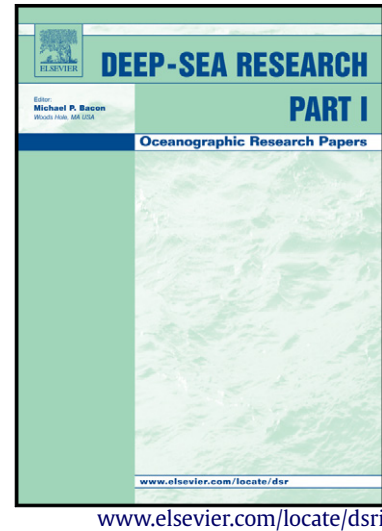


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School characteristics of mesopelagic fish at South Georgia

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Abstract

In this paper, we describe the variation in myctophid schools characteristics at South Georgia using multi-frequency acoustic data collected annually between November 2007 and January 2012. We studied the relationship between the proximity of land and the distribution and schooling characteristics of myctophid fish. We also examined patterns in schooling behaviour in relation to oceanographic data. Fish schools were identified using a dual-frequency dB identification method ($S_{V120-38\text{ kHz}}$), where negative $S_{V120-38\text{ kHz}}$ is indicative of gas-bearing organisms, such as swimbladdered fish. Available net data were used to provide information on the mesopelagic fish community in the region. School morphometrics (e.g. length, thickness, area) data were extracted and pooled according to their distance from the shore (0-30 km, 30-60 km, 60-90 km, 90-120 km). A total of 578 schools were detected in the survey region and there was high variation in school backscattering strength (NASC), length, height, perimeter, depth and horizontal distribution between surveys, including distinct inter-annual variation in these parameters when surveys were conducted in the same season (2009-2012). Schools were distributed predominantly on-shelf (0-500 m isobaths) during some summer surveys (2007 and 2012) and predominantly off-shelf on others (>500

m isobaths; 2009, 2010 and 2011). There was also evidence of bathymetric separation in the horizontal distribution of schools. Schools observed in the late-season in 2008 had the greatest NASC, largest height and the deepest depth distribution. Most schools occurred at depths between ~60-300 m, but they did not occupy the same water masses during each survey. Schools became progressively thinner, shallower and acoustically weaker with increasing distance to land, whilst school length and perimeter increased correspondingly. The change in fish schooling behaviour between environments could be a response to a combination of local predatory threats over short spatial/temporal scales and differences in oceanographic conditions, such as current velocity. The trend could also be evidence of spatial habitat partitioning of myctophids, with different schooling species, or different life-stages, orientating along a bathymetric gradient at South Georgia.

Keywords

Acoustics, Myctophid fish, Predator foraging, Schooling behaviour, South Georgia

1. Introduction

Lantern fish or myctophids (Family Myctophidae) are the dominant mesopelagic fish in most of the world's oceans, including the Southern Ocean (Gjøsaeter and Kawaguchi, 1980). They play a key role in oceanic food webs linking primary consumers such as copepods and macro-zooplankton to higher predators such as birds, marine mammals and large pelagic fish (Gjøsaeter and Kawaguchi, 1980; Mann, 1984). Despite their ecological importance, there is a scarcity of data on the ecology of myctophids around the globe and data are particularly lacking in high latitude regions, such as the Southern Ocean.

The South Georgia region of the Southern Ocean (54°S, 37°W) is characterised by high biomass and productivity of phytoplankton that sustains high levels of zooplankton and vertebrate predators (Atkinson et al., 2001). The food web at South Georgia is centred on Antarctic krill (*Euphausia superba*), which is pivotal in the transfer of energy from primary consumers to a number of abundant higher predators (Murphy et al., 2007). Against this

background of high productivity, marked seasonal and inter-annual variation in krill abundance occurs at the island and this has a profound impact on the breeding success and population levels of several krill-dependent marine predators in the region (Brierley et al., 1999; Croxall et al., 1999; Everson et al., 1997; Reid et al., 2005). During times when krill abundances are low, many of these predators must switch to alternative food sources, such as mesopelagic fish, and it is now clear that other trophic pathways are both regionally and seasonally important at South Georgia (Murphy et al., 2007).

Myctophids are the most dominant mesopelagic fish families in the South Georgia region in terms of abundance and diversity (Collins et al., 2012; Collins et al., 2008; Hulley, 1981). Myctophid fish form an important dietary component of many higher predators at South Georgia, including penguins (*Aptenodytes patagonicus* and *Eudyptes chrysolopus*), seals (*Arctocephalus gazella* and *Mirounga leonina*), squid (*Martialia hyadesi*) and toothfish (*Dissostichus eleginoides*) (Cherel et al., 2002; Collins et al., 2007; Dickson et al., 2004; Olsson and North, 1997; Reid et al., 2006). In turn, they are also predators of copepods, amphipods and euphausiids, including *E. superba*, with evidence of dietary specialisation occurring in different species (Pakhomov et al., 1996; Pusch et al., 2004; Shreeve et al., 2009). Despite the ecological importance of myctophid fish, there is a distinct paucity of data on their distribution of abundance, biology and ecology at South Georgia. Recent trends in ocean warming in the Scotia Sea have raised concerns about major long-term reductions in Antarctic krill abundance and its potential consequences for the South Georgia ecosystem (Atkinson et al., 2004; Murphy et al., 2007). With the possibility of large-scale reductions in krill availability at the island under currently predicted ocean warming scenarios, the importance of krill-independent food web pathways, such as myctophid fish, is likely to increase (Murphy et al., 2007). Therefore, there is clearly a pressing need for more data on the ecology of myctophid fish and food web dynamics at South Georgia to provide new insight into the likely outcomes of environmental change and aid effective ecosystem management strategies.

One important aspect of mesopelagic fish ecology that is highly relevant to food web dynamics at South Georgia is schooling behaviour. The formation of schools (we use “schools” generically here to mean pelagic fish aggregation) is common in many pelagic fish

species and several biological and physical drivers of this complex behaviour have been proposed, including predator avoidance, oxygen acquisition, reproduction and food acquisition (Brierley and Cox, 2010; Kaartvedt et al., 1998; Krause and Ruxton, 2002). The pattern of schooling has a strong influence on the horizontal and vertical distribution of their predators. Birds, mammals and large predatory fish often aggregate in regions where dense schools are predictable and sustained, and changes in predator foraging behaviour often occur in response to variations in prey schooling patterns (Certain et al., 2011; Fréon and Misund, 1999; Matley et al., 2012; Ritz et al., 2011). Therefore, understanding the nature of schooling behaviour in the prey field is an essential step to interpreting foraging behaviour and success in myctophid predators. Recent studies have further highlighted that pelagic fish and their schooling behaviour could be impacted directly by increasing ocean temperatures and subsequent reductions in oxygen content (Brierley and Cox, 2010; Cheung et al., 2012), which is of particular relevance at South Georgia where there has been a 2.3 °C increase in winter temperatures over the past 81 years (Whitehouse et al., 2008).

Underwater acoustics provide an effective way of observing pelagic fish schools and the use of acoustic school descriptors have provided new insight into the schooling behaviour of many species around the world (Barange, 1994; Coetzee, 2000; Lawson et al., 2001; Petitgas et al., 2001; Tsagarakis et al., 2012). However, most of these studies have focussed upon commercially targeted species in a fisheries management context and there are few data on myctophid fish schools, particularly in the remote Southern Ocean, where any patterns in schooling behaviour remain unresolved for almost all myctophid species. Acoustic studies of myctophids and their schooling behaviour have been limited primarily due to difficulties in sampling them appropriately. For example, myctophid fish often reside in mixed-species communities at depths where it is difficult to collect discrete single-target detection data and the concurrent net samples necessary to resolve species-specific target-strength (TS) relationships (Simmonds and MacLennan, 2005). As a consequence, there are few robust TS relationships available to establish multi-frequency acoustic signatures for myctophid fish species and it is not yet possible to scale measurements of myctophid fish echo intensity to units of density (or biomass) for any species in the Southern Ocean. Myctophids also vary in behaviour and physiology and are therefore complex acoustic targets (Godø et al., 2009). Gas-filled swimbladders constitute between 90 and 95% of the acoustic backscatter from fish with such organs (Foote, 1980). Differences in myctophid swimbladder structure,

composition (e.g. gas-filled or lipid-filled) and orientation between, and within, species can have a large impact on their acoustic response (Butler and Percy, 1972; Godø et al., 2009; Marshall, 1960; Yasuma et al., 2003), which further confounds our ability to identify and quantify myctophids using acoustic techniques. Despite the challenges associated with myctophid fish, acoustic techniques offer the best available window of observation into their schooling behaviour in the natural environment at the appropriate temporal/spatial scales. New studies are therefore warranted to develop acoustic techniques for monitoring myctophids and their schooling behaviour robustly.

To our knowledge, there has only been one study that has attempted to describe myctophid fish schools in the Southern Ocean. Fielding et al. (2012) characterised myctophid schools from discrete short transects in a line across the Scotia Sea (from South Georgia to Signy Island, South Orkneys) and reported distinct latitudinal and seasonal trends in school numbers, size and depth distribution. The study showed that the number and backscattering strength of myctophid fish schools was highest in the northern Scotia Sea regions and this was correlated with increasing sea temperature and dynamic height. There was also evidence that schools were deeper and smaller in autumn than in spring and summer. In this paper, we continue the work of Fielding et al. (2012) and describe the inter-annual variation in distribution and size of myctophid fish schools at South Georgia using data collected during routine acoustic surveys between 2007 and 2012. These data provide important baselines for investigating the possible impacts of broad-scale environmental change on the myctophid component of the South Georgia ecosystem. Another aim of this investigation was to describe variation in myctophid schooling patterns in relation to one of the most important variables from the perspective of a land-based predator, the distance it must travel from its land-base in order to reach its prey. We also compare observations of school characteristics with hydrographic data to examine whether environmental conditions influenced the distribution and size of schools. Such analyses are important for understanding, and ultimately predicting, the foraging patterns of land-based predators at South Georgia, and for providing new insight into the ecology of myctophid fish.

2. Methods

2.1. Survey details

We use data from six acoustic surveys carried out by The British Antarctic Survey around South Georgia onboard the RRS *James Clark Ross* between 2007 and 2012 (see Table 1 for survey timing). Each survey was conducted in a standard 80×100 km box to the northwest of South Georgia (the western core box; hereafter WCB), which consisted of eight 80 km transects that were orientated perpendicular to the continental shelf-break (Brierley et al., 1999) (Figure 1). Acoustic transects were run in sequence from west to east against the prevailing current solely during daylight hours to avoid potential bias from diel vertical migration (DVM) or changes in target orientation (Godø et al., 2009). Net samples for krill were collected regularly during the surveys to ground-truth the acoustic observations using a Rectangular Mid-water Trawl (RMT8) net (Roe and Shale, 1979). However, this net does not sample large nekton, such as myctophid fish, effectively, and trawling with nets appropriate for catching these organisms was beyond the confines of the routine monitoring programme, which was principally aimed at Antarctic krill. There are consequently few robust net data on myctophids available from these surveys. However, we draw upon published data from myctophid surveys conducted around South Georgia during time periods coinciding with the present study to support our observations where possible (Collins et al., 2012; Collins et al., 2008). Although these surveys were not conducted during our WCB surveys, the data are the most contemporary and comprehensive available for mesopelagic fish in the region to date. Hydrographic data were collected regularly in the survey region using a SeaBird 911 Conductivity, Temperature, Depth (CTD) profiler that was also equipped with a fluorometer (a proxy for chlorophyll *a* concentration) and an SBE 43 oxygen sensor (Figure 1). The fluorometer and oxygen sensors were uncalibrated on the surveys, so they provide only relative estimates of these parameters. The CTD was deployed at six fixed locations (three on-shelf and three off-shelf; Figure 1) to either ~ 10 m above the sea bed in on-shelf regions, or to maximum depth of 1000 m at off-shelf stations.

2.2. Acoustic sampling and processing

Mean volume backscattering data (S_v dB re 1 m^{-1}) were collected using a Simrad EK60 scientific echosounder operating three split-beam transducers at frequencies of 38, 120 and 200 kHz. All transducers were hull-mounted and positioned no further than 4.9 m apart. The echosounder was configured so that all frequencies pinged simultaneously at an interval of

1.5-3.0 seconds (dependent on synchronisation with other shipboard sounding instruments) and echosounder power settings were consistent across all years (see Table 2 for echosounder settings and properties). Acoustic data were collected to a maximum depth of 500 m at a speed of ~10 knots, where weather and sea state permitted. All frequencies were calibrated at least once per cruise using standard reference targets (60.0, 23.0 and 13.7 mm copper spheres for the 38, 120 and 200 kHz, respectively) following the method of Foote et al. (1987). Only data at 38 and 120 kHz were used in the present study.

All raw acoustic data were processed using Echoview v4.80 software (Myriax, Hobart, Australia). Echograms were first edited to mask bad data arising from the seabed and the transducer near-field, surface noise, false-bottom echoes and periods of interference (a 3×3 median convolution algorithm was used to identify and remove cells within single pings greater than 40 dB different from surrounding cells), and time-varied-gain-amplified noise was then subtracted using the method described by Watkins and Brierley (1996). Following Cox et al. (2011), a moving matrix-based mean (convolution) of samples from the 38 and 120 kHz frequencies was applied on a grid of a common one ping by 0.5 m vertical range using a uniform (top hat) three-by-three kernel filter where the kernel element values are set to 1 (Reid and Simmonds, 1993). This procedure was applied to reduce the sampling volume mismatch between the two frequencies, increase the signal-to-noise ratio and reduce the effect of dropped pings on the location of fish school boundaries.

2.3. Fish school detection

The Echoview schools detection module implements the Shoal Analysis and Patch Estimation System (SHAPES; Coetzee 2000), and this was used to detect schools (pelagic aggregations) in the moving matrix-based mean 120 kHz echograms. Schools were identified as a group of cells that met minimum criteria for length and height, based on the sampling rate, echosounder operation parameters and ships speed, following Tarling et al. (2009) and Fielding et al. (2012). The software was configured to detect schools with a minimum length

of 15 m and height of 2 m, and the detection threshold was set to -70 dB. Schools were linked if they were less than 15 m apart horizontally or 5 m apart vertically (Appendix Table 1). These values were selected partially to match the resolution of our acoustic data and to facilitate comparisons with other studies in the region (Fielding et al., 2012; Klevjer et al., 2010; Tarling et al., 2009). A sensitivity analysis was conducted to examine the impacts of variations in these parameters on the number of schools detected with the SHAPES algorithm following Cox et al. (2011). The analysis was conducted on a representative echogram from one transect by varying one SHAPES parameter at a time, whilst holding the other six at fixed values (Appendix Table 1). The sensitivity analysis showed that the number of schools detected was relatively stable to variations in most parameters, although the analysis was sensitive to changes in values for school height (Appendix Figure 1). Halving or doubling the minimum school height parameter values increased and decreased the number of detected schools by ~34-46% in each instance, in agreement with the level of variation described by and Cox et al. (2011) and Tarling et al. (2009).

Physical and acoustic descriptors for the detected schools were exported from both the 38 and 120 kHz data, including corrected school length (m), thickness (m), area (m²), perimeter (m), depth (m) and mean area backscattering strength (NASC; m² nmi⁻²). All exported schools morphometrics were scrutinized for errors resulting from the schools geometry correction process and any erroneous data were removed (Diner, 2001). Not all acoustically detected aggregations were necessarily attributable to fish. A validated mean volume backscattering difference technique ($\Delta S_v = S_{v, 120 \text{ kHz}} - S_{v, 38 \text{ kHz}}$) was therefore used to identify fish/non-fish schools (Watkins and Brierley, 2002). Schools were identified as fish schools if the difference in mean S_v for the entire school ($S_{v, 120-38 \text{ kHz}}$) was less than 0 dB (Madureira et al., 1993). As there are no multi-frequency acoustic species-discriminators, or TS models, available for Southern Ocean myctophid fish, it was not possible to differentiate between schooling species or calculate the packing concentration/abundance of fish within schools. The acoustic backscatter of myctophid schools was therefore expressed simply as NASC at 38 kHz in this paper following Fielding et al. (2012). This frequency was selected because backscatter measurements from swimbladdered fish are less impacted by changes in target orientation than at 120 kHz (Simmonds and MacLennan, 2005).

2.4. Spatial and statistical analyses

The minimum distance between fish schools was calculated from the midpoint of each school using a great circle algorithm implemented in the R package ‘sp’ (Bivand et al., 2008). This package was also used to compute the minimum distance between the fish schools and the nearest point on the shoreline around South Georgia. All coastline data and bottom depths were taken from the GEBCO_08 grid (version 20091120, www.gebco.net). Data were then collated according to estimated distance to shoreline into the following zones to investigate relationships between school morphology and proximity to land: 0-30, 30-60, 60-90 and 90-120 km. These zones broadly match those of Cresswell et al. (2007) and Klevjer et al. (2010) where aggregation and vertical migration behaviour of pelagic nekton (Antarctic krill) is predicted to change over this cline as a function of different levels of land-based predation and food availability. Data were first compiled for each survey to evaluate the possibility of inter-annual variations in school morphology along this cline. Although the numbers of observations were low during some surveys, our analyses showed that the underlying relationship between school morphology and proximity to land was consistent across all surveys. Therefore, data were collated from all surveys for further analysis. We also extracted data on underlying bathymetry (GEBCO_08) at each school position using ArcGIS v9 mapping software to assess whether or not schools were associated with certain bathymetry zones.

Statistical differences in schools properties between years and spatial zones were tested for using a combination of a Mann-Whitney rank sum test and a Kruskal-Wallis ANOVA by ranks test. Following significant outcomes from the Kruskal-Wallis ANOVA tests, a multiple pairwise comparison test was conducted to explore which factors contributed most to the observed variation (Siegel and Castellan, 1988). All statistical tests were conducted in R software (R Development Core Team, 2010).

3. Results

3.1. Oceanography in the WCB

All CTD data were resampled (mean) into 2.5 m depth bins and data were subsequently aggregated to give mean on-shelf and off-shelf temperature, salinity, oxygen and fluorescence profiles for each survey (Figure 2). The CTD was not equipped with an oxygen sensor or fluorometer in 2007, so no oxygen or fluorescence data were available for that year.

Each off-shelf profile collected during the mid-season surveys (2009-2012) consistently showed the presence of three major water masses: Antarctic Surface Water (AASW) above 80 m, Winter Water (WW) around 110 m and Circumpolar Deep Water (CDW) deeper than ~200 m (Figure 2a). Profiles varied by around ± 0.5 °C at most depths, with variations in salinity of around ± 0.3 and oxygen concentration (± 1.0 ml l⁻¹) between years. Profiles of fluorescence in the photic layers (~0-80 m) varied by around ± 1.0 μ g l⁻¹ at most depths.

Mean temperature and salinity in the AASW ranged between 2-4 °C and 33.7-34.1, respectively, and these waters had the highest oxygen levels (>6.0 ml l⁻¹) and greatest fluorescence (up to ~ 3 μ g l⁻¹). WW was predominantly cooler (0-2 °C) and slightly fresher (34.0-34.3) than the AASW, with distinct temperature minima occurring at around 110 m. Oxygen levels in the WW decreased by ~ 2 ml l⁻¹ over the depth range 100-200 m. Environmental conditions in the CDW were relatively stable with depth compared to the surface-induced AASW and WW, with temperatures around 2 °C, salinities around 34.5 and oxygen levels in the order of ~ 3.5 ml l⁻¹. All three of these water masses were also evident during the early-season (November 2007) and late-season (April 2008) surveys, but there were clear seasonal differences in the upper water mass properties due to thermal mixing by surface conditions. For example, AASW waters were notably cooler (by ~ 0.6 -2 °C) and more mixed during the early-season and late-season than during mid-summer, and the base of the AASW occurred predominantly deeper in the water column (~ 120 m compared to ~ 80 m). Fluorescence levels were also comparatively low during the late-season (<1.0 μ g l⁻¹).

On-shelf profiles were comparable to those observed off-shelf and the level of inter-annual variation in temperature, salinity and oxygen levels was broadly similar in the two regions. The on-shelf waters were marginally cooler (by ~ 0.5 °C) and often higher in chlorophyll *a* concentration than those in off-shelf regions, and there were some slight differences in the

boundaries of the water masses present on-shelf during the mid-season surveys. AASW occurred predominantly above ~50 m at the on-shelf sites whilst the WW occurred at around 75 m. There was no evidence of CDW extending on-shelf. The on-shelf water masses were relatively well-mixed throughout the water column during the early- and late-season surveys.

3.2. Schools morphological characteristics

A total of 578 fish schools were identified from the six acoustic surveys using the dual-frequency dB method. The density of schools detected in the WCB varied between surveys (0.04 - 0.23 schools km^{-1}) and there was significant ($P < 0.01$) inter-annual variation in median school length, thickness, depth, perimeter and NASC between surveys conducted during the same season (mid-summer 2009-2012; Figure 3 and Table 3). However, there was no significant difference ($P > 0.05$) in either the minimum distance between schools, or the area of schools between surveys. An all pairwise comparison test of all school descriptors between surveys indicated that schools observed during the 2008 (late-season) and 2009 (mid-season) surveys had the greatest differences in morphology and depth distribution when compared to schools on all other surveys. The greatest densities of fish schools were detected during the mid-season surveys in 2009 and 2011 (~ 0.23 schools km^{-1}), and these schools had the greatest median length (127.9 and 106.5 m) and largest median perimeter (340.0 and 286.8 m; Figure 3 and Table 3). However, schools observed on these surveys also had the lowest median NASC (13.4 and 23.5 $\text{m}^2 \text{ nmi}^{-2}$) and shallowest median depth (29.4 and 46.9 m). School density was lowest during the 2010 mid-season survey (0.04 schools km^{-1}). The largest schools in terms of thickness (7.0 m), area (416.9 m^2) and NASC (304.3 $\text{m}^2 \text{ nmi}^{-2}$) occurred during the late-season survey in 2008, and these schools were distributed much deeper in the water column than on any other survey (234.7 m).

The maximum school depth observed during the surveys was ~400 m. However, most schools were distributed much higher in the water column, the overall median depth being 126.4 m (Table 4), and few schools were positioned below 300 m (Figure 3). Although a few schools occurred in the surface layers (above 50 m), the majority of schools were positioned below ~60 m. Comparisons of school depth distribution with the underlying oceanographic data (off-shelf profiles were used to cover the full depth range of the schools) showed that

schools did not occupy the same water masses on each survey (Figure 4). In some instances, such as on the 2007 (early-season) and 2012 (mid-season) surveys, schools were situated in WW and the median (and mean) depth of fish schools corresponded with the depth at which the temperature minima occurred (~100-120 m). In contrast, schools observed on the 2009 mid-season survey were positioned above the temperature minima in the AASW, whilst schools observed on the 2008 (late-season) and 2010 (mid-season) surveys occurred predominantly below the temperature minima, occupying CDW and WW, respectively. The mean depth of schools on the 2011 mid-season survey broadly corresponded with the temperature minima at 105 m in WW, but the median depth occurred much higher in the water column (~50 m) and coincided with the AASW. Almost all schools on each survey were positioned in the regions of the water column where oxygen concentrations were above ~3.5 ml l⁻¹ (Figure 4).

3.3. Schools horizontal distribution

Myctophid schools were observed regularly on most transects in the WCB, but there were distinct differences in the horizontal distribution of schools around South Georgia between surveys, including significant ($P < 0.05$) inter-annual variation between surveys that were conducted in the same season (2009-2012; Figure 5). During the 2007 (early-season), 2008 (late-season) and 2012 (mid-season) surveys, schools were predominantly distributed in on-shelf regions that were landward of the 500 m isobaths, whilst schools were distributed much further off-shelf during the mid-season surveys in 2010 and 2011. Not many schools extended landward of the 500 m contour during the 2010 and 2011 surveys. Schools occurred predominantly off-shelf during the 2009 mid-season survey, however, a relatively large proportion of schools were also situated on-shelf in the most south-westerly regions of the survey area. The underlying bathymetry value at each school position was extracted from the spatial plots and these data were subsequently binned into 100 m bathymetry zones to investigate whether or not schools were orientated along particular bathymetry gradients (Figure 6). Although the number of schools observed on each survey was relatively low (Table 3), the distribution of schools appeared to be separated into zones according to underlying bathymetry during most surveys. For example, there were three distinct peaks in school abundance that occurred around the 500 m, 2500 m and 3400 m isobaths during the 2009 survey. A similar trend was evident on the 2011 survey, with schools mostly distributed

along the 1600 m, 2700 m and 3000 m isobaths. There was predominantly one peak in school abundance during both the 2007 and 2012 surveys which occurred around the 300 m and 500 m contours, respectively, whilst two distinct peaks occurred at 500 m and 1700 m on the 2008 survey. The total number of schools observed on the 2010 survey was particularly low compared to the other surveys, however, the schools present at this time still appeared to be separated into two peaks along the 2000 m and 3400 m depth contours.

3.4. Properties of schools in relation to proximity of land

The NASC of fish schools was significantly greater ($P < 0.01$) inshore (0-60 km) compared to offshore (90-120 km) and there was a distinct decline in NASC with increasing distance from land after 60 km (Figure 7a). The median NASC of fish schools was around seven times greater in the 30-60 km zone ($104.2 \text{ m}^2 \text{ nmi}^{-2}$) than in the 90-120 km zone, ($13.4 \text{ m}^2 \text{ nmi}^{-2}$; Table 5). A similar trend was observed in the depth distribution of fish schools. Schools occurred progressively higher in the water column with increasing distance from land after 60 km, with the difference between the 30-60 km and 90-120 km zones being significant ($P < 0.01$; Figure 7b and Table 5). Comparisons of schools characteristics in the two inshore regions indicated that schools in the 0-30 km zone had a significantly lower ($P < 0.05$) NASC and shallower depth distribution than those in the 30-60 km zone, but these schools still had a greater NASC and depth distribution than the offshore schools at 90-120 km. Bathymetry in the 0-30 km zone (median: 182 m) was notably shallower than in the 30-60 km zone (median: 480 m), so school depth distribution and morphology in this region may have been impacted by constrained water depth, or by bio-physical processes occurring in the epi-benthic zone.

There were marked differences in fish school morphology along the proximity to land gradient (Figures 7 and Table 4). Schools were significantly greater ($P < 0.01$) in length (102.4 m compared to 73.8 m) and perimeter (318.8 m compared to 156.1 m) in the offshore regions (90-120 km) compared to inshore zones (0-30 m), but schools were thinner in the outermost zone (3.8 m) than in the more inshore regions (30-60 m: 5.4 m). However, the thickness of schools in the 0-30 km was an exception to this trend. There was also some evidence that the cross-sectional area of schools was greater inshore than offshore, as schools in the 0-30 km zone had a significantly smaller ($P < 0.01$) median area than those in the 90-

120 km zone. However, the trend in the variation of school area with increasing distance from land was not statistically significant ($P>0.05$; Figure 7f). There were also no significant differences in the minimum distance between schools along the proximity to land gradient and schools were generally positioned around 0.11 to 0.17 km apart (Table 4).

4. Discussion

There is little data on myctophid fish schools in the Southern Ocean, which is primarily due to issues in sampling them appropriately using acoustics and nets. Myctophid species identification through TS relationships is presently unresolved and remains a challenge for acoustic techniques. Our approach was to consider myctophid schools as a single generic category and examine how schools properties changed on an inter- and intra-annual basis around South Georgia.. Our results indicate that myctophid fish form regular schools in this region and that there were distinct differences in myctophid schools characteristics at the island amongst surveys. In particular, we found that the horizontal distribution of schools varied from on-shelf to off-shelf between surveys and that myctophid schools often occurred in discrete peaks that appeared to be related to underlying bathymetry. The vertical distribution of schools varied amongst surveys, and schools appeared not to occupy the same water masses within the same seasons. There were also distinct changes in depth distribution and school morphology with increasing distance from land. Offshore schools appeared to be positioned higher in the water column than onshore schools, and the offshore schools tended to be longer, thinner, greater in perimeter, and acoustically weaker than those in inshore regions. These differences in school characteristics suggest that myctophids could be responding to a combination of predatory threat and variations in the physical properties of the water column. Alternatively, there could be spatial habitat partitioning of myctophids at South Georgia, with species of different schooling behaviour, or different life-stages within a species, orientating along a bathymetric gradient.

4.1. Target identification

In this paper, we identified mesopelagic fish schools using a validated dual-frequency technique (Madureira et al., 1993; Watkins and Brierley, 2002) and we attributed these

schools to the myctophid component of the South Georgia fish community based on available net data obtained during the study and from published sources (Collins et al., 2012; Collins et al., 2008). Biological targets with negative $S_{v120-38 \text{ kHz}}$ backscatter around South Georgia are most likely to be organisms with gas-filled organs such as siphonophores, swimbladder fish, or possibly squid (Korneliussen and Ona, 2003; Madureira et al., 1993; Martin et al., 1996; Woodd-Walker et al., 2003). Net samples collected in the WCB as part of a long-term monitoring programme for krill and zooplankton provided strong evidence that gelatinous organisms were unlikely to comprise a major component of the acoustic backscatter we measured (Ward et al., 2012). Furthermore, our study focussed only on acoustic targets that formed discrete and regular schools, which reduces the likelihood of siphonophores biasing our results because they do not aggregate densely. Although squid, such as *Martial hyadesi* and *Loligo gahi*, have been reported around South Georgia, particularly during austral winter (June), these organisms have a distribution that is highly associated with the Antarctic Polar Front and are found predominantly in regions beyond the WCB (Anderson and Rodhouse, 2001; Gonzalez and Rodhouse, 1998; Rodhouse et al., 1996). Ground-truthed acoustic observations also showed that aggregations of squid in the region tended to have a relatively weak acoustic response and exhibit positive $S_{v120-38 \text{ kHz}}$ backscatter (Goss et al., 2001; Goss et al., 1998), so we advocate that squid were an unlikely source of bias in the study. All available net data from around South Georgia collected around the timeframe of the study period showed that the dominant group of swimbladder fish in the mesopelagic community was Myctophidae (Collins et al., 2012; Collins et al., 2008). Other swimbladder fish groups, such as some Bathylagidae, were observed in the region, but these groups were comprised of predominantly deep-dwelling fish that occurred below our vertical observation window (>600 m) (Collins et al., 2012; Collins et al., 2008). These groups often occur only in relatively low abundance at South Georgia and they are not known to exhibit daytime vertical migrations that would result in them being detected above 500 m during our surveys (Collins et al., 2012; Gon, 1990). We therefore maintain that the predominant acoustic signal within our observation windows was from swimbladder myctophid fish.

4.2. Possible schooling species

There are few data on the ecology of most myctophid species in the Southern Ocean, and it is not fully known which species form regular, sustained schools, or which species remain

solitary. Several high latitude pelagic fish species, such as Atlantic herring (*Clupea harengus*), do not always form single species schools and often occur within mixed species assemblages (ICES, 2008). Whether or not myctophid fish form mono-specific schools is presently unknown. Furthermore, it is possible that there is high intra-specific variation in myctophid schools characteristics as different life stages within the same species could form unique schools. Such schools may form at different times of year, in different spatial zones and under different environmental conditions, thus adding further complexity to the situation. In this section we evaluate some of the available lines of evidence that cast light on which schooling species were detected around South Georgia during this study.

Two species that are possible candidates for the schools observed in the study are *Electrona carlsbergi* and *Krefftichthys anderssoni*. These two species have prominent gas-filled swimbladders throughout their life cycle (Marshall, 1960), making them strong acoustic targets that would fall readily within the negative backscatter range of our dual-frequency identification technique. They are also both distributed predominately in the upper 500 m of the water column during the daytime, which is within the observation window of this study (Collins et al., 2008). Acoustic observations have shown that both *E. carlsbergi* and *K. anderssoni* form distinct schools in the Southern Ocean (Perissinotto and McQuaid, 1992; Zasel'sliy et al., 1985) and there is evidence from fish larval surveys that *K. anderssoni* also exhibit this behaviour around South Georgia (Belchier and Lawson, 2013). *E. carlsbergi* and *K. anderssoni* were found regularly in net samples at South Georgia during the timeframe of this study, but there was clear variation in their presence at the island between years (Collins et al. 2008; Collins et al. 2012; Figure 8). Although some of this variation may be attributable to temporal variation in net sampling, the available data showed that *E. carlsbergi* comprised a relatively high proportion of the myctophid community in 2004 and 2006, but was notably absent, or in low abundance, in 2008 and 2009. *K. anderssoni* occurred regularly within the community in most years where net samples were taken and the species was one of the most abundant myctophids at South Georgia, particularly in 2006 and 2009. RMT8 nets hauls deployed for krill and zooplankton during our surveys often contained small numbers (<27 individuals) of *K. anderssoni*, with a few individuals (<18) of *Electrona antarctica* and *Gymnoscopelus braueri* also occurring on occasion. Therefore, *K. anderssoni* is the more likely of the two to be detected throughout this study, whilst *E. carlsbergi* was probably detected intermittently. It has been suggested that *K. anderssoni* regularly form aggregations

along the shelf-break at South Georgia before moving to the more inshore regions and deep-water fjords around the island to spawn (Belchier and Lawson, 2013). *K. anderssoni* larvae occur regularly in plankton trawls taken around Cumberland East Bay during the mid- to late season, which might indicate that the species undertakes distinct on-shelf/off-shelf spawning migrations throughout its lifecycle. It is also possible that there are ontogenetic variations in distribution for this myctophid, as predator species that forage in more inshore regions tend to consume much smaller sized *K. anderssoni* than predators that have a greater foraging range in more oceanic regions (Cherel et al., 2007). Available data on *E. carlsbergi* suggest that main distribution of the species occurs around the Polar Front (Efremenko, 1987; Hulley, 1981; Zasel'sliy et al., 1985), a region targeted frequently by predator species based at South Georgia (Scheffer et al., 2012). The presence of *E. carlsbergi* at South Georgia could therefore be intermittent, either as part of a broad-scale migration, or due to variations in environmental conditions, such as temperature and changes in the oceanic circulation (Collins et al., 2012; Fielding et al., 2012).

Other species that occurred regularly in the upper 500 m of the water column around South Georgia were *E. antarctica* and *G. braueri* (Figure 8). However, these species are unlikely to be responsible for the schools observed in this study because certain features of their swimbladder structure/composition make them relatively weak acoustic targets that would not register within the negative $S_{v120-38}$ backscatter range of our dual-frequency identification technique. In *E. antarctica* the swimbladder is much reduced and almost absent throughout its life cycle, so the acoustic response from this species would be markedly low due to the low volume of gas in this organ (Marshall, 1960). Species within the *Gymnoscopelus* genus have swimbladder properties that change throughout the life cycle. Swimbladders in this genus are relatively large and predominantly gas-filled in the early larval stages, but the volume of gas within this organ reduces rapidly with age and there is a pronounced transition in swimbladder composition from gas-filled to lipid-filled by the early juvenile stages (Marshall, 1960). Furthermore, the swimbladder wall becomes thicker with age, such that the inner cavity of this organ becomes much reduced and many species in this group, including *G. braueri* and *G. nicholsi*, are not considered to possess a swimbladder as adults (Marshall, 1960). The reasons for this switch in swimbladder composition and structure are presently unclear, but the reduced gas component in this organ in the later life stages causes these fish to have a low acoustic response for the majority of their life cycle. Evidence from the

available net data suggested that fish within the *Gymnoscopelus* genus around South Georgia were predominantly in the adult stages, so *G. braueri*, *G. nicholsi* and *G. fraseri* are unlikely to be contributors to the schools measured in this study (Belchier and Lawson, 2013; Collins et al., 2012; Collins et al., 2008). Other fish observed occasionally in the region that are likely to have a low acoustic response due to such changes in physiology and swimbladder morphology are the myctophids *Lampanyctus*, and the non-myctophid groups *Channichthyidae* and *Nototheniidae*, which have a pelagic phases in the juvenile life stages (Marshall, 1960). These fish can therefore be differentiated easily from gas-bearing myctophids and were excluded from the analysis due to their markedly low TS.

Myctophids within the genus *Protomyctophum* were also often observed around South Georgia during this study, with *P. bolini* comprising a relatively high proportion of the fish community in most years (Figure 8). All species within this genus possess gas-filled swimbladders throughout their life cycle, and are therefore strong acoustic targets, and they reside predominantly in the upper 400 m of the water column, making them possible contributors to the schools analysis. Although *P. bolini* has been reported in the diet of predators at South Georgia (Reid et al., 2006), very little is known about the schooling behaviour of the species in the region. It has been suggested that *P. choriodon* is possibly a schooling species in the Scotia Sea (pers. comm., M. Collins, South Georgia Government, Falkland Islands), but this species comprised a relatively small proportion of the myctophid community between 2006 and 2009. However, greater proportions of *P. choriodon* were observed in 2004, so it is possible that the species might have also contributed to our analyses. Neither of these species were observed in high quantities in the RMT8 nets used for krill catches during the surveys. However, the RMT8 nets are not effective at sampling myctophid fish and it is therefore not possible to discount these species from our analysis based on these observations. In conclusions, and based on the available net data, observations from fish larval/zooplankton surveys and evidence from detailed swimbladder studies, we propose that the most probable schooling species we detected throughout this study were *K. anderssoni*, *E. carlsbergi*, and *P. bolini*. However, there is a clear need for further acoustic and netting studies to substantiate our hypotheses.

4.3. Insight into myctophid ecology

Although we are not able to resolve the species observed during the schools analysis, our results still provide new insight into the general ecology of myctophid schools at South Georgia. Myctophid schools, regardless of species or life cycle stage, were deeper and acoustically stronger in onshore regions where predation pressure from shore-based predators can be expected to be highest (Staniland et al., 2004). An acoustic study at Marion Island, Southern Ocean, reported an onshelf/offshelf gradient in the presence of a deep scattering layer (DSL) attributable to *K. anderssoni* whereby the DSL was strong in offshelf waters but faded gradually towards the island's shelf (Perissinotto and McQuaid, 1992). These authors suggested that increased predation pressure from land-based predators in the inshore regions was responsible for this trend. In our study, schools appeared to position themselves deeper in the water column and become more compact, or denser which could reduce the chances of being encountered and eaten by diving predators. A similar trend was observed for Antarctic krill across the Scotia Sea indicating that predation pressure is a key driver of the distribution and behaviour of schools of nektonic organisms in the region (Cresswell et al., 2007; Klevjer et al., 2010). Other than a response to predation pressure, the observed trends in depth distribution and echo strength of the schools could also have resulted from shifts in myctophid species or lifecycle stages between zones, with each different species/stage having a different depth distribution and swimbladder morphology in each zone. However, the underlying trend remains that myctophid school depth and backscatter strength are greatest in the zones closest to land.

An interesting observation from these results is that myctophid schools also occurred often in the upper 100 m of the water column during daylight hours in the more offshore zones (90-120 km). This contrasts with netting studies around South Georgia that showed that myctophids seldom occur above 200 m during the daytime (Collins et al., 2008). Thus our results support the notion that there is a high degree of net avoidance by myctophids in the upper regions of the water column during periods of high daylight intensity (Collins et al., 2008). Other studies have reported daylight near-surface schooling of mesopelagic fish that perform DVM in high latitude and equatorial regions and it has been suggested that this could be related to local light regimes (Alverson, 1961; Kaartvedt et al., 1998; Marchal and Lebourges, 1996). For example, both these regions represent an extreme regarding light climate, such as the absence of darkness in summer at high latitudes and rapid changes between daylight and darkness in equatorial regions. Periods of prolonged daylight and short

dusk and dawn periods imply short anti-predation windows, such that myctophids could be rapidly exposed to diurnal predators in these regions. Therefore schooling as a strategy to extend the feeding period in the upper layers, or as an immediate response when encountered by predators, may be beneficial to vertically migrating myctophid fish (Kaartvedt et al., 1998).

Schools were significantly longer, thinner and greater in perimeter in offshore regions. Offshore regions were also observed to have higher current velocities compared to inshore during the study (Figure 9). Schools in offshore regions may therefore be experiencing more shear stress and are consequently elongated. Similar trends have been suggested for Antarctic krill swarms (Zhou et al., 1994). A further explanation could be that schools in the inshore regions reduce their horizontal dimensions by extending vertically so that they become narrower in shape and are therefore less visible to predators from above. Such behaviour has been suggested for *K. anderssoni* in shallow waters off Marion Island as an anti-predatory mechanism to avoid predation from above when DVM becomes constrained by bathymetry (Perissinotto and McQuaid, 1992). It is also possible that the onshore and offshore trends were simply a function of variations in school shape and size due to schooling of different species or different life stages within the same species. Indeed, our results provided some evidence that myctophid school distribution was separated horizontally according to underlying bathymetry in most years, and this could be evidence of spatial habitat partitioning of different myctophid species or separation of different life cycle stages. The trend could also be indicative of pulsed migration of myctophid species or stages between inshore and offshore regions around South Georgia.

4.4. Inter-annual variation in myctophid schools at SG

The WCB annual acoustic survey was designed so that the same regions could be surveyed repeatedly using consistent methodology at approximately the same times of year (where possible). Our results showed that, despite this continuity in survey design and timing, there were distinct inter-annual variations in school size, depth and horizontal distribution. All surveys except for that of 2008 were conducted at similar times of year either during mid-summer (2009-2012), or within ~7 weeks of mid-summer (2007). The 2008 survey was

conducted in the late-season, so the increased depth distribution, thickness and NASC of schools observed during this time could be due to seasonal effects. For example, studies have shown that there is a distinct seasonal deepening of acoustic scattering layers in the wintertime at high latitudes that could be related to a corresponding seasonal deepening of food resources, such as small zooplankton (Anderson et al., 2005; Chereskin and Tarling, 2007). Distinct seasonal deepening of myctophid schools was also reported by Fielding et al. (2012) across the Scotia Sea.

Our results showed that, although school size can be relatively large, these schools do not always have the greatest backscattering strength. Therefore school size is not necessarily indicative of myctophid biomass at South Georgia. Overall, there was a high degree of concordance between school dimensions in the present study to those of Fielding et al. (2012) from across the Scotia Sea, suggesting that our results have relevance over greater spatial scales than that of the WCB. We also found that myctophid schools were not always associated with the same water masses in each year, and the depth of the temperature minima and oxygen maxima was not a robust indicator of school depth. The reasons for these inter-annual differences in size and depth distribution were not clear from our data set and it is possible that differences in species composition and life stages could be a major factor. However, there is a clear requirement to quantify the level of inter-annual variation in these parameters for robust predator foraging models and analysis into food web dynamics. For example, our results indicated that predators would have to travel further from their land-bases and dive deeper in order to reach their prey sources in some years more than others. The results also showed that there were years where school abundance at South Georgia was relatively low, such as in 2010, so these episodes could correspond to periods of low food availability for some myctophid predators. The relevance of these periods of low myctophid school abundance could have particular significance for a range of predators during krill-poor years. Understanding the scale and timing of low school abundance and biomass around the island is therefore important for understanding the extent to which these alternative trophic pathways can buffer periods of low krill abundance at South Georgia.

4.5. Conclusions

Myctophids and their schooling behaviour are difficult to study using both nets and underwater acoustics. These fish are deep-dwelling, avoid nets during the daylight, and are complicated acoustic targets and this has restricted studies of this important component of the food web. In particular, myctophids are difficult to identify to species level using underwater acoustics and further studies are required to gain new insight into the TS relationships and acoustic backscattering properties of myctophid species. New approaches, such as acoustic morphometric descriptors/classification (Charef et al., 2010; Korneliussen and Ona, 2003), *in situ* TS probes and theoretical TS modelling (Yasuma et al., 2003; Yasuma et al., 2010), together with continued acoustic surveys and scientific netting, are likely to develop the field of myctophid acoustics. However, there is clearly a pressing need to acquire basic data on these fish and their schooling behaviour in these high latitude regions that are experiencing rapid environmental change. In this paper, we provide useful baselines on myctophid fish schools at South Georgia and give some indication of the levels of inter-annual variability in myctophid school characteristics. Despite uncertainties with species identification, our analyses provide information on the ecology of schooling myctophids of use to predator foraging models and ecosystem studies. Our parameterisations of acoustically-detected myctophid schools also give scientists some quantitative means with which to monitor the response of myctophid schooling behaviour over time in an ocean-warming context.

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Table and figure legends

Figure 1. Map of the island of South Georgia showing the eight acoustic transects, hydrographic stations (open circles) and the standard Western Core Box survey region (dashed line). The 100, 500, 1000, 1500 and 2000 m isobaths are also shown.

Figure 2. Hydrographic properties in the Western Core Box during 2007-2012. (A) mean potential temperature, (B) mean salinity, (C) mean oxygen concentration and (D) mean fluorescence data are shown for on-shelf (left plots) and off-shelf (right plots) stations. No oxygen or fluorometer data were collected in 2007.

Figure 3. Fish school parameters: mean (dashed line), median (solid line), 25th to 75th percentile (grey box) and outliers (filled circles) of (A) density of schools (no. km⁻¹), (B) Nautical Area Scattering Coefficient (NASC, m² nmi⁻²), (C) depth (m), (D) length (m), (E) thickness (m), (F) area (m²), (G) perimeter (m) and (H) minimum distance between school (km)

Figure 4. Depth distribution of fish schools (box plot) in relation to mean temperature (black line) and oxygen levels (dashed line) during each survey (A-F). Values shown in the box plot are: mean (dotted line), 95% CI (whiskers), median (solid line), 25th and 75th percentiles (grey box), and outliers (filled circles).

Figure 5. Distribution of fish schools during (A) 2007, (B) 2008, (C) 2009, (D) 2010, (E) 2011 and (F) 2012. Filled circles are proportional to the square root of the Nautical Area Scattering Coefficient ($\text{m}^2 \text{nmi}^{-2}$) of the schools. The 100, 500, 1000, 1500 and 2000 m isobaths are also shown.

Figure 6. Distribution of fish schools in relation to underlying bathymetry around South Georgia. The number of schools detected in each year is shown in Table 3.

Figure 7. Fish school parameters in relation to proximity to land: mean (dashed line), median (solid line), 25th to 75th percentile (grey box) and outliers (filled circles) of (A) Nautical Area Scattering Coefficient (NASC, $\text{m}^2 \text{nmi}^{-2}$), (B) depth (m), (C) length (m), (D) thickness (m), (E) perimeter (m), (F) area (m^2).

Figure 8. Myctophid species composition at South Georgia between 2004 and 2009. Data were summarised from Collins et al. (2008) and Collins et al., (2012). Bar fill colours denote species that possess swimbladders that are, a) prominently gas-filled and have a strong acoustic response (black), b) reduced or predominantly lipid-filled and have a weak acoustic response (white), and c) gas-filled in the juvenile stages, but predominantly lipid-filled in adulthood such that the acoustic response varies from strong to weak based on ontogeny (grey) (Marshall, 1960).

Figure 9. Inshore and offshore variation in current velocities (m s^{-1}) in the Western Core Box measured using an Acoustic Doppler Current Profiler (ADCP) during a survey in 2004. Westward current flow is shown in purple and eastward current flow is in green.

Figure A1. Schools length sensitivity analysis showing the variation in the number of schools detected in a representative echogram using the SHAPES detection algorithm. The filled circle denotes the selected value for each SHAPES parameter used in the analysis

Table 1. Western Core Box survey details.

Cruise	Year	Season	Start date	End date	No. transects	Total transect length (km)
JR184	2007	Early	07/11/2007	10/11/2007	8	643.70
JR186	2008	Late	19/04/2008	22/04/2008	8	641.92
JR188	2009	Mid	31/12/2008	03/01/2009	8	641.26
JR228	2010	Mid	20/12/2009	23/12/2009	7	559.34
JR245	2011	Mid	26/12/2010	30/12/2010	8	632.29
JR260	2012	Mid	02/01/2012	05/01/2012	8	638.66

Table 2. Scientific echosounder system parameters during data collection. Mean values (standard deviations in parenthesis) are given for variable calibration parameters for brevity, but cruise-specific values were used during the acoustic analysis.

Specification	Frequency (kHz)		
	38	120	200
Transducer type	ES38	ES120-7	ES200-7
Transducer depth (m)	5	5	5
Max. power (W)	2000	1000	300
Pulse duration (ms)	1.024	1.024	1.024
Sample length (m)	0.1867	0.1867	0.1867
Ping interval (s)	1.5	1.5	1.5
Bandwidth (Hz)	2425	3026	3088
Sv transducer gain (dB)	24.89 (0.98)	21.64 (0.58)	23.48 (0.82)
2-way equivalent beam angle (dB)	-20.7	-20.7	-19.6
3 dB beamwidth alongship (deg)	6.96 (0.13)	7.59 (0.11)	6.44 (0.18)
3 dB beamwidth athwartship (deg)	6.95 (0.10)	7.54 (0.11)	6.44 (0.16)
Absorption coefficient (dB/km)	9.55 (0.19)	26.58 (1.33)	40.25 (1.10)
Sound velocity (m/s)	1455.75 (5.50)	1455.75 (5.50)	1455.75 (5.50)
Sa correction	-0.56 (0.04)	-0.41 (0.02)	-0.46 (± 0.17)

Table 3. Summary statistics for fish schools. Values are presented as 25th percentile/**median**/75th percentile. NASC is the Nautical Area Scattering Coefficient ($\text{m}^2 \text{ nmi}^{-2}$).

Year	Season	N	NASC ($m^2 nmi^{-2}$)			Depth (m)			Length (m)			Thickness (m)			Perimeter (m)			Area (m^2)			Minimum distance to next school (km)			Bathymetry zone (m)			Distance to land (km)		
2007	Early	92	23.4	60.2	202.1	63.2	164.3	214.9	67.0	76.1	95.7	2.1	3.5	7.4	145.4	173.9	403.3	125.0	196.0	604.2	0.00	0.11	0.39	-347	-290	-201	25.40	31.85	48.49
2008	Late	83	134.8	304.3	730.4	214.8	234.7	253.4	59.9	72.7	101.0	4.8	7.0	11.7	160.2	245.6	393.8	229.4	416.9	699.8	0.04	0.11	0.24	-1670	-470	-321	46.49	49.56	60.65
2009	Mid	149	8.3	13.4	102.4	24.2	29.4	172.1	82.1	127.9	166.2	2.4	3.8	7.9	219.9	340.0	472.8	135.3	274.2	671.7	0.03	0.13	0.39	-3292	-3035	-857	73.88	76.53	82.21
2010	Mid	38	19.1	58.3	90.7	131.9	166.7	188.2	74.3	81.7	88.3	1.8	3.5	5.5	158.8	170.1	201.0	138.1	270.0	374.5	0.02	0.48	0.88	-3368	-2002	-1752	57.46	65.39	78.29
2011	Mid	146	8.8	23.5	119.2	38.0	46.9	203.0	73.5	106.5	175.4	2.4	5.2	9.2	159.8	286.8	480.1	135.9	400.7	892.7	0.01	0.14	0.43	-3380	-2730	-1710	59.43	75.51	85.59
2012	Mid	70	33.8	85.7	184.5	68.6	95.4	138.6	49.2	59.2	78.5	3.0	4.9	8.5	112.1	151.0	273.3	118.7	197.3	469.9	0.03	0.1	0.53	-348	-426	-348	42.84	75.47	77.2
All	-	578	13.6	49.9	188.0	37.0	126.4	210.5	66.6	84.9	147.8	2.4	4.7	8.6	153.1	235.8	448.5	153.1	282.3	675.6	0.01	0.13	0.38	-3157	-1670	-390	48.82	71.02	79.09

Table 4. Summary statistics for fish schools in four zones according to proximity to land.

Values are presented as 25th percentile/**median**/75th percentile. NASC is the Nautical Area Scattering Coefficient ($m^2 nmi^{-2}$).

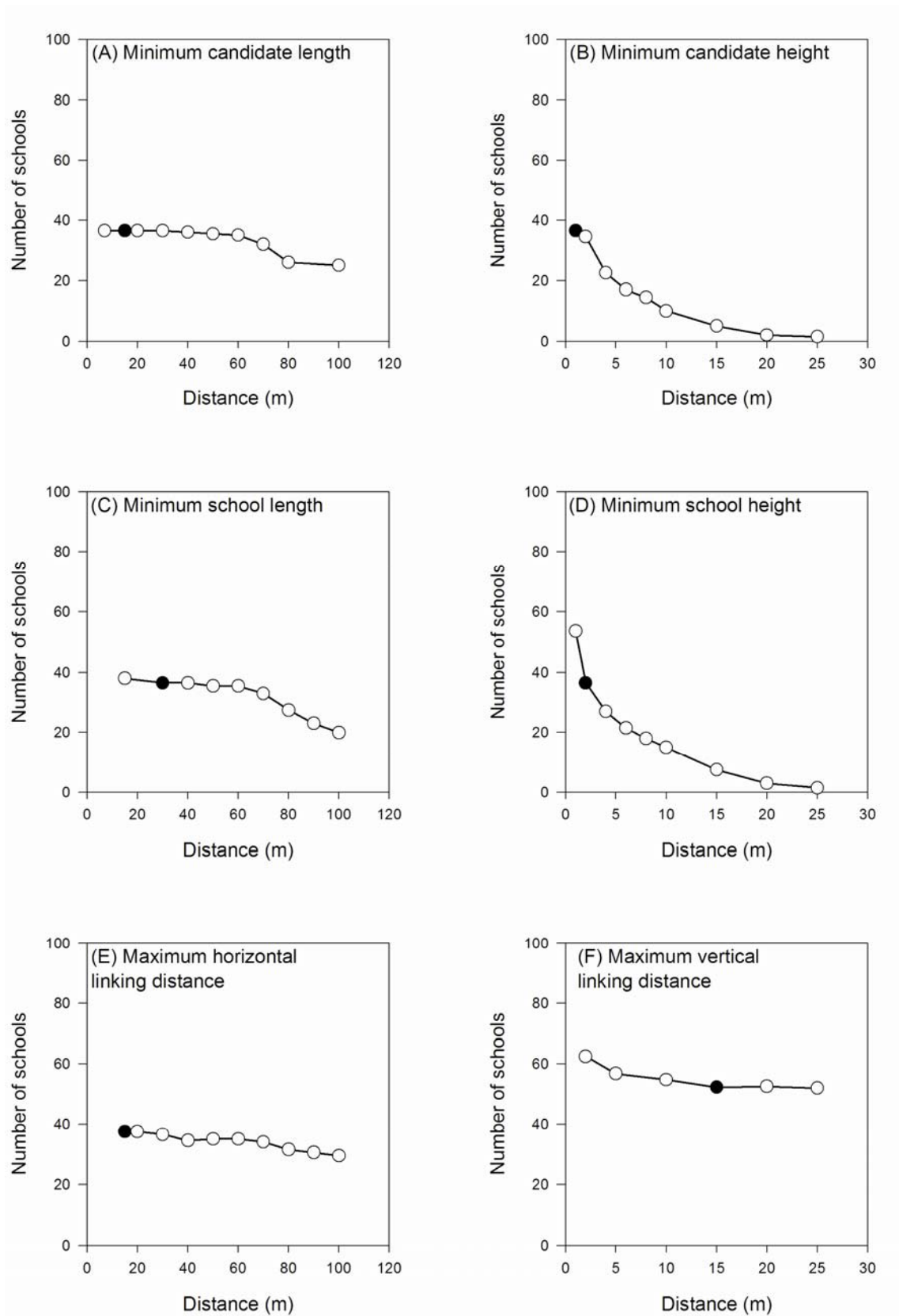
Zone (km)	N	NASC ($m^2 nmi^{-2}$)			Depth (m)			Length (m)			Thickness (m)			Perimeter (m)			Area (m^2)			Minimum distance to next school (km)		
0-30	46	21.4	37.7	121.1	43.1	139.7	191.9	65.1	73.8	85.1	2.1	2.7	4.8	143.8	156.1	202.0	131.6	167.8	262.3	0.05	0.17	0.53
30-60	183	23.5	102.4	364.4	100.1	196.0	234.7	65.1	80.1	129.3	2.7	5.4	9.6	152.1	229.3	416.5	154.4	320.2	718.2	0.00	0.11	0.54
60-90	298	10.9	40.3	143.5	33.2	94.7	188.3	67.1	94.5	156.7	2.4	4.6	8.7	158.7	265.1	490.1	132.4	299.9	667.7	0.02	0.14	0.32
90-120	51	7.8	13.4	30.4	21.3	31.1	108.9	74.4	102.4	203.9	2.3	3.8	8.2	179.7	318.5	581.3	126.0	277.2	888.9	0.05	0.15	0.33
All	578	13.6	49.9	188.0	37.0	126.4	210.5	66.6	84.9	147.8	2.4	4.7	8.6	153.1	235.8	448.5	153.1	282.3	675.6	0.01	0.13	0.38

Table A.1. SHAPES detection parameters used in the sensitivity analysis and in the schools analysis. Schools parameters were selected to facilitate comparisons with Fielding et al. (2012), Tarling et al. (2009) and Klevjer et al. (2010)

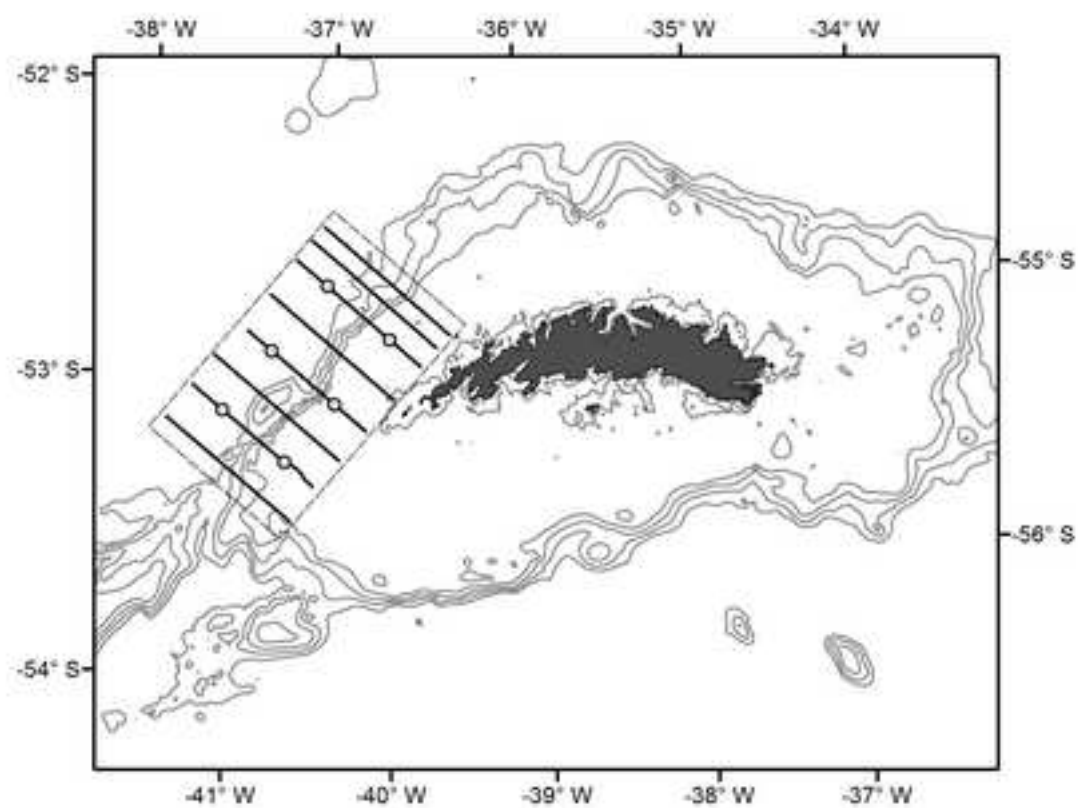
School detection parameter	Sensitivity investigation values			
	Fixed value	Test range	Test step size	Selected values
Minimum school length (m)	30	10 to 100	10	30
Minimum school height (m)	2	1 to 25	2 and 5	2
Minimum candidate length (m)	15	5 to 80	5 and 10	15
Minimum candidate height (m)	1	1 to 25	2 and 5	1
Maximum horizontal linking distance (m)	5	15 to 10	10	5
Maximum vertical linking distance (m)	15	1 to 25	5	15
Threshold (S_v ; dB re $1 m^{-1}$)	-70	-65 to -80	5	-70

Highlights

- Myctophid fish formed regular schools at South Georgia and their schooling characteristics varied inter-annually.
- Schools were distributed on-shelf in some years, but off-shelf in others. They also appeared to be separated by bathymetry.
- Offshore schools occurred higher in the water column than onshore schools, and they were longer, thinner, and acoustically weaker.
- This might be related to a) predatory pressure b) oceanographic variation, or c) habitat partitioning of different species/life stages.
- Our study provides new information on the ecology of myctophids of use to predator foraging models and ecosystems studies.



Appendix Figure 1



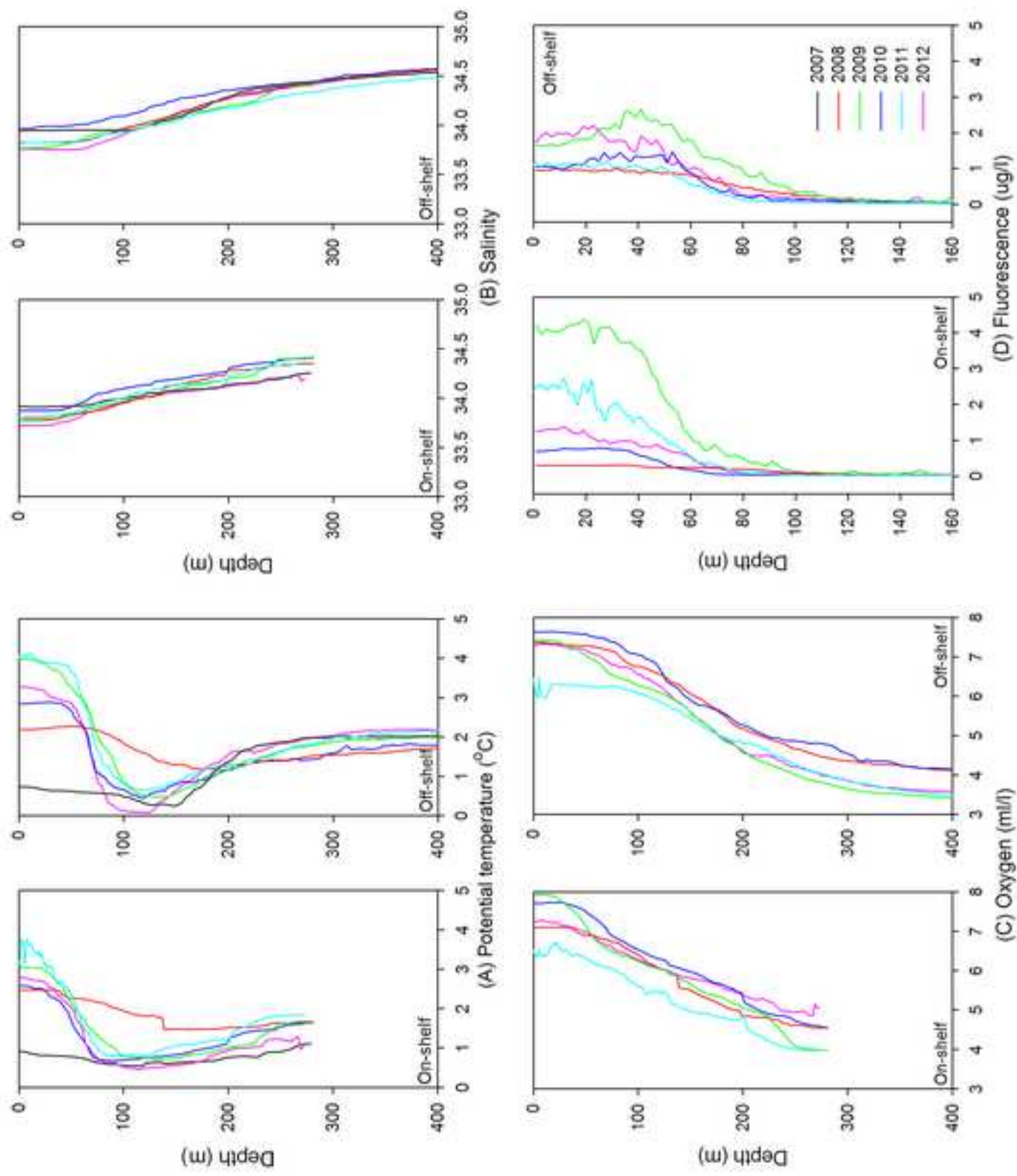


Figure 2

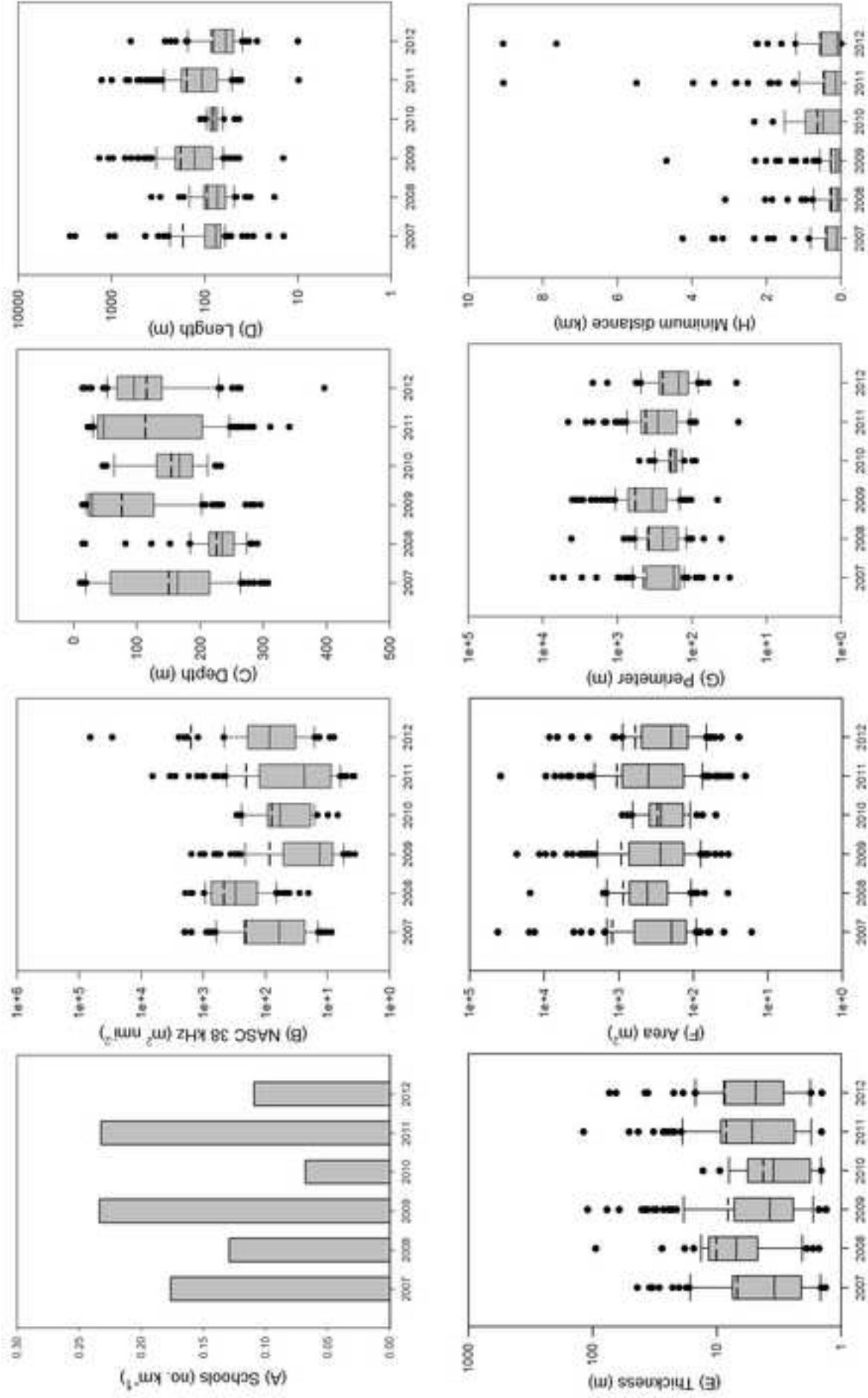


Figure 3

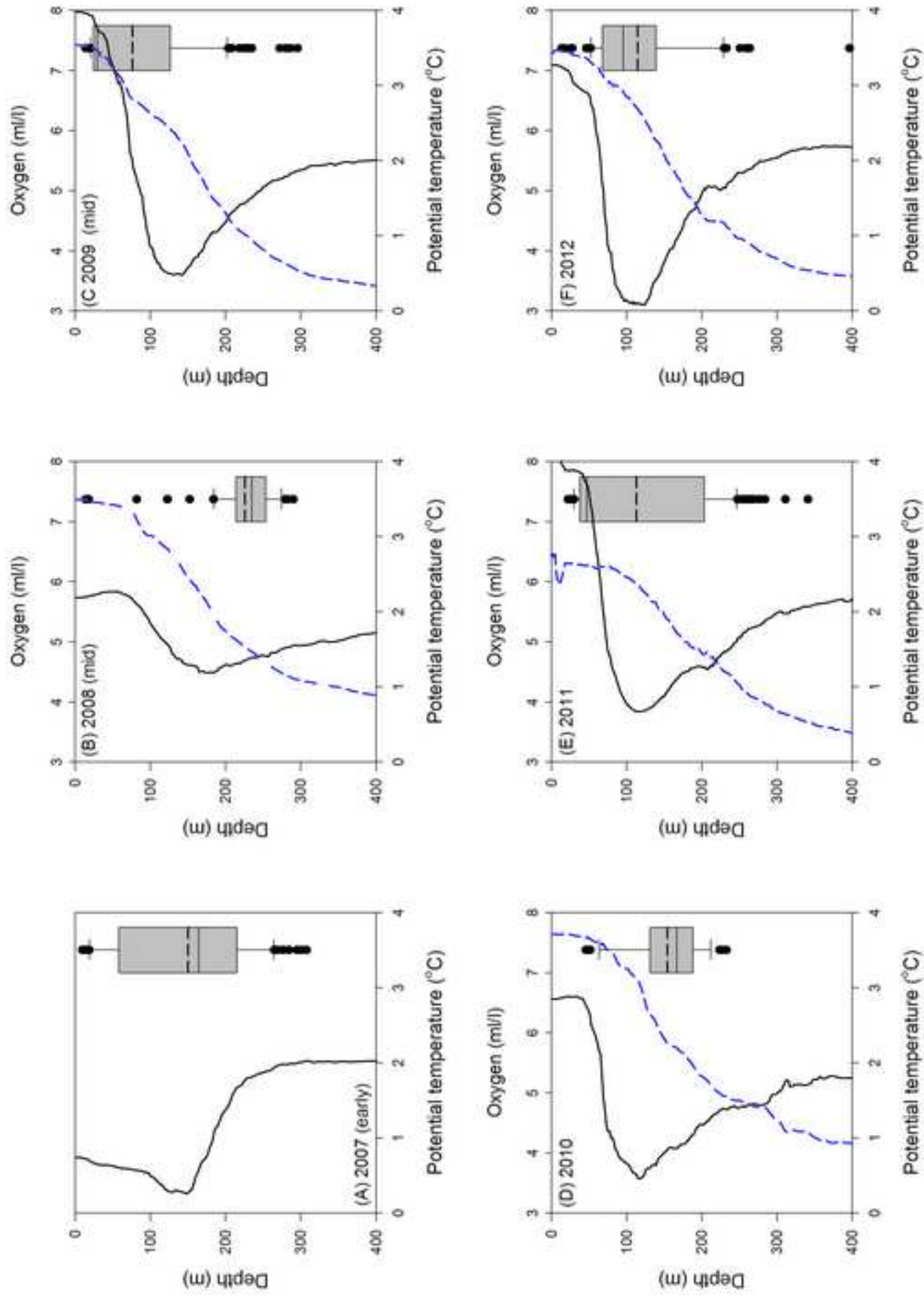


Figure 4

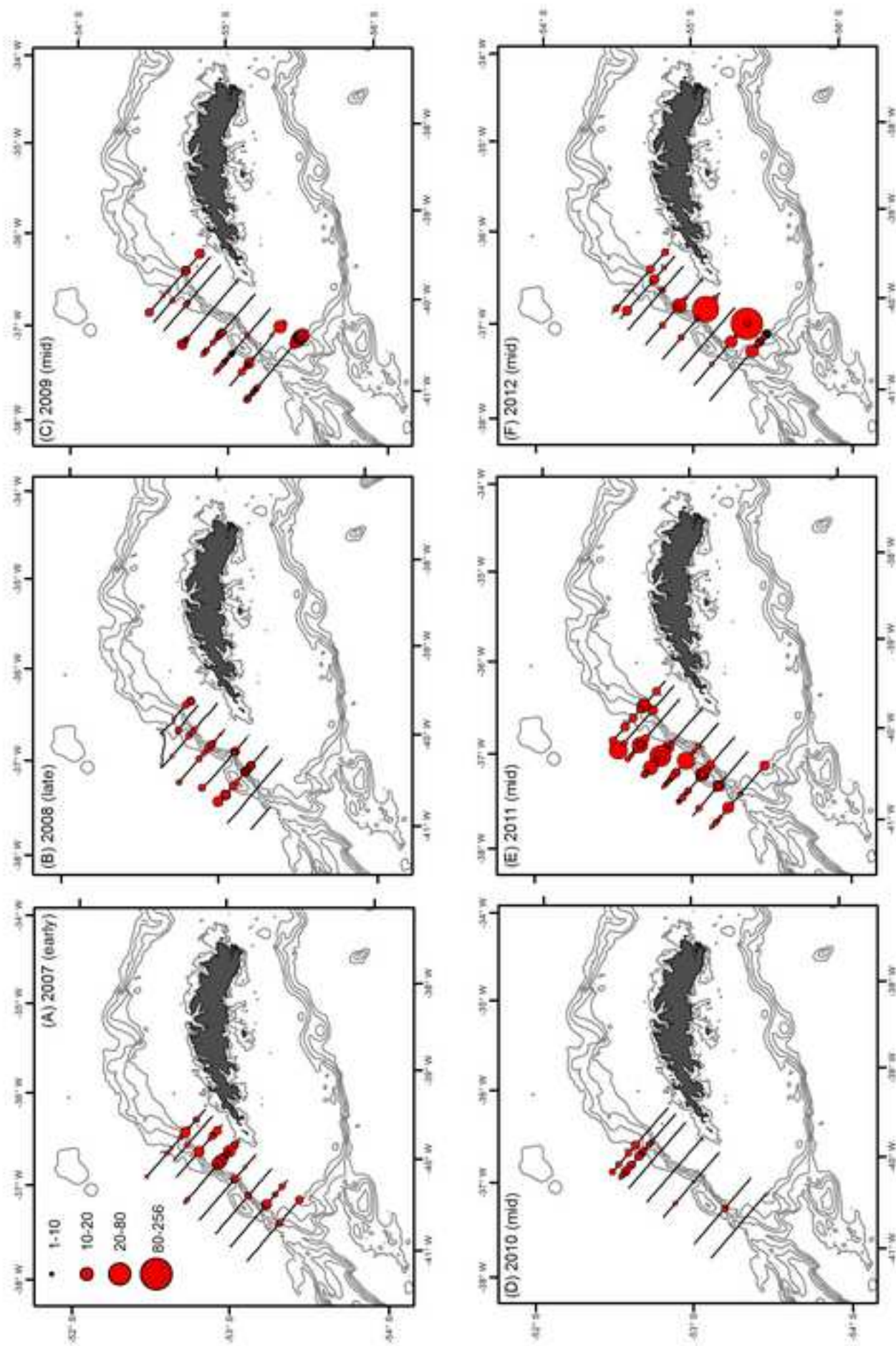


Figure 5

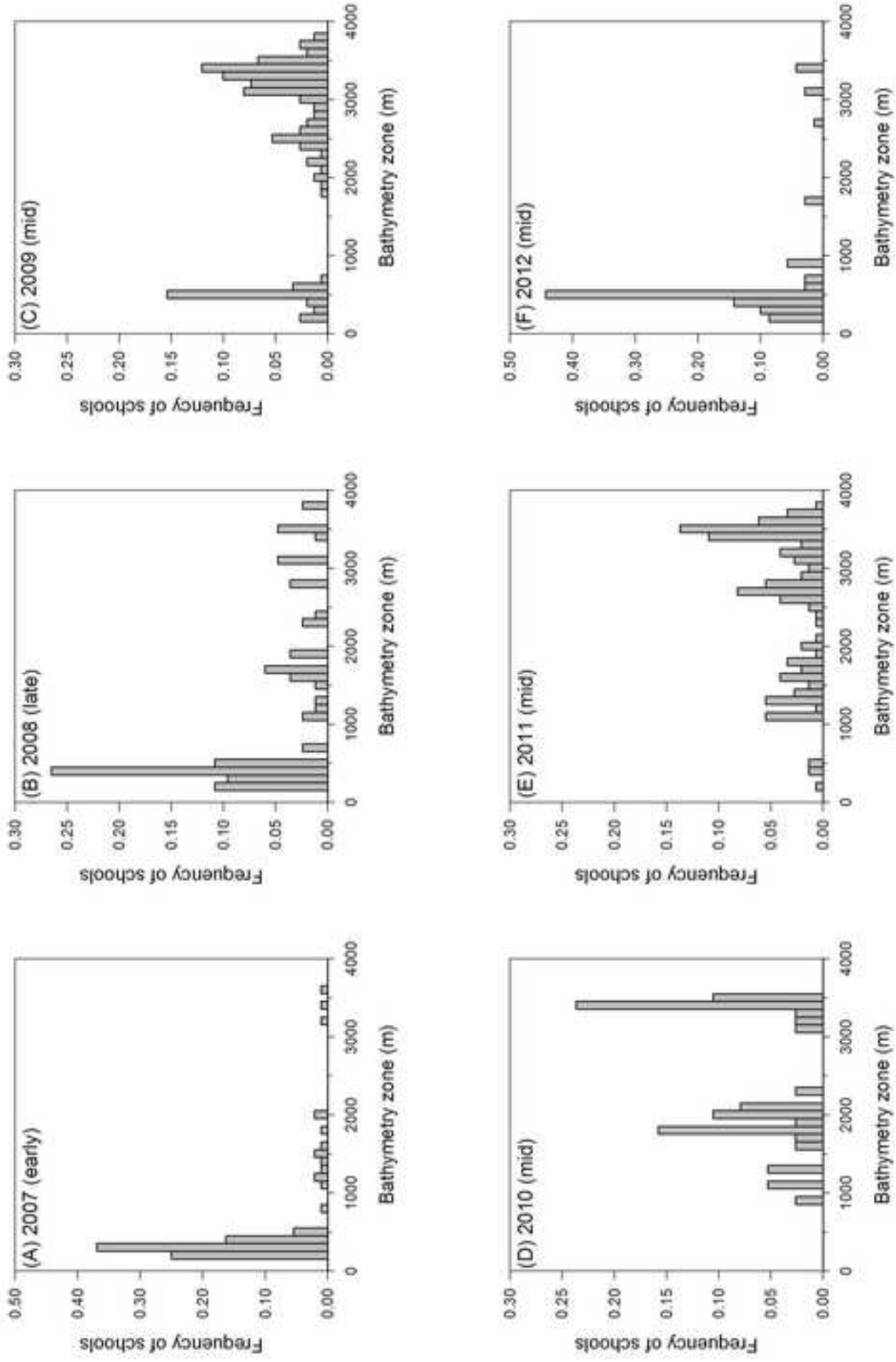


Figure 6

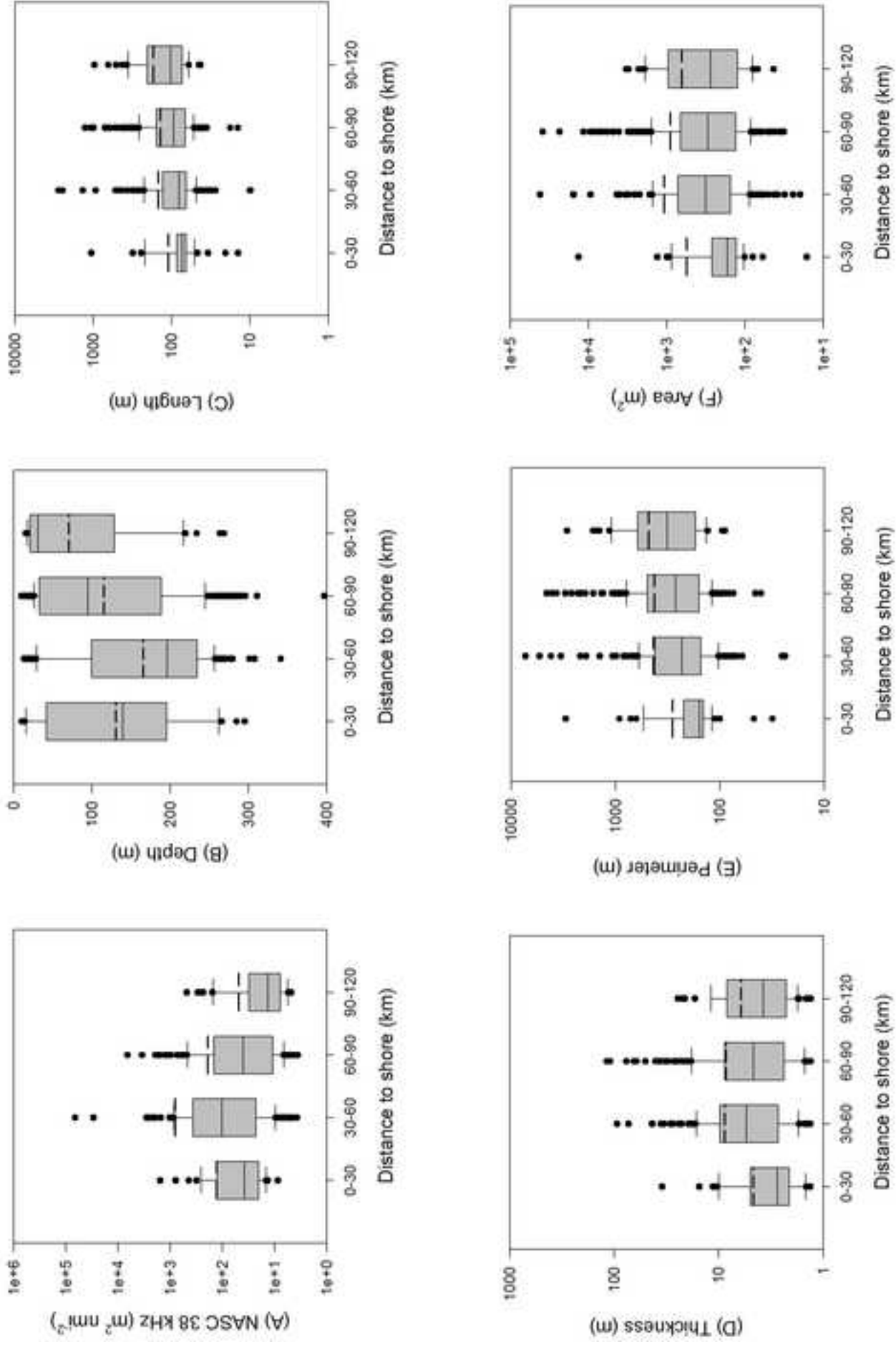


Figure 7

A

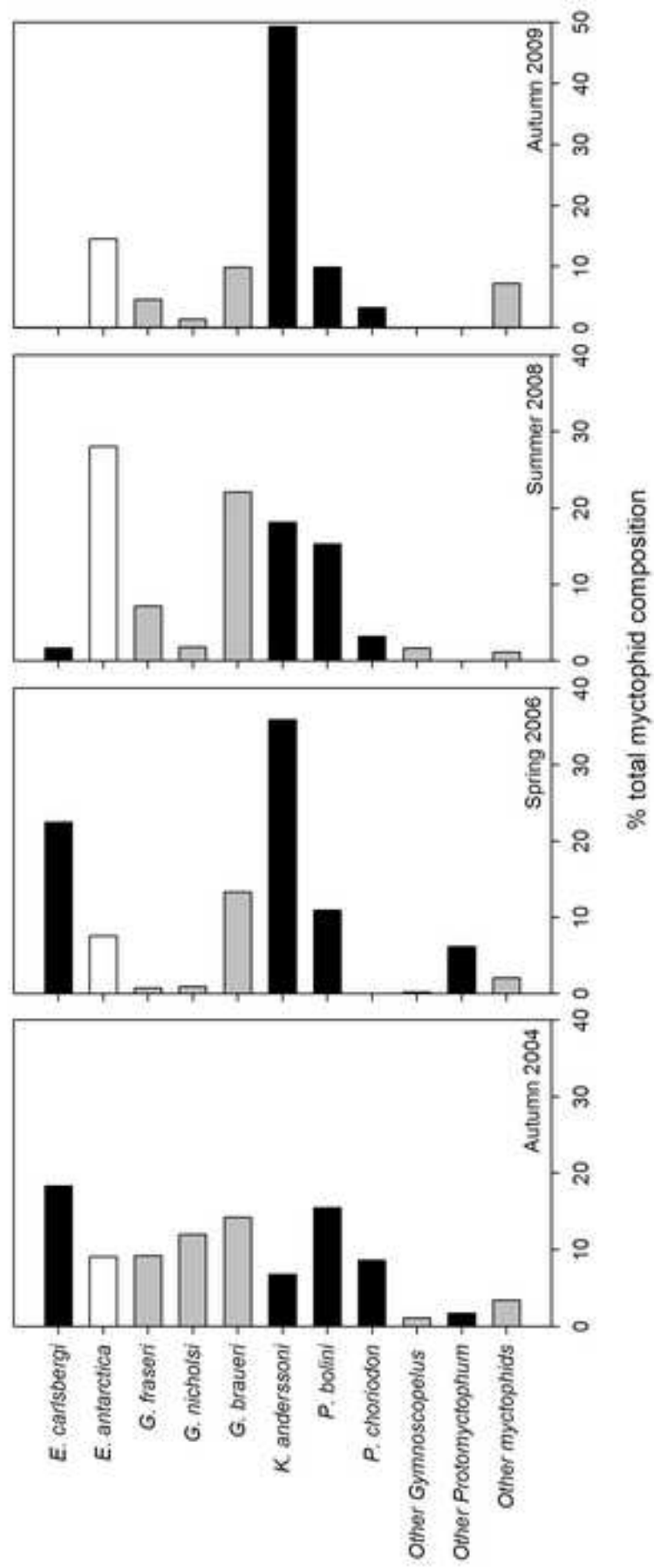


Figure 8

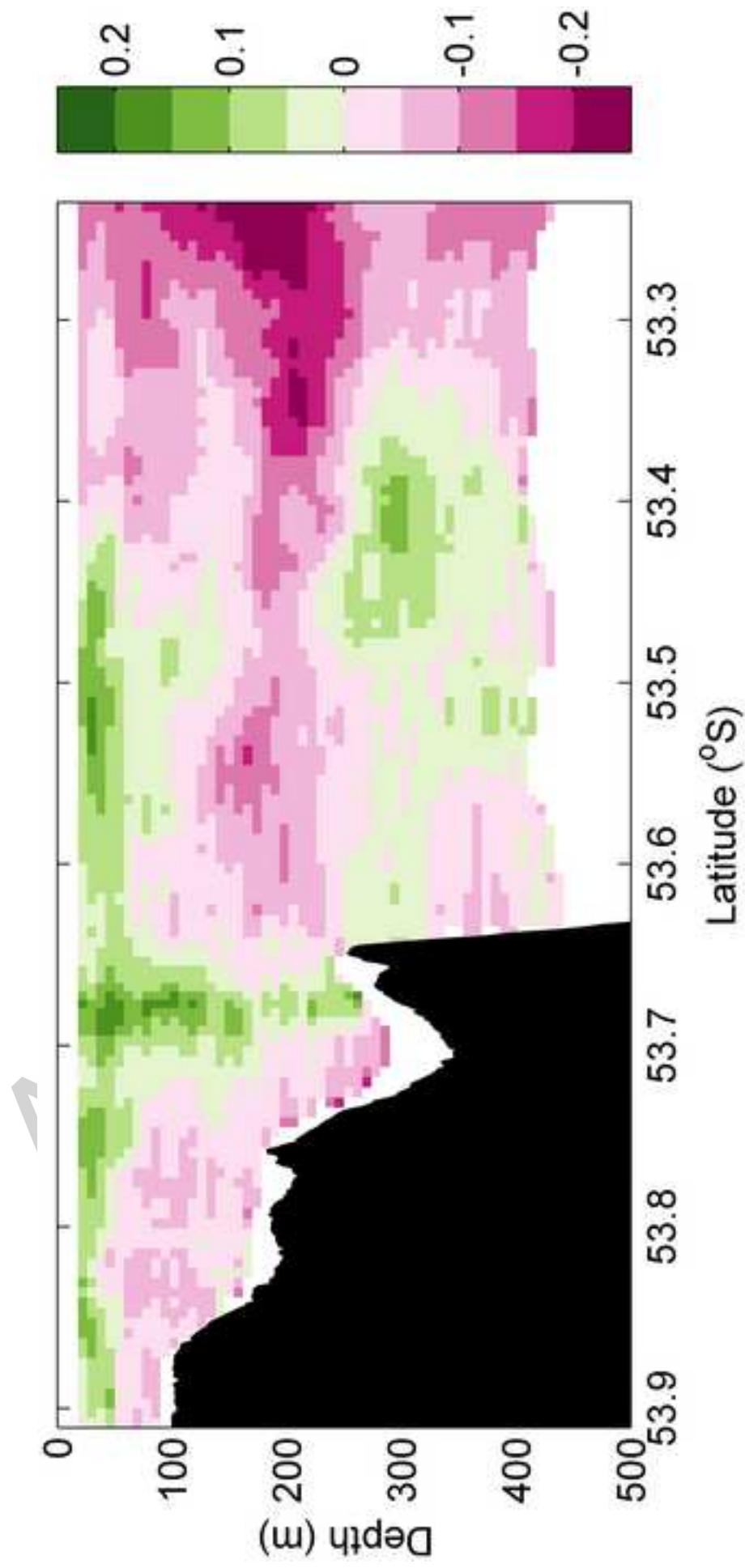


Figure 9