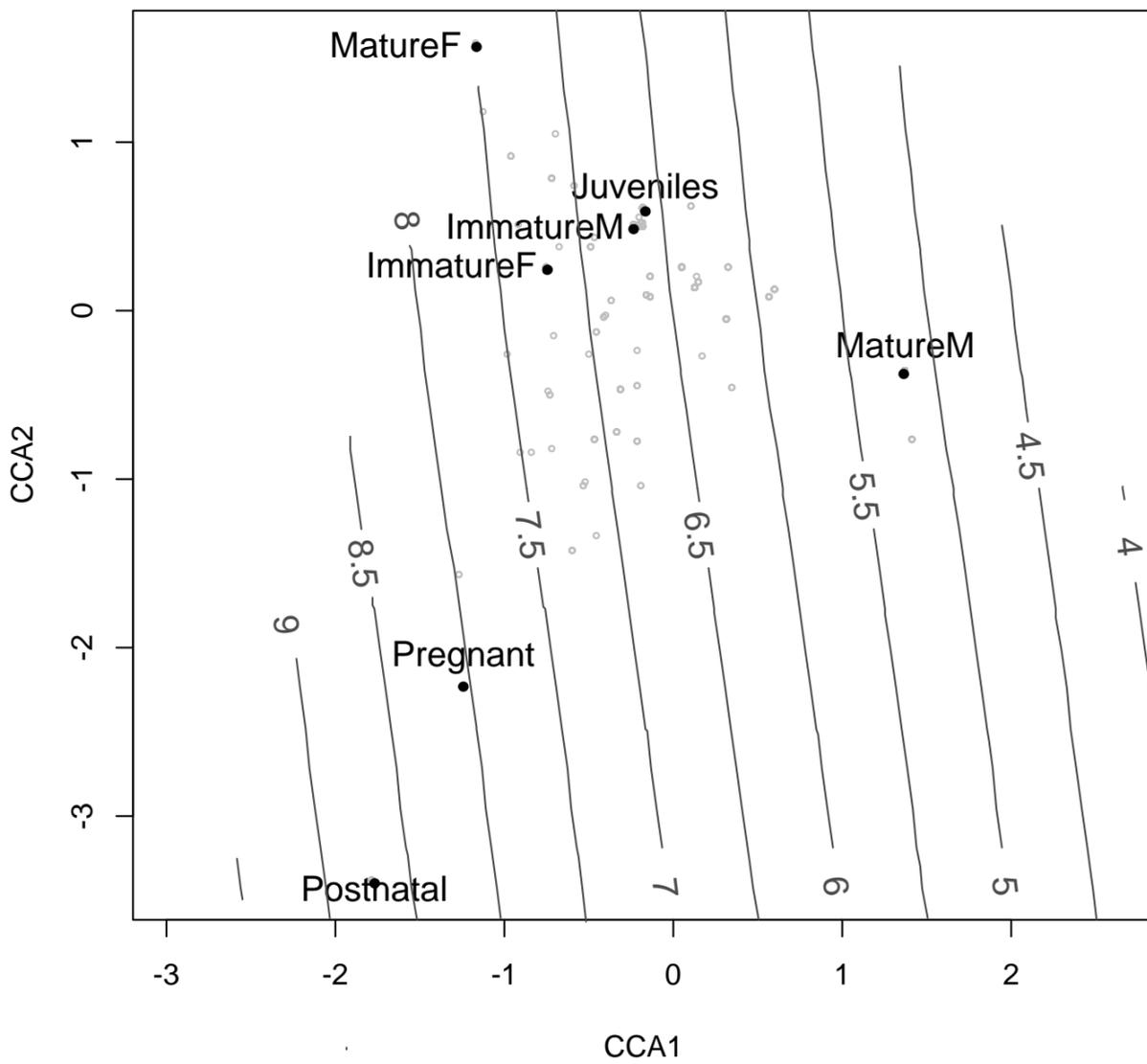
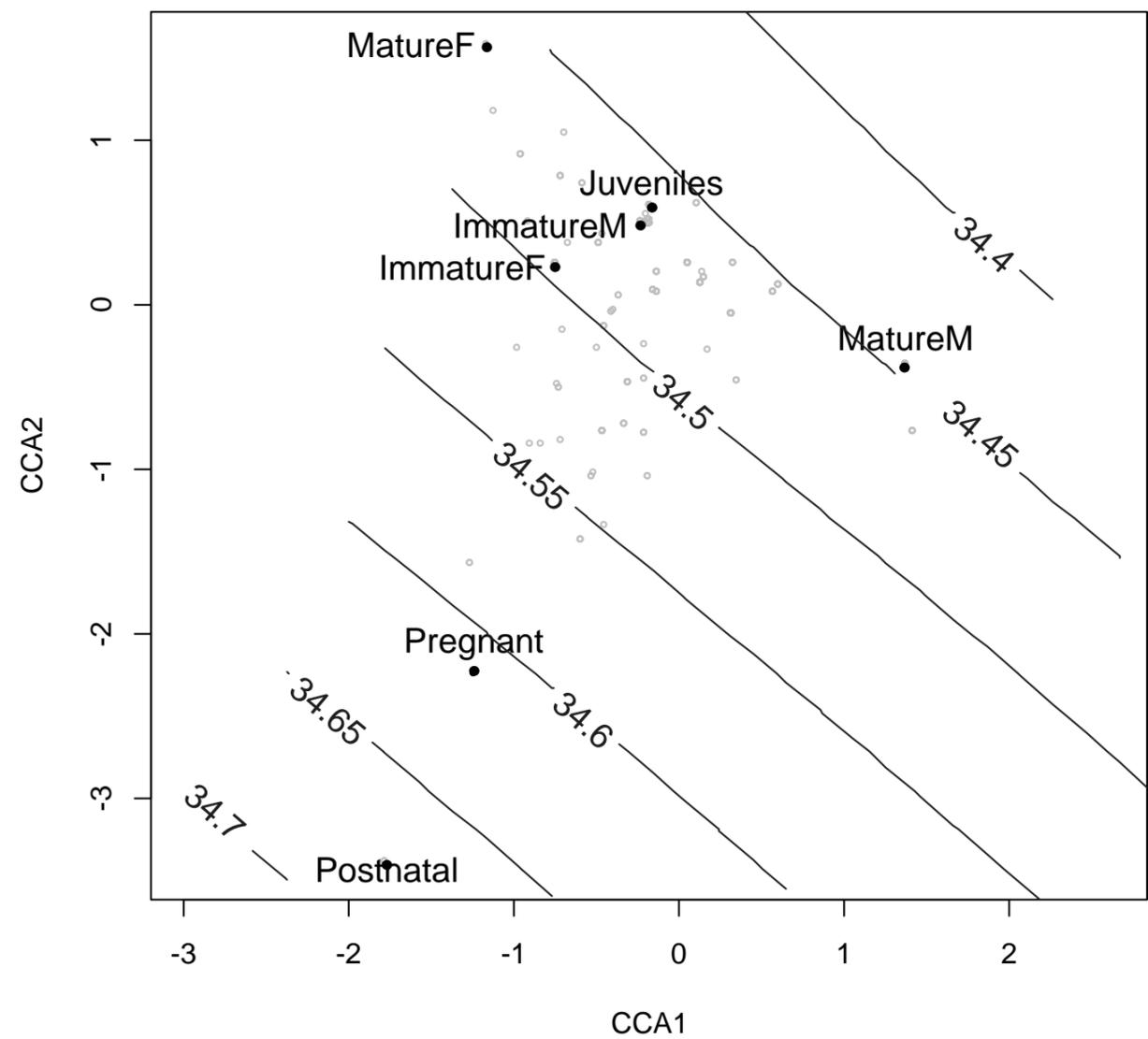
a**Birdbeak dogfish, NE Atlantic****b****Birdbeak dogfish, SW Pacific****c****Birdbeak dogfish, SW Pacific**

Table A1

Identification of the datasets available for the Portuguese dogfish (PD), leafscale gulper shark (LGS) and birdbeak dogfish (BD). Region: NE, northeast; CE, center-east, SE, southeast, NW, northwest; SW, southwest. Geographical area: CGFZ, Charlie-Gibbs Fracture Zone. Data source: Comm., sampling of commercial catches; Res. Surv., research survey; Trial Fish., trial fisheries.

Region	Geographical area	R/V or Project/ sampling port	Data source	Gear	Period	PD	LGS	BD
NE ATLANTIC	Greenland	F/V Skarheim, Husøy	Trial Fish.	Longline	1993, 1995	✓		
	Iceland	Autumn Groundfish Survey	Res.Surv.	Trawl	1996-2010	✓	✓	✓
	Iceland: Reykjanes Ridge	F/V Borgarin	Trial Fish.	Longline	1996	✓		✓
	Mid-Atlantic Ridge: North CGFZ	F/V Skarheim	Trial Fish.	Longline	1997	✓		
	West of Scotland , Ireland	R/V Scotia	Res.Surv.	Trawl	2000, 2005-2008	✓	✓	✓
	Ireland, West of Scotland	F/V Mary M	Res.Surv.	Trawl	1996-1999	✓	✓	✓
	Hatton Bank, Rockall Bank	R/V Koralmes	Res.Surv.	Trawl	1998	✓	✓	✓
	Ireland, Hatton Bank, Rockall Bank	MS Loran	Res.Surv.	Longline	1996, 1999-2000	✓	✓	✓
	Bay of Biscay (West Brittany), West of Scotland, Ireland	R/V Thalassa	Res.Surv.	Trawl	1999	✓	✓	✓
	Bay of Biscay (West Brittany), Rockall and Hatton Banks	Lochinver port, W Scotland	Comm.	Trawl	2000-2001	✓	✓	✓
	Bay of Biscay (Cantabrian Sea)	Ondarroa port, Basque Country	Comm.	Longline	2001-2002	✓	✓	✓
	Portugal	Profundidade, R/V Noruega	Res.Surv.	Trawl/Longline	1994-95,1997,2003		✓	✓
	Portugal	TUBAPROF, Sesimbra port	Comm.	Longline	2006-2007	✓	✓	
	Mid-Atlantic Ridge: north and south Azores	MS Loran	Res.Surv.	Longline	1996, 2004	✓	✓	✓
	Madeira Archipelago	Funchal port	Comm.	Longline	2004		✓	
Canarias Archipelago	MARE, R/V G. W. Pierce II	Res.Surv.	Longline	1986	✓		✓	
Canarias Archipelago	Experimental fishing	Res.Surv..	Longline	1991-1999, 2010	✓	✓	✓	
CE ATLANTIC	Mauritania	R/V Vizconde de Eza	Res.Surv.	Trawl	2007-2008	✓	✓	✓
SE ATLANTIC	Namibia	R/V Vizconde de Eza	Res.Surv.	Trawl	2006-2007	✓	✓	✓
NW ATLANTIC	USA East Coast	Multiple VIMS Research Surveys	Res.Surv.	Trawl/ Traps	1973-1979	✓		✓
	Gulf of Mexico	FSU BP-11 cruise, R/V Weatherbird II	Res.Surv.	Longline	2011			✓
SW INDIAN	Mozambique Plateau, Madagascar Plateau	Experimental fishing	Comm.	Longline	2004	✓		
SW PACIFIC	New South Wales, Tasmania (Australia)	Several F/V and ports	Comm.	Trawl	1986-2002	✓		
	North Island, Challenger Plateau (New Zealand)	F/V Wanaka	Res.Surv.	Trawl	1985-1986			✓
	North Island, South Island, Chatham Rise, Campbell Plateau (New Zealand)	R/V Tangaroa	Res.Surv.	Trawl	1996-2010	✓	✓	✓

Table A2

Compiled data available for the Portuguese dogfish by region and geographical Area. Data presented includes the number of sampled specimens (n), total length range (TL, in cm) by sex and depth range of capture (in m) for all the specimens; the number (n), total length range (TL, in cm) and depth range of capture (in m) of all the sampled juveniles; the number of specimens used in the analysis (n) and the analysis carried out for each geographical area. Since there were some gaps for some variables in the datasets the number of sampled specimens might differ between analyses. CCA: constrained correspondence analysis; CGFZ: Charlie-Gibbs Fracture Zone; MAR: Mid-Atlantic Ridge; NA: information not available.

Region	Geographical Area	All specimens				Juveniles information			Analysis information			
		n	Males TL range (cm)	Females TL range (cm)	Depth range (m)	n	TL range	Depth range (m)	notes	n	Sex ratio	CCA
NE ATLANTIC	Greenland	21	89	83-114	840-1247	1	58	1213	a, b			
	Iceland	311	62-112	49-120	407-1404	1	49	880		307	*	*
	Rockall & Hatton Banks	2556	66-117	72-130	627-1930				c, b	773	*	*
	Scotland	408	31-109	37-126	416-1800	4	31-58	1500		408	*	*
	Ireland	931	70-114	37-130	562-1823	1	37	1600	c, b	793	*	*
	Bay of Biscay	80	78-99	84-113	1151-1947					65	*	*
	Portugal	367	69-99	73-118	1119-1640					367	*	*
	North CGFZ (MAR)	44	59-97	102-122	566-866				d			
	North Azores (MAR)	64	81-101	85-121	883-1929					49	*	*
Canarias Archipelago	295	71-100	67-125	750-2715					269	*	*	
CE ATLANTIC	Mauritania	1381	32-92	30-123	1006-1835	796	30-60	1006-1835	e	1381	*	
SE ATLANTIC	Namibia	944	33-100	28-110	798-1882	695	28-60	798-1882	e	944	*	
NW ATLANTIC	U.S. East Coast	62	32-47	30-123	670-2624	53	37-49	670-2624	b, e	42		
SW INDIAN	Mozambique Plateau	1400	69-126	79-118	1007-1481					436	*	(f)
	Madagascar Plateau	106	69-120	72-121	1112-1606					106	*	(f)
SW PACIFIC	New South Wales (Australia)	85	48-98	55-110	NA	8	48-58	NA	g	85	(g)	(g)
	Tasmania (Australia)	241	67-122	72-120	NA				g	241	(g)	(g)
	North Island & Challenger Plateau (New Zealand)	92	72-121	77-118	835-1256				a			

^a Maturity staging information not available

^b Some/all specimens unsexed

^c Maturity staging information incomplete

^d Insufficient number of specimens for analysis

^e The representation of each maturity stage is inadequate – predominance of immature and juveniles

^f Insufficient number of hauls

^g Geographical position and depth not available

^h Depth not available

* Analysis performed

Table A3

Compiled data available for the leafscale gulper shark by region and geographical Area. Data presented includes the number of sampled specimens (n), total length range (TL, in cm) by sex and depth range of capture (in m) for all the specimens; the number (n), total length range (TL, in cm) and depth range of capture (in m) of all the sampled juveniles; the maximum number of specimens used in the analysis (n) and the analysis carried out for each geographical area. Since there were some gaps for some variables in the datasets the number of sampled specimens might differ between analyses. CCA: constrained correspondence analysis; MAR: Mid-Atlantic Ridge; NA: information not available.

Region	Geographical Area	All specimens				Juveniles information			Analysis information			
		n	Males TL range (cm)	Females TL range (cm)	Depth range (m)	n	TL range (cm)	Depth range (m)	notes	n	Sex ratio	CCA
NE ATLANTIC	Iceland	46	63-113	98-145	228-915					46	*	*
	Rockall & Hatton Banks	2056	64-136	70-135	500-1930				b, c	627	*	*
	Scotland	720	65-143	82-166	416-1540					713	*	*
	Ireland	847	87-119	77-138	610-1459				b, c	570	*	*
	Bay of Biscay	16	91-110	82-109	1202-1293				h			
	Portugal	260	84-140	35-139	560-1606	3	35-59	550-650		255	*	*
	North Azores (MAR)	333	95-120	90-123	467-3366				b, c	83		
	Madeira Archipelago	205	89-118	92-146	1200					205	*	*
	Canarias Archipelago	74	83-115	76-133	750-3150					74	*	*
CE ATLANTIC	Mauritania	86	41-101	43-116	650-930	45	41-60	621-1639		86	*	
SE ATLANTIC	Namibia	13	44-112	49-142	504-1553	4	44-60	551-793	d			
SW PACIFIC	Chatham Rise & North Island (New Zealand)	407	37-115	31-140	361-1251	170	31-60	361-1096		407	*	*
	South Island, Campbell Plateau (New Zealand)	417	25-121	39-142	477-999	260	25-60	477-999		417	*	*

^a Maturity staging information not available

^b Some/all specimens unsexed

^c Maturity staging information incomplete

^d Insufficient number of specimens for analysis

^e The representation of each maturity stage is inadequate – predominance of immature and juveniles

^f Insufficient number of hauls

^g Geographical position and depth not available

^h Depth not available

* Analysis performed

Table A4

Compiled data available for the birdbeak dogfish by region and geographical Area. Data presented includes the number of sampled specimens (n), total length range (TL, in cm) by sex and depth range of capture (in m) for all the specimens; the number (n), total length range (TL, in cm) and depth range of capture (in m) of all the sampled juveniles; the number of specimens used in the analysis (n) and the analysis carried out for each geographical area. Since there were some gaps for some variables in the datasets the number of sampled specimens might differ between analyses. CCA: constrained correspondence analysis; MAR: Mid-Atlantic Ridge; NA: information not available.

Region	Geographical Area	All specimens			Juveniles information			Analysis information				
		n	Males TL range (cm)	Females TL range (cm)	Depth range (m)	n	TL range (cm)	Depth range (m)	notes	n	Sex ratio	CCA
NE ATLANTIC	Iceland	259	71-97	66-126	437-921				b, c	251	*	*
	Rockall & Hatton Banks	1504	42-94	35-112	262-1355	10	35-49	1092-1355	b, c	377	*	*
	Scotland	332	58-97	66-114	416-1504					330	*	*
	Ireland	2426	55-109	52-162	500-1378	2	52-55	883	b, c	1503	*	*
	Bay of Biscay	172	73-93	62-113	1151-1339				h	166	*	*
	Portugal	33	---	28-142	660-1000	5	28-32	660-740		33	*	*
	North Azores (MAR)	67	81	85-105	651-1100				b, c			
	South Azores (MAR)	82	85-90	97-111	412-691				b, c			
	Canarias Archipelago	56	80-88	57-113	600-1300					51	*	*
CE ATLANTIC	Mauritania	1264	27-99	26-136	738-1412	490	26-55	739-1399		1264	*	*
SE ATLANTIC	Namibia	324	38-93	41-111	551-1492	133	38-60	551-1900		324	*	*
NW ATLANTIC	U.S. East Coast	23	59-89	38-101	830-1141	2	37-38	830-1141	d, e			
	Gulf of Mexico	4	---	78-102	524-714				d			
SW PACIFIC	Chatham Rise & North Island (New Zealand)	7540	28-100	20-120	350-1478	1769	20-55	350-1120		7508	*	*
	South Island, Campbell Plateau (New Zealand)	382	29-96	29-116	457-984	11	29-39	670-959		382	*	*

^a Maturity staging information not available

^b Some/all specimens unsexed

^c Maturity staging information incomplete

^d Insufficient number of specimens for analysis

^e The representation of each maturity stage is inadequate – predominance of immature and juveniles

^f Insufficient number of hauls

^g Geographical position and depth not available

^h Depth not available

* Analysis performed

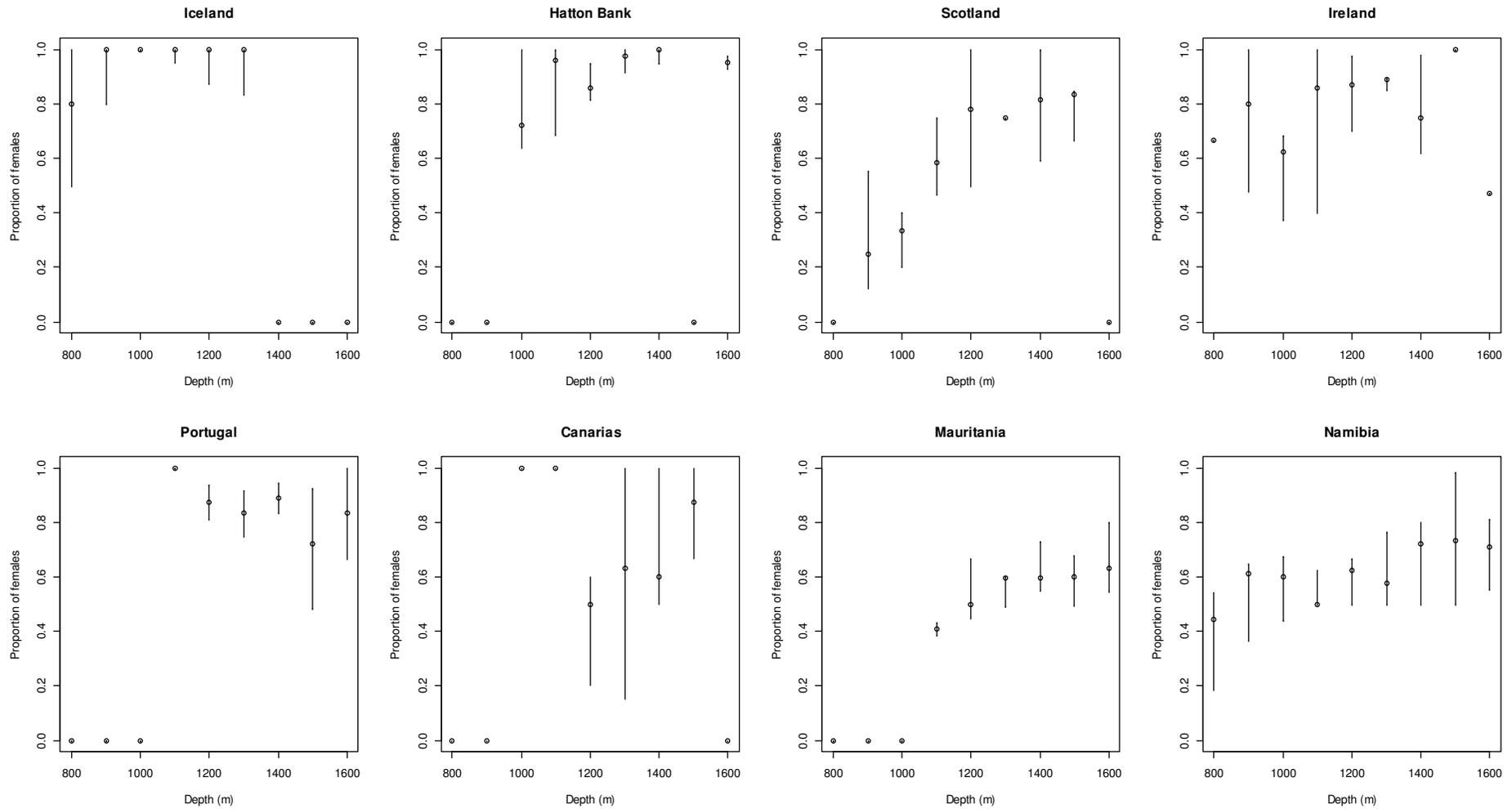


Fig. A1. Portuguese dogfish. Median and interquartile range of the proportion of females by depth strata (100 m) by geographical area. Depth was constrained to 800 to 1700 m. Only hauls with two or more individuals were selected and among these, only geographical areas with 25 or more hauls were selected for the analysis.

Portuguese dogfish, NE Atlantic

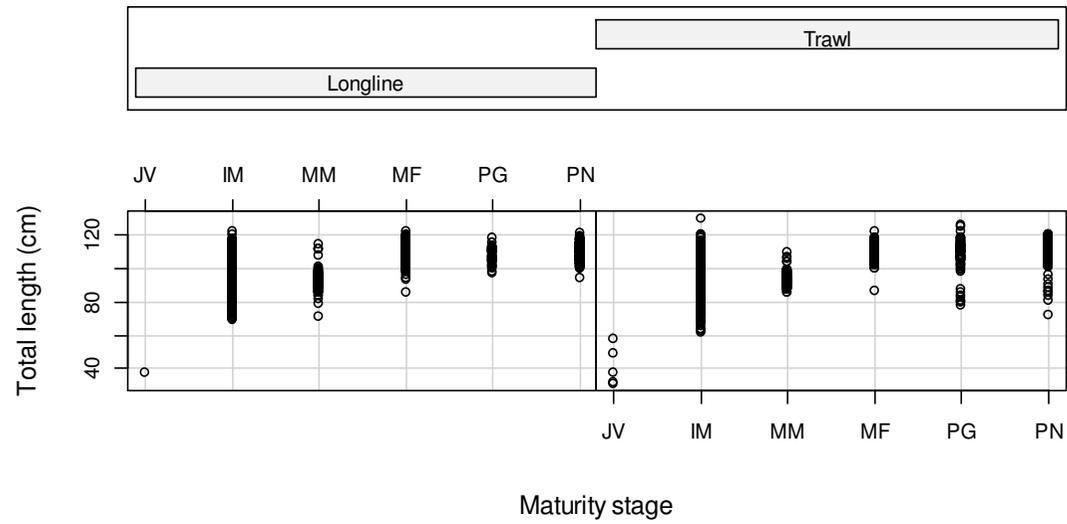


Fig. A2. Portuguese dogfish. Relationship Total length (cm) by maturity stage and type of gear (longline or trawl) in the NE Atlantic (n= 2887). JV: juveniles; IM: immatures; MM: mature males; MF: mature females; PG: pregnant females; PN: post-natal females.

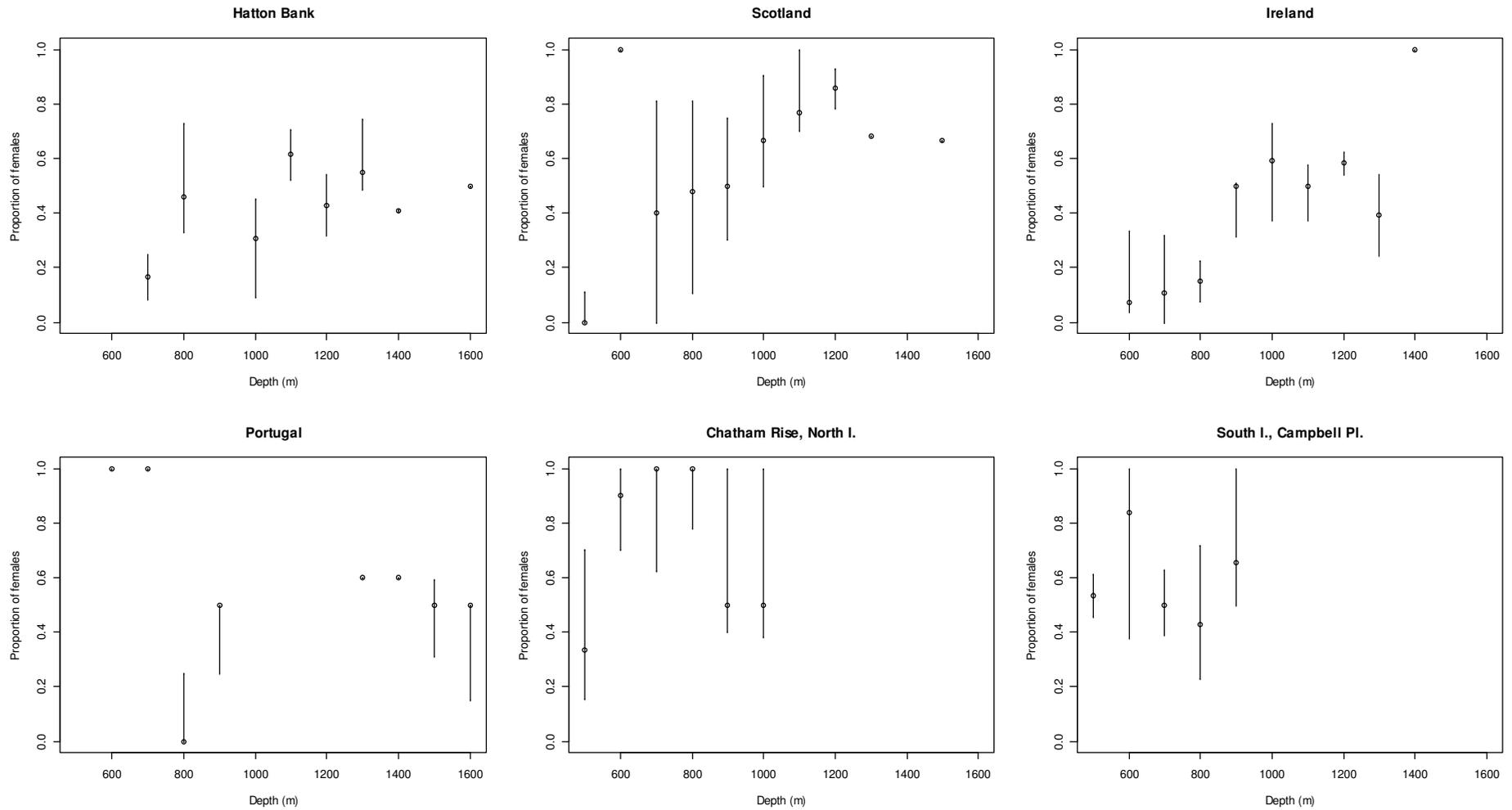


Fig. A3. Leafscale gulper shark. Median and interquartile range of the proportion of females by depth strata (100 m) by geographical area. Depth was constrained to 500 to 1700 m. Only hauls with two or more individuals were selected and among these, only geographical areas with 25 or more hauls were selected for the analysis.

Leafscale gulper shark, NE Atlantic

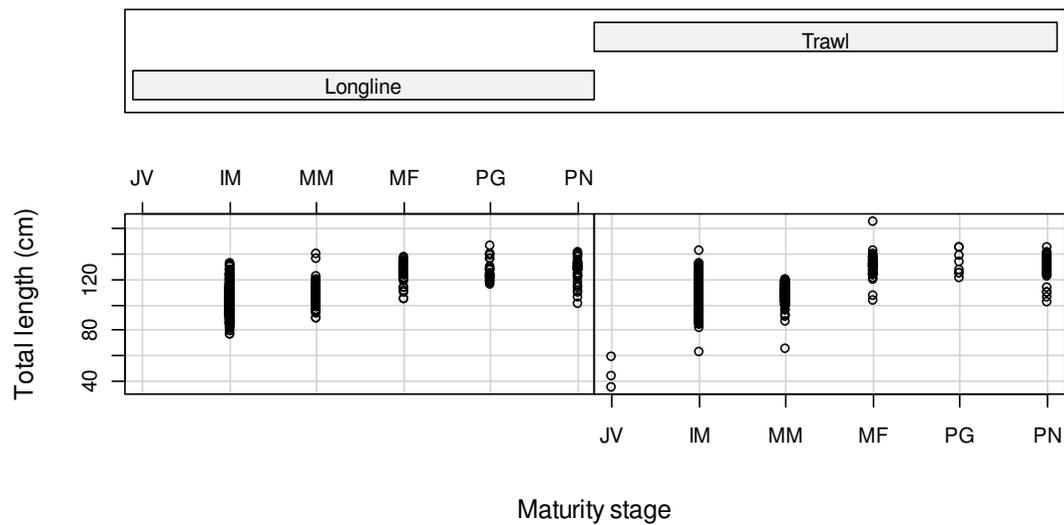


Fig. A4. Leafscale gulper shark. Total length (cm) by maturity stage and type of gear (longline or trawl) in the NE Atlantic (n= 2573). JV: juveniles; IM: immatures; MM: mature males; MF: mature females; PG: pregnant females; PN: post-natal females.

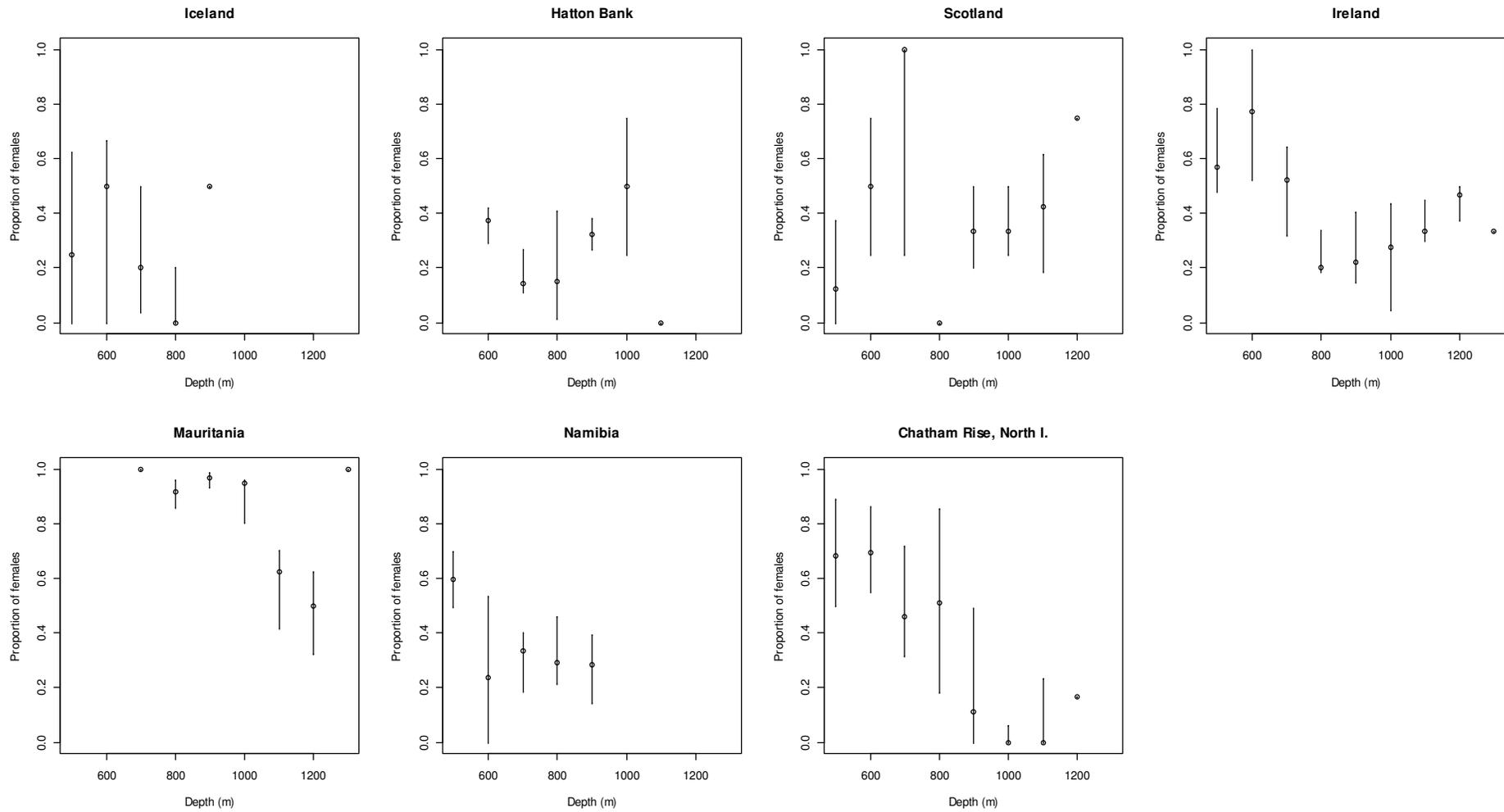


Fig. A5. Birdbeak dogfish. Median and interquartile range of the proportion of females by depth strata (100 m) by geographical area. Depth was constrained to 500 to 1400 m. Only hauls with two or more individuals were selected and among these, only geographical areas with 25 or more hauls were selected for the analysis.

Birdbeak dogfish, NE Atlantic

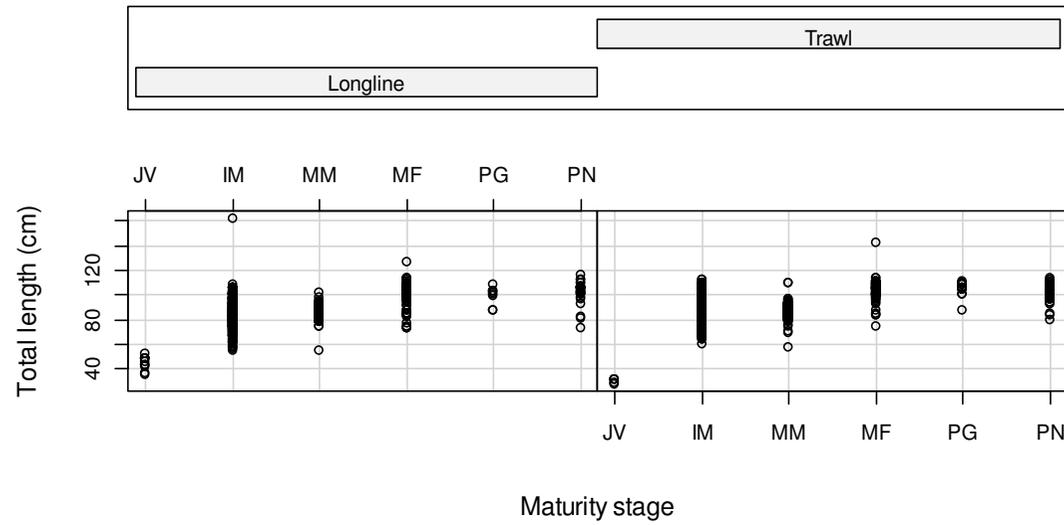


Fig. A6. Birdbeak dogfish. Total length (cm) by maturity stage and type of gear (longline or trawl) in the NE Atlantic (n=2711 JV: juveniles; IM: immatures; MM: mature males; MF: mature females; PG: pregnant females; PN: post-natal females).