Biogeography of cephalopods in the Southern Ocean using habitat suitability prediction models

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Abstract

Our understanding of how environmental change in the Southern Ocean will affect marine diversity, habitats, and distribution remain limited. The habitats and distributions of Southern Ocean cephalopods are generally poorly understood, and yet such knowledge is necessary for research and conservation management purposes, as well as for assessing the potential impacts of environmental change. We used net-catch data to develop habitat suitability models for 15 of the most common cephalopods in the Southern Ocean. Using modelled habitat suitability, we assessed favourable areas for each species and examined the relationships between species distribution and environmental parameters. The results compared favourably with the known ecology of these species and with spatial patterns from diet studies of squid predators. The individual habitat suitability models were overlaid to generate a "hotspot" index of species richness, which showed higher numbers of squid species associated with various fronts of the Antarctic circumpolar current. Finally, we reviewed the overall distribution of these species and their importance in the diet of Southern Ocean predators. There is a need for further studies to explore the potential impacts of future climate change on Southern Ocean squid.

Keywords: Biogeography, Southern Ocean, Cephalopods, Habitat suitability models

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Introduction

Habitat suitability models can contribute significantly to our understanding of species niche requirements and can predict the potential distributions of species (Hirzel et al., 2006). Certain regions of the Antarctic are among the most rapidly warming areas on Earth (Turner et al., 2009). However, our understanding of how these changes affect marine diversity, habitats, and distribution remain limited, particularly regarding pelagic taxa in the Southern Ocean (Xavier et al., 2006; Griffiths, 2010).

In the Southern Ocean, defined here as the region south of the Subtropical Front, all known squid are oceanic pelagic species with high levels of endemism (Collins and Rodhouse, 2006). As most pelagic cephalopods have a short life span, rapid and labile growth, and semelparous maturation patterns (Boyle and Rodhouse, 2005), it seems likely that they will respond relatively rapidly to environmental change. Antarctic squid are also a poorly studied group despite considered to be commercially exploitable in the future (Xavier et al., 2007). For the Southern Ocean, it has been suggested that predicted temperature increases, and/or changes in sea ice extent, are unlikely to have major effects on squid other than changes in distribution near the limits of their range (Rodhouse, 2013). However, the likely consequences of ecosystem change on the distribution of squid fauna in the Southern Ocean are not well understood (Constable et al., 2014; Kennicutt II et al., 2014; Xavier et al., 2014).

The objective of this study was to estimate the spatial distribution of suitable habitats of a number of common squid species from the Southern Ocean. We review our predicted distributions against previously published distribution estimates (Xavier et al., 1999; Rodhouse et al., 2014), the known distribution of the sampling effort (Griffiths, 2010), and the presence of the studied species in the diet of key top predators in different areas of the

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Southern Ocean.

Materials and Methods

Occurrence data were taken from the SCAR Biogeographic Atlas of the Southern Ocean (De Broyer et al., 2014). This compilation was based upon Xavier et al. (1999), with additional data drawn from the Ocean Biogeographic Information System (OBIS, 2013), biodiversity.aq, the Australian Antarctic Data Centre, and the National Institute of Water and Atmospheric Research (NIWA, 2014). Duplicate records (identified by exact matches in species name and position) were removed. Figure 1 shows the study region and the names of features mentioned in the text. Figure 2 shows the complete set of occurrence records used.

The available species occurrence records were in presence-only form, and so the habitat suitability modelling was conducted using the Maxent software package (v3.3.3k) (Phillips et al., 2006). Maxent does not provide a direct estimate of the probability of presence of the species across its range, but rather an index of habitat suitability (effectively, utilized habitat relative to the background environmental conditions). This index is nonlinearly related to the probability of presence (Phillips et al., 2009). Maxent allows for nonlinear model terms by formulating a series of features from the predictor variables. Due to relatively limited sample sizes, we constrained the complexity of most models by considering only linear, quadratic, and product features. A multiplier of 3.0 was used on automatic regularization parameters to discourage overfitting (Radosavljevic and Anderson, 2014); otherwise, default Maxent settings were used. A 10-fold cross-validation procedure was used to assess model performance (using the area under the receiver-operating curve) and variable permutation importance, with values averaged over the 10 fitted models. The final predicted

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distribution for each species was based on a single model fitted using all data. The squid presence records come from a mixture of sources: some dedicated marine science surveys with a designed sampling strategy, but also other sources such as fishing vessels. The presence records are therefore biased, in that they were not drawn at random from across the range of each species. To reduce the effects of this bias on the fitted models, the background points were sampled from the locations of all squid records, rather than randomly sampled from across the region of interest (Phillips et al., 2009). 1000 background points were used for each model.

Species distribution and habitat suitability modelling in the Southern Ocean relies on predictor variables drawn from remote-sensing and model sources in order to obtain synoptic coverage at suitable spatial and temporal resolution. Predictor variables (**Error! Reference source not found.**)(Smith and Sandwell, 1997; Spreen et al., 2008; Feldman and McClain, 2010; Garcia et al., 2010; Rio et al., 2011; Trübenbach et al., 2013) were chosen from a collection of Southern Ocean layers (Raymond, 2012). These variables were selected as indicators of ecosystem structure and processes including water mass properties, sea ice dynamics, and productivity (see biological relevance, **Error! Reference source not found.**). We used a combination of predictive performance and expert opinion, including interpretation of the fitted responses, to select appropriate variables for each model. The selection process was also used to avoid including multiple, highly-correlated predictor variables within any one model.

Records of squid as prey items were extracted from the Southern Ocean dietary database (Raymond et al., 2011). These data were not used as part of the model fitting process, which was based entirely on the net catch data, but rather as informal evaluation of the predicted habitat distributions from the models. This comparison between the spatial

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distribution of the diet records and the spatial pattern of predicted habitat was not done in a formal manner, because the geographic location of a diet record indicates where that diet sample was obtained (usually a breeding colony); the prey item in question may not be local to that colony. Some predators (e.g. sperm whales, wandering albatrosses) retain squid beaks in their stomachs for long periods of time (Clarke, 1980; Xavier et al., 2005) and/or have long foraging ranges (e.g. albatrosses) (Phillips et al., 2008), so they may have consumed that prey item a considerable distance from the colony. Further, the absence of a prey item from a predator's diet may be due to factors such as availability (e.g. deep prey beyond the diving reach of air-breathing predators) or prey preference, rather than disjunct spatial distributions (Xavier et al., 2013).

We identified cephalopod hotspots using an index of species richness derived from the individual species habitat models. We then converted the predicted habitat suitability for each species to a binary presence/absence layer by applying a threshold, such that habitat suitability values above the threshold were converted to presences. The threshold used for each species was the average of the thresholds (for each of the 10 training models) chosen to maximize the test area under the receiver-operating curve (Phillips et al., 2006). The binary layers were summed to give the number of species estimated to be present in each pixel (Ballard et al., 2012). The results of this study are available from the Australian Antarctic Data Centre.

Results

The results of the modelling, including the predictor variables used in each model, are summarised in Table 2. For each species we provide two maps: one showing the

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catch data used to fit the model as well as the diet data available for that squid species as prey, and the second figure for each species showing the predicted habitat suitability map.

Family Bathyteuthidae

Bathyteuthis abyssicola (Figure 3a,b). The predicted habitat suitability suggests a circumpolar distribution (i.e. occurring in all three sectors of the Southern Ocean). The most favourable habitat was predicted to lie between the Southern Antarctic Circumpolar Current Front (SACCF) and the Sub-Antarctic Front (SAF), with more moderate values of habitat suitability extending from roughly 45°S up to the Antarctic shelf.

Family Brachioteuthidae

Slosarczykovia circumantarctica (Figure 4a,b). The predicted habitat suitability suggests a circumpolar distribution, with meridional limits between approximately the SACCF and the SAF. Zonally, the most favourable habitat was predicted in the Scotia Sea in the Atlantic sector, particularly around the Antarctic Peninsula and South Georgia, in the Indian sector (with higher values at Kerguelen shelf and eastern waters) and south of the Tasman Sea between Tasmania and New Zealand. While net catches of this species were sparse outside of the southwest Atlantic sector, diet records were present in the Indian and Pacific sectors, broadly matching the predicted habitat distribution.

Family Cranchiidae

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Galiteuthis glacialis (Figure 5a,b). The predicted habitat suitability clearly indicates a circumpolar distribution, bounded to the south by the Antarctic continent and to the north by the SAF.

Mesonychoteuthis hamiltoni (Figure 6a,b). The predicted habitat suitability suggests a circumpolar distribution extending relatively close to the Antarctic continent but not into shallow areas such as the continental shelf or the Kerguelen Plateau. To the north, suitable habitat appears to be delimited by the SAF. The highest values of habitat suitability extended from the Weddell Sea in the Atlantic sector to 60 °E (west of the Kerguelen archipelago), and between 180 °E and 120 °W in the Ross/Amundsen seas region.

Family Gonatidae

Gonatus antarcticus (Figure 7a,b). The predicted habitat suitability suggests a circumpolar distribution, with patches of highly suitable habitat over the south part of the Patagonian shelf (around the Falkland Islands and Cape Horn), in the Scotia Sea and to the east in the Atlantic sector, in the Indian sector (northern Kerguelen Plateau and Prydz Bay) and in the Pacific sector (the Ross Sea, and eastwards along the continental shelf to the Antarctic Peninsula). Similarly to *S. circumantarctica*, catch records were almost exclusively restricted to the southwest Atlantic sector, whereas diet records were circumpolar, as was the predicted habitat distribution.

Family Histioteuthidae

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Histioteuthis atlantica (Figure 8a,b). The predicted habitat suitability indicated a circumpolar distribution north of approximately 60 °S (50 °S in the Atlantic sector), away from the coldest waters of the Southern Ocean. The predicted distribution of *H. atlantica* was restricted to more northerly regions than that of the closely-related *H. eltaninae*.

Histioteuthis eltaninae (Figure 9a,b). The model predictions indicated that suitable habitat is widespread across the Southern Ocean, excluding shallow areas such as continental shelves and undersea banks and ridges.

Family Loliginidae

Doryteuthis gahi (Figure 10a,b). Predicted habitat for this species was limited to continental shelves, particularly the Patagonian shelf (agreeing well with all net capture and predator diet locations), and in South Chilean waters (in the Pacific). Areas of suitable habitat, albeit more restricted in extent, were also predicted around South Georgia, the Kerguelen Islands, and New Zealand.

Family Neoteuthidae

Alluroteuthis antarcticus (Figure 11a,b). Predicted habitat was circumpolar, bounded approximately by the SACCF to the north, and by the Antarctic continental shelf to the south.

Family Ommastrephidae

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Martialia hyadesi (Figure 12a,b). The model predicted spatially-patchy areas of suitable habitat, generally downstream of land masses. The principal areas of predicted habitat were around the South American shelf, in the north Scotia Sea close to South Georgia, in the Indian sector (Prince Edward, Crozet and Kerguelen shelf archipelagos and to the east of the latter islands) and south and southwest of New Zealand.

Todarodes filippovae (Figure 13a,b). The predicted habitat suitability was clearly circumpolar, bounded to the south by the SAF, away from the coldest waters of the Southern Ocean. While catches were largely confined to the eastern Indian and Pacific sectors (Tasmania through to South America), a small number of diet and catch records from the western and central Indian sectors (approximately 30–80 °E) provided some corroboration of the circumpolar habitat prediction.

Family Onychoteuthidae

Kondakovia longimana (Figure 14a,b). The predicted habitat suitability was circumpolar, consistent with the catch and diet records, but spatially patchy. Areas of most suitable habitat were found in the Scotia Sea, particularly around South Georgia and the South Sandwich islands, in the Indian sector (Kerguelen waters and further south) and south of the Tasman Sea around 60 °S. Patches of suitable habitat were also predicted for parts of the Antarctic continent shelf (e.g. the western Antarctic Peninsula, Prydz Bay, and the Dumont d´Urville Sea).

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Moroteuthis ingens (Figure 15a,b). Predicted areas of suitable habitat were patchy, generally restricted to regions around 50 °S or further north. Oceanic waters were generally predicted to be unsuitable habitat, compared to areas above and around continental or island shelves, particularly around the Falkland Islands, Crozet, the Kerguelen Plateau in the Indian sector, south of Tasmania, and on the New Zealand shelf in the Pacific sector. North of about 60 °S, the shelf distribution of *M. ingens* is complementary to that of *H. atlantica*.

Moroteuthis robsoni (Figure 16a,b). The predicted habitat suitability was broadly circumpolar with a southern boundary at approximately the SAF, away from the coldest waters of the Southern Ocean, and with an affinity for mid-depth regions (e.g. shelf slopes).

Family Psychroteuthidae

Psychroteuthis glacialis (Figure 17a,b). Suitable habitat was predicted to be circumpolar, extending northwards from the Antarctic continent to approximately the APF. Areas of highest habitat suitability were found in patches in the southern Scotia Sea, Weddell, and Ross seas, and in coastal waters around the Antarctic continent.

“Hotspot” regions in the distribution of cephalopods from the Southern Ocean

The individual species habitat suitability predictions were combined to produce an index of species richness (Figure 18). The highest predicted values (8 or more

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species) occurred in a largely-circumpolar band, approximately from the Polar Front south to the northernmost extent of sea ice. Areas of nine or more species were found in the southwest Atlantic sector. The lowest values occurred over the shelf around the Antarctic continent, and to the north of the sub-Antarctic front (but note that these latter waters are home to other species of squid not considered in this study).

Discussion

Biases and uncertainties

To our knowledge, this is the first study to develop habitat suitability predictions for these common cephalopod species of the Southern Ocean. The modelling component of this study presented a number of challenges. Data systems such as OBIS currently provide the most comprehensive occurrence data for biogeography but are aggregated from a variety of diverse sources with differences in aspects such as survey design and sampling techniques. One possible approach is to use the aggregated dataset merely as an index of the available data and follow each component dataset back to its original, detailed source. However, this is rarely practical for large-scale studies. Although we have attempted to account for the spatial distribution of survey efforts in the modelling procedure, these results should still be treated with caution, particularly for species with small sample sizes or where one particular area dominates the occurrence record.

The predictor variables used were drawn from satellite and similar sources. The information from such variables rarely provides direct characterization of the primary processes affecting the species distribution. For example, there are no direct estimates of squid prey distributions. Instead, these variables typically provide proxy information such as

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water mass properties or primary productivity. The spatial and temporal scales of this information often do not match the scales experienced by the animals. Furthermore, predictor variables in the Southern Ocean are typically highly correlated because of the strong latitudinal and seasonal gradient that affects oceanic and atmospheric conditions. Because of these factors, it is rarely obvious which particular predictor variable is the most appropriate proxy to use in a given model. Predictive performance offers some guidance, but should not be relied upon exclusively (Raymond et al., 2014). Squid are also notorious for their net avoidance ability, and scientific nets typically catch only juvenile individuals (Collins and Rodhouse, 2006).

In order to help assess the influence of these issues on the results, we used *Doryteuthis gahi* as a validation species, because it is well known to be coastally distributed (up to 350 m depth) in areas of the Patagonian shelf and eastern Pacific Ocean from southern Peru to Southern Chile (Arkhipkin et al., 2013). The predicted habitat suitability for this species broadly matched the expected pattern. Small areas of suitable habitat were predicted in a few locations where this species is unlikely to be present (e.g. around New Zealand). This highlights the fact that the outputs from these models are predictions of suitable habitat and do not take into account other processes that govern species distributions such as dispersion, competition, and trophic dependencies. Indeed, combining food web models with species distribution models to predict spatial variation in community composition remains an active area of research in biodiversity modelling (Pellissier et al., 2013; Constable et al., 2014).

Generally, each predicted habitat distribution matched the picture provided by the combination of occurrence and predator diet records. For *Kondakovia longimana*, the predicted habitat was much more circumpolar in nature than the observed catch records, but that circumpolar pattern was consistent with predator diet observations. Similarly, suitable

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habitat for *Gonatus antarcticus* was predicted to include areas close to the Antarctic continent, well away from observed net catches. However, emperor penguins have been recorded to feed on this species there (Cherel and Kooyman, 1998). Some minor discrepancies were also noted. The sea ice zone was not predicted to be suitable habitat for *Moroteuthis ingens*, apparently contradicting an emperor penguin diet record from Auster colony, near Mawson station (Robertson et al., 1994). However, this species has never been recorded in any other emperor diet studies (Xavier and Cherel, 2009) and so this record may have been a misidentified *M. knipovitchi*, an Antarctic species of the same family with broadly similar beak characteristics (Xavier and Cherel, 2009). Finally, *S. circumantarctica* has occasionally been caught by nets in warm waters near New Zealand (around 45 °S) but this was not predicted to be a suitable habitat (Figure 4b).

The models showed that ocean areas with generally higher levels of habitat suitability exist around 50 °S in the Atlantic and Indian sectors and 60 °S in the Pacific sector, where the majority of the fronts are distributed (i.e. Polar Front, sub-Antarctic Front and subtropical Fronts; see Xavier et al. 1999), reinforcing that these areas regions are broadly ecologically relevant, including for cephalopods.

Physical and biogeochemical ocean mechanisms influencing the distribution of squid in the Southern Ocean

The Southern Ocean is characterized by high surface macro-nutrient concentrations and relatively low iron concentrations, and so iron input typically leads to increased productivity. Several low-latitude species (e.g. *Doryteuthis gahi*, *Martialia hyadesi*) were associated with regions where atmospheric iron deposition is strongly correlated with

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increased productivity (as measured by satellite-based chlorophyll, e.g. east of Patagonia, on the Falkland plateau) (Erickson et al., 2003). Away from land in the open Southern Ocean, areas of elevated productivity tend to be driven by upwelling of nutrients, often caused by the interaction of the Antarctic circumpolar current flow with large-scale bathymetric features, such as mid-ocean ridges (Sokolov and Rintoul, 2007). Some such areas are known to be foraging grounds for predators such as seabirds (Raymond et al., 2010). Thus water depth can potentially influence cephalopod distribution, even in deep, mid-ocean areas well away from shelves.

Broadly speaking, cold, nutrient-rich waters upwell south of the Polar Front and subduction (i.e. downwelling) occurs north of the Polar Front (Sarmiento et al., 2004). Several species in this study (e.g. *Todarodes filippovae, Galiteuthis glacialis*) featured a strong contrast across the Subantarctic Front. Upwelling in the Weddell and Ross gyres may also play a role in forming suitable habitat for some species, such as *Psychroteuthis glacialis* (Figure 17a,b). Three species (*Mesonychoteuthis hamiltoni*, *Bathyteuthis abyssicola* and *Slosarczykovia circumantarctica*) were found to have a potential affinity for areas with low oxygen minima, suggesting that these species may use this ecological niche close to or within the oxygen minimum zone. Although low oxygen levels are known to greatly limit the abundance, vertical distribution, and ecology (e.g. predation, food competition) of numerous marine animals, some species of squid (e.g. jumbo squid *Dosidicus gigas*) are known to thrive in such harsh environments (Trübenbach et al., 2013).

This study indicates that large-scale physical and biogeochemical properties can influence the suitability of a given region, often in remarkably different ways for different cephalopod species. The 15 species modelled here can be discussed in terms of three broad spatial groupings: those distributed in cold waters close to the Antarctic continent, those in

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relatively warm waters to the north, and those with less constrained distribution (i.e. extending into both warm and cold waters).

Habitat suitability of "cold" water cephalopod species

The species that clearly have suitable habitat close to the Antarctic continent were *Alluroteuthis antarcticus*, *Galiteuthis glacialis*, *Mesonychoteuthis hamiltoni*, *Psychroteuthis glacialis*. These species have been recognized as typical Antarctic water species with a suggested circumpolar distribution (Xavier et al., 1999; Rodhouse et al., 2014), consistent with our results. *A. antarcticus* is occasionally caught in nets in the Atlantic and Indian sectors of the Southern Ocean (Rodhouse, 1989; Lu and Williams, 1994) but also in the diet of albatrosses in the Pacific sector (Xavier et al., 2014). *G. glacialis* is one of the most abundant (i.e. most commonly caught in midwater research nets) and widely distributed squid species in the colder waters of the Southern Ocean. *M. hamiltoni* is arguably the largest squid species in the world, growing to ten metres or more in length (Collins and Rodhouse, 2006). Its habitat is typically in circumpolar colder waters (see results; Xavier et al. 1999). It is occasionally caught by longline fisheries (as a by-catch), and is found in top predator diets (Xavier and Cherel, 2009). Finally, *P. glacialis* is considered to be abundant with a circumpolar distribution in high Antarctic areas (Filippova and Pakhomov, 1994; Xavier et al., 1999). This is supported by our habitat suitability predictions, suggesting that this species may be abundant close to the continent as previously thought, but also in oceanic waters (see results). Evidence of *P. glacialis* living near the bottom at the shelf break area (300–1000 m) (Lu and Williams, 1994; Collins et al., 2004), applies particularly for the Scotia Sea region in our habitat suitability predictions. *P. glacialis*, like *A. antarcticus*, *G. glacialis* and *M.*

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hamiltoni, is also found in the diets of a wide range of top predators, including albatrosses, penguins, seals, whales and toothfish species (Xavier and Cherel, 2009).

Habitat suitability of “mixed” (i.e. cold and warm) water cephalopod species

A group of species were predicted to be broadly distributed, from close to the Antarctic continent to warmer waters north of 60 °S: *Bathyteuthis abyssicola*, *Slosarczykovia circumantarctica, Histioteuthis eltaninae, Kondakovia longimana* and *Gonatus antarcticus*.

B. abyssicola occurs in all three sectors of the Southern Ocean (Roper, 1969), but occurs very rarely in the diet of top predators (Xavier and Cherel, 2009), probably because it lives at great depths (Roper, 1969). *S. circumantarctica* is considered to be the most abundant squid in the upper layers of pelagic waters in the Southern Ocean, generally deeper than 400 m by day and migrating towards the surface by night (Collins and Rodhouse, 2006). The suitable habitat of *S. circumantarctica* in this study predicted to be circumpolar but not close to the Antarctic continent (only at the Antarctic Peninsula islands; see results) occuring regularly in research nets in the Scotia Sea (Rodhouse and Piatkowski, 1995; Rodhouse et al., 1996; Collins et al., 2004). *S. circumantactica* is the most important squid species (by frequency of occurrence and by number) in the diet of Antarctic fur seals breeding at South Georgia in most years (British Antarctic Survey, unpubl. data). *H. eltaninae* is distributed the furthest south of the species of the family Histioteuthidae, with a circumpolar distribution (Rodhouse and Piatkowski, 1995; Rodhouse et al., 1996; Xavier et al., 1999; Collins and Rodhouse, 2006), occurring in small numbers in research nets (Rodhouse and Piatkowski, 1995; Xavier and Cherel, 2009), but never close to the Antarctic continent (matching model predictions here; see results). Although it has been suggested that *H. eltaninae* is more

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abundant in proximity to land and oceanic ridges (Roper et al., 1984), this is not expressed in our predictions (but note that the habitat suitability model for this species used only a single predictor variable (depth), and so should be treated with caution). *H. eltaninae* occurs in a wide range of predator diets (Cherel and Klages, 1998; Xavier and Cherel, 2009). *K. longimana* has a circumpolar distribution (Xavier, 1997; Xavier et al., 1999), matched by our study results, ranging from close to the Antarctic continent coasts to north of 60 °S (Cherel and Weimerskirch, 1999). This species also reaches large sizes (Rodhouse et al., 2014), but not as large as *M. hamiltoni*. Although rare in research nets (Collins et al., 2004), *K. longimana* is one of the most important species (by number and by mass) in numerous predators in the Southern Ocean, including wandering and grey-headed albatrosses (Clarke, 1980; Croxall and Prince, 1996; Xavier et al., 2003b; Cherel et al., 2004; Xavier and Cherel, 2009). *G. antarcticus* has a circumpolar distribution reaching as far south as the Antarctic continent (Xavier et al., 1999), a finding mirrored by our results. This species occurs occasionally in nets (Rodhouse et al., 1996; Collins and Rodhouse, 2006) but is more commonly found in the diet of seabirds and seals (Croxall and Prince, 1996; Cherel and Klages, 1998; Xavier et al., 2002; Cherel et al., 2004; Xavier and Cherel, 2009).

Habitat suitability of “warm” water cephalopod species

Five species were predicted to be distributed in the warmer waters of the Southern Ocean: *Histioteuthis atlantica*, *Martialia hyadesi*, *Todarodes filippovae*, *Moroteuthis ingens* and *Moroteuthis robsoni*. *H. atlantica* has a circumpolar distribution (Xavier et al., 1999; Rodhouse et al., 2014), and is more northerly distributed than *H. eltaninae*, as reflected by our predicted habitat suitability for both histioteuthid species. *H. atlantica* is known to occur in oceanic waters (Roper et al., 1984), as suggested by our predictions (see results) but it has

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also been caught in shallow waters (Voss et al., 1998). *H. atlantica* is important in the diet of albatrosses, sharks and many other predators that forage in the warmer waters of the Southern Ocean (Xavier and Cherel, 2009). *M. hyadesi* is found further south than *H. atlantica*, but never close to the Antarctic continent (Rodhouse, 1998a; Xavier et al., 1999). Our results are consistent with this, indicating that the sea ice zone comprises unsuitable habitat for this species. *M. hyadesi* is the squid species that has attracted most attention with regard to future commercial exploitation (Rodhouse, 1997), and is present in the diet of a wide range of top predators (Xavier and Cherel, 2009), being particularly important in the diet of grey-headed albatrosses in some years (Xavier et al., 2003a). *T. filippovae* has a similar circumpolar distribution to *H. atlantica*, and extending further north than the region modelled here (to 35 °S) (Pethybridge et al., 2013). It is common around seamounts and slope waters, up to a 1000 m depth (Roeleveld, 1998; Xavier et al., 1999). While generally found in relatively warm waters, *T. filippovae* is periodically caught further south (Rodhouse, 1998b). *Todarodes* spp. are present in the diet of toothed whales, wandering albatrosses, seals, sharks and fish (Smale, 1996; Xavier and Cherel, 2009). *M. ingens* is mostly associated with shelves (Cherel and Duhamel, 2003) but is also found in bathyal waters (Rodhouse et al., 2014). Given these depth differences, more sampling and genetics work must be carried out to verify if it is truly a single species and not a group of similar species. *M. ingens* is common in the diet of penguins, albatrosses, petrels, whales, seals and the southern opah (Clarke, 1980; Green and Burton, 1993; Cherel et al., 1996; Croxall and Prince, 1996; Cherel and Klages, 1998; Xavier and Cherel, 2009). *M. robsoni* may exhibit a circumpolar distribution (Rodhouse, 1990; Rodhouse et al., 2014), extending as far south as the Scotia Sea but nevertheless still a warm water cephalopod species. Like *M. ingens*, most specimens of *M. robsoni* have been caught in shelf/near shelf waters with a small number specimens being caught in oceanic waters, and so more sampling and genetics work must be carried out to verify the nature of this species. *M.*

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robsoni is an oceanic species (Roper et al., 1984) that occurs occasionally in the diets of Southern Ocean predators that forage sufficiently far north (Imber, 1992; Cherel et al., 2004; Xavier and Cherel, 2009).

The "hotspots" in the distribution of cephalopods in the Southern Ocean are related to oceanic waters, across various fronts. This is consistent with the tendency of top predators to target oceanic fronts, potentially to catch squid (Rodhouse et al., 1996; Xavier et al., 2004). Further research should concentrate on these areas to improve our understanding of the abundance and population dynamics of Southern Ocean cephalopods (Xavier et al., 2015). Several species (e.g. *K. longimana*, *G. antarcticus*, *M. hyadesi*, *M. knipovitchi*) have commercial potential in the future (Xavier et al., 2007), although the biology and ecology of some species (particularly *M. knipovitchi*) remain poorly known (Collins et al., 2004; Collins and Rodhouse, 2006). There is also a need for studies to explore the potential impacts of future climate change on Southern Ocean squid.

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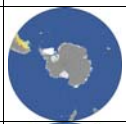
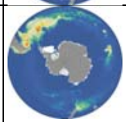
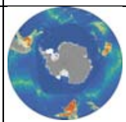
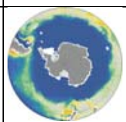
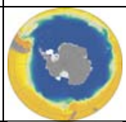
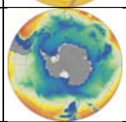
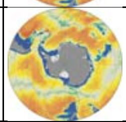
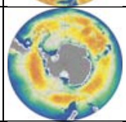
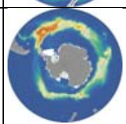
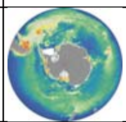
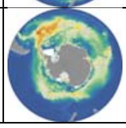
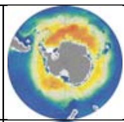
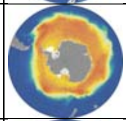
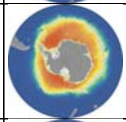
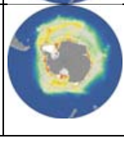
Table 1. Predictor variables used in the species distribution habitat suitability modeling.

Variable	**Description**	**Source and references**	**Biological relevance**
Sea surface temperature (SST)	Sea surface temperature summer climatology, calculated over the 2002/03 to 2012/13 austral summer seasons	MODIS Aqua (Feldman and McClain 2010)	General water mass properties including positions of fronts, which can represent areas of different prey and of prey-aggregation
Sea ice cover	The average proportion of the year for which sea ice is present. Concentration data from 1-Jan-2003 to 31-Dec-2010 was used. The fraction of time each pixel was covered by sea ice of at least 85% concentration was calculated	AMSR-E satellite estimates of daily sea ice concentration (Spreen et al. 2008)	Indicator of sea ice cover, including polynyas, which affects ecosystem structure and prey availability
Depth	Measured and estimated seafloor topography from satellite altimetry and ship depth soundings	Smith and Sandwell (1997) V15.1	Water mass properties
Sea surface height (SSH)	Mean dynamic topography (sea surface height relative to geoid)	CNES-CLS09 Mean Dynamic Topography v1.1 (Rio et al. 2011)	Water mass properties
Chlorophyll-*a* (Chl-*a*)	Near-surface chlorophyll-*a* summer climatology, calculated over the 2002/03 to 2012/13 austral summer seasons	MODIS Aqua (Feldman and McClain 2010)	Productivity, ecosystem structure
Oxygen minimum	Minimum dissolved oxygen value in the top 1000m of the water column	World Ocean Atlas 2009 annual climatology (Garcia et al. 2010)	Water mass properties, potential habitat niche for cephalopods (Trübenbach et al. 2013)

Table 2. Habitat suitability modeling results summary (N occ.: Number of occurrences, AUC: area under the receiver-operating characteristic, OW: open water, PF: polar front, SAF: Sub-Antarctic Front, SIZ: sea ice zone. For variable names see Table 1). The thumbnail maps are reproductions of figures 3b-17b, and are included here to allow a convenient comparison of the broad spatial patterns in the modelling results.

Species	**N occ.**	**Train /test AUC**	**Variables used in model (permutation importance, %)**		**Typical habitat from model predictions**					
					SST (°C)	**Depth (m)**	**Ice**	**O_2 min. (ml/l)**	**Chl-*a* (mg m^{-3})**	**Water mass**
Doryteuthis gahi	149	0.99/ 0.99	Chl (60.5) Depth (34.3) Ice (5.1)		≥9	<400	OW		>0.75	
Martialia hyadesi	260	0.94/ 0.94	Chl (47.2) SST (43.8) Ice (5.8) Depth (3.2)		3–15		OW		>0.3	PF to SAF
Moroteuthis ingens	3808	0.61/ 0.61	Depth (65.5) SST (27.4) SSH (4.8) Ice (2.3)		3–16	300–1500	OW		>0.2	
Moroteuthis robsoni	342	0.75/ 0.75	SSH (41.5) Chl (32.5) O_2min (16.4) Depth (9.7)		7–18	>1000	OW		0.15–0.55	SAF and north
Todarodes filippovae	1173	0.62/ 0.61	SSH (84.9) Depth (15.1)		≥10		OW			SAF and north
Histioteuthis atlantica	106	0.89/ 0.89	Depth (85.4) SST (14.6)		≥5	>3000	OW		<0.6	
Histioteuthis eltaninae	110	0.90/ 0.90	Depth (100)			>3000	OW–70% cover		<0.65	
Bathyteuthis abyssicola	548	0.91/ 0.91	Depth (53.8) SST (37.2) O_2min (9.0)		≤12	>2500	OW–70% cover	<4.8	<0.7	
Slosarczykovia circumantarctica	1304	0.96/ 0.96	SSH (74.4) Ice (19.6) Chl (4.2) SST (1.8)		0–7	>1500	OW–20% cover	4–4.5	0.15–0.65	SAF to parts of SIZ
Gonatus antarcticus	120	0.83/ 0.82	SST (66.2) Chl (33.8)		< 12				>0.4	
Kondakovia longimana	100	0.95/ 0.94	SSH (82.8) Chl (12.1) Ice (5.2)		<6	>500	OW–70% cover		>0.15	PF and south

Mesonychoteuthis hamiltoni	234	0.93/ 0.92	SSH (57.5) Depth (37) O_2min (5.4)		≤11	>2200		<4.75		SAF and south
Galiteuthis glacialis	1449	0.88/ 0.88	SST (79.5) SSH (20.5)		≤6	>500	SIZ–OW			PF and south
Alluroteuthis antarcticus	124	0.93/ 0.93	SST (98.6) Depth (1.4)		≤3	>500	SIZ and OW			South of PF
Psychroteuthis glacialis	316	0.94/ 0.93	SST (66.6) SSH (24.0) Chl (7.4) Ice (2.0)		≤3	>500	SIZ and OW			South of SAF