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Chapter 2: Decapod Shimps in the Antarctica

Nature of contribution by PhD candidate	Compilation of observation records, generation of distribution maps, writing the manuscript
Extent of contribution by PhD candidate (%)	90

CO-AUTHORS

Name	**Nature of Contribution**
Assoc. Prof. Mark J. Costello	Advice and guidance in the design, execution and interpretation of the research

Certification by Co-Authors

The undersigned hereby certify that:

- the above statement correctly reflects the nature and extent of the PhD candidate's contribution to this work, and the nature of the contribution of each of the co-authors; and
- in cases where the PhD candidate was the lead author of the work that the candidate wrote the text.

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Chapter 3: Diversity and distribution of deep-sea shrimps in the Ross Sea region of Antarctica

Nature of contribution by PhD candidate	Original hypothesis, analysis of specimens, analysis of video from IPY-CAML cruise TAN0802, compilation of observation records and environmental layers, generation of species distribution models, statistical analysis. Preparation of the manuscript, figures and maps
Extent of contribution by PhD candidate (%)	85

CO-AUTHORS

Name	Nature of Contribution
David A. Bowden, PhD	Provision of samples, video and photograpy data from IPY-CAML cruise TAN0802 in the Ross Sea. Suggestions on the focus and presentation of the data and manuscript. Advice and guidance in the design, execution and interpretation of the research and preparation of the paper. Improvement of written English in the paper.
Assoc. Prof. Mark J. Costello	advice and guidance in the design, execution and interpretation of the research and prepartion of the paper.

Certification by Co-Authors

The undersigned hereby certify that:

❖ the above statement correctly reflects the nature and extent of the PhD candidate's contribution to this work, and the nature of the contribution of each of the co-authors; and

❖ in cases where the PhD candidate was the lead author of the work that the candidate wrote the text.

Name	Signature	Date
Mark Costello		23/06/2014
David Bowden		24/06/2014
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Chapter 1

Thesis Overview

1.1 Natant Decapods

Natant decapods are shrimp and prawns that belongs to the suborder natantia, and are ubiquitous in the world's oceans. They are found from shallow seas to abyssal depth, including the Antarctic, where other decapod taxa are largely absent (Clarke, 1990; Briggs, 1995; Arntz *et al.*, 1999; Gorny, 1999; Thatje & Arntz, 2004; Griffiths, 2010). As they are predominantly benthic particulate feeders and predators, they can be important in the processing of material on the seabed (Coull & Bell, 1983; Field, 1983; Cartes *et al.*, 2007). The composition and distribution of decapods in the Antarctica have been the subject of more intense study during the past decade, revealing their wider distribution around the Antarctic (Clarke, 1990; Briggs, 1995; Arntz *et al.*, 1999; Gorny, 1999; Thatje & Arntz, 2004; Griffiths, 2010; Griffiths *et al.*, 2013). While decapods are known to be playing an important role in controlling the flow of energy in an ecosystem (Wenner, 2001), knowledge about ecology and in particular the role of decapods and their distribution in the Southern Ocean ecosystems remains limited due to the difficulty of sampling in extreme weather conditions (i.e. strong currents, ice coverage round the year).

In recent years, species distribution models (SDM) were used widely in modelling biogeography, ecology, conservation biology and identifying species' response to climate change (Guisan & Zimmermann, 2000; Peterson & Vieglais, 2001; Elith *et al.*, 2006; Pearson *et al.*, 2007; Elith & Leathwick, 2009; Feeley & Silman, 2011; Varela *et al.*, 2011; Selig *et al.*, 2014; Vierod *et al.*, 2014; Zhang *et al.*, 2014). They can also be used to identify environmental variables influencing the distribution of a particular species or group of species and model their potential geographic distributions (Dambach *et al.*, 2012; González-Salazar *et al.*, 2013).

Although shrimps were captured frequently in research cruises around the Antarctic, previous studies on the shrimp focused in the West Antarctic regions (Weddell Sea and Antarctic Peninsula) (Arntz & Gorny, 1991). No such information is available in current literature for shrimp distribution and diversity in the Eastern Antarctic regions i.e. the D'urville Sea and the Ross Sea. Information on the distribution and population densities of shrimps is necessary for producing ecosystem models which will improve understanding of trophic interactions and producing informed environmental management (Pinkerton *et al.*, 2010). A considerable amount of information about shrimps was collected during the recent International Polar Year-Census of Antarctic Marine Life (IPY-CAML) cruise in the Ross Sea. With these new datasets and well-timed maturity of SDM algorithms to successfully model species distribution in a wider area, gave me the opportunity to update the existing biogeography knowledge of decapod shrimps and proceed with understanding more complex physiological and ecological processes in the Southern Ocean.

This thesis has addressed and expanded on the knowledge about the decapod shrimps in the Ross Sea, Antarctica, in relation to their diversity and distribution in the surrounding environment in the past, present and future climatic condition. It also addressed the lack of information about the role and importance of the shrimps in the Antarctic benthic ecosystem. Here I introduce:

- the physical and environmental characteristics of the Southern Ocean and the Ross Sea;
- biodiversity studies in the Southern Ocean;
- decapod diversity in the Southern Ocean;
- The use of SDM to predict species distributions;
- the objectives of this thesis;
- and the aims and hypothesis of the following chapters.

1.2 The Southern Ocean

The Southern Ocean is one of the most clearly defined marine ecosystems on earth, being bounded by the Antarctic Continent to the south and the Polar Front to the north. It covers an area of 34.8 million km^2 (Clarke & Johnston, 2003; Griffiths, 2010). The continental shelf around Antarctica is on average 450–500 m deep, but exceeds 1000 m in places. Of the total SO area, the continental shelf (<1000m in depth) covers 4.59 million km^2, the continental slope (1000–3000 m in depth) covers 2.35 million km^2 and the deep sea (>3000m in depth) covers approximately 27.9 million km^2 (Clarke & Johnston, 2003).

The Southern Ocean marine environment is characterized by low but stable temperatures. Surface water temperature of the most variable sites (e.g. Signy Island) ranged between -1.8°C in winter and around +1.0°C in summer while at high Antarctic (e.g. McMudro Sound) it goes down to maximum -2.0°C in some years (Clarke, 1988). The total annual fluctuation in sea temperature rarely exceeds 3°C in the region of the Antarctic Peninsula and Scotia Sea and is half this or less at high Antarctic (continental coast)(Peck, 2005). Sea surface temperatures in the Southern Ocean have been well studied using both traditional and satellite-based methods. The different temperature regimes of the upper waters are separated by marked gradients across various fronts (Orsi *et al.*, 1995). There is a change of around 4–5°C across the Subtropical Front from subtropical waters of >11.5°C to sub-Antarctic waters of 5–7.5°C (Orsi & Whitworth, 2004). The Antarctic Circumpolar Current (ACC) developed during the Oligocene and led to climatic cooling of the Southern Ocean (Lawver & Gahagan, 2003). At about 50°S cold water masses coming from the South (surface temperature ca. 2°C) meet warmer waters from the North (surface temperature ca. 8°C (Orsi *et al.*, 1995)). The sharp change in water temperature is detectable to a significant depth and may pose an oceanographic barrier, called the Polar Front (Figure 1.1). However, near the bottom this difference will be less distinct, depending on the depth of the seabed (Orsi *et al.*, 1995). Potential seabed temperatures at 50°S are ca. 2°C on continental shelf (0–1,000 m), 0–2°C on continental slope (1,000–3,000 m) and -1–0°C in deep-sea areas (>3,000 m) (Clarke *et al.*, 2009). At high southern latitudes, seabed potential temperature is highest on the shelf of the western Antarctic Peninsula (ca. 1°C), whereas it is lowest on the shelves of the Weddell and Ross Seas (ca. -1.5°C at Clarke *et al.*, 2009). The cold waters of the shelf and deep regions of the Weddell Sea and East Antarctica are made up of Antarctic bottom water, whereas the warmer waters of Western Antarctic Peninsula are explained by incursions of circumpolar deep water onto the shelf. There is also distinct latitudinal variation in the difference between bottom temperatures on the shelf, slope, and deep sea, of which the deep sea is warmer by up to ~2°C at high latitudes and colder by ~2°C around sub-Antarctic islands (Griffiths, 2010).

The waters south of the Polar Front have a distinct chemical signature (Orsi & Whitworth, 2004). The upper and surface waters have low salinity (less than 34.0 PPT), except in the Weddell and Ross Seas, where sea ice formation removes freshwater, increasing the overall salt content. At the seafloor the Antarctic bottom water was highly saline, as it is also created during sea ice formation. In general oxygen levels were significantly higher than most other regions of the world (>320 µmol/kg at 50 m depth) (Orsi & Whitworth, 2004). In general, the SO is considered high in nutrients but low in chlorophyll. One of the most important factors controlling primary production in the SO is iron. Iron availability is limited and phytoplankton blooms occur near natural sources of mineral iron, such as islands (Korb *et al.*, 2004).

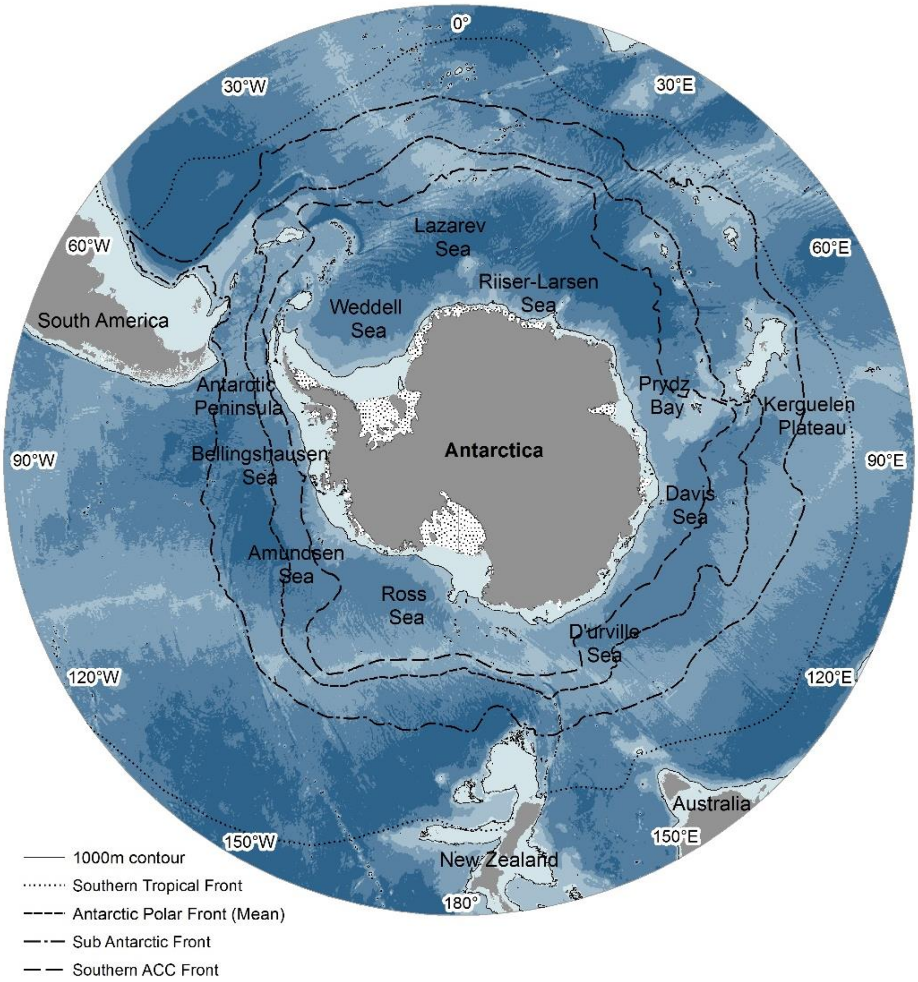

Figure 1.1. Map of the Southern Ocean showing various fronts following Sokolov & Rintoul (2009) and bathymetry from General Bathymetric Chart of the Oceans, GEBCO08 (shallow to deep water presented in white to blue colour gradient).

Typical to polar regions, the annual light varies between seasons with no direct sunlight in winter (end Nov – March) and 24 h direct sunlight in summer (end May – September) producing radiation levels similar or above the values of tropical regions. Antarctic sea-ice formation and melting varies between ca.10 and 15 million km^2 in winter and summer respectively. This result in intense seasonality of phytoplankton productivity, especially in near shore waters reaching chlorophyll standing stock levels in excess of 25 mg Chl a m^{-3} at sites around the South Orkney, Signy and Adelaide Island (Clarke *et al.*, 1988). Open ocean productivity is often associated with the edge of the sea-ice, and a significant portion of overall oceanic productivity occurs in these areas (Comiso *et al.*, 1990; Smith & Comiso, 2008). Higher Chlorophyll concentration in combination with algal productivity on the sea ice (Garrison *et al.*, 2003) can be a more significant source of resource supply to the benthic communities on the seabed (Mcminn *et al.*, 2004; Convey *et al.*, 2014).

1.2.1 Biodiversity studies in the Southern Ocean

Despite covering about 10% of the world ocean, large areas of the SO still lack a basic biodiversity inventory. The majority of the Southern Ocean taxa appear to have a circum-Antarctic distribution, but not all species will be found in all places, even where apparently suitable habitat exists. Dell (1972) and White (1984) first published about the species richness of the SO marine fauna and it was recently reviewed by others (Arntz *et al.*, 1997; Clarke & Johnston, 2003; De Broyer *et al.*, 2003; Griffiths, 2010; Kaiser *et al.*, 2013). Although many authors have described the composition and biodiversity of SO marine taxa (Dayton, 1990; Arntz *et al.*, 1997; Brandt, 1999a, 1999b; Clarke & Johnston, 2003; De Broyer *et al.*, 2003; Griffiths *et al.*, 2009), there are still relatively few places in the SO for which comprehensive faunal lists exist. Few of the relatively well-studied areas are the northern west Antarctic Peninsula, Weddell Sea and Admiralty Bay (Barnes & Conlan, 2007). A comparison of species richness for the SO with the fauna known for the Weddell Sea, the Ross Sea, and very preliminary data for the much smaller areas of Admiralty Bay, Arthur Harbour and Signy Island show dominance of certain taxonomic groups reflected at all scales (Table 1.1).

Littoral and shallow littoral zones have been relatively well studied in several places (Sicinski *et al.*, 2011) but deeper regions of the SO remain relatively under-sampled (Brandt, 1999a; Clarke & Johnston, 2003; Brandt *et al.*, 2004; Brandt, 2005; Griffiths, 2010; Griffiths *et al.*, 2011). The estimations of the biodiversity of the Antarctic shelf are still weak because many geographic areas are not sampled representatively until today (e.g. East Antarctic, Bellingshausen and Amundsen seas) (Gutt *et al.*, 2004; Griffiths, 2010). This significant gap of deep sea sampling in the past was convincingly demonstrated by Griffiths *et al.* (2003) with the Southern Ocean bivalve distribution using SOMBASE. The SO deep sea differs in faunal composition from the Antarctic continental shelf. Contrary to the shelf, which is zoogeographically well isolated through the ACC, the SO deep-sea faunal elements may freely move in and out of the SO abyssal plains of the world oceans (Brandt, 2005). Data from the SO deep sea obtained so far have shown that the fauna does not differ generally in composition at the higher taxonomic level from that of other deep-sea regions of the world oceans (Brandt, De Broyer, *et al.*, 2007). In general, the species composition of abyssal (4000 - 6000 m) deep sea communities is poorly known in comparison with shelf and upper-slope environments (Gage, 1991; Griffiths, 2010).

Table 1.1. A comparison of species richness in two regions and three smaller areas of the Southern Ocean with the total regional fauna (From Clarke & Johnston, 2003 and citations therein).

	Southern Ocean	Region	Areas			
		Weddell Sea	Ross Sea	Admiralty Bay	Signy Island	Arthur Harbour
Annelida						
Polychaeta	645	225	97	~100	78	142
Urochordata	118	24	40	nd	nd	4
Bryozoa						
Cheilostomatida	249	180	163	nd	87	nd
Cnidaria						
Hydrozoa	186	36	25	nd	nd	nd
Anthozoa	86	33	19	nd	nd	nd
Brachiopoda	19	nd	7	nd	od	nd
Crustacea						
Decapoda	8	4	nd	2	nd	nd
Amphipoda	496	174	nd	99	nd	48
Isopoda	257	68	33	nd	nd	38
Pycnogonida	175	69	64	nd	nd	6
Echinodermata						
Asteroidea	108	50	28	15	nd	nd
Crinoidea	28	6	9	nd	nd	nd
Echinoidea	49	nd	nd	4	nd	2
Ophiuroidea	119	43	nd	15	nd	6
Holothuroidea	106	35	nd	3	nd	2
Mollusca						
Gastropoda	530	145	nd	35	82	8
Bivalvia	110	43	nd	27	nd	20
Porifera + Symplasma	279	nd	57	nd	nd	nd
Total taxa with No Data	0	3	7	9	15	6

* nd = no data

Among the few investigations of deep-sea biology that have been carried out in the Southern Ocean, none has been devoted exclusively to the deep water. The Antarctic deep-sea regions have been explored by some scattered Russian and American investigations (R.V.s *Eltanin*, *Glacier*, Akademik *Kurchatov*, and Akademik *D. Mendeleiev*) mostly in the 1960's (mainly focused on the shelf off the South Orkneys and South Sandwich Islands (Clarke, 2003; Malyutina, 2004 and citations therein). Among other regions of the Southern Ocean, the Beagle Channel was sampled including several deep sea stations in 1873–1876 (HMS Challenger), and later during IBMANT (interactions between the Magellan Region and the Antarctic) in 1994 (Arntz *et al.*, 1999; Arntz & Rios, 1999). A wealth of benthic data on species of all taxonomic groups and functional guilds collected from Weddell Sea and the Antarctic Peninsula region by more recent programmes such as EPOS (European Polarstern Studies) and EASIZ (Ecology of the Antarctic Sea Ice Zone), which also collected deep-sea data from the slope but rarely from abyssal sites (Brandt & Ebbe, 2009). More significantly, the ANDEEP expeditions between 2002-2005 in the Atlantic Sector (Brandt *et al.*, 2004; Brandt, De Broyer, *et al.*, 2007; Brandt, Gooday, *et al.*, 2007) and most recent NZ IPY-CAML expedition at 2008 in the Ross Sea collected a significant amount of data of deep sea slopes and abyssal regions.

1.2.2 Decapods in Southern Ocean

The order decapoda consists of shrimps, crayfishes, lobsters, and crabs. The members of this group have ten legs and are distinguished from other crustaceans by a well-developed carapace that covers the head and thorax. Decapod crustaceans are known to play a critical role in metabolizing and controlling the flow of energy in an ecosystem (Wenner, 2001). They are preyed upon by a variety of predators from alligators to fishes. Depending on its intensity, predation is a factor in controlling population density, as well as structuring species assemblages within a habitat. Decapods are also important predators themselves, consuming phytoplankton, benthic algae, macrobenthos and species in deepest marine region: marine snow derivatives (Coull & Bell, 1983; Cartes *et al.*, 2007). Decapod particulate feeders consume detritus derived from fragments of organic matter and faeces, thereby making detritus available to several different trophic levels and processing particles in such a way that substrate is enhanced for accelerated growth by diatoms and bacteria (Field, 1983). While there is some information on the role of specific decapod species in aquatic systems, our understanding of decapod crustacean populations and communities is limited. As more information is collected on life histories, demography, and species interactions, a better understanding of the role of decapods in ecosystems will emerge.

The higher Crustacea, particularly the Decapoda, were believed to be scarce in the SO (Figure 1.2), being replaced by a rich pycnogonid and peracarid fauna (Brandt, 2005; Brandt, De Broyer, *et al.*, 2007). The low species numbers of the Decapoda compared to other species were regarded to be the prime reason for the success of the brooding peracarid crustaceans in the SO (Thatje *et al.*, 2005). However, recent study in the species composition and distribution of decapods in the Antarctic during the past decade have revealed their wider distribution around the Antarctic (Clarke, 1990; Briggs, 1995; Arntz *et al.*, 1999; Gorny, 1999; Thatje & Arntz, 2004; Thatje *et al.*, 2005; Griffiths, 2010; Griffiths *et al.*, 2013). The recent absence of many groups of decapods in Antarctic waters is in contrast to fossil records found at various locations around the Antarctic Peninsula and indicate the presence of brachyuran crabs and a thalassinoid during the late Eocene (Zinsmeister & Feldmann, 1984; Clarke *et al.*, 1992). The presence of large anomuran crabs in the SO is limited to the Lithodidae, which have been found in several deep-water locations including the continental slope of the West Antarctic Peninsula (Klages *et al.*, 1995; Thatje & Arntz, 2004; Ahyong & Dawson, 2006; Thatje *et al.*, 2008; Griffiths *et al.*, 2013). Three genera of deep-sea lithodids (*Lithodes, Neolithodes and Paralomis*) have been found at latitudes above 60°S, although species number was lower than in the adjacent sub-Antarctic regions (Lovrich *et al.*, 2005; Thatje *et al.*, 2005). Diversity of lithodids in the region 45–60°S is higher than 60–70°S, and species *Neolithodes yaldwyni* and *Paralomis stevensi* are both endemic to waters south of 60°S. This indicates that some adaptations to very low temperatures are present in lithodids living at the lowest end of the family's temperature range (Hall & Thatje, 2009; Hall & Thatje, 2010). Another study by Arntz *et al.* (1999) suggested that the southern tip of the Magellan region (or northern slope of the Drake Passage) acted as a transitional area between the Antarctic and cold-temperate faunas particularly in case of decapods.

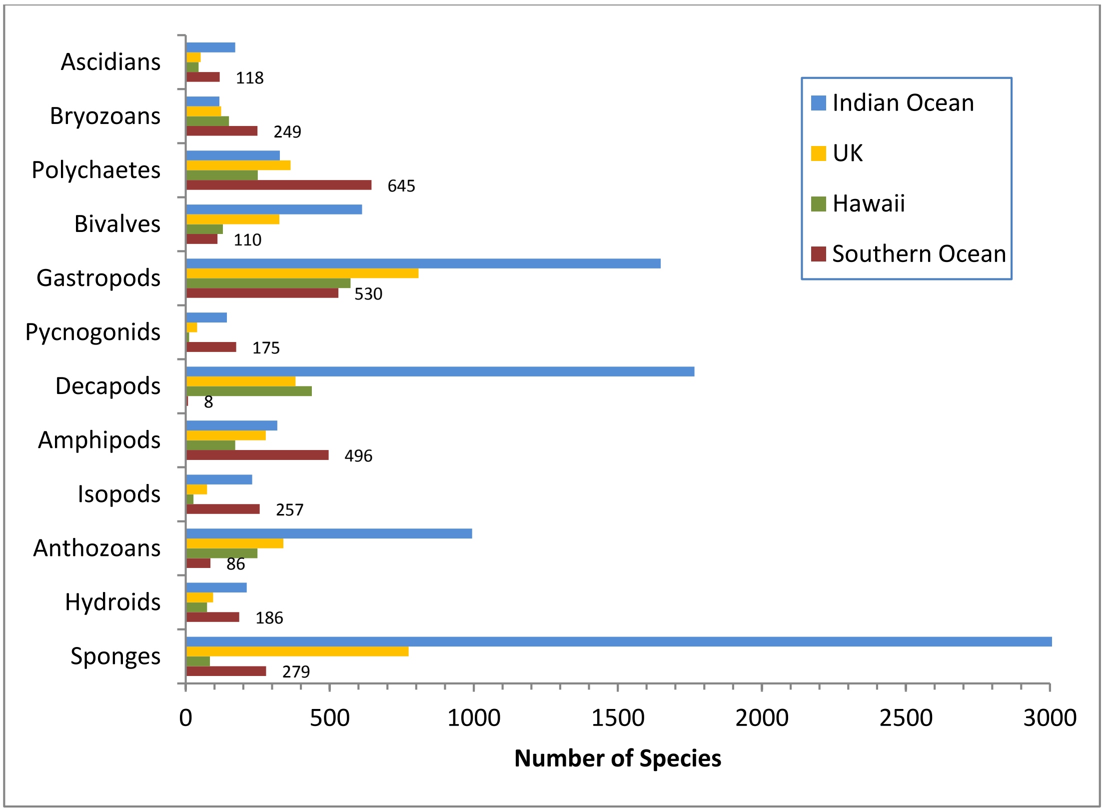

Figure 1.2. Species diversity for selected benthic marine invertebrate groups in the Southern Ocean (Clarke & Johnston, 2003), with Hawaii (Eldredge & Miller, 1995), UK and waters around Indian Ocean (Appeltans *et al.*, 2011).

The first Antarctic caridean shrimp species, namely *Chorismus antarcticus and Notocrangon antarcticus*, were discovered by the expedition of the German Polar Commission to South Georgia in 1882–1883 (Pfeffer,1887) (Thatje & Arntz, 2004). Since then, a few new species and records of decapods have been reported from the SO (Yaldwyn, 1965; Kirkwood, 1984; Wasmer, 1986; Iwasaki & Nemoto, 1987; Tiefenbacher, 1990; Thatje, 2003; Komai & Segonzac, 2005; De Grave & Fransen, 2011) but still the knowledge about the diversity of the decapods remained poor, only a dozen of species represented in further studies.

The difficulty to describe the biogeography of marine invertebrates in the higher latitudes of the SO has been outlined by various authors (Crame, 1996 and citations therein). Biogeographical studies of living invertebrates, such as imphimediid amphipods and serolid and arcturid isopods suggest strongly that they may have originated in the Southern Ocean and dispersed subsequently into lower latitude regions through the later Cenozoic (Clarke *et al.*, 1992). Gorny (1999) attempted to define the biogeography and ecology of decapods in the SO using data available from all past expeditions. Studies by Arntz & Gorny (1991) using *'Polarstern'* cruise data and Gutt *et al.* (1991) using underwater photography described species composition, distribution pattern and habitat ecology of three frequently occurring natant decapods species in the Weddell Sea region. Since then our knowledge on the distribution has been increased considerably in recent years through numerous expeditions carried out in various regions of the SO (as explained above). Even after all these expeditions particularly in terms of available records for decapods, the Ross Sea region remains the least studied (Table 1.1).

1.3 The Ross Sea

Ainley *et al.* (2010) followed the Ross Sea boundary used by Davey (2004), as the waters overlying the continental shelf and slope extending in a wavering line, including the northward projecting Pennell Bank, from Cape Adare, Victoria Land (71°17'S, 170°14'E), to Cape Colbeck, Marie Byrd Land (77°07'S, 157°54'W). Some authors also included the waters around the Balleny Islands (66°55'S, 163°20'E), which are the summits of deep-rising sea mounts, 200 km to the northwest of Cape Adare, whereas others also included this area, as well as waters between 130°E to 150°W and as north as 60°S (Hanchet *et al.*, 2008). "Biologically, the Ross Sea is divided into two components, the continental shelf (neritic) and the continental slope (pelagic)."(Ainley *et al.*, 2010) Defined as above, the ice- free portion of the Ross Sea is 433,061 km^2 (delineated by 800 m isobath and the Ross Ice Shelf front) and 647,194 km^2 when the continental slope is included. This area comprises 3% of the Southern Ocean (determined to be ~20 million km^2, Costello *et al.*, 2010). Part of the Ross Sea basin is covered by Ross Ice Shelf to the south equal in size to the open-water portion in the north. The mean depth of the exposed shelf is about 500 m, although this varies widely between deep troughs and shallow banks, which are roughly running in a north-south direction (Figure 1.3).

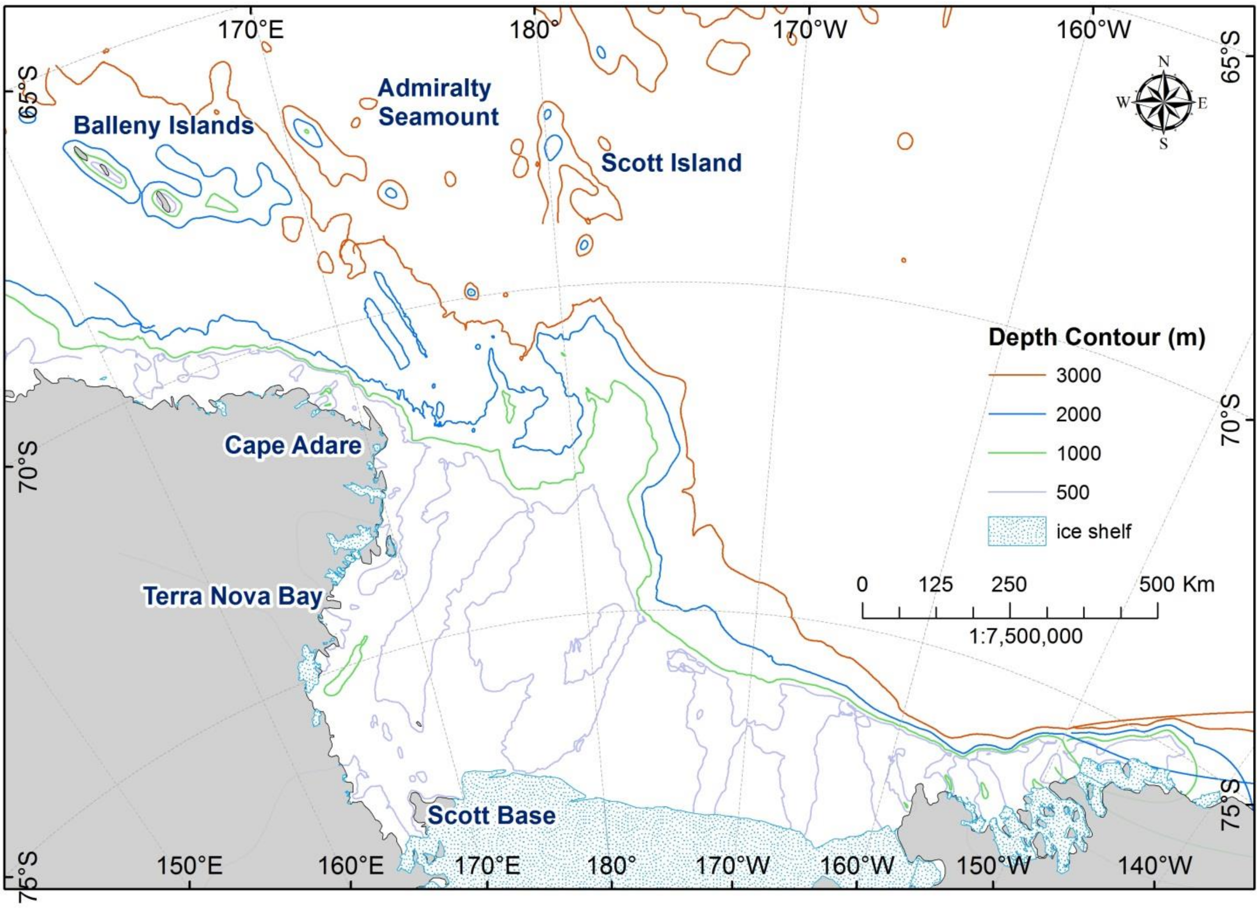

Figure 1.3. Map of the Ross Sea showing the bathymetry with depth contours.

Water circulation patterns in the Ross Sea are closely related to the formation of sea-ice and polynyas (open ocean areas in between the ice-sheets) in summer months (Smith *et al.*, 2012). The prevalent katabatic winds blow across the Ross Sea and push northwards the newly formed sea-ice at the edge of the Ross Ice Shelf. This establishes polynyas and areas of low sea-ice density east of Ross Island (Ross Sea polynya) and to the north of the Kryglinsky ice tongue (Terra Nova Bay polynya). During winter, cold air temperatures result in the formation of new sea-ice in the polynya, which again is pushed northwards (Arrigo & van Dijken, 2004). This cycle of polynyas formation during winter months generates ~450 cubic kilometres of sea-ice each year – the highest annual sea-ice contribution in Antarctica (Jacobs & Comiso, 1989).

The primary production in the Ross Sea is mostly generated by photosynthesis and is therefore limited to the summer months. Benthic primary production is limited in the Ross Sea, as most of the shelf surface is below the euphotic zone or covered in fast ice reducing light penetration. In the intertidal, only cyanobacteria and diatoms thrive during summer, restricted to rock pools fed by melted ice (Cattaneo-Vietti *et al.*, 2000), whereas green macroalgae are limited to areas sheltered from ice abrasion (Smith *et al.*, 2007). Phytoplankton assemblages change their composition across summer months in the Ross Sea. In the early summer it is dominated by

Phaeocystis antarctica while in the late summer diatoms are common over the shelf. (Smith *et al.*, 2014). Both of these species thrive in ice-free areas, whereas cryophilic algae, which develop in the sea ice, account for 20% of the total primarily productivity in the Ross Sea (Arrigo *et al.*, 2003).

1.3.1 Studies on the Ross Sea ecosystem

The Ross Sea has a diverse biota in both the neritic and the benthic realms, and includes a substantial contribution to the overall diversity from both the ice and the shallow water littoral. Much is known of each of the trophic levels, but despite the long history of study (dating from the explorations of James Clark Ross in the mid-1800s), a great deal remains poorly known (Smith *et al.*, 2007). Bradford-Grieve and Fenwick (2002b) carried out an extensive review of the biodiversity of the Ross Sea covering over 3000 publications. They concluded that much is still unknown about biodiversity and ecosystem functioning of the Ross Sea and adjacent regions. The patterns of biodiversity that are known have arisen from sparse sampling and usually incomplete analysis of sporadic collections dating back over 150 years. They identified the need for wider ranging integrated biodiversity sampling programmes and analyses that take into account the important probable forcing factors (i.e. resilience and vulnerability of Ross Sea biodiversity, biomass, characteristics of the biota etc). They also noted that much more knowledge is required of the standing stocks and the rates of biological processes to understand the resilience of Ross Sea biodiversity.

Until recently most of the benthic research in the Ross Sea has been in the coastal waters, particularly in the McMurdo Sound and Terra Nova Bay regions (Dayton *et al.*, 1974; Pearse *et al.*, 1986; Mcclintock, 1994; Carli & Pane, 2000; Chiantore *et al.*, 2002; Berkman *et al.*, 2005; Thrush *et al.*, 2006; Choudhury & Brandt, 2007). Relatively few studies have investigated the benthic macrofauna of the deeper waters of the Ross Sea, two exceptions being Gambi & Bussotti (1999) who visited three locations in the non-coastal Ross Sea in 1994–1995, and the ROAVERRS series of voyages (Barry *et al.*, 2003). More recently, the Research Vessel Italica visited coastal areas in the vicinity of Cape Hallett, Cape Adare, Coulman Island and Cape Russell in 2004, and carried out transect-based sampling of stations 100–500 m deep (Cummings *et al.*, 2005). Also in 2004, the Research Vessel Tangaroa visited areas from Cape Adare to Cape Hallett, and sampled five across-shelf transects, targeting three depth strata (50–250, 250–500 and 500–750 m;Mitchell & Clark, 2004; Pinkerton *et al.*, 2010).

De Broyer *et al.* (2011) highlighted the zone between Amunden Sea and Ross Sea as one of the regions having the most important sampling gaps in Antarctic biodiversity. In common with most other sectors of the Antarctic, deeper benthic habitats of the shelf edge, slope and abyssal depths remain under-sampled (Arntz *et al.*, 1994; Clarke & Johnston, 2003; Brandt, De Broyer*, et al.*, 2007). Pinkerton *et al.* (2006) found no data from the deeper benthic habitats from the Ross Sea region after a comprehensive search of the scientific and grey literature. The authors believed that the highest priority for each trophic group was the spatial distribution and abundance of the key species across the study area. If data on the above components are gathered then it will considerably help fill the gaps in knowledge of the Ross Sea ecosystem identified in reviews by (Bradford-Grieve, 2002b, 2002a) and modelling by (Pinkerton *et al.*, 2005; Pinkerton *et al.*, 2006). Information on decapod invertebrate distributions and population density in the Ross Sea is necessary for producing ecosystem models which will give us important insights about the past, present and future resilience abilities of these organisms, and thus the communities as a whole to respond to the effect of environmental change. Previous studies on decapods' biogeography were discussed in relation to multivariate cluster analysis (Gorny, 1999; Boschi & Gavio, 2005), physiological difference (Crame, 1999; Frederich *et al.*, 2001; Wittmann *et al.*, 2010), and habitat preferences (Gutt *et al.*, 1991). However, as SDM provide a new method to quantify the distributions, we used past and new data on decapod shrimps to generate species distribution models to understand about their distribution pattern in the Ross Sea and in the Southern Ocean.

1.4 Species Distribution Modelling to predict species potential distribution

Species distribution models (SDM) have a wide variety of uses in biogeography, ecology and conservation biology (Elith & Leathwick, 2009). In many cases they are regarded as a method of providing an index of environment or habitat suitability. Relatively higher values indicate more suitable conditions, but exact values of the index are not imbued with any meaning. In SDM's, species climate niches or envelopes have been defined by assessing the relationship between known occurrences and climate related variables. They may be used to predict species' responses to climate change (Guisan & Zimmermann, 2000; Peterson & Vieglais, 2001; Elith *et al.*, 2006; Pearson *et al.*, 2007; Elith & Leathwick, 2009; Feeley & Silman, 2011). In reality, additional factors not considered in the modelling (including biotic interactions, geographic barriers and history) mean that species rarely occupy all areas within suitable environments. The output from niche-based distribution models therefore must be interpreted carefully (as discussed by

Anderson *et al.*, 2002; Phillips *et al.*, 2006; Pearson *et al.*, 2007). Despite these caveats, distribution models have been shown to yield highly informative biogeographical information (e.g. Fleishman *et al.*, 2003; Pearson *et al.*, 2007; Monk *et al.*, 2010). SDM's utilize presence-absence records for predicting species distributions. There has been a wide discussion prompted by using presence-only data for modelling species distribution (Elith *et al.*, 2011 and citations therein for brief overview). Elith *et al.* (2006) demonstrated that non–parametric models such as Boosted Regression Trees (BRT), Maximum Entropy (MaxENT) and Generalised Dissimilar Model (GDM), performed better than regression models (e.g. Generalized Linear Model - GLM and Generalised Additive model - GAM), which in turn performed better than BIOCLIMatic (BIOCLIM), Limiting Variable and Environmental Suitability (LIVES) and Domain models that used presence only data.

I used Maximum Entropy (MaxEnt) to generate SDM's in two chapters in this study. MaxEnt is a machine-learning technique based on the principle of maximum entropy (Jaynes, 1982 and citations therein) it was adapted for species distribution modelling by Phillips *et al.* (2004; 2006). The method seeks to find the probability distribution of species presence over all cells of the study area that best agrees with the constraints given by the observed species locations and, at same time, is closest possible to uniform (maximum entropy) in order to avoid any unfounded constraints. MaxEnt's predictive performance is consistently competitive with the highest performing methods (Elith *et al.*, 2006). Since becoming available in 2004, it has been utilized extensively for modelling species distributions. Published examples include finding correlates of species occurrences, mapping current distributions, and predicting distribution in future times and places across many ecological, evolutionary, conservation and biosecurity applications. Government and nongovernment organizations have also adopted MaxEnt for large-scale, real-world biodiversity mapping applications (Elith *et al.*, 2011).

In general with SDM, the environmental variables and functions thereof (features) from various sources are used as predictors with regularisation functions: constraining the average value for a given feature so as to be close (i.e. within the confidence intervals) to its empirical average. MaxEnt as a generative approach is especially advantageous when processing small and noisy data sets (Elith *et al.* 2006, Phillips *et al.* 2006). The assessment of models predictive performance has been dependent on the availability of observed absence data, which as negative data can be problematic, or on the partitioning of data into training and test data sets, which can become very small (e.g. Anderson *et al.*, 2002; Anderson *et al.*, 2003). In practice, available occurrence records are often split into test and training sets using a partitioning method such as bootstrapping, randomization or k-fold partitioning (Fielding & Bell, 1997). Perhaps the simplest and most common approach is to split the available data into training and test sets, using either a random (e.g. Pearson *et al.*, 2002) or spatially stratified (e.g. Peterson & Shaw, 2003) partition. However, such approaches are not appropriate when available data are limited, since both training and test data sets become very small.

The limited number of occurrence records has meant that the possibility of independent tests of model quality become difficult to carry out in many occasions. Whilst some studies (Stockwell & Peterson, 2002) have mentioned deterioration in predictive performance as sample sizes are decreased, Pearson *et al.* (2007) demonstrated using low numbers of records (minimum sample size from two to seven) produced results with as high as 90% of the areas of that achievable with models using over 200 records. MaxEnt also generally predicted a larger proportion of the study area as being present, thus making the approach suited to the identification of a species' potential distribution. Thus, it offers excellent potential for extracting useful biogeographical information from small samples of locality records (Pearson *et al.*, 2007). As the presence records used in this study were distributed over 160,000 km^2, which is sufficiently spatially segregated to reduce the probability of spatial-correlation between observations (Mateo *et al.*, 2010).

The limited number of natant decapods in the Southern Ocean in comparison with other fauna and regions (Table 1.1 and Figure 1.1) highlighted the need for further research to investigate the current decapods distribution pattern in the Southern Ocean. Updating the existing biogeography knowledge would enable us to proceed with more complex physiological and ecological approaches to explain the presence or absence of decapods in different regions.

The intention of this thesis was to investigate the finer detail of natant decapods diversity, habitats, associated assemblages and their spatial distribution in the Ross Sea as well as in the Southern Ocean. From the outcomes of this study we expect to advance the scientific knowledge and understanding about natant decapods and their contribution into the Antarctic ecosystem so as to better inform the relevant policy making bodies to help guide resource management of the Ross Sea ecosystem (i.e. particularly in case of crustaceans). It will also facilitate the development of management policies and tools in similar regions in the Southern Ocean.

1.5 Thesis objectives

The main focus of this thesis is to understand the diversity, distribution and ecology of decapod shrimps in the Ross Sea, Antarctica. Due to the availability of materials and data collected for analysis during the recent IPY-CAML Voyage in 2008 from the Ross Sea, we have focused our study into this region and provided discussion in wider context of the Southern Ocean. The dissertation has four main objectives:

- **Objective one:** *To identify the decapod shrimp diversity and geographic distribution in the Ross Sea and predict their potential distribution range and compare them with historical records from literature and other sources of known locations in similar regions (i.e. Weddell Sea, Antarctic Peninsula).*

  To accomplish this, observations records from all previous survey in the Antarctic were collated (Chapter 2). Specimens, video and photography data collected during surveys were analysed and SDM was used to predict potential present distributions (Chapter 3)

- **Objective two:** *Is there any difference in shrimp species composition, diversity and size frequency within the Ross Sea region or with other regions in the SO? How abundant are the shrimps? What was the community composition and what role do they play in the wider trophic ecosystem?*

  To accomplish this, specimen data from trawls, underwater video and photography data from the same cruise were used to estimate the abundance and densities of shrimps in the Ross Sea. Stable Isotope analysis following Pinkerton *et al.* (2010) was used to identify their trophic position in the Ross Sea ecosystem (Chapter 4).

- **Objective three:** *Which environmental variables influence the distribution of shrimps in the marine environment and does their source or spatial resolution matter when using them for Species Distribution Models?*

  To accomplish this, environmental dataset from two different sources with different resolutions were used in SDM to investigate their influence and the effect of resolution with different shrimp species (Chapter 3). Moreover, a comprehensive compendium of marine environmental dataset was compiled and standardized using modified data processing protocol (Chapter 5) and the dataset was subsequently used in generation of species distribution models in other chapter (Chapter 6).

- **Objective four:** *To identify whether deep sea shrimps are susceptible to changing environmental conditions over the millennia and how they will react with projected climate change scenario in the future.*

  To accomplish this SDM were used with a novel approach in predicting refugia and how a species' distribution may change by 2100 in the Southern Ocean (Chapter 6).

1.6 Chapters overview and aims

The thesis is presented as a series of self-contained chapters, which are grouped under the major questions posted in the thesis objectives.

1.6.1 Chapter 2: Decapod Shrimps in the Antarctica

Aim: To summarize current knowledge and location of shrimps in the Antarctica (within Antarctic polar front) and identify their distribution range.

Species' distribution records were compiled from the literature and databases. This chapter summarized previous and current knowledge about decapod shrimp locations in the Antarctica, and reviewed their diversity based on family, genera, depth range and geographic locations. This chapter has been published in the SCAR Biogeographic Atlas of the Southern Ocean with the title of "Chapter 5.22. Shrimps (Crustacea: Decapoda)" (In K. P. De Broyer C., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', Van de Putte A.P., Danis B., David B., Grant S., Gutt J., Held C., Hosie G., Huettmann F., Post A., Ropert-Coudert Y. (Ed.), Biogeographic Atlas of the Southern Ocean (pp. 190-194). Cambridge: Scientific Committee on Antarctic Research). I was the lead author of this manuscript and it was produced in collaboration with my supervisor, Mark J. Costello. (Co-authorship form attached after the Table of Contents)

1.6.2 Chapter 3: Diversity and distribution of decapod shrimps in the Ross Sea region Antarctica

Aim: To explore the diversity and distribution of shrimps in the Ross Sea region, model distribution of suitable habitat for two common shrimp species and investigate the effect of using datasets with differing spatial resolution on the outputs of species distribution models in the marine environment.

Specimen information was collected from 28 sites across the Ross Sea continental shelf, slope, abyssal plain, and seamounts. High definition digital video and still images were collected using NIWA's Deep Towed Imaging System (DTIS), which was followed by physical sampling gears including: beam trawl, large demarsal fish trawl, and two types of epibenthic sled; one on flat and another on seamount sites. Two different sets of environmental dataset with different spatial resolutions were used for SDM. The effect of using environmental datasets with different spatial resolution was also investigated in the study. This chapter has been accepted for publication in the journal PLoS One (doi: 10.1371/journal.pone.0103195). I was the lead author of this manuscript and it was produced in collaboration with my supervisor Mark J. Costello and Advisor at NIWA, David A. Bowden (Co-authorship form attached after the Table of Contents).

1.6.4 Chapter 4: Dispersion and faunal association pattern of common Antarctic shrimps

Aim: To summarize and update the species composition, relative abundance, size frequency distribution and habitat of three common decapod shrimps in the Ross Sea and compare the data with other Antarctic regions.

In this chapter, data about shrimps' density, body size frequency, habitat, and associated fauna were collected from video and photographs, which complemented the size and isotopic signature values collected from physical specimens caught with the same IPY-CAML cruise. Image analysis software was used to analyse still images to calculate specimen size, record substratum and estimate local population densities of individual taxa. For a wider comparison, preserved specimens of the same species from other museums around the world were also measured.

1.6.5 Chapter 5: Global marine environment datasets (GMED) for environment visualisation and species distribution modelling.

Aim: To create a comprehensive standardized publicly available compendium of climatic, biological and geophysical environmental datasets including present, past and future environmental conditions in a form suitable for visualization and SDM without additional processing.

The idea of this chapter initiated when compiling datasets to use with SDM for Chapter 3. It was discovered that marine datasets were found in different formats and resolution. A considerable amount of time was needed to process all of the datasets into SDM ready format. A compendium of SDM ready environmental datasets were created from *in-situ* measured, remotely sensed and modelled environmental variables into standardized dataset using geodatabase, raster interpolation and modified data processing protocol in ArcGIS. The dataset produced in this chapter has been published online with the same title. Global Marine Environment Datasets (GMED). World Wide Web electronic publication. Version 1.0 (Rev.01.2014). Available at: http://gmed.auckland.ac.nz.

1.6.6 Chapter 6: Past, present and future distribution of deep-sea shrimp in the Antarctica

Aim: To identify whether deep-sea shrimp distributions are susceptible to changing environmental conditions in the deep-ocean and to determine how they may respond to changing climatic conditions in the future.

In this chapter, I used a novel approach to predict the location of refugia during the last glacial maximum, and the change in distribution with the predicted future climatic conditions. Species occurrence data of the most common deep-sea shrimp *Nematocarcinus lanceopes* was collated as described in Chapter 1 with environmental predictors in Chapter 5. Then SDM models were generated for past, present and future climate conditions.

1.6.7 Chapter 7: General discussion, conclusions and future directions

This chapter provides a synthesis of the previous chapters and future directions based on the finding of this study.

The references, tables, figures and appendices are presented at the end of each chapter for the reader's convenience.

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Chapter 2

Decapod Shrimps in the Antarctica

2.1 Introduction

Decapod shrimps are ubiquitous in the world oceans, with most species in tropical and subtropical regions and a marked decline towards temperate and polar regions (e.g. Boschi, 2000; Van Dover, 2000; Bauer, 2004). They have a wide distribution around the Antarctic continent and to abyssal depths in the Southern Ocean (Clarke, 1990; Tiefenbacher, 1990b, 1990a; Briggs, 1995; T. Komai *et al.*, 1996; W. E. Arntz *et al.*, 1999; Gorny, 1999; Thatje & Arntz, 2004; Boschi & Gavio, 2005; Thatje, Anger, *et al.*, 2005; Ahyong, 2009; Griffiths, 2010; Dambach *et al.*, 2012; Griffiths *et al.*, 2013; Linse *et al.*, 2013). Historically, Antarctic shrimps may have persisted through several glaciation events by surviving in the deep-sea during glacial maxima and recolonizing the continental shelf as ice shelves retreated during interglacials (A. Brandt, Linse, K., Mühlenhardt-Siegel, U., 1999; A. Brandt, 2005). They may be able to tolerate extremely low sea-water temperatures through their ability to regulate magnesium levels in the haemolymph (Frederich *et al.*, 2001; Wittmann *et al.*, 2010); a capacity which other crabs and lobsters lack (Gorny *et al.*, 1992; Frederich *et al.*, 2000).

Although predominantly benthic, they also occur in the water column and in symbiotic relationships (Bauer, 2004). Their feeding habits range from deposit feeding to carnivory (Lagardère, 1977; Cartes *et al.*, 2002; Fanelli & Cartes, 2004), and they can contribute significantly to the processing and recycling of materials at the seabed (Coull & Bell, 1983; Field, 1983; Cartes *et al.*, 2007). Some shrimps species comprised 20% of the weight and occurred in 70% of the diet of Weddell seals (Green & Burton, 1987). Thus if widespread and abundant they could play a significant role in Antarctic food webs.

This chapter illustrates the distribution of decapod shrimp species in the Southern Ocean, defined here as the region south of the Antarctic Polar Front, and comment on their ecology. The data were compiled from the literature and from follow up chapters have been published through the SCAR-MarBIN.

2.2 Biodiversity

Two Antarctic caridean shrimp species, *Chorismus antarcticus* (Pfeffer, 1887) and *Notocrangon antarcticus* (Pfeffer, 1887), were first discovered during the German Polar Commission expedition to South Georgia in 1882–1883 (Thatje & Arntz, 2004). Since then, 19 publications have reported new species and records of shrimps from the Southern Ocean (Yaldwyn, 1965;

Zarenkov, 1968; Makarov, 1970; Vinuesa, 1977; Boschi *et al.*, 1981; Kirkwood, 1984; Wasmer, 1986; Iwasaki & Nemoto, 1987; Tiefenbacher, 1990b; Branch *et al.*, 1991; Gorny, 1999; Boschi, 2000; Wolf E. Arntz, 2003; M. Retamal & Gorny, 2003; Thatje, 2003; T. Komai & Segonzac, 2005; Ahyong, 2009; De Grave & Fransen, 2011; Nye *et al.*, 2013).

To date, 23 shrimp species belonging to 10 families and 14 genera have been reported from the region (Table 2.1). There are approximately 4,050 decapod shrimp species reported world-wide (De Grave & Fransen, 2011). Twenty of the Antarctic species belong to the infraorder Caridea, which is globally the second most species–rich decapod group after Brachyuran crabs (De Grave & Fransen, 2011), and about half of these species belong to just three families; Acanthephyridae, Hippolytidae and Pasiphaeidae(Figure 2.2).

2.3 Geographic distribution

The Atlantic, Indian, and Pacific Ocean sectors of the Southern Ocean have 18, 16, and 15 decapod shrimp species respectively. Nine (40% of) species occur in all three sectors. Four species were only reported from the Atlantic sector, two to the Pacific sector and none to the Indian Ocean sector (Table 2.1). In the Atlantic sector, there were more benthic (56%) than pelagic (44%) species, whereas in the Pacific and Indian Ocean sectors pelagic species were more numerous (60-61%) (Figure 2.3a, Table 2.1). The regions with the lowest numbers of shrimp records were from the Amundsen Sea to the eastern Ross Sea, the Bellingshausen Sea, the western Weddell Sea, and East Antarctica from the Mawson Sea to the D'Urville Sea (Figure 2.3).

The northern distribution boundary for more than half the Antarctic species was at about 55°S, coinciding with the Polar Front (Figure 2.4 and 2.5). The pelagic species' had wider geographic ranges than benthic. Some extended up to the tropical zones of Asia, Africa and South America, or even towards the Arctic seas (i.e. *Acanthephyra pelagica*) (Gorny, 1999). *Pasiphaea acutifrons* has been reported around the Chilean coast and further north in the Pacific Ocean, off the coasts of Japan and Hawaii (Gorny, 1999; Tomoyuki Komai *et al.*, 2012). *Nematocarcinus longirostris and Campylonotus vagans* are the only two benthic species whose range extended to the temperate waters north of the antiboreal region of South America. *Eualus kinzeri* and *E. amandae* were the only two species endemic to south of the Polar Front (Gorny 1999; Nye *et al.* 2013).

2.4 Depth distribution

For this study the continental shelf, slope and deep-sea (or abyssal) zones were defined as between 0-1000 m depth, 1000-3000 m, >3000 m, respectively. Shrimps have been recorded from the shallow continental shelf to the abyssal in the Southern Ocean (Figure. 2.6, Figure 2.7). Two-thirds of the pelagic but only one-sixth of the benthic, species were in all depth zones (i.e. eurybathic) (Table 2.1). Four species occurred in all three depth zones (shelf, slope and deep-sea) (Table 2.1, Figure 2.5). The Acanthephyridae family covered the widest depth range, from 122 m to 3934 m (Figure. 2.6). Species found deeper than 500 m had a wider depth range compared to species occurring in shallow waters (<500 m). The pelagic species exhibited wider geographic and depth ranges than the benthic species (Figure 2.3a; Figure. 2.7). Iwasaki & Nemoto (1987) similarly found that deep-water pelagic species tended to be distributed from sub-tropical regions southwards. Species richness decreased with depth; with 19, 17, and 9 species in the continental shelf, slope and abyssal zones (Figure 2.3b, Figure. 2.7, Table 2.1).

2.5 Ecology

In situ observations of benthic shrimp species in the Antarctic show they may be associated with a wide range of habitats (Gorny, 1999; Chapter 3). Caridean shrimps are mostly associated with debris, sponges, or sediments covered with detritus. The maximum density of benthic shrimps recorded in seabed camera surveys is 9 individuals*m^{-2} in the Weddell sea (Gutt *et al.*, 1991) but only 4 individuals*m^{-2} in the Ross Sea (Chapter 3). *Nematocarcinus lanceopes* is solitary and lives on or above the substratum; *Notocrangon antarcticus* tends to be partially buried in muddy sediments; and *Chorismus antarcticus* is associated with sponges (Gutt *et al.*, 1991), bryozoans, and other sessile epifauna (Chapter 3).

Detailed studies of Antarctic shrimps have focused to date on reproductive biology and larval development (Gorny *et al.*, 1992; Gorny & George, 1997; Thatje, Bacardit, *et al.*, 2005; Lardies & Wehrtmann, 2011), biochemical or metabolic characteristics (Dittrich, 1990; Bluhm *et al.*, 2002), digestive systems (Storch *et al.*, 2001) and their infestation by ectoparasites (Raupach & Thatje, 2006). There is no information on their trophic ecology and how they might contribute to ecosystem function, for example by re-cycling nutrients from deposited organic matter in sediments. In the recent International Polar Year (2007–2008), numerous shrimp specimens and datasets were collected from different regions around Antarctica. Results from studies of these datasets will improve understanding of the decapod shrimps' overall role in the Antarctic ecosystem.

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Table 2.1. The decapod shrimp species recorded south of the Antarctic Polar Front, including their occurrence in depth zones, whether adults are pelagic or benthic, present in the Atlantic (Atl, longitude 72°W–15°E), Indian (Ind, longitude 15°E–150°E), and Pacific (Pac, longitude 150°E–72°W) sectors, and maximum reported depth.

Family	**Species**	**Depth Zones**	**Habitat**	**Sectors**			**Maximum Depth (m)**	**References**
				Atl	Ind	Pac		
Acanthephyridae	*Acanthephyra pelagica* (Risso, 1816)	Shelf, Slope, Deep-sea	Pelagic	•	•	•	3635	1-5
	Hymenodora gracilis (Smith, 1886)	Shelf, Deep-sea	Pelagic		•	•	3733	2, 4, 5, 8
	Hymenodora glacialis (Buchholz, 1874)	Deep-sea	Pelagic	•	•	•	3925	4, 5
Benthesicymidae	*Gennadas kempi* (Stebbing, 1914)	Slope, Deep-sea	Pelagic	•	•		3143	2, 3, 6, 5
Campylonotidae	*Campylonotus vagans* (Bate, 1888)	Shelf	Benthic	•	•	•	506	5, 7-13 , 21, 34
	Campylonotus arntzianus (Thatje, 2003)	Shelf	Benthic	•			589	33, 34
Crangonidae	*Notocrangon antarcticus* (Pfeffer, 1887)	Shelf, Slope	Benthic	•	•	•	2350	5, 15-24, 34
Hippolytidae	*Chorismus antarcticus* (Pfeffer, 1887)	Shelf, Slope	Benthic	•	•	•	860	5, 15, 17-22, 24-26, 34
	Chorismus tuberculatus (Bate, 1888)	Shelf, Slope	Benthic	•			815	5, 8-10, 27
	Eualus kinzeri (Tiefenbacher, 1990)	Slope	Benthic	•			782	5, 15, 28
	Eualus amandae (Nye, 2013)	Slope, Deep -sea	Benthic	•			2401	32
	Lebbeus antarcticus (Hale, 1941)	Shelf, Slope	Benthic	•	•		2087	5, 7, 15, 22, 24, 32
	Lebbeus n. sp. (S. Ahyong, unpublished)	Slope, Seamount	Benthic			•	1235	20
Nematocarcinidae	*Nematocarcinus lanceopes* (Bate, 1888)	Shelf, Slope, Deep-Sea, Seamount	Benthic	•	•	•	3432	5,7, 8, 15, 18, 19, 20-22, 24, 34

	Nematocarcinus longirostris (Bate, 1888)	Shelf, Slope, Deep-sea	Benthic		•	•	3635	2, 5, 8, 24
Oplophoridae	*Systellaspis braueri* (Balss, 1914)	Shelf, Slope	Pelagic	•		•	1130	4, 5, 6, 31
Pandalidae	*Austropandalus grayi* (Cunningham, 1871)	Shelf	Benthic	•	•		413	5, 7-9, 11-13, 24, 26, 29, 30
Pasiphaeidae	*Pasiphaea acutifrons* (Bate, 1888)	Shelf, Slope Deep-sea	Pelagic	•	•	•	1560	2, 5, 7-9, 11 -13, 26
	Pasiphaea cf. ledoyeri (Hayashi, 2006)	Slope, Seamount	Pelagic			•	1587	20
	Pasiphaea scotiae (Stebbing, 1914)	Slope, Deep-sea	Pelagic	•	•	•	3660	2, 3, 5, 6, 20
	Pasiphaea berentsae (Kensley, Tranter & Griffin, 1987)	Shelf	Pelagic		•	•	1150	35
Sergestidae	*Eusergestes arcticus* (Krøyer, 1855)	Shelf, Slope, Deep-sea	Pelagic	•	•	•	3935	2, 3, 5, 29
	Petalidium foliaceum (Bate, 1888)	Slope, Deep-sea	Pelagic	•	•		3935	2, 3, 5, 6, 8, 22

References: 1 (Boschi *et al.*, 1981); 2 (Iwasaki & Nemoto, 1987); 3 (Tiefenbacher, 1994); 4 (Wasmer, 1986); 5 (Gorny, 1999); 6 (Tiefenbacher, 1991); 7 (W. E. Arntz *et al.*, 1999); 8 (Bate, 1888); 9 (Boschi *et al.*, 1981); 10 (Boschi, 1997); 11 (Holthuis, 1952); 12 (Milne-Edwards, 1891); 13 (M. A. Retamal, 1974); 14 (Miers, 1881), 15 (Gorny, 1992); 16 (Gorny, 1994); 17 (Gorny, 1998); 18 (Gutt *et al.*, 1991); 19 (Gutt *et al.*, 1994); 20 Chapter 3; 21 (Wolf E. Arntz, 2003); 22 (Hale, 1941); 23 (Makarov, 1970); 24 (Zarenkov, 1968); 25 (Branch *et al.*, 1991); 26 (Vinuesa, 1977); 27 (Spivak, 1997); 28 (Tiefenbacher, 1990b); 29 (Doflein & Balss, 1912); 30 (Mutschke & Gorny, 1999); 31 (Foxton, 1970); 32 (Nye *et al.*, 2013) 33 (Thatje, 2003) 34 (Lovrich *et al.*, 2005) 35 (Wasmer, 1993).

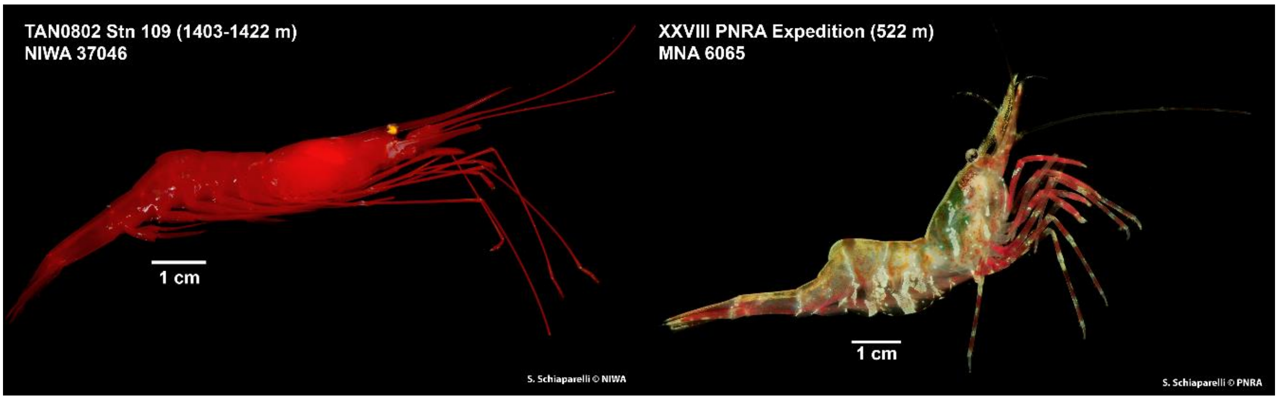

Figure 2.1. *Nematocarcinus lanceopes* (Bate, 1888) (left) *and Chorismus antarcticus* (Pfeffer, 1887) (right).

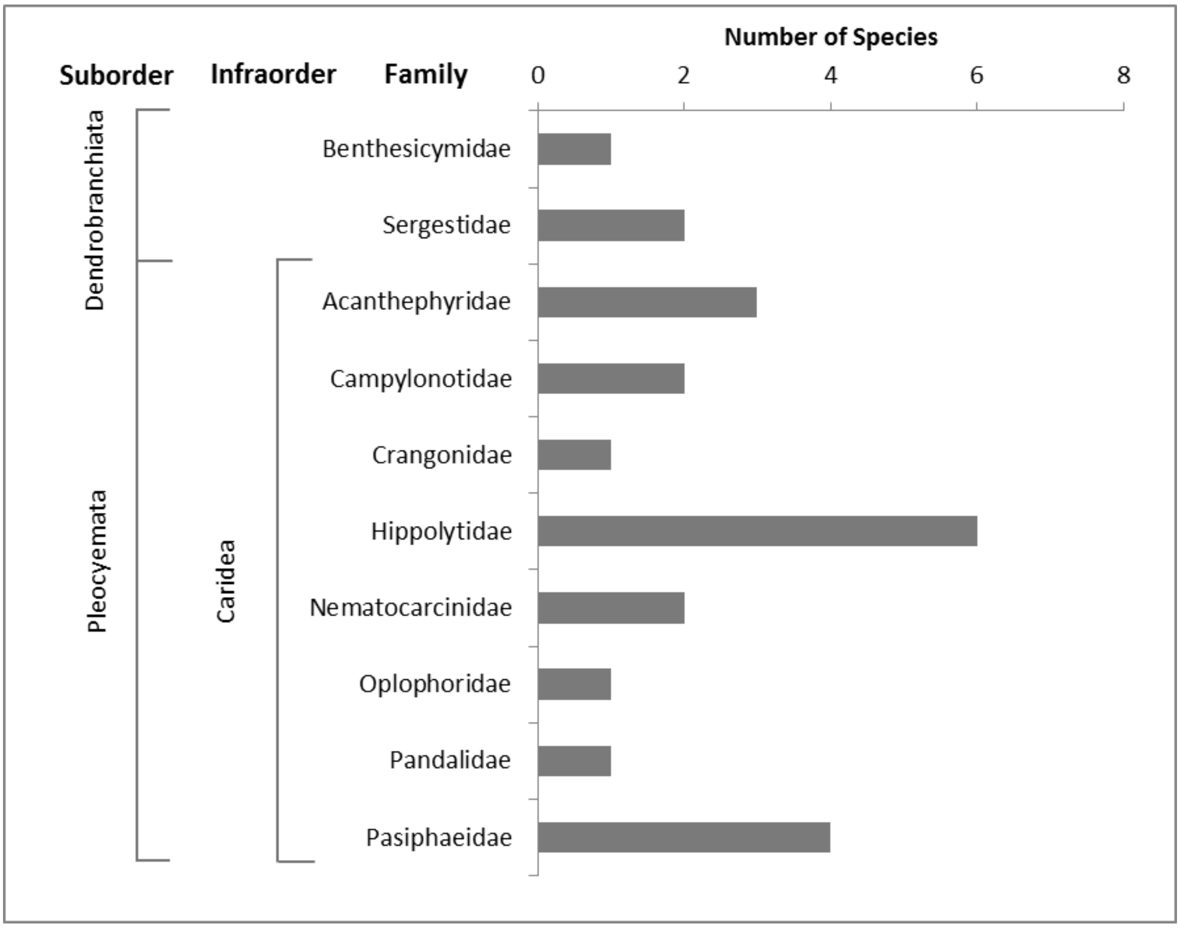

Figure 2.2. Number of species in the families of decapod shrimps in the Antarctic, south of the Antarctic Polar Front.

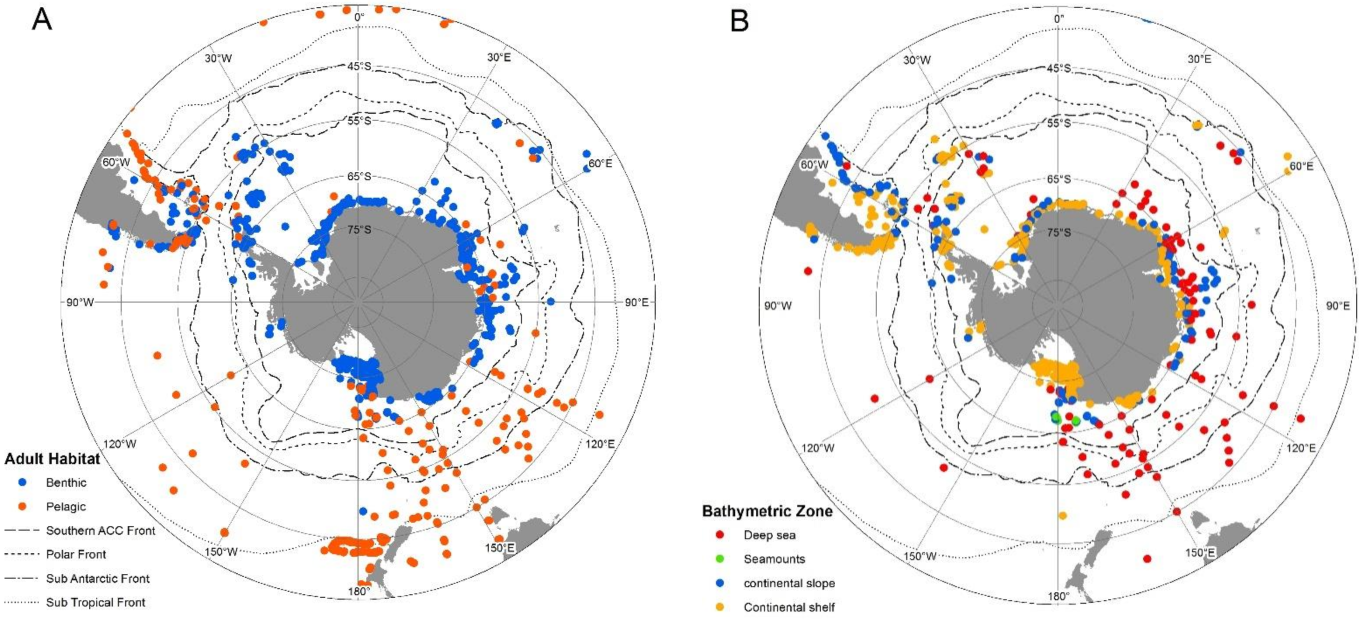

Figure 2.3. Map of the Southern Ocean showing all individual records of (a) Antarctic benthic (blue) and pelagic (red) shrimp species, and (b) their recorded depth zone and occurrence on seamounts (see Table 1 for details). The Southern Ocean fronts in all maps (Polar front: --- ;Southern Polar front :— — —; Sub-Antarctic Front: —·—; Sub-Tropical front: ····) follow Sokolov & Rintoul (2009).

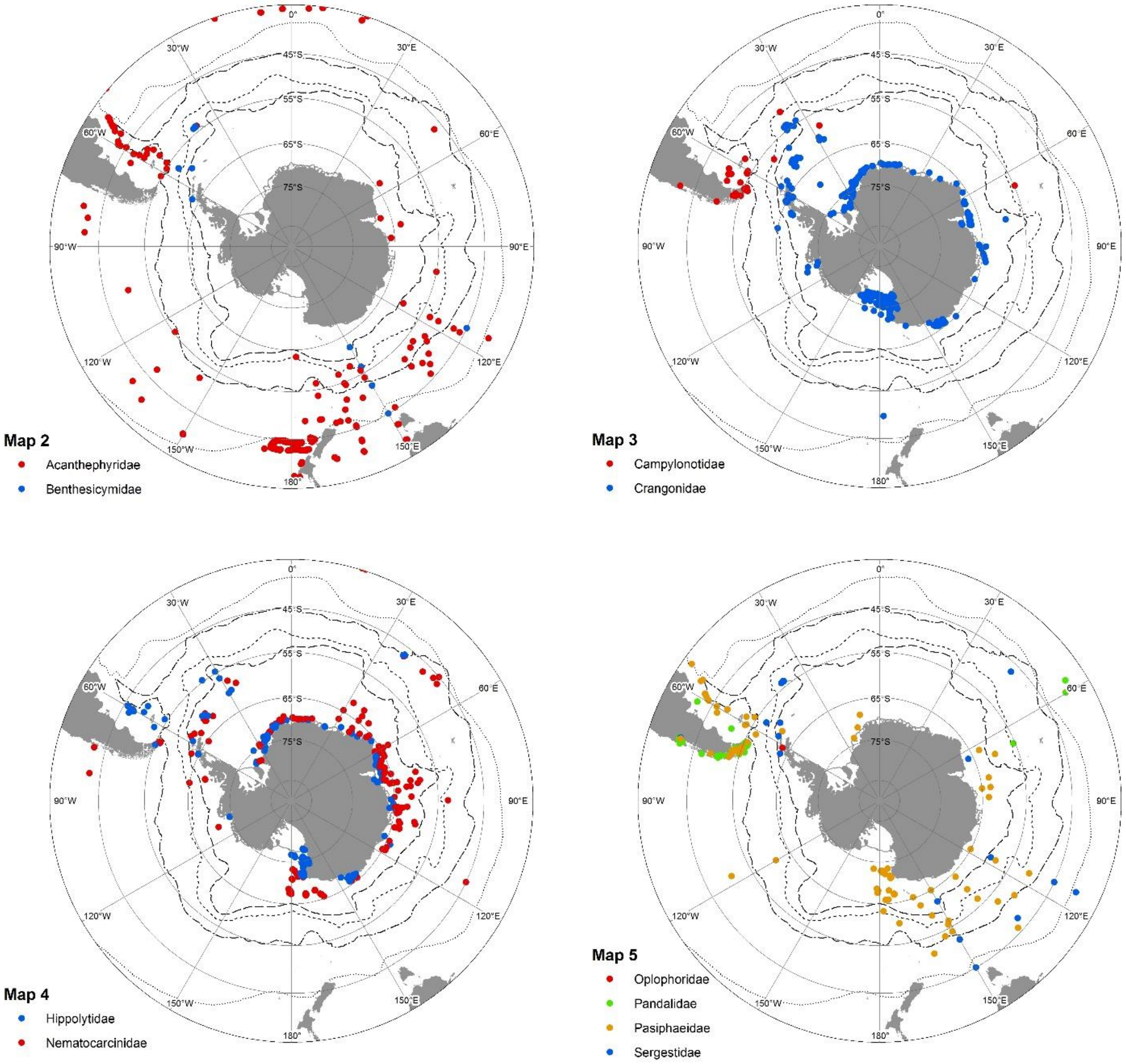

Figure 2.4. **Map 2.** Distribution of Acanthephyridae (red, n=283) and Benthesicymidae (blue, n=23). **Map 3**. Distribution of Campylonotidae (red, n=30) and Crangonidae (blue, n=892). **Map 4.** Distribution of Hippolytidae (blue, n=474) and Nematocarcinidae (red, n=1228). **Map 5.** Distribution of Oplophoridae (red, n=2), Pandalidae (green, n=68), Pasiphaeidae (orange, n=126) and sergestidae (blue, n=44).

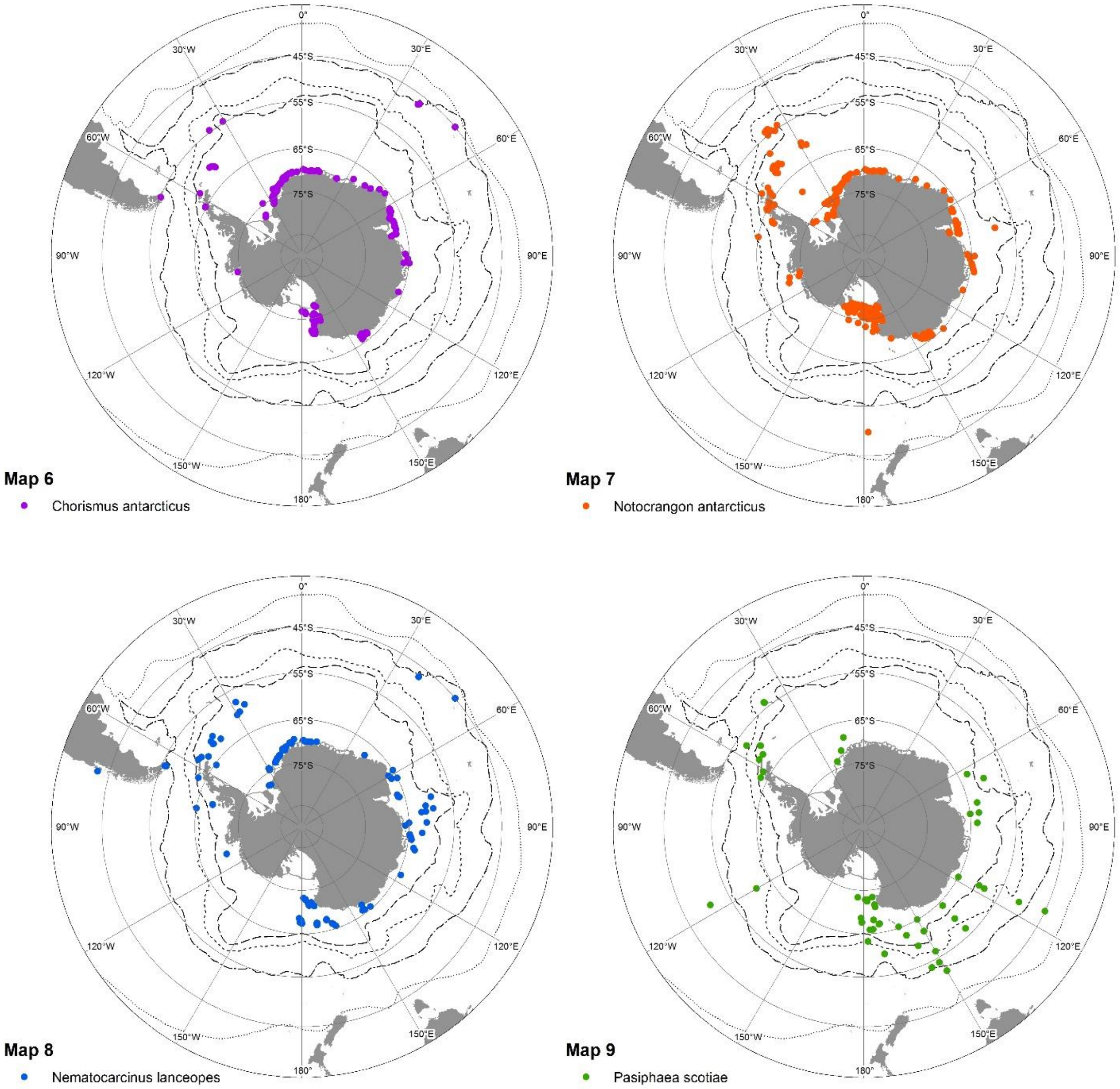

Figure 2.5. **Map 6.** Distribution of *Chorismus antarcticus* (Pfeffer, 1887). **Map 7.** Distribution of *Notocrangon antarcticus* (Pfeffer, 1887). **Map 8.** Distribution of *Nematocarcinus lanceopes* (Bate, 1888). **Map 9.** Distribution of *Pasiphaea scotiae* (Stebbing, 1914).

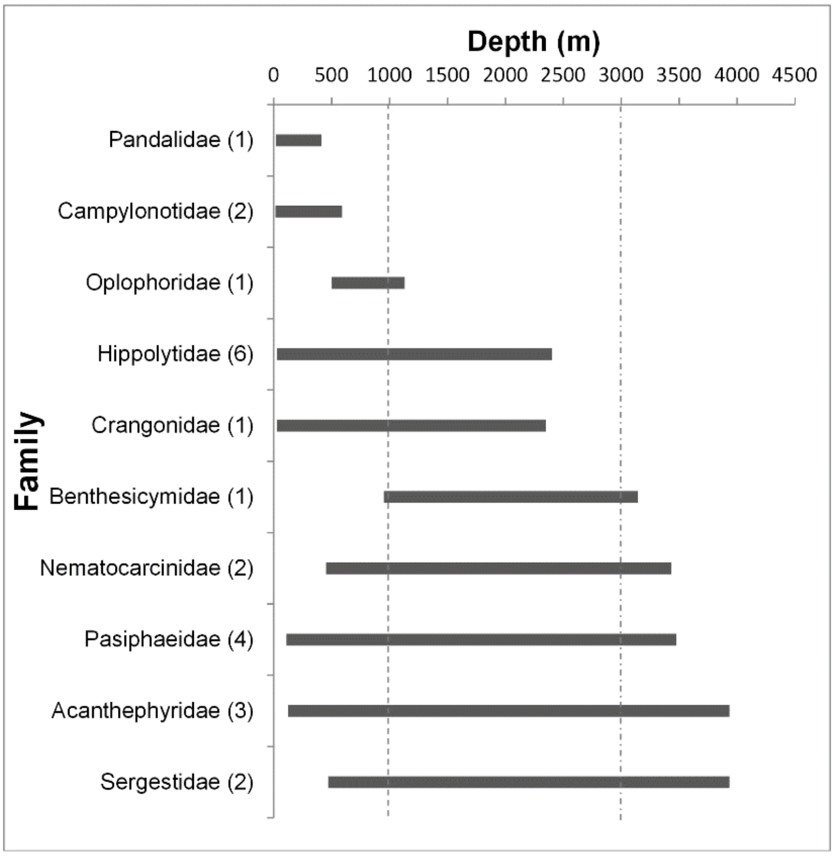

Figure 2.6. Depth ranges of the decapod shrimp families. In parentheses are the numbers of species per family in this study. Dashed lines show the average depth of the continental shelf edge and the start of the deep sea at 1000 m and 3000 m respectively.

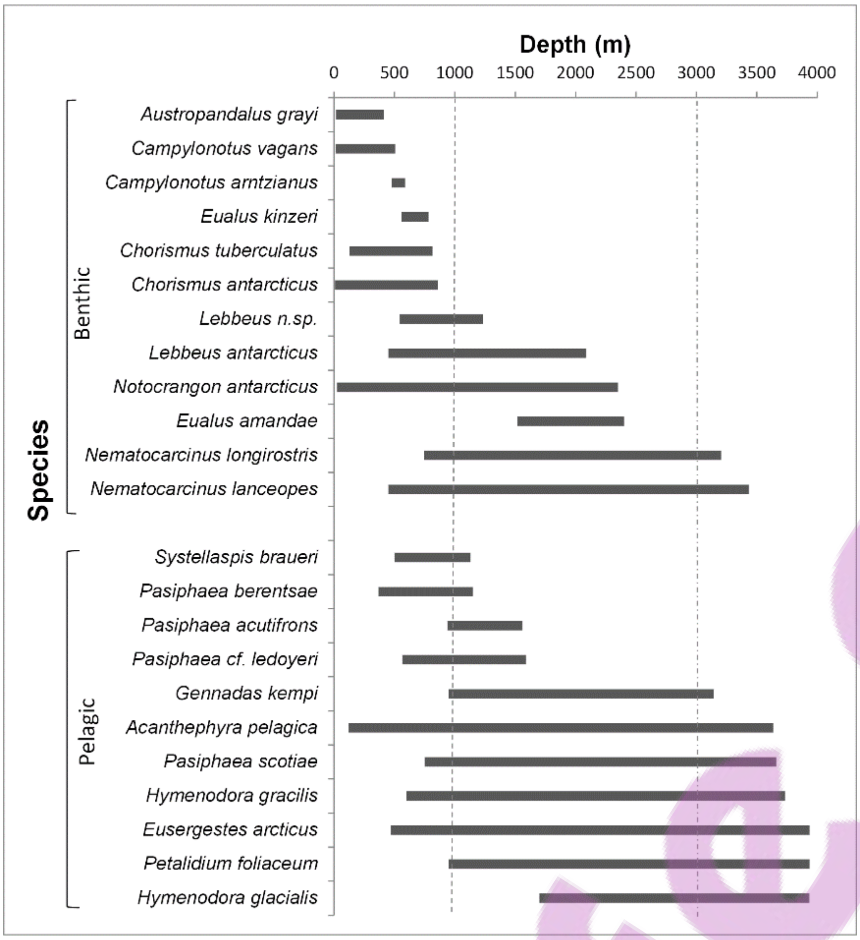

Figure 2.7. Depth ranges of the decapod shrimp species. Dashed lines show the average depth of the continental shelf edge and the start of the deep sea at 1000 m and 3000 m respectively.

Chapter 3

Diversity and Distribution of deep-sea shrimps in the Ross Sea Region of Antarctica

Abstract

Although decapod crustaceans are widespread in the oceans, only Natantia (shrimps) are common in the Antarctic. Because remoteness, depth and ice cover restrict sampling in the South Ocean, species distribution modelling is a useful tool for evaluating distributions. We used physical specimen and towed camera data to describe the diversity and distribution of shrimps in the Ross Sea region of Antarctica. Eight shrimp species were recorded: *Chorismus antarcticus; Notocrangon antarcticus; Nematocarcinus lanceopes; Dendrobranchiata*; *Pasiphaea scotiae*; *Pasiphaea* cf. *ledoyeri*; *Petalidium* sp., and a new species of *Lebbeus*. For the two most common species, *N. antarcticus* and *N. lanceopes*, maximum entropy modelling was used, based on records of 60 specimens and over 1130 observations across 24 sites in depths from 269 m to 3433 m, to predict distributions in relation to environmental variables. Two independent sets of environmental data layers at 0.05° and 0.5° resolution respectively, showed how spatial resolution affected the model. *Chorismus antarcticus* and *N. antarcticus* were found only on the continental shelf and upper slopes, while *N. lanceopes, Lebbeus* n. sp*.,* Dendrobranchiata*,* Petalidium sp*., Pasiphaea* cf. *ledoyeri,* and *Pasiphaea scotiae* were found on the slopes, seamounts and abyssal plain. The environmental variables that contributed most to models for *N. antarcticus* were depth, chlorophyll-*a* concentration, temperature, and salinity, and for *N. lanceopes* were depth, ice concentration, seabed slope/rugosity, and temperature. The relative ranking, but not the composition of these variables changed in models using different spatial resolutions, and the predicted extent of suitable habitat was smaller in models using the finer-scale environmental layers. Our modelling indicated that shrimps were widespread throughout the Ross Sea region and were thus likely to play important functional role in the ecosystem, and that the spatial resolution of data needs to be considered both in the use of species distribution models.

3.1 Introduction

Natant decapod crustacea (shrimp and prawns) are ubiquitous in the world's oceans and shallow seas, including the Antarctic, where other decapod taxa are largely absent (Clarke, 1990; Briggs, 1995; Arntz *et al.*, 1999; Gorny, 1999; Thatje & Arntz, 2004; Griffiths, 2010). As they are predominantly benthic particulate feeders and predators, they can be important in processing of material at the seabed (Coull & Bell, 1983; Field, 1983; Cartes *et al.*, 2007). Studies by Arntz & Gorny (1991) and Gutt *et al.* (1991) using underwater photography, have described species composition, distributions, and habitats of three shrimp species in the Weddell Sea but no similar studies have been conducted for the Ross Sea. The benthic fauna of the Ross Sea continental shelf has been relatively well-studied, particularly in coastal regions, and shares many taxa with other sectors of the Antarctic (Berkman *et al.*, 2005; Thrush *et al.*, 2006; Smith *et al.*, 2007; Cummings *et al.*, 2010), but deeper benthic habitats of the shelf edge, slope and abyssal depths remain little-sampled (Arntz *et al.*, 1994; Clarke & Johnston, 2003; Brandt *et al.*, 2007). Brandt *et* *al.* (2007) have highlighted the high rate of discovery for new species from the deep Southern Ocean, where up to 86% of isopod crustacean species were new to science, and argued that priority should be given to identifying the spatial distribution and abundance of key species in each trophic group across the region. Decapods are key species in the functioning of marine ecosystems, world-wide, as predators, scavengers, detritivores, and prey (Welsh, 1975; Coleman & Williams, 2002). In the Ross Sea region, information on the distributions and population densities of shrimps is necessary for producing ecosystem models which will improve understanding of trophic interactions and inform environmental management (Pinkerton *et al.*, 2010).

Because sampling in the Antarctic is restricted by remoteness, intense seasonality, and sea-ice, species distribution models (SDM) may provide a useful tool for estimating species' occurrences from limited field sample data. The basic assumption of SDM is that the fundamental niche of a species, defined by physiological and ecological tolerances, is the primary driver of its realized distribution (Soberón & Peterson, 2005; Soberón & Nakamura, 2009). Few SDM studies have focused on marine invertebrates, yet these groups have several attributes that make them well suited to species distribution modelling. Restricted availability of marine data (Kaschner *et al.*, 2006), and a limited number of high quality species occurrence records were considered as obstacles behind the application of SDM in the ocean (Elith & Leathwick, 2009; Tyberghein *et al.*, 2012). In recent years, as more sophisticated modelling algorithms have become available, the potential to model species' distributions across un-sampled marine regions is now realistic. In this study, we used MaxEnt, a machine-learning algorithm based on the principle of maximum entropy (Jaynes, 1982), which has been shown to have superior performance among presence-only algorithms (Elith *et al.*, 2006) for species distribution modelling (Phillips *et al.*, 2004; Phillips *et al.*, 2006).

Marine environmental datasets available for use in SDM have varying spatial resolutions and are frequently provided in different file formats, making the data assembly a time-consuming aspect of SDM studies (Tyberghein *et al.*, 2012). Studies in the terrestrial domain have found that coarser spatial resolution resulted in reduced accuracy of predicted area although overall in SDM performance was not affected (Tobalske, 2002; Guisan *et al.*, 2007; Seo *et al.*, 2009; Song *et al.*, 2013). However, the effect of spatial resolution on the relative influence of environmental variable on species distributions has not been assessed. The availability of several environmental datasets for the present study area, each with different spatial resolution provided an opportunity to investigate the effect of spatial resolution on the influence of environmental variables and the accuracy of the predicted area in the marine environment for the first time. In this study we used sample data on shrimp distribution in the Ross Sea, Antarctica, with historical records of occurrence, and two sets of environmental variables to (a) explore the diversity and distribution of shrimps in the Ross Sea region, (b) model distributions of suitable habitat for two common species, and (c) investigate the effect of using datasets with differing spatial resolutions on model predictions in the marine environment.

3.2 Methods

3.2.1 Study area

Our study area was bounded by 65° S, 150° E, 140° W, and the Ross ice shelf in the south. It included the entire Ross Sea continental shelf area, the Balleny Islands, and Scott and Admiralty seamounts (Figure 3.1). The mean depth of the Ross Sea continental shelf is about 500 m, although depth varies widely between deep troughs and shallow banks, and the area free of glaciers and permanent ice shelves is ca. 433,061 km^2 (delineated by 800m isobath and the Ross Ice Shelf).

3.2.2 Sampling

Samples were collected from 12 February to 11 March 2008 during New Zealand’s 2008 International Polar Year – Census of Antarctic Marine Life voyage (IPY-CAML, RV Tangaroa, TAN0802) at 10 sites on the Ross Sea continental shelf, 10 sites on the northern continental slope, 3 sites on the abyssal plain (>3000 m depth), and 5 seamounts to the north (Figure 3.1). At each site, at least one, and up to 7, 1 hour deployments of a towed camera system with high definition digital video and still image cameras were made (Hill, 2009). The camera array (NIWA’s Deep Towed Imaging System, DTIS) was held ca. 2.5 m above the seabed and towed at 0.25–0.5 ms^{-1}. In total, 55 camera transects were run. The seabed position was recorded in real time using an ultra short baseline (USBL) acoustic transponder system (Simrad HPR 410). Camera transects at each site were followed by physical sampling gear including a beam trawl (4 m width, 25 mm mesh), a large demersal fish trawl (25 m wing spread, 40 mm mesh), and two types of epibenthic sled; a fine mesh (1 m width, 0.5 mm mesh) sled used on flat, smooth seabeds (Brenke, 2005), and a coarse mesh (1 m width, 25 mm mesh) sled used on seamounts. In addition, a fine-mesh midwater trawl, was used following acoustic surveys. It had a circular mouth opening of about 12 m diameter and a cod end mesh of 10 mm and was generally towed for 20-30 min at 3-4 knots. All shrimp specimens collected by trawls and sleds were preserved (except in large hauls where representative 2-5 specimens/station were preserved) in 99% ethanol and were identified to species level.

Post-voyage analyses of video transects were run using Ocean Floor Observation Protocol (OFOP; www.ofop-by-sams.eu) software. Raw USBL transponder positions were first smoothed using a running mean and splined with associated metadata (e.g., time, depth, heading, vehicle altitude) to yield corrected seabed tracks with position coordinates and metadata values at 1 -s intervals. The digital video files were then synchronised with the corrected position data to enable re-running of transects in the laboratory with full video playback control and precise spatial and temporal logging of events. All shrimps on all transects were recorded and identified as close to species level as possible, using the high-resolution still images to confirm identities.

3.2.3 Environmental variables

We compiled environmental variables from two different sources (referred to hereafter as SET 1 and SET 2), each with different spatial resolution (Table 3.1, 3.2 and Figure 3.2). We selected variables that were likely to be ecologically relevant to benthic distributions: depth; seabed slope or rugosity; bottom temperature; ice concentration (proportion of the year with >85% ice cover in SET 1, annual mean in SET 2); chlorophyll-a concentration (mean summer in SET 1, mean annual concentration in SET 2) and for SET 1 only, bottom current speed.

SET 1 had a spatial resolution of 0.05˚ longitude and 0.05˚ latitude (Grant *et al.*, 2006; Rickard *et al.*, 2010), representing approximately 5.5 km by 2 km at areas between 67˚S and 68˚S , and consisted of 7 variables derived from satellite observations and modelled climatologies. SET 2 had a spatial resolution of 0.5˚ and consisted of 6 variables obtained from AquaMaps (Kaschner *et al.*, 2008) (Table 3.1).

All datasets were received in raw csv format, and interpolated to raster layers at the respective spatial resolutions using the “Spatial Analyst” extension in ArcGIS 10. Inverse distance weighted (IDW) multivariate interpolation (Shepard, 1968; Daly, 2006) was used in the ArcGIS Spatial Analyst extension with default setting and smoothing (p=2) option to assign the final interpolated cell value in the generated raster layers. Chlorophyll-a was transformed to natural log to improve normality in SET 1 (Table 3.2). Raster layers were converted to ASCII grid with WGS84 Antarctic Polar Stereographic projection. The finer resolution dataset (SET 1) had almost 45 times more grid cells across the study region than the coarser resolution dataset (ca. 450,000 vs 10,000).

There were missing values in some layers in SET 2 but not in SET 1. During raster interpolation, these ‘no data’ pixels were assigned average values of 12 surrounding (ocean) cells using ArcGIS raster calculator. The "Band Collection Statistics" multivariate toolset function (Snedecor & Cochran, 1968) of Spatial Analyst was used to calculate Pearson's correlation coefficient between the variables in each dataset (Appendix I). Correlation coefficients over ± 0.7 were considered significant (Cohen, 1988; Dormann *et al.*, 2013) and are known to affect model prediction capability (Jiménez-Valverde *et al.*, 2009; Veloz, 2009).

3.2.4 Modelling fitting procedure

Using all occurrence data from TAN0802 physical and photographic samples, we modelled the two most commonly-occurring shrimp species, *Notocrangon antarcticus* and *Nematocarcinus lanceopes*, using MaxEnt version 3.3.3e (http://www.cs.princeton.edu/~schapire/maxent/), with each of the two sets of environmental variables as predictors in consecutive runs for each species (Table 3.1 and Figure 3.2). Our occurrence records were distributed over 160,000 km^2, which is sufficiently spatially segregated to reduce the probability of spatial-correlation between observations (Phillips *et al.*, 2004; Mateo *et al.*, 2010). MaxEnt is flexible with respect to the types of variables used and the form of their relationship to a species' presence (e.g. linear, nonparametric, etc.). A review comparing 16 models of >200 taxa found that machine-learning methods including MaxEnt consistently outperformed traditional linear methods (Elith *et al.*, 2006) and that presence-only models were preferable because limited sampling may mean that apparent absences may not be true. We selected the 'Auto features' function for model fit in MaxEnt, which automatically applies the feature or features estimated to be appropriate for the particular sample size of occurrence records (Phillips & Dudik, 2008). As the number of records varied depending the resolution of the datasets in this study, only linear, quadratic and hinge features (See Elith *et al.*, 2011 for definitions) were utilized for model fitting.

MaxEnt models were generated using 100 bootstrap replicates run with the 'random seed' option turned on. The 'Remove duplicate presence records' feature was enabled to exclude duplicate records that fell within individual pixels of background environment layers on each dataset and the occurrence records were split into 75% for training and 25% for testing for bootstrap replications. The Maximum number of background points (randomly selected in each replication) was increased to 100,000 instead of the default value of 10,000 because of our large-scale mapping objective. Maximum iterations were also increased to 1000 allowing enough time for model convergence. As suggested by Phillips & Dudik (2008) the default regularisation value was used because it results in better performance of evaluation data for presence-only datasets. We also used the settings 'fade by clamping' option to minimize unreliable extrapolation into areas with environmental conditions that were not encountered during model training. The relative contributions of variables were calculated in the MaxEnt models in training steps where the algorithm keeps track of how much each environmental variable contributes to fitting the model and adjusts the overall gain to calculate contributions of individual variables.

3.2.5 Model evaluation

Various test statistics are available to test the ability of models to discriminate suitable versus unsuitable habitat (Fielding & Bell, 1997; Ferrier *et al.*, 2007). Several studies have highlighted issues with using only one statistic to evaluate model performance (Elith & Graham, 2009; Merow *et al.*, 2013). Options for model validation include: (1) internal validation, or cross-validation in which the data are partitioned randomly into 'training' and 'test' sets, thus creating quasi-independent data for model evaluation (Fielding & Bell, 1997; Guisan *et al.*, 2007) using the Area Under the receiver operating Curve (AUC; Phillips & Dudik, 2008; Elith *et al.*, 2011; Dambach *et al.*, 2012) criterion; (2) omission rates (Anderson *et al.*, 2003; Shcheglovitova & Anderson, 2013); (3) low presence threshold (LPT; Pearson *et al.*, 2007), and (4) completely independent datasets (Fleishman *et al.*, 2003; Elith *et al.*, 2006; Williams *et al.*, 2009; Newbold *et al.*, 2010; Wilting *et al.*, 2010). We validated our models using all four of these methods.

AUC measures the quality of a ranking of sites (Elith & Burgman, 2002). Use of AUC analysis with presence-only evaluation datasets has been justified for the presence versus random classification problem (Wiley *et al.*, 2003). AUC is measured on a scale of 0–1, where 1 indicates no errors of omission or commission, 0.5 indicates no better than random selection, and 0.9 indicates that there is a 90% chance that predicted habitat suitability for a randomly drawn species presence will be higher than that of randomly drawn absence (Wiley *et al.*, 2003; Fawcett, 2006; Williams *et al.*, 2009). MaxEnt provides AUC values based on the evaluation localities used in each model run. In this study, mean AUC values calculated from 100 bootstrap models were used to measure model performance. MaxEnt's built-in Jack-knife validation method was also used as an independent estimate of each variable's contribution to overall model performance allowing comparison with AUC values for each variable.

The threshold-dependent intrinsic (based on training data) or extrinsic (based on test data) omission rate, is the fraction of the known presence localities that fall into pixels not predicted as suitable for the species. A low omission rate is indicative of a good model (Anderson *et al.*, 2003). High-quality models should show zero or low omission of evaluation localities, or at least predict evaluation localities statistically better than random.

LPT sets the lowest threshold value of the prediction for any of the presence localities in the training dataset (measured on a scale of 0-1) (Pearson *et al.*, 2007). This yields a binary prediction that includes all pixels that are at least as suitable (according to the model) as those where the species was known to be present (in the training dataset). These threshold values generally vary by model. We also checked the models using a fixed threshold value of 10 out of 100 for the cumulative output. MaxEnt provides a convenient interpretation for the output of cumulative probabilities, where the expected omission rate for localities of the species is equal to the threshold employed. For example, an ideal model and a threshold of 10 would be expected to yield approximately 10% omission in an independent, unbiased sample of localities of the species. Hence, use of the fixed threshold of 10 is expected to lead to omission levels of approximately 10%.

Using an independent dataset is the optimal method for evaluating model performance (Phillips & Dudik, 2008; Kumar & Stohlgren, 2009). We used 6 *N. lanceopes* and 58 *N. antarcticus* occurrence records in the Ross Sea area extracted from the Ocean Biogeographic Information System (OBIS, www.iobis.org), the SCAR-Marine Biodiversity Information Network (SCAR-MarBIN, www.scarmarbin.be), and the published literature (Appendix II). Records were filtered to remove duplicates (i.e. same co-ordinates or same records from different sources) and apparent geographic errors (i.e. co-ordinates plotting on land or in different regions) before combining them into a single data set for model verification using GIS. Probability of occurrence values, which ranged from 0 to 1, where 0 meant no probability of presence and 1 meant highest probability of presence at that particular location, were extracted from the average of all bootstrap models on each data set using the "Extract Values to Point" function of Spatial Analyst in ArcGIS. We evaluated model accuracy with the independent dataset by seeing how successfully the model predicted the species' potential distribution outside its sampled distribution using six model evaluation metrics (each measured on a scale of 0-1), namely: Percent Correct Classification (PCC, overall accuracy); Sensitivity (the proportion of actual presences that are accurately predicted); Specificity (the proportion of actual absences that are accurately predicted); False Positive Rate; False Negative Rate, and True Skill Statistics (TSS, correct classification rate in relation to false positive rate) (Franklin & Miller, 2009).

3.3 Results

3.3.1 Sampled diversity and distribution

In total, 921 shrimp specimens (91 preserved) were collected and 1249 individuals observed in video transects across 24 different sites (Table 3.3). Eight species were identified; *Chorismus antarcticus* (Pfeffer, 1887); *Notocrangon antarcticus* (Pfeffer, 1887); *Nematocarcinus lanceopes* (Bate, 1888); *Pasiphaea scotiae* (Stebbing, 1914); *Pasiphaea cf. ledoyeri* (Hayashi, 2006); Petalidium sp.; an unidentified damaged specimen of the suborder Dendrobranchiata; and a new species of Lebbeus (S. Ahyong, unpublished data). *Chorismus antarcticus* and *Notocrangon antarcticus* were found only on the continental shelf in depths shallower than 1000 m. *Chorismus antarcticus* was largely restricted to depths shallower than 700 m, whereas *N. antarcticus* was found down to ca 1000 m at sites out to the edge of the continental slope. None of the other species were found on the continental shelf or at depths shallower than 450 m. *Nematocarcinus lanceopes*, Petalidium sp., *Pasiphaea cf. ledoyeri* and *Pasiphaea scotiae* were found on the continental slope and northern seamounts, but only *N. lanceopes* and *P. scotiae* were found at abyssal depths. Dendrobranchiata was found only at one site on the continental slope, and *Lebbeus n. sp.* was found only on the northern seamounts (Table 3.3 & Figure 3.3). *Notocrangon antarcticus* was the most frequently recorded species on the continental shelf (440 individuals, depth range 269–930 m) and *N. lanceopes* was the most frequently recorded species elsewhere (1554 individuals, depth range 570–3433 m). Larvae of *N. lanceopes* were also recorded from MOCNESS (Wiebe *et al.*, 1976) samples on the slope and seamounts (4 individuals, 110-800 m). The distributions of these two species overlapped at one site (D27) on the northern continental slope (Table 3.3 &Figure 3.3).

3.3.2 Modelled distributions

A total of 281 *N. antarcticus* and 909 *N. lanceopes* occurrence records were available from the TAN0802 cruise, including both physical specimens and records from video transects. When duplicate presence records within each grid cell were excluded there were 22 and 41 presence records at the fine spatial resolution (SET 1) for *N. antarcticus* and *N. lanceopes*, respectively, and 12 and 17 records for the two species, respectively, at the coarser resolution (SET 2) (Table 3.4). For both *N. antarcticus* and *N. lanceopes*, the extent of predicted suitable habitat was greater in the coarser spatial resolution model (SET 2) and less in the finer model (SET 1). There were also differences in the locations of highest probability of occurrence values between SET 1 and

SET 2 models. This was particularly noticeable for *N. antarcticus*, for which the coarser resolution SET 2 models show wider distribution of suitable habitat across northern and western areas of the continental shelf than do the finer resolution SET 1 models (Figure 3.5). Both of the modelled distributions indicated geographic separation of the two species at the shelf break (Figure 3.5). The predicted distribution for *N. antarcticus* was restricted to the Ross Sea continental shelf, whereas suitable habitat for *N. lanceopes* was predicted to occur on the continental slope, Scott and Admiralty seamounts, and around the Balleny Islands, with lower probability of occurrence on the abyssal plain near these features (Figure 3.5).

3.3.3 Model evaluation

AUC values for both models were high (>0.9) and significantly different from a random prediction (Wilcoxon rank-sum test, $p < 0.01$) (Table 3.4). High test gain (all values > 1), indicated that $<0.1\%$ of the withheld test presences were misclassified. Intrinsic omission rates for all models were zero and extrinsic omission rates were <0.1, indicating acceptable model performance (Phillips *et al.*, 2006).

LPT and 10th percentile presence threshold values were lowest at the finer spatial scale of SET 1 for both species; 0.168 and 0.291 for *N. antarcticus*, and 0.031 and 0.141 for *N. lanceopes*, respectively. Corresponding values using the coarser spatial scale in SET 2 were higher (0.431 and 0.431 for *N. antarcticus*, and 0.432 and 0.438 for *N. lanceopes*, Table 3.4). Because LPT is considered more suitable than the 10th percentile in cases where presence records have been collected in a short period of time and with high spatial accuracy (Rebelo & Jones, 2010) as in the present study, we used the LPT values as the suitability cut-off value for model validation using independent records.

For both species, mean probability of independent location records plotting within the predicted habitat suitability area was highest at the coarse spatial scale (SET 2, mean ± SD; 46.7 ± 0.19% and 80.9 ± 0.21% for *N. antarcticus* and *N. lanceopes*, respectively) and somewhat lower at the finer spatial scale (SET 1, 24.03 ± 0.11% and 19.6 ± 0.08%, respectively) (Table 3.4). Models of *N. lanceopes* had the highest accuracy based on the independent record evaluation metrics; in particular, PCC scores of 0.86 and 0.93 and TSS scores of 0.54 and 0.92 for SET 1 and SET 2 models, respectively. Corresponding values for *N. antarcticus* models were lower, at 0.62 and 0.60 for PCC and 0.27 and 0.17 for TSS, respectively.

3.3.4 Environmental variables

Temperature and depth were correlated with each other in SET 1 (r = 0.75), and salinity and slope were correlated with each other in SET 2 (r = 0.88) (Appendix I). MaxEnt has robust mechanisms integrated in the algorithm to deal with interactions of correlated variables (Phillips *et al.*, 2009; Elith *et al.*, 2011) so we did not exclude any variables from our variable pool.

MaxEnt model response curves show how the logistic prediction changed across the sampled range of each environmental variable, while keeping other variables at their average value (Figure 3.6). Each of these response curves represents a separate MaxEnt model created using only the named variable. The principal differences in environmental envelopes between the models of each species were in temperature range, chlorophyll-a, and ice concentration (Figure 3.6). The response curves indicated that *N. antarcticus* was likely to be found in lower seabed rugosity and slope areas that had colder waters with higher chlorophyll-a concentrations and lower ice concentrations than *N. lanceopes*.

In fine scale models of *N. antarcticus* using SET 1 variables, temperature, chlorophyll-a concentration, and depth had the highest contributions to the models, whereas using the coarse-scale SET 2 variables highest contributions were from depth, salinity, and chlorophyll-a concentration (Table 3.5). In the fine-scale SET 1 *N. lanceopes* models, highest variable contributions were from ice concentration, seabed rugosity, and depth, whereas in the coarse-scale SET 2 model, highest variable contributions were from depth, ice concentration, and temperature (Table 3.5). The maximum contribution of an individual variable to any model was 46.67 % (depth, SET 2, for *N. antarcticus*). Jack-knife analyses of model gains, and test AUC scores for models generated with a single variable indicated that the same variables listed above were the top predictors regardless of covariation.

3.4 Discussion

3.4.1 Diversity and distribution

The NZ IPY-CAML survey has extended the number of known sites with species-level records of deep-sea shrimps in the Ross Sea and provided the first such records from seamounts and abyssal regions in the north of the region (Appendix II, Figure 3.3 and Figure 3.4). These new observations have enabled us to re-evaluate known shrimp diversity and distribution in the Ross Sea region. Shrimps occurred throughout the region, with *N. antarcticus* being the most abundant species on the continental shelf, and *N. lanceopes* on the continental slope and seamounts to the north. *Notocrangon antarcticus* and *Chorismus antarcticus* occurred only on the shelf, whereas the five other species were only recorded off-shelf. These distributions reaffirm previous findings (Kirkwood, 1984; Childress *et al.*, 1990; Arntz & Gorny, 1991; Gutt *et al.*, 1991; Gorny *et al.*, 1992 and citations therein; Gorny *et al.*, 1993; Gorny & George, 1997; Gorny, 1999; Guzmán & Quiroga, 2005; Dambach *et al.*, 2012). However, previous surveys (Bullivant, 1959, 1967; Gambi & Bussotti, 1999) did not find *N. lanceopes*, Petalidium sp. and Dendrobranchiata in the Ross Sea region, although a 2004 survey (NIWA unpublished data, Pinkerton *et al.*, 2010) found *N. lanceopes* in six locations at north western Ross Sea around slopes near Cape Adare and Balleny Islands (Appendix II). Our results also show distinct depth zonation of *C. antarcticus*, *N. antarcticus*, and *N. lanceopes*, with a broad overlap between *C. antarcticus* and *N. antarcticus* in shelf regions, and between *N. antarcticus* and *N. lanceopes* on the upper slope; *N. lanceopes* being widely distributed in depths greater than 1000 m but less frequent in depth shallower than this (Figure 3.4). The new records of *N. lanceopes* and Pasiphaea spp. on seamounts north of the Ross Sea show that their distributions are more widespread than previously reported.

3.4.2 Modelled distributions

Although the present data increase the number of records of the shrimps in the Ross Sea region considerably, the available data remain insufficient to map their distributions with confidence. Therefore, we used species distribution models to predict the geographic distribution of the two most common shrimps, *N. antarcticus* and *N. lanceopes*, based on their occurrences at 23 different locations in the Ross Sea region. This study is also the first in the marine environment to assess of the effect on species distribution model performance of using different environmental datasets at different spatial resolutions.

For all MaxEnt models of the predicted habitat suitability for both *N. antarcticus* and *N. lanceopes*, independent validation records plotted into areas with predicted maximum probability of presence between 59-86 %, and all models had high AUC scores supported by high training gain and low omission rates, regardless of environmental dataset resolution. The AUC value tends to increase when the selected background area is larger than the species observed presence area (Phillips & Dudik, 2008; Merow *et al.*, 2013). Thus, inclusion of other validation metrics is required for a thorough evaluation of model performance, particularly when our modelled species are known to have restricted distribution ranges (*N. antarcticus* in the shelf and *N. lanceopes* off-shelf) in a large geographic area. These results suggest that any of the modelled predictions are likely to be useful indications of distributions for these species, regardless of the spatial resolution of the underlying environmental data (Phillips *et al.*, 2006; Anderson & Gonzalez Jr, 2011; Davies & Guinotte, 2011). However, there was appreciable variation between outputs of the different models (Figure 3.5, Table 3.4) and it is important both to understand which environmental variables are influencing the models and to consider factors that might underlie the differences between the models.

A recent study that modelled the distributions of *N. antarcticus* and *N. lanceopes* over the entire Southern Ocean using MaxEnt showed depth, ice concentration and salinity to have the highest explanatory power for models of *N. antarcticus*, while *N. lanceopes* distribution was better explained by depth, ice concentration and temperature (Dambach *et al.*, 2012). In our study, at the scale of the Ross Sea region, depth, temperature, chlorophyll-a concentration, and salinity had highest explanatory power for *N. antarcticus*, whereas for *N. lanceopes*, ice concentration, depth, seabed rugosity, and temperature contributed most to the models. Given the spatial separation of these two species between the extreme high-Antarctic environment of *N. antarcticus* on the Ross Sea shelf and the more moderate oceanic environment of *N. lanceopes* beyond the shelf-break front, it is perhaps not surprising that these variables should contribute most to the models. Depth and seawater temperature are obvious distinctions between the two environments, shelf habitats being characterised by temperatures <0°C and depths <1000 m whereas beyond the shelf break temperatures are always >0°C and depths, other than on the seamounts, are >1000 m. However, the influence of the Ross Sea polynya also causes strong distinctions in ice concentration, salinity, and chlorophyll-a concentration between the environments of the two species (Figure 3.2). Seabed slope and rugosity are also important influences on benthic faunal distributions in the deep sea, e.g. by influencing food supply via current flow amplification (Mohn & Beckmann, 2002). Their influence in models, however, is likely to be strongly influenced by the spatial scales at which they are calculated. In our regional-scale models, the continental shelf break and slope, and the northern seamounts, are areas with high computed values for both slope and rugosity which contrast strongly with the comparatively uniform morphology of continental shelf and abyssal environments.

Because the steepest gradients in several potentially important variables coincide at the Ross Sea shelf break (depth, temperature, slope/rugosity, ice concentration, Chlorophyll-a concentration), determining which of these variables are most ecologically important to the realised distributions of the two species is problematic. Adaptation to cold has been postulated as the primary reason why Antarctic shrimps are capable of living at the extremely low temperatures of the continental shelf where other decapod taxa are absent (Wittmann *et al.*, 2010), and as an explanation of why they were able to re-colonize high southern latitudes after past glaciation cycles (Gutt *et al.*, 1991; Frederich *et al.*, 2001; Wittmann *et al.*, 2010). That only two of the eight species identified here have distributions on the continental shelf, and that there is strong demarcation between species' ranges at the shelf break, suggests either that such adaptation is species-specific or that factors other than physiological adaptation to low temperature per se have a stronger influence on realised distributions.

Physiological studies have suggested that many Antarctic benthic invertebrates on the continental shelf are highly stenothermal, and thus have limited capacity to withstand future environmental warming (Peck, 2004). If the shrimp species studied here were currently range-limited by temperature, predicted warming might be expected to result in southward range shifts of those species currently found only in warmer waters north of the shelf break front (e.g. *N. lanceopes*, Figure 3.3). Conversely, for the two species with shelf-only distributions (*C. antarcticus* and *N. antarcticus*) at present, the only potential range shift would be southward into the region currently covered by the Ross Ice Shelf.

In addition to the suite of environmental variables used in species distribution modelling, three other factors were likely to affect the final outputs of the models and how well individual models rated in evaluation metrics. First, the number of independent records used to validate models can influence the test statistics (Newbold *et al.*, 2010). In the present study, only 6 independent presence records were available to validate the *N. lanceopes* models, compared to 58 records for *N. antarcticus*, and it is likely that this will have had some effect on their respective validation metrics. Second, validation using independent records assumes geographic accuracy of the independent records; i.e., that the position data associated with these records are both accurate and precise. The accuracy of records derived from biodiversity databases can be uncertain, however (Feeley & Silman, 2010; Mesibov, 2013), and in the present study none of the records used for independent validation had spatial accuracy information associated with them. Therefore, it is possible that some of the independent records that plotted outside predicted areas of suitable habitat here might be as a consequence of such inaccuracies. Finally, the spatial resolution of the environmental datasets used in the models clearly influenced the predictions of the resulting models; this is discussed in more detail below.

3.4.3 Effects of spatial resolution

Guisan *et al.* (2007) suggested model performance depends more on the type of species, scale of the study area and modelling techniques than the spatial resolution of the used dataset. Although the four model validation techniques used here all suggested that the models in this study were useful predictions of potential distribution for the two shrimp species, there were some noticeable differences between models generated with datasets of different spatial resolutions. Models using the finer spatial scale dataset (SET 1) predicted areas of suitable habitat that closely matched the distributions of the observation records. By contrast, predicted areas with the coarser resolution dataset (SET 2), were broader. This is because that a decrease in the dataset resolution increases the size of individual grid cells and thus increases the probability that a given sample point will fall within areas of predicted suitable habitat. This was reflected during independent model evaluation, when mean probability of presence values were higher in coarse resolution datasets than finer resolution ones. Thus, finer resolution environmental data will tend to predict more restricted areas of occurrence, whereas coarse resolution data will predict wider potential biogeographic range, at least when using the default settings in MaxEnt. In addition to the influence of spatial resolution, it is also relevant here that the fine-scale data in SET 1 were developed more recently than those of SET 2 and were based on more extensive and detailed data from the most up-to-date observational and modelling sources (Rickard *et al.*, 2010). While comparisons show that most layers are very similar between the two datasets (Figure 3.5), there are obvious differences in the summaries for Chlorophyll-a concentration that might be expected to have some influence on model results. Our results agree with the findings of terrestrial studies where model performance was not significantly affected by the coarsening of spatial resolution (Song *et al.*, 2013). However, we found that the relative importance of environmental variables in predicting a species distribution varies with spatial resolution of dataset.

The most appropriate spatial resolution for modelling a species' distribution will differ depending on that species' ecological characteristics (Mitchell *et al.*, 2001; McPherson & Jetz, 2007), the amount and spatial accuracy of sample data available (Elith *et al.*, 2010; Merow *et al.*, 2013), and the purpose of the modelling exercise. In this study, the relative importance of the environmental variables in explaining the species' distributions differed depending on spatial resolution of the environmental data (Table 3.5), indicating that changing spatial resolution can influence the perceived importance of environmental variables. Environmental variables that characteristically change rapidly over short distances (e.g., in this case, depth, temperature, and ice concentration at the shelf break) are likely to have more influence in the finer resolution models than variables having more gradual rates of change over the study region (e.g., salinity).

More fundamentally, models using coarser resolution data layers for SDM will not identify fine-scale variations in habitat suitability. This might have a strong effect in relation to the ecology of the modelled species as well. If relatively fine-scale topographic features (e.g. seamounts, canyon walls), are important habitat for a species and such features are appreciably smaller than the grid scale of the model, they will not be represented in the environmental data and thus will not be predicted in SDM predicted distributions. It is important, therefore, that the spatial resolution of species distribution models should be appropriate to the purpose of the modelling exercise.

Selection of a particular resolution (i.e. coarser or finer), for a species distribution modelling exercise in a practical application such as protected area design would depend on the specific management aim and whether or not decisions were to be based solely on the available data (Downie *et al.*, 2013). If the management aim is broad, for example, aiming to identify the best strategy for conservation of a poorly-sampled species with uncertain distribution, then using coarser resolution datasets would rapidly delineate regions of potentially suitable habitat with sufficient detail for decision-making purposes and be computationally less demanding. However, predicting core habitat areas of a species with well-understood environmental niche requirements will be more accurate with finer spatial resolution data.

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Table 3.1. Details and sources of environmental variables used for modelling. SET 1 was at 0.05°and SET 2 at 0.5° latitude-longitude.

Set	Data Layer	Description	Reference
1	Depth	Water depth taken from GEBCO_O8 Digital Atlas	IOC *et al.* (2003)
	Rugosity	The rugosity layer is an approximation to true rugosity defined as the actual area of seabed divided by the area projected onto an equipotential (horizontal) plane.	Burrough & McDonnell (1998)
	Chlorophyll-*a*	Mean SeaWiFS surface Chl-a in Summer (Dec-Feb), natural log averaged between 1997-2007	Hooker *et al.* (1992) , NASA (2009)
	Temperature	Bottom temperature from HIGEM 1.1 Model	Shaffrey *et al.* (2009) & Rickard *et al.* (2010)
	Salinity	Bottom salinity from HIGEM 1.1 Model	Shaffrey *et al.* (2009) & Rickard *et al.* (2010)
	Ice Concentration	Fraction of the year for which a given pixel was covered with >85% from Nmbus-7 & DMSP satellites dated 1979/80 to 2006/07 seasons.	U.S. National Snow and Ice Data Centre (Cavalieri *et al.*, 1996, Updated 2007)
	Current	Current speed (*speed*) by combining the modelled meridional and zonal velocities from HiGEM 1.1 model	Shaffrey *et al.* (2009) & Rickard *et al.* (2010)
2	Depth	Mean ETOPO 2min bathymetry (negative) elevation in 30min cell	Smith and Sandwell (1997)
	Slope	Slope derived from depth layer using ArcGIS Spatial Analyst	This study
	Chlorophyll-*a*	Proportion of annual primary production in a cell in mgC·m-²·day $^{-1}$.	Bouvet *et al.* (2002), Hoepffner *et al.* (1999) , Longhurst *et al.* (1995)
	Temperature	Mean annual sea bottom temperature as derived from WOA 2001 Bottom Source Information for all coastal and oceanic cells. Coverage 1990-1999	Stephens *et al.* (2002)
	Salinity	Mean annual bottom salinity in Practical Salinity Scale (PPS), as derived from WOA 2001 Bottom Source Information for all coastal and oceanic cells. Coverage 1990-1999	Boyer *et al.* (2002)
	Ice Concentration	Mean annual ice cover in percent as derived from the National Snow and Ice Data Centre (1979-2002)	U.S. National Snow and Ice Data Centre (Cavalieri *et al.*, 1996, Updated 2006)

Table 3.2. Summary statistics for the environmental variables in each dataset used in models (SD = Standard deviation, SE= Standard error, CV=Coefficient of variance). All variables except ice and Chlorophyll-a concentration were for the seabed or near seabed.

	Variable	**Unit**	**Min**	**Max**	**Mean**	**SD**	**SE**	**CV**
SET 1 (0.05°)	Depth	m	3.25	6044.70	2461.74	1557.52	2.23	0.63
	Rugosity	% (0-1)	0	0.70	0.08	0.05	0	0.67
	Temperature	Degree C	-1.79	0.73	-0.46	0.67	0.001	-1.48
	Salinity	ppt	34.13	34.85	34.66	0.07	0	0
	Chlorophyll-*a* (Summer mean)	ln (mgC·m^{-2}·day^{-1})	-0.94	0.91	-0.27	0.37	0	-1.36
	Ice Concentration	% (0-1)	0	0.78	0.27	0.23	0	0.85
	Current	cm s^{-1}	0.05	57.00	2.02	2.20	0.003	1.09
SET 2 (0.50°)	Depth	m	0	5304.00	2559.47	1621.75	16.17	0.63
	Slope	Degree	0	4.52	0.17	0.31	0.003	1.79
	Temperature	Degree C	-2.01	1.57	0.03	0.71	0.007	26.45
	Salinity	ppt	33.72	34.94	30.99	10.68	0.105	0.34
	Chlorophyll-*a* (Annual mean)	mgC·m^{-2}·day^{-1} cell^{-1}	0	2.50	0.62	0.40	0.004	0.65
	Ice Concentration	% (0-1)	0	1.00	0.42	0.37	0.003	0.87

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Table 3.3. Number of shrimp specimens collected or observed at each station, site and region. **Gear type:** FT= Fish Trawl; BT= Beam Trawl; MOC=MOCNESS; MWT=Mid-water Trawl; HBS=Hyperbenthic Sled; EBS=Epibenthic Sled; DTIS=Deep Towed Imaging System. [a] Total number of specimens caught in the haul, not all specimens preserved for further analysis; [b] Larval specimen collected from pelagic MOCNESS see Wiebe *et al.* (1976) for gear specification and Gallego *et al.* (2013) for specimen details) deployment.

Region	Site	Station	Co-ordinates	Gear	Depth (Mean)	*Chorismus antarcticus*	*Dendrobranchiata*	*Lebbeus* n. sp.	*Nematocarcinus lanceopes*	*Notocrangon antarcticus*	*Pasiphaea cf. ledoyeri*	*Pasiphaea scotiae*	*Petalidium* sp.
Abyssal	C30	186	-68.52, -178.3	DTIS	3227				5				
		189	-68.56, -178.3	BT	3207							2	
	C33	228	-67.61, -178.8	DTIS	3366				3				
		230	-67.61, -178.8	BT	3480							1	
	C35	285	-66.73, 171.18	DTIS	2711				7				
Seamount	C24	276	-67.01, 171.07	DTIS	695				12				
		278	-67.01, 171.07	DTIS	771				7				
		280	-67.16, 171.16	DTIS	587			30					
		281	-67.16, 171.16	EBS	604			2[a]					
		293	-66.99, 171.08	MWT	1032							2	1
		294	-66.94, 170.99	DTIS	2055				5				
		295	-66.93, 170.82	DTIS	553			2					
		301	-67.13, 171.16	DTIS	1024				7				
		302	-67.13, 171.14	EBS	947				7[a]				
		303	-67.12, 171.09	FT	743			8			5[a]		
		304	-67.16, 171.18	DTIS	642			11	9				
		305	-67.16, 171.17	EBS	634			2[a]					
		307	-67.17, 171.12	EBS	616			4[a]					
		309	-67.12, 170.89	EBS	738			1	5[a]				
		312	-67.00, 170.69	MWT	1078							1	
	C31	194	-68.13, -179.3	MOC	110				2[ab]				
		199	-68.10, -179.3	EBS	634			1					
		201	-68.09, -179.2	EBS	730				2				
		202	-68.07, -179.3	DTIS	1138				34				
		203	-68.08, -179.2	EBS	895				1				
		205	-68.11, -179.2	DTIS	864				54				
		206	-68.12, -179.2	EBS	876				10				
		207	-68.14, -179.2	DTIS	1191				46				
		210	-68.11, -179.3	EBS	662				3				
		211	-68.10, -179.2	FT	867				65[a]		3[a]		
	C32	218	-67.72, -179.7	EBS	1173				2				
		219	-67.78, -179.7	DTIS	1180				8				
		220	-67.78, -179.7	EBS	1189				2				
		224	-67.73, -179.6	EBS	841				1				
	C33	227	-67.60, -178.8	MWT	1000							1	

	C34	237	-67.40, -179.8	EBS	1540				4				
		244	-67.38, -179.8	DTIS	718				224				
		245	-67.38, -179.8	EBS	660				7				
		250	-67.37, 133.82	DTIS	1440				39				
		251	-67.38, 179.98	EBS	1496				3				
		255	-67.34, -179.9	DTIS	1027				42				
		256	-67.34, -179.9	EBS	1183			1	1				
	C35	283	-66.94, 171.33	MOC	800				1[b]				
		284	-66.79, 171.24	MWT	1004								1
Shelf	C1	26	-74.58, 170.24	FT	285	2[a]							
		31	-74.59, 170.27	BT	283	11[a]				8			
	C2	40	-74.73, 167.01	DTIS	898					34			
		41	-74.72, 167.01	FT	923					41[a]			
		43	-74.77, 167.05	HBS	800					1			
		46	-74.73, 167.06	BT	865					4			
	C3	55	-75.63, 169.78	DTIS	530	4				79			
		56	-75.63, 169.85	FT	528					18[a]			
		61	-75.62, 169.80	BT	521					9[a]			
	C4	93	-76.19, 176.29	DTIS	450	41				44			
		94	-76.19, 176.29	FT	447	1				33[a]			
		100	-76.20, 176.24	BT	449	1				10[a]			
	C5	80	-76.60, 176.77	DTIS	368	26				65			
		81	-76.59, 176.82	FT	367					17			
		82	-76.59, 176.88	HBS	363					8			
		84	-76.60, 176.80	BT	360					7			
	D2	22	-74.11, 170.79	FT	636					1			
	D3	65	-75.62, 167.33	DTIS	269	4				4			
		66	-75.62, 167.32	FT	477					10[a]			
	D34	76	-76.83, -179.9	DTIS	664	1				3			
		77	-76.83, -179.9	FT	664	1				7[a]			
	D4	69	-76.80, 167.87	DTIS	706					23			
		70	-76.77, 167.83	FT	731					11[a]			
Slope	C17	130	-72.08, 175.55	DTIS	1565				159				
		133	-72.09, 175.57	FT	1577				50		3[a]		
		139	-72.08, 175.55	BT	1620				5				
	C18	169	-71.38, 174.73	DTIS	2213				60				
		171	-71.38, 174.73	FT	2282				5				
	C25	158	-72.07, 172.92	MOC	450				1[b]				
	C27	142	-71.98, 173.39	MWT	1005								1
	D28	108	-72.82, 177.13	DTIS	1369				110				
		109	-72.80, 177.19	FT	1413				20[a]			1	
	D45	166	-71.84, 174.00	DTIS	1917				44				
		167	-71.85, 174.03	FT	1972		1		479[a]				
Upper Slope	C26	150	-72.02, 173.17	DTIS	795					1			
	D27	105	-73.25, 178.72	DTIS	775				3				
		106	-73.24, 178.72	FT	757					2			

Table 3.4. Results of model performance evaluation using different validation methods.

	Notocrangon antarcticus		*Nematocarcinus lanceopes*	
Records	**SET 1**	**SET 2**	**SET 1**	**SET 2**
Training	17	9	31	13
Testing	5	3	10	4
Independent	58	58	6	6
AUC (Area Under Curve)				
Training AUC	0.988	0.970	0.993	0.975
Test AUC	0.963	0.963	0.983	0.960
Training Gain	2.836	2.095	3.952	1.563
Test Gain	1.215	2.313	3.930	2.057
Threshold				
Low Presence Threshold (LPT)	0.168	0.431	0.031	0.432
P-Values for LPT	0.001	0.005	<0.001	0.001
10^{Th} percentile Threshold	0.291	0.431	0.141	0.484
Omission Rate				
Intrinsic	0	0	0	0
Extrinsic	0.09	0.07	0.05	0.07
Independent Records				
Maximum probability of presence (%)	64.66	74.40	59.56	86.19
Mean probability of presence (%)	24.03	46.74	19.60	80.92
Minimum probability of presence (%)	0.02	0.11	1.17	65.23
Standard deviation	0.11	0.18	0.08	0.21
Confidence Interval (95%)	0.03	0.05	0.06	0.17
Percent correct classification (PCC)	0.62	0.60	0.86	0.93
Sensitivity	0.52	0.66	0.67	1.00
Specificity	0.76	0.51	0.87	0.92
False positive rate	0.24	0.49	0.13	0.08
False negative rate	0.48	0.34	0.33	0
True Skill Statistics (TSS)	0.27	0.17	0.54	0.92

Table 3.5. Influence of environmental variables on the models generated using two datasets (SET1 and SET 2) for (a) *Notocrangon antarcticus* and (b) *Nematocarcinus lanceopes*. The top three environmental variables in terms of relative contributions are highlighted in **bold** for each species. Higher values for the regularised training gain of the jack-knife test indicated greater contribution to the model for a variable (these values were not directly comparable between the different species).

(a) *Notocrangon antarcticus*	**Contribution (%)**		**Jack-knife (Training gain)**		**Test AUC (Single variable)**	
Variable	**SET 1**	**SET 2**	**SET 1**	**SET 2**	**SET 1**	**SET 2**
Depth	**9.22**	**46.67**	**1.607!**	0.812*	**0.924**	0.770
Rugosity	1.44	-	0.085	-	0.568	-
Slope	-	10.35	-	0.080	-	0.345
Ice Concentration	7.89	3.63	0.396*	0.135	0.735	0.692
Temperature	**45.24**	13.08	**1.436**	**0.976**	**0.923**	**0.820**
Salinity	1.10	**21.80**	0.894	**1.210**	0.898	**0.916**
Chlorophyll-a	**27.66**	**14.69**	**1.415**	**1.260!**	**0.911**	**0.941**
Bottom Current	7.45	-	0.167	-	0.648	-

(b) *Nematocarcinus lanceopes*	**Contribution (%)**		**Jack-knife (Training gain)**		**Test AUC (Single variable)**	
Variable	**SET 1**	**SET 2**	**SET 1**	**SET 2**	**SET 1**	**SET 2**
Depth	**15.67**	**29.55**	**1.250**	**0.496**	**0.881**	**0.806**
Rugosity	**29.14**	**-**	**1.290!**	**-**	**0.885**	**-**
Slope	-	10.35	-	**0.391**	-	**0.830**
Ice Concentration	**32.17**	**26.72**	**1.043***	**0.922!***	**0.883**	**0.897**
Temperature	11.89	**25.53**	0.423	0.164	0.801	0.592
Salinity	7.61	6.58	0.215	0.142	0.699	0.627
Chlorophyll-a	5.51	1.28	0.178	0.017	0.692	0.558
Bottom Current	3.34	-	0.167	-	0.601	-

* indicates the variable that reduced the gain the most when omitted and thereofore contained the most information that was not present in other variables.

! Indicates the variable with the highest gain when used in isolation and had the most useful information by itself.

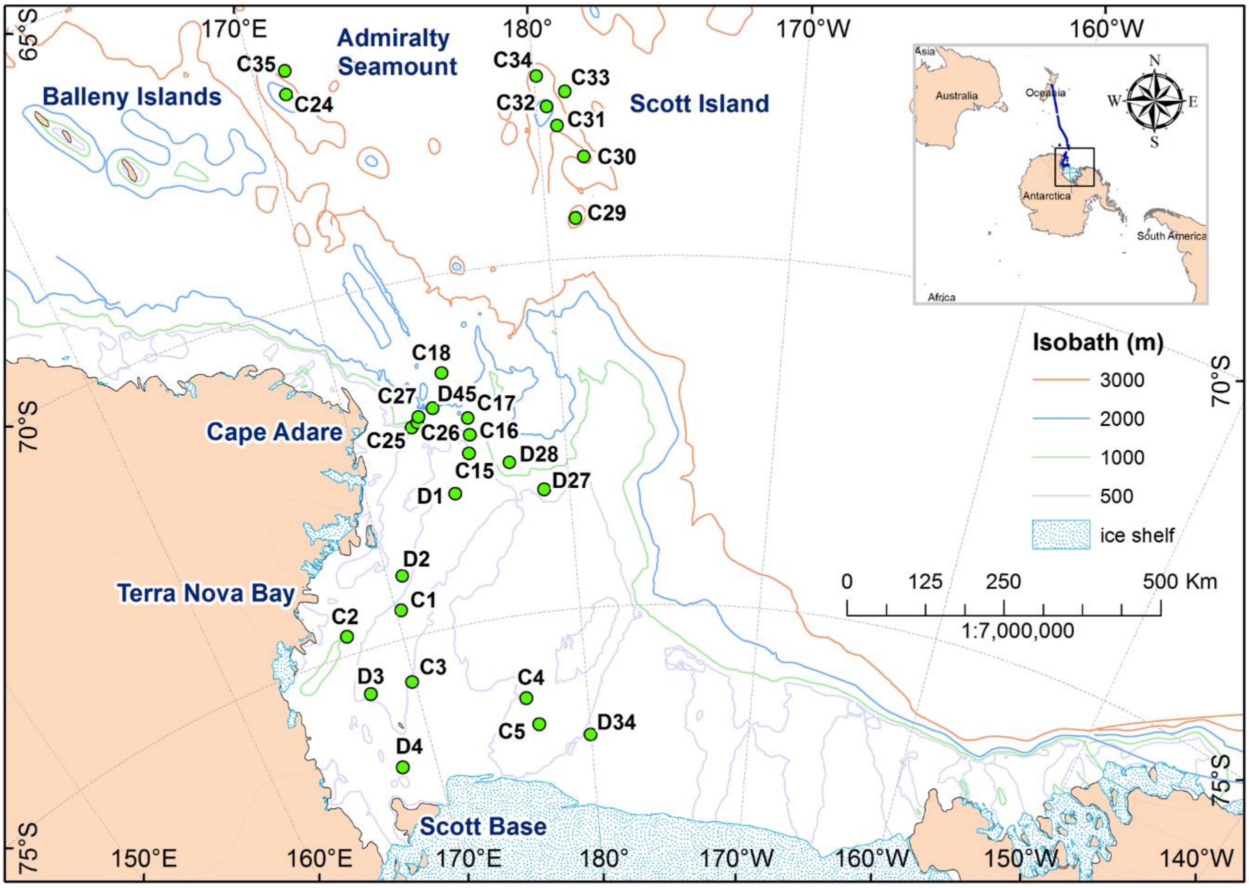

Figure 3.1. Map of Ross Sea region showing sampling sites of the New Zealand International Polar Year – Census of Antarctic Marine Life (NZ IPY-CAML) voyage TAN0802.

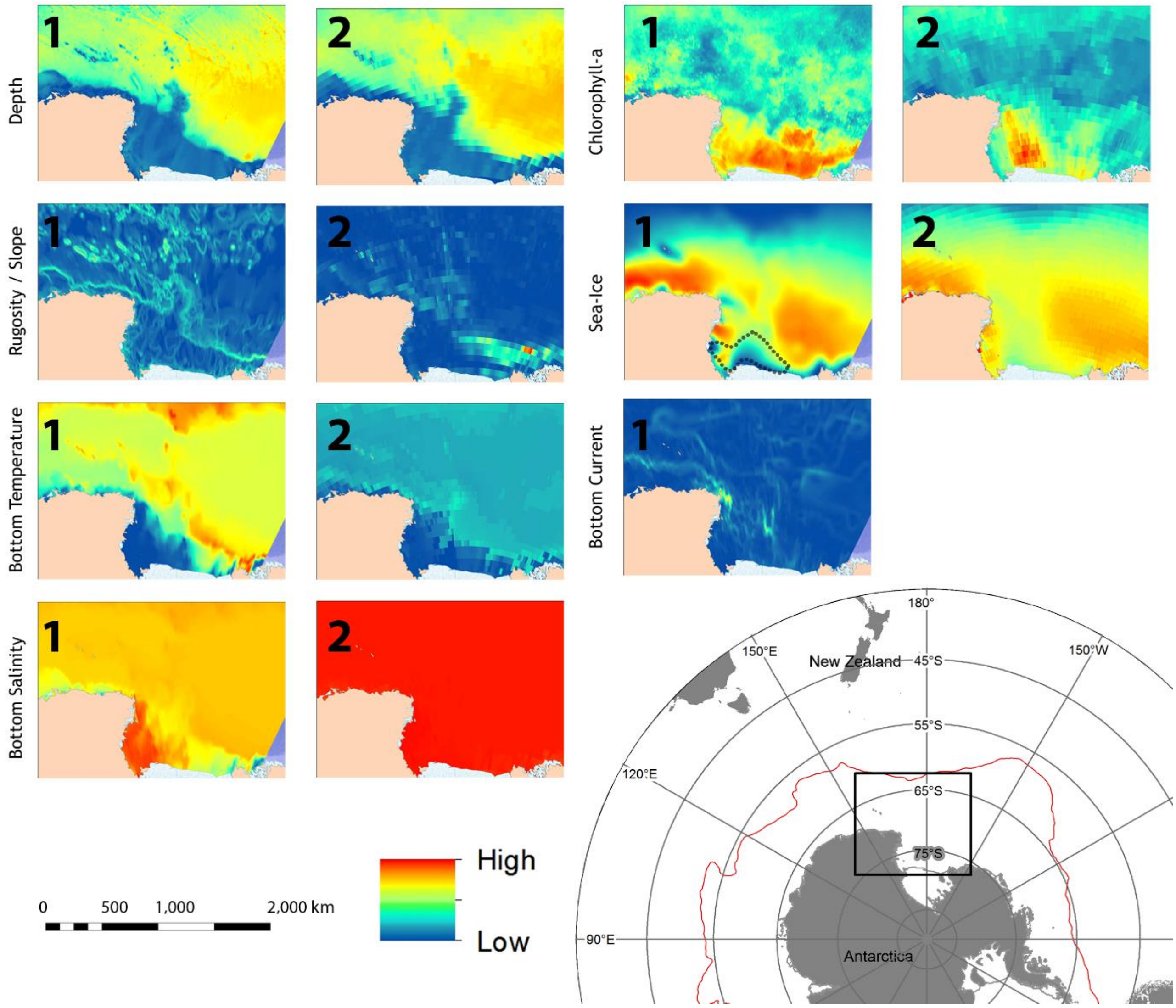

Figure 3.2. Environmental layers used for modelling. Numbers denote respective environmental datasets. The location of the Ross Sea polynya is marked with dash in the ‘sea ice’ layer.

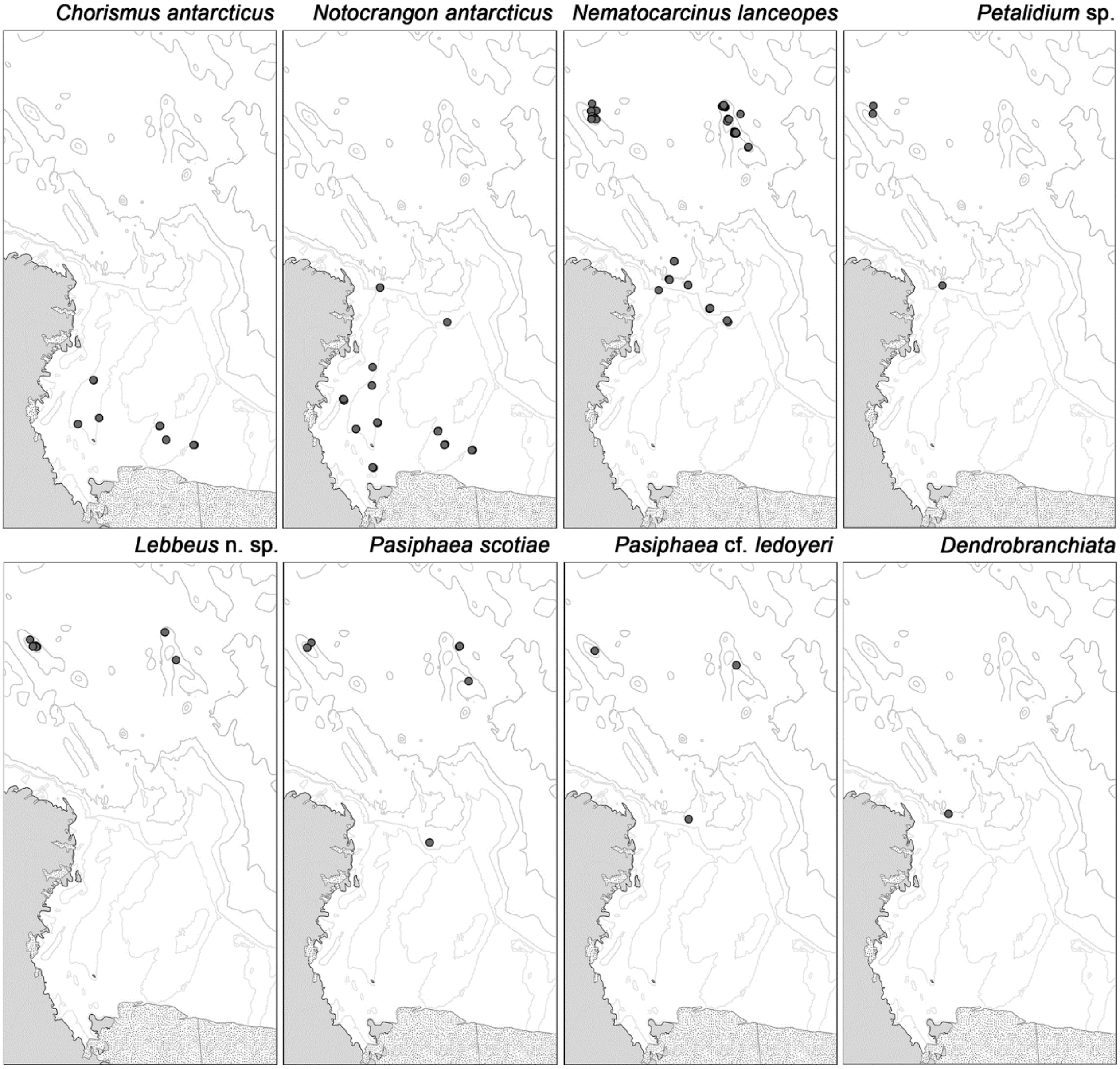

Figure 3.3. Spatial distribution of shrimp species sampled during NZ IPY-CAML voyage TAN0802 in the Ross Sea region.

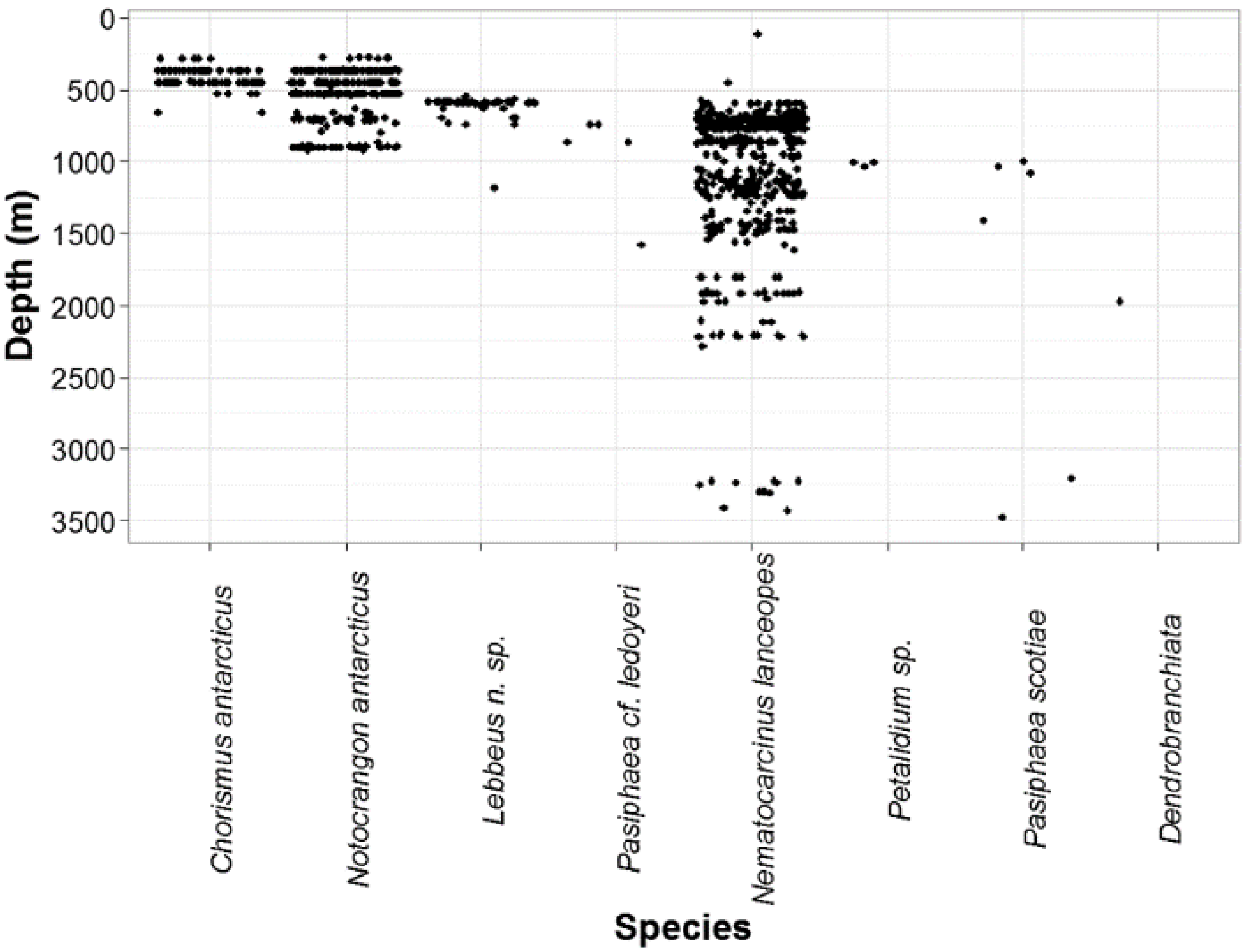

Figure 3.4. Depth ranges of sampled shrimp species during NZ IPY-CAML voyage TAN0802 in the Ross Sea Region.

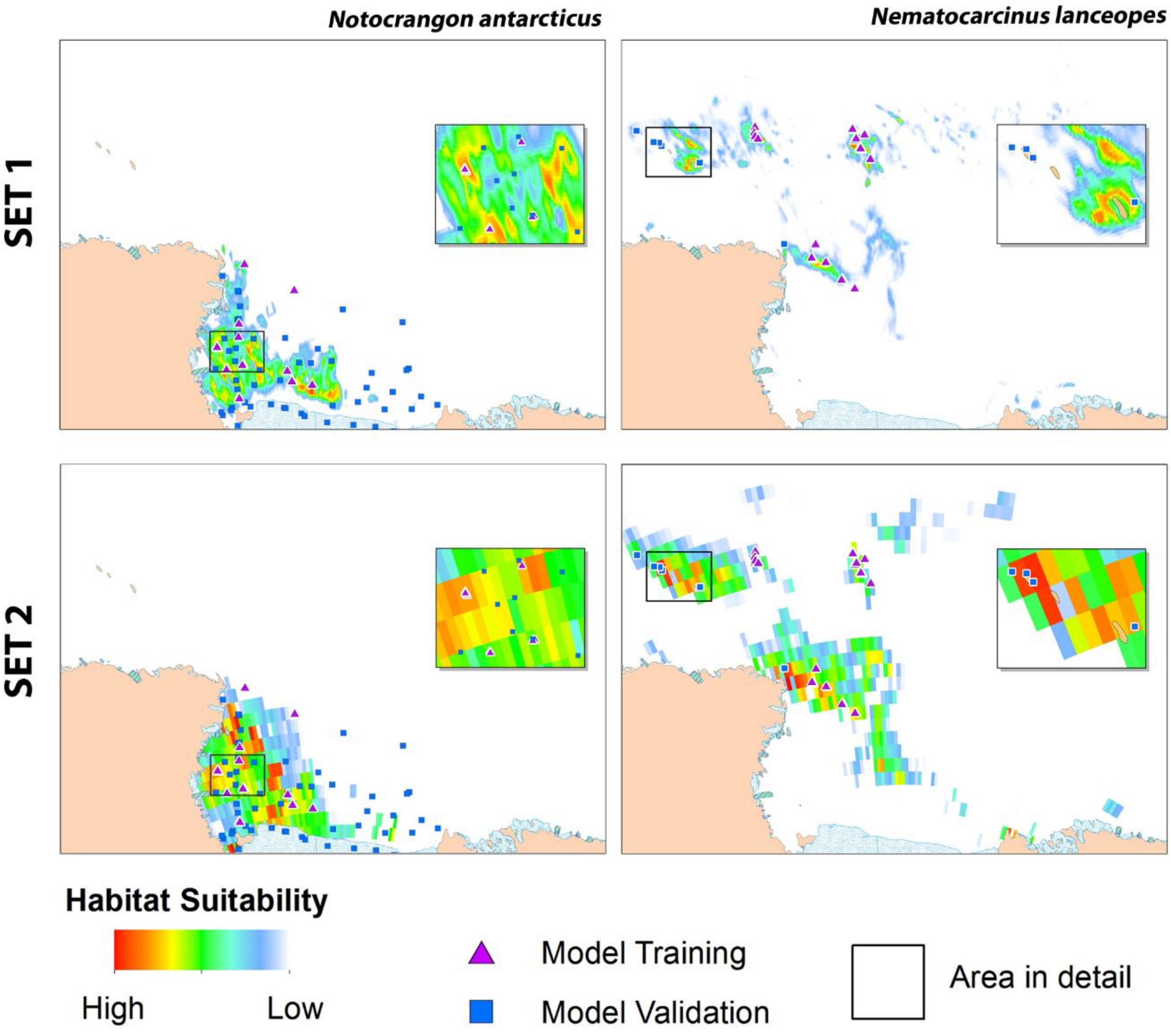

Figure 3.5. MaxEnt habitat suitability maps for *N. lanceopes* and *N. antarcticus* using two different resolutions of environmental data (SET 1, fine; and SET 2, coarse) in the Ross Sea region, showing predicted areas having values above low presence threshold value (LPT, see Table 3.4).

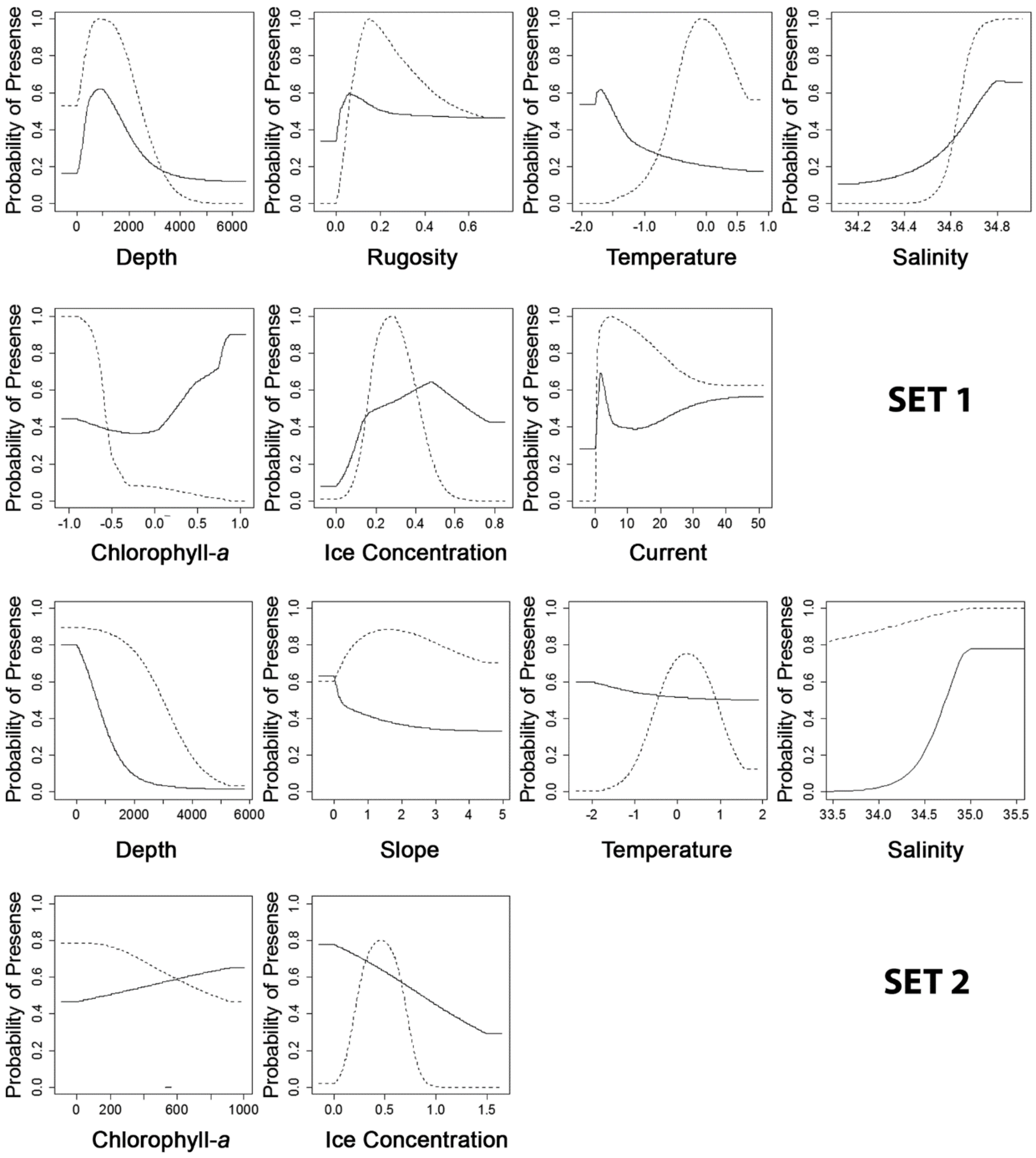

Figure 3.6. Response curves of environmental variables at two different spatial resolutions (SET 1 and SET 2) in MaxEnt models for *N. antarcticus* (solid line) *and N. lanceopes* (dotted line), showing how each variable affected model prediction performance.

Chapter 4

Dispersion and Faunal association pattern of common Antarctic shrimps

Abstract

Three Antarctic shrimps (*Chorismus antarcticus, Notocrangon antarcticus, Nematocarcinus lanceopes*) from the Ross Sea and other regions of the Southern Ocean were investigated using over 500 underwater video and photography observations complemented with 159 specimens collected in various expeditions. *Notocrangon antarcticus* and *N. lanceopes,* but not *C. antarcticus,* grew to a larger size at greater depth in the Ross Sea comparing to other regions of Antarctic. *C. antarcticus* were observed between 0-900 m depth while *N. antarcticus* and *N. lanceopes* were observed between 250-950 m and 500-2500 m depth respectively. In the Ross Sea, maximum density of *ca.* 16 individual * 1000m^{-2} was found for *N. lanceopes* on the seamounts and 5 individual.*1000 m^{-2} for *N. antarcticus* on the shelf area. *Chorismus antarcticus* was observed mostly close to bryozoan, crinoid and ophiuroid on muddy sediment, *N. antarcticus* often buried in muddy sediments mostly near holothurian, sponge and bryozoan, and *N. lanceopes* on sandy or rocky sediments close to seleractinia, ophiuroid and anemone. Potential reasons behind their habitat preference and their role in Ross Sea trophic ecosystem were discussed using information extracted from video, photographs and stable isotope data.

4.1 Introduction

Antarctic shrimps though not as abundant as other common benthic groups, have a circumpolar eurybathic distribution in the Southern Ocean (SO) (A. Clarke, 1990; Brey *et al.*, 1994; Briggs, 1995; Brey *et al.*, 1996; Gorny, 1999; Carli & Pane, 2000; A. Clarke & Johnston, 2003; Thatje & Arntz, 2004; Griffiths, 2010; Basher & Costello, 2014). Caridean shrimp species, namely *Chorismus antarcticus* (Pfeffer,1887), *Notocrangon antarcticus* (Pfeffer,1887) and *Nematocarcinus lanceopes* (Bate, 1888) were the three most common species, in cruises around the (Arntz & Gorny, 1991; Gorny *et al.*, 1992; Thatje & Arntz, 2004; Basher *et al.*, 2014). Although, studies on shrimp population density are rare, it is necessary to obtain a completed picture of the systems trophic flow in which bottom-loving crustacean play an important role (Bluhm & Brey, 2001). Previous studies in the population structure of these common shrimps around Antarctic were focused on high Antarctic areas between Terra del Fuego and Lazarev Sea where considerable variation in numbers, size frequency distributions and occurrence in different depths found between the studies (Yaldwyn, 1966; Maxwell, 1977; A. Clarke & Lakhani, 1979; J .M. Kirkwood, 1984; Arntz & Gorny, 1991; Lovrich *et al.*, 2005). Despite advances in making inventory of benthic decapods shrimps around the Ross Sea, information on adult shrimp distribution has been limited to few studies in past decades (Bullivant, 1959; Dearborn, 1965; Bullivant, 1967; Gambi & Bussotti, 1999; Berkman *et al.*, 2005; Cummings *et al.*, 2010) and one study regarding larvae population from Terra Nov Bay (Carli & Pane, 2000). Information on shrimp population densities, habitat and depth distribution, body size variation, species associations, and trophic ecology is necessary to understand their overall role in the Ross Sea food web, but it has not been addressed to date.

In benthic ecosystems, decapods occupy a variety of ecological niches and exhibit wide variety of feeding habits or guilds ranging from deposit feeders to carnivores in similar range of trophic levels to fish (Lagardère, 1977; Gorny *et al.*, 1993; Polunin *et al.*, 2001; Cartes *et al.*, 2002). Thus, shrimps can have a marked impact on abundance and population structure of their prey taxa, as well as on food competitors e.g. echinoderms (Jarre-Teichmann *et al.*, 1997). Information about the prey and predators of the shrimps is necessary to determine the position of shrimps in trophic webs of the Antarctic ecosystem. To date, Weddell Seals, Antarctic cods (ice fish), and dragon fish are known as the predators of shrimps from studies in various regions of the SO (Targett, 1981; Green & Burton, 1987; Schwarzbach, 1988; Arntz & Gorny, 1991; La Mesa *et al.*, 2004; Davis *et al.*, 2013). Gorny (1992) suggested *C. antarcticus* prey upon amphipods and isopods and Carli & Pene (2000) suggested *C. antarcticus* and *N. antarcticus* larvae might prey on abundant copepod and ostracod in the Ross Sea shelf but no conclusive evidence about prey of the shrimps were available in the literatures. Determining diets of marine invertebrates by gut content analysis is problematic as many organisms post consumption become unrecognizable once partly digested, while those with hard remains (e.g. diatom skeletons) may bias the analysis and limit the estimation of long term average diets of marine invertebrates (Cortés, 1997; Blankenship & Yayanos, 2005). Moreover, complex processes within food chains are elucidated by energy flux in an ecosystem, but this does not provide information at species metabolic and molecular levels (Noguchiaita *et al.*, 2011). Stable Isotope (SI) analyses have allowed ecologists to study biogeochemical cycles as well as ecosystem structure from entirely new perspectives. We can determine the structure of food webs and the interactions between organisms using distributions and variation in Carbon/Nitrogen (C/N) isotope ratios together with their fractionations (Wada, 2009). Isotopic distribution in animals is generally closely related to dietary isotopic compositions. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope enrichment occurs between animals and their foods. Heavy isotope $\delta\ ^{13}C$ enrichment is estimated to be about 1‰ per trophic level for carbon and $\delta^{15}N$ enrichment at 3-4‰ for nitrogen (Minagawa & Wada, 1984; Fry, 1988).

The present study updates information on the species composition, depth distribution, relative abundance, size frequency distribution and habitat composition of three common decapod shrimps in the Ross Sea. The study also compare size frequency distributions with information gathered from other cruises around the Antarctic. Additional knowledge of faunal association and trophic ecology of shrimps are furthermore discussed based on detailed community level data extracted from video transects and isotopic signatures.

4.2 Methods

4.2.1 Study area

Shrimps were collected from New Zealand's 2008 IPY voyage (TAN0802) from 12 February to 11 March 2008 by the RV Tangaroa in the Ross Sea, Antarctica. Our study area was bounded by 65° S, 150° E, 140° W, and the Ross ice shelf in the south, including the entire Ross Sea continental shelf area, the Balleny Islands, and the Scott and Admiralty seamounts. A total of 644 individuals (55 from specimens and 589 from photographs) of species of *Chorismus antarcticus* (Pfeffer, 1887), *Notocrangon antarcticus* (Pfeffer, 1887) and *Nematocarcinus lanceopes* (Bate, 1888) were measured out of more than 66 specimens and several thousand photographs from 23 sites in the Ross Sea. An additional, 112 specimens were measured from museum collections around the world for comparison.

4.2.2 Sampling

Sampling was carried out using at least one deployment of a towed camera array (NIWA Deep Towed Imaging System, DTIS) with high definition digital video and still image cameras (Hill, 2009) at 23 sites. Camera transects were then followed by physical sampling gear including a beam trawl (4 m width, 25 mm mesh), a large demersal fish trawl (25 m wing spread, 40 mm mesh), and two types of epibenthic sled; a fine mesh (1 m width, 0.5 mm mesh) sled used on flat, smooth seabeds, and a coarse mesh (1 m width, 25 mm mesh) sled used on seamounts. Standard gear tows were of 20-minute duration at a speed over the ground of approximately 3 knots and the distance covered was measured by GPS on the surface. The tow was deemed to have started when the net monitor indicated the net was on the bottom, and was completed when hauling began. Each camera transect were of one hour duration at target altitude of 2.5 m above the seabed and 0.25–0.5 ms^{-1} tow speed and high definition still photographs were taken at 15-second interval.

All collected shrimps were weighed fresh and then preserved in 99% ethanol on board and registered with relevant metadata (including exact co-ordinates of collection) in the NIWA Invertebrate Collection (NIC) database. Preserved specimens were identified to species level (when possible) in the lab by a taxonomist and samples of different sizes from each species groups were photographed individually and measured to nearest mm. Carapace length (CL) was measured using vernier calipers, from the rear of the eye socket to the posterior dorsal edge of the carapace. Total length (TL) was measured as the distance between the tip of the rostrum and the end of the telson.

Furthermore, decapod specimens available at Smithsonian Institution National Museum of Natural History, in Washington D.C. and Muséum National d'Histoire Naturelle, in Paris were also checked for this study to compare Antarctic regional populations. Full details of repository and station data were listed in Appendix IV.

4.2.3 Data analysis

Post-voyage analyses of video transects were run using Ocean Floor Observation Protocol (OFOP; www.ofop-by-sams.eu) software. Raw USBL transponder positions were first smoothed using a running mean and splined with associated metadata (e.g., time, depth, heading) to yield corrected seabed tracks with position coordinates and metadata values at 1-s intervals. The digital video files (in n.avi format) were then synchronised with the corrected position data to enable re-running of transects in the laboratory with full video playback control and precise spatial and temporal logging of events. A total of ca. 55 hours of video and ca. 13000 photographs collected by DTIS were analysed to identify the shrimps and their surrounding habitat condition. All shrimps on all transects were recorded and identified to the finest practicable taxonomic resolution using the high-resolution still images to confirm identities. ImageJ (Schneider *et al.*, 2012) software was used to analyse still images, in order to confirm the identities of surrounding benthic fauna, calculate specimen sizes, and estimate local population densities of individual taxa and record substrate type. Small specimens of three species were clearly distinguishable in the photographs. Photographs where the entire specimens without a ventrally flexed tail were present were exclusively used in this study. Abundance for each species was calculated by dividing their number in the catch or observation by the total area covered with the representative gear of that particular sampling station.

To investigate multimodality of the shrimp population in relation to depth, non parametric Kernel Density Estimation (Silverman, 1986) was used and differences in size frequency distributions of shrimps at different stations were analysed by means of the non-parametric Kolmogoroff- Smirnoff test (Justel *et al.*, 1997) in R-statistical software (R Core Team, 2014). One species matrix with presence absence and a second matrix for abundance) by station was constructed for fauna's associated with shrimps as seen in the photographs. This data formed the basis of the multivariate statistical analysis using PRIMER 6 (K. R. Clarke, 1993). Faunistic similarity between species was measured by quantitative Bray-Curtis similarities of presence absence transformed data using SIMPER analysis (K. R. Clarke & Ainsworth, 1993). Non-metric multidimensional scaling (MDS), and cluster analysis were applied to the similarity data to reflect faunistic similarity in a two-dimensional plane. Faunal association between the species in different station were analysed by Principal Component Analysis (PCA).

4.2.4 Stable Isotope Analysis

Shrimp diets may change seasonally and spatially in response to prey availability so that stomach/gut contents may not be consistent over time. There may also be significant variation in diets between individuals in a population in a given area at a particular period. The interaction of physical, biological and chemical processes in an ecosystem results in distinct isotopic signature in the tissue of an organism (M. H. Pinkerton *et al.*, 2011). These distinct natural signatures are increasingly used as tracers in environmental studies, with carbon and nitrogen isotope ratios used to track nutrient fluxes between trophic levels and provide information on the trophic structure of food webs. Stable isotope analysis was used to provide a long-term view of the tropic position of shrimps.

Specimens were dissected to obtain samples of tissue and gut to determine both tissue-specific and gut content isotopic signatures. The gut and its contents were considered to represent recently ingested food, while signatures derived from intestine represent an integration of food sources consumed over a longer period of time (Lorrain *et al.*, 2002). This tissue-specific approach is especially important in the Antarctic environment where the input of food and feeding activity is likely to be pulsed and highly seasonal (Norkko *et al.*, 2007). Tissues from gut and intestinal tracts of *N. lanceopes* (n=10) and *N. antarcticus* (n=4) were analysed with Delta^{Plus} mass spectrometer and ISODAT (Thermo-Finnigan) software to calculate δ^{15}N and δ^{13}C values (See M. H. Pinkerton *et al.*, 2011 for details).

Trophic levels are usually calculated based on two rules: (1) primary producers and bacteria are defined as having a trophic level of one; (2) the trophic level of a consumer is the sum of the trophic levels of the prey items weighted by diet fraction plus one (Lindeman, 1942; Odum & Heald, 1975; Christensen & Pauly, 1992). Pinkerton *et al.* (2010) added a third rule, namely, that carcasses have the average trophic levels of their source biota (see Lorrain *et al.*, 2002). Fractionation of 15N results in an increased of δ^{15}N ranging from 1.4 to 3.4‰ per trophic level (e.g. Post, 2002; McCutchan *et al.*, 2003). In this study I assume a +3.2‰ change in δ^{15}N per successive trophic transfer and hence use differences in δ^{15}N to infer relative trophic levels (*sensu* Hobson & Welch, 1992). Trophic level of shrimps were calculated based on the following formula.

Trophic level = 1 + (dN-dNphytoplankton)/) dN change per trophic level)

Where, ‘dN’ is the δ^{15}N value of the organism tissue, ‘dNphytophankton’ is the δ^{15}N of the primary producers of the area, which is 0.4 for the Ross Sea (Bury *et al.*, 2008); ‘dN change per tropic level’ is the delta value of each successive trophic transfer which is 3.2 ‰ for this study.

4.3 Results

4.3.1 Species Composition

Chorismus antarcticus, Notocrangon antarcticus and *Nematocarcinus lanceopes* were the most common species of shrimp found across all regions of southern ocean out of 23 reported shrimp species from the Antarctica (Basher & Costello, 2014). A total of 878 specimens of *Chorismus antarcticus, N. antarcticus and N. lanceopes* were captured from 46 out of 126 trawling stations. In addition, there species were photographed 632 times from 30 out of 58 stations.

4.3.2 Dispersion pattern

4.3.2.1 Distribution

Geographically, *Chorismus antarcticus* specimens were frequently captured from the Weddell Sea, Lazarev Sea, Ross Sea, Prydz Bay and the D'urville Sea area; *N. antarcticus* were obtained from the Antarctic Peninsula, the Southern Orkney and the Ross Sea area; and *N. lanceopes* were mostly located near the Karguelen plateau, Davis Sea and from slope and seamount regions of the Ross Sea (Figure 4.1). All three species were most abundant between 65 and 75°S latitude and shrimps caught in the Ross Sea were present in deeper water in general comparing to other regions (Figure 4.2). In the Ross Sea, *Chorismus antarcticus* and *Notocrangon antarcticus* distributed around the entire area of continental shelf from north to south except the seamount areas in the north where shrimps populations were dominated by *Nematocarcinus lanceopes* and a few other species (Basher *et al.*, 2014). Depth stratified distribution of their occurrence in catches and observations in the Southern Ocean indicate depth stratification exists between the three species despite a large overlap in the ranges. *Chorismus antarcticus* occurrence decreased with depth > 500 m while that of *N. lanceopes* increased. *Notocrangon antarcticus* occurred regularly between depth ranges of 300-800 m (Figure 4.3). Considerable overlap existed between the depth distribution of *C. antarcticus* (269 and 664 m) and *N. antarcticus* (269 and 930 m) and they frequently occurred together in the shelf areas with depth < 500 m. Whereas, *N. lanceopes* mostly occurred alone in slopes and deep-sea areas (570 – 3500 m), there was overlap with *N. antarcticus* near shelf edge region (500-900 m) (Figure 4.3). In terms of number of available records, *Chorismus antarcticus* was found abundantly over a wide depth range between 200 and 500 m, *N. antarcticus* appeared at greater concentrations below 400 m to about 800 m and large catches *of N. lanceopes* were hauled above 1000 m.

4.3.2.2 Size frequency distribution

A total of 134, 274 and 338 individuals of *C. antarcticus*, *N. antarcticus* and *N. lanceopes* respectively were measured from specimens collected and photographed during the IPY expedition at the Ross Sea and from the specimens preserved at the museums.

Chorismus antarcticus: The smallest specimen caught was 8.5 mm CL. Specimens up to 36 mm CL (101 mm TL) were captured in recent cruises. Most of the specimens were measured between 15 to 30 mm CL (70 to 90 mm TL) (Figure 4.4).

Notocrangon antarcticus: Carapace length of the smallest specimen caught was 8.9 mm. Most specimens were within 20-30 mm CL (80 - 100 mm TL), only a few specimens exceeded >30 mm CL or < 40 mm TL range. The largest specimen measured 36.6 mm CL (107 mm TL) (Figure 4.4).

Nematocarcinus lanceopes: The smallest specimen detected in the trawl was 17.31 mm carapace length. The largest specimen, measured 71.8 mm CL (171 mm total length). Majority of the specimens measured between 25-55mm CL (95-140 mm TL) (Figure 4.4).

Medium specimens of *Chorismus antarcticus* (TL: 70mm, CL: 20mm) and *N. antarcticus* (TL: 80 mm, CL: 30mm) were more frequently captured, while larger individual of *N. lanceopes* (TL: 180mm, CL: 50mm) was captured across all regions. Comparison between shrimps captured in different regions in the Antarctica revealed that *C. antarcticus* and *N. antarcticus* specimens captured in areas outside the Ross Sea were larger in size ($P > 0.01$ and higher CL to TL ratio) and *N. lanceopes* specimens were smaller ($P < 0.01$) (Figure 4.4). The regression of TL vs. CL indicates *C. antarcticus* population was divided into two size cohorts (Figure 4.6) and *Notocrangon antarcticus* and *N. lanceopes* population had positively allometric relationship across all populations around the Antarctica (Figure 4.5). Gears with the biggest mesh size (40 mm) captured most of the *N. lanceopes*. The frequency of *C. antarcticus* captured was reduced from smaller (10 mm) to bigger mesh (40 mm) size. *Notocrangon antarcticus* capture frequency was not affected by mesh size of the gear (Figure 4.7). There were differences in size of shrimps which were captured in trawls and observed in photographic transects. Smaller specimens of *C. antarcticus* and *N. lanceopes* (CL: 32.64mm, 59.84mm respectively) were observed in photographs comparing to minimum size specimens captured in trawls (CL: 36mm and 71.81mm respectively). The trend was opposite for *N. antarcticus* i.e. trawls captured more of the smaller specimens than photographs (CL: 36.66 mm for DTIS and 34 mm for trawl).

4.3.2.3 Abundance

Shrimp abundance in the Ross Sea varied from shelf to abyssal regions; shelf had 5 times more shrimp than the abyssal regions (Table 4.1). The length of transects where shrimps were present ranged between 0.5 to 0.8 nautical miles and covered areas between 1342 m^2 (DTIS) to 31,522 m^2 (trawl). Neglecting the escape factor, and assuming that all the shrimps were collected from the catches or observed in videos, average densities of individuals*1000 m^{-2} for *C. antarcticus*, *N. antarcticus* and *N. lanceopes* were 0.68, 3.16 and 9.12 respectively. Maximum densities of individuals*1000 m^{-2} encountered in a single transect were 14.21 for trawl hauls and 145.55 for photographic observations (Table 4.1). Highest density of *N. lanceopes* were observed (up to 16 individuals*1000 m^{-2}) in the video transects while the highest 9 individuals*1000 m^{-2} captured in trawl hauls were *N. antarcticus*. Densest concentration in one photograph was four *N. antarcticus* at a shelf site, constituting almost 1 per m^2 and the overall density up to 50 individuals per 1000 m^2 was estimated for the whole transect (Figure 4.8). In general, beam trawl captured the most individuals of the three species compared to other gears. A comparison of shrimp density estimates with previous studies shown on Table 4.2.

4.3.3 Fauna, substrate and sediment associations

Habitat of *C. antarcticus* and *N. antarcticus* consisted of homogenous muddy substrate with the very little identifiable debris present. However, *N. lanceopes* habitats had substrate, mostly composed of sand and rocky outcrops and often covered with shell hash, dead barnacle plate and echinoid shells (Figure 4.10). *Chorismus antarcticus* mostly found close to bryozoans, crinoids, ophiuroids, sponges and worms; whereas *N. antarcticus* were often observed buried in the mud and close to holothurians, sponges and bryozoans. *Nematocarcinus lanceopes* were observed close to seleractinia, ophiuroids, anemones and bryozoans (Figure 4.13, Figure 4.15). MDS analysis revealed groups of stations with faunal assemblage very similar to the groups identified from cluster analysis (Figure 4.11) i.e. locations (shelf, slope, seamount and abyssal) have similar assemblage composition. All regional groups were separated along two MDS axes (stress=0.11) except the slopes. The slope assemblage of six stations was included in three minor clusters (Figure 4.12) with stations that separated in both analyses. Dissimilarity between geographically distant regions (shelf and seamounts) reached 73% while the greatest dissimilarity 80% was between two adjacent regions (shelf and slope). It was mainly driven by the abundance of ophiuroid and bryozoan (Table 4.3). Slope and seamount sites have the least amount of dissimilarities (69%). A SIMPER analysis between faunal composition next to species showed each species has 36 - 38% similar species occurring next to them (Table 4.3). The compositions were driven mainly by the presence of sponge, ophiuroid and bryozoans. In overall variation in the abundance of the ophiuroid, bryozoan, sponge and worms were responsible for the greatest dissimilarity between the regions and shrimps (Table 4.3).

4.3.4 Faunal association in relation to isotope data

Analysis of isotopic signature from shrimps illustrated variation in trophic level position of individual shrimp species. I have analysed 12 gut and 10 intestinal tissue samples from 14 shrimp specimens collected from five sites located in the shelf, slope and seamounts of the Ross Sea. The average $\delta^{13}C$ value for *N. lanceopes* and *N. antarcticus* were similar, mean ± SD; 28.41 ± 0.81‰ and 27.47 ± 2.04‰ respectively but the average $\delta^{15}N$ value was lower for *N. lanceopes* (6.92 ± 0.37‰) than *N. antarcticus* (10.4 ± 1.39‰) (Table 4.4). The average value of $\delta^{13}c$ for Particulate organic matter (POM) was -27.09 ± 0.62 ‰. Values of $\delta^{13}C$ for ostracod, copepod and amphipod overlapped with those of both shrimp species (Figure 4.15, Table 4.4). The value of $\delta^{15}N$ for phytoplankton in the Ross Sea was 0.4 ± 0.6‰. This was used as a food-web baseline (.i.e. equivalent to trophic level of 1). Particulate organic matter, the primary food item for deep-sea invertebrates has an average $\delta^{15}N$ value of 4.7 ± 1.48‰. Considering +3.2‰ of change in nitrogen at each successive trophic level, other organisms, after death might be preyed upon by shrimps should have $\delta^{15}N$ values between 4.3 to 8.0‰. This is equivalent to a trophic level between 2 to 3.3 representing the group amphipod, holothurian, ophiuroid and copepod (Table 4.4). However, known predators of shrimp, Weddell seals and ice fish have an average $\delta^{15}N$ values of 13.1 and 9.3 respectively Trophic level calculation estimated *N. antarcticus* (Trophic Level = 4.1 ± SD 0.53) in the same trophic level as Antarctic silver fish (*Pleuragramma antarcticum*). *Nematocarcinus lanceopes* (Trophic level = 3.0 ± SD 0.12) was estimated to be similar to Antarctic Krill (*Euphausia superba*) and ophiuroids (Table 4.4, Figure 4.15). Correlation between depth and $\delta^{13}C$ (R=0.001, 0.02; P=0.94, 0.71) was not significant for both species.

4.4 Discussion

In the Antarctic benthic ecosystem, *C. antarcticus* and *N. antarcticus* appear to be abundant in the shelf regions while *N. lanceopes* in regions outside of the continental shelves. Without using any special gears to capture the shrimps, 35 - 50% of the trawl catches or video transects in the Ross Sea yielded shrimps and the mean densities reached up to 50 individuals per 1000m^2. Faunal association in the Ross Sea showed species *C. antarcticus* and *N. antarcticus* have faunal composition dominated by bryozoans and ophiuroid when *N. lanceopes* is surrounded by sponges, ophiuroid and anemones. Stable isotope analysis of the shrimps for the first time positively identified their carnivorous and detrivorous feeding habit and trophic level in the Ross

Sea trophic web. Despite our compiled dataset having information about shrimp size and frequency around number of sites in the Antarctic, a direct comparison of the distribution of sizes at different depths and latitudes has been possible only in a few cases. The shrimp density was low but the overall size of all of the species were larger in the Ross Sea in comparison with populations found elsewhere in the Antarctica (Arntz & Gorny, 1991; Gutt *et al.*, 1991; Gorny, 1992; Arntz *et al.*, 1999). This agrees with the past studies; however we cannot give any reason for this distribution pattern.

4.4.1 Distribution

Depth preference for *C. antarcticus* and *N. antarcticus* is similar in the Ross Sea as described by Arntz and Gorny (1991) and Gutt *et al.* (1991) for the Weddell Sea. This indicates that the preference of different depth ranges is due to the variation of surrounding environment, e.g. substratum, which can change with depth and therefore influences indirectly the composition of the shrimp fauna. No true vertical zonation for both of these species exists. *Nematocarcinus lanceopes* was also observed in random dispersion pattern. The comparison of the distribution patterns on different spatial scales (between areas, within one area and within one station) indicate that the size in a one dimensional extension of significant shrimp patches lies between a few hundred meters and a few kilometres. Similar results were obtained by Arntz and Gorny (1991) and Gutt *et al.* (1991) for the same species in the Gould Bay, Weddell Sea.

In general, our results agree with those of former, Antarctic and sub-Antarctic studies, demonstrating Chorismus-Notocrangon-Nematocarcinus distributed from shallower to deeper waters, with a broad overlap between the former two species at shelf and latter two species in the slope around the SO (Arntz & Gorny, 1991; Basher *et al.*, 2014). Arntz and Gorny (1991) hypothesized seasonal vertical, horizontal or ontogenetic migrations of adults in the Weddell Sea to provide improved feeding conditions for the larval shrimps. In shallower waters of Antarctic, food input from pelagic zone to the shelf and slope benthos sharply decreased with depth (J. M. Kirkwood & Burton, 1988). Primary production and sedimentation is extremely seasonal (A. Clarke, 1988; Smith Jr *et al.*, 2000) in the deeper open waters. This uncertainty of food availability might explain why most of the shrimp larvae were found in pelagic shallower waters in the past. Although, *Nematocarcinus lanceopes* larvae was captured from shallow pelagic sampling stations in the same cruise (Gallego *et al.*, 2013) and larvae of *N. antarcticus* and *C. antarcticus* were captured from the shallow waters in the Terra Nova Bay (Carli & Pane, 2000), the knowledge about the spawning and early life history of particularly the deep-sea shrimps *N. lanceopes* in the Ross Sea remains unknown.

Sampling in the Antarctic is mostly restricted to summer season, therefore catches outside of the season is limited and the presence of pack ice hampered sampling in the eastern slope and deep sea regions at the edge of the Ross Sea shelf. This should be considered when comparing our findings of the Ross Sea to those from similar areas, e.g. the Weddell Sea and the Antarctic Peninsula region. Further catches are needed to determine whether these shrimps are really absent from different areas around the Antarctic i.e. the eastern Ross Sea, western Weddell Sea and Riiser-Larsen Sea.

4.4.2 Size frequency distribution

Latitudinal differences in sizes were minimal for all of the shrimp species. Growth in benthic species tended to be isometric, meaning that greater increase in depth results greater increase in size (Company & Sarda, 2000).. In general, *Chorismus antarcticus* and *N. antarcticus* seem to attain greater size in the inner Ross shelf than coastal regions similar to the observation of Maxwell (1977) where they attained maximum size in the inner Weddell Sea rather than South Georgia. This trend may be due to predation pressure near the coastal waters. Our maximum carapace length for *C. antarcticus, N. antarcticus* and *N. lanceopes* were 36 mm, 36.6 mm and 71.8mm respectively which was much bigger than previously known maximum CL of 21.5 mm, 27.1 mm and 35 mm respectively at the Weddell Sea (Arntz & Gorny, 1991). Former two species seemed to attain larger sizes comparing to the shrimps even found at South Georgia (Maxwell, 1977) and Tierra del Fuego (Yaldwyn, 1966). Total length of the largest specimen of *N. lanceopes,* 171mm (from trawl) and 189 mm (from DTIS) exceeded known maximum size of 163 mm from eastern Weddell sea (Arntz & Gorny, 1991; Gutt *et al.*, 1991) and 150mm from high Antarctic waters (J .M. Kirkwood, 1984). The size frequency distributions for all shrimps show similar modes for specimens captured or observed in photographs. However, size ranges for *C. antarcticus* and *N. lanceopes* species was skewed towards smaller sizes on photographs while the opposite was observed for species *N. antarcticu*s. Frequency of smaller specimens occurring in shallower water was higher for all the species in both trawls and photographs in spite of both gears covering different depth strata across the transects. Specimens caught from the Ross Sea region seem to be bigger and found at greater depth when comparing with catches from other regions as length of at least two species exceeded the previously known maximum size of same species caught at the Weddell Sea (Arntz & Gorny, 1991) (Figure 4.5). The trend of linear regression between TL and CL were significant for *N. antarcticus* ($R^2 = 0.79$) and *N. lanceopes* ($R^2 = 0.78$) but for *C. antarcticus* it was ($R^2 = 0.15$) which is due to the reason of population structure being divided into male and female size cohorts.

4.4.3 Abundance

Trawling and standard catch methods are often used in fisheries biology to measure relative standing stock population (Gutt *et al.*, 1991). Considering our methods of data collection and restrictions in survey route in the north-western part of the Ross Sea, it seems difficult to arrive at a reliable estimate of absolute shrimp abundance in the entire Ross Sea area. Shrimps are highly motile crustaceans; therefore escape behaviour might be important mechanism to avoid predators. We have noticed clouds of suspension in collected videos and photographs at several stations, this sudden and intense swimming behaviour by reaction of propulsion indicates the escaping of the shrimps from the visible area. However, the underwater video or photography proved to provide better density estimates for shrimps compared to other methods in the past as it can be expected to cause less escape reactions than a trawl (Voß, 1988; Arntz & Gorny, 1991; Gutt *et al.*, 1991). This was reflected in our result where more than 479 shrimps were caught by a bottom trawl in station '167' resulted density of ca. 4 individual per 1000 m^2, whereas the same site observed in photographs showed density of 40 individual per 1000 m^2 (Table 4.1).

The highest shrimp abundance, four specimens of *N. antarcticus*, was observed in one photograph (0.88 m^2) at a shelf site. Small–scale patches like this were recorded at stations where shrimp were common in several instances but in general, for many cases no shrimps were found at adjacent stations. This was true also for *Nematocarcinus lanceopes*, in several images of slope transects, where both species were found aggregate in patches that cover greater area than the photographic observations. Voß (1988) using Agassiz trawl and Gutt *et al.* (1991) using underwater photography arrived at similar average density values for *C. antarcticus*. However, all previous studies had higher density values for both *N. lanceopes* and *N. antarcticus* (Table 4.2). All of all these density figures appear low against the density value of 3.31 m^{-2} in the top 32 m of Ellis Fjord (Antarctica) derived from 836 samples by Kirkwood and Burton (1988). These figures contrast in comparison to shrimp density in other regions. For example, the stock assessment of the brown shrimp (*Crangon crangon*) along the coast of Netherlands with traditional trawl gear resulted in average densities of 1000 - 6000 specimen per 1000m^2 (Boddeke, 1978; Welleman & Daan, 2001). In another study at a west Swedish fjord by means of underwater video observed average densities of 33 pandalid shrimps (*Pandalus borealis*) per 100m^2 (Bergstrom *et al.*, 1987). Comparing distributions in different gears must take into account of the size of the sampling area. In our study, not all the gears were deployed in all of the stations, so estimates based on photographic transects are higher than those calculated from the trawl catches. This may be due to low catchability by the trawl or different mesh size. Bream trawl (25 mm mesh) transects captured shrimps on average ca. 8 ind.*1000 m^{-2}, whereas the average for photographic transects was more than 16 ind.*1000 m^{-2}. This is probably due to the photographic transects usually referring to the smallest areas (1 - 3 m^2) in comparison to the trawls (few hundred m^2). A trawl catch integrates patches of different sizes as well as areas with a poor shrimp concentration, which might result in lower maximum values for large total areas.

4.4.4 Faunal composition

Notothenioid fishes dominate the shelf areas in the western Ross Sea, a known habitat of the *C. antarcticus* (Ainley *et al.*, 2010). Cod ice fish *(e.g. Trematomus scotti, T. leonnbergii)* dominates the deeper shelf areas, known habitat of the *N. antarcticus. Nematocarcinus lanceopes* was most abundant in slope and seamount areas known to be dominated by mobile and sessile benthic fauna (e.g. gorgonians, crinoids, ophiuroids, asteroids and sponges) (Bowden *et al.*, 2011).

The epifaunal coverage observed was highest on the shelf and gradually decreasing in number at seamount, slope and abyssal sites (Gambi & Bussotti, 1999; Hanchet *et al.*, 2008). Shrimps were either solitary or in small groups on the photographic transects, similar to the pattern of same species in the Weddell Seas (Gutt *et al.*, 1991) and *Pandalus* sp. in video films taken in the Gullmarfjord (Bergstrom *et al.*, 1987). *Chorismus antarcticus* was observed next to bryozoans and crinoids in muddy sediments, whereas Gutt *et al.* (1991) observed them living epizoically on sponges in the Weddell Seas. Kirkwood and Burton (1988) observed strong association with the colonies of serpulid tubeworms in Ellis Fjord, which they may use as protection against predation. Barnes and Conlan (2007) also mentioned that the shrimp *Chorismus antarcticus* and the holothurian (*Taeniogyrus contortus*) feed on organic matter deposited between bryozoans and on sponge surfaces (presumably providing a cleaning service to the host). *Notocrangon antarcticus* was often found buried ventrally in the mud in stations with poor epifaunal coverage and mostly next to holothurians and sponges. *Nematocarcinus lanceopes* seems to prefer diverse types of substrates and epifaunal coverage and was often found either stalking or standing on its legs, which are comparatively longer than those of the other species (Figure 4.10). While all the shrimp species can be associated with other benthic fauna, there was no evidence of obligate associations. The shrimps may benefit from 3-D habitat structure and/or food provided by other epifauna.

Chorismus antarcticus was abundant near the Cape Adare where Weddell seals and Adelie penguins are also present. Shrimps are known to be exposed to higher predation rates in inshore and shallower waters than in the deep-sea (King & Butler, 1985). Green and Burton (1987) observed seals feeding on prawns in shallower water, but feeding on more fish in deeper waters. Weddell seals and emperor penguins prey on shrimps within a specific size range (Arntz

& Gorny, 1991). *Chorismus antarcticus* and *N. antarcticus* had a 11 % frequency of occurrence in the diets of 36 Weddell seals from McMurdo Sound (Dearborn, 1965). However, *C. antarcticus* and *N. antarcticus* constituted 21% by weight in 16 Weddell seals from Davis (Vestfold Hills) and a high frequency (> 70%) of occurrence in 845 Weddell Seal faeces from the same site (Green & Burton, 1987). These authors' studies did not report the presence of any shrimps in 5 seals from Mawson and 20 seals from McMurdo Sound area of the Ross Sea. Shrimps were not observed in the diet of emperor penguins or Weddell seals from the Weddell Sea (Plötz *et al.*, 1991). Other known occurrences of shrimps in the diet of predators includes, Antarctic cod *Notothenia nudifrons* (5 - 20%), dragon fish *Parachaenichthys georgianus* (10 - 40%) and small eye moray cod *Muraenolepis microps* (10 - 20%) from South Georgia Island (Targett, 1981); and in *Trematomus* spp. stomachs (up to 20%) from the south-eastern Weddell Sea (Schwarzbach, 1988) and Terra Nova Bay (La Mesa *et al.*, 2004). Le Mesa (1997; 2004) recorded *C. antarcticus* and *N. antarcticus* as the most common pray of *Trematomus* spp. in the Terra Nova Bay area indicating their importance in the shallow continental shelf marine food chain around the Antarctic. Understanding the impact of predation on shrimps at deeper depths remains unknown for the Antarctic until a larger investigation of potential predators is conducted.

4.4.5 Isotope Analysis

Isotopic measurements to study trophic structure are based on the method of documenting a regular and consistent pattern of isotopic enrichment with increasing trophic level. At high latitudes, such as the Antarctic, phytoplankton $\delta^{15}N$ exhibit rather low values of -1‰ to 3‰ by nitrogen isotope fractionation under high nitrate concentrations with $\delta^{15}N$ of ca. 6‰, whereas nitrate $\delta^{15}N$ increases with decreasing utilization of nitrate by phytoplankton (Sigman & Casciotti, 2001). The wide range of $\delta^{15}N$ values (6.9-10.4‰) exhibited by shrimps in the Ross Sea confirmed the variety of feeding strategies that this group can adopt. High abundance of particulate organic matter and zooplankton, such as copepods and ostracods in the shallower areas of the Ross Sea are known to support the development *N. antarcticus and C. antarcticus* larvae (Fabiano *et al.*, 1993; Hecq *et al.*, 1993; Zunini Sertorio *et al.*, 1994). Ross Sea zooplankton biomass is dominated by smaller zooplankton, such as copepods, rather than the larger krill (Deibel & Daly, 2007), which have more abundance in ice-free areas compared to ice covered zones (Guglielmo *et al.*, 1987; Hecq *et al.*, 1993). Based on the $\delta^{15}N$ value range we assume the adult carnivorous shrimps feed on the smaller zooplankton in shallower waters. No significant relationship between $\delta^{15}N$ and $\delta^{13}C$ value ($R^2=0.091$, $P=0.34$) among the shrimp species were observed, suggesting shrimps depend on multiple food sources (Polunin *et al.*, 2001;

Cartes *et al.*, 2007). Correlation between depth and δ^{13}C (R=0.001, 0.02; P=0.94, 0.71) was not significant for both species, indicating no relationship with shrimps and fresher food source at any depth.

Adult *N. antarcticus* in our study exhibited very high δ^{15}N value indicating a Trophic Level of 4.1, which placed it in the same trophic level as one of the key predatory species, Antarctic silverfish, in the Ross Sea ecosystem. This is not surprising as crangonoid shrimps (*N. antatrcticus*) are known to exhibit high δ^{15}N values among decapods. This has been observed in the case of *Glyphocrangon sculpta*, a species yielding δ^{15}N value of 13-13.2‰ at 2500m depth in NE Atlantic (Van Dover *et al.*, 1992) and *Glyphocrangon sp.,* which showed the highest δ^{15}N value among decapods on the Porcupine Abyssal plain (Iken *et al.*, 2001). The high degree of complexity in the benthic component of deep–sea food chains may explain why the highest δ^{15}N value among deep-sea decapods are always found amongst the specialized benthos feeds like crangonids. The δ^{15}N values of *N. lanceopes* was 6.9 indicating a Trophic Level of 3.0, implying an omnivore, scavenger and detrital feeding behaviour. Other species in a similar trophic level include ophiuroids (*Ophionotus victoriae) which* have been observed frequently in our photographic transects. The shrimp diet could be the same as the ophiuroids which consisted of euphasids, polychaetes, sponges, nematodes, mysids, isopods, bryozoans, echinoids and detritus (Norkko *et al.*, 2007). At highly productive locations like the Ross Sea, the majority of primary production is not consumed by herbivores, but is returned to the ecosystem as detritus and consumed by detrivores (Polis & Strong, 1996; Moore *et al.*, 2004). Furthermore, the benthic food web in Antarctica seems to be sustained with persistent availability of a detritus ‘food bank’ in the sediments. Thus, shrimps may play an important role in the benthic food web by using their carnivorous, omnivorous and scavenging feeding behaviour to utilize food resources that may temporally and spatially constrained and unpredicted.

4.5 References

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Table 4.1. Shrimps captured and photographed by different gears in the Ross Sea. Swept area indicates the total area covered by gear transect in each of the station. Abundance of shrimps are given as n.1000m^{-2}. Gear type: FT = Fish Trawl, BT= Beam Trawl, DTIS = Deep Towed Imaging System, HBS=Hyperbenthic sled, EBS=Epibenthic sled.

Region	**Gear**	**Site**	**Station**	**Co-ordinates (average)**	**Swept area (m^2)**	**Abundance**			**Total Abundance**
						C. antarcticus	*N. antarcticus*	*N. lanceopes*	
Shelf	FT	C1	26	-74.58, 170.24	37040	0.05			0.05
	BT	C1	31	-74.59, 170.27	1111.20	9.90	7.20		17.10
	DTIS	C2	40	-74.73, 167.01	679.73		50.02		50.02
	FT	C2	41	-74.72, 167.01	45837		0.89		0.89
	HBS	C2	43	-74.77, 167.05	740.80		1.35		1.35
	BT	C2	46	-74.73, 167.06	1185.28		3.37		3.37
	DTIS	C3	55	-75.63, 169.78	2262.78	1.77	35.80		37.56
	FT	C3	56	-75.63, 169.85	45837		0.41		0.41
	BT	C3	61	-75.62, 169.80	888.96		10.12		10.12
	DTIS	C4	93	-76.19, 176.29	2322.47	17.65	18.95		36.60
	FT	C4	94	-76.19, 176.29	50930	0.02	0.65		0.67
	BT	C4	100	-76.20, 176.24	888.96	2.25	12.37		14.62
	DTIS	C5	80	-76.60, 176.77	2475.93	10.50	26.25		36.75
	FT	C5	81	-76.59, 176.82	49078		0.35		0.35
	HBS	C5	82	-76.59, 176.88	592.64		13.50		13.50
	BT	C5	84	-76.60, 176.80	814.88		8.59		8.59
	FT	D2	22	-74.11, 170.79	24076		0.04		0.04
	DTIS	D3	65	-75.62, 167.32	2494.54	1.60	2.00		3.61
	FT	D3	66	-75.62, 167.32	46300		0.22		0.22
	DTIS	D34	76	-76.83, 179.94	3123.63	0.32	0.96		1.28
	FT	D34	77	-76.83, 179.95	40281	0.02	0.17		0.20
	DTIS	D4	69	-76.79, 167.87	2111.41		10.89		10.89
	FT	D4	70	-76.77, 167.83	46300		0.24		0.24
Slope	DTIS	C17	130	-72.08, 175.55	2756.22			58.05	58.05
	FT	C17	133	-72.09, 175.57	28243			1.77	1.77
	BT	C17	139	-72.08, 175.55	1555.68			3.21	3.21
	DTIS	C18	169	-71.38, 174.74	1317.48			47.82	47.82
	BT	C18	171	-71.38, 174.73	1777.92			2.81	2.81
	DTIS	C26	150	-72.02, 173.18	1417.50		0.71		0.71
	DTIS	D27	105	-73.20, 178.63	1040.37			1.92	1.92
	FT	D27	106	-73.24, 178.72	47226		0.04		0.04
	DTIS	D28	108	-72.82, 177.14	1623.96			69.58	69.58
	FT	D28	109	-72.80, 177.19	45374			0.44	0.44
	DTIS	D45	166	-71.84, 174.00	2460.37			40.24	40.24
	FT	D45	167	-71.85, 174.03	116213			4.12	4.12

Seamount	DTIS	C24	276	-67.02, 171.06	2749.15	4.36	4.36
	DTIS	C24	278	-67.01, 171.07	2763.67	2.53	2.53
	DTIS	C24	280	-67.16, 171.16	3812.37	7.87	7.87
	DTIS	C24	294	-66.91, 171.01	4627.04	1.08	1.08
	DTIS	C24	301	-67.13, 171.15	2560.19	2.73	2.73
	DTIS	C24	304	-67.17, 171.17	3163.78	2.84	2.84
	EBS	C24	302	-67.13, 171.14	592.64	11.81	11.81
	EBS	C24	309	-67.12, 170.89	444.48	11.25	11.25
	DTIS	C31	202	-68.07, 180.67	4069.68	8.35	8.35
	DTIS	C31	205	-68.11, 180.75	3830.62	14.10	14.10
	DTIS	C31	207	-68.14, 180.79	2216.86	20.30	20.30
	EBS	C31	201	-68.09, -179.26	648.20	3.09	3.09
	EBS	C31	203	-68.08, -179.29	629.68	1.59	1.59
	EBS	C31	206	-68.12, -179.24	703.76	14.21	14.21
	EBS	C31	210	-68.11, -179.31	1296.40	2.31	2.31
	FT	C31	211	-68.10, -179.23	54634	1.19	1.19
	DTIS	C32	219	-67.78, 180.22	3909.43	2.05	2.05
	EBS	C32	218	-67.72, -179.71	722.28	2.77	2.77
	EBS	C32	220	-67.78, -179.76	814.88	2.45	2.45
	EBS	C32	224	-67.73, -179.63	722.28	1.38	1.38
	DTIS	C34	244	-67.38, 180.15	1538.94	145.55	145.55
	DTIS	C34	250	-67.37, 179.95	2479.96	15.73	15.73
	DTIS	C34	255	-67.34, 179.93	1018.28	41.25	41.25
	EBS	C34	245	-67.38, -179.84	574.12	12.19	12.19
	EBS	C34	251	-67.38, 179.98	555.60	5.40	5.40
	EBS	C34	256	-67.34, -179.93	592.64	1.69	1.69
	DTIS	C35	285	-66.74, 171.17	2099.72	3.33	3.33
Abyssal	DTIS	C30	186	-68.52, 181.60	702.80	7.11	7.11
	DTIS	C33	228	-67.61, 181.16	2724.77	1.10	1.10
	EBS	C33	237	-67.40, -179.80	351.88	11.37	11.37

Table 4.2. Comparison of mean and maximum densities of shrimps obtains by different gears. This study: Trawl and DTIS; (Gutt *et al.*, 1991): Underwater photography; (Arntz & Gorny, 1991): bottom trawl; (Voß, 1988): Agassiz trawl. The densities refer to the samples area sizes and to one square meter for comparison.

	C. antarcticus	***N. antarcticus***	***N. lanceopes***
This study Density for total sampled area mean n.1000m^{-2}| n.m^{-2}	0.68 | 0.001	3.16 | 0.003	9.12| 0.009
This study Density per station (trawl) maximum n.1000m^{-2}| n.m^{-2}	9.90 | 0.010	13.50 | 0.014	14.21 | 0.014
This study Density per station (DTIS) maximum n.1000m^{-2}| n.m^{-2}	17.65 | 0.015	50 | 0.050	145.55 | 0.146
Gutt *et.al.* (1991) Density for total sampled area mean n.1000m^{-2}| n.m^{-2}	11 | 0.011	64 | 0.064	38 | 0.038
Gutt *et.al.* (1991) Density per station maximum n.100m^{-2}| n.m^{-2}	40 | 0.400	73 | 0.730	135 | 1.350
Arntz & Gorny (1991) Density for total sampled area mean n.100 000m^{-2}| n.m^{-2}	300 | 0.003	1200 | 0.012	2000 | 0.020
Arntz & Gorny (1991) Density per trawl catch maximum n.10 000m^{-2}| n.m^{-2}	80 | 0.008	330 | 0.330	350 | 0.035
Voß (1988) Density for total sampled area mean n.10 000m^{-2}| n.m^{-2}	20 | 0.002	110 | 0.011	-
Voß (1988) Density per trawl catch maximum n.1000m^{-2}| n.m^{-2}	≥ 10 | ≥ 0.01	< 100 | < 0.1	36 | 0.004

Table 4.3. Summary of SIMPER analysis between fauna assemblages found in different Ross Sea regions (Shelf, Slope, Seamount: Scott Seamount, SeamountA: Admiralty Seamount) and next to shrimps (three studied species), showing the species most contributing to similarities within region and dissimilarities between them. Stars note contribution of each species: ****, more than 30%;***, between 20-30%;**, between 10 - 20%; *, less than 10%. Full results can be found in Appendix 3 and 4.

Species	**Region**				**Shrimp**		
	Shelf	Slope	Seamount	Seamount A	*Chorismus antarcticus*	*Notocrangon antarcticus*	*Nematocarcinus lanceopes*
Sponge	**	****	****	****	**	**	****
Ophiuroid	***	***	*	****	****	****	**
Bryozoan	***		*		****	****	*
Worms	**				**	**	
Anemone	*		****	*			**
Seleractinia		*	**				*
Brachiopod		*		**			
Asteroid		**					
Mollusc		*					
Holothurian	*						

Table 4.4. Calculated trophic level of shrimp species in the Ross Sea from the stable isotope data. Except shrimp all other values were compiled from Bury *et al.* (2008), Pinkerton *et al.* (2011) and Norkko *et al.* (2007). Code: fsh= Fish, mam= Mammal, cep= Cephalopod, ast= Asteroid, cru= Crustacea, cop= Copepod, hol= Holothurian, oph= Ophiuroid, cni= Cnidaria, mol= Mollusc, tun= Tunicate, pom= Particulate organic matter, pp= Primary producer.

Code	**Common name**	**Scientific Name / Group**	**δ^{13}C (mean)**	**δ^{15}N (mean)**	**Trophic Level**
fsh	Antarctic Tooth fish	*Dissostichus mawsoni*	-24.6	13.6	5.1
mam	Killer Whale	*Orchinus orca*	-23.7	13.3	5.0
mam	Weddell Seal	*Leptonychotes weddellii*	-22.5	13.1	5.0
mam	Leopard Seal	*Hydrurga leptonyx*	-21.8	12.3	4.7
cep	Colossal Squid	*Mesonychoteuthis hamiltoni*	-23.0	11.5	4.5
cru	Shrimp	***Notocrangon antarcticus***	-27.5	10.4	4.1
fsh	Antarctic Silverfish	*Pleuragramma antarcticum*	-25.0	10.3	4.1
ast	Starfish	Acanthaster spp.	-19.3	9.9	4.0
cru	Mysid	Antarctomysis spp.	-24.1	9.7	3.9
fsh	Antarctic Icefish	*Chionobathyscus dewitti*	-25.2	9.3	3.8
fsh	Lantern Fish	Myctophids	-24.3	9.1	3.7
cop	Copepods	*Paraeuchaeta antarctica*	-22.5	8.1	3.4
cru	Seed Shrimp	Ostracod	-27.6	7.8	3.3
hol	Sea Cucumbers	Bathyplotes spp.	-25.9	7.8	3.3
oph	Brittle Star	*Ophiosparte gigas*	-16.2	7.1	3.1
cru	Shrimp	***Nematocarcinus lanceopes***	-28.4	6.9	3.0
oph	Brittle Star	*Ophionotus victoriae*	-20.2	6.7	3.0
cni	Jelly Fish	Scyphozoa spp.	-23.4	6.5	2.9
pp	Ice Algae	Macro algae	-20.7	5.6	2.6
cru	Antarctic Krill	*Euphausia superba*	-25.7	4.8	2.4
pom	General Mass	Particulate organic matter	-27.1	4.7	2.3
cru	Amphipods	Amphipod	-28.3	4.4	2.3
mol	Sea slugs	Gymnosomata *spp.*	-24.6	4.4	2.2
tun	Salps	Salpidae spp.	-29.0	3.8	2.1
pp	Algae	Phyllophora antarctica	-23.0	3.3	1.9
pp	Plankton (Surface)	Phytoplankton	-28.2	0.4	1.0

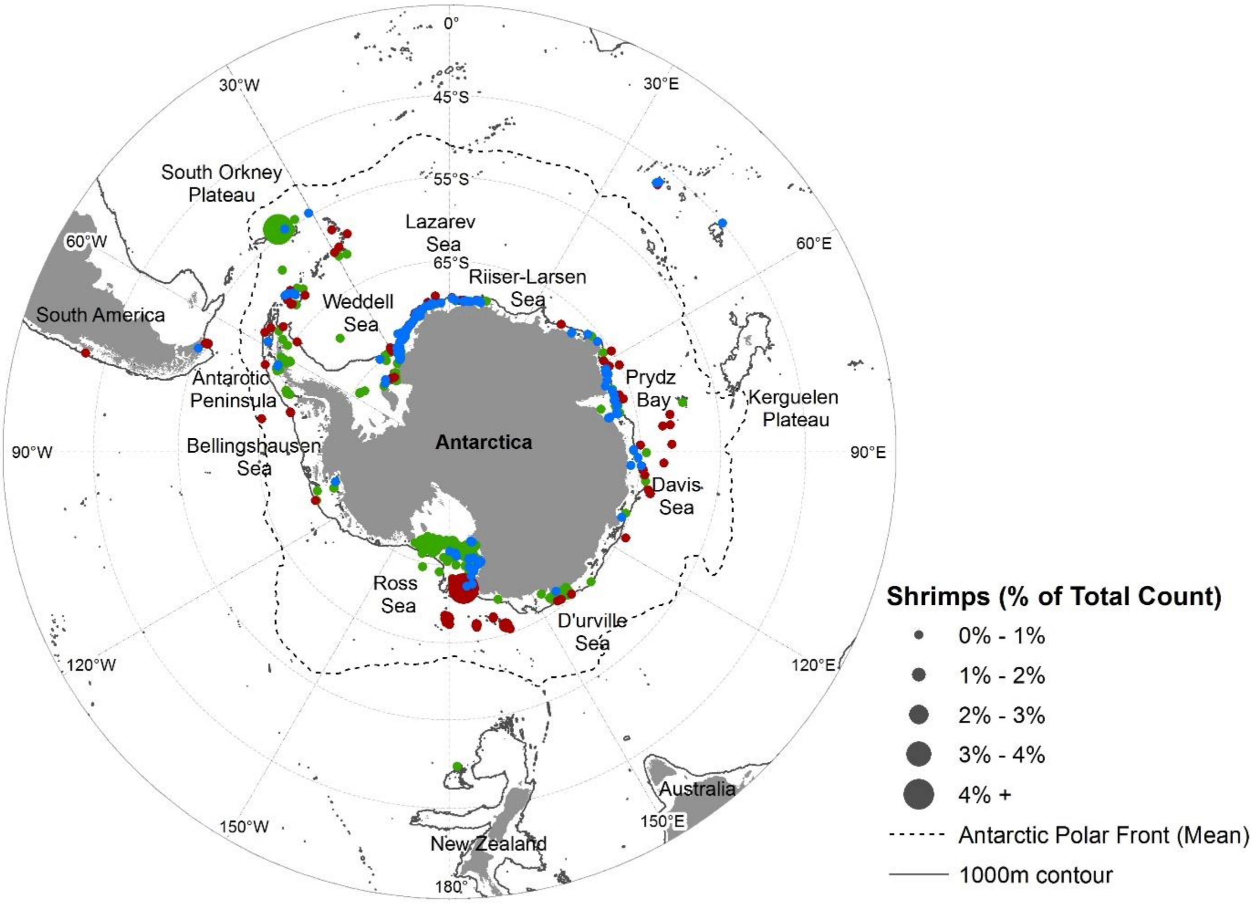

Figure 4.1. Geographic distribution of *Chorismus antarcticus* (blue), *Notocrangon antarcticus* (green) and *Nematocarcinus lanceopes* (red) in the Southern Ocean. Counts in each station presented as the percent of total specimens found in all stations.

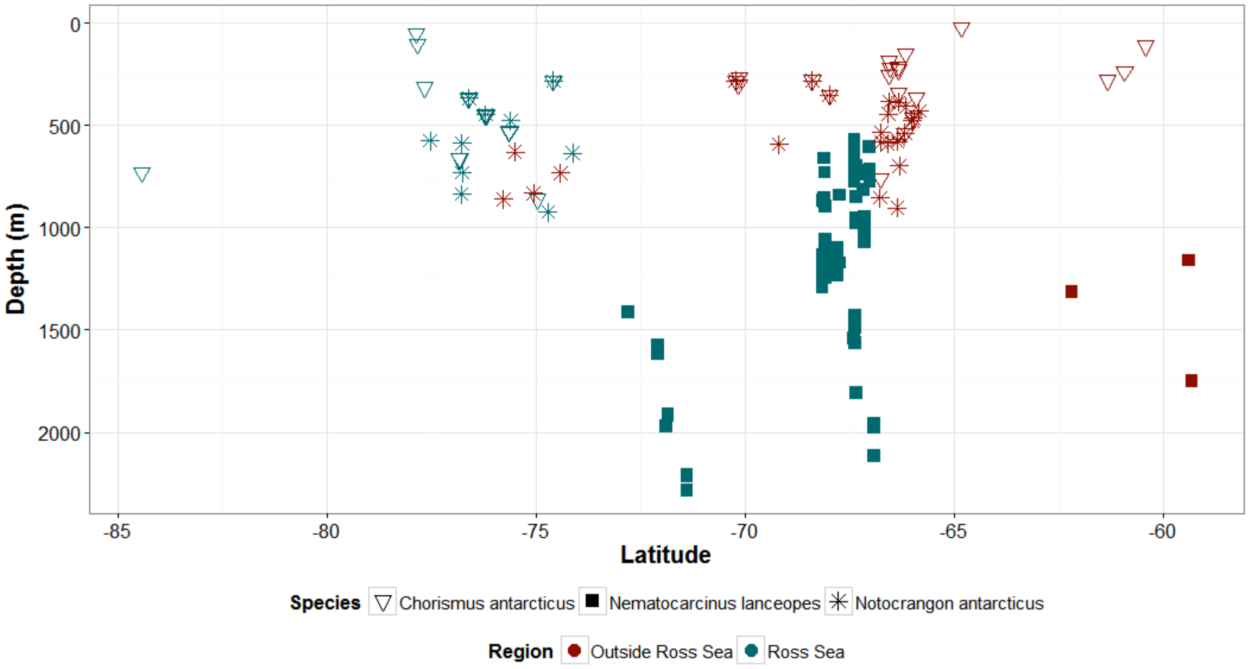

Figure 4.2. Common Antarctic shrimps in the Southern Ocean with reference to latitude, depth and region.

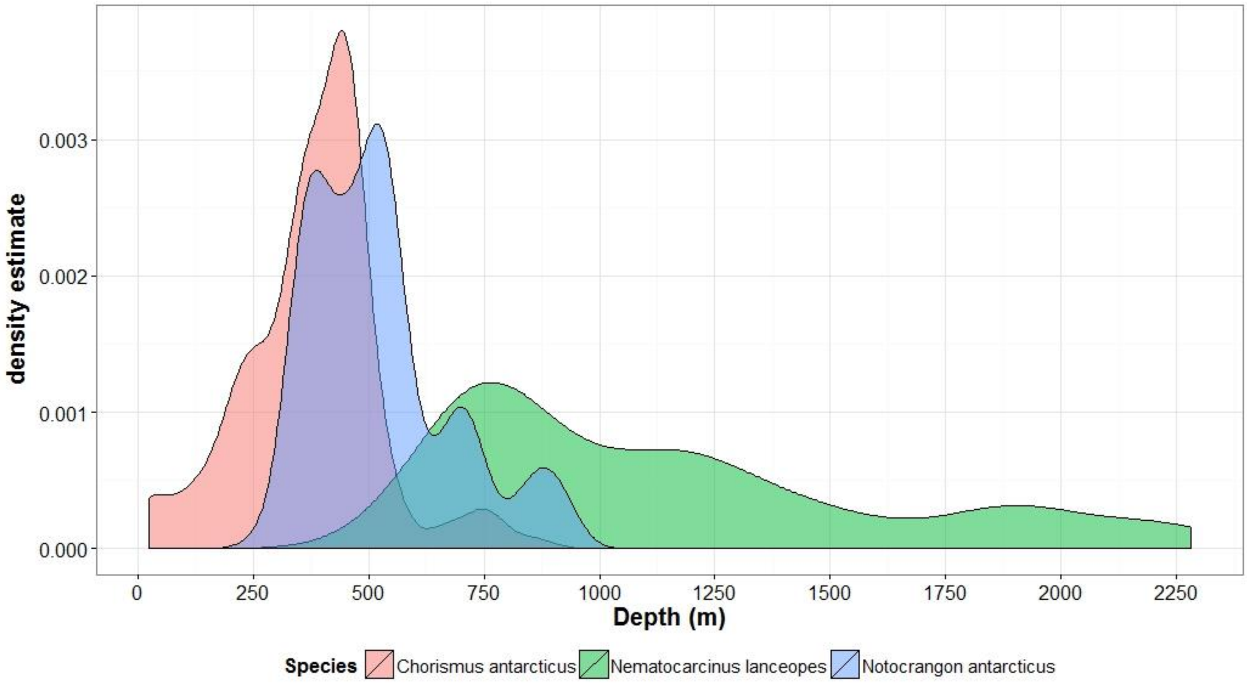

Figure 4.3. Kernel density estimate of common Antarctic shrimps in the Southern ocean with reference to depth.

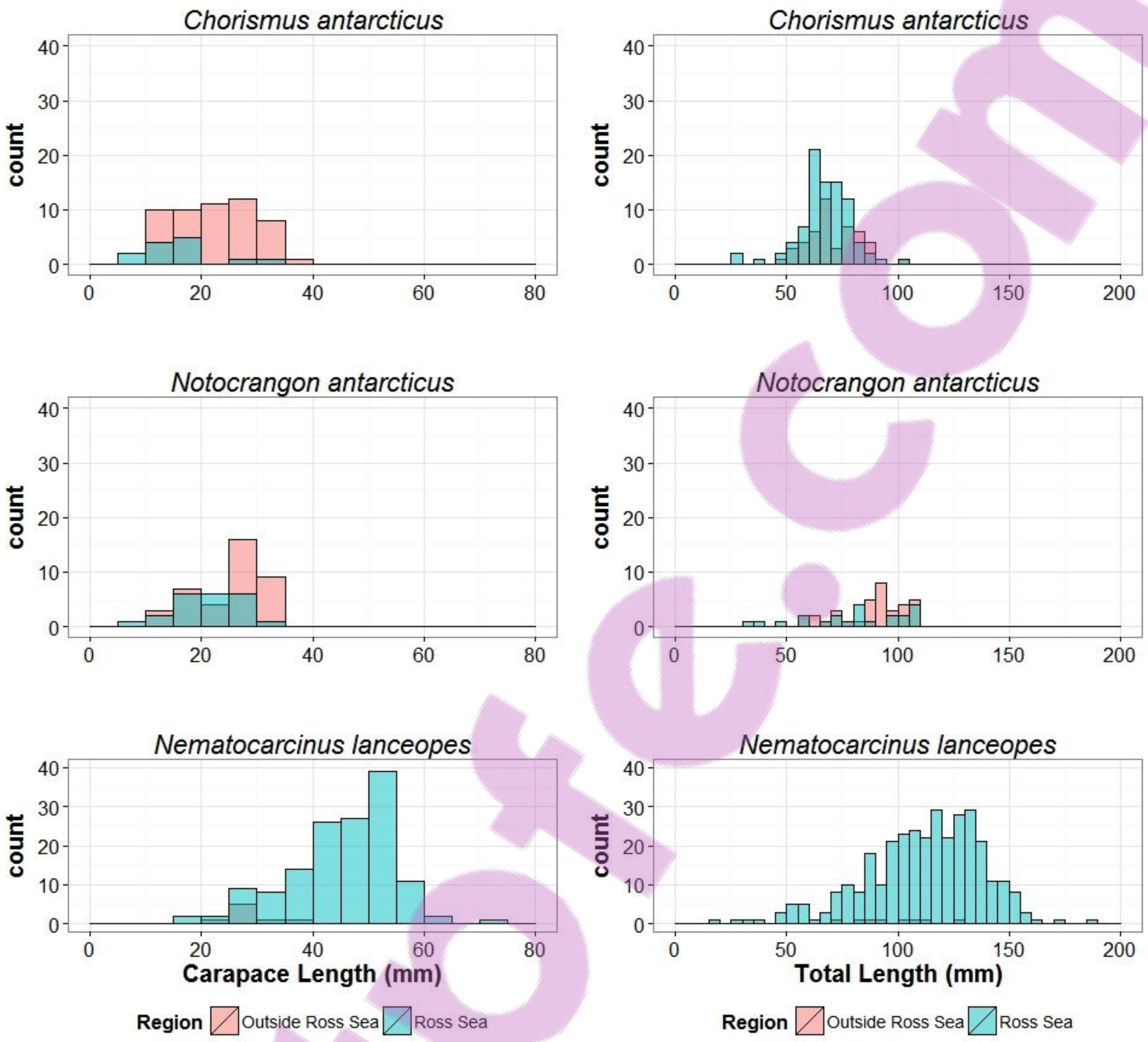

Figure 4.4. Frequency distribution of, carapace length on the left (*C. antarcticus*, n=65; *N. antarcticus*, n=90; *N. lanceopes*, n=149) and Total length on the right (*C. antarcticus*, n=134; *N. antarcticus*, n=274; *N. lanceopes*, n=338).

Figure 4.5. Total length of Antarctic shrimps in relation to depth in different regions of the Southern Ocean.

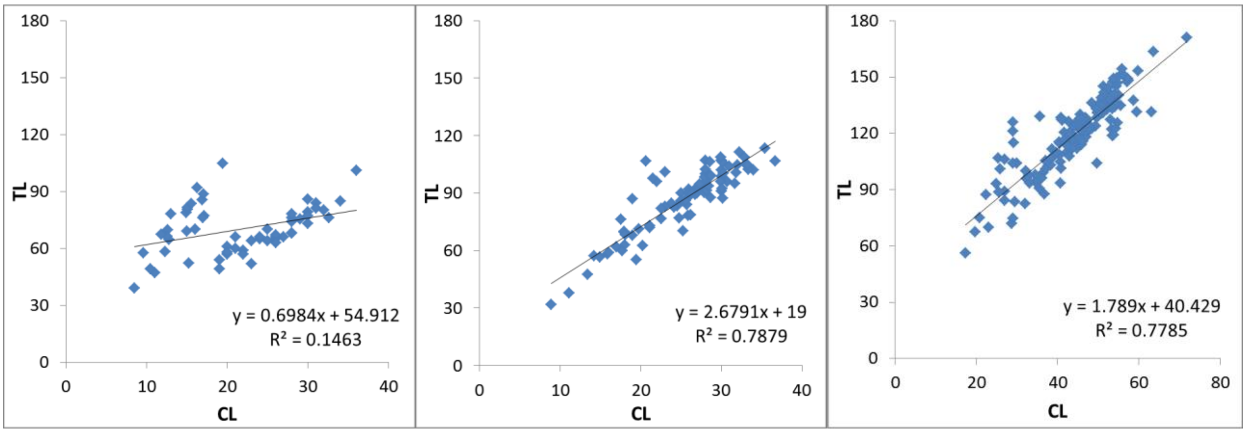

Figure 4.6. Total length (mm) vs. carapace length (mm) in all regions of Southern Ocean for (a) *C. antarcticus* (n=65), (b) *N. antarcticus* (n=90), and (c) *N. lanceopes* (n=149).

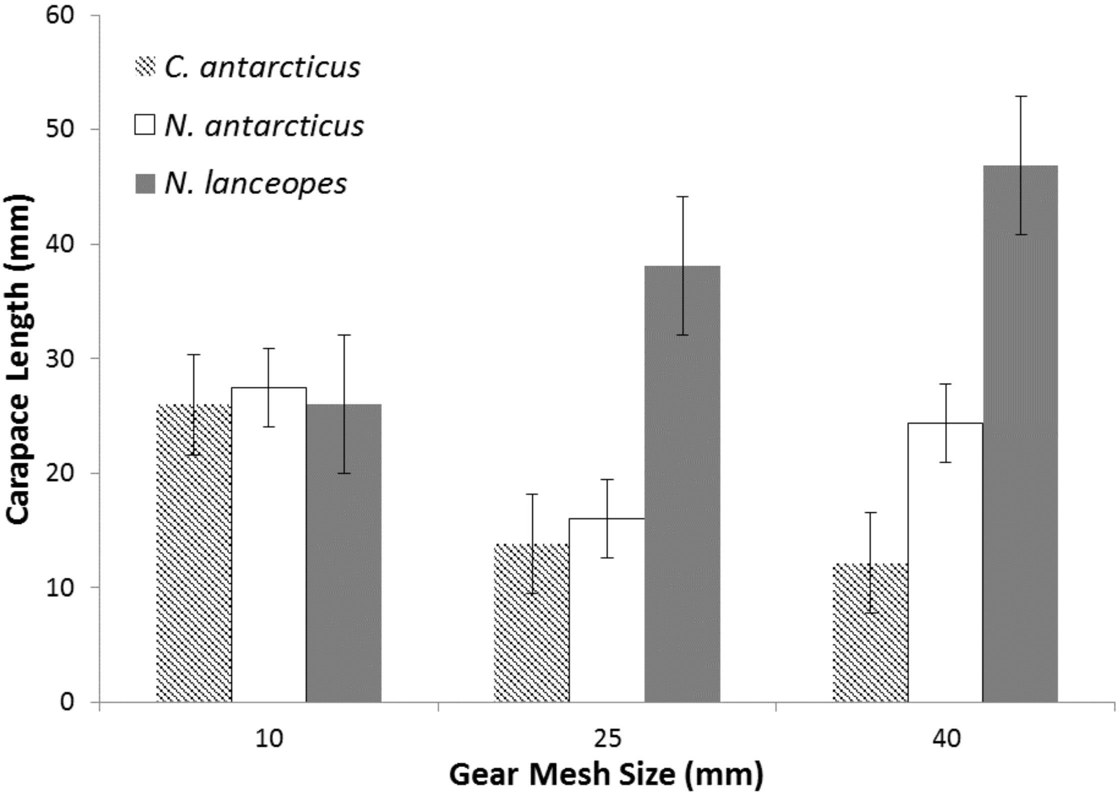

Figure 4.7. Length of Antarctic shrimps captured using various trawling gears [Gear mesh size: Fish trawl (40 mm), Beam trawl & Epibenthic sled (25 mm) and Trawl (10 mm)].

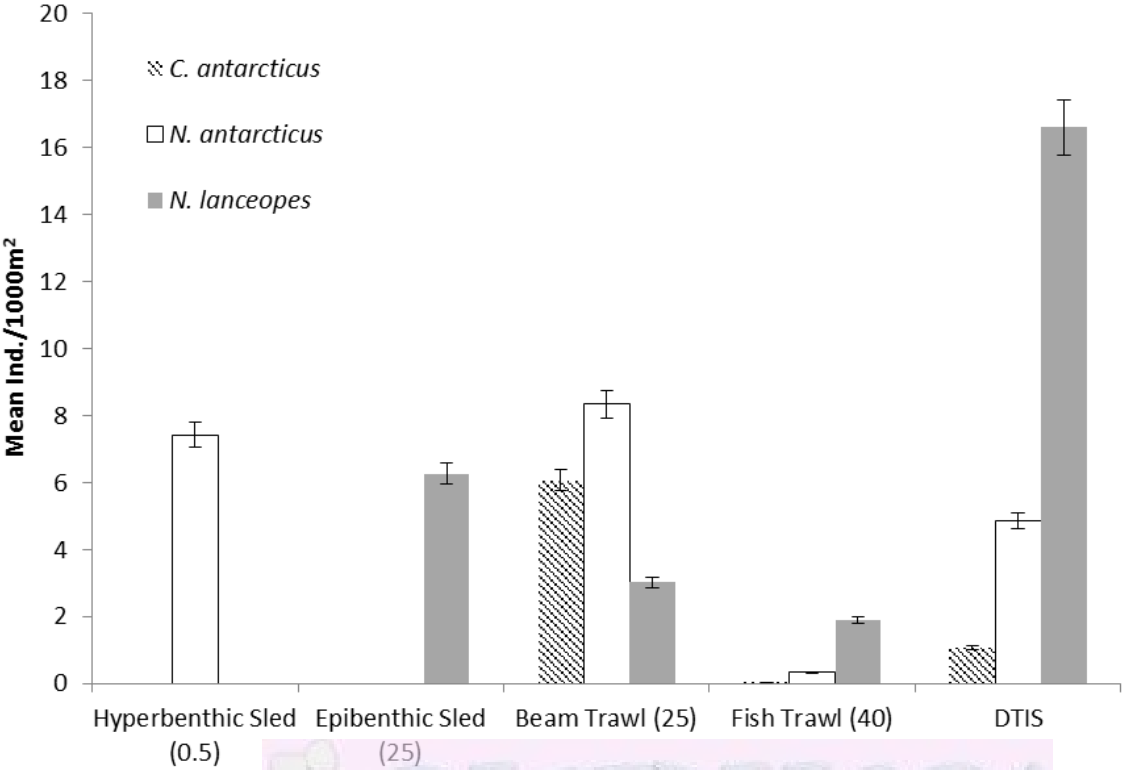

Figure 4.8. Abundance of shrimps captured using different gears.

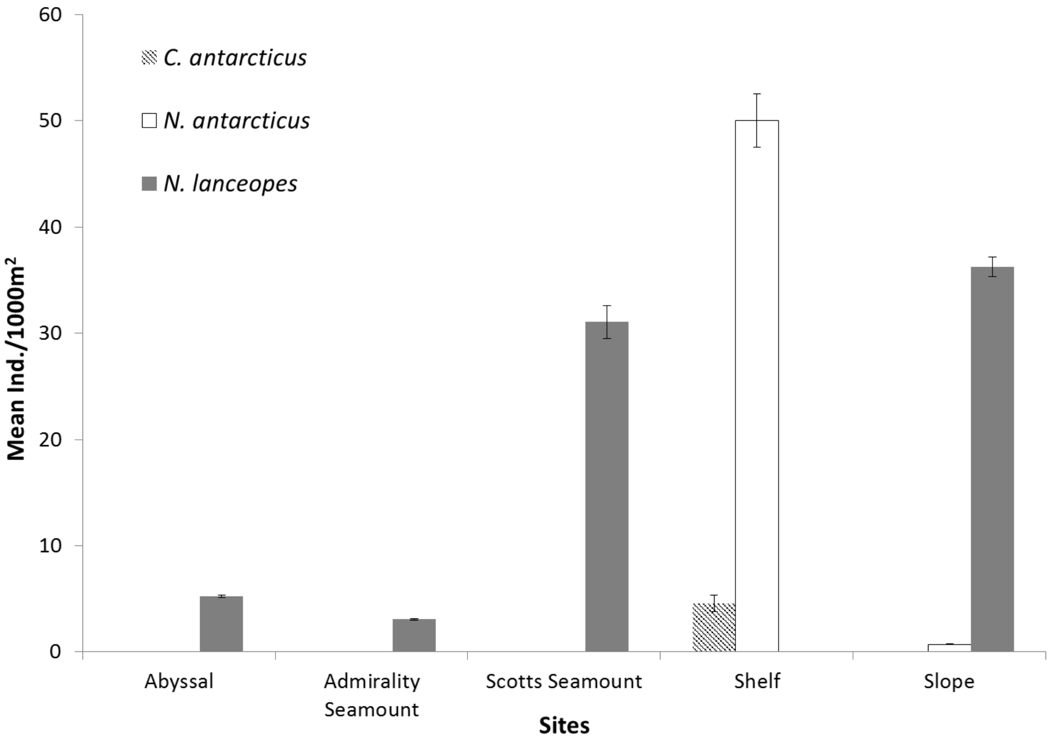

Figure 4.9. Abundance of shrimps in different regions of the Ross Sea.

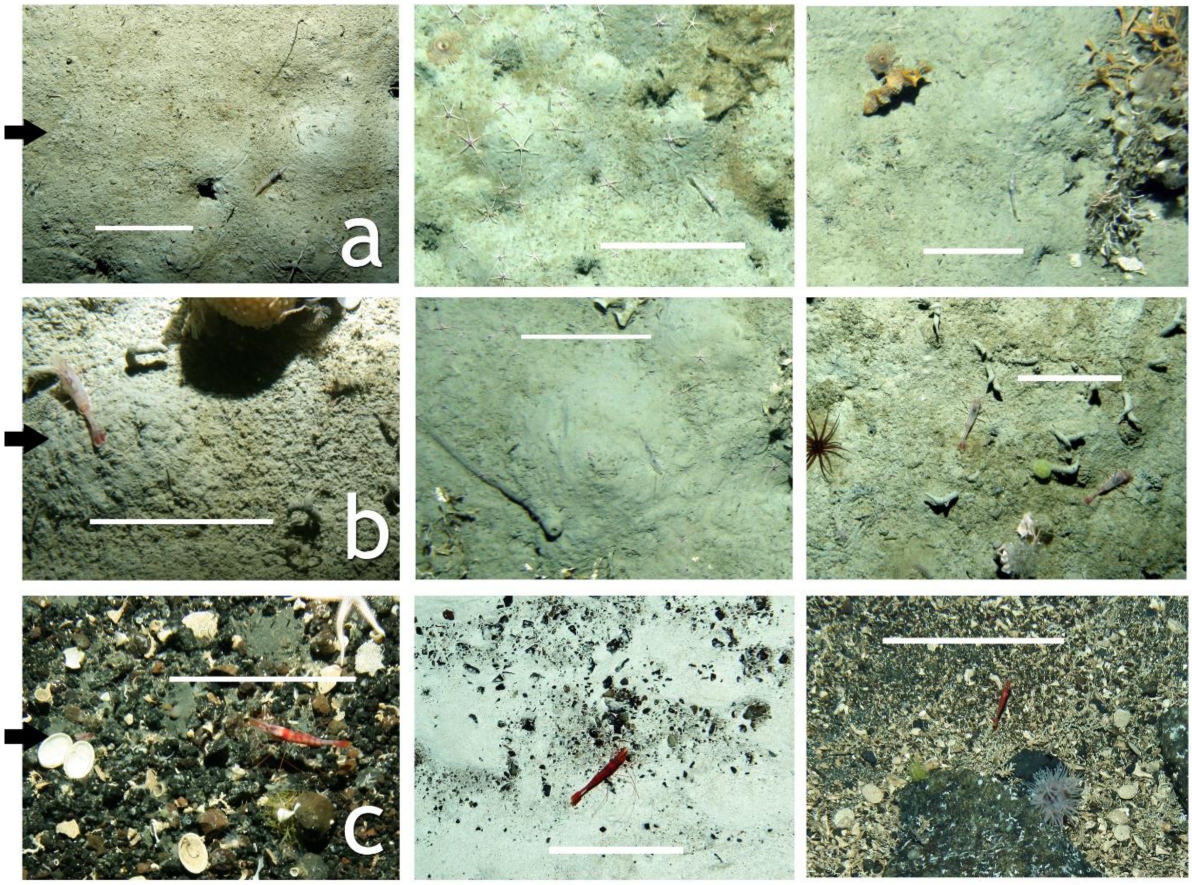

Figure 4.10. Typical habitat of shrimps (a) *C. antarcticus*, (b) *N. antarcticus* and (c) *N. lanceopes* from different stations in the Ross Sea as seen in the photographs. White bar indicates 20 cm at seafloor.

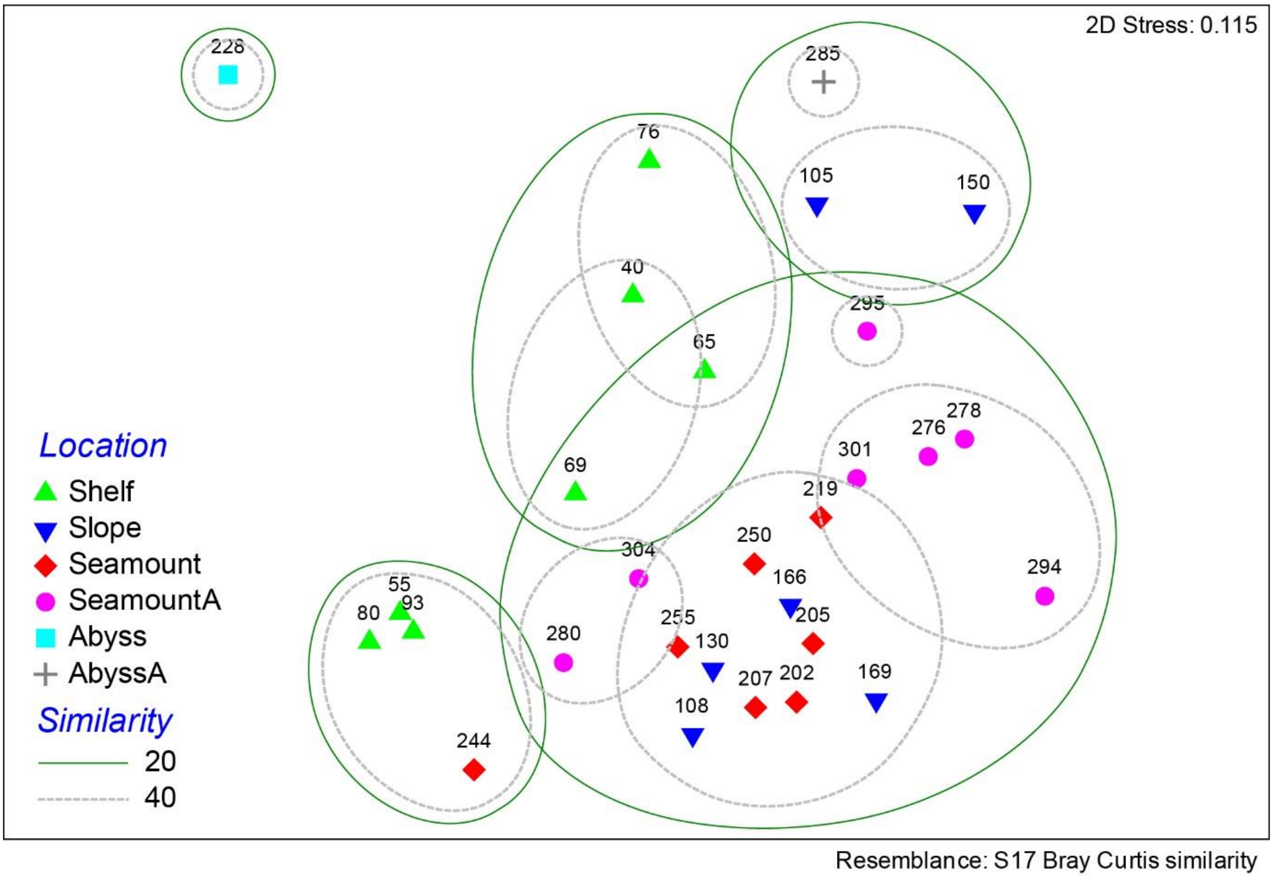

Figure 4.11. Multidimensional scaling of faunal distribution in the stations of video transects where shrimps were present. Different symbol represent location of stations (Shelf: Ross Sea Shelf; Slope: Ross Sea Slope; Seamount: Scott Seamount; SeamountA: Admiralty Seamount; Abyss: Abyssal Plane; AbyssA: Abyssal Plane near Admiralty seamount), and circles represent assemblage grouping determined by cluster analysis. See Table 1 for reference to station numbers.

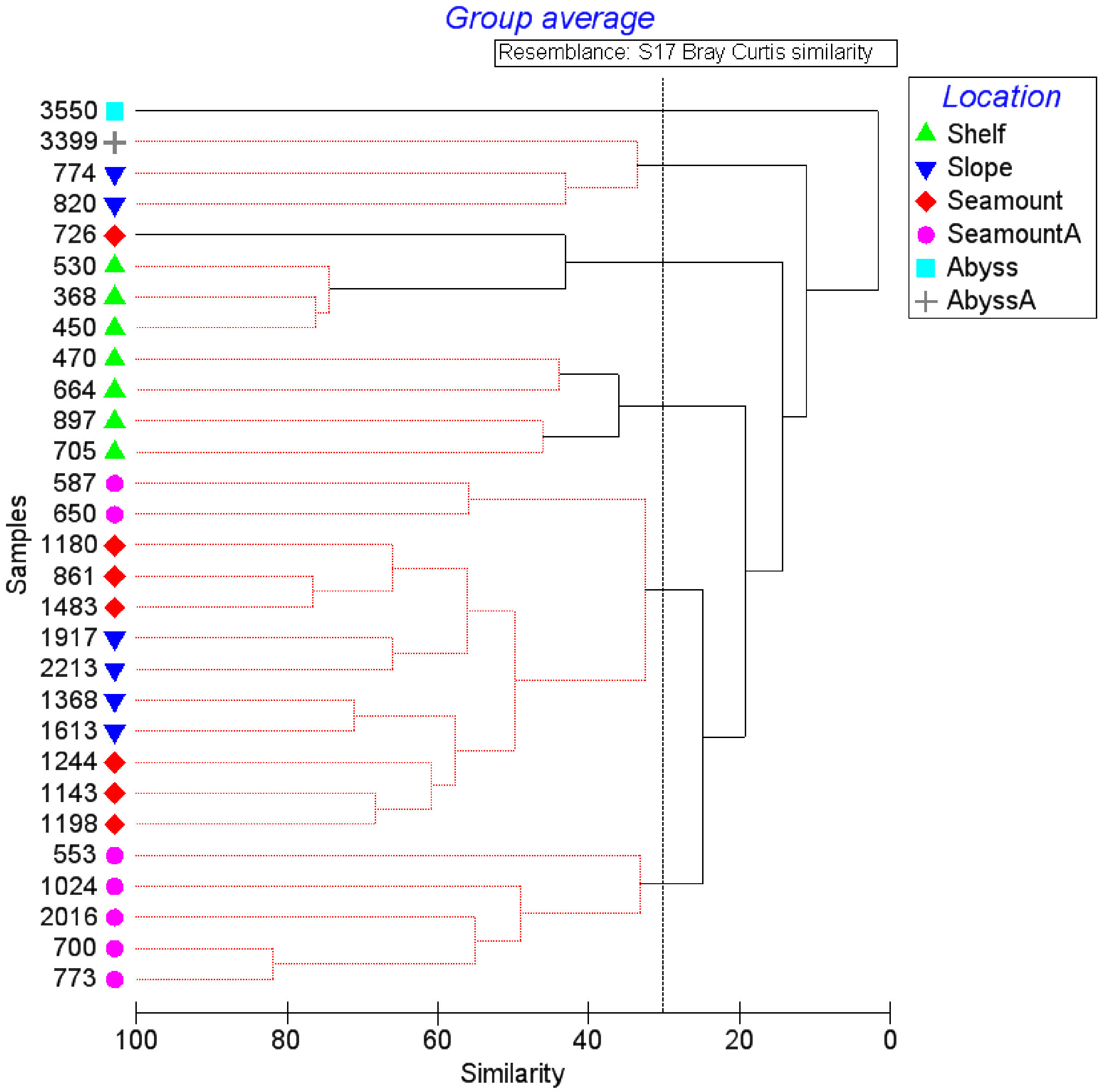

Figure 4.12. Dendogram of faunal distribiutions in video transect stations grouped by depth for different locations I nthe Ross Sea. Different symbol represent location of stations (Shelf: Ross Sea Shelf; Slope: Ross Sea Slope; Seamount: Scott Seamount; SeamountA: Admiralty Seamount; Abyss: Abyssal Plane; AbyssA: Abyssal Plane near Admiralty seamount).

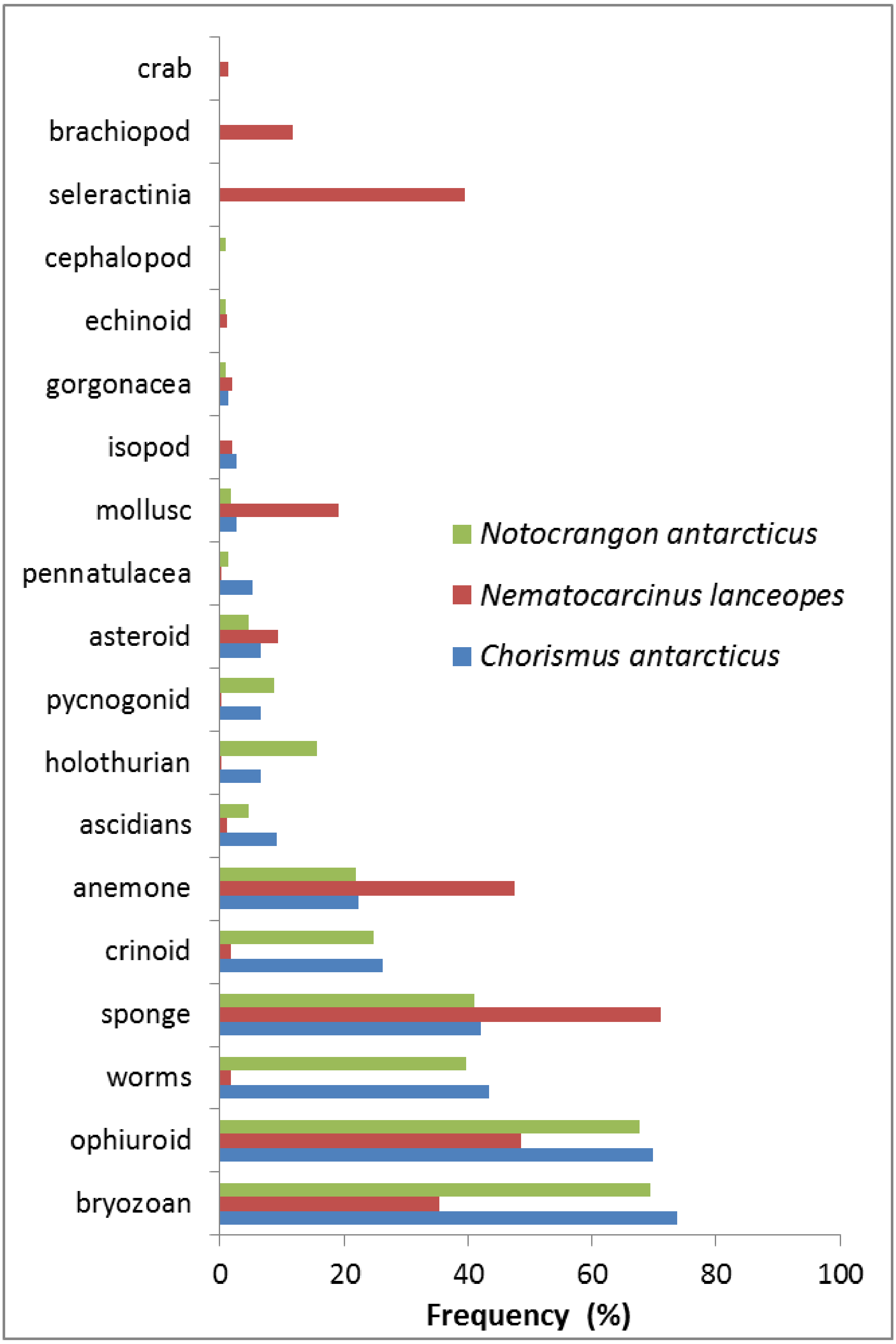

Figure 4.13. Faunal composition of shrimp habitats in the Ross Sea. *C. antarcticus* n= 76, *N. lanceopes* n= 299, *N. antarcticus* n= 219.

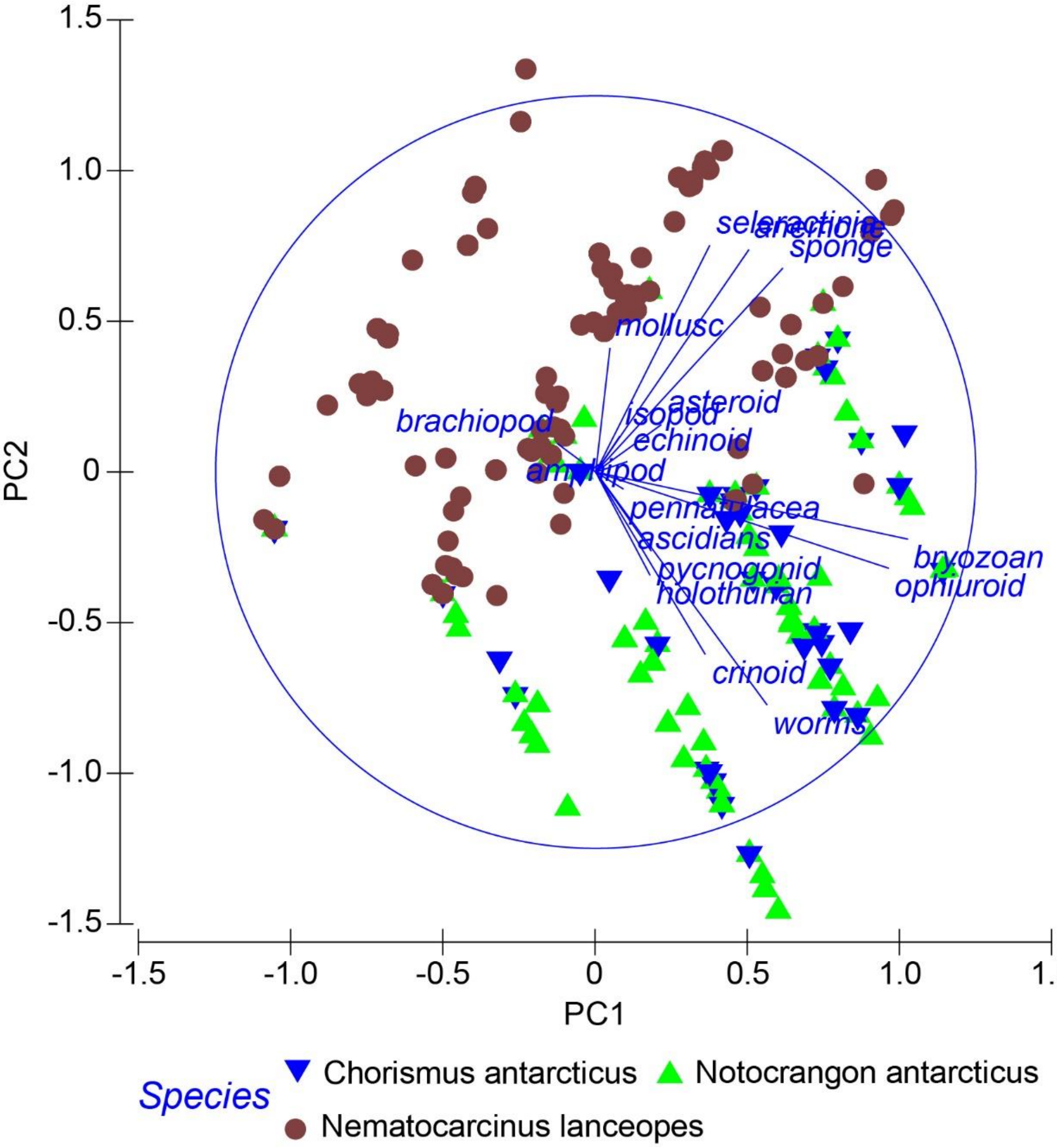

Figure 4.14. Principal component analysis (PCA) of faunal composition in the photographic transects .

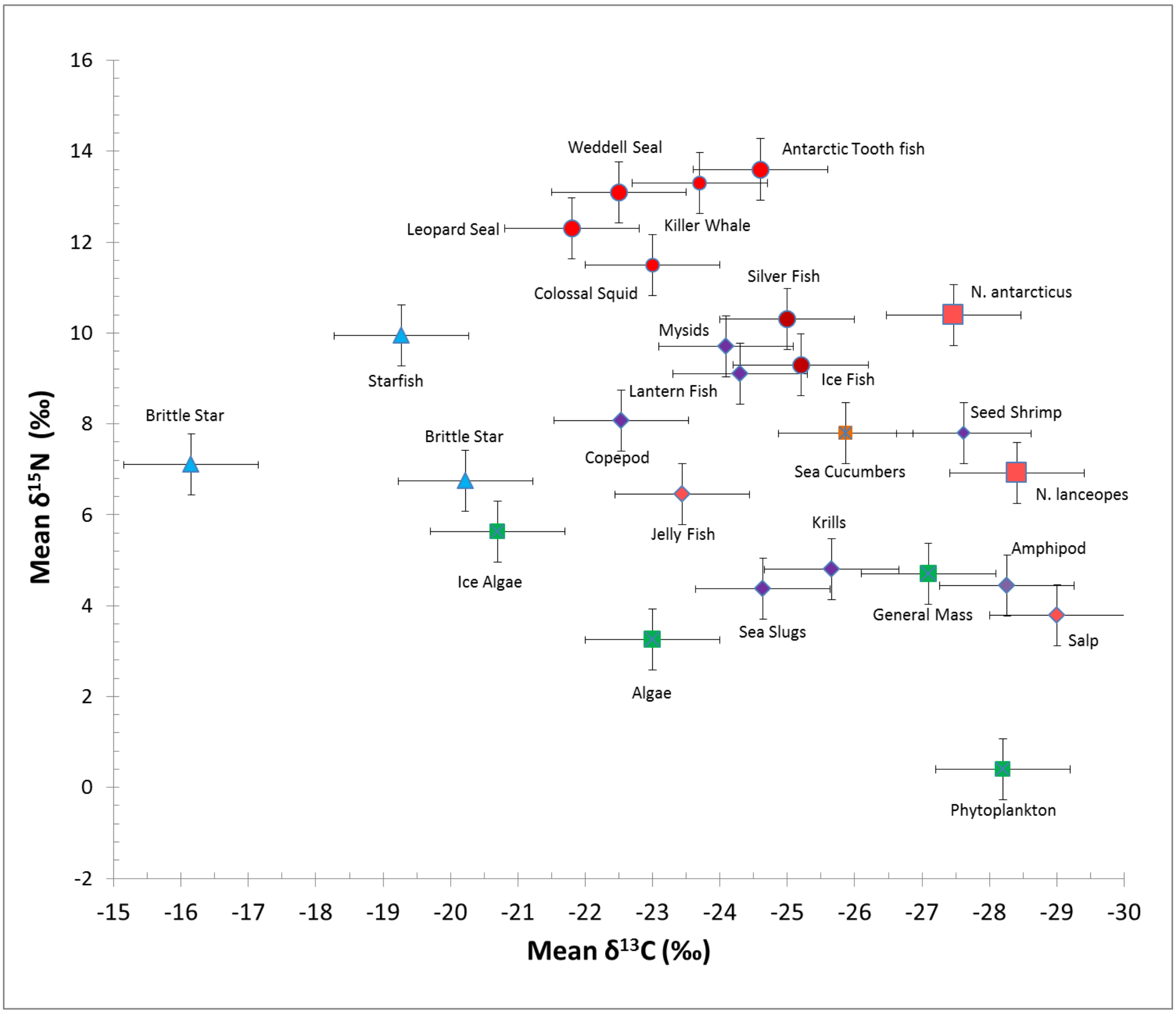

Figure 4.15. Carbon-nitrogen staple isotope values for *Notocrangon antarcticus* and *Nematocarcinus lanceopes* (red squares) and selected other biota from Ross Sea (mean ± S.D.). Except shrimps all other values were compiled from Bury *et al.* (2008), Pinkerton *et al.* (2011) and Norkko *et al.* (2007).

Chapter 5

Global Marine Environment Datasets for environment visualisation and species distribution modelling

Abstract

The Global Marine Environment Datasets (GMED) is a compilation of publicly available climatic, biological and geophysical environmental layers featuring present, past and future environmental conditions. Marine biologists have increasingly utilized geo-spatial technologies with modelling algorithms to predict and visualize species biodiversity at a global scale. Marine environmental datasets available for Species Distribution Modelling (SDM) have different spatial resolutions and are frequently provided in assorted file formats. This makes data assembly one of the most time-consuming parts of any study using multiple environmental layers for biogeography visualization or SDM applications. GMED covers the widest available range of environmental layers from a variety of sources from the surface to the deepest part of the ocean. It has a uniform spatial extent, high-resolution land mask (to eliminate land areas in the marine regions), and high spatial resolution (5 arc-minute, c. 9.2 km near equator). The free online availability of GMED enables rapid map overlay of species of interest (e.g. endangered or invasive) against different environmental conditions of the past, present and the future, and expedites mapping distributions ranges of a species using popular SDM algorithms.

5.1 Introduction

Understanding how the environment determines species distributions is necessary to assess the impacts of threats to habitats, species invasions and climate change (Millennium Ecosystem Assessment, 2005). Because sample data is spatially biased (Phillips *et al.*, 2009), species distribution models (SDM), which predict the occurrence of suitable habitat based on correlations between species' records and environmental parameters (Elith & Leathwick, 2009), are used increasingly to predict distributions in un-sampled areas based on environmental variables. SDM's have a wide variety of uses in biogeography, ecology and conservation biology (Elith & Leathwick, 2009). Successful prediction of species ecological niche preference using SDM algorithms depends on both high-quality species occurrence records and related environmental information (Elith & Leathwick, 2009). Relatively few studies have focused on SDM of marine species in contrast to strong interest in SDM and their wide adoption in terrestrial ecosystem studies (Robinson *et al.*, 2011). Predictions of geographic distributions of marine organisms using SDM include studies on fish (Wiley *et al.*, 2003; Guinotte *et al.*, 2006), coral reefs (Tittensor *et al.*, 2009; Davies & Guinotte, 2011; Bridge & Guinotte, 2013; Tong *et al.*, 2013; Rinne *et al.*, 2014), jellyfish (Bentlage *et al.*, 2013), benthic invertebrates (Compton *et al.*, 2010; Reiss *et al.*, 2011; Dambach *et al.*, 2012; Compton *et al.*, 2013; Basher *et al.*, 2014), and algae or seaweeds (Graham *et al.*, 2007; Verbruggen *et al.*, 2009; Tyberghein *et al.*, 2012; Downie *et al.*, 2013). Issues that restricted the application of SDM in the marine compared with the terrestrial environment are limited availability of high quality marine species observation records (Kaschner *et al.*, 2006), extensive spatio-thermal variability characterizing the ocean environment (Valavanis *et al.*, 2008; Franklin & Miller, 2009), and complexities involved in processing environmental data for SDM applications (Tyberghein *et al.*, 2012).

Marine environmental data have been derived from combinations of observations and modelled values of ocean surface (e.g. current, wave height), water column (e.g. temperature, salinity, nutrients), sea floor (e.g. depth, slope, distance to shore)(Valavanis *et al.*, 2008), *in-situ* observations (e.g. survey cruise, AUV and Argo floats), and remotely sensed satellites data (e.g. chlorophyll-a, surface temperature etc.)(Costello, 2009). Numerical oceanographic process or circulation models are another source of environmental data for SDM applications (Robinson *et al.*, 2011). Because available marine environmental datasets occur in assorted file formats and differ in their accuracy, and temporal and spatial resolution, it is common for a large portion of time in SDM studies to be spent on assembling compatible environmental data (Tyberghein *et al.*, 2012). Among the commonly available marine environmental datasets, sea surface temperature observations are relatively consistent, accurate, well spatially resolved and have a long global time series. Chlorophyll-a concentration has similarly good consistency apart from data gaps in the polar-regions. In contrast, most of the deep-sea and less well-sampled variables (e.g. dissolved oxygen and nutrient concentrations), are patchy in their spatial distribution and cannot be measured from satellite imagery. Generally, data accuracy will be poorer for more remote areas, which have less primary data. Hence, continuous global layers for such variables are predicted from ocean circulation models and by extrapolation of in situ sample data. Ocean circulation models generally have relatively coarse resolution, primarily because of computational capacity, and thus are often inadequate to model environmental conditions on finer time and spatial scales (Redfern *et al.*, 2006). However, when available at finer resolution, ocean circulation models can simulate realistic features and dynamics, such as variability in frontal and eddy structures and its effect on biogeochemical fields (McGillicuddy *et al.*, 2003).

WorldClim (http://www.worldclim.org), a global terrestrial climate environment dataset is a freely available and widely accessible online repository that has served the need for terrestrial SDM researchers for the last few years. Initiatives to establish equivalent marine environment data repositories include (1) the KGS mapper (Hexacoral project, Fautin & Buddemeier, 2011), (2) Aquamaps (Kaschner *et al.*, 2008) (3) the human impact on marine ecosystems layers (Halpern *et al.*, 2008), (4) Bio-Oracle (Tyberghein *et al.*, 2012), and (5) MARSPEC: Ocean climate layers for marine spatial ecology (Sbrocco & Barber, 2013). However, except Bio-Oracle other datasets have not been widely adopted due to the complexity of processing the data for modelling applications. Although, Bio-Oracle has the most number of independent variables among the datasets but it lacked bathymetry and other ecologically significant layers (e.g. slope, deep sea: below surface layers) (Table 5.4). The accuracy and resolution of various ocean circulation models and survey data are continually increasing, particularly through assimilation of observations from global ocean observing programmes (e.g. the Global Ocean Observing System, http://www.ioc-goos.org; Marine explore, http://www.marinexplore.com) and integration of oceanographic data into regional portals (e.g. NODC http://www.nodc.noaa.gov, BODC, http://www.bodc.ac.uk). Millions of marine species observation records are available from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org) and Ocean Biogeographic Information Systems (OBIS, http://www.iobis.org; Costello *et al.*, 2007; Costello *et al.*, 2013). The need for easier access to marine species occurrence records and environmental data prompted the science community to launch the Group on Earth Observations Biodiversity Observation Network (GEO BON, https://www.earthobservations.org/geobon.shtml) (Andrefouet *et al.*, 2008), which aims to make biodiversity and earth observation data readily accessible.

Despite these advances, recent experience with developing compatible, comprehensive environmental layers for use with SDM in the deep sea (Basher *et al.*, 2014) demonstrated that considerable work is needed to collate and match environmental data layers from disparate sources. Based on this experience, we have developed an extensive on-line repository of marine environmental data layers with consistent resolution and global coverage that are ready to use in SDM and other spatial analyses. The repository is called the Global Marine Environment Dataset (GMED) and is freely available on-line at http://gmed.auckland.ac.nz. This chapter describes the source data and procedures used to generate GMED.

5.2 Methods

Development of the GMED layers followed 3 main steps (Figure 1): (1) compilation, quality control, and land-masking of source data; (2) interpolation and projection to generate continuous data surfaces at uniform resolution; (3) evaluation of derived data layers against source data.

5.2.1 Source data

I compiled data *in-situ* measured, remote sensed, and modelled datasets for a broad range of quantitative and qualitative environmental variables (Table 5.1). I extracted spatially interpolated i*n-situ* measured and remotely sensed data from Aquamaps (Kaschner *et al.*, 2008), KGS mapper environmental data (Hexacoral project, Fautin & Buddemeier, 2011), NOAA Ocean Color (Feldman & McClain, 2009), and World Ocean Database 2009 (Boyer *et al.*, 2009). Modelled datasets were sourced from Bio-Oracle (Tyberghein *et al.*, 2012), paleoclimatic reconstructions from Peltier (1993) and Paul & Schafer-Neth (2003)IPCC future climatology layers from Jungclaus (2006), Tyberghein *et al.* (2012), and Kaschner *et al.*(2013). All compiled datasets were converted into ESRI grid format before adding into ArcMap workspace for further processing. Several of the deep-sea datasets (e.g. bottom salinity, nutrients) had marine pixels with 'no data' value. These missing pixel values were calculated using the 'raster calculator' in ArcGIS, as the average values of the 12 surrounding (ocean) cells. Variable values were then extracted from each raster grids into a single global five arc-minute point geodatabase. A uniform land mask was then applied before final interpolation by extracting high-resolution land area from GEBCO 30 arc-second bathymetry (IOC *et al.*, 2003) (Figure 5.1).

5.2.2 Interpolation and Projection

Methods used to produce smooth interpolated environmental surfaces may combine regression analyses and distance-based weighted averages (Hartkamp *et al.*, 1999). Such approaches includes: Gaussian weighting filter (Thornton *et al.*, 1997), PRISM method (Daly *et al.*, 2002), Spline (New *et al.*, 2002; Hijmans *et al.*, 2005) and Inverse Distance Weighting and Kriging (see Hartkamp *et al.*, 1999, for an overview). Inverse Distance Weighting (IDW) multivariate interpolation (Shepard, 1968; Daly, 2006) was used to generate environmental surfaces using the "Spatial Analyst" extension in ArcGIS 10. We selected IDW instead of other interpolation techniques because it is computationally efficient and its ability to interpolate equal distance points has been demonstrated in other studies (Dirks *et al.*, 1998; Lu & Wong, 2008; Joseph & Kang, 2011). IDW interpolates environmental surfaces based on surrounding measured values that determine the smoothness of the resulting surface (interpolated values are decreased by distance weightings). In contrast, kriging, the other commonly used method, produces an environmental surface based on statistical models and is more suitable for capturing fine-scale local variability (Gong *et al.*, 2014). IDW interpolation was used with the default smoothing option in Spatial Analyst (p=2) which assigns the final interpolated cell values as weighted averages of the values of 12 surrounding points.

Most currently, datasets were usually available in equidistant projections (same distance from north to south in any pixel of the map). This may be suitable for some mapping applications, however to measure species richness, abundance and density estimate in a particular region, an equal–area projected (same area in any pixel of the map) dataset is preferred (Tittensor *et al.*, 2009; Elith *et al.*, 2010). Following Tyberghein *et al.* (2012), GMED rasters were interpolated into Behrmann equal area projection as well as WGS84 world geographic equidistant projection. Both equal area and geographically projected data layers were converted into ASCII grid format before making them available for downloading from the GMED website (Figure 5.1).

5.2.3 Descriptive statistics and evaluation

In ArcGIS, the "band statistics" tool was used to measure the standard deviation, standard error and coefficient of variation within each datasets. The same tool was used to calculate Pearson correlation coefficients (r) for all pairwise comparisons between datasets. To compare GMED with other available datasets we calculated the range of depth, temperature, salinity, chlorophyll-a annual mean for a half degree resolution grid were calculated. This resolution was chosen because with the exception of the Bio-Oracle, other available marine environmental datasets are generally closer to this resolution. Mean values of the above variables were aggregated from KGS Environment Dataset (Fautin & Buddemeier, 2011) for comparison.

5.2.4 Data Quality

All of the primary datasets used in the GMED compilation had undergone quality control checks by the primary data collectors and processors (Table 5.1). Here, we checked only the interpolation quality of the generated layers were checked to ensure no further errors were introduced during the re-interpolation process. The interpolation quality for all of the data layers were tested by extracting interpolated values into randomly generated 10,000 evaluation points over the global ocean area using 'extract to points' tool in the ArcGIS 'Spatial Analyst' extension. Coefficient of variation and standard errors of individual data layers were then calculated from this point grid using the 'pastecs' package in R v2.15 (R Core Team, 2014) and compared with statistics derived from the original source layers (Table 5.4).

5.3 Results

After initial data cleaning, the primary GMED point grid had ca. 5.7 million data points. Fifty-three global marine environment raster's were generated from these point records (Table 5.1). A detailed description of the data layers, their sources and interpolated surface images are available in the supporting materials sections.

5.3.1 Descriptive statistics

Sea ice coverage had a negative correlation with temperature and positive correlations with nutrients, while oxygen layers had a strong positive correlation with temperature and negative correlations with nutrients (Pearson Correlation coefficient $r > 0.5$). The nutrients nitrate, phosphate and silicate were negatively correlated with temperature and depth, while photosynthetically active radiation (PAR) was greater in warmer waters (Table 5.2). Thus, there were less dissolved nutrients in seawater in warmer and shallower seas and more nutrients in polar and deeper regions. Chlorophyll-*a* was positively correlated with the diffuse attenuation coefficient (DA), a measure of water clarity, and decreased with depth (Table 5.2) and salinity. DA increased with depth and decreased with salinity. The above correlations reflect the effects of phytoplankton growth (greater in warmer waters) on available nutrients. Apart from the strong effect of temperature on oxygen saturation, correlations between the physical data were weak; i.e. slope, distance from land, tide, wind, wave, pH, salinity and depth.

The depth and primary productivity dataset had the highest variation of values across the globe and had highest standard deviation and standard errors (Table 5.3). Surface current, chlorophyll-*a* and ice layers had higher variation compared to all other datasets (Table 5.3).

5.3.2 Comparison with other dataset

Differences were observed in extreme values by comparison with the source datasets. For instances, the GMED depth layer values ranged between 0 and 10415 m, while compared to 0 to 8672 m in KGS Mapper () (Figure 5.2). This effect of overall higher resolution GMED dataset was also visible in sea surface temperature, salinity, and chlorophyll-a layers. Sea surface temperature had values between −1 and 31°C, compared to those of KGS (−1.9 to 29.9 °C). Similarly, salinity had maximum value of 41 and 40.3 PSS, and chlorophyll-a maximum values were 60.3 and 64.5 mg.m^{-3} respectively in GMED and KGS mapper datasets (Figure 5.3).

5.3.3 GMED Data quality

Interpolation error of GMED's environment surface by comparison with the source data layers was minimal, as assessed by consistent standard error and coefficients of variation across most of the datasets when verified using the random evaluation points (Figure 5.4). Depth, LGM depth, and primary productivity datasets showed higher standard error in GMED evaluation data than in the source data. These increases were probably due to downgrading the spatial resolution of the interpolated surface into GMED's standard five arc-minute resolution from their primary data resolution of 30 arc-second. Visual inspection of the layers revealed that the Arctic regions had more data gaps compared to the Antarctic, which caused interpolation errors to be more visible in the higher latitudes of northern hemisphere, especially above 70°N latitude (Figure 5.5).

5.4 Discussion

GMED has 6 to 12 times higher spatial resolution than most previously available major marine environment datasets, with the exception of Bio-Oracle, which is at the same resolution. However, GMED has 30 more data layers than Bio-Oracle (Table 5.1, 5.3). GMED environmental surfaces were also derived from a more diverse set of sources than any other publicly available compilation of marine environment datasets (Table 5.4) (Figure 5.5 to Figure 5.9). Applications such as analysis of species population densities using SDM will benefit from equal-area projected dataset while rapid mapping of species will benefit from more the commonly used geographically projected equidistant dataset (Table 5.4). The inclusion of depth, slope, and several deep-sea variables with past and future climatic scenario layers in GMED will enable researchers to model distributions of species across broad spatial and temporal scales. More data layers will be integrated with GMED from climatic, anthropogenic variables and modelled datasets as they become available in the future.

5.4.1 Comparison with other datasets

The existing marine environment datasets were compiled for specific objectives. In the case of, AquaMaps datasets represented long-term averages of temporally varying environmental variables to support SDM (Ready *et al.*, 2010). The KGS mapper marine datasets were developed to enable environmental classification and to understand spatial and temporal patterns in biogeochemistry and biogeography (Guinotte *et al.*, 2006). The Bio-Oracle dataset was developed to facilitate modelling the distribution of shallow water marine species (Tyberghein *et al.*, 2012). GMED provides the most comprehensive environmental dataset resource to date, for support of SDM applications. A comparison of strengths and weaknesses of GMED by comparison with other freely available marine environment datasets is given in Table 5.4.

Although there was an overall agreement between all marine datasets in the tropical and sub-tropical regions, differences shown in interpolated surface near the polar and coastal areas were still large. This clearly indicates that some uncertainty exists about the true values of any particular grid cell in these areas. The differences I found likely reflect the difference between a pure statistical and a more mechanistic expert-driven approach in interpolation. Future work focusing on model comparison in these geographic areas would be useful because in my comparison the effects of interpolation method may be confounded with differences in primary dataset resolution, used climate and depth data sources, and the temporal resolution of datasets.

5.4.2 Dataset extent and quality

The comparatively high spatial resolution of GMED does not imply that data quality is high in all locations. The quality of the interpolated environmental surfaces is, therefore, spatially variable and depends on local environmental variability and the quality and density of the underlying observations (reviewed by Costello *et al.*, 2010 for bathymetry). GMED environmental data do not capture all the variation that may occur at a resolution of 9 km considering the overall low density of real-time ocean observing globally (for most variable), and ignoring locally important drivers such as the fine scale bathymetric or environmental conditions.

The data layers derived from remotely sensed data only included information with the highest available quality (from Level-3 processed data products, see Hooker & McClain, 2000 for details). However, even here, data gaps existed due to irregular temporal sampling of the ocean colour sensors (MODIS and SeaWiFS), sparse observational networks in the polar regions (IPCC Climate Change, 2007), clouds, thick aerosols, inter-orbit gaps, sun glint and high solar zenith angles (Gregg & Casey, 2007). Filing these data gaps by interpolation makes them disappear but could lead to unpredictable errors. The overall interpolation error was small (Figure 5.4), and the highest uncertainty(i.e. the highest predicted error) was pronounced in regions with low data coverage such as at high latitude areas (e.g. Arctic, some regions of Antarctica) (Kennedy, 2014). For example, chlorophyll-a, photosynthetically available radiation and diffuse attenuation, which are measured at relatively short wavelengths (in the visible spectrum), cannot be accurately measured during the winter season at high latitudes due to high solar zenith angles (Gregg & Casey, 2007). Surface temperature data do not suffer from this effect because they are measured in longer wavelengths (the thermal infrared part of the spectrum). Data gaps were also visible in some non-sampled areas in the middle of the oceans, particularly for the less commonly reported variables e.g. the sea bed salinity and nutrient variables of Figure 5.5. Although interpolation and extrapolation of data for pixels with missing data could affect the quality of interpolation, our verification data indicates that the GMED layers are reliable representation of the source data (Figure 5.4).

The extent to which missing data could create a problem in analyses depends on the application. Uncertainty in the prediction of species ranges may be offset by the gradient of change in the dominant variables. For example, a small error in a region with a shallow environmental gradient can lead to a more incorrect prediction of a larger species range compared to a similar error in a regions with steep environment gradient. A cropped version (70°N on the top) of GMED dataset was provided as well as a full version of dataset covering all latitudinal ranges. We recommend using the cropped version of the dataset for modelling. The full extent dataset should only be used with careful consideration of possible model anomalies in the Polar Regions.

Marine species distribution models are susceptible to faulty predictions into land areas when the underlying environmental data does not have a uniform land area. As we masked the GMED datasets using land areas extracted from the very high-resolution (30 arc-second, ca. 930 m in equator) GEBGO data, model prediction in coastal areas should minimise such errors. We made all data available ASCII Grid format, frequently used by common SDM algorithms (e.g. MaxEnt, Random Forest, GARP). GMED is published in 5 arc-min (c. 9.2 km near equator) resolution affording, (1) convenience of managing the rasters in common desktop computing environments, (2) Interoperability with other recently available datasets like Bio-Oracle, (3) having sufficient resolution to model near-shore environments, and (4) resolution fine enough to address species distribution questions at a global scale for implementing management decisions.

5.5 Conclusion

This study have documented the construction of GMED, a comprehensive compilation of 53 high-resolution marine environmental data rasters comprised of environmental variables - Depth, Slope, Land distance, Ice cover, Tide average, Wave height, Wind speed, Surface current, Diffuse attenuation coefficient, Temperature, Salinity, Chlorophyll-a, Primary productivity, Photosynthetically active radiation, pH, Calcite, Nitrate, Phosphate, Silicate, Dissolved oxygen, Saturated oxygen, Utilized oxygen, past climate of Last Glacial Maxima (Depth, Temperature, Salinity, Ice thickness) and future climate scenario of year 2100 (Temperature, Salinity, primary productivity, Ice concentration) for marine SDM and visualisation application. The dataset has a spatial resolution of 5’ latitude-longitude, which approximates to about 9.2 km x 9.2 km near equator. The gridded raster’s are available for download from the GMED website (http://gmed.auckland.ac.nz/).

There are opportunities to refine and improve the interpolation methods in future versions. Additional efforts to compile and capture more environmental data sets are needed to improve temporal and spatial coverage of the dataset. Availability of online tools might enable researchers to explore the full strength of GMED. Future work planned for the GMED is likely to include development of an open geospatial consortium (OGC) compliant database, online data extraction tool allowing users to download dataset of any defined extent and an online workbench to run SDM algorithms instantaneously using user provided species dataset with GMED.

5.6 References

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Table 5.1. GMED Dataset source data and description.

Layer	*Description*	*Unit*	*Original Spatial Resolution*	*Temporal Range*	*Derivatives*	*Primary Data Source*
Physical						
Depth	From GEBCO 08 Digital Atlas.	m	30 arc-seconds	-	Mean	IOC (IOC et al., 2003)
Slope	From GEBCO 08 using ArcGIS Spatial Analyst.	degree	5 arc-min (9.2 km)	-	-	-
Land distance	Distance (km) to the nearest land cell (water cells only) calculated using Euclidean distance formula using ArcGIS.	Euclidean (km x 100)	5 arc-min (9.2 km)	-	-	-
Ice cover	Mean annual ice cover in percent was derived from the National Snow and Ice Data Centre. Interpolation covered missing cells and values for the ice shelves in the Antarctic were set to 1.5.	% (0-1.0)	0.5° x 0.5°	1979-2002	Mean, Summer, Winter	U.S. National Snow and Ice Data Centre (Cavalieri et al., 2003)
Tide average	Average of maximum tidal amplitude. These tide model results are from a global 0.25-degree tide model which assimilated tide estimates derived from the TOPEX/Poseidon altimeter.	m	0.25° x 0.25°	-	Mean	(Stewart, 2000)
Wave height	Height of waves in scaled discrete classes as provided by the Original LOICZ Database, for all coastal and oceanic cells.	m	0.5° x 0.5°	-	Mean	KGS (Fautin & Buddemeier, 2011)
Wind speed	Yearly variations of the surface wind velocity over the ocean	$m\cdot s^{-1}$	0.5° x 0.5°	1945-1989	Mean	(Da Silva et al., 1994)
Surface current	Monthly average of Zonal velocity (UVEL), meridional velocity (VVEL) values in the ocean surface.	$m\cdot s^{-1}$	0.25° x 0.25°	2009-2010	Mean	NASA JPL Laboratory

Layer	*Description*	*Unit*	*Original Spatial Resolution*	*Temporal Range*	*Derivatives*	*Primary Data Source*
Diffuse attenuation coefficient	The diffuse attenuation coefficient is an indicator of water clarity. It expresses how deeply visible light in the blue to the green region of the spectrum (490 nm) penetrates in to the water column.	m^{-1}	5 arc-min (9.2 km)	2002 - 2009	Mean	(Feldman & McClain, 2010)
Temperature	Sea surface temperature is the temperature of the water at the ocean surface. This parameter indicates the temperature of the topmost meter of the ocean water column.	°C	5 arc-min (9.2 km)	2002 - 2009	Mean, Minimum, Maximum, Range, Summer, Winter	(Feldman & McClain, 2010)
	Temperature of water near the sea bed.	°C	1° x 1°	1874-2000	Mean (Bottom)	(Stephens et al., 2002)
	Long term monitoring of temperature on multiple depth levels.	°C	2° x 2°	1871-2008	Mean (Water column)	20th Century Reanalysis V2 data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA
Salinity	Salinity indicates the dissolved salt content in the ocean surface.	pss	1° x 1°	1961-2009	Mean	(Boyer et al., 2009)
	Long term monitoring of salinity on several depths	ppt	2° x 2°	1871-2008	Mean (Bottom)	20th Century Reanalysis V2 data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA

Layer	*Description*	*Unit*	*Original Spatial Resolution*	*Temporal Range*	*Derivatives*	*Primary Data Source*
Biochemical						
Chlorophyll-a	Chlorophyll A concentration indicates the concentration of photosynthetic pigment chlorophyll A (the most common “green” chlorophyll) in oceans. Please note that in shallow water these values may reflect any kind of autotrophic biomass.	$mg \cdot m^{-3}$	5 arc-min (9.2 km)	2002 - 2009	Mean, Minimum, Maximum, Range	(Feldman & McClain, 2010)
	Chlorophyll-a concentration data consists of satellite measurements of global and regional ocean color data.	$mg \cdot m^{-3}$	~ 5 arc-min (9 km)	1997-2006	Max, Mean, Summer Max, Winter max	(Feldman & McClain, 2006)
Primary Productivity	Proportion of annual primary production in a cell. See reference for details about the productivity calculation methods.	$mgC \cdot m^{-2} \cdot$/day/cell	~ 5 arc-min (9 km)	-	Mean	(Longhurst et al., 1995; Hoepffner et al., 1999; Bouvet et al., 2002)
Photosynthetically Active Radiation	Photosynthetically Active Radiation (PAR) indicates the quantum energy flux from the sun (in the spectral range 400-700 nm) reaching the ocean surface.	Einstein/m^2/day	5 arc-min (9.2 km)	1997-2009	Mean	(Feldman & McClain, 2010)
pH	Measure of acidity in the ocean surface.	-	1° x 1°	1910-2007	Mean	(Boyer et al., 2009)
Nutrients						
Calcite	Calcite concentration indicates the concentration of calcite ($CaCO_3$) in surface seawater.	$Mol \cdot m^{-3}$	5 arc-min (9.2 km)	2002 - 2009	Mean	(Feldman & McClain, 2010)
Nitrate	This surface layer contains both $[NO_3]$ and $[NO_2]$ data. By this we mean chemically reactive dissolved inorganic nitrate and nitrite.	$\mu mol \cdot l^{-1}$	1° x 1°	1922 - 1986	Mean	(Boyer et al., 2009),.
	Nitrate concentration.	$\mu mol \cdot l^{-1}$	0.5° x 0.5°	1874-2000	Mean (Bottom)	(Saving, 2006)

Layer	*Description*	*Unit*	*Original Spatial Resolution*	*Temporal Range*	*Derivatives*	*Primary Data Source*
Phosphate	Phosphorous (PO_4)concentration.	µmol·l^{-1}	0.5° x 0.5°	1874-2000	Mean (Surface, Bottom)	(Saving, 2006)
Silicate	This variable indicates the concentration of silicate or ortho-silicic acid [$Si(OH)_4$] in the ocean surface.	µmol·l^{-1}	1° x 1°	1930 - 1986	IDW Interpolation	(Boyer et al., 2009)
	Silicate concentration.	µmol·l^{-1}	0.5° x 0.5°	1874-2000	Mean (Bottom)	(Saving, 2006)
Dissolved Oxygen	Dissolved oxygen concentration [O_2] in the surface.	ml·l^{-1}	1° x 1°	1898 - 2009	Mean	(Boyer et al., 2009)
	Dissolved oxygen concentration	ml·l^{-1}	0.5° x 0.5°	1874-2000	Mean (Bottom)	(Conkright et al., 2002)
Saturated Oxygen	Amount of dissolved oxygen as a percentage of maximum potential oxygen amount that could be present for the given temperature and salinity at standard atmospheric pressure (760 mmHg) (i.e., sea level).	ml·l^{-1}	0.5° x 0.5°	1874-2000	Mean (Surface)	(Conkright et al., 2002)
Utilized Oxygen	Apparent oxygen utilization (AOU) =oxygen saturation concentration minus measured dissolved oxygen concentration.	ml·l^{-1}	0.5° x 0.5°	1874-2000	Mean (Surface, Bottom)	(Saving, 2006)
Past						
Last Glacial Maxima Depth	Water depth calculated from GEBCO 08 (using formula current depth-130 m; the average depth decrease mentioned in literature).	m	30 arc-seconds	-	Mean	(IOC et al., 2003; Bintanja et al., 2005)
Last Glacial Maxima Temperature	Sea surface temperature during last glacial maxima (22 thousand years ago)	°C	1° x 1°	19-22 cal.KYrBP	Mean (Surface)	(Paul & Schäfer-Neth, 2003)

Layer	*Description*	*Unit*	*Original Spatial Resolution*	*Temporal Range*	*Derivatives*	*Primary Data Source*
Last Glacial Maxima Salinity	Sea surface salinity during last glacial maxima (22 thousand years ago)	PSS	1° x 1°	19-22 cal.KYrBP	Mean (Surface)	(Paul & Schäfer-Neth, 2003)
Last Glacial Maxima Ice Thickness	Thickness of ice sheets during last glacial maxima (22 thousand years ago)	km	1° x 1°	19-22 cal.KYrBP	Mean (Surface)	(Peltier, 1993)
Future						
Temperature at 2100	Future 4 grids of monthly mean sea surface temperature, A1B (720 ppm stabilization) scenario.	°C	1.25° x 1.25°	2087–2096	Mean	Based on IPCC (WCRP CMIP3) multi-model database (http://esg.llnl.gov:8080/index.jsp)
	Predicted sea bottom temperature for year 2100.	°C	0.5° x 0.5°	2090-2099	Mean	IPSL model, A2 scenario (http://icmc.ipsl.fr/)
Salinity at 2100	Future grid of average monthly mean sea surface salinity	PPT	2.75°x 3.75°	2087–2096	Mean	Based on IPCC (WCRP CMIP3) multi-model database (http://esg.llnl.gov:8080/index.jsp)
	Predicted sea bottom salinity for year 2100.	PSU	0.5° x 0.5°	2090-2099	Mean	IPSL model, A2 scenario (http://icmc.ipsl.fr/)
Primary productivity at 2100	Predicted primary productivity for year 2100.	mgC·m-^{2}·/day	0.5° x 0.5°	2090-2099	Mean	IPSL model, A2 scenario (http://icmc.ipsl.fr/)
Ice Concentration at 2100	Predicted ice cover (area proportion) for year 2100.	% (0-1)	0.5° x 0.5°	2090-2099	Mean	IPSL model, A2 scenario (http://icmc.ipsl.fr/)

Table 5.2. Pearson correlation matrix of GMED data layers.

	Depth	Slope	Land Distance	Ice Mean	Ice Summer	Ice Winter	Tide average	Wave Height	Wind Speed	Surface Current	DA Mean	SST Maximum	SST Mean	SST Minimum	SST Range	SST May_Oct	SST Nov_Apr	Seabed Temp	Bottom Temp	Salinity	Bottom Salinity	Chla Mean	Chla Max	Chla Min	Chla Range	Chla Sum_Max	Chla Win_Max	Chla PrimProd	PAR	pH	Calcite	Nitrate	Bottom Nitrate	Phosphate	Bottom Phosphate	Silicate	Bottom Silicate	Dissolved O2	Bottom Dissolved O2	Saturated O2	Bottom Utilized O2
Depth	1.000																																								
Slope	0.078	1.000																																							
Land Distance	-0.464	-0.074	1.000																																						
Ice Mean	0.252	0.015	-0.201	1.000																																					
Ice Summer	0.155	0.040	-0.155	0.929	1.000																																				
Ice Winter	0.334	-0.024	-0.211	0.816	0.644	1.000																																			
Tide average	0.264	-0.041	-0.272	0.346	0.289	0.365	1.000																																		
Wave Height	0.473	0.009	-0.334	-0.022	-0.062	0.053	0.126	1.000																																	
Wind Speed	-0.259	0.028	0.344	-0.177	-0.116	-0.197	-0.237	-0.236	1.000																																
Surface Current	-0.009	0.019	0.134	-0.026	-0.010	-0.040	-0.117	-0.029	0.297	1.000																															
DA Mean	0.505	-0.053	-0.338	0.294	0.211	0.306	0.173	0.443	-0.175	0.013	1.000																														
SST Maximum	-0.126	-0.021	-0.099	-0.573	-0.569	-0.404	-0.048	0.064	-0.419	-0.311	-0.235	1.000																													
SST Mean	-0.161	-0.008	-0.080	-0.540	-0.520	-0.406	-0.038	0.016	-0.430	-0.320	-0.300	0.984	1.000																												
SST Minimum	-0.181	-0.001	-0.068	-0.498	-0.474	-0.383	-0.028	-0.022	-0.435	-0.327	-0.341	0.955	0.991	1.000																											
SST Range	0.197	-0.066	-0.125	-0.210	-0.283	-0.037	-0.066	0.292	0.029	0.046	0.370	0.129	-0.043	-0.169	1.000																										
SST May_Oct	-0.167	-0.007	-0.063	-0.539	-0.520	-0.411	-0.052	0.003	-0.431	-0.320	-0.315	0.967	0.991	0.988	-0.089	1.000																									
SST Nov_Apr	-0.150	-0.012	-0.091	-0.506	-0.515	-0.367	-0.029	0.027	-0.445	-0.326	-0.269	0.969	0.979	0.968	-0.014	0.969	1.000																								
Seabed Temp	0.484	-0.069	-0.293	-0.196	-0.181	-0.130	0.089	0.464	-0.300	-0.055	0.303	0.327	0.298	0.259	0.219	0.283	0.256	1.000																							
Bottom Temp	0.014	0.003	-0.113	-0.536	-0.548	-0.373	-0.081	0.118	-0.306	-0.209	-0.214	0.841	0.828	0.801	0.113	0.816	0.824	0.346	1.000																						
Salinity	-0.270	0.039	0.140	-0.246	-0.144	-0.300	-0.030	-0.180	0.022	-0.083	-0.536	0.316	0.370	0.393	-0.282	0.370	0.323	0.031	0.354	1.000																					
Bottom Salinity	-0.172	0.034	0.069	-0.049	-0.022	-0.076	-0.029	-0.165	0.078	-0.013	-0.162	0.074	0.092	0.103	-0.102	0.088	0.087	-0.108	0.127	0.242	1.000																				
Chla Mean	0.505	-0.053	-0.338	0.294	0.211	0.306	0.173	0.443	-0.175	0.013	1.000	-0.235	-0.300	-0.341	0.370	-0.315	-0.269	0.303	-0.214	-0.536	-0.162	1.000																			
Chla Max	0.306	-0.031	-0.208	0.134	0.075	0.152	0.055	0.319	-0.196	-0.017	0.816	-0.051	-0.095	-0.126	0.260	-0.103	-0.071	0.212	-0.050	-0.438	-0.103	0.816	1.000																		
Chla Min	0.151	-0.029	-0.100	0.074	0.021	0.080	0.000	0.172	-0.132	-0.006	0.620	-0.008	-0.036	-0.056	0.166	-0.036	-0.012	0.147	-0.006	-0.376	-0.022	0.620	0.715	1.000																	
Chla Range	0.293	-0.024	-0.200	0.126	0.079	0.144	0.059	0.303	-0.184	-0.019	0.731	-0.051	-0.092	-0.119	0.235	-0.100	-0.073	0.189	-0.051	-0.376	-0.111	0.731	0.948	0.465	1.000																
Chla Sum_Max	0.323	-0.044	-0.218	0.101	0.034	0.139	0.064	0.357	-0.210	-0.010	0.715	-0.030	-0.072	-0.102	0.256	-0.077	-0.048	0.298	-0.013	-0.437	-0.110	0.715	0.713	0.652	0.604	1.000															
Chla Win_Max	0.321	-0.045	-0.207	0.030	0.017	0.068	0.078	0.375	-0.187	0.004	0.604	0.003	-0.036	-0.071	0.253	-0.047	-0.046	0.399	-0.022	-0.267	-0.111	0.604	0.544	0.398	0.498	0.618	1.000														
Chla PrimProd	0.466	-0.070	-0.339	-0.126	-0.165	-0.022	0.168	0.513	-0.173	-0.026	0.682	0.121	0.050	-0.007	0.423	0.031	0.051	0.494	0.119	-0.296	-0.157	0.682	0.525	0.285	0.513	0.526	0.581	1.000													
PAR	-0.097	-0.022	-0.121	-0.436	-0.428	-0.329	-0.005	0.031	-0.498	-0.422	-0.230	0.892	0.920	0.927	-0.122	0.924	0.907	0.246	0.729	0.322	0.083	-0.230	-0.036	-0.008	-0.032	-0.030	-0.022	0.062	1.000												
pH	-0.100	0.027	0.004	-0.287	-0.310	-0.156	0.012	-0.032	-0.122	-0.100	-0.260	0.446	0.429	0.409	0.106	0.423	0.429	0.010	0.438	0.205	0.013	-0.260	-0.151	-0.172	-0.108	-0.198	-0.113	-0.088	0.354	1.000											
Calcite	-0.272	0.022	0.068	-0.288	-0.277	-0.221	-0.077	-0.164	-0.296	-0.248	-0.438	0.653	0.680	0.689	-0.128	0.677	0.678	-0.043	0.553	0.333	0.144	-0.438	-0.172	-0.072	-0.166	-0.187	-0.198	-0.292	0.653	0.343	1.000										
Nitrate	0.027	0.044	0.122	0.549	0.621	0.287	0.054	-0.131	0.347	0.275	0.139	-0.906	-0.865	-0.823	-0.257	-0.844	-0.872	-0.314	-0.816	-0.216	-0.044	0.139	0.006	-0.019	0.015	-0.027	-0.014	-0.171	-0.771	-0.476	-0.573	1.000									
Bottom Nitrate	-0.516	0.117	0.309	-0.065	0.021	-0.178	-0.114	-0.435	0.179	-0.008	-0.446	-0.012	0.043	0.084	-0.331	0.064	0.030	-0.632	-0.134	0.083	0.045	-0.446	-0.274	-0.191	-0.236	-0.339	-0.351	-0.429	0.033	0.032	0.155	0.170	1.000								
Phosphate	0.011	0.068	0.098	0.454	0.516	0.231	0.022	-0.127	0.357	0.284	0.091	-0.826	-0.779	-0.736	-0.286	-0.759	-0.785	-0.258	-0.746	-0.213	-0.043	0.091	-0.006	-0.024	0.003	-0.037	-0.018	-0.176	-0.687	-0.447	-0.498	0.887	0.165	1.000							
Bottom Phosphate	-0.435	0.104	0.261	-0.018	0.045	-0.111	-0.076	-0.377	0.117	-0.015	-0.359	-0.028	0.019	0.054	-0.279	0.039	0.010	-0.599	-0.154	-0.019	-0.005	-0.359	-0.211	-0.156	-0.176	-0.276	-0.301	-0.361	0.019	0.022	0.120	0.170	0.957	0.170	1.000						
Silicate	0.099	0.057	-0.065	0.762	0.821	0.464	0.235	-0.092	0.109	0.146	0.202	-0.781	-0.740	-0.698	-0.245	-0.732	-0.739	-0.247	-0.755	-0.246	-0.048	0.202	0.060	0.006	0.068	0.024	0.016	-0.152	-0.632	-0.429	-0.455	0.871	0.123	0.789	0.148	1.000					
Bottom Silicate	-0.560	0.056	0.339	-0.056	0.023	-0.163	-0.144	-0.402	0.170	0.005	-0.367	-0.045	-0.002	0.030	-0.255	0.017	-0.012	-0.523	-0.212	-0.037	0.023	-0.367	-0.222	-0.125	-0.203	-0.261	-0.277	-0.408	-0.011	-0.045	0.099	0.197	0.899	0.212	0.900	0.156	1.000				
Dissolved O2	0.189	0.010	0.035	0.552	0.526	0.417	0.049	0.005	0.378	0.302	0.329	-0.952	-0.967	-0.959	0.044	-0.963	-0.943	-0.273	-0.811	-0.413	-0.104	0.329	0.119	0.049	0.114	0.095	0.050	-0.026	-0.891	-0.417	-0.656	0.830	-0.065	0.748	-0.033	0.730	-0.015	1.000			
Botttom Dissolved O2	0.053	-0.108	-0.002	0.331	0.270	0.292	0.069	0.019	0.161	0.128	0.205	-0.451	-0.457	-0.450	0.012	-0.458	-0.424	-0.159	-0.334	-0.042	0.072	0.205	0.091	0.080	0.068	0.090	0.049	-0.039	-0.387	-0.121	-0.232	0.310	-0.549	0.234	-0.583	0.271	-0.547	0.445	1.000		
Saturated O2	-0.100	-0.046	0.020	-0.720	-0.772	-0.462	-0.213	0.105	-0.017	-0.057	-0.118	0.608	0.546	0.495	0.359	0.529	0.562	0.151	0.565	0.127	0.012	-0.118	-0.022	0.004	-0.030	0.017	0.000	0.189	0.461	0.362	0.331	-0.695	-0.085	-0.624	-0.093	-0.801	-0.108	-0.516	-0.202	1.000	
Bottom Utilized O2	-0.296	0.130	0.153	-0.197	-0.148	-0.197	-0.110	-0.255	-0.004	-0.090	-0.328	0.245	0.268	0.281	-0.132	0.276	0.255	-0.339	0.109	-0.011	-0.016	-0.328	-0.177	-0.136	-0.144	-0.217	-0.229	-0.205	0.232	0.087	0.223	-0.114	0.842	-0.070	0.863	-0.106	0.804	-0.267	-0.867	0.094	1.000

Table 5.3. Descriptive statistics for the GMED environmental layers. All values are in annual means and refer the ocean surface unless noted otherwise. * Summer = May – October; Winter = November – April. (see table 5.1 for detailed layer descriptions)

Layers	**Minimum**	**Maximum**	**Mean**	**Standard Deviation**	**Standard Error**	**Coefficient of Variation**
Physical						
Depth	-10415.08	0.00	-3650.32	1623.20	0.70	-0.44
Slope	0.00	21.65	0.98	1.16	0.00	1.18
Land distance	0.00	24.92	6.80	5.22	0.00	0.77
Ice Mean	0.00	1.50	0.06	0.18	0.00	2.89
Ice Summer*	0.00	1.50	0.07	0.23	0.00	3.02
Ice Winter*	0.00	1.50	0.04	0.14	0.00	3.72
Tide average	0.00	6.38	0.51	0.44	0.00	0.87
Wave height	0.00	7.00	0.29	1.02	0.00	3.57
Wind speed	0.00	12.07	7.51	1.80	0.00	0.24
Surface current	-0.93	1.00	0.00	0.08	0.00	15.83
Diffuse Attenuation Coefficient	0.00	0.90	0.05	0.04	0.00	0.81
Temperature Maximum	-1.00	35.19	18.45	10.48	0.00	0.57
Temperature Mean	-1.00	31.54	15.89	10.44	0.00	0.66
Temperature Minimum	-2.00	30.76	13.84	10.31	0.00	0.74
Temperature Range	0.00	27.81	4.26	3.08	0.00	0.72
Temperature Summer*	-2.10	30.72	16.05	10.71	0.00	0.67
Temperature Winter*	-2.10	30.73	15.83	10.56	0.00	0.67
Seabed Temperature	-2.08	29.46	2.24	4.05	0.00	1.81
Water column Temperature	-2.30	26.03	5.99	3.42	0.00	0.57
Salinity	0.00	41.00	33.96	2.09	0.00	0.06
Bottom Salinity	6.36	40.62	34.59	1.66	0.00	0.05
Biochemical						
Chlorophyll-a Mean	0.00	60.38	0.18	1.34	0.00	7.60
Chlorophyll-a Max	0.00	64.00	0.45	2.34	0.00	5.15
Chlorophyll-a Min	0.00	57.80	0.07	0.81	0.00	12.45
Chlorophyll-a Range	0.00	62.16	0.33	1.78	0.00	5.31
Chlorophyll-a Summer Maximum*	0.00	64.57	0.55	1.96	0.00	3.54
Chlorophyll-a Winter Maximum*	0.00	64.57	0.43	1.39	0.00	3.22
Primary Productivity	0.00	4875.00	385.08	285.55	0.12	0.74
Photosynthetically Active Radiation	0.00	64.82	35.22	8.55	0.00	0.24
pH	6.73	8.62	8.19	0.06	0.00	0.01
Nutrient						
Calcite	0.00	9.00	2.87	3.18	0.00	1.11
Nitrate	0.00	45.96	5.52	6.13	0.00	1.11
Bottom Nitrate	0.00	55.78	30.34	8.44	0.00	0.28
Phosphate	0.00	2.00	0.26	0.44	0.00	1.67
Bottom Phosphate	0.00	4.50	2.12	0.57	0.00	0.27
Silicate	0.00	69.00	9.85	13.86	0.01	1.41

Bottom Silicate	0.32	267.50	107.16	46.78	0.02	0.44
Dissolved O_2	2.00	9.86	5.29	1.27	0.00	0.24
Bottom Dissolved O_2	0.00	9.48	4.61	1.12	0.00	0.24
Saturated O_2	76.05	113.11	100.10	3.23	0.00	0.03
Bottom Utilized O_2	-1.32	7.69	3.06	1.14	0.00	0.37
Past						
Depth	-10411.84	0.49	-3836.29	1571.24	0.68	-0.41
Temperature	-1.56	28.59	14.76	10.47	0.00	0.71
Salinity	4.65	41.32	35.63	1.75	0.00	0.05
Ice thickness	0.00	4735.79	31.25	262.76	0.11	8.41
Future						
Temperature (A1B Scenario)	-1.61	35.05	18.04	10.91	0.00	0.60
Temperature (A2 Scenario)	-2.19	31.91	17.58	11.12	0.00	0.63
Bottom Temperature	-2.08	31.33	2.43	4.25	0.00	1.75
Salinity (A1B Scenario)	3.37	40.05	34.37	1.99	0.00	0.06
Salinity (A2 Scenario)	3.37	40.05	34.37	1.99	0.00	0.06
Bottom Salinity	3.38	41.07	34.60	1.44	0.00	0.04
Primary Productivity	0.00	5004.00	354.76	277.07	0.12	0.78
Ice concentration	0.00	1.50	0.05	0.16	0.00	3.16

Table 5.4. Comparison of features of freely available online marine environment datasets. Legend: (√ Present, × Absent). [1] AquaMaps (Kaschner *et al.*, 2008), [2] KGS Hexacoral Project (Fautin & Buddemeier, 2011), [3] Global Map of Human Impact on Marine Ecosystems (Halpern *et al.*, 2008), [4] MARSPEC: Ocean Climate Layers for Marine Spatial Ecology (Sbrocco & Barber, 2013; Sbrocco, 2014), [5] Bio-Oracle Marine SDM Raster (Tyberghein *et al.*, 2012).

	AquaMaps[1]	**KGS[2]**	**Halpern[3]**	**Marspec[4]**	**Bio-Oracle[4]**	**GMED**
Resolution						
arc minute	30'	15-30'	0.5'	0.5'	5'	5'
ca. km	55	22-55	1	1	9	9
Uniform file format	√	√	√	√	√	√
Uniform land area mask	×	√	×	√	√	√
GIS ready Format (ASCII Grid or Raster)	×	×	√	√	√	√
Common geographic extent	√	×	×	√	√	√
Suitable for coastal studies	×	×	√	√	√	√
Bathymetry	√	√	×	√	×	√
Deep-Sea datasets	√	√	×	×	×	√
Equal-area grids available	×	×	×	×	√	√
Future climate scenario	√	×	×	×	√	√
Past climate condition	×	×	×	√	×	√
Descriptive statistics of dataset	×	×	×	×	×	√
Individual dataset download option	×	×	×	√	×	√

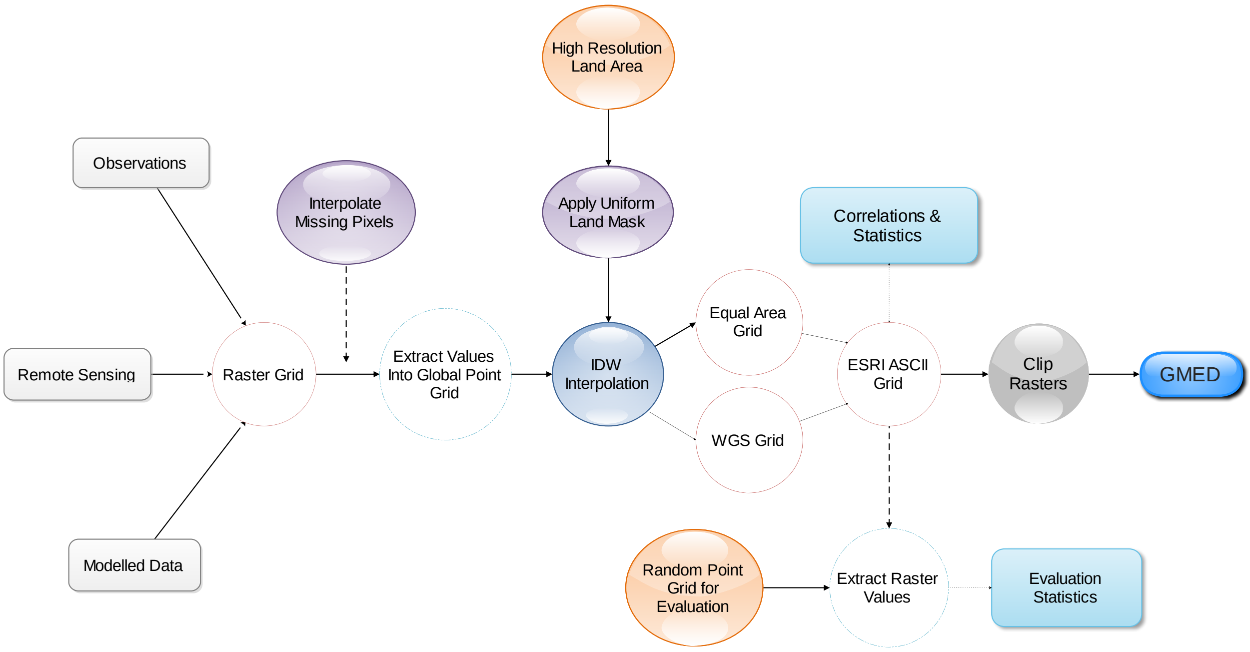


Figure 5.1. Data processing steps used to produce GMED.

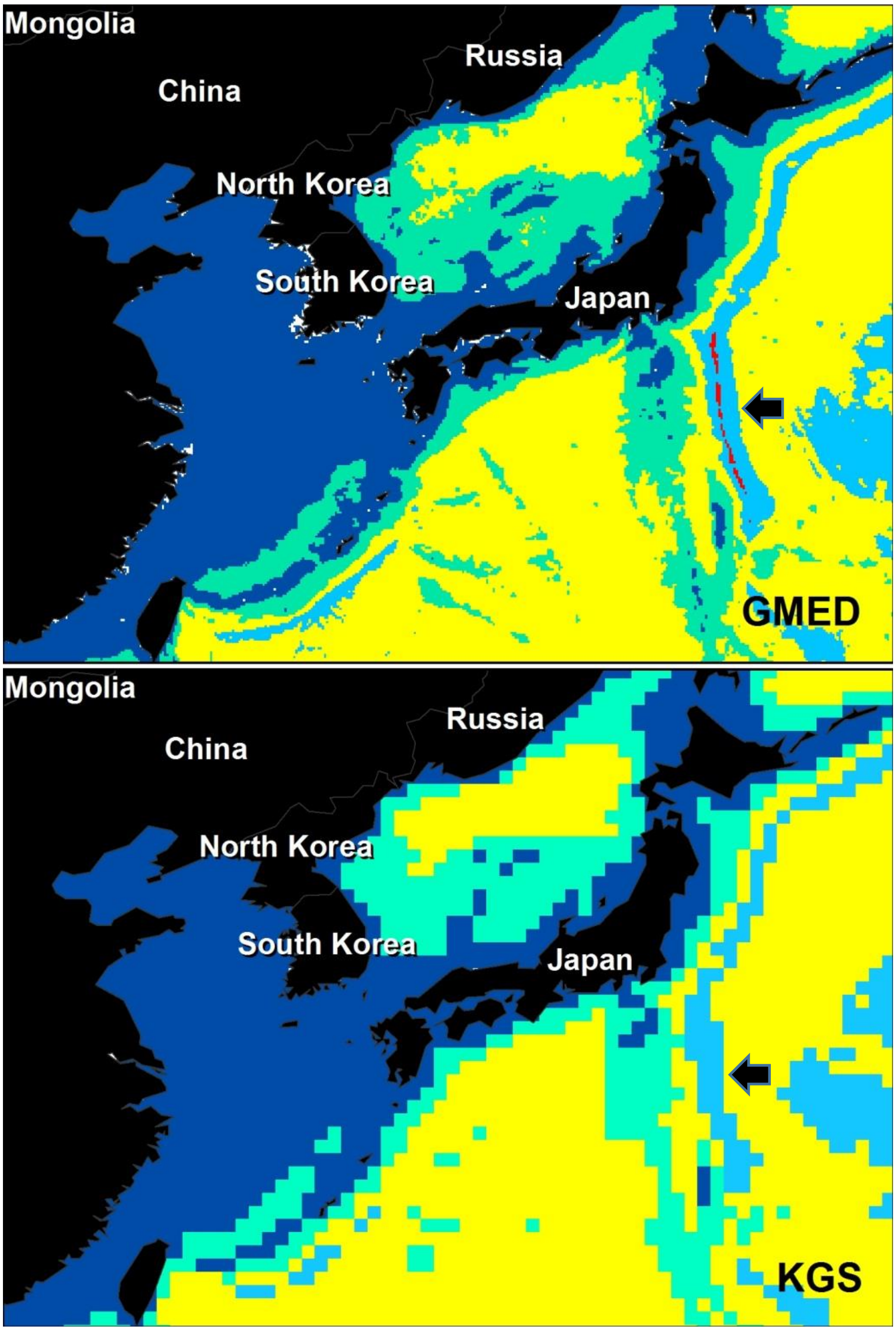


Figure 5.2. Comparison of Depth layers in GMED (top) KGS Mapper (bottom). The Mariana Trench near the east coast of Japan is clearly visible (black arrow) in GMED but absent in KGS Mapper (Scale, 1:30,000,000)

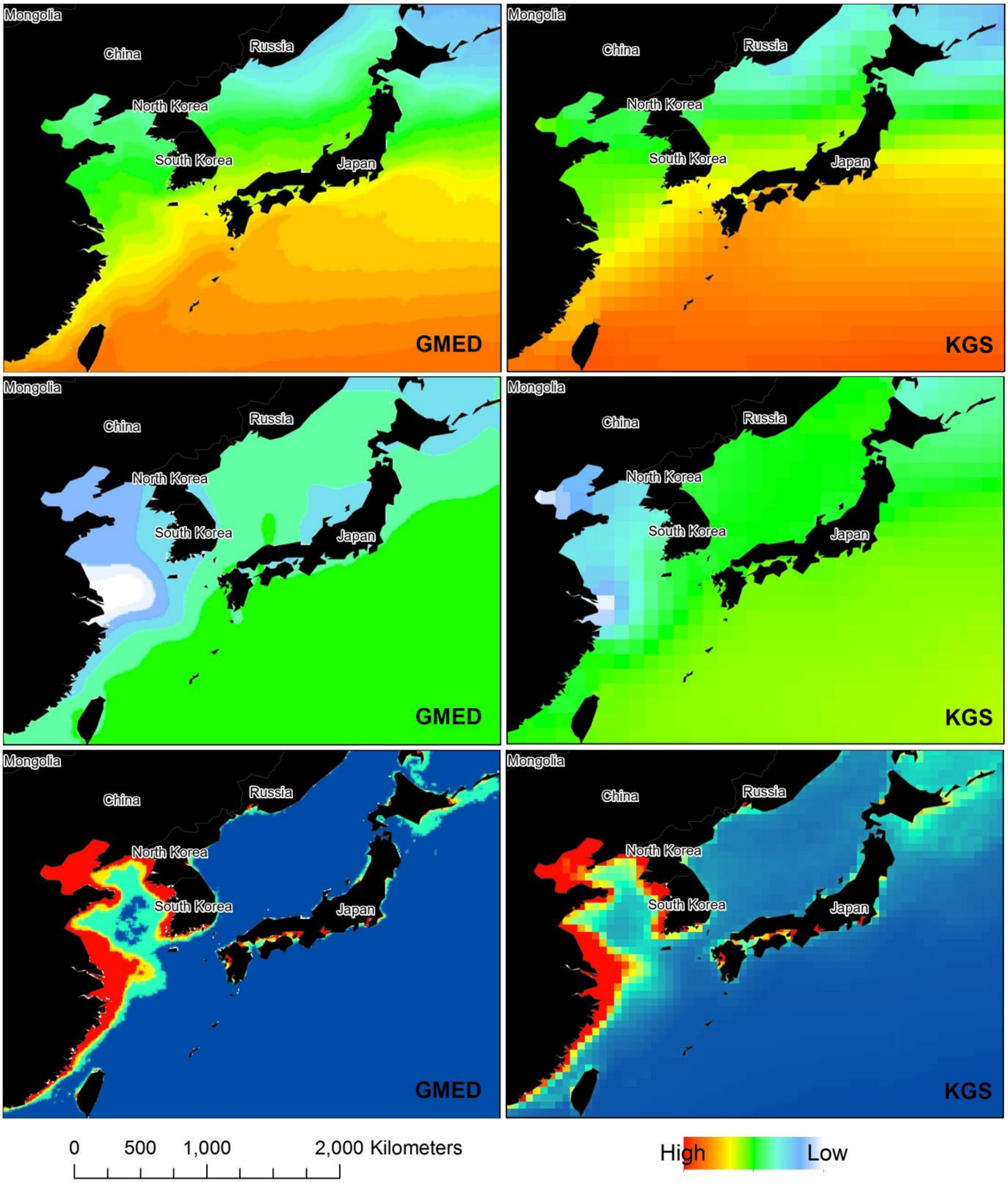


Figure 5.3. Comparison of mean surface temperature, salinity and chlorophyll-a of GMED with the KGS Mapper dataset. Data range high (red) to low (blue); 0 - 32°c surface temperature (top), 0 - 40 ppt surface salinity (middle) and 0 - 65 mg.m^{-3} chlorophyll-a (bottom).

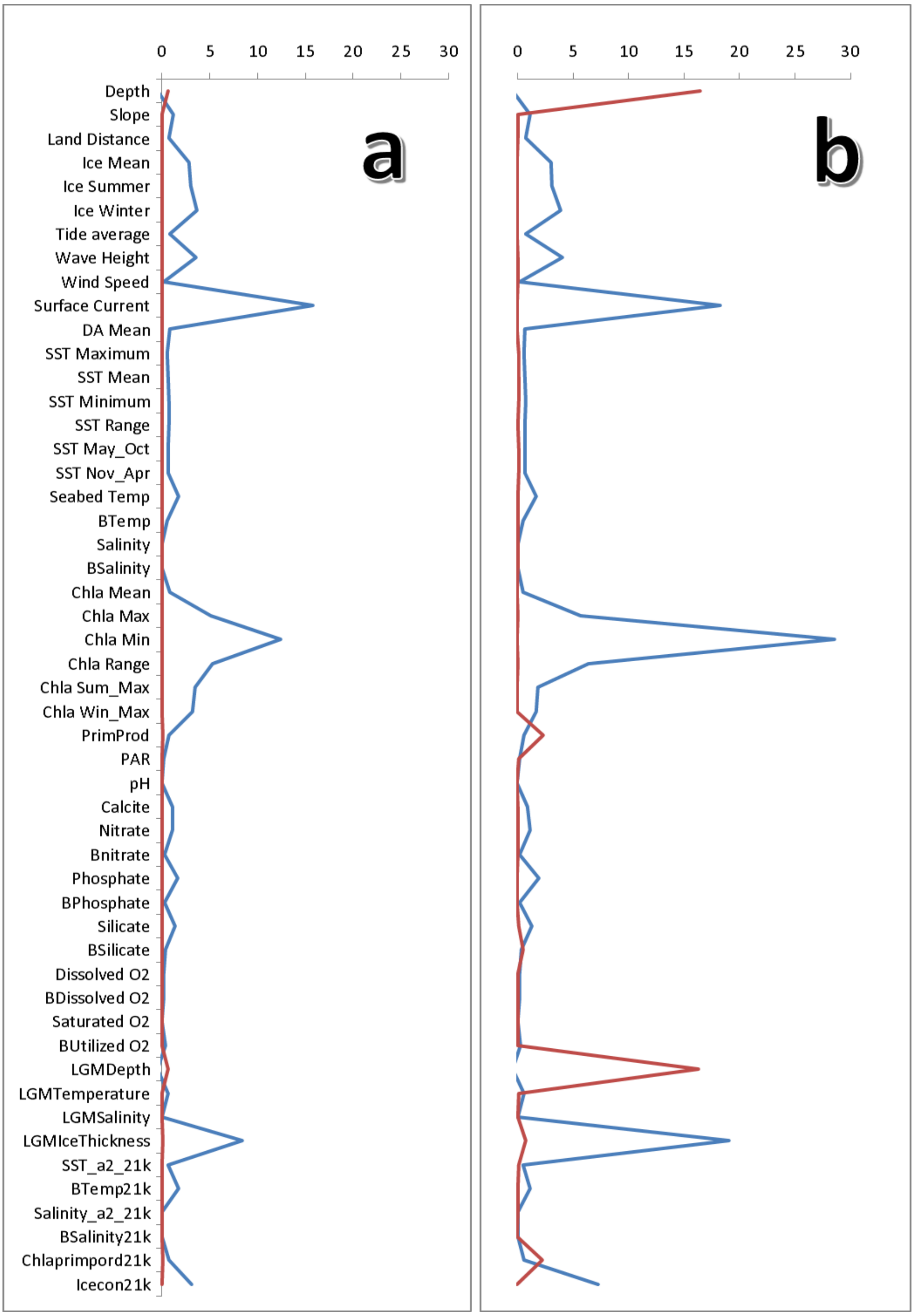
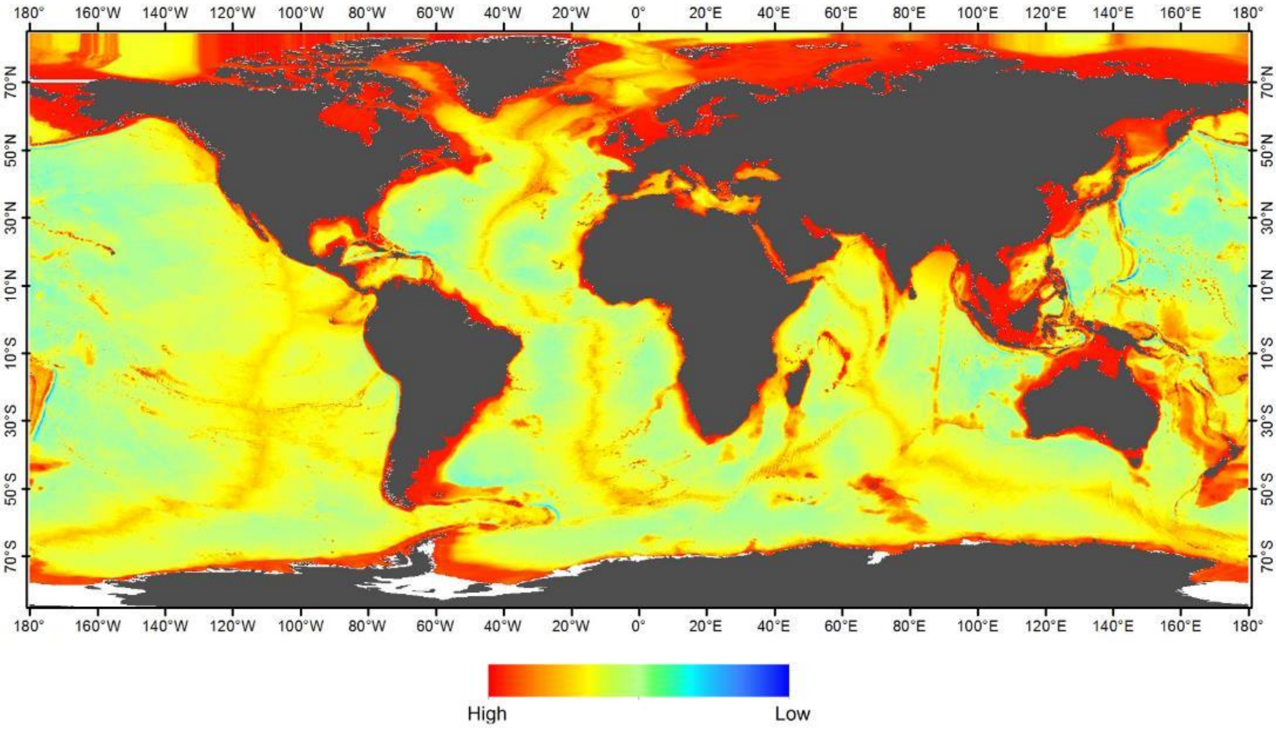


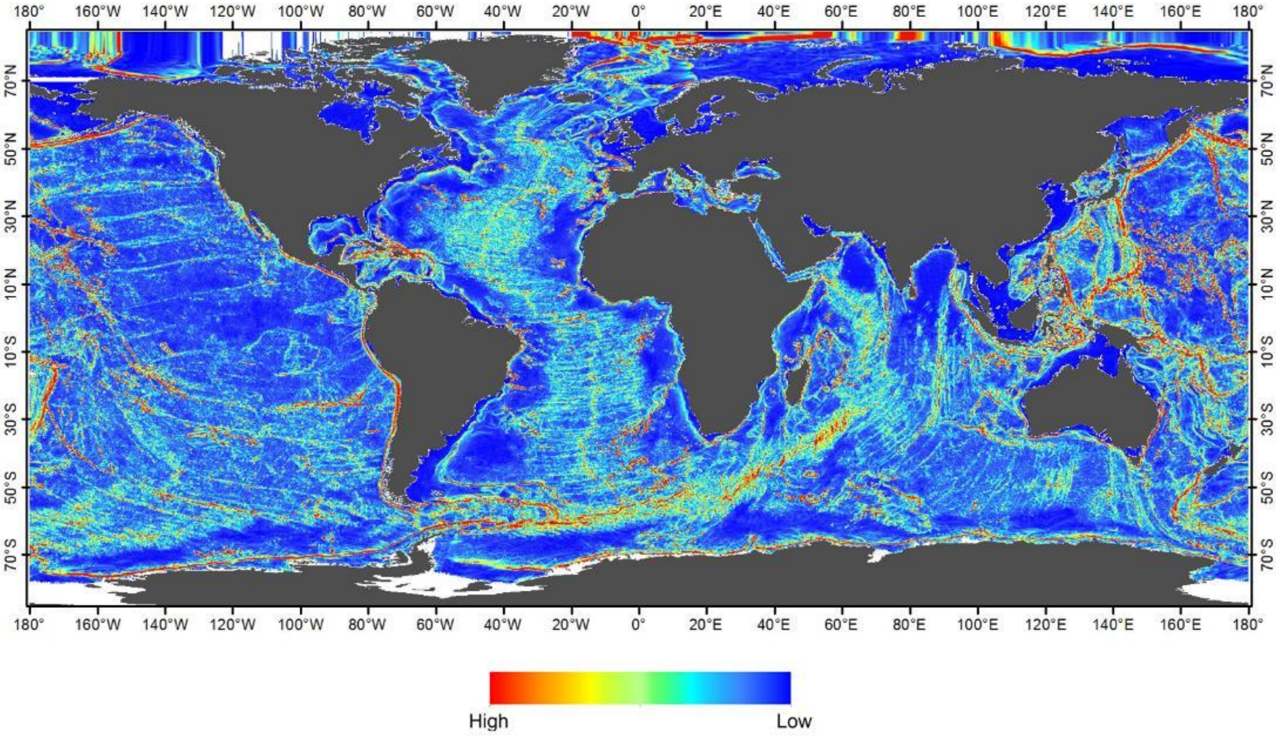
Figure 5.4. Coefficient of variation (blue), mean standard error (red) of environmental variables in *a*. source dataset, and *b*. evaluation dataset.

Figure 5.5. Visualization of GMED physical data layers.

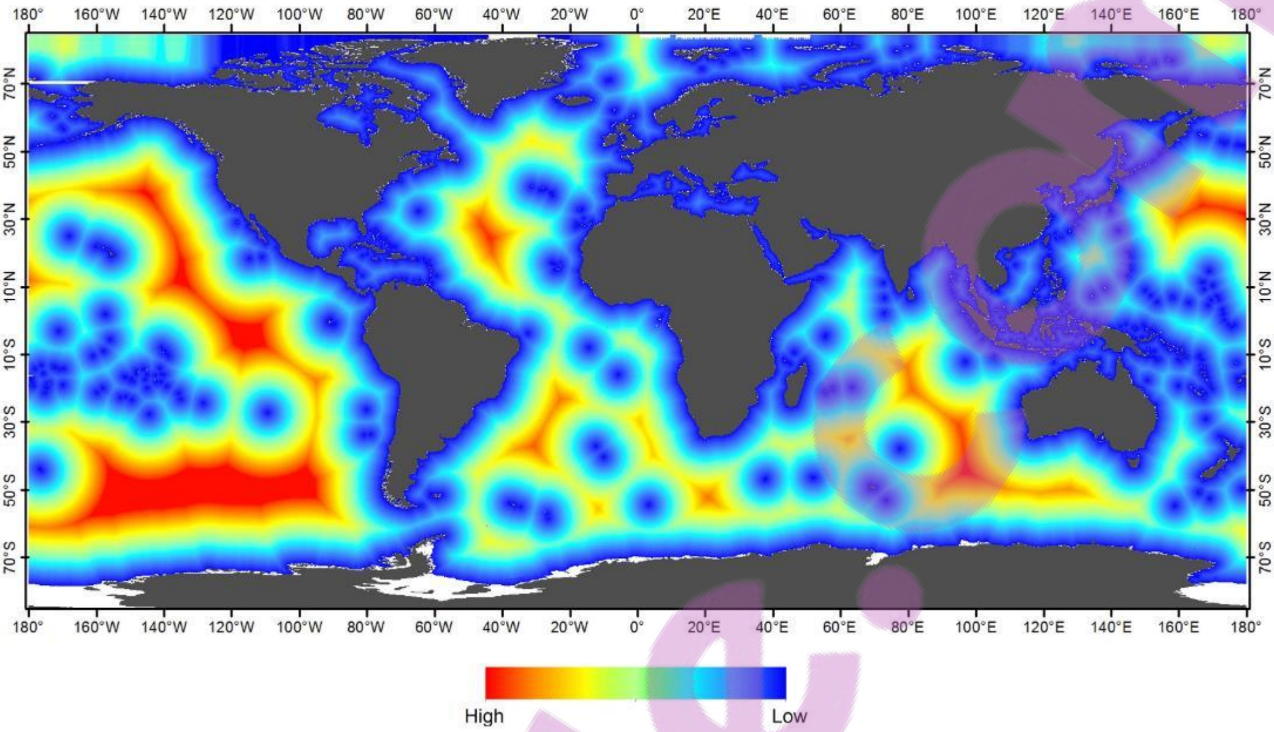
Depth



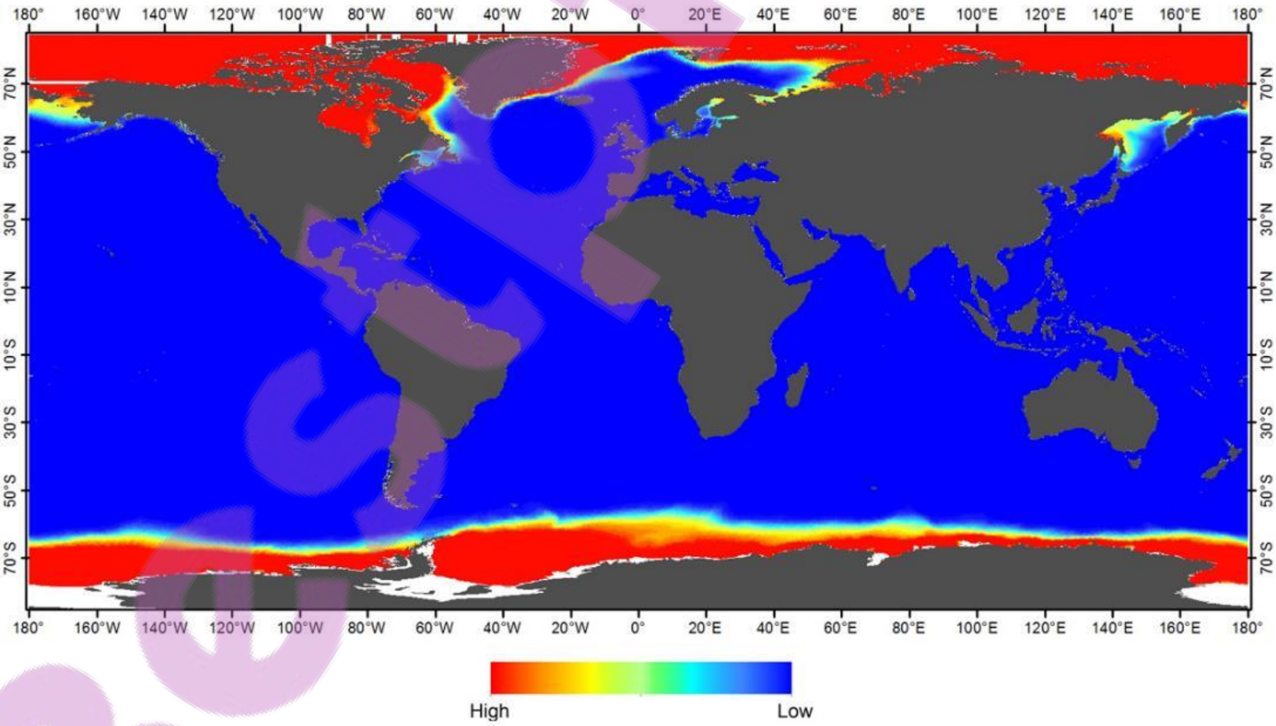
Slope



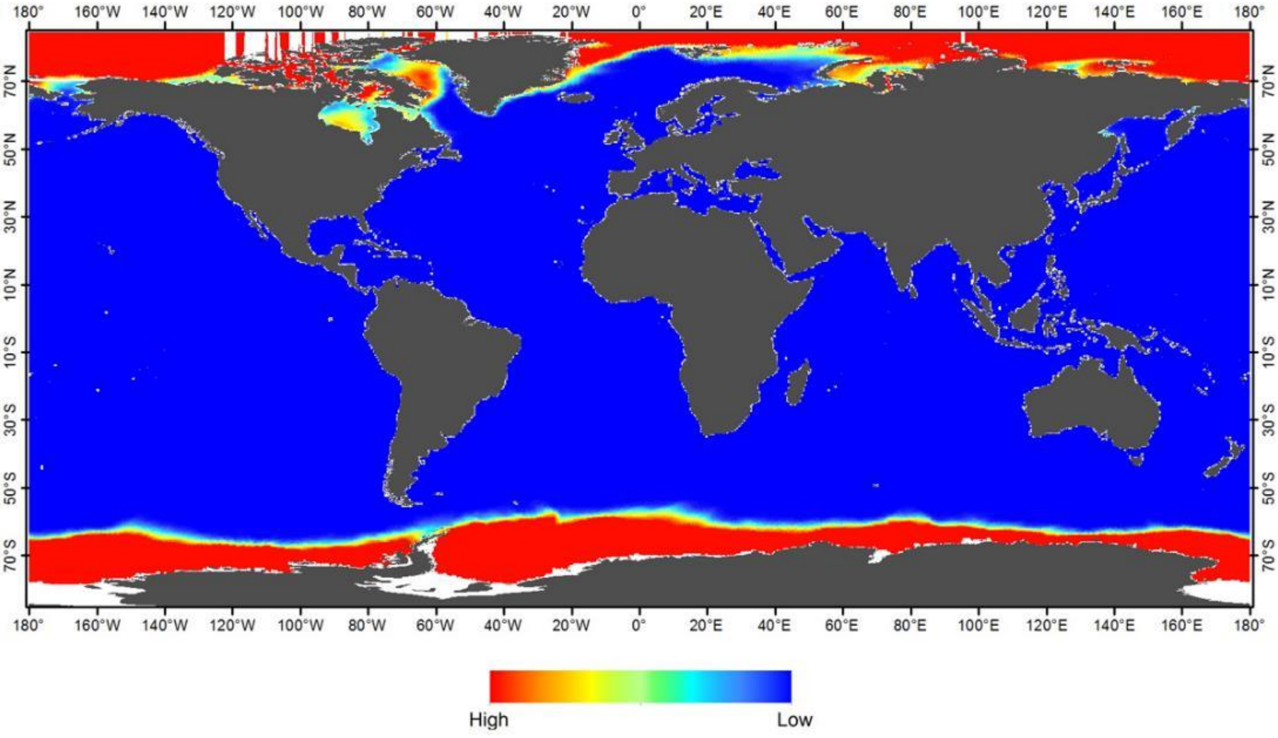
Land Distance



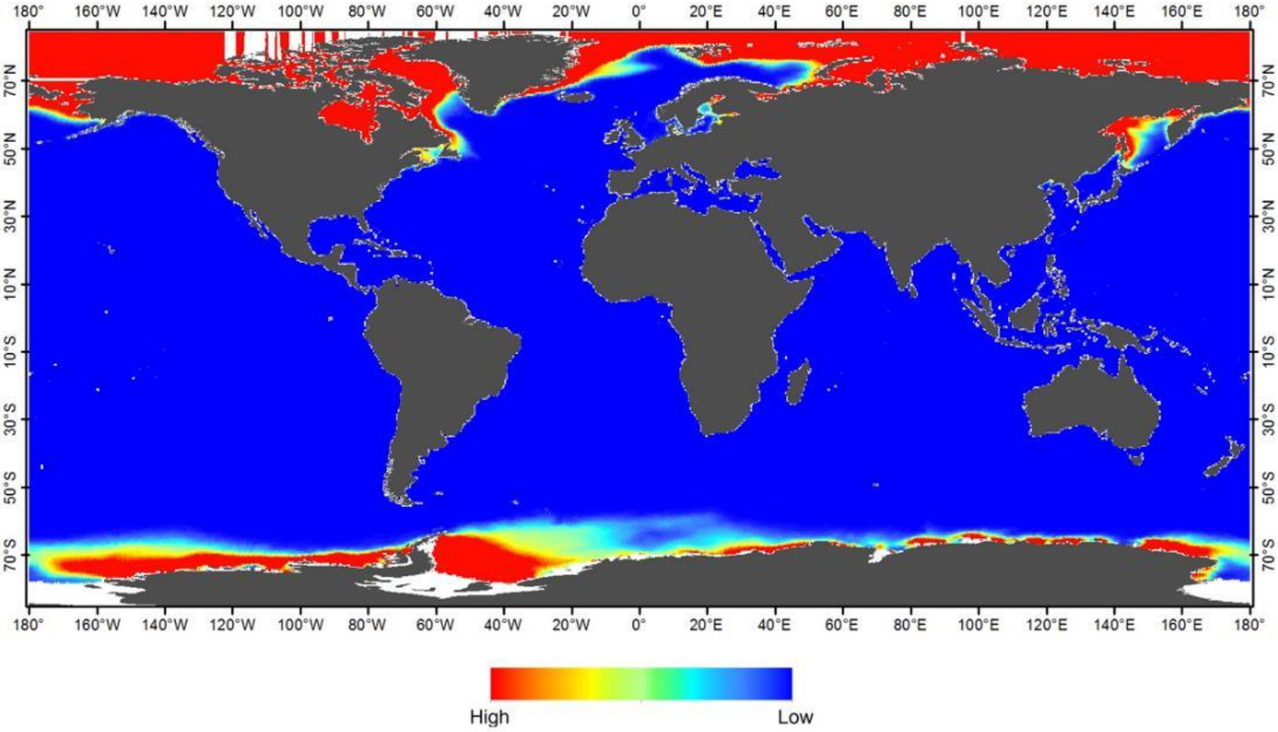
Ice cover Mean



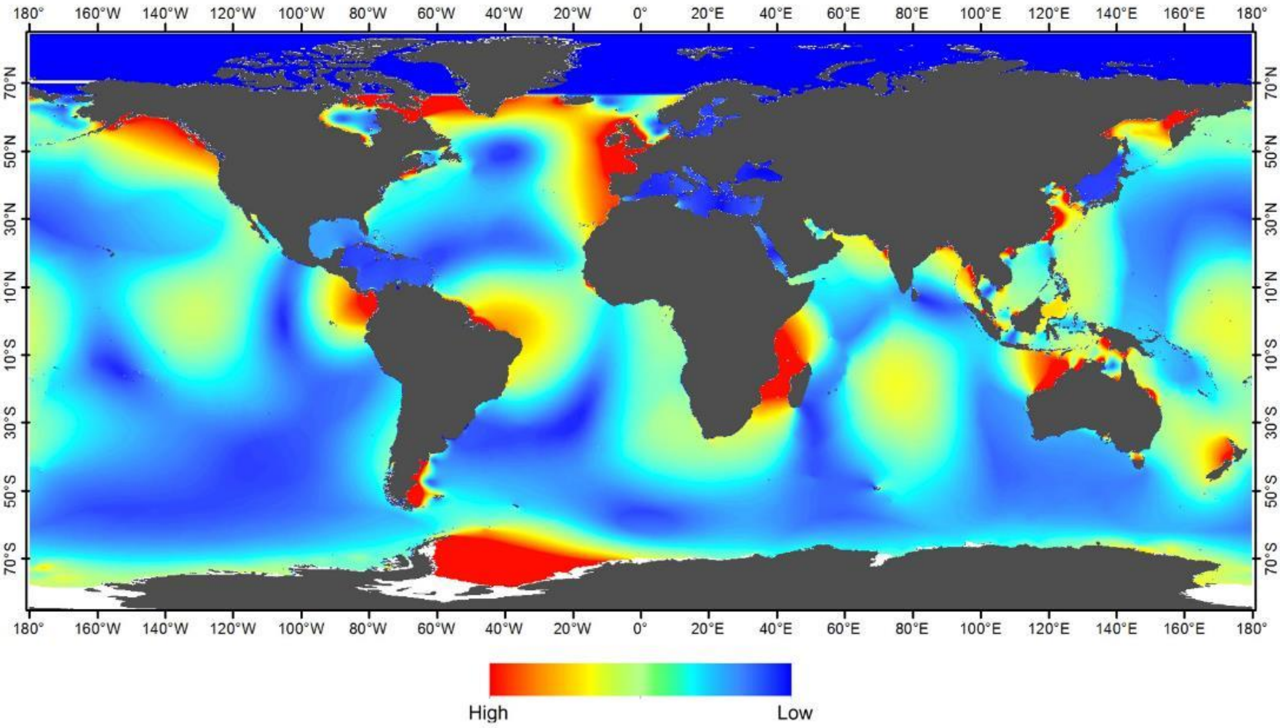
Ice Cover Summer (May-Oct)



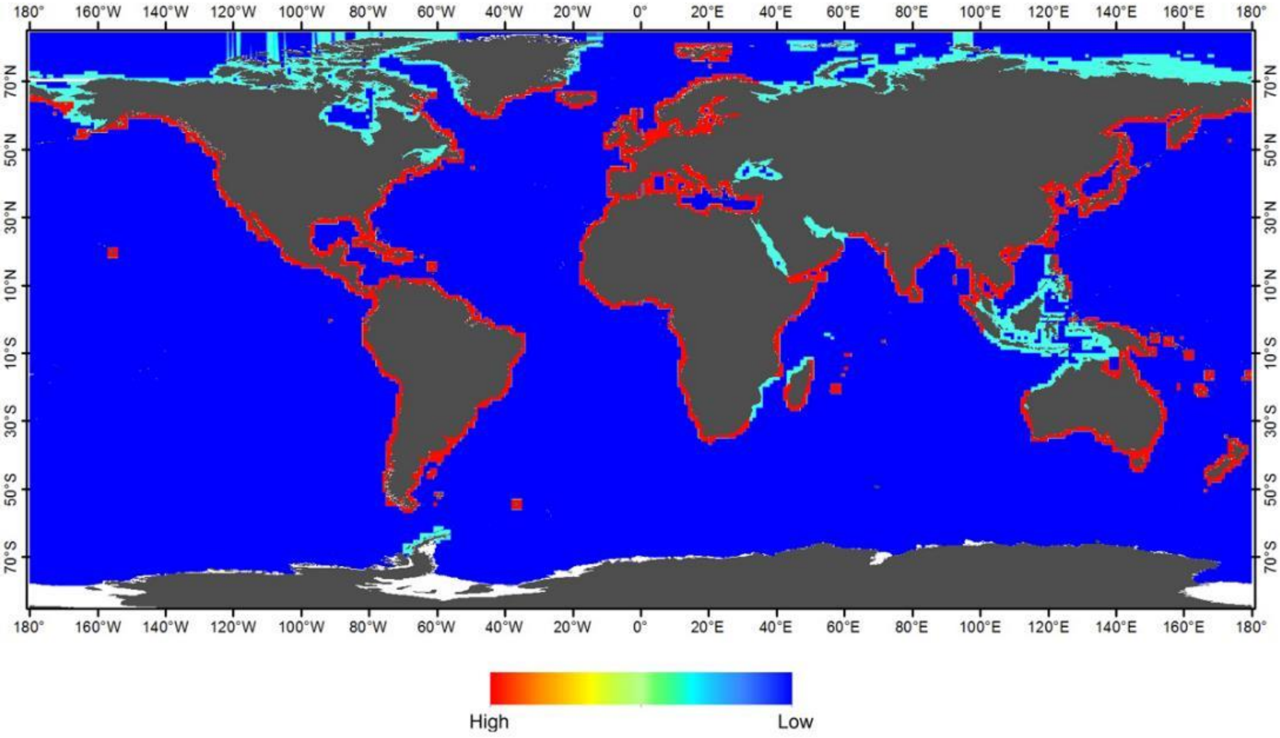
Ice Cover Winter (Nov- Apr)



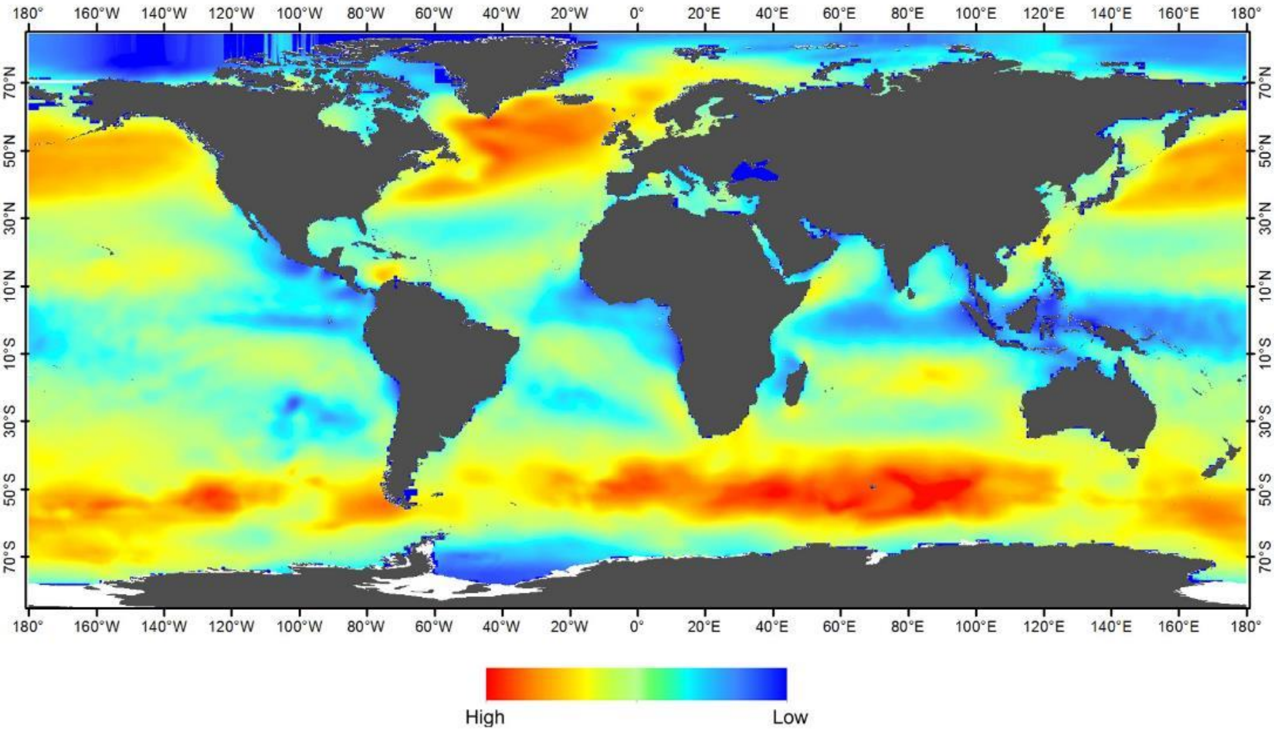
Tide Range average



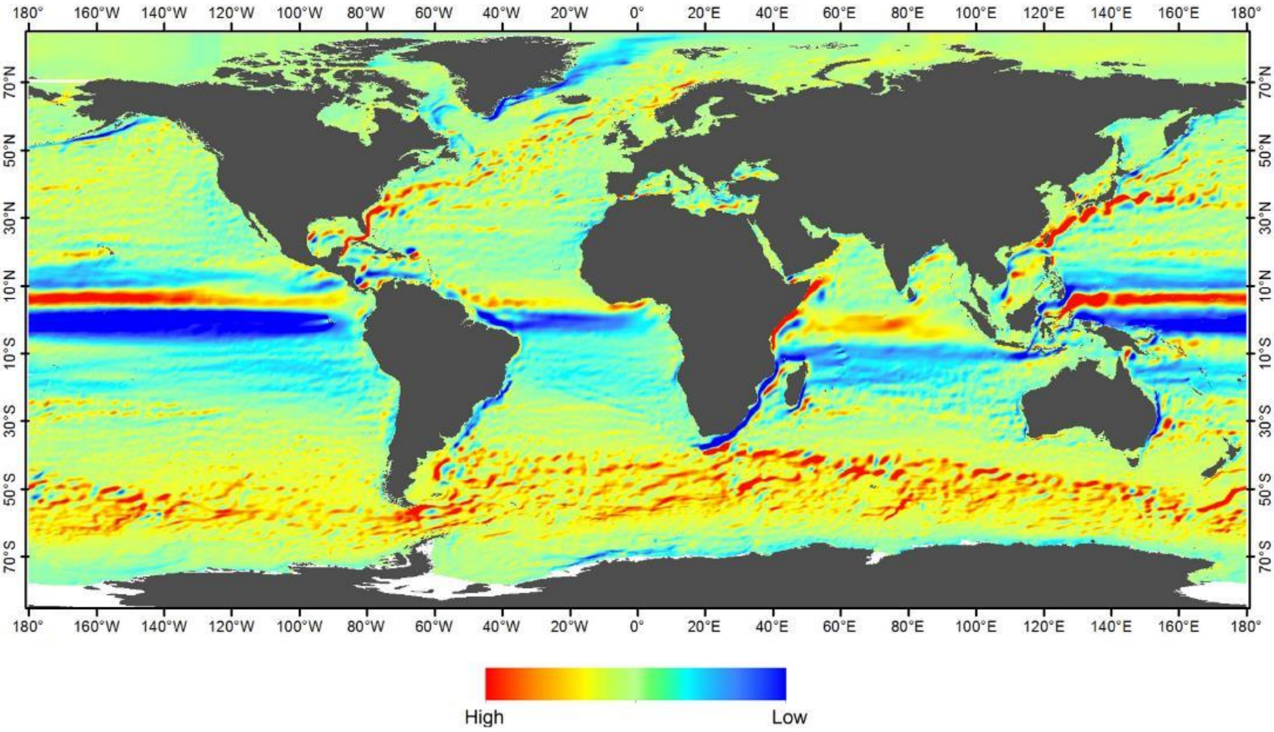
Wave Height



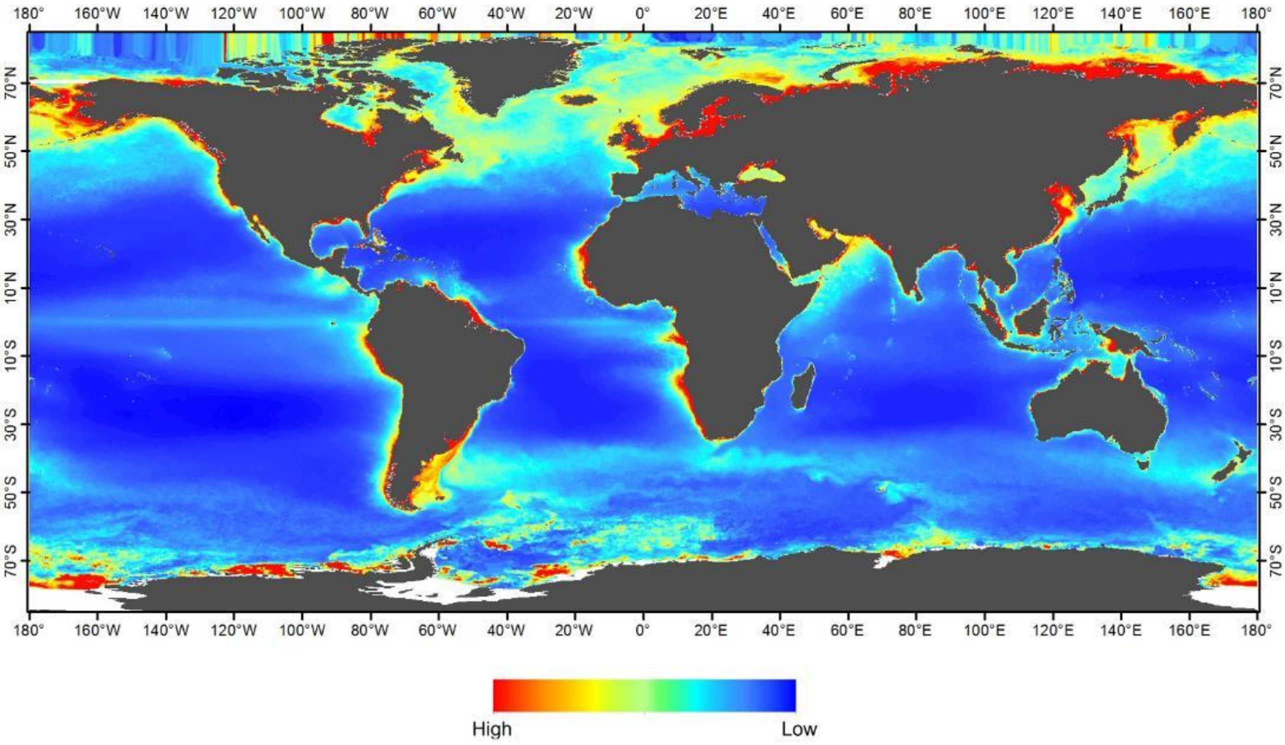
Wind Speed



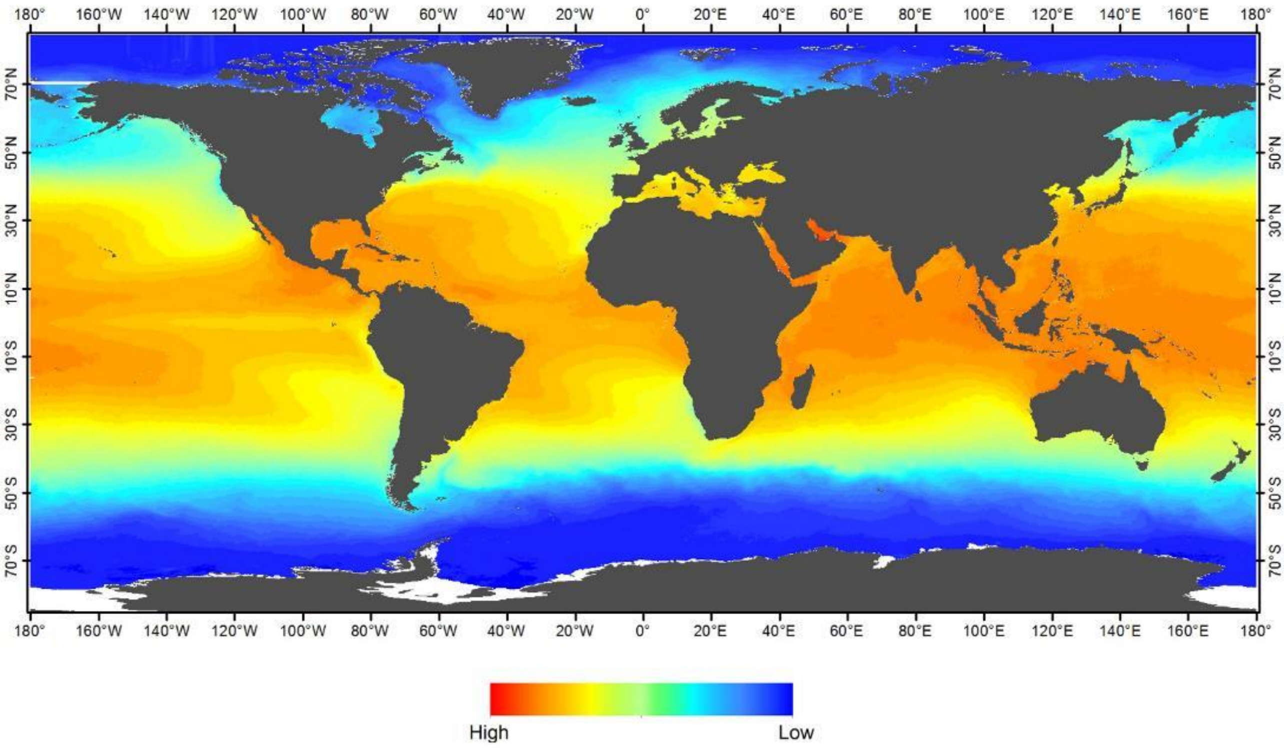
Surface Current



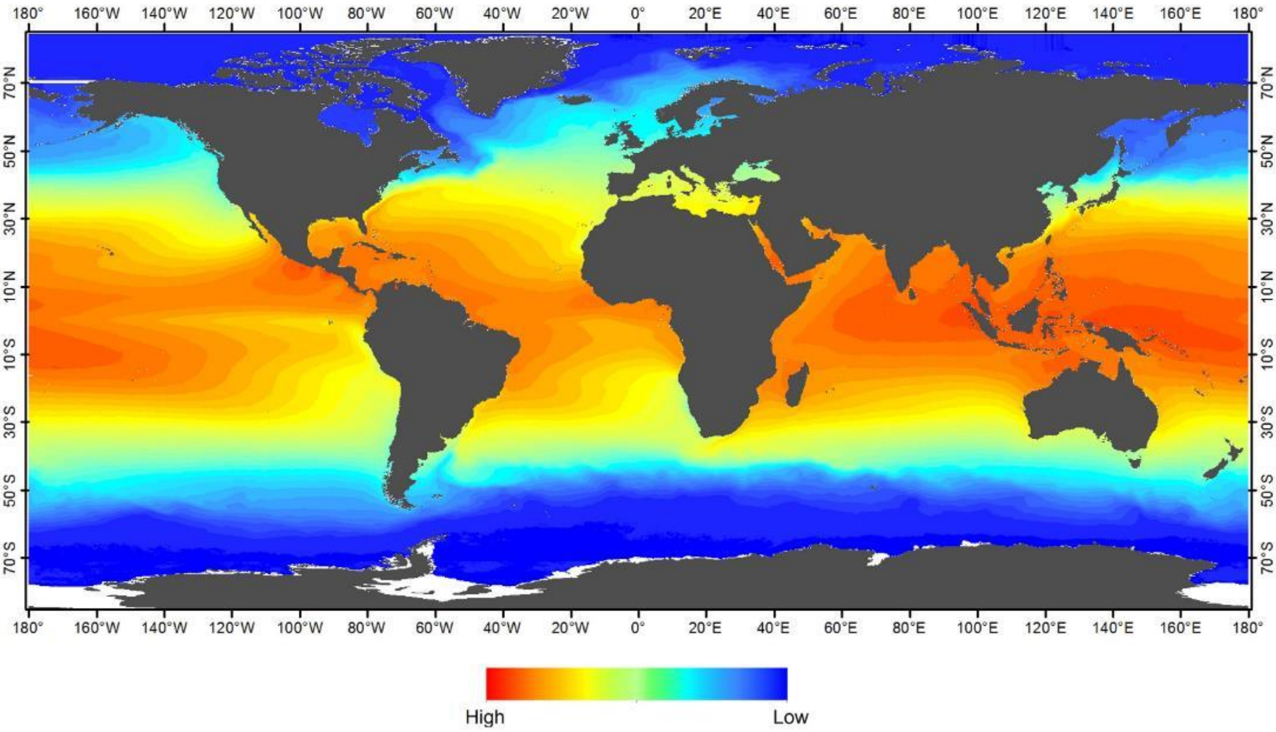
Diffuse Attenuation Coefficient Mean



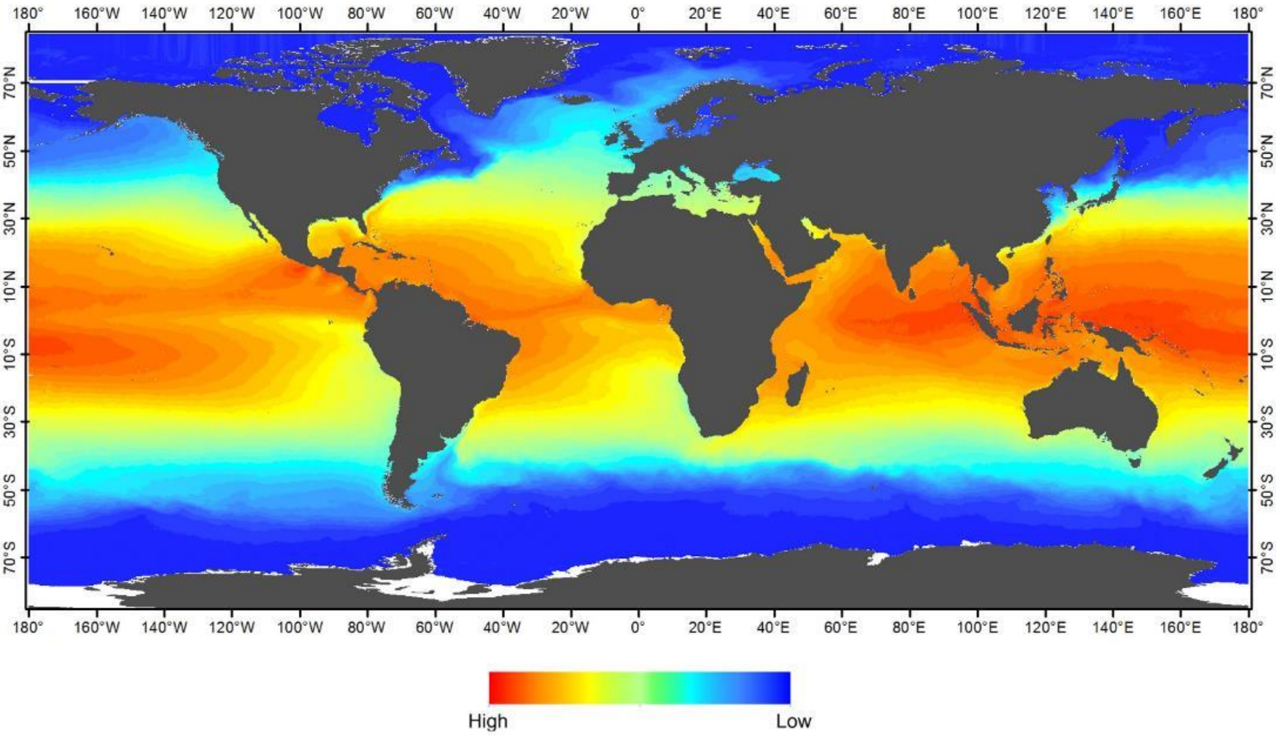
Sea Surface Temperature Maximum



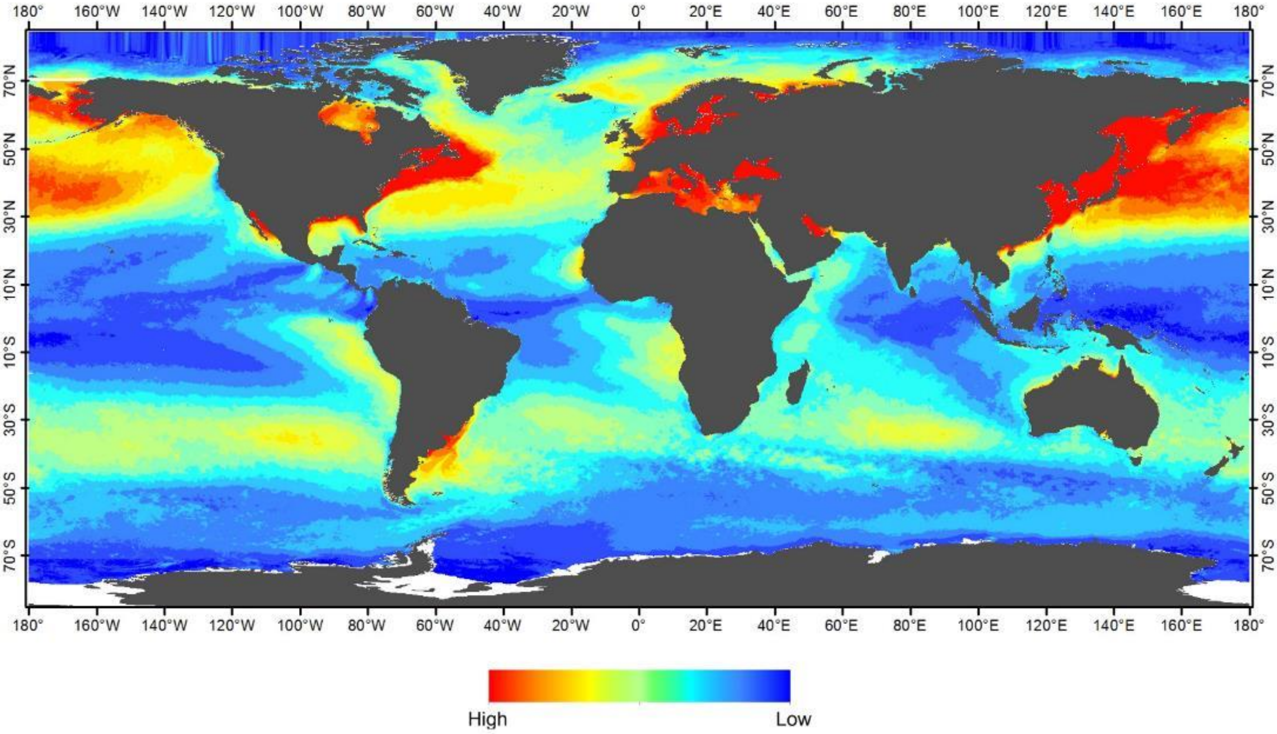
Sea Surface Temperature Mean



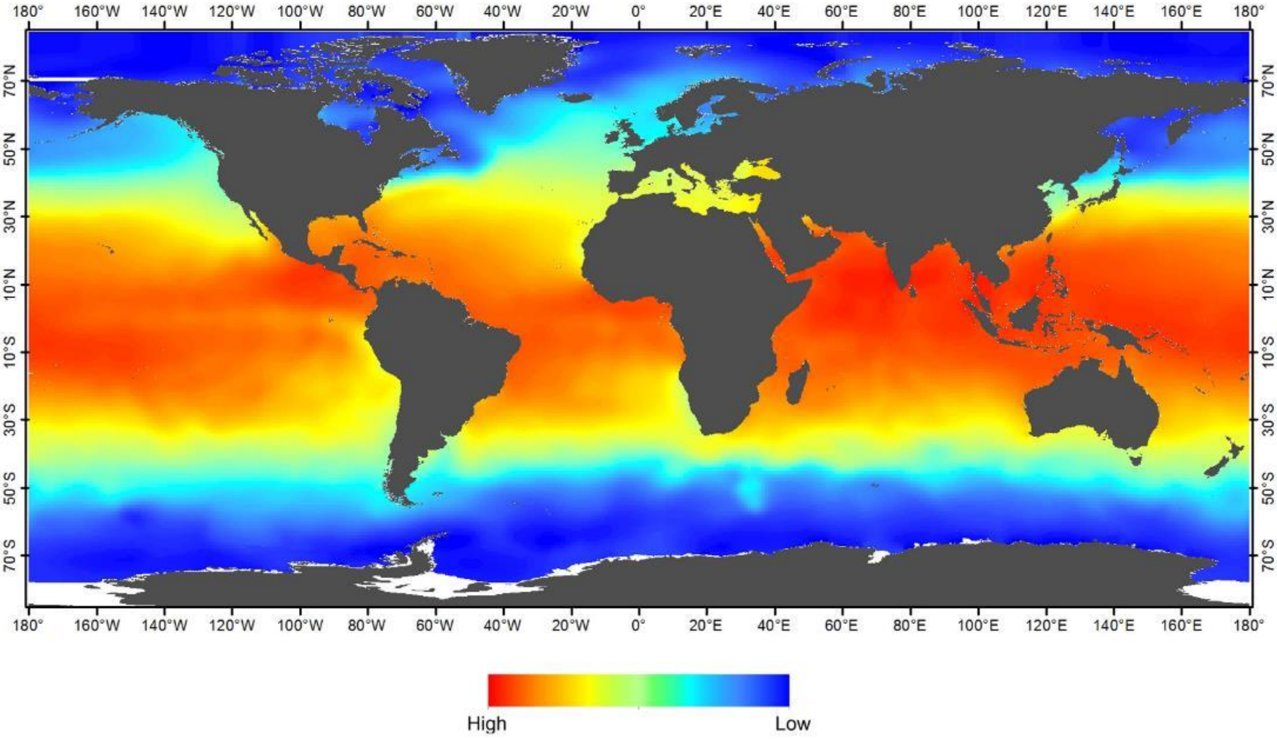
Sea Surface Temperature Minimum



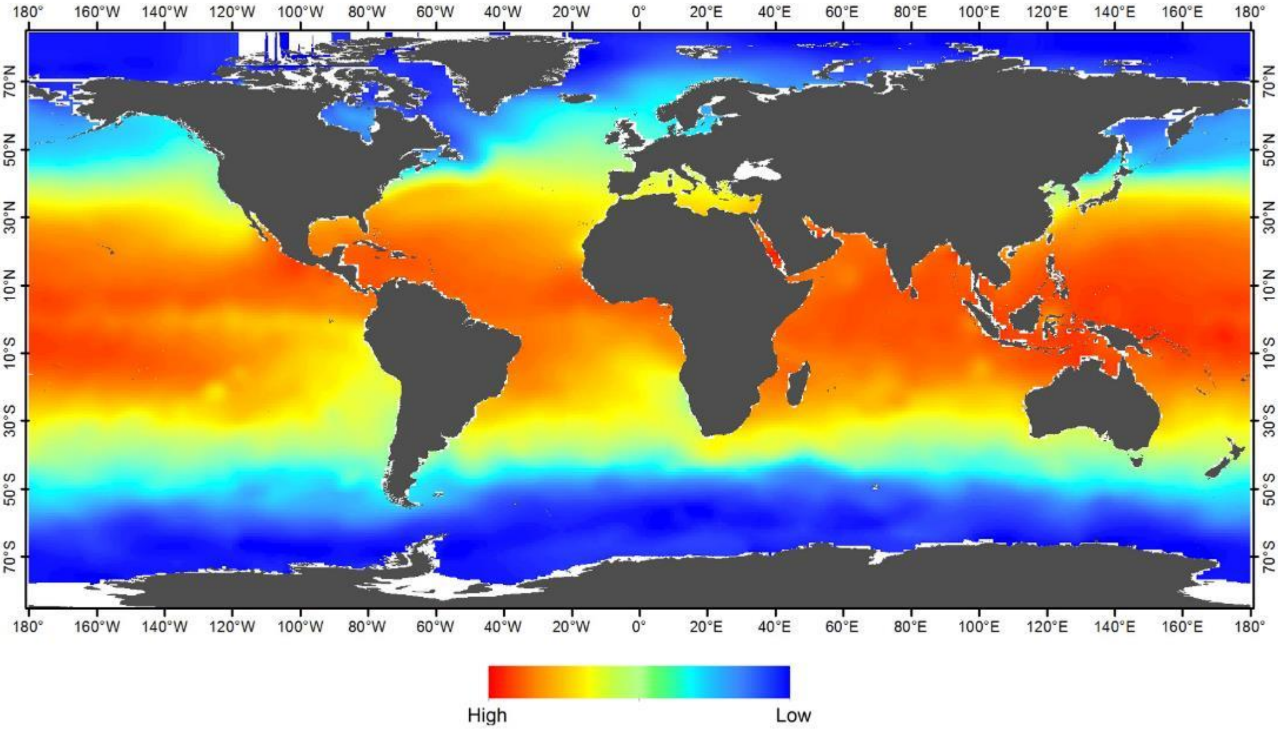
Sea Surface Temperature Range



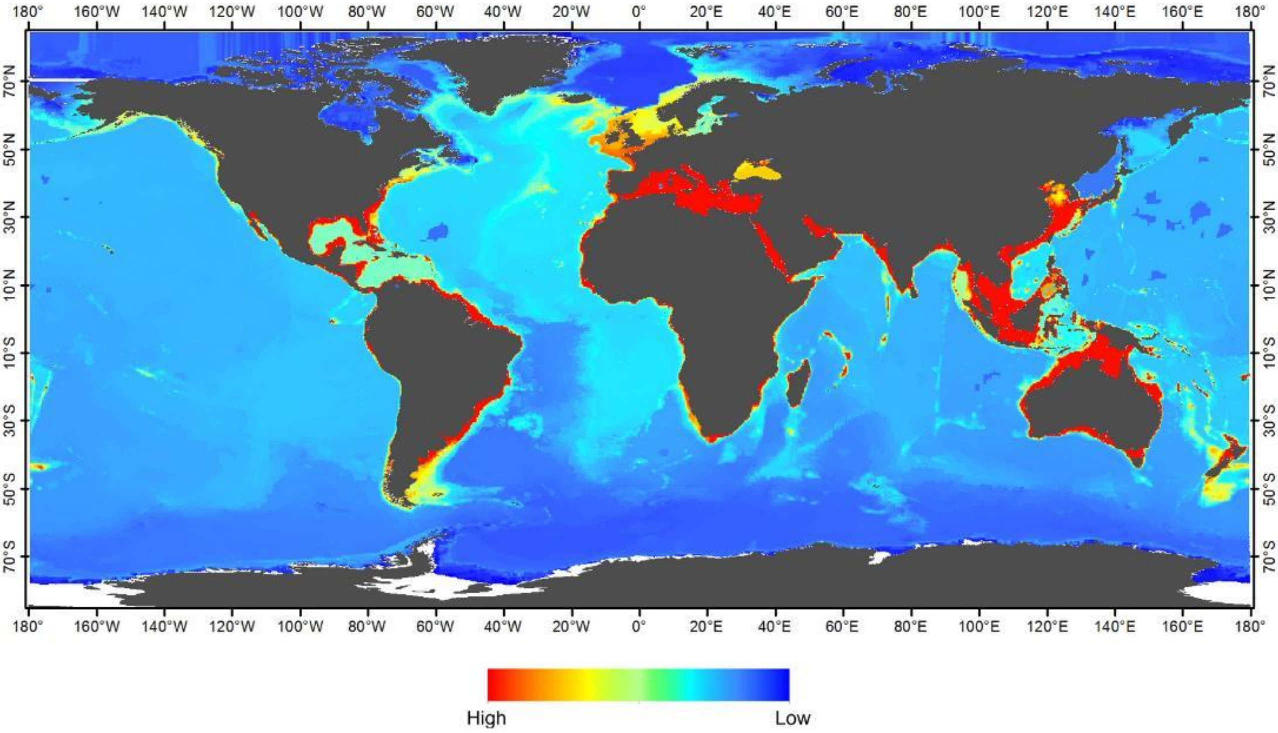
Sea Surface Temperature Summer (May-Oct)



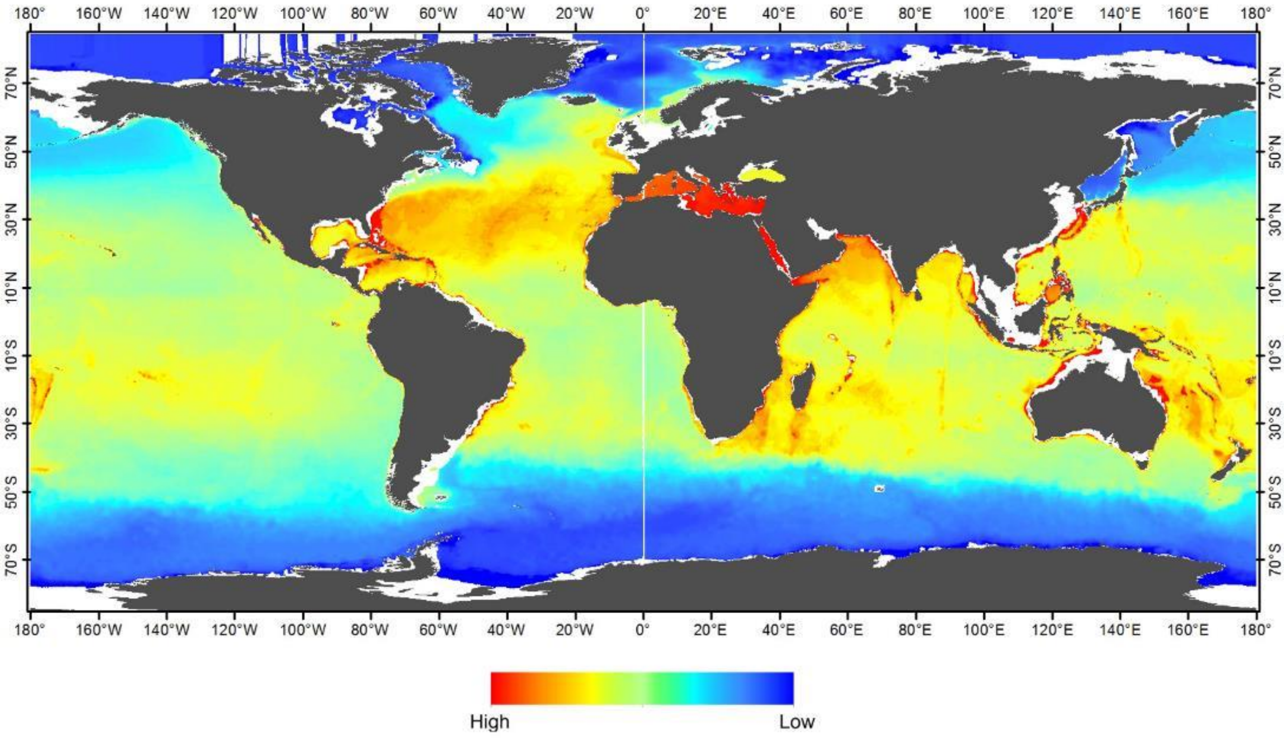
Sea Surface Temperature Winter (Nov-Apr)



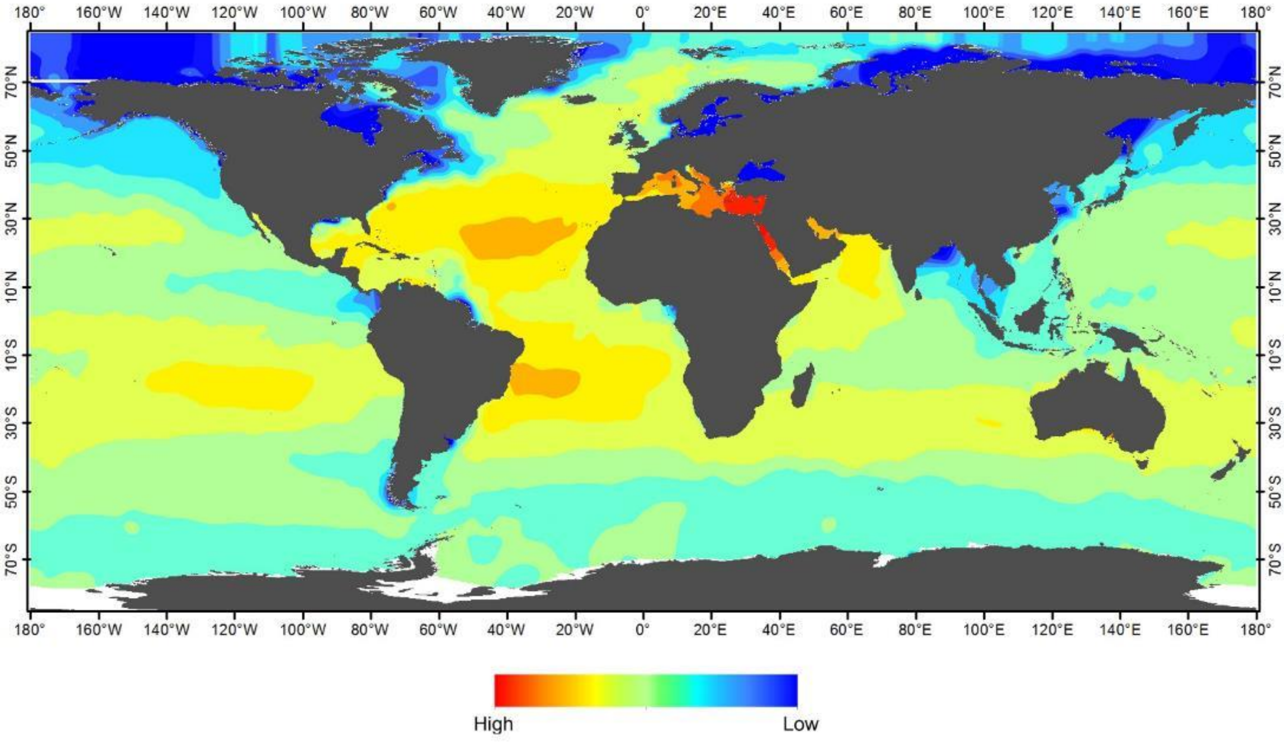
Seabed Mean Temperature



Water Column Temperature Mean



Salinity



Bottom Salinity

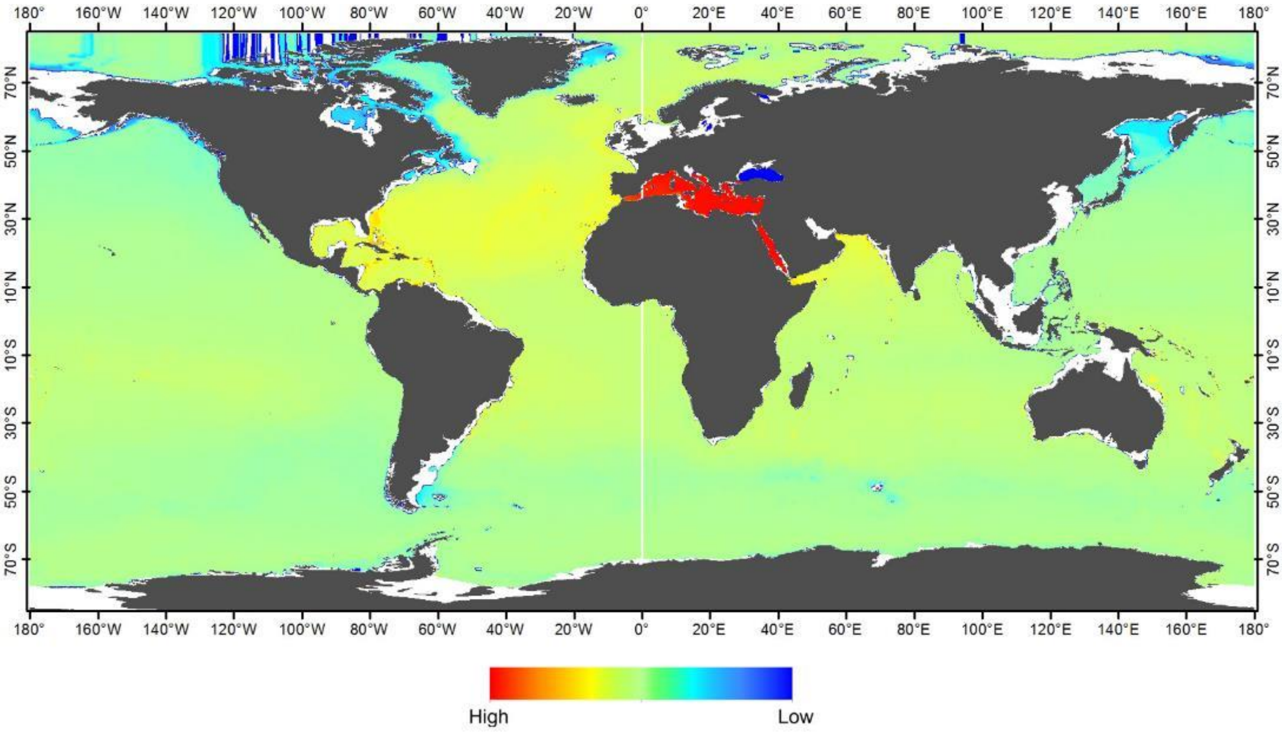
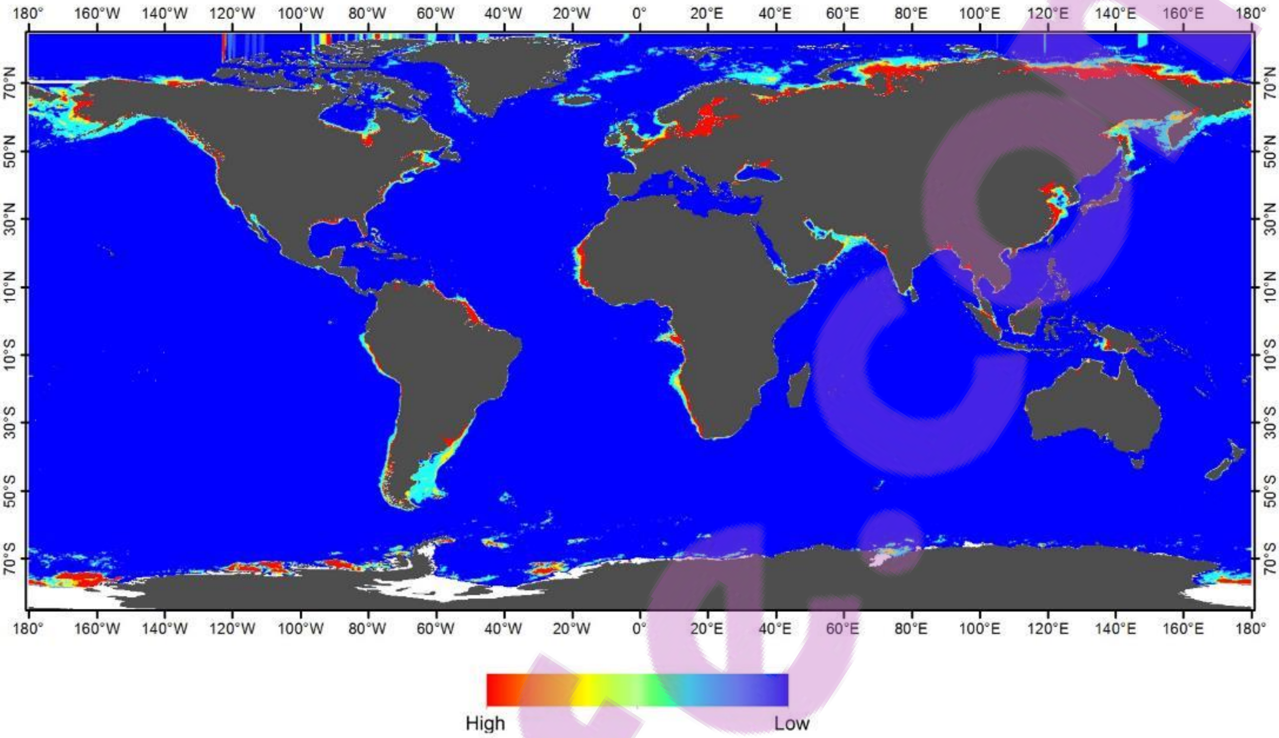
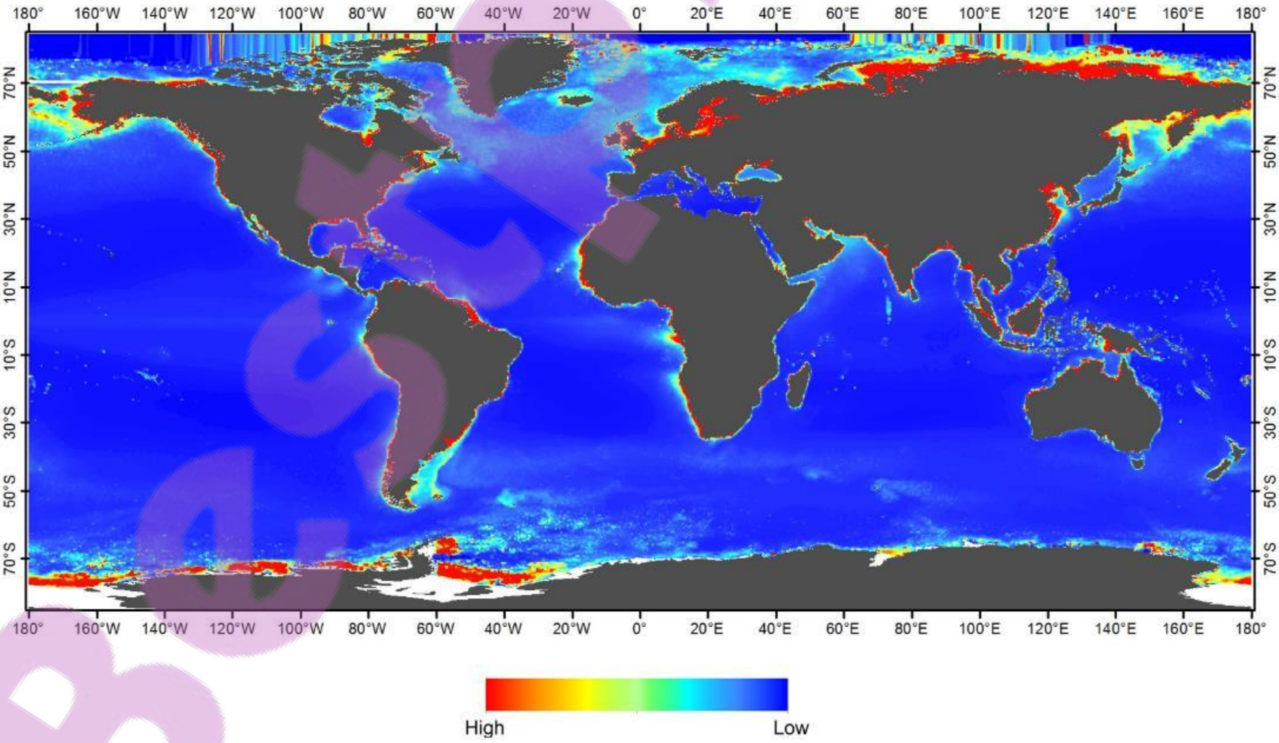


Figure 5.6. Visualization of GMED biochemical data layers.

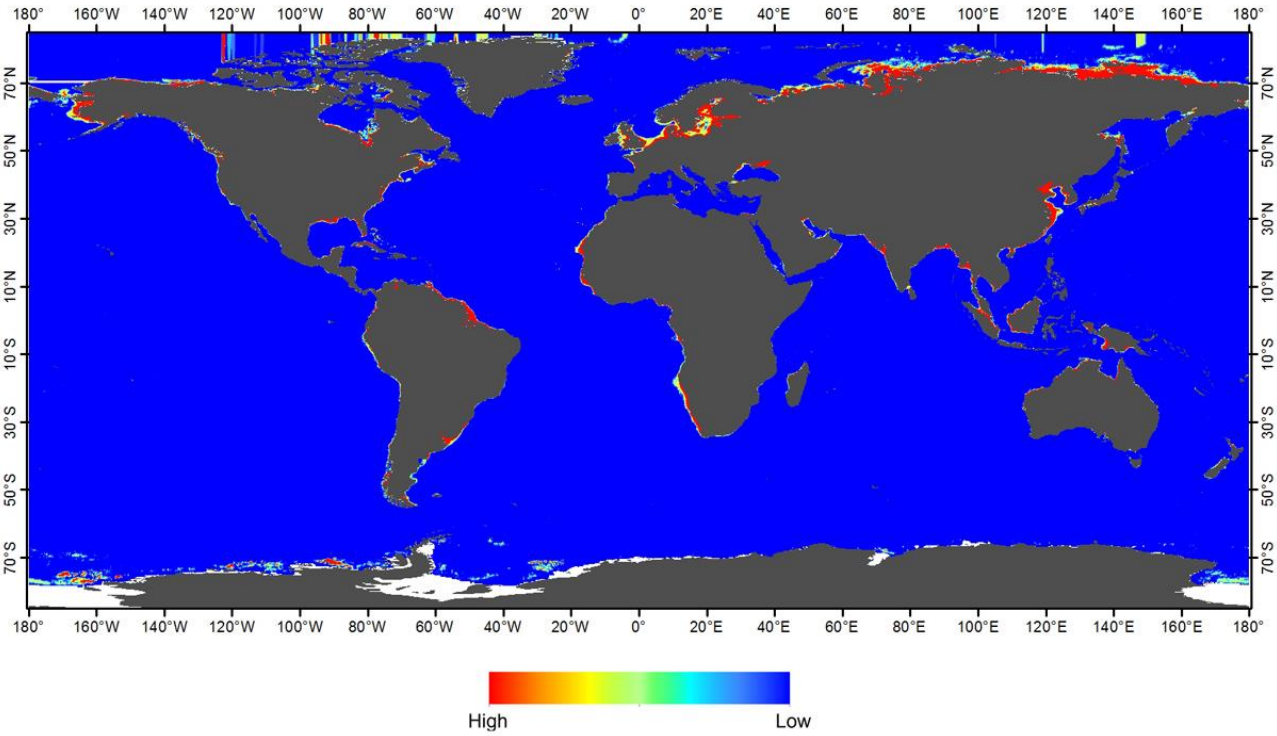
Chlorophyll-a Mean



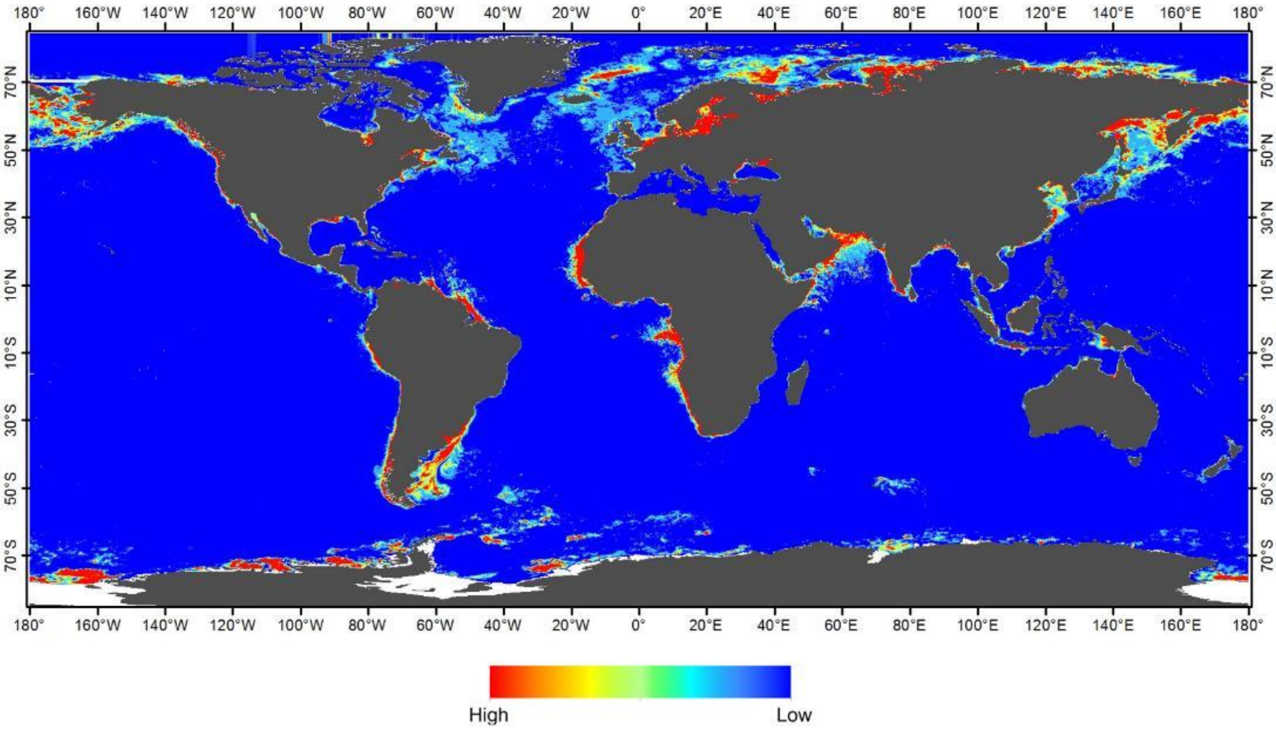
Chlorophyll-a Maximum



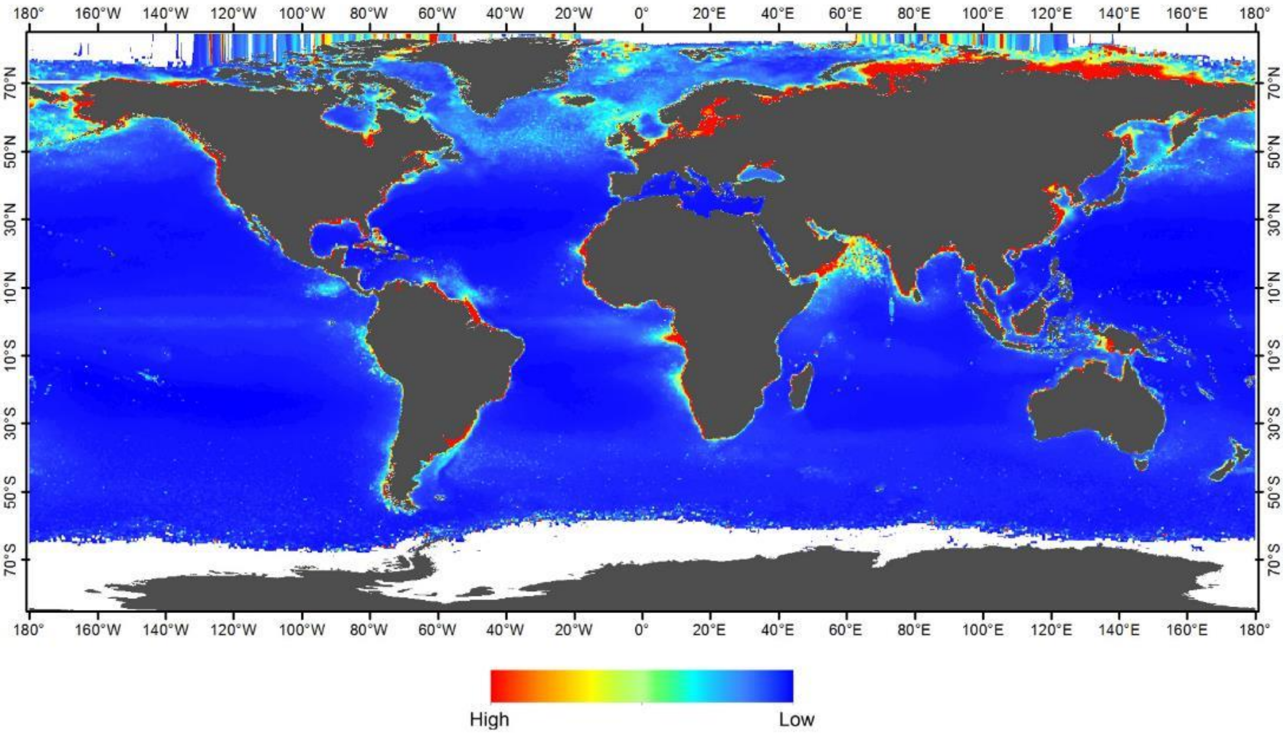
Chlorophyll-a Minimum



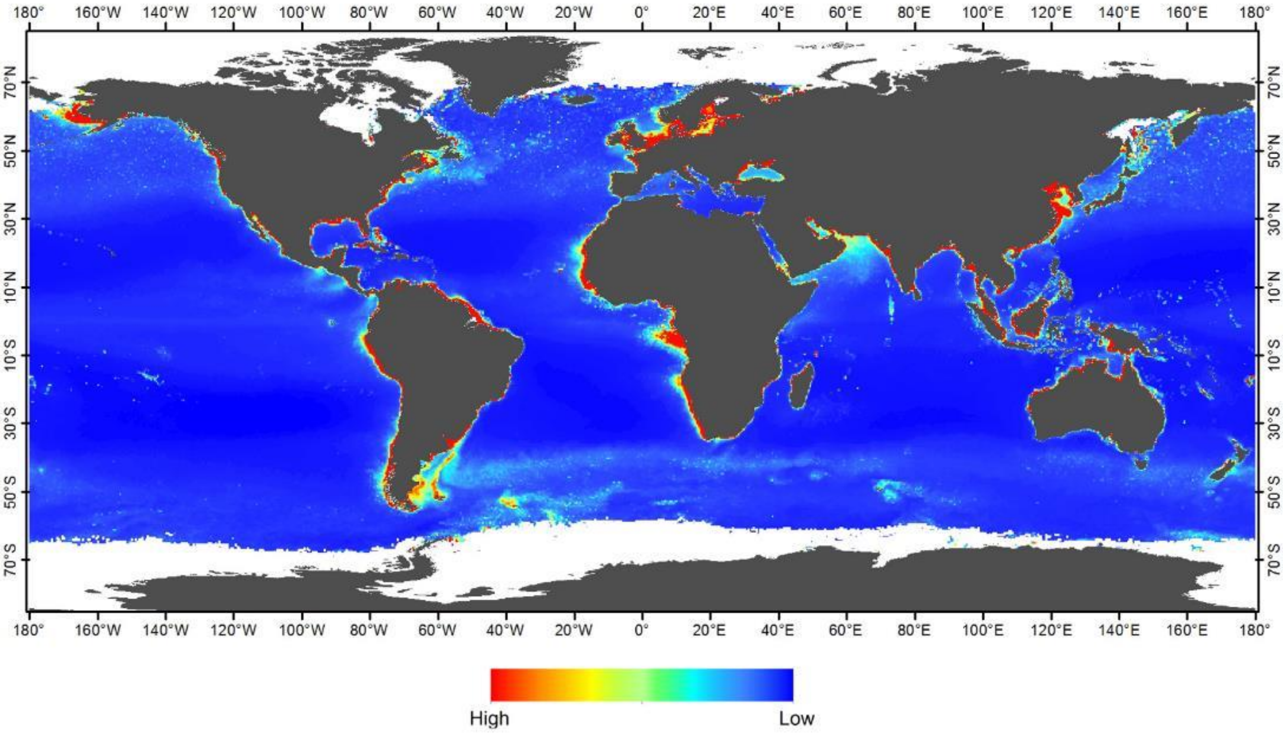
Chlorophyll-a Range



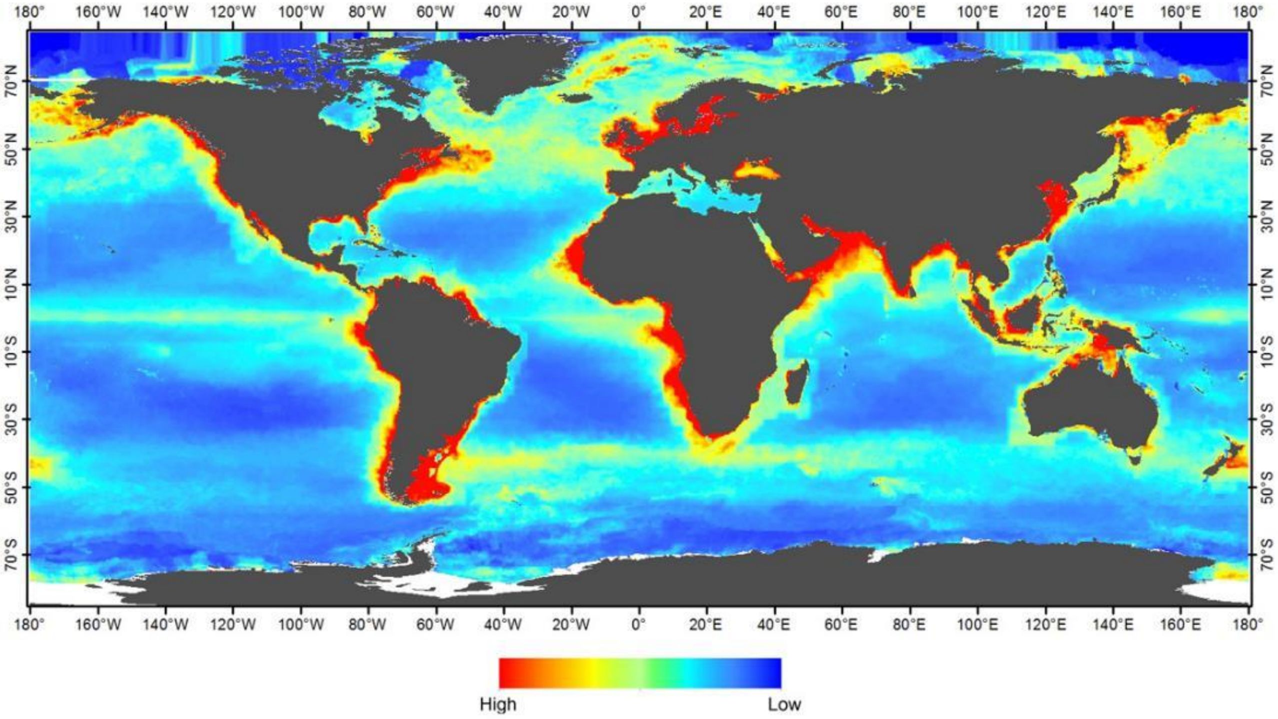
Chlorophyll-a Summer (May-Oct) Maximum



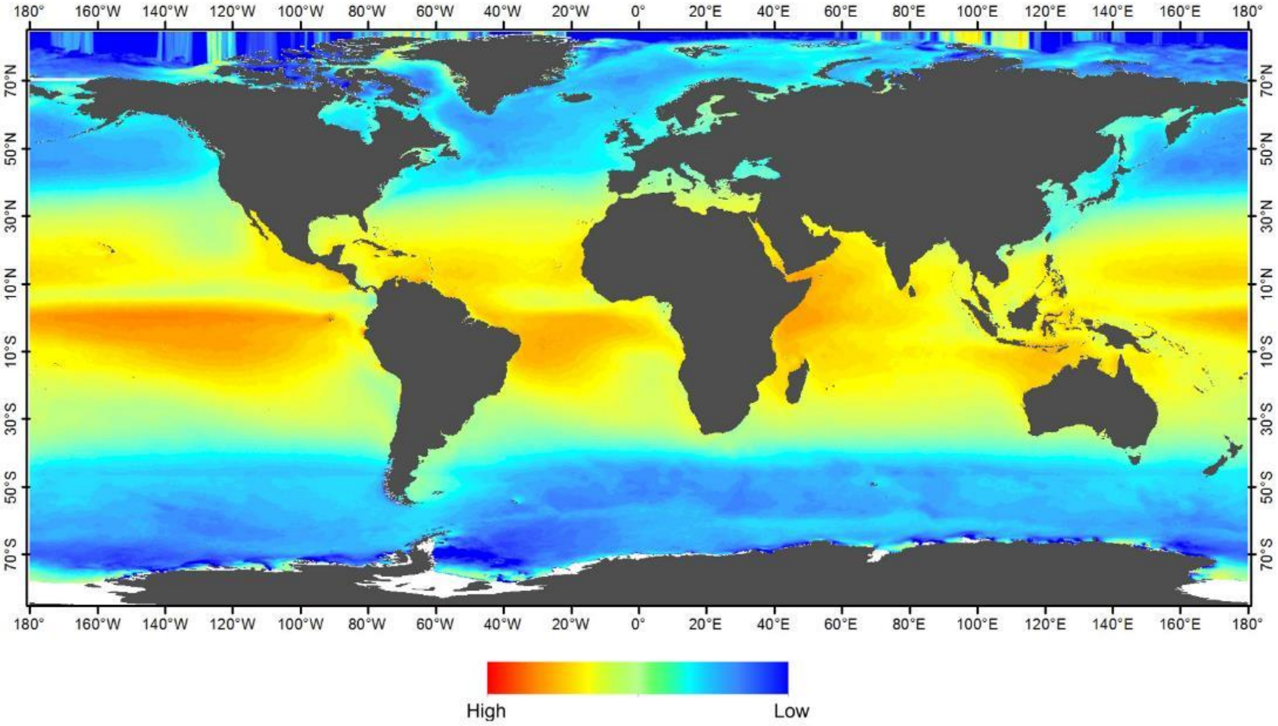
Chlorophyll-a Winter (Nov-Apr) Maximum



Primary Productivity



Photosynthetically Active Radiation Mean



pH

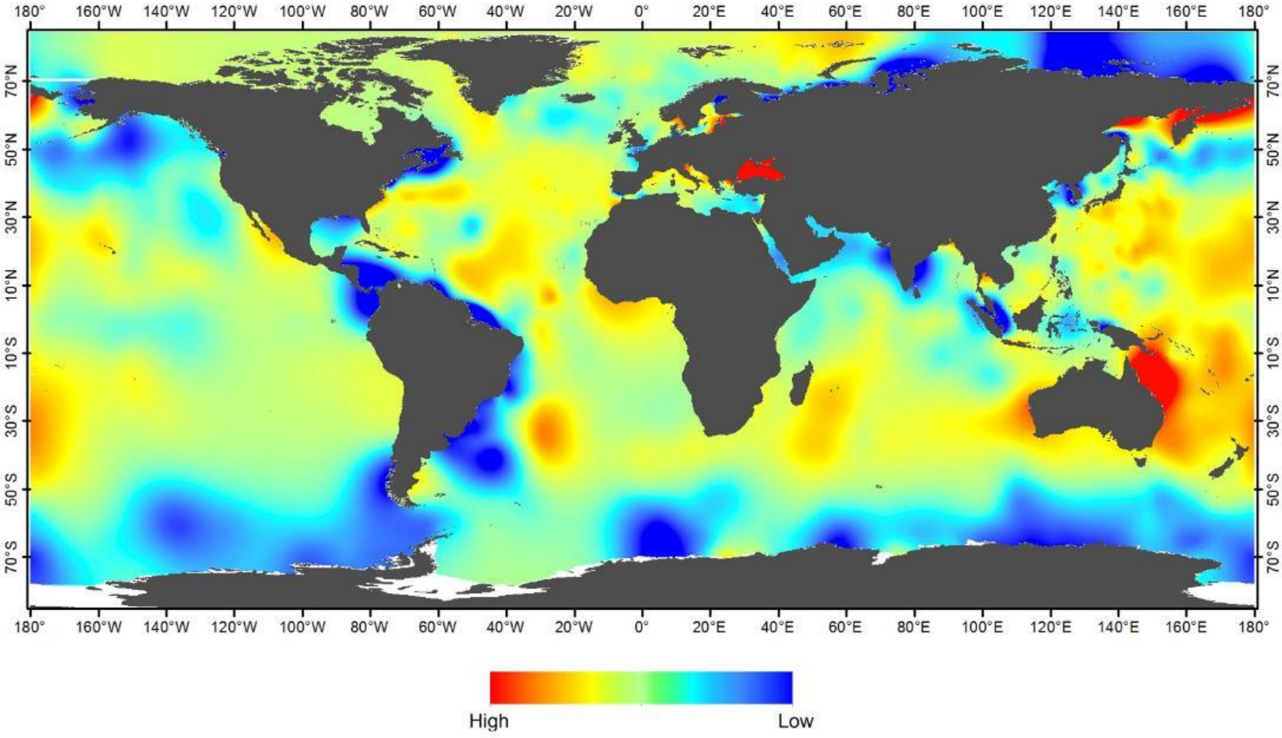
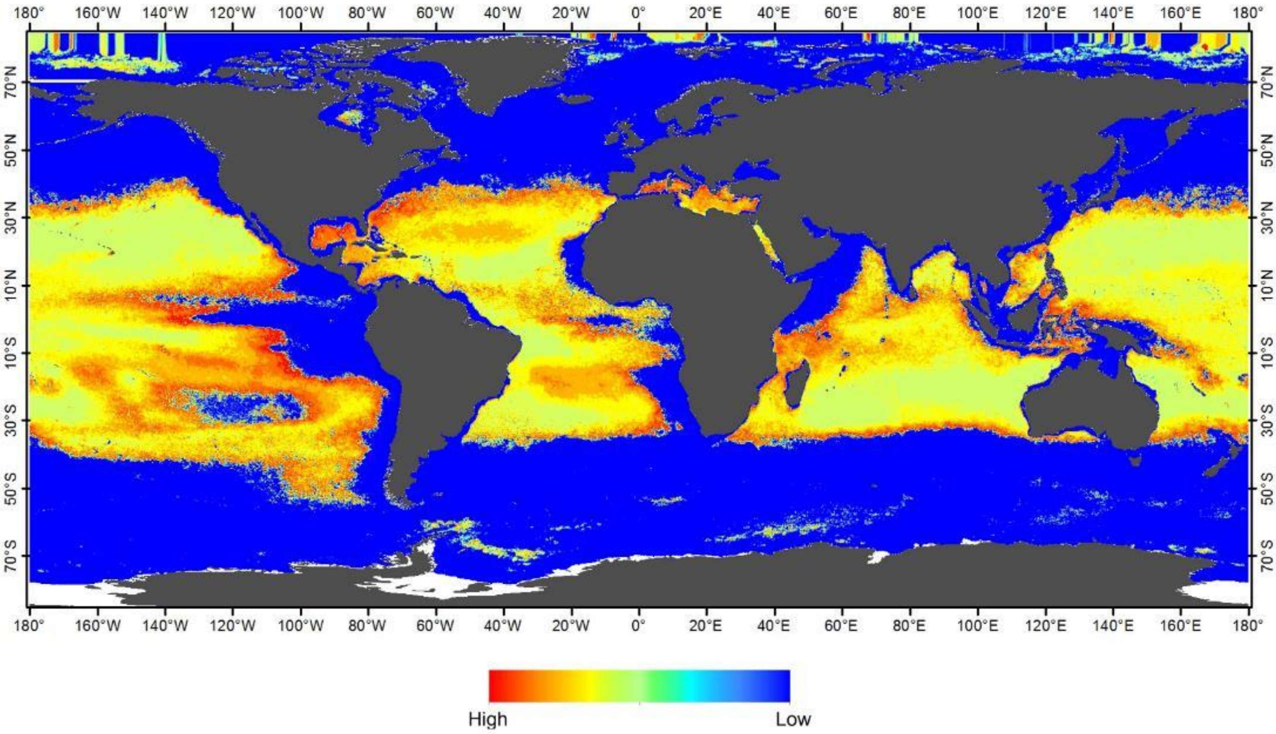
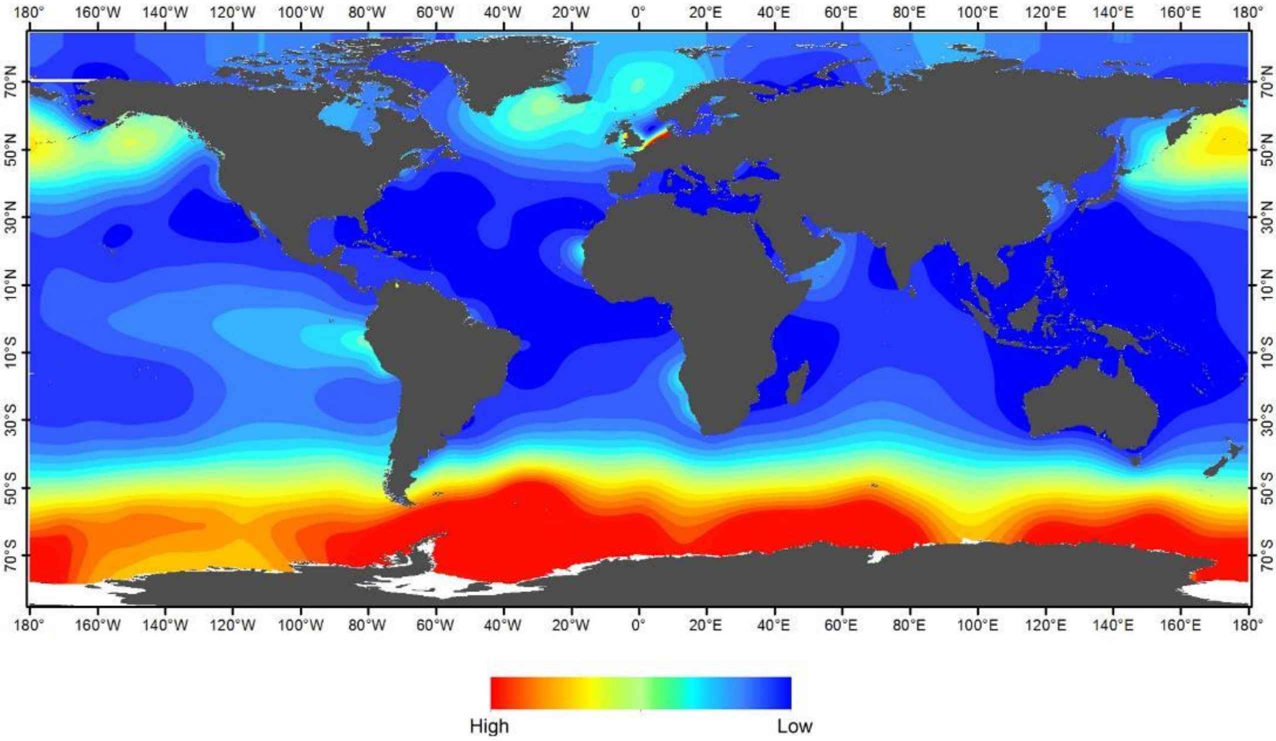

180°
160°W
140°W
120°W
100°W
80°W
60°W
40°W
20°W
0°
20°E
40°E
60°E
80°E
100°E
120°E
140°E
160°E
180°
70°N
50°N
30°N
10°N
10°S
30°S
50°S
70°S
High
Low

Figure 5.7. Visualization of GMED nutrient data layers.

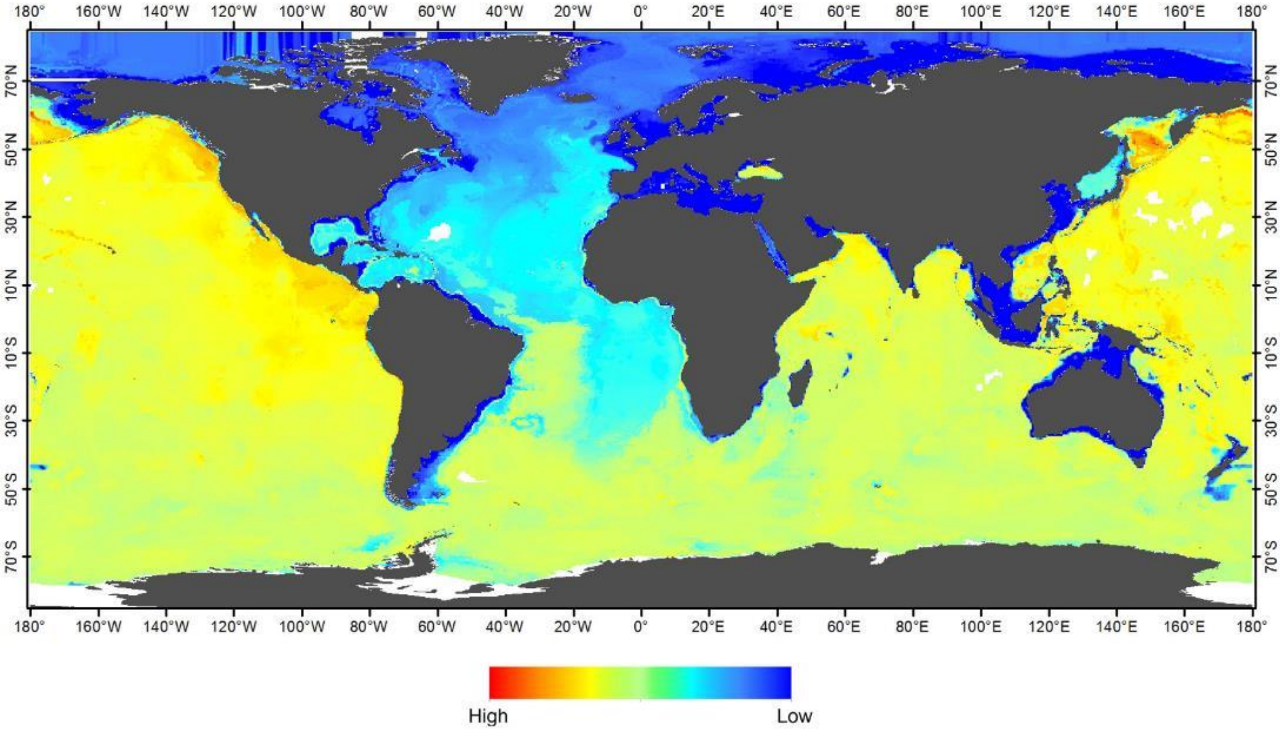
Calcite



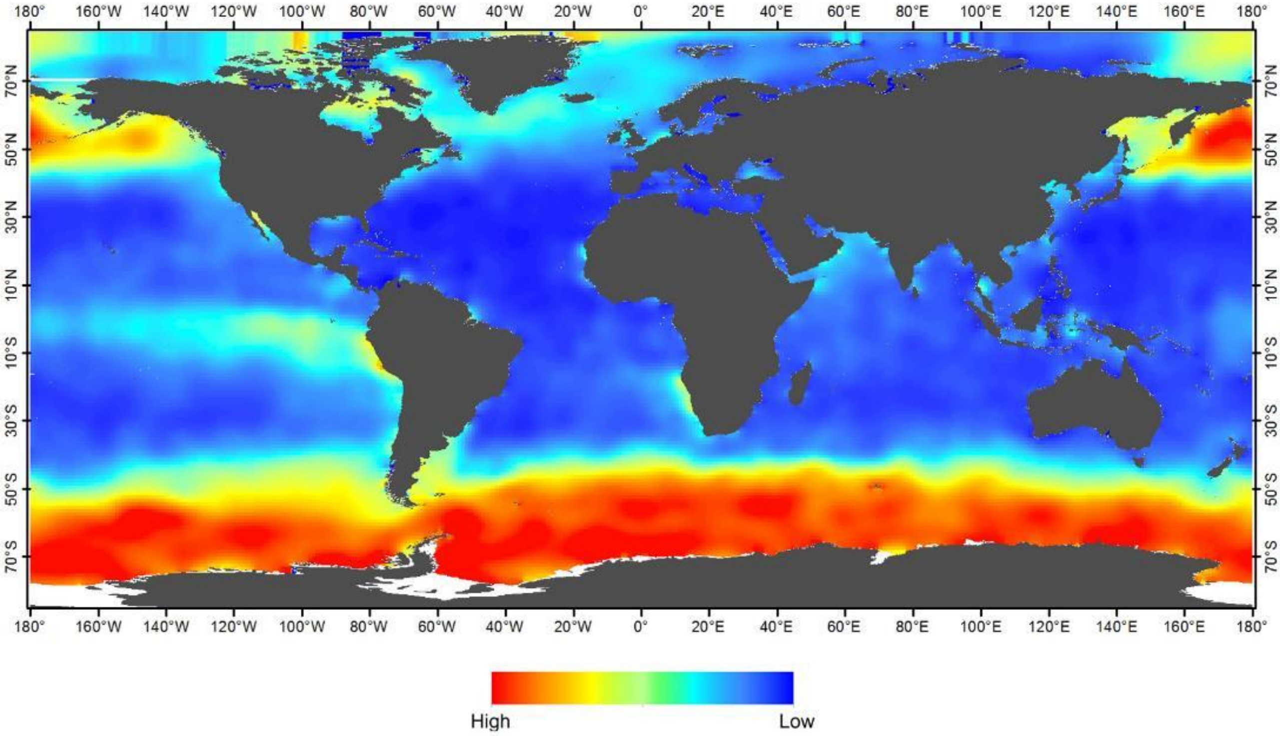
Nitrate



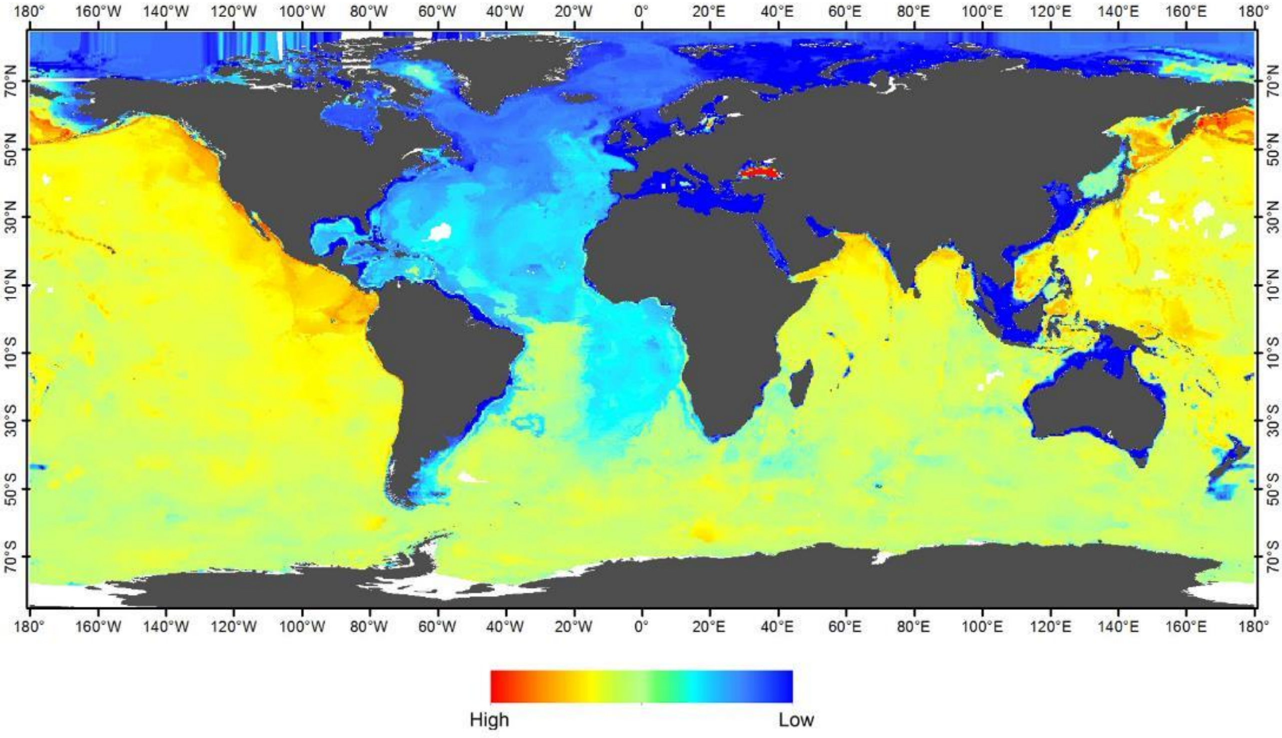
Bottom Nitrate



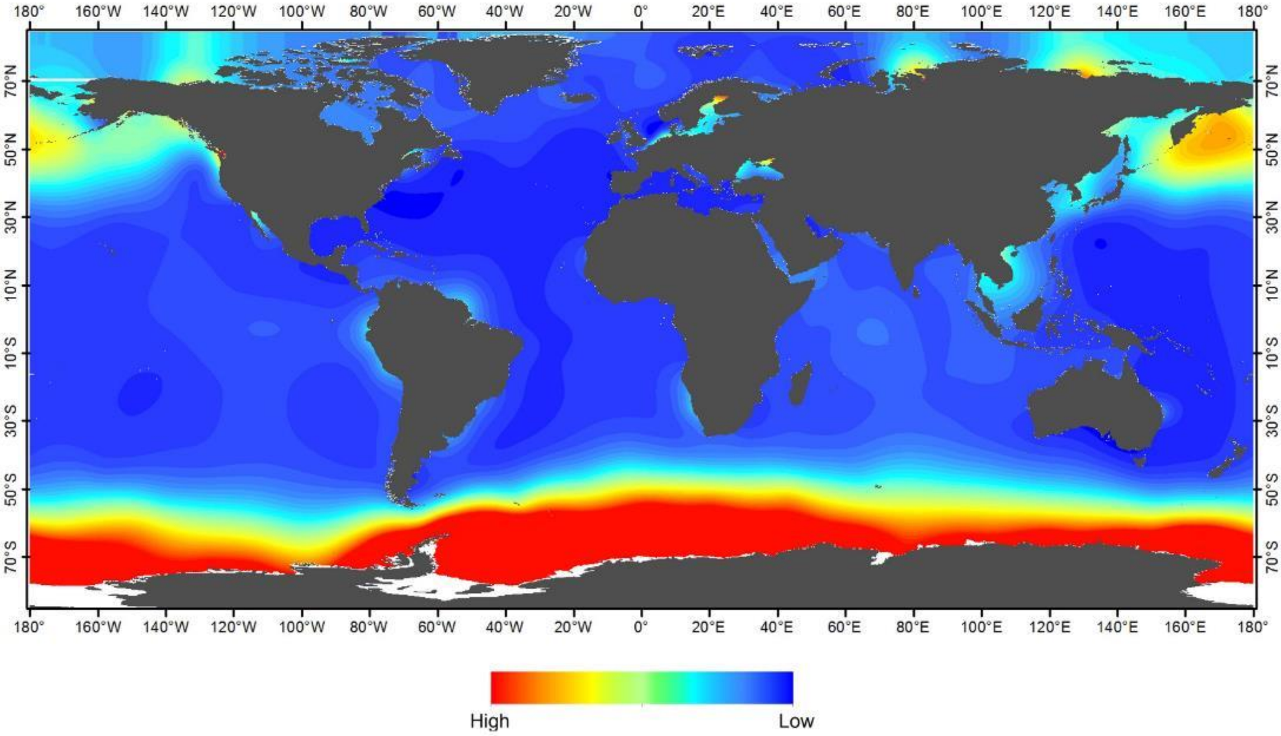
Phosphate



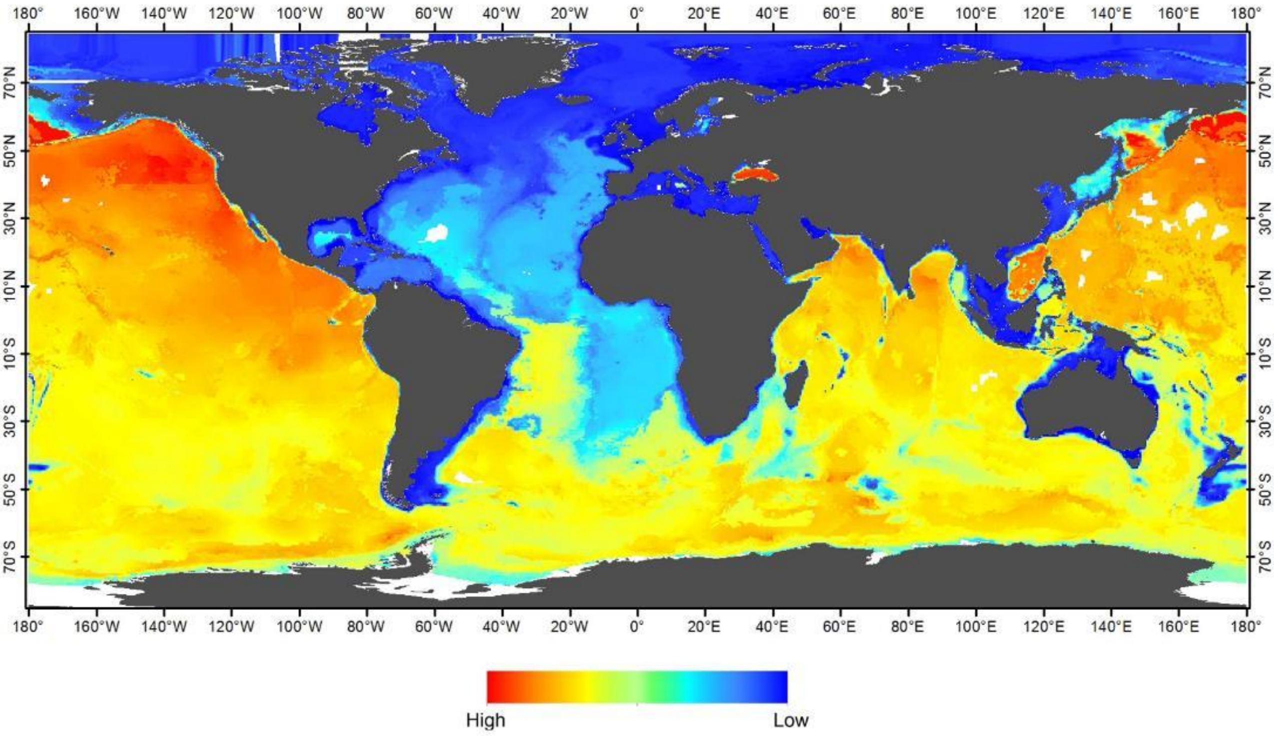
Bottom Phosphate



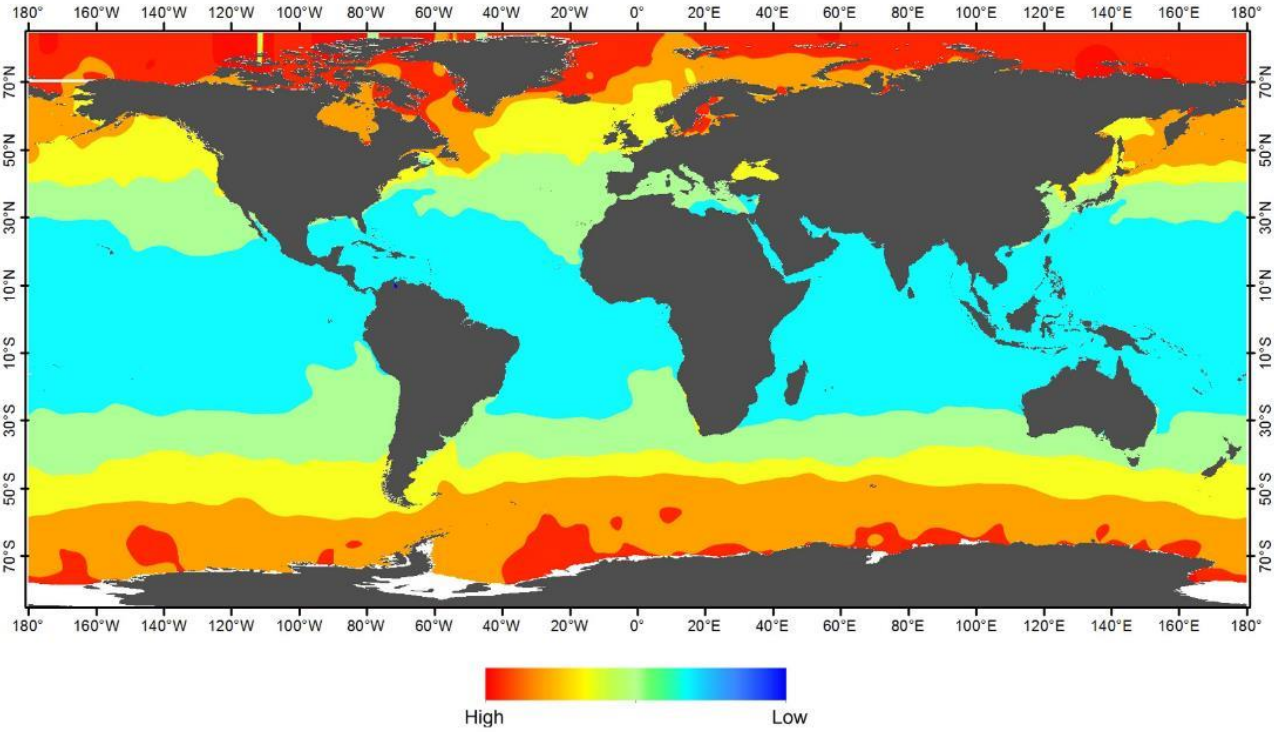
Silicate



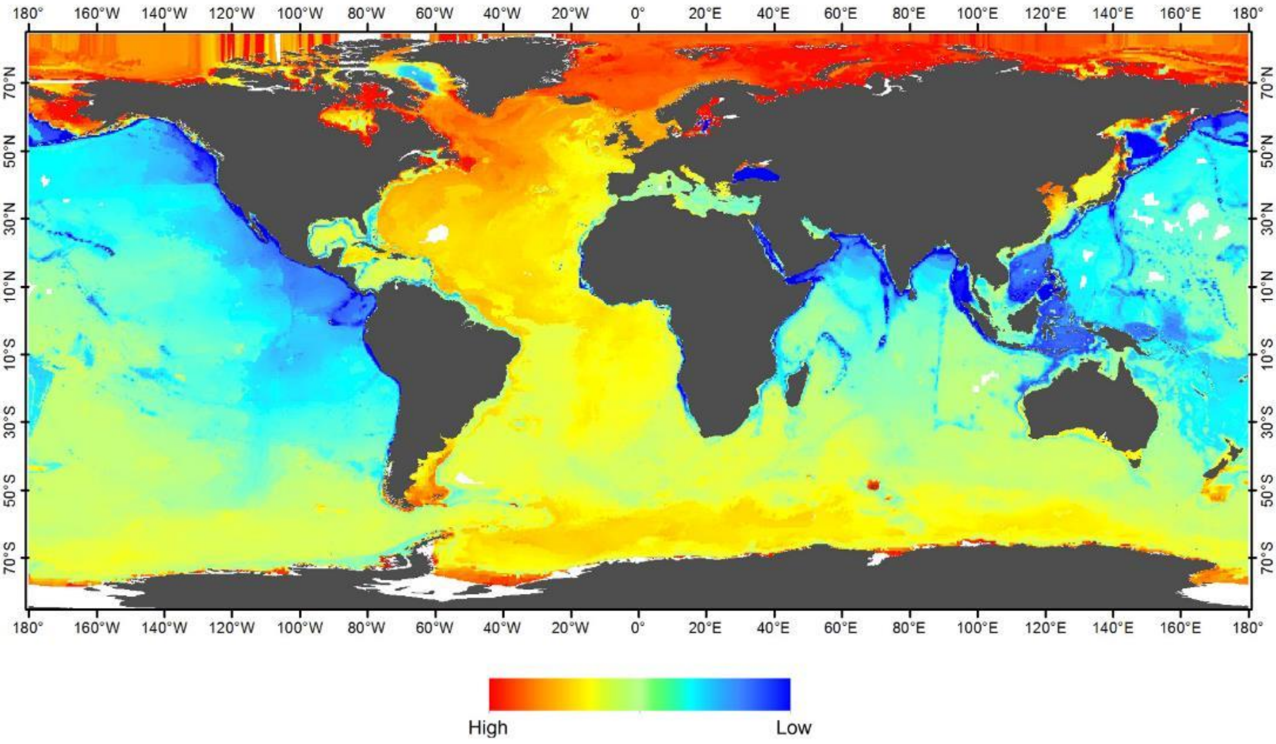
Bottom Silicate



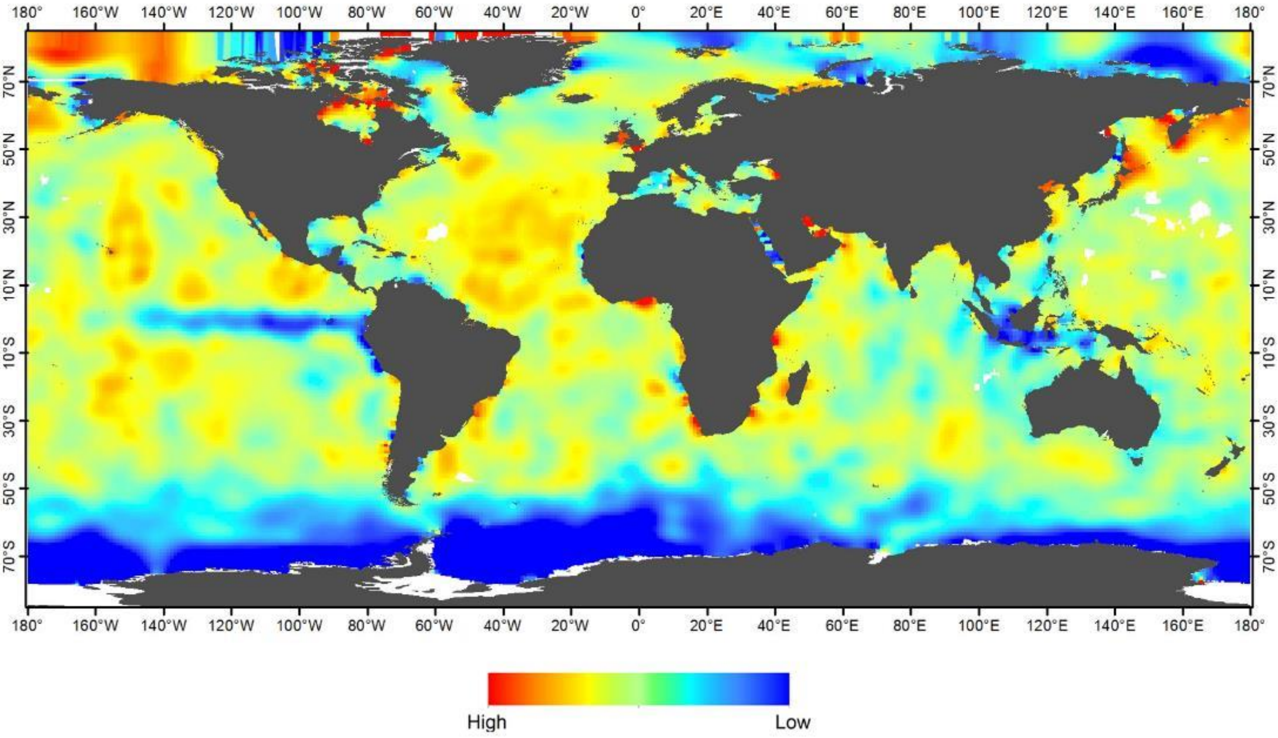
Dissolved O_2



Bottom Dissolved O_2



Saturated O_2



Bottom Utilized O_2

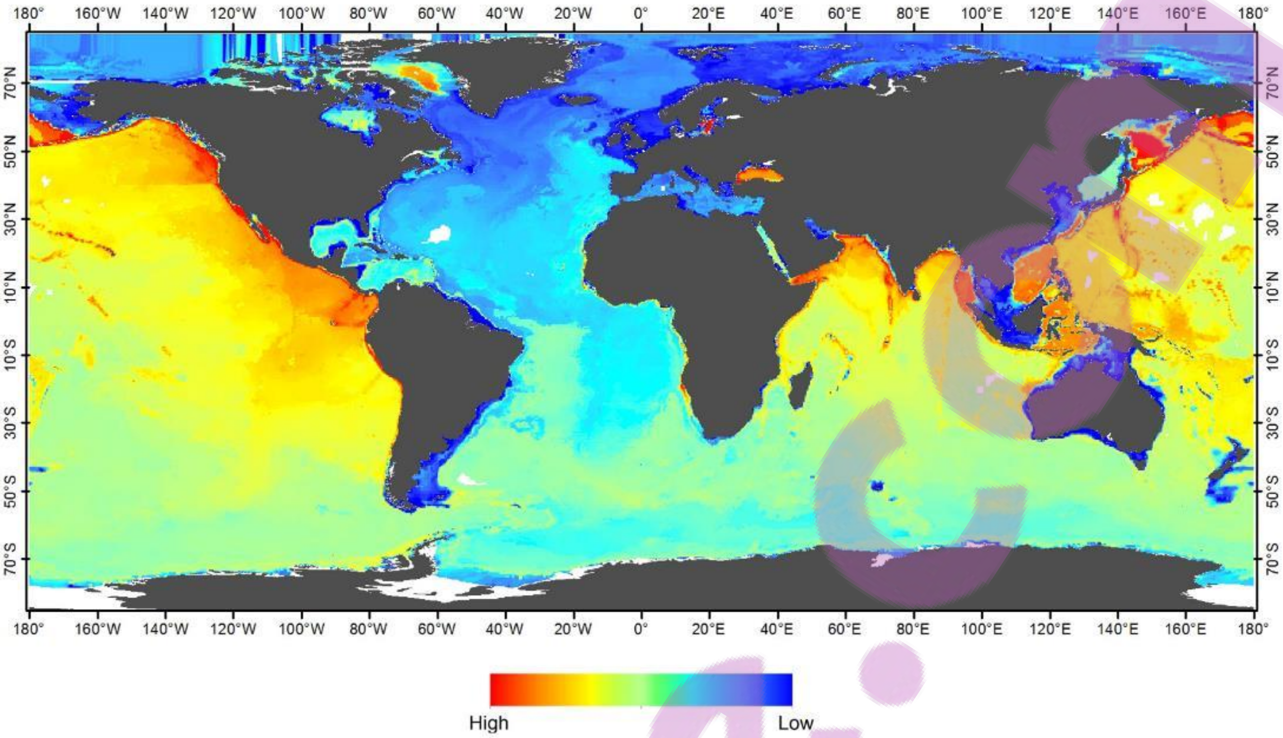
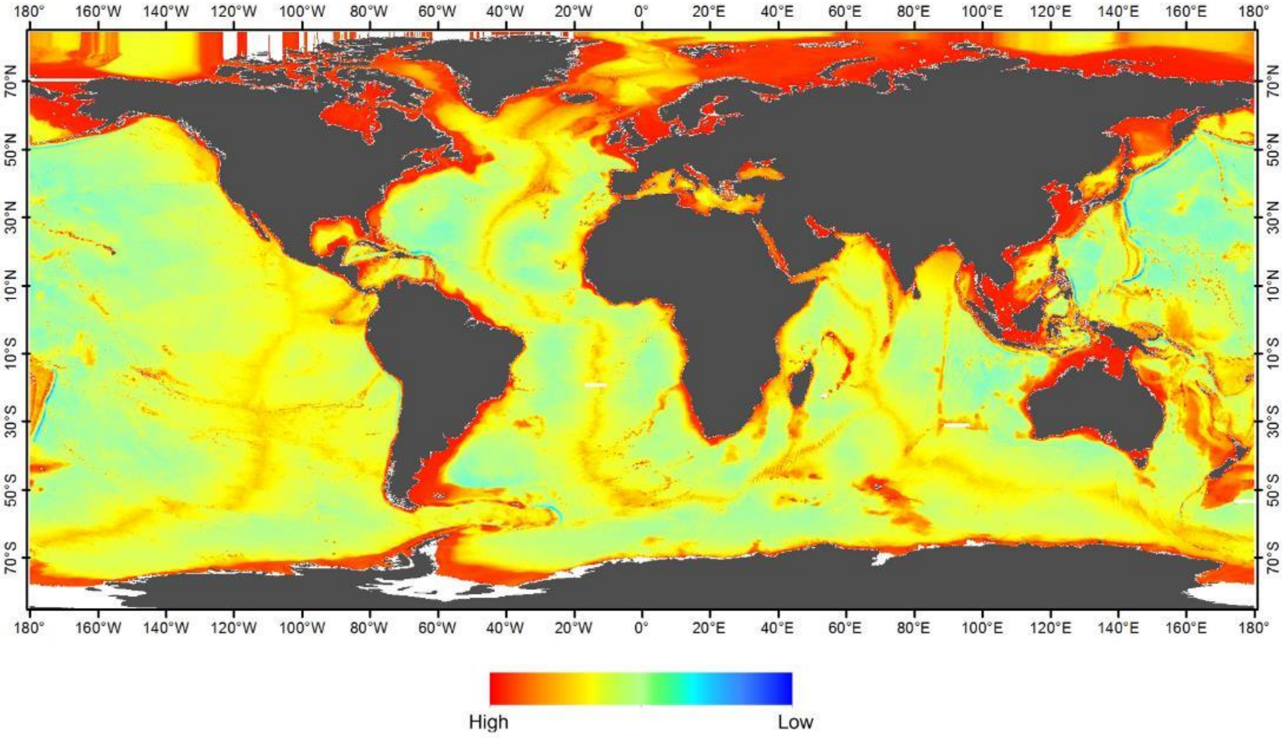
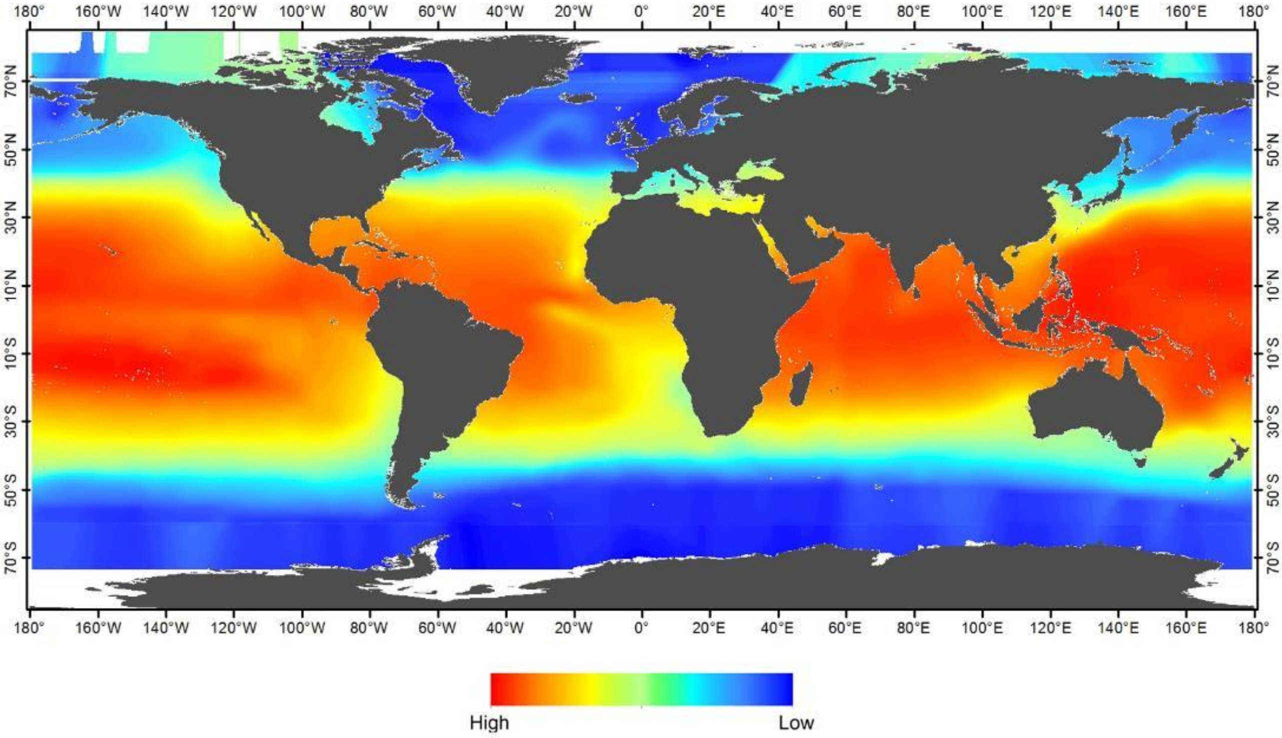


Figure 5.8. Visualization of GMED Past (Last Glacial Maximum, 22 mya) data layers.

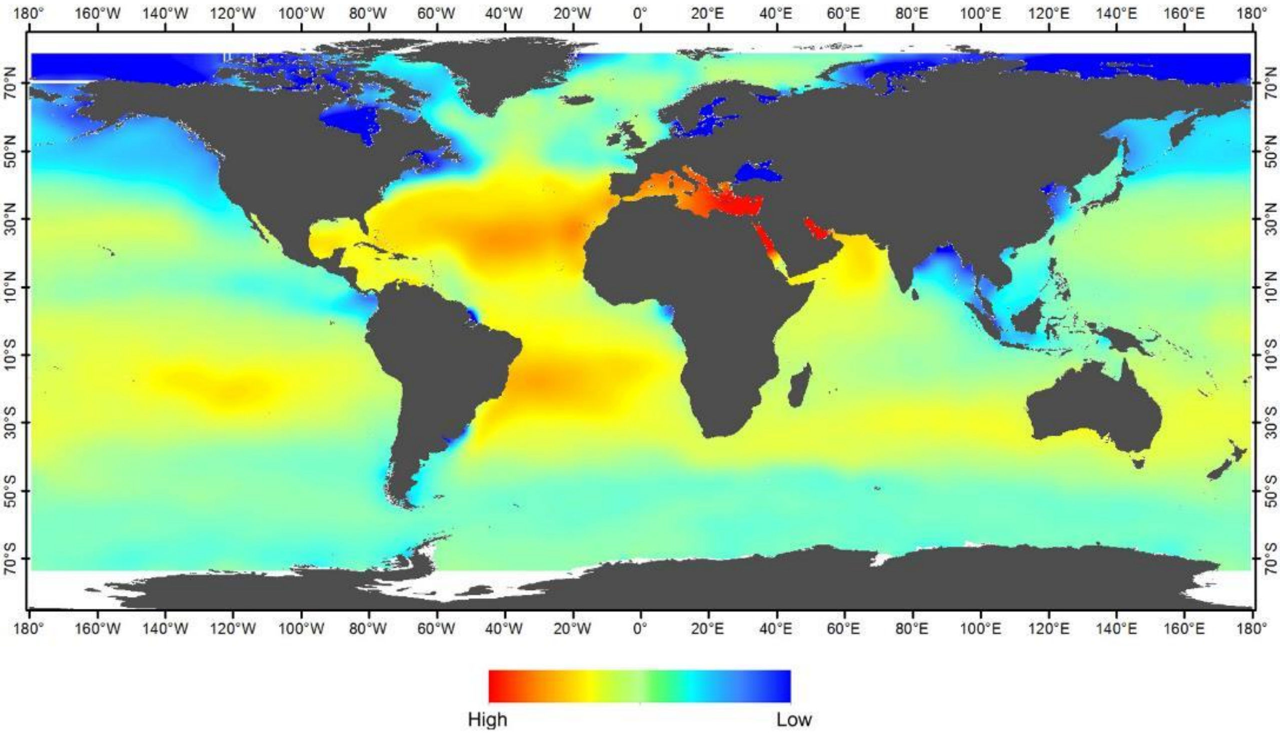
Depth



Temperature



Salinity



Ice Thickness

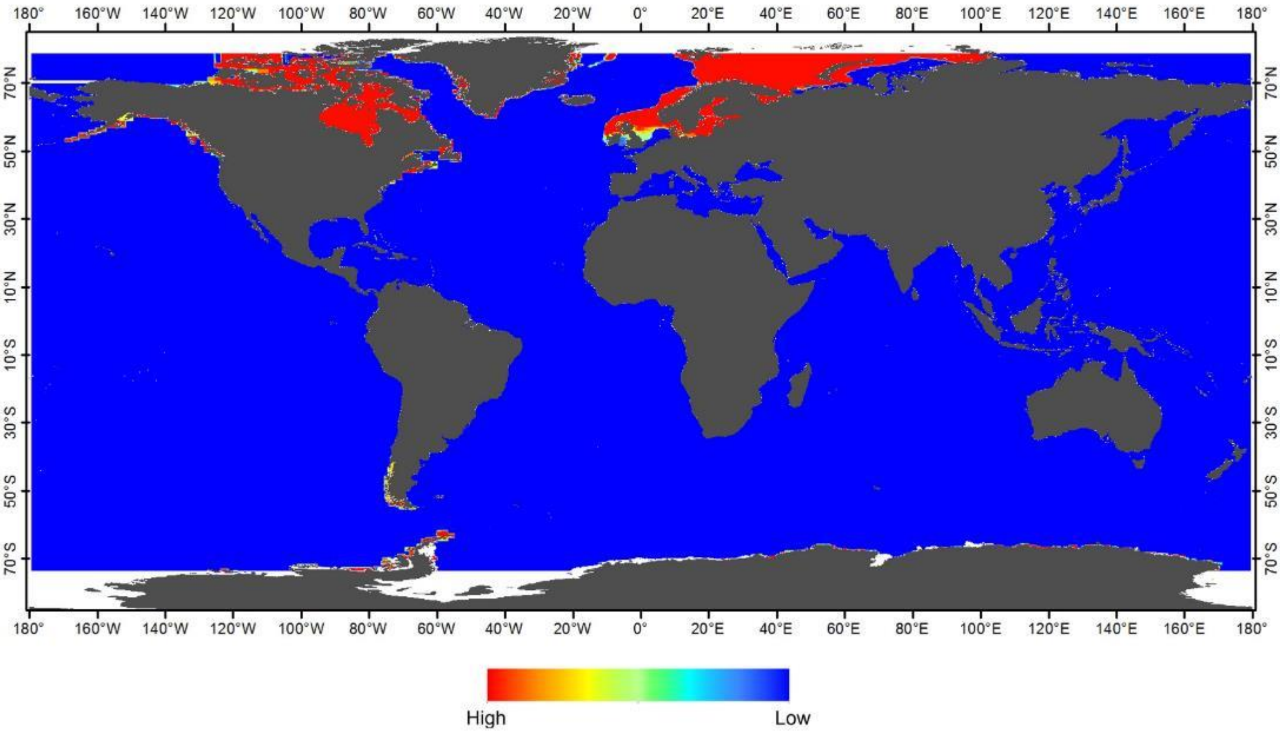
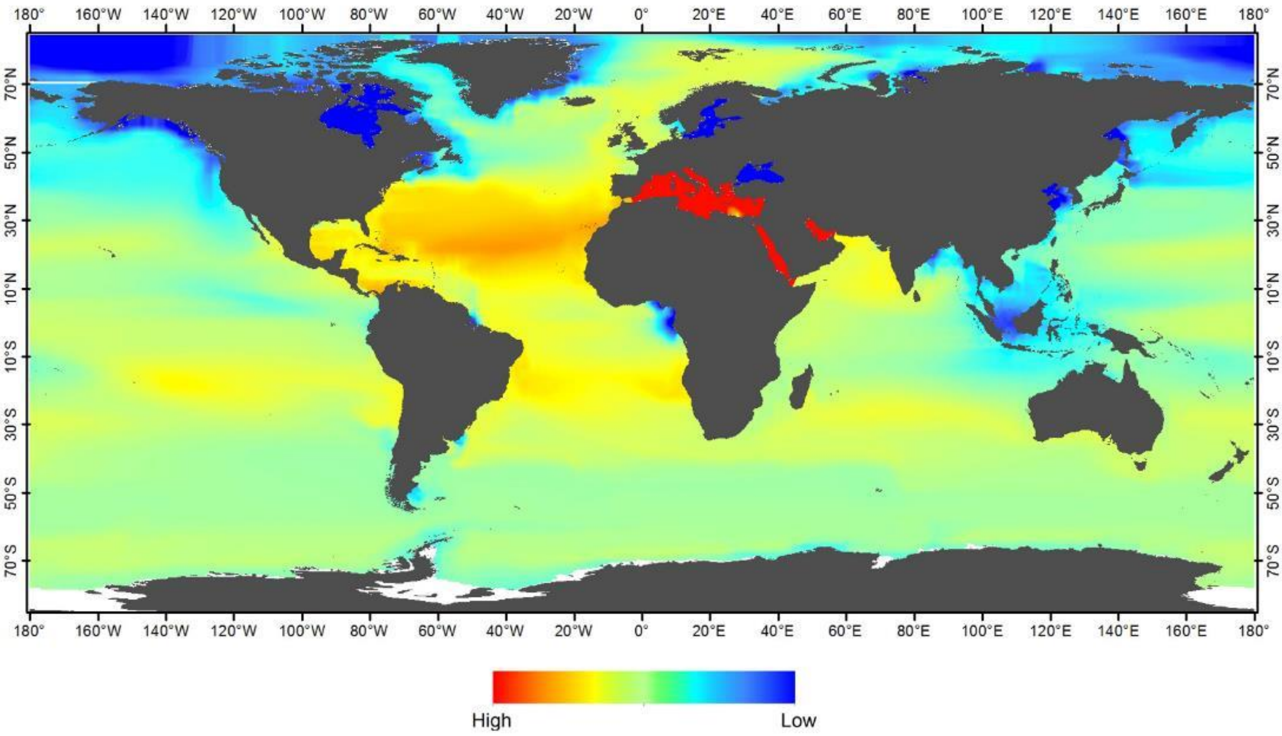
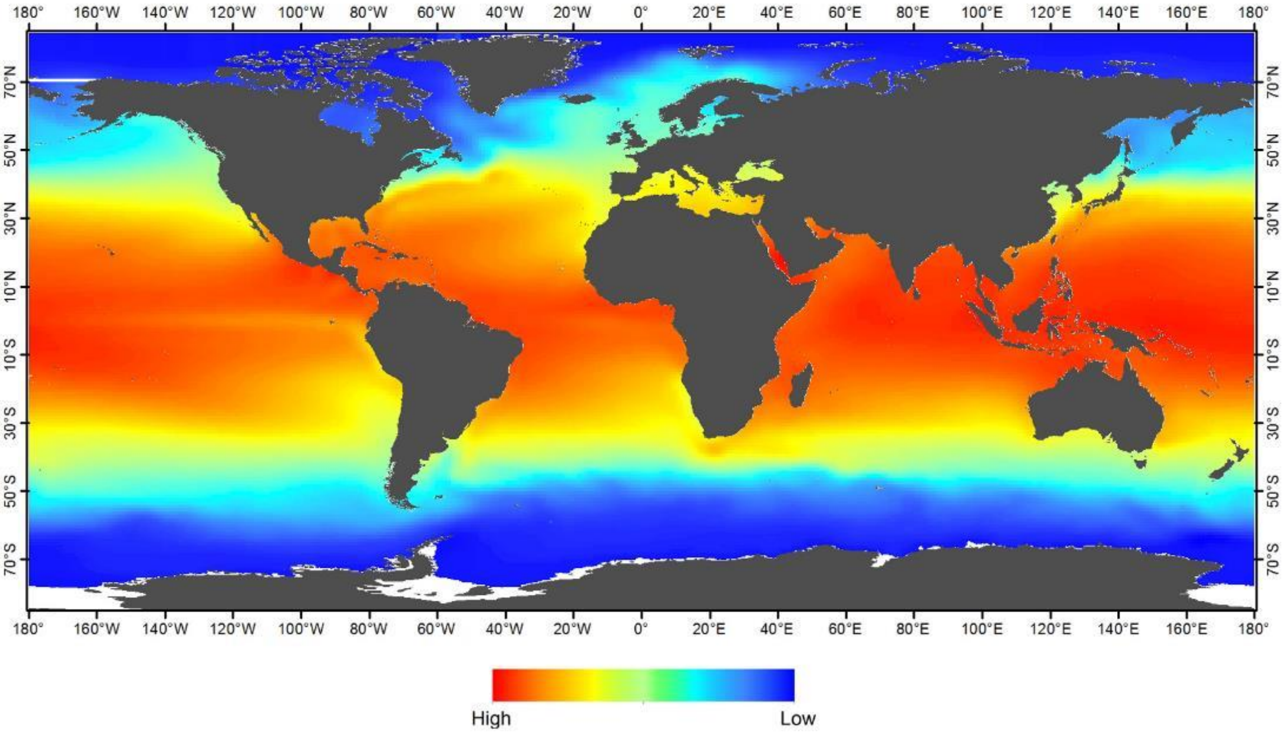


Figure 5.9. Visualization of GMED Future (Year 2100) data layers.

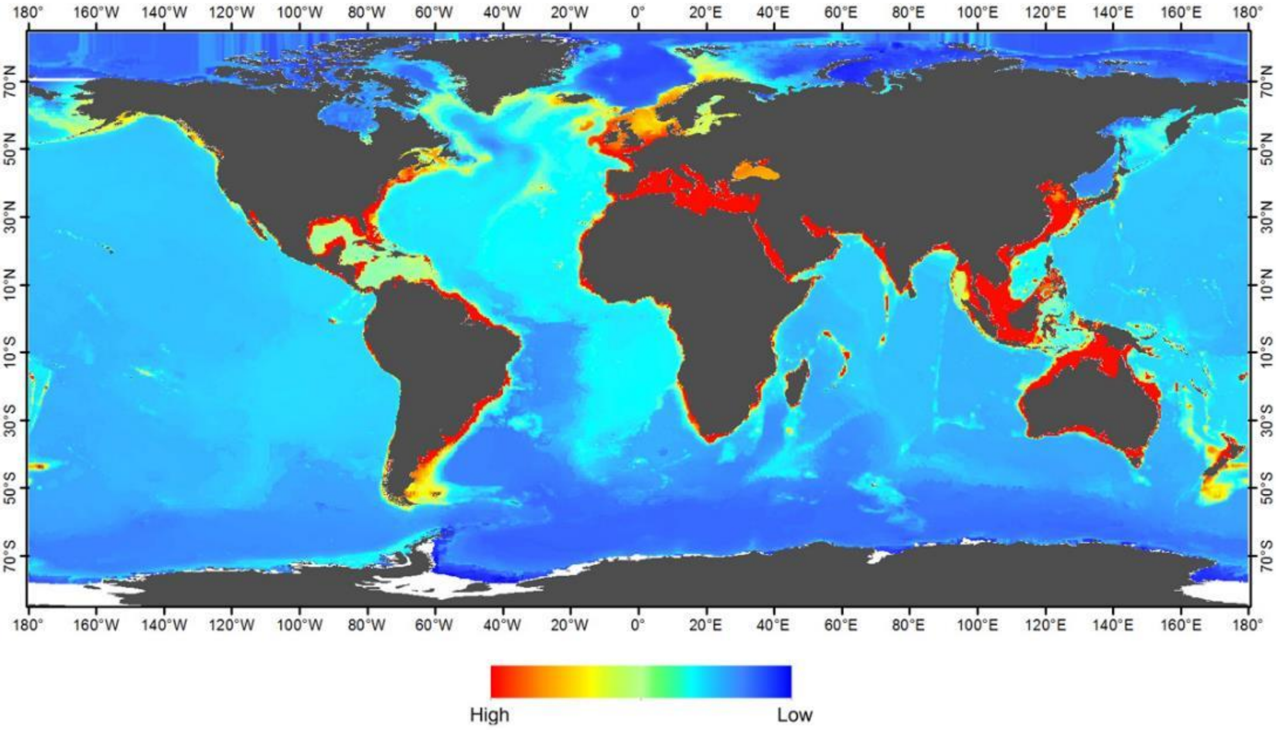
Temperature A1B Scenario



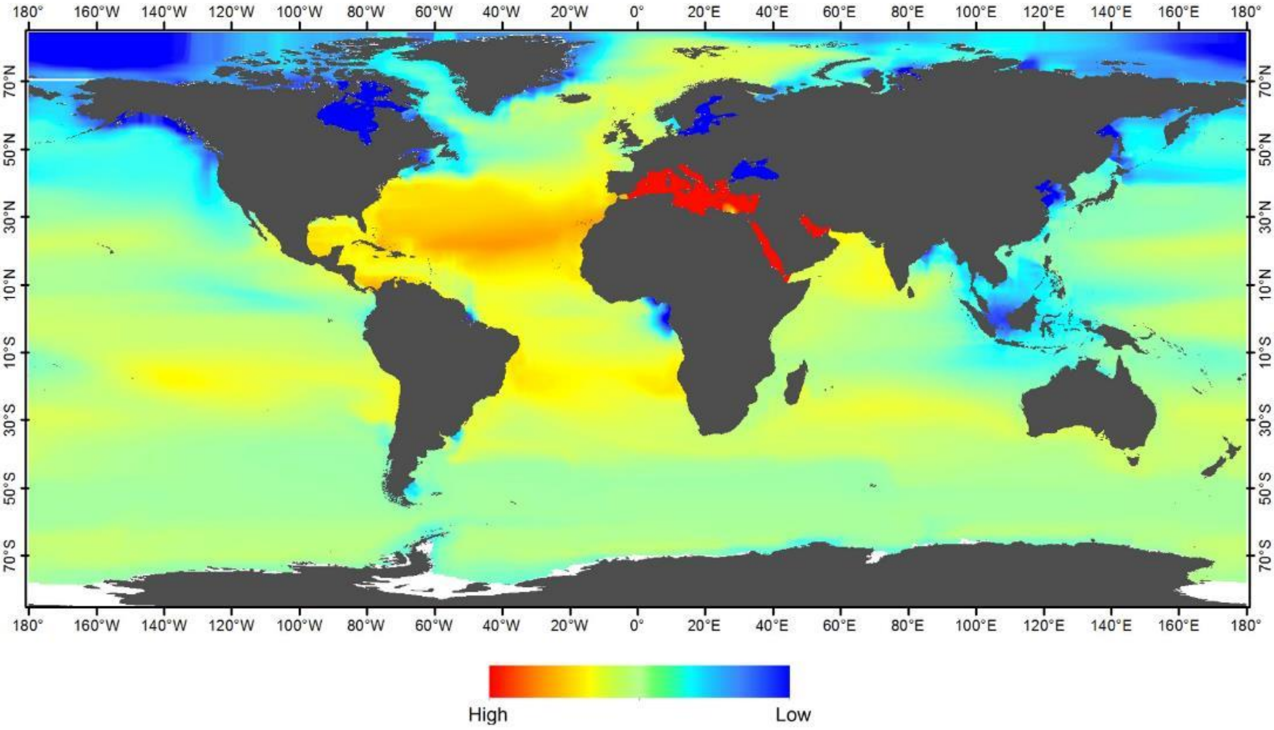
Temperature A2 Scenario



Bottom Temperature A2 Scenario



Salinity A1B Scenario



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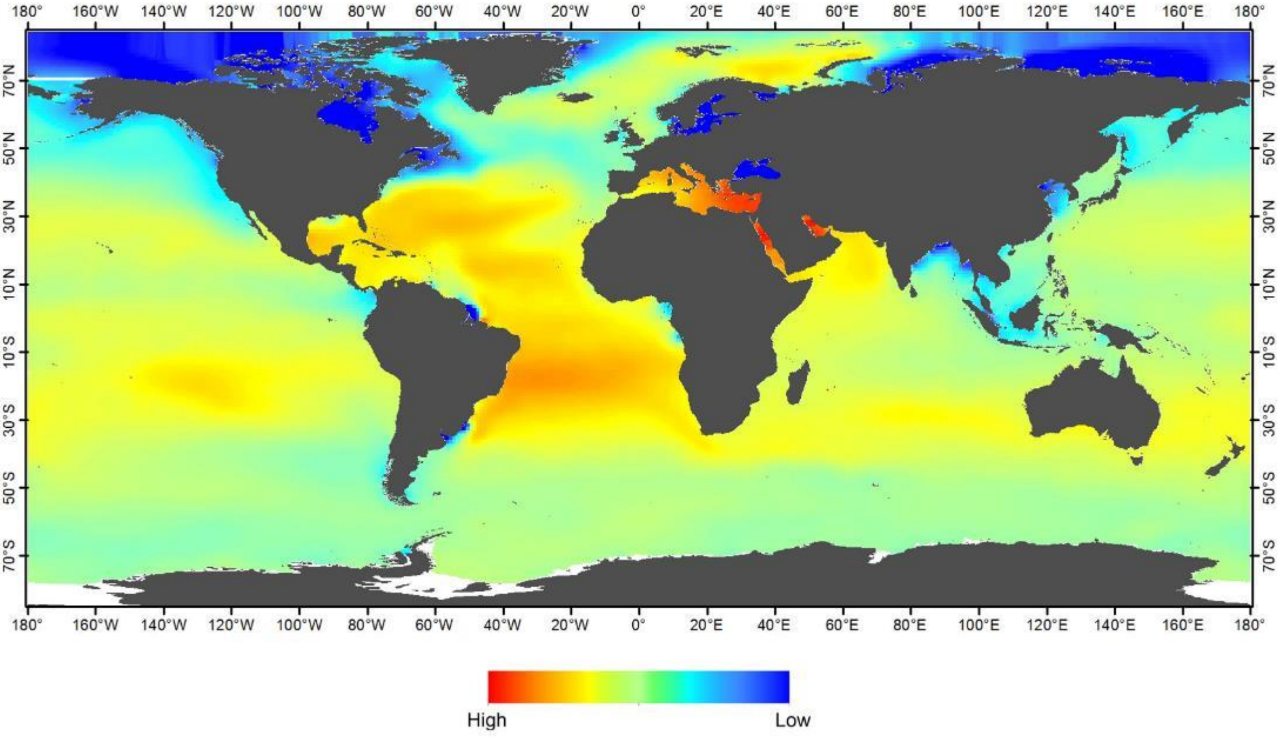
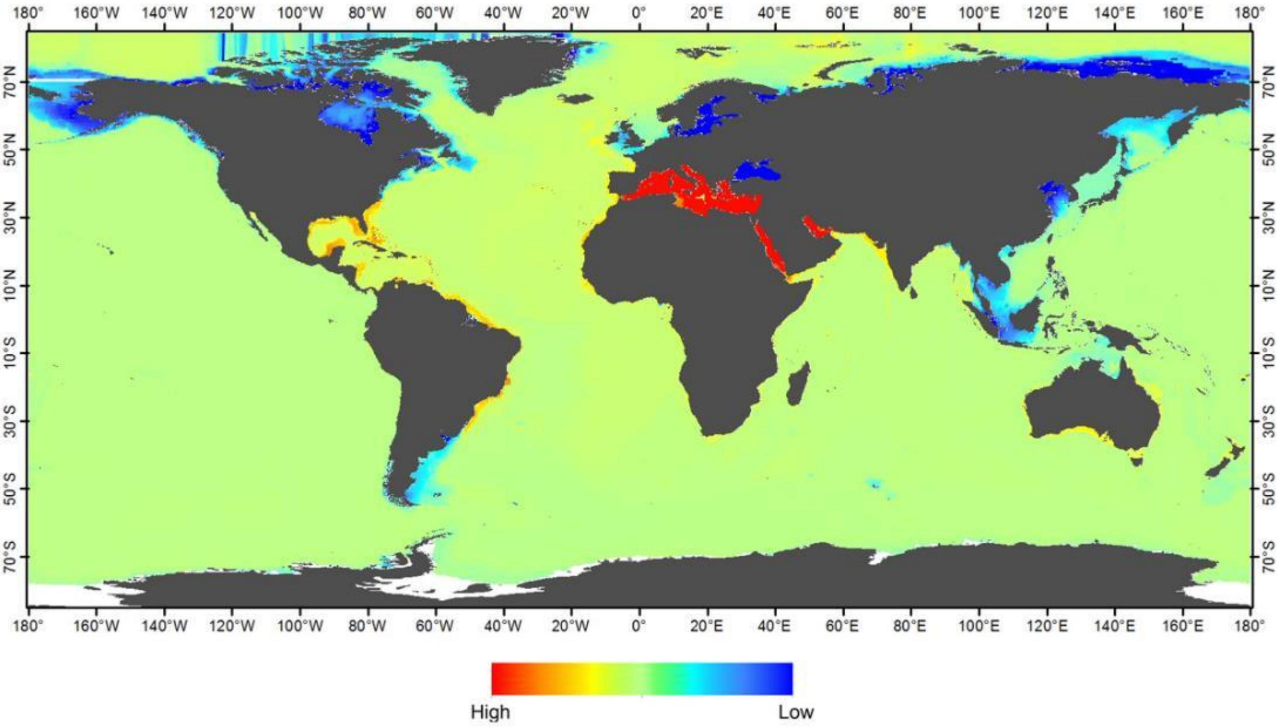
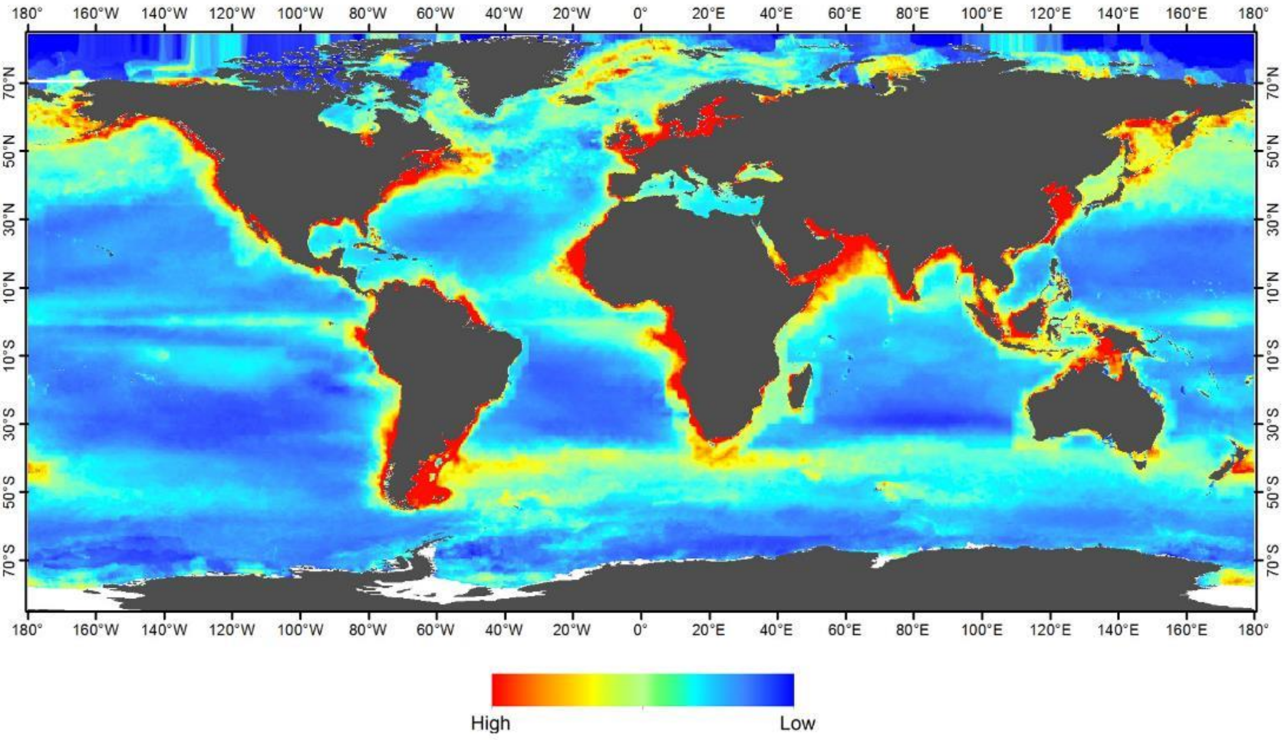


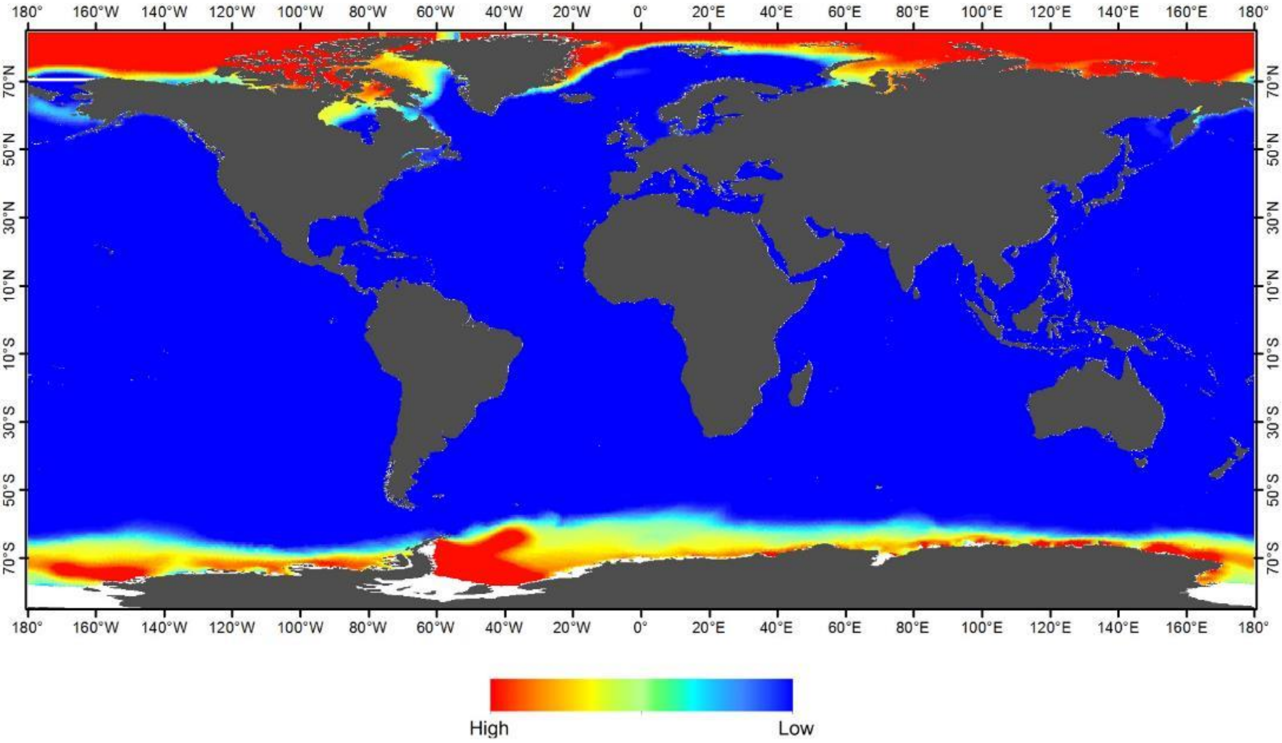
Bottom Salinity A2 Scenario



Primary Productivity A2 Scenario



Ice concentration A2 Scenario



Chapter 6

Past, Present and Future distribution of deep-sea shrimp in the Antarctica

6.1 Introduction

Climate warming is one of the most significant threats to biodiversity. The changing environmental conditions often affect species geographical distributions and the persistence of populations (Moore, 2003; Parmesan & Yohe, 2003; Cheung *et al.*, 2009). Species generally react to their changing surrounding environment by shifting their latitudinal range (Perry *et al.*, 2005; Parmesan, 2006; Dulvy *et al.*, 2008; Hiddink & Ter Hofstede, 2008; Cheung *et al.*, 2012; Cheung *et al.*, 2013). In extreme environments at the higher latitudes physical factors become dominant in delimiting species distributions and putting some polar species at risk from climate change (Peck, 2004). Many organisms living in the Antarctic evolved to survive the combined physiological and ecological constraints of the cold environment (Thatje *et al.*, 2008). In the last glacial maximum (LGM, ca. 19.5-16 ka; Gersonde *et al.*, 2005), Antarctic marine life was challenged by even more extreme environmental conditions with reduced suitable area in the shelf and scarcity of food in the open ocean. This forced them to take refuge in ice free regions, and then re-colonize their present range (Aronson *et al.*, 2007; Barnes & Conlan, 2007; Thatje *et al.*, 2008). At present, polar ecosystems are experiencing significant environmental changes with the retreat of glaciers and the disintegration of ice shelves due to climate warming forecasting a shift of pelagic and benthic communities towards the south in the future (Turner *et al.*, 2009). With a projected global temperature change on average by 2°C in the next 100 years (IPCC Climate Change, 2007), there will be marked regional variation with some areas warming more and others not changing or possibly cooling following the movement of the large scale ocean currents (Peck, 2005). Although, satellite data indicate sea-ice extent has not changed markedly over last 25 years (Bjørgo *et al.*, 1997), the Intergovernmental Panel for Climate Change has predicted that a decrease of around 25% sea-ice extent over the next 100 years would result in a reduced extent of phytoplankton productivity around the Southern Ocean (SO).

The presence of a strong Antarctic Circumpolar Current facilitates the dispersal of pelagic life stages (Raupach *et al.*, 2010). However, several studies on Antarctic species stated that their distributions were often more restricted (Allcock *et al.*, 1997; Sands *et al.*, 2003; Kuhn & Gaffney, 2006). The first phylogeographic study of Antarctic shrimps suggested that postglacial expansion of the shelf-inhabiting species *Chorismus antarcticus* while the deep-water shrimp *Nematocarcinus lanceopes* was less affected (Raupach *et al.*, 2010). It is likely that benthic shelf species have been more affected by glaciations than pelagic or deep sea inhabiting species (Janko *et al.*, 2007). Increasing evidence suggests deep-sea ecosystems, which have long been thought to be extremely stable in terms of physiochemical conditions, may experience abrupt changes due to changing environment (Smith & Kaufmann, 1999). Studies in tropical deep-sea ecosystems indicated that the deep-sea fauna is vulnerable to a small change in temperature (Danovaro *et al.*, 2004). In the Antarctic it has been suggested that the re-colonization of the deep-sea by some predators was possible due to climate warming (Aronson *et al.*, 2007; Aronson *et al.*, 2009). Barnes *et al.* (2009) suggested mollusc species at higher latitudes tend to have wider latitudinal ranges; which helps them to shift ranges under changing climatic conditions.

Various methodological approaches are available for examining the potential effects of climate change on the distribution of species and often ranges from spatially explicit mechanistic models for single species range-shifts (Hill *et al.*, 2001) to physiologically based (Walther *et al.*, 2005) and correlative bioclimatic envelope or species distribution models (SDM) (Peterson & Vieglais, 2001; Pearson *et al.*, 2002; Pearson & Dawson, 2003; Graham *et al.*, 2004; Thuiller *et al.*, 2005; Waltari *et al.*, 2007; Peterson *et al.*, 2011; Bentlage *et al.*, 2013). SDM is very valuable for providing insights into potential climate warming effects on biodiversity when range-limiting physiological factors for species are poorly known (Crumpacker *et al.*, 2001; Elith *et al.*, 2010). Dambach *et al.* (2012) used SDM to predict that Antarctic shrimp ranges contracted during the last glacial maximum (LGM), but did not predict future ranges under climate change. In order to understand how shrimps survived through numerous climatic events in the past and how they will react with the changing climate in future a more comprehensive set of distribution records of the shrimp *Nematocarcinus lanceopes* and environmental variables were used. *Nematocarcinus lanceopes* was selected because it has the most distribution records, and a range north to the sub-Antarctic islands and off Chile (Kirkwood, 1984; Arntz *et al.*, 2006; Basher & Costello, 2014). This species may be an example of how Antarctic species distributions have changed due to glaciations and may change due to climate change.

The objective of this study is to identify whether deep-sea shrimps are susceptible to changing environmental conditions in the deep-ocean and to determine how they may respond to changing climatic conditions in the future.

6.2 Methods

6.2.1 Study area and observation data

Our study area lies in the north of the Antarctic Circumpolar Current zone close to 40°N and the Antarctic coast in the south, known as the Southern Ocean (Figure 6.1). Southern Ocean is the largest semi-enclosed ecosystem on the planet (Knox, 2006). A strong temperature gradient of 4°C over 0.5° of latitude across the Subtropical front (Sikes *et al.*, 2009) and the Antarctic circumpolar current (ACC) uniquely characterises Southern Ocean form the northern temperate waters. Connecting all ocean basins, without interruption, the ACC is the strongest current on earth (Rintoul *et al.*, 2001). It creates a physical barrier that has isolated the Southern Ocean for the last 25 million years (Clarke *et al.*, 2005). Bathymetry is dominated by deep ocean ridges and a continental shelf that is unusually deeper with a shelf break lying two to four times deeper than in other oceanic regions (Knox, 2006).

A total of 87 *N. lanceopes* observation records were extracted from the Ocean Biogeographic Information System (OBIS, 2011), the SCAR-Marine Biodiversity Information Network (De Broyer *et al.*, 2011), and literature (Figure 6.1 and Appendix VII). Additionally, 30 *N. lanceopes* records from IPY-CAML cruise in the Ross Sea area were used for model validations (Basher *et al.*, 2014a). All records were filtered to remove apparent geographic errors (i.e. coordinates plotting on land or in different regions) before combining them into a single data set for model training or validation using GIS.

6.2.2 Environmental data

Environmental data were obtained from the Global Marine Environment Datasets, (GMED) (Basher *et al.*, 2014b), and consisted of the five oceanographic variables depth, temperature, salinity, ice cover and primary productivity. The variables were derived from remotely sensed and in situ measured datasets, and had a spatial resolution (pixel size) of 5 arc min or ca. 9 x 9 km near the equator. These variables were chosen because of their relevance to species' distributions and were common to most of the past, present and future datasets. The dataset for past (LGM) comprised of LGM Depth (DepthL, m), ice thickness (IceT, m), surface salinity (sSal, ppt) and sea surface temperature (SST, °C). The dataset for present and future data comprised of depth (Depth, m), sea bottom salinity (bSal, ppt), sea bottom temperature (bTmp, °C), ice cover (IceC, 0-1%) and primary productivity (PPD, mgC·m^{-2}·/day). For the future environmental predictors, the environmental layers from IPSL model, A2 scenario (http://icmc.ipsl.fr/) for the year 2100 were used. Depth in future scenario was considered the same as present depth since future predictions are currently not available. All the temperature and salinity values were annual average, whereas all other variables were interpolation of in-situ measurements (See Basher *et al.*, 2014b for layer details). High correlations among environmental predictors may negatively affect SDM performance and its transferability through space and time (Heikkinen *et al.*, 2006; Jiménez-Valverde *et al.*, 2009). None of the environmental variables used in our models have significant correlations ($R^2 > 0.7$) when tested for pair-wise correlations using Pearson's correlation. Thus, all of them are suitable for large-scale species distribution models and hind casting projections (Bigg *et al.*, 2008).

6.2.3 Model building

MaxEnt 3.3.3e (Phillips *et al.*, 2006) was used to model the potential current distribution of *N. lanceopes* and to project it for past and future environmental conditions. The program uses a machine learning algorithm following the principles of maximum entropy (Jaynes, 1982). A review comparing 16 models of >200 taxa found that machine-learning methods including MaxEnt consistently outperformed traditional linear methods (Elith *et al.*, 2006) and that presence-only models were preferable because limited sampling may mean that apparent absences may not be true. MaxEnt starts with a uniform distribution during the modelling process, and successively fits the model to the data (occurrence records and environmental variables). MaxEnt repeatedly tests the predictive capability and improves the model by iteratively permuting and varying the input variables and features thereof. This is measured in the log likelihood or "model gain" which displays the increasing distance from the uniform distribution (Elith *et al.*, 2011). Note that MaxEnt does not predict the actual prevalence of the taxon, but rather the relative suitability of the environment, which is interpreted as the potential geographic distribution of the taxon under study.

MaxEnt models were generated using 10 bootstrap replicate runs with a total of 100,000 random background points automatically selected in each replicate run. The average predictions across all replicates were used for further analysis. The maximum number of points to be used for modelling were increased to 100,000 instead of the default value of 10,000 because of our large-scale mapping objective. The 'Remove duplicate presence records' feature was enabled to exclude duplicate records that fell within individual pixels of background environment layers on each dataset and the occurrence records were split into 75% for training and 25% for testing for bootstrap replications. Maximum iterations were also increased to 1000 allowing enough time for model convergence. As suggested by Phillips & Dudik (2008) the default regularisation value was used because it results in better performance of evaluation data for presence-only datasets. The option 'fade by clamping' was used to minimize unreliable extrapolation into areas with environmental conditions that were not encountered during model training. Any area having prediction value below the Minimum Presence Threshold (MPT) value were considered as a 'not suitable' area for the species. Species range shift was calculated by subtracting predicted LGM distribution raster from present day raster and then subtracting present day raster with future raster using ArcGIS 'Raster Calculator' (ESRI, 2011).

6.2.4 Model evaluation

The logistic model output format gives predicted suitability value ranging from 0 (unsuitable) to 1 (optimal) (Phillips & Dudik, 2008). The final output raster was classified into four classes based on the range of predicted suitability value: HS, High Suitability (0.75-Maximum); MS, Medium Suitability (0.5-0.75); LS, Low Suitability (MPT-0.5) and NS, Not suitable (Values below MPT), these classified raster files were used to interpret the suitability of *N. lanceopes* habitat in the Southern Ocean. MaxEnt allows for model evaluation by the Area under the Receiver Operation Characteristic curve (AUC) (Phillips *et al.*, 2004). The AUC is a threshold-independent measure of a model's ability to discriminate presence from absence (or background). It varies from 0.5 to 1; an AUC value of 0.5 shows that model predictions are not better than random and AUC >0.9 indicates high performance (Peterson *et al.*, 2011). MaxEnt software used a random data split approach to evaluate model performance using bootstrap procedure with an evaluation dataset (25% of the entire present dataset records). Percent variable contribution and jack-knife procedures in MaxEnt were used to investigate the relative importance of different environmental predictors. The jack-knife procedure in MaxEnt repeatedly produces a model by using variables in isolation to examine how well the result fits the known model gain (for both training and test data). Response curves were used to study the relationships between environmental variables and the predicted probability of the presence of *N. lanceopes*. Confidence maps were generated using the ratio of the standard deviation of the MaxEnt prediction maps to the mean habitat suitability map of 10 replicate run to ensure prediction performance was consistent.

6.3 Results

6.3.1 Predicted distributions

All the SDM had a high predictive performance with AUC > 0.95 (AUC ± SD, Past 0.950 ± 0.01; Future 0.968 ± 0.008). The lowest predicted suitability value observed at the training records was zero for all of the models but the minimum presence threshold (MPT) values were 0.012 and 0.015 for past and future models respectively. Relative importance of the environmental variables to the SDM showed that depth had the highest explanatory power 61 - 79% for both past (Figure 6.2) and future (Figure 6.4) climate conditions. The second most important variables were temperature (26% for past) and ice cover (9% for future) (Table 6.1) (Appendix IX).

6.3.1.1 LGM distribution

The predicted distribution for the LGM period suggested that *N. lanceopes* would have been widely distributed in the Sub-Antarctic regions near the Scotia Arc (South Georgia, South Orkney, South Sandwich Islands), Kerguelen plateau, Mawson Sea, D'urville Sea and in the Bellingshausen Sea (Figure 6.2). The maximum predicted value for training record was 0.875 (Table 6.1). The high confidence in predicted areas indicated optimum model performance in identifying potential area glacial refugia (Figure 6.8). More than half of the pixels (57%) were identified as not suitable for *N. lanceopes*. The percent of pixels indicating areas with low, medium and high suitability varied from 40%, 2% and 0.5% respectively (Figure 6.5).

6.3.1.2 Present distribution

The predicted present distribution covers the current known distribution range of the species very well. The highest predicted suitability was in areas near the Mawson sea, Kerguelen plateau, Ross Sea slope, Davos sea, Prydz bay, South Orkney Islands, Bellingshausen Sea and at Gunnerus Ridge in between Riiser-Larsen and the Cosmonaut Sea (Figure 6.3). The present distribution range highlighted a pole-ward shift of the *N. lanceopes* population after the last glaciation period by re-colonizing previously unoccupied slope areas. Independent model validation with observation records collected during the IPY-CAML Ross Sea cruise confirmed the high predictive performance, whereas none of the validation records plotted into regions outside of this predicted *N. lanceopes* distribution (Figure 6.1). Overall, the *N. lanceopes* population distribution seemed to contract further into certain geographic areas as the model predicted a high number of pixels (71%) as 'not suitable' areas in the present day compared to the past (Figure 6.5). This was followed by a further decrease of pixel numbers with low (26%), medium (1.17%) and high (0.34%) suitability, which showed the increased endemic nature of the present population.

6.3.1.3 Future distribution

The SDM under 2100 climate conditions showed contraction of distribution but there was an increase in suitable areas in the deeper slope regions (Figure 6.4, Figure 6.9). The potential range predicted by the model showed range expansion into the deeper sections of the eastern Ross sea shelf, areas between Amundsen Sea and Ross Sea, slopes of D'urville Sea, Prydz bay, Maud rise, bathyal regions of Mawson Sea, Prydz bay and to the Aurora Canyon near eastern tip of Antarctic Peninsula (Figure 6.4). The maximum predicted value for training record was 0.940 (Table 6.1). However, the predicted pixels with 'high suitability' values continued to decrease (0.18%) and pixels with 'low suitability' increased slightly (33%) which reduced the 'not suitable' area to 65% when compared to present day predictions (Figure 6.5). The model predicted all of the potential expansion areas in close distance to existing *N. lanceopes* populations. There is a projected increase in suitable areas forecasted for the eastern Ross Sea (Figure 6.4, Figure 6.7).

6.3.2 Effect of climate change

The results predicted a contraction and expansion of *N. lanceopes* distribution from the past, to present and future. The model suggested a pole-ward shift between the predicted distribution of LGM and present day, and present to future. The highly suitable LGM areas located in the Sub-Antarctic (South Sandwich, South Orkney Islands, and South Georgia), Bouvet Island, Western Weddell Sea and the Kerguelen plateau regions became contracted into smaller areas now. The model also suggested colonization of the slope areas of the east Antarctica (D'urville Sea, Davis Sea, and Ross Sea) and in the tip of Antarctic Peninsula (Figure 6.6).

The predicted distribution for the year 2100 followed the previous trend of pole-ward range shift of *N. lanceopes* populations. However, a range expansion was suggested into newer regions of deeper slope areas near the Scott seamount at Ross Sea, Marie Byrd seamounts at the Amundsen Sea, Aurora canyon at eastern tip Antarctic Peninsula and Maud rise off at north of the Lazarev Sea (Figure 6.9). Nevertheless, the predicted change in area was not same for all Antarctic regions. It contracted more in the western Antarctic (Antarctic peninsula) and expanded more in the Eastern Antarctic regions, i.e. Bellingshausen Sea and eastern Ross Sea. The eastern Ross Sea area which is at present mostly covered by ice all year round is predicted to have more open ocean areas in the future (future ice cover, Appendix VIII) which would facilitate *N. lanceopes* colonization from the nearby slope areas in the west (Figure 6.6).

6.4 Discussion

This study reports the first attempt to explain the geographic shift of a deep-sea Antarctic shrimp in changing climatic conditions using species distribution models. *Nematocarcinus lanceopes* is one of the most widely distributed deep-sea shrimp in the Southern Ocean (Arntz & Gorny, 1991; Gutt *et al.*, 1991; Arntz *et al.*, 1999; Guzmán & Quiroga, 2005; Lovrich *et al.*, 2005; Thatje *et al.*, 2005a; Donnelly *et al.*, 2006; Basher & Costello, 2014). In our study, predicted geographic distribution of *N. lanceopes* was influenced by depth, ice cover and temperature, which is similar to previous studies looking at regional and global scale distribution of the same species using SDM (Dambach *et al.*, 2012; Basher *et al.*, 2014a), however our models predicted new areas of distribution which expanded our understanding of the species wide distribution range. The models showed good predictive performance when they are validated using internal and independent datasets. Similar to other Antarctic benthos (Barnes *et al.*, 2009), *N. lanceopes* population in the Southern Ocean showed a contraction and expansion of distribution following the variation of ice cover in the Antarctic marine ecosystem. The model predicted a range shift of *N. lanceopes* populations from the last glacial maximum to present and then from present to future conditions at year 2100 (Figure 6.9).

6.4.1 SDM to predict species range extension over time

Species distribution models can predict the direction of range contractions or expansions (Araújo *et al.*, 2005) but projections beyond the temporal range of a training dataset require a cautious interpretation to avoid potential pitfalls. Furthermore, using AUC as the only method of model validation has its own caveats (Jiménez-Valverde & Lobo, 2007; Lobo *et al.*, 2008; Pineda & Lobo, 2009) but it has been used widely in studies involving SDM application in paleo and future climate conditions (Lobo *et al.*, 2010; Varela *et al.*, 2011; Dambach *et al.*, 2012; Weinmann *et al.*, 2013). To maximize confidence on the predict potential distribution of the species in different temporal resolution, in addition to AUC , confidence maps were used to identify regions in the predicted suitability maps that contain less variation in prediction among all the replications (Figure 6.8). All of the three confidence maps gave high confidence values (less variation between the predictions in replicates) to highly suitable regions in our predictions.

Compared to taxa elsewhere, many shelf and slope inhibiting Antarctic fauna have an extended bathymetric range (Brey *et al.*, 1996) as they have to endure the same type of physiological adaptations to pressure that parallel those found in truly deep–sea organisms in other oceans (Clarke, 2003). This suggests that Antarctic fauna may represent an evolutionary history of movement in and out of deep water, driven by glacial cycles (Aronson *et al.*, 2007; Fraser *et al.*, 2012). During the last glacial maximum turbidity currents severely affected the survival of fauna on the continental slope around Antarctica (Thatje *et al.*, 2005b; Thatje *et al.*, 2008). For most benthic taxa, survival was possible in the circum-Antarctic deep sea i.e. refugia close to the Antarctic continent which had consistent food supply with open ocean polynya in the surface (Thatje *et al.*, 2008). The agreement between past and present day predicted area by the models highlighted these potential refugia which could be explained by relative climate stasis in those areas. Our past LGM model suggested potential refugia areas located around the northern part of Scotia Arc, southern tip of South America, South Georgia, Bouvet Island, southern tip of the Campbell plateau and Kerguelen plateau (Figure 6.2). The refugia near Campbell plateau and Bouvet island were not identified in a previous study by Dambach *et al.* (2012), is due to our the expanded dataset used in this study. The extent of photosynthetic primary production reducing with the increase of sea ice and thus reduces the survival chance of planktonic larvae of the shrimps (Arrigo & van Dijken, 2004). The predicted *N. lanceopes* LGM distribution is located in many of the highly suitable areas outside of the known LGM ice extent and these areas retained these high suitability characteristics today.

The Antarctic Peninsula (AP) has warmed up to 3.7 ± 1.6°C over the last century (Vaughan *et al.*, 2003; Clarke *et al.*, 2007) while areas in Halley and Amundsen-Scott at the South Pole showed a cooling trend (Turner *et al.*, 2005). The Amundsen Sea has a declined sea ice coverage over the last three decades and the trend seems to continue in the future (future sea ice coverage map at Appendix B and Rignot *et al.*, 2013). Food availability in the deep sea is dependent upon the surface productivity and vertical supply of organic matter from the upper ocean (Smith & Comiso, 2008). Thus, an increase in food availability in the deep sea generally triggers a significant meiofaunal response (Gooday, 2002) resulting in an increase of overall biodiversity in the productive seafloor area (Levin *et al.*, 2001). It is assumed with the melting of sea ice, new habitat areas will become available in the shelf and slope for re-colonization which will be supported with increased projected Chlorophyll-a production in these areas (Shepherd *et al.*, 2004; Whitehouse *et al.*, 2008; Gerringa *et al.*, 2012).

This study hypothesise ongoing range contraction and expansion of *N. lanceopes* due to climate warming. Previous ‘highly suitable’ habitat in the AP showed reduced availability of suitable habitat in the present and future models compared to the past model (Figure 6.2, 6.3, 6.9). Environment suitability in the Amundsen Sea has increased gradually from the past to the future models (Figure 6.3, 6.4, 6.9). Other areas where habitat suitability is projected to increase in the future includes the deeper slopes of the Kerguelen plateau and the eastern Ross Sea. The Kerguelen plateau is one of the major linear shelves near Antarctica and has strong temperature gradient comparing to the AP and Victoria Land areas. This makes it one of the sensitive region to experience thermally driven range shifts by Antarctic fauna (Barnes *et al.*, 2009). The eastern Ross Sea is known as an incredibly hostile place for marine sampling as the area is mostly covered by sea ice and ice bergs (Griffiths, 2010). With projected warming of the temperature and decreased ice coverage around these regions in the coming 100 years, there is a predicted increase of suitable environment for *N. lanceopes*.

SDM is a useful tool for identifying locations and species that may be at greater risk and provide first approximations as to the impact of climate change on species distribution ranges (Pearson & Dawson, 2003; Thuiller *et al.*, 2004; Araújo *et al.*, 2005). However, due to numerous sources of uncertainty, the models and their outputs should only be interpreted with a thorough understanding of the limitations involved with modelling species distribution at different temporal scale (Heikkinen *et al.*, 2006). We should acknowledge that natural systems are not confined to certain measurable parameters and it is not possible to account for all probable driving forces that shape a species distributions over a longer period. There can be no assurance that models that show good predictive ability for past range shifts will produce reliable predictions of future shifts, as climate change over the next century is projected to be potentially more rapid and of greater magnitude than has been experienced during the last 1000 years (Houghton *et al.*, 2001; IPCC Climate Change, 2007).

6.5 Conclusion

This study modelled the potential distribution of the deep-sea shrimp *Nematocarcinus lanceopes* in the Southern Ocean. Past model for *N. lanceopes* suggested contraction of habitat from the Sub-Antarctic regions and pole ward expansion on the continental slopes. Future models for *N. lanceopes* forecast further pole-ward expansion in the continental slope in response to ocean warming. Increases in suitability values suggest that the species will thrive in future environments of the eastern Antarctic but areas will contract further in the Western Antarctic. Potential impact on the marine ecosystems due to range expansion of *N. lanceopes* needs to be investigated in future studies to identify how increased abundance in certain regions will affect the community structures with potential implications to ecosystem functioning.

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Table 6.1. MaxEnt result summary of past and future models. Permutation importance for predictors and result of the jackknife test for the training and test data. Note the high values for Depth, Temperature and Ice cover concerning permutation importance. This indicates their importance as prime factors regulating the distribution of *N. lanceopes* in the SO. This was supported with strong decrease in gain and AUC values for Depth/DepthL and SST when omitted from SDM for *N. lanceopes* (without). When variables are used in isolation (with only) model again and AUC values are most similar to the original values for them.

Model Summary	**Past**				**Future**				
Training Samples	54				54				
Test Samples	18				18				
Training Gain	2.17				2.51				
Training AUC ± SD	0.950± 0.01				0.968 ± 0.008				
Test AUC ± SD	0.903± 0.03				0.956 ± 0.02				
Minimum Presence Threshold	0.012				0.015				
Omission Rate	0				0				
Predictor Influence									
	DepthL	SST	sSal	IceT	Depth	bTmp	bSal	PPD	IceC
Contribution	79.57	18.42	1.02	0.99	61.03	5.27	0.07	2.51	31.12
Permutation Importance	71.91	26.43	1.49	0.16	88.29	0.74	0.02	2.1	8.84
Training Gain without	0.53	1.89	2.15	2.15	1.28	2.44	2.51	2.43	2.22
Test Gain without	-0.56	0.68	0.4	1.74	1.43	2.53	2.63	2.6	2.28
AUC without	0.699	0.91	0.904	0.922	0.902	0.954	0.956	0.962	0.944
Training Gain with only	1.75	0.47	0.14	0.04	1.76	0.92	0	0.13	0.76
Test Gain with only	1.77	-0.02	0.13	-0.03	1.78	1.06	0	0.09	0.86
AUC with only	0.92	0.704	0.63	0.493	0.928	0.866	0.528	0.658	0.845

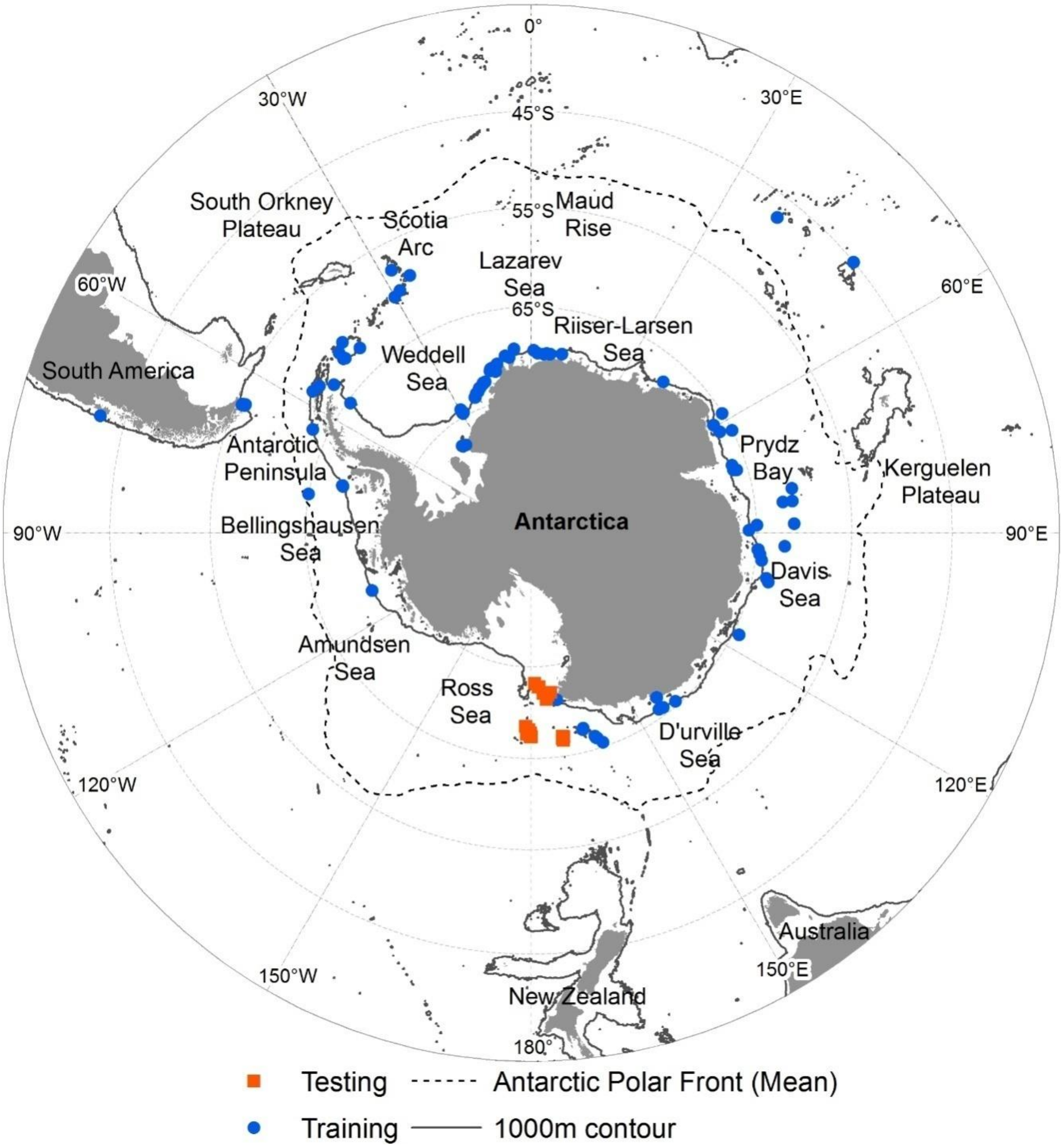

Figure 6.1. Occurrence of *N. lanceopes* in the Southern Ocean. Circles represent the locations used for model training and squares represent the locations used for independent model testing.

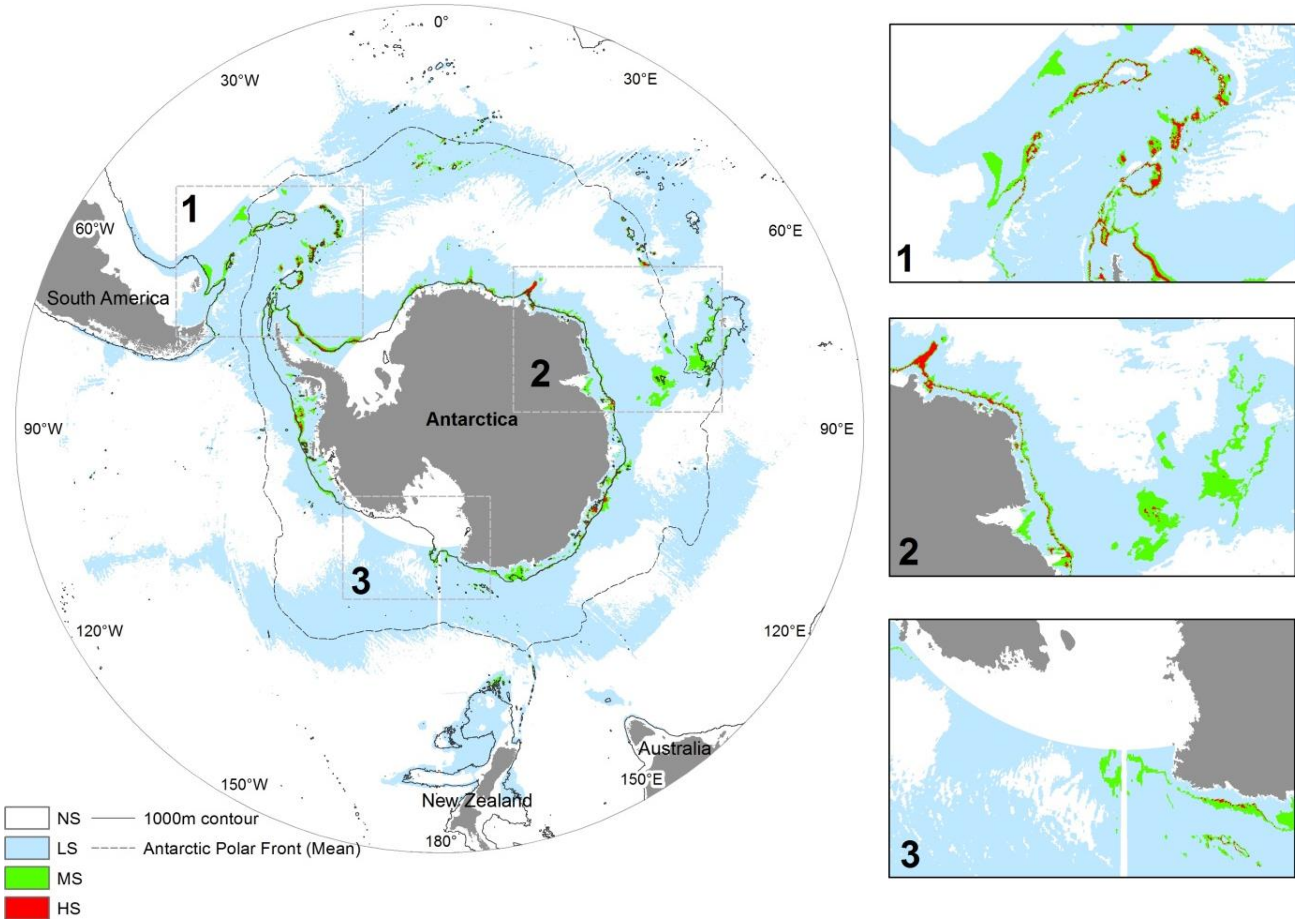

Figure 6.2. Predicted distribution of *N. lanceopes* in the Last Glacial Maximum. Habitat suitability: HS, High suitability (red); MS: Medium suitability (green); LS: Low suitability (sky); NS: Not suitable (white). Detailed prediction map of three different Antarctic regions 1. Scotia Arc and Antarctic Peninsula; 2. Prydz bay and Kerguelen plateau; 3. Ross Sea and Amundsen Sea showed in the close up boxes on the right.

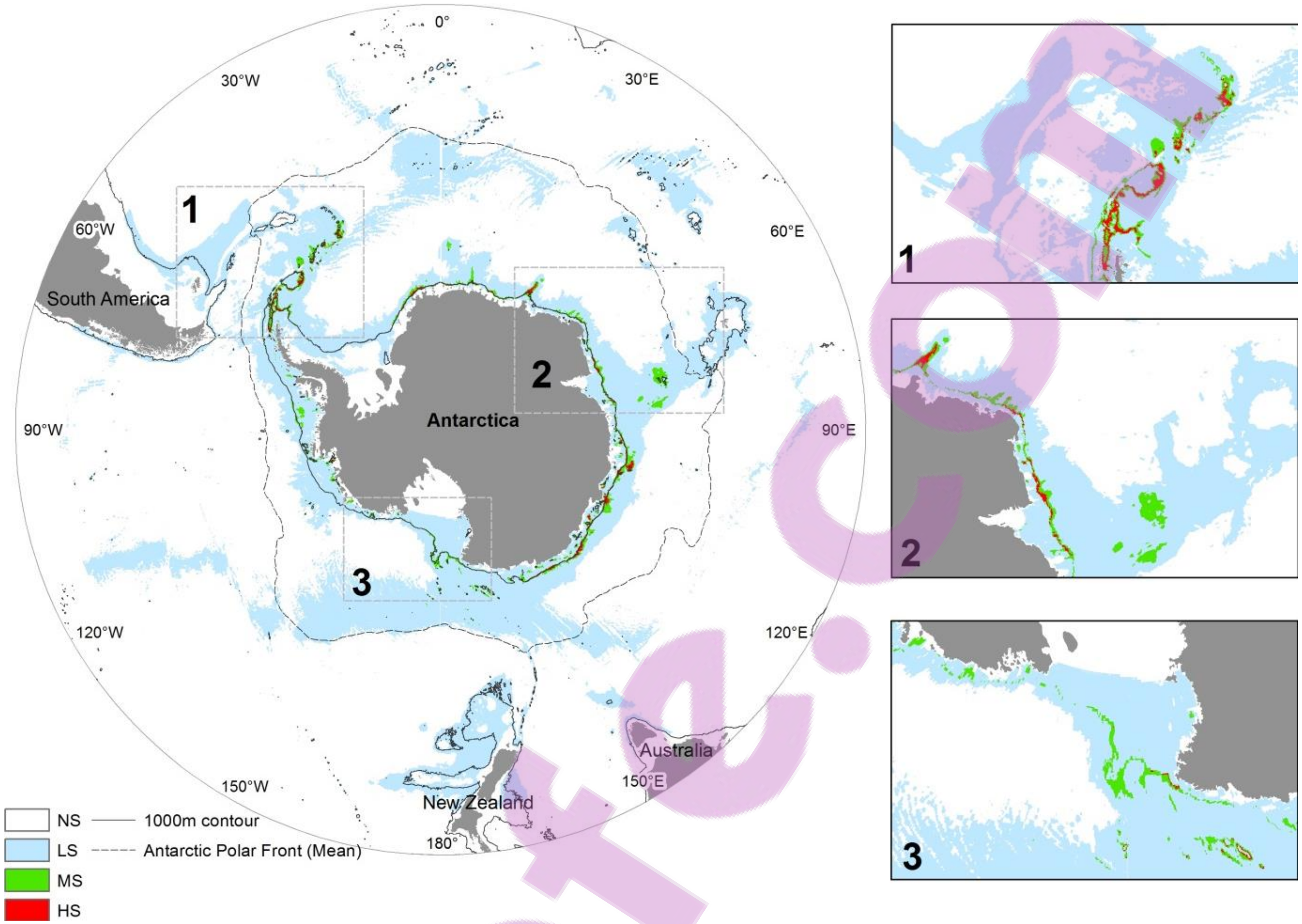

Figure 6.3. Predicted distribution of *N. lanceopes* at present. Habitat suitability: Habitat suitability: HS, High suitability (red); MS: Medium suitability (green); LS: Low suitability (sky); NS: Not suitable (white). Detailed prediction map of three different Antarctic regions 1. Scotia Arc and Antarctic Peninsula; 2. Prydz bay and Kerguelen plateau; 3. Ross Sea and Amundsen Sea showed in the close up boxes on the right.

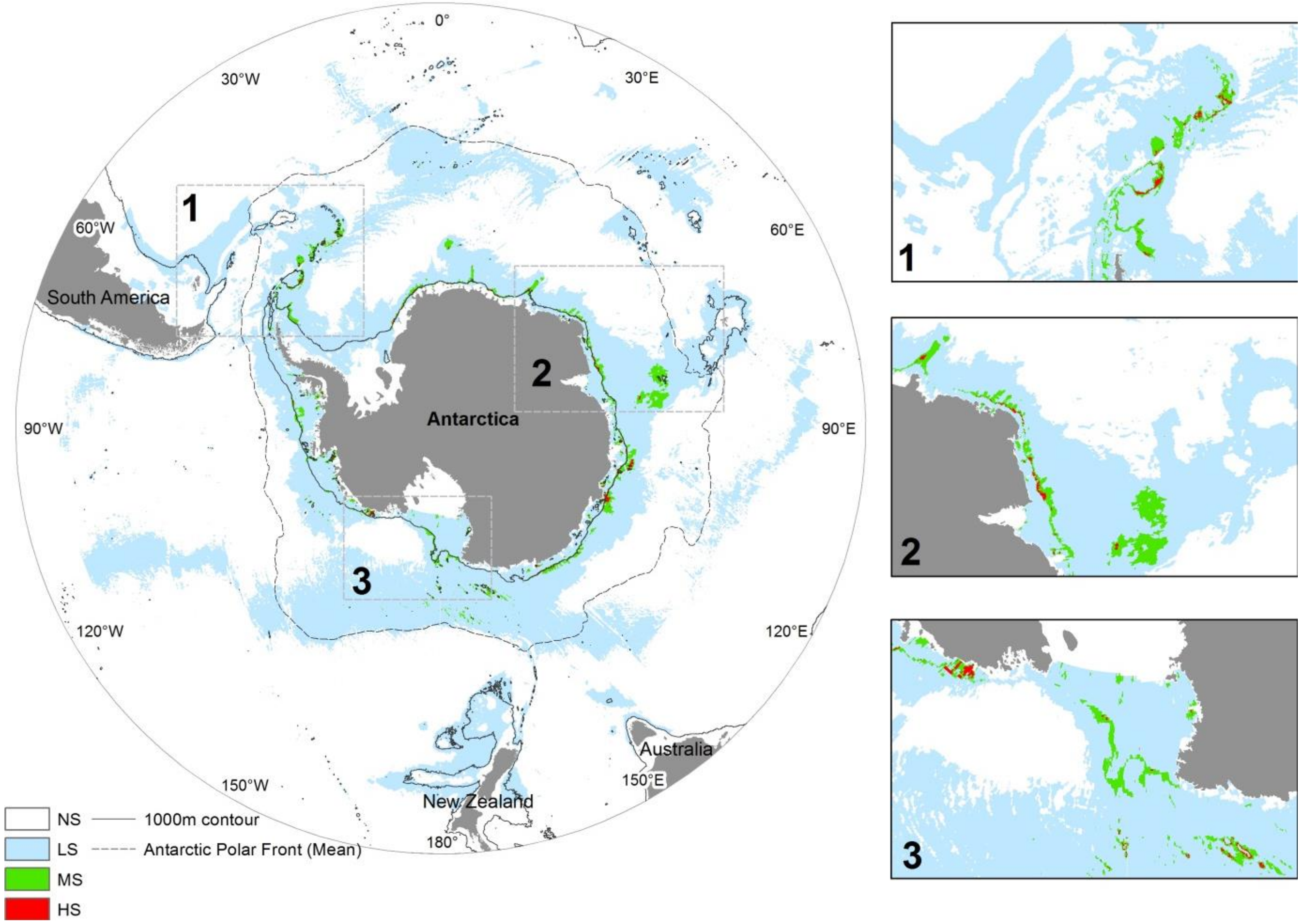

Figure 6.4. Predicted distribution of *N. lanceopes* in the future (year 2100). Habitat suitability: HS, High suitability (red); MS: Medium suitability (green); LS: Low suitability (sky); NS: Not suitable (white). Detailed prediction map of three different Antarctic regions 1. Scotia Arc and Antarctic Peninsula; 2. Prydz bay and Kerguelen plateau; 3. Ross Sea and Amundsen Sea showed in the close up boxes on the right.

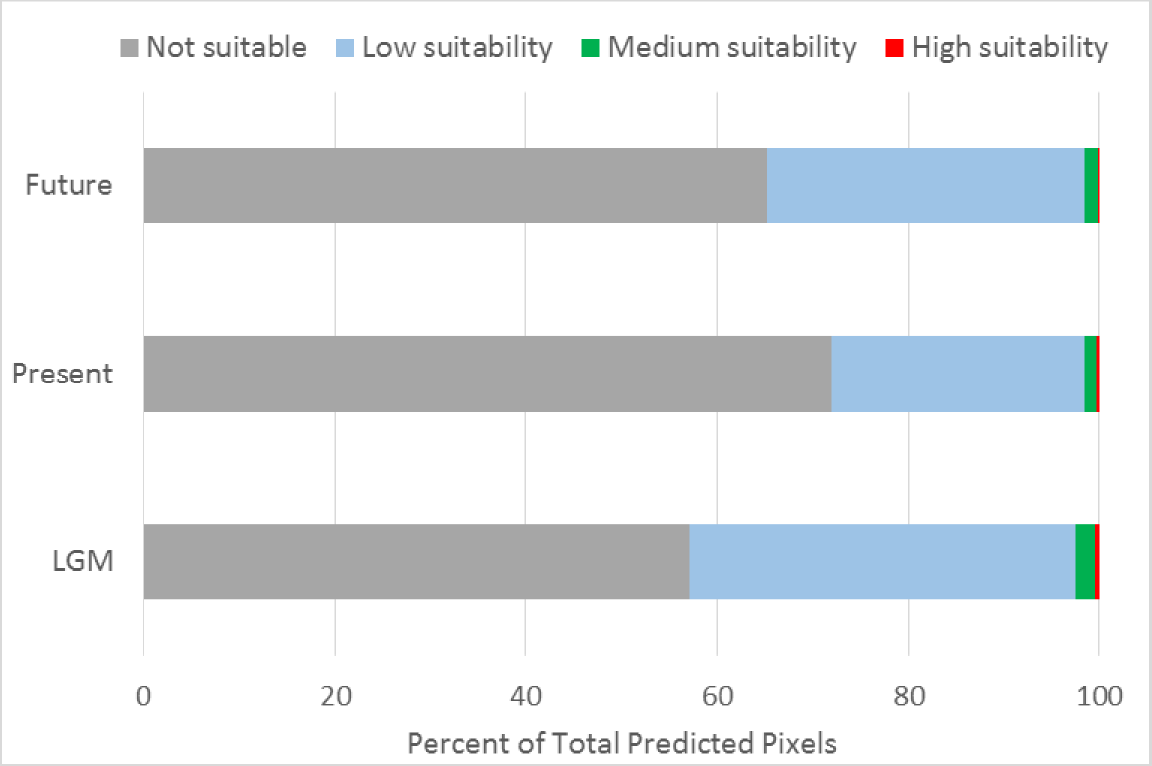

Figure 6.5. Variation in number of pixels identified as the suitable environment for *N. lanceopes* in the MaxEnt model predictions.

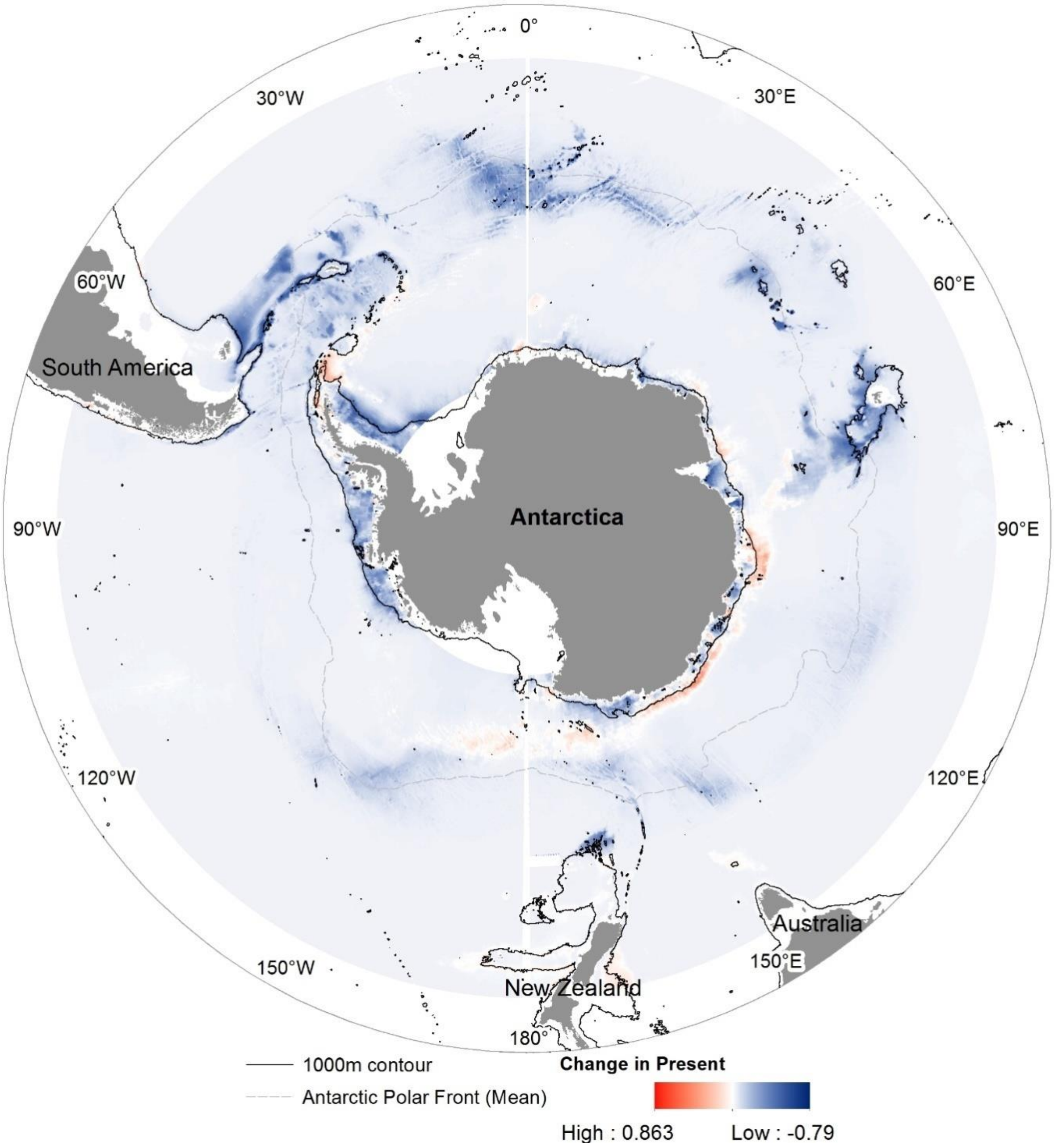

Figure 6.6. *Nematocarcinus lanceopes* range loss and gain from past last glacial maxima period to present day. Areas in red indicates gained range and areas in blue lost range.

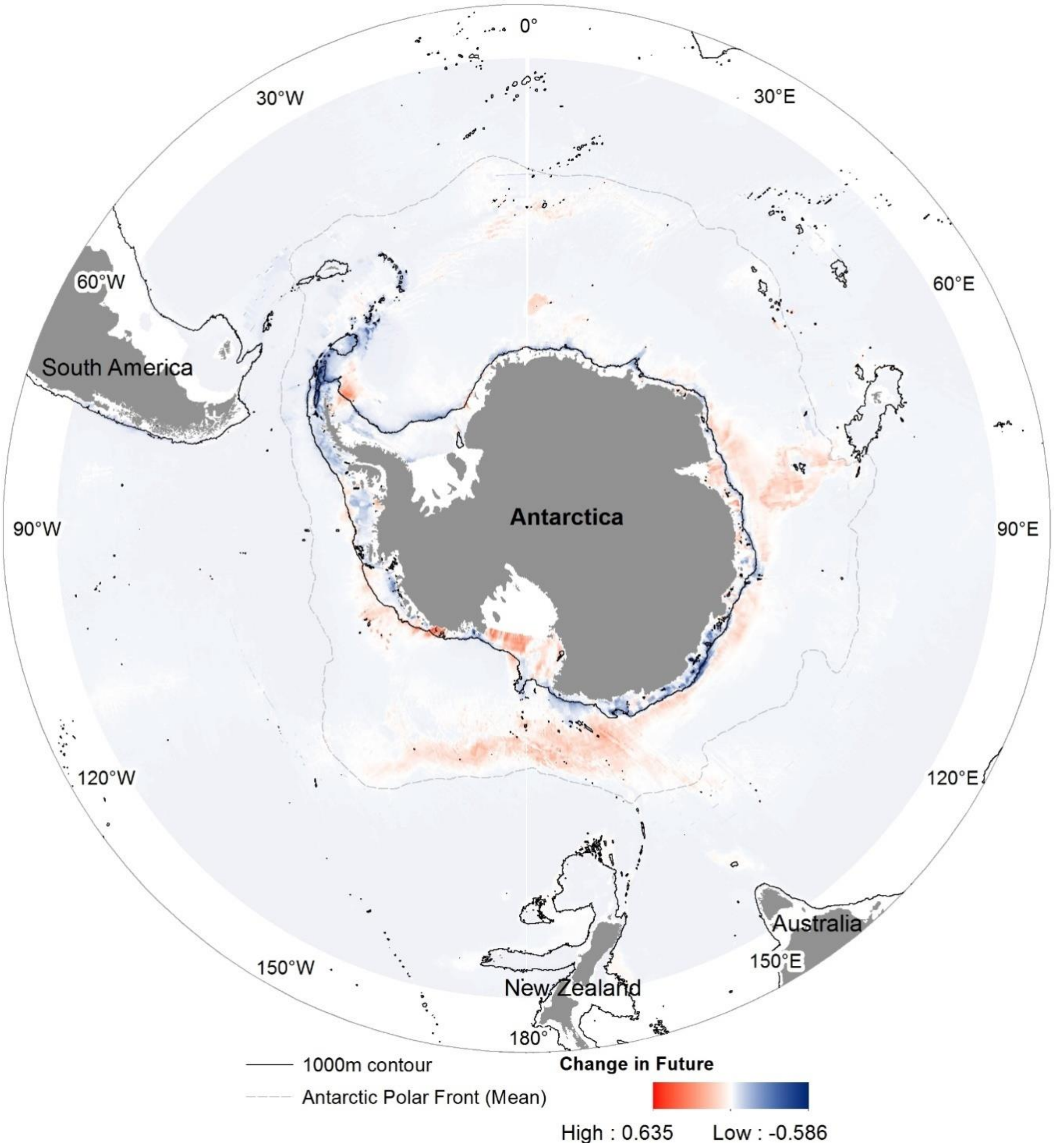

Figure 6.7. Potential habitat change of *N. lanceopes* in the future. Areas in red will gain range and areas in blue will lost range.

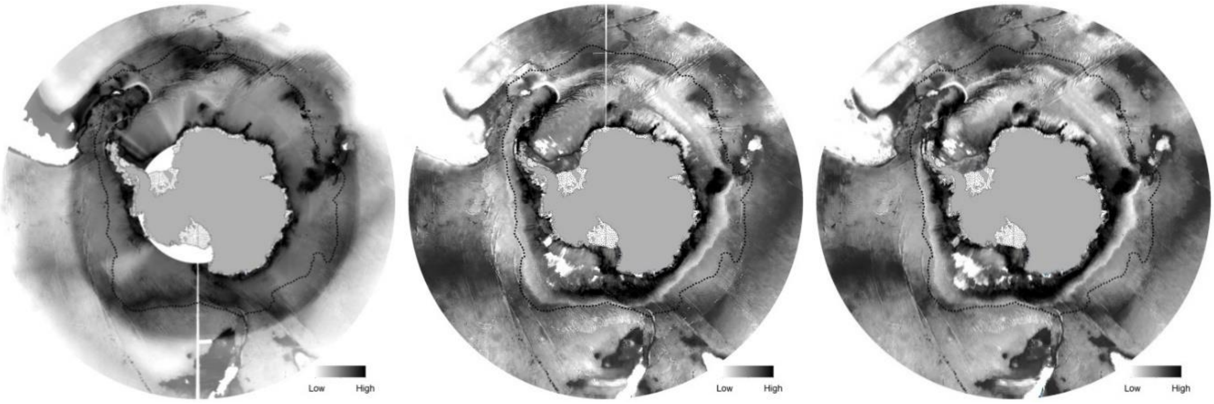

Figure 6.8. Prediction confidence maps of past, present and future MaxEnt models of *N. lanceopes* (from left to right). Black indicates high confidence or less variation in predicted performance among all replicates.

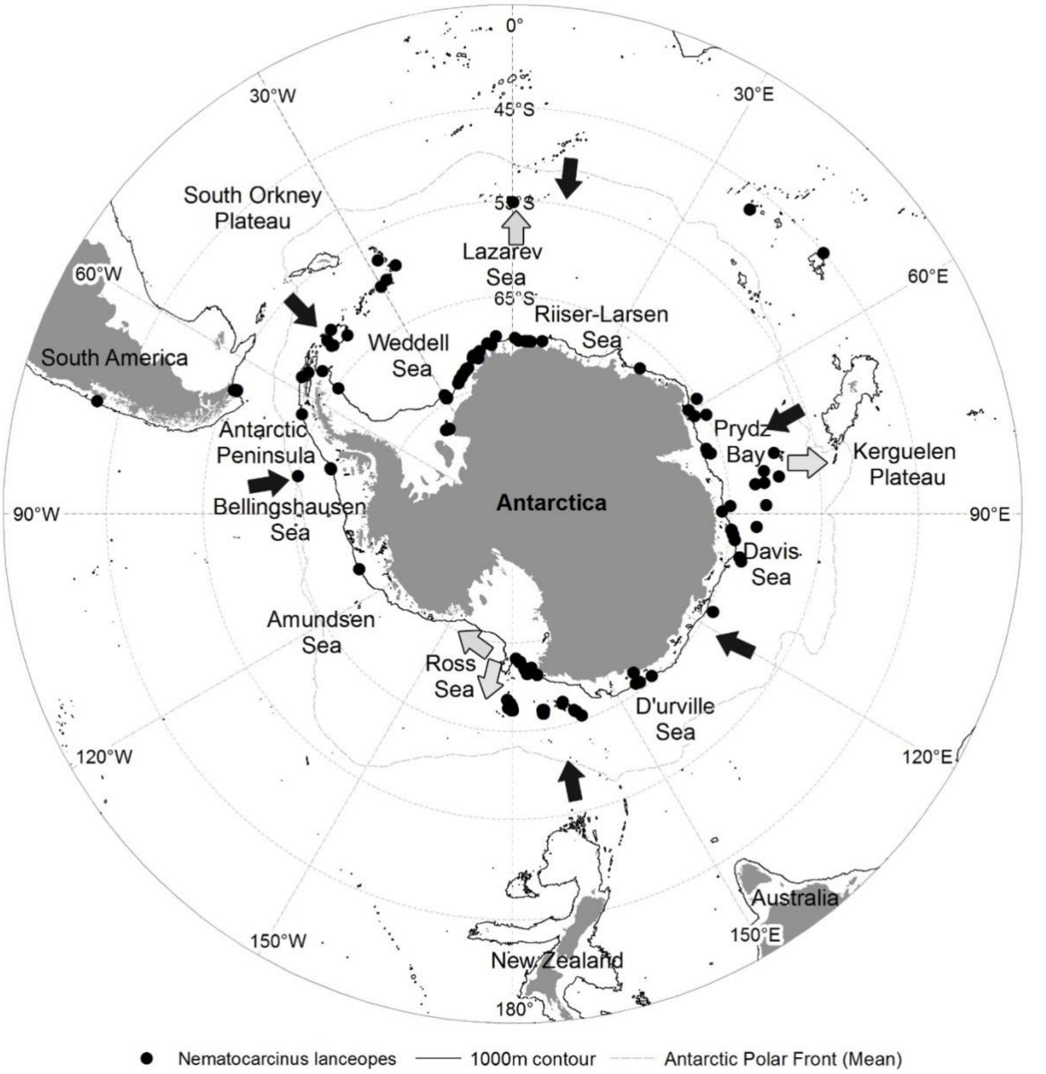

Figure 6.9. Predicted range contraction (black arrow) and expansion (grey arrow) direction of *N. lanceopes* populations in the Southern Ocean based on the predictions of past, present and future climate conditions.

Chapter 7

General Discussion, Conclusion and Future direction

7.1 General Discussion

This thesis has made significant contributions to our understanding of decapod shrimp populations from the Ross Sea, Antarctica. The updated knowledge about their diversity and distribution has allowed us to re-evaluate a common misconception about their scarcity in the Southern Ocean ecosystem. Their widespread distribution around the Southern Ocean and new information about the importance of their role in the food web necessitates their inclusion in ecosystem food web models.

7.1.1 Fulfilment of the objectives of the thesis

7.1.1.1 **Objective one:** To identify the decapod shrimp diversity and geographic distribution in the Ross Sea and predict their potential distribution range and compare them with historical records from literature and other sources of known locations in similar regions (i.e. Weddell Sea, Antarctic Peninsula) (Chapter 2 and Chapter 3) .

Prior to this study, the literature reported between 8 to 12 different shrimp species in the high southern latitudes (Arntz & Gorny, 1991; Arntz *et al.*, 1997; De Grave & Fransen, 2011; Dambach *et al.*, 2012). After the review of recent literature and collating distribution records of the shrimps from various sources in Chapter 2, the total number of known shrimp species in the Antarctic almost doubled. Now, 23 different shrimp species are known to exist in the Antarctic and about half of the species have their northern distribution limit coinciding with the Polar Front suggesting it is a biogeographic boundary. They have been recorded from the shallow continental shelf (ca. 50 m) to abyssal depths (ca. 4000 m) in all areas around the Pacific, Atlantic and Indian Oceans.

In the Ross Sea, this thesis has significantly increased the known locations of deep-sea shrimps. The distribution range of eight shrimp species were identified from collected specimens and this study provided the first record of shrimps from seamounts and the abyssal plain. We reported the existence of at least three species in the Ross Sea which were not found in past studies (Bullivant, 1959, 1967; Gambi & Bussotti, 1999; Pinkerton *et al.*, 2010), and extended the known distribution range of two other species. The SDM predicted a widespread distribution of two species in the shelf, slope and seamount regions. This new knowledge about their region wide distribution emphasized their potential functional role in the Antarctic ecosystem.

7.1.1.2 **Objective two:** Is there any difference in shrimp species composition, diversity and size frequency within the Ross Sea region or with other regions in the SO? How abundant are the shrimps? What was the community composition and what role do they play in the wider trophic ecosystem? (Chapter 4)

The composition of shrimp species was varied at different sites in the Ross Sea. *Chorismus antarcticus* and *N. antarcticus* appear to be abundant in the shelf while *N. lanceopes* were abundant in the regions outside of the continental shelves. Without using any special gear to target shrimps, they were captured in 35 - 50% of the trawl catches or video transects. The mean densities reached up to 50 individuals per 1000 m^2. However, the shrimp density was low but the overall size of all of the species were larger in the Ross Sea in comparison with populations found elsewhere in the Antarctica (Kirkwood & Burton, 1988; Arntz & Gorny, 1991; Gutt *et al.*, 1991; Gorny, 1992; Arntz *et al.*, 1999).

The community composition of shrimps' habitat in the Ross Sea showed *C. antarcticus* and *N. antarcticus* habitats were associated with bryozoans and ophiuroids. While, *N. lanceopes* habitat was dominated by sponges, ophiuroids and anemones. More than one in three occasions, shrimps were found in same community composition in all the sites (where they are present), although the type of species composing those communities varied in the continental shelf, slope, seamount and abyssal depths. The main drivers of the faunal composition at different locations were driven by the presence of ophiuroid, bryozoan and sponges. Other studies on the benthic fauna of the Ross Sea found similar faunal dominance at sites in shelf, slope and abyssal depths (Barry *et al.*, 2003; Cummings *et al.*, 2010; Bowden *et al.*, 2011), suggesting shrimps may also or will occur in these regions.

The stable isotope analysis of the shrimps identified a carnivorous and detrivorous diet in the Ross Sea. This finding fills an important knowledge gap in the existing Ross Sea Food Web model by Pinkerton *et al.* (2010), where the role of benthic invertebrates were previously unknown.

7.1.1.3 **Objective three:** Which environmental variables influence the distribution of shrimps in the marine environment and do their source or spatial resolution matter when using them for Species Distribution Models? (Chapter 3, Chapter 5 and Chapter 6).

Species distribution models are empirical models relating field observations to environmental predictor variables based on statistically or theoretically derived response surfaces (Guisan & Zimmermann, 2000). They also identify variables that might influence a species distribution over time and space (Guisan & Thuiller, 2005). However, the influence of individual variables might vary depending on the resolution of the environmental datasets used for modelling. This trait was not assessed prior to this study and our results suggest the relative ranking, but not the composition of these environmental variables change in models at different spatial resolutions. The predicted extent of suitable habitat was smaller in models using the finer-scale environmental variables (Chapter 3).

It is important to select the most relevant environmental predictors in SDM's to understand factors influencing a species biogeography (Pearson & Dawson, 2003; Thuiller *et al.*, 2004; Stanton *et al.*, 2012). Therefore, to address the limited availability of most ecologically relevant set of marine environmental datasets that could be used with species distribution models; a new compendium of marine environment datasets was created as a part of this thesis (Chapter 5). These new online high-resolution marine environment datasets are free and publicly available, which have been compiled to give marine researchers a useful resource to expedite the mapping of species distribution ranges using the popular SDM algorithms. The utility of this new compendium dataset was demonstrated in Chapter 6, where distribution of a deep-sea shrimp species was predicted for the past and future climatic conditions.

7.1.1.4 **Objective four:** To identify whether deep sea shrimps are susceptible to changing environmental conditions over the millennia and how they will react with projected climate change scenario in the future. (Chapter 6).

Species distribution models (SDM) have been used to predict the change of species distribution in terrestrial and marine studies over the years (Araújo *et al.*, 2005; Bond *et al.*, 2011; Robinson *et al.*, 2011; Mellin *et al.*, 2012; Rapacciuolo *et al.*, 2012; Olson *et al.*, 2014). However, it has not been used for predicting the range shift for any Antarctic species to date. In Chapter 6, I predicted the range shift of deep-sea shrimp *Nematocarcinus lanceopes* using SDM.

The main findings of this chapter include prediction of new glacial refugia around the Southern Ocean which were not predicted in a previous study by Dambach *et al.* (2012). In addition, they predicted continued pole-ward range shift following other Southern Ocean fauna in response to climate change (Aronson *et al.*, 2009; Cheung *et al.*, 2012; Fraser *et al.*, 2012). The future models predicted a range expansion in the east Antarctica but continued contraction will in west Antarctica. This implies the species will survive in future climate conditions by changing its current distribution.

7.2 General conclusions of the thesis

This study extended the number of known locations of deep-sea shrimps in the Southern Ocean (Chapter 2) and in the Ross Sea (Chapter 3). These new observations have enabled us to re-evaluate the known shrimp diversity and their distribution in the Southern Ocean and Ross Sea region. Shrimps occurred throughout the Ross Sea region, with *N. antarcticus* being the most abundant species on the continental shelf, and *N. lanceopes* on the continental slope and on seamounts to the north. *Notocrangon antarcticus* and *Chorismus antarcticus* occurred only on the shelf, whereas the five other species were only recorded off-shelf. The predicted distribution of *N. antarcticus* and *N. lanceopes* showed both species have their distribution range restricted to certain regions; the former one at the shelf and the latter one at the slope and seamount sites. Overall, they were widespread throughout the Ross Sea region. Models generated with different spatial resolution showed changes in the relative ranking, but not the composition of, variables. The predicted suitable area was shown to be smaller in models using finer scale environmental layers.

Shrimps were present in 35-50% of the catches in the Ross Sea, showing a lower density in comparison to other Antarctic regions. Specimens captured in the Ross Sea were bigger and found in greater depth compared to catches from other regions as the length of at least two species exceeded the previously known maximum. In terms of community composition, this new data showed it differed from species to species but the composition was dominated by ophiuroid, bryozoan and sponge abundance. The advantages of using isotope analysis to identify benthic invertebrates' diet was demonstrated. Isotopic signatures of individual shrimps showed they were carnivorous and detrivorous in the Ross Sea. *Notocrangon antarcticus* have one of the highest (i.e. carnivorous) trophic levels in the Antarctic food web.

The compilation of the high-resolution marine environment datasets also opened a new opportunity to investigate the utility of SDM to predict potential range expansion or contraction directions of a species under past and future climate conditions. By using species distribution records with high geographical accuracy I have been able to predict the past glacial refugia locations and the future range shift directions of deep-sea shrimp *Nematocarcinus lanceopes* in the Southern Ocean.

7.3 Future direction

The work presented here has answered four important questions regarding Antarctic shrimps. But it has also shown the need for further research in the following areas.

7.3.1 Shrimp population in the Ross Sea and Antarctica

Additional samples will determine whether shrimps are really absent from other areas around the Antarctic, in particular the eastern Ross Sea, western Weddell Sea and Riiser-Larsen Sea. Furthermore, the sampling stations were limited to the western Ross Sea shelf, slope and seamount regions and with the low number of shrimp specimens (*n=92*) captured in the IPY-CAML cruise at the Ross Sea, it was not possible to undergo a comprehensive study on the population dynamics of shrimps. It should be attempted when more specimens from unsampled locations around the region become available with future cruises to understand the population structure of shrimps in the region.

Although, *Nematocarcinus lanceopes* larvae were captured from shallow pelagic sampling stations in the same IPY-CAML cruise (Gallego *et al.*, 2013), and the larvae of *N. antarcticus* and *C. antarcticus* have been previously captured from the shallow waters in the Terra Nova Bay (Carli & Pane, 2000), the knowledge about the spawning and early life history of the Southern Ocean deep-sea shrimps in the Ross Sea is largely unknown.

7.3.2 Temporal variation

Sampling in the Antarctic is very expensive and limited to a few days in campaign years due to logistical reasons. The specimens used for this study were collected from a single cruise during the Austral summer in the year 2008. No information about the temporal variation of shrimp abundance on the sampled sites were available to compare seasonal variation over a longer period. Other sites where shrimps were not captured during the cruise might discover a shrimp population in different months of the year. A year-round study on the shrimp population at least for the shallow shelf region could highlight the temporal variation in adult shrimp density in the Ross Sea. Perhaps this could be aided by in-situ time-lapse photography.

7.3.3 Species observation records

Observation records are limited for any deep-sea species and this is more evident when the species resides in high latitudes. Since sampling is expensive in high-latitudes, government-funded cruises are the main source of these records. In this thesis, we have used geo-referenced observation records of specimens to generate SDM. Their usefulness was shown when the model outputs were validated with independent records, showing very high accuracy by matching the species predicted distribution with fundamental distribution. Although in recent years, more government-funded projects have required the publication of the biodiversity dataset on collected species be made available to the public, often time independent collectors or museums did not follow the same path. Thus, observation records collected by the researchers from independent projects in the Sub-Antarctic and Antarctic regions should be made accessible to the wider scientific community through biodiversity databases (Costello *et al.*, 2013). This will enrich the geographic coverage of the distribution records and will result in better SDM models to explore regional and global questions for Antarctic species.

7.3.4 Improved environmental layers

There are opportunities to refine and improve the interpolation methods in future versions of the marine environmental dataset presented in this thesis. Continuing efforts to compile and capture more environmental data sets are needed to improve temporal and spatial coverage of the dataset. The availability of online tools might enable researchers to explore the full strength of the datasets. Future products could include the development of an open geospatial consortium (OGC) compliant database, an online data extraction tool allowing users to download the dataset of any defined extent and an online workbench to run SDM algorithms instantaneously using user-provided species datasets with selected environmental datasets.

7.3.5 Impact of range shift in the ecosystem

Our study predicted past and future range shifts of shrimps due to warming climate. Other species may show similar responses but remain to be assessed. Such studies would help predict the potential impact of climate change on the marine ecosystems on community structure and food webs, and their implications to the overall functioning of the ecosystem.

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Chapter 8

Appendices

Appendix I

Pearson correlation matrix of environmental variables. Variables with high correlation highlighted in **bold**.

SET 1	*Depth*	*Rugosity*	*Temperature**	*Salinity**	*Chlorophyll-a*	*Ice Concentration*	*Current**
Depth	-						
Rugosity	-0.307	-					
Temperature*	**0.751**	-0.108	-				
Salinity*	0.346	-0.015	0.195	-			
Chlorophyll-*a*	-0.381	0.021	-0.386	0.111	-		
Ice Concentration	-0.228	-0.029	-0.305	-0.237	0.344	-	
Current*	-0.125	-0.028	-0.083	0.016	0.108	0.070	-

SET 2	*Depth*	*Slope*	*Temperature **	*Salinity**	*Chlorophyll-a*	*Ice Concentration*
Depth	-					
Slope	0.495	-				
*Temperature **	0.580	0.037	-			
Salinity *	0.548	0.879	0.018	-		
Chlorophyll-*a*	-0.114	0.464	-0.384	0.529	-	
Ice Concentration	-0.174	0.318	-0.550	0.391	0.305	-

*** Bottom layers**

Appendix II

Independent location records used for model validation. Citations (a) Department of Invertebrate Zoology, Research and Collections Information System, NMNH, Smithsonian Institution. See: http://www.mnh.si.edu/rc/db/collection_db_policy1.html, 05-14-2010 ; (b) De Grave, S., C.H.J.M. Fransen (2011) Carideorum Catalogus: The Recent Species of the Dendrobranchiate, Stenopodidean, Procarididean and Caridean Shrimps (Crustacea: Decapoda). Zoologische Mededelingen Leiden, 84, 195-589; (c) Dambach, J., Thatje, S., Rödder, D., Basher, Z. & Raupach, M.J. (2012) Effects of Late-Cenozoic Glaciation on Habitat Availability in Antarctic Benthic Shrimps (Crustacea: Decapoda: Caridea). PLoS ONE, 7, e46283; (d) NIWA OBIS (nzobis.niwa.co.nz).

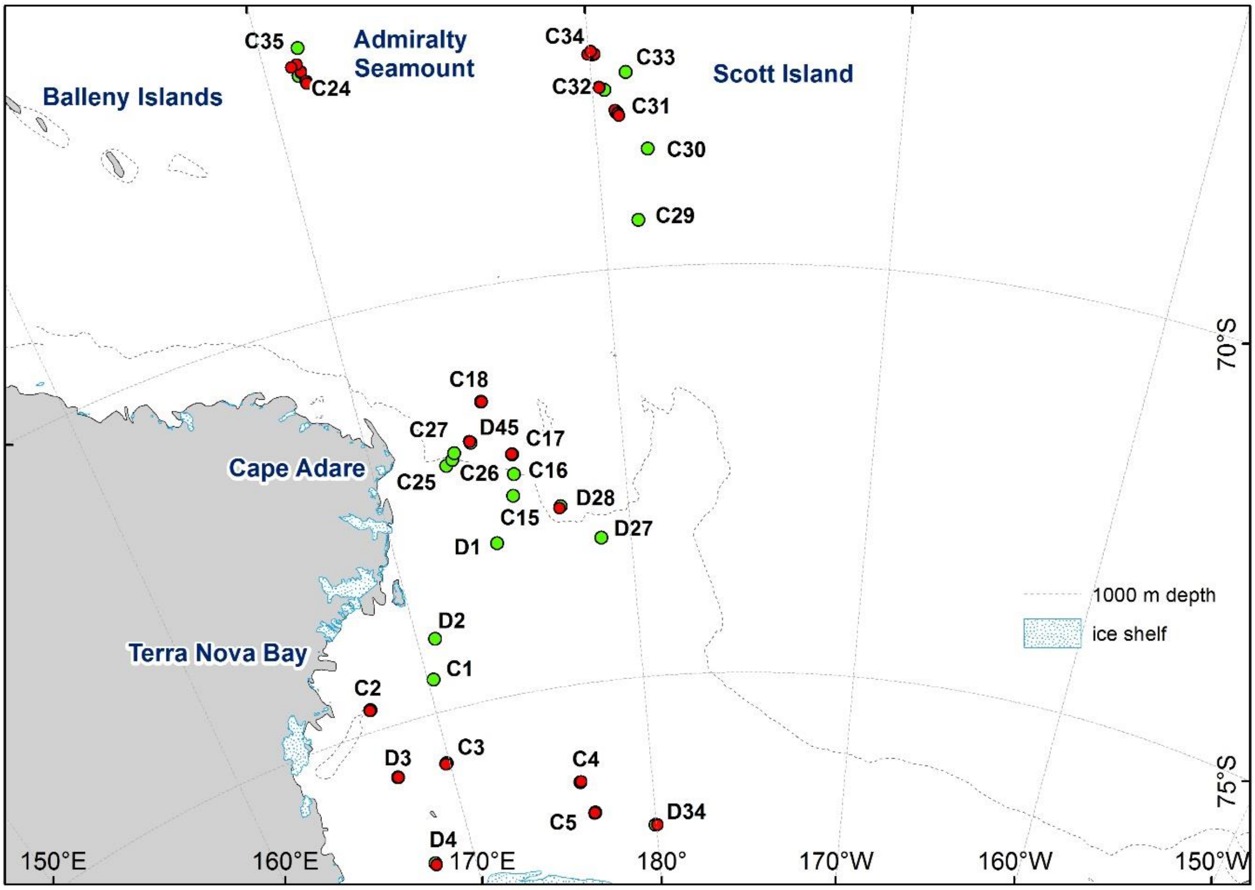
Catalogue #	Scientific name	Latitude	Longitude	Year collected	Depth Min	Depth Max	Basis of record	Institution code	Citation
1124840	*Notocrangon antarcticus*	-77.058	166.233	1967	891	891	S	USNM	a
1124848	*Notocrangon antarcticus*	-77.558	174.758	1967	728	728	S	USNM	a
1124853	*Notocrangon antarcticus*	-77.717	-167.692	1968	547	552	S	USNM	a
1124860	*Notocrangon antarcticus*	-77.233	169.2	1967	930	930	S	USNM	a
1124864	*Notocrangon antarcticus*	-77.867	177.6	1967	769	770	S	USNM	a
1124865	*Notocrangon antarcticus*	-76.075	-164.808	1968	513	550	S	USNM	a
1124866	*Notocrangon antarcticus*	-76.975	-171.117	1968	430	433	S	USNM	a
1124867	*Notocrangon antarcticus*	-75	176.683	1968	335	338	S	USNM	a
1009761	*Notocrangon antarcticus*	-76	172.067	1968	565	569	S	USNM	a
1009762	*Notocrangon antarcticus*	-73.983	170.708	1967	598	613	S	USNM	a
1011061	*Notocrangon antarcticus*	-75.5	165.733	1958	631	631	S	USNM	a
1124829	*Notocrangon antarcticus*	-76.492	170.733	1967	640	646	S	USNM	a
1124827	*Notocrangon antarcticus*	-75.533	-178.767	1967	474	496	S	USNM	a
1124830	*Notocrangon antarcticus*	-73.533	171.458	1967	527	538	S	USNM	a
1124838	*Notocrangon antarcticus*	-74.517	170.183	1967	311	328	S	USNM	a
1124955	*Notocrangon antarcticus*	-78.383	-173.067	1968	473	475	S	USNM	a
1124957	*Notocrangon antarcticus*	-74.817	172.25	1968	535	535	S	USNM	a
1124959	*Notocrangon antarcticus*	-76.525	174.933	1967	445	448	S	USNM	a
1124960	*Notocrangon antarcticus*	-73	171.717	1968	580	580	S	USNM	a
1124962	*Notocrangon antarcticus*	-78.475	-165.508	1968	491	493	S	USNM	a
1124963	*Notocrangon antarcticus*	-76.008	-176.767	1968	566	569	S	USNM	a
1124964	*Notocrangon antarcticus*	-76.142	168.167	1967	362	375	S	USNM	a

1124966	*Notocrangon antarcticus*	-77.142	165.9	1968	820	826	S	USNM	a
1124868	*Notocrangon antarcticus*	-77	-161.983	1968	525	537	S	USNM	a
1124901	*Notocrangon antarcticus*	-77.533	-163.058	1968	606	638	S	USNM	a
1124903	*Notocrangon antarcticus*	-77.975	178.083	1968	655	655	S	USNM	a
1124909	*Notocrangon antarcticus*	-77.033	-166.733	1968	408	415	S	USNM	a
1124932	*Notocrangon antarcticus*	-77.033	168.508	1968	909	923	S	USNM	a
1124946	*Notocrangon antarcticus*	-76.417	-170.467	1968	568	568	S	USNM	a
1124948	*Notocrangon antarcticus*	-78.4	-168.992	1968	562	564	S	USNM	a
1124949	*Notocrangon antarcticus*	-75	169.45	1967	324	329	S	USNM	a
1124950	*Notocrangon antarcticus*	-72.958	171.608	1967	573	576	S	USNM	a
1124952	*Notocrangon antarcticus*	-74.1	-175.025	1968	2350	2350	S	USNM	a
1124953	*Notocrangon antarcticus*	-74.533	168.283	1968	876	876	S	USNM	a
1124954	*Notocrangon antarcticus*	-76.475	167.933	1967	741	747	S	USNM	a
1124870	*Notocrangon antarcticus*	-77.667	-176.825	1968	595	600	S	USNM	a
1124872	*Notocrangon antarcticus*	-76.15	-165.117	1968	494	498	S	USNM	a
1124875	*Notocrangon antarcticus*	-77.583	174.975	1968	731	731	S	USNM	a
1124880	*Notocrangon antarcticus*	-75.45	168.833	1967	364	366	S	USNM	a
1124883	*Notocrangon antarcticus*	-75.025	168.458	1968	334	335	S	USNM	a
1124886	*Notocrangon antarcticus*	-73.975	170.908	1968	589	608	S	USNM	a
1124887	*Notocrangon antarcticus*	-75.975	178.233	1968	513	517	S	USNM	a
1124888	*Notocrangon antarcticus*	-78.283	-177.942	1968	636	637	S	USNM	a
1124919	*Notocrangon antarcticus*	-77.525	-172.458	1968	468	482	S	USNM	a
1124967	*Notocrangon antarcticus*	-49.85	178.575	1968	2010	2100	S	USNM	a
1124968	*Notocrangon antarcticus*	-77.342	172.683	1967	662	664	S	USNM	a
1124878	*Notocrangon antarcticus*	-77.1517	-158.998	1972	344	357	S	USNM	a
1124882	*Notocrangon antarcticus*	-76.035	-179.95	1972	347	358	S	USNM	a
TNSTN294	*Notocrangon antarcticus*	-74.4167	-166.783		0	1750	S	AWI	b
TNSTN338	*Notocrangon antarcticus*	-77.2167	164.3		379	379	S	AWI	b
TNSTN355	*Notocrangon antarcticus*	-77.7667	166.1333		547	547	S	AWI	b
TBSTN339	*Notocrangon antarcticus*	-77.0833	164.2833		256	256	S	AWI	b

JD1	*Notocrangon antarcticus*	-76.6023	176.802				S	AWI	c
JD2	*Notocrangon antarcticus*	-76.594	176.828				S	AWI	c
JD3	*Notocrangon antarcticus*	-76.591	176.883				S	AWI	c
JD4	*Notocrangon antarcticus*	-76.202	176.248				S	AWI	c
JD5	*Notocrangon antarcticus*	-76.1931	176.2961				S	AWI	c
JD9	*Notocrangon antarcticus*	-75.6217	169.8045				S	AWI	c
JD15	*Notocrangon antarcticus*	-72.2875	170.2333				S	AWI	c
TAN0402/203b	*Nematocarcinus lanceopes*	-71.1562	171.1742	2004	1165	1158	O	NIWA	d
TAN0402/214	*Nematocarcinus lanceopes*	-67.4228	165.2637	2004	1389	1444	O	NIWA	d
TAN0402/254b	*Nematocarcinus lanceopes*	-66.3598	162.5418	2004	720	985	O	NIWA	d
TAN0402/257	*Nematocarcinus lanceopes*	-66.2162	162.4415	2004	1261	1395	O	NIWA	d
TAN0402/263b	*Nematocarcinus lanceopes*	-66.1195	162.013	2004	960	1176	O	NIWA	d
TAN0402/270	*Nematocarcinus lanceopes*	-65.4983	161.044	2004	755	764	O	NIWA	d

Appendix III

Sampling site locations for the IPY-CAML Survey in the Ross Sea. Sites with red dots indicated the locations from where shrimp specimens were measured in photography or trawls.



Appendix IV

Details of shrimp specimens from IPY-CAML and other museums, used for population density estimate in the study. Abbreviations: LAT = Latitude; Lon = Longitude; CL= Carapace Length (mm); TL=Total Length (mm); Type=I (Image), S (Specimen)

SN	TYPE	COLLECTION	SPECIES	LAT	LON	CL	TL	DEPTH_MAX
1	S	SMHN	*Chorismus antarcticus*	-77.6567	166.27	16.23	92.07	315
2	S	SMHN	*Chorismus antarcticus*	-74.97	164.07	12.3	58.25	860
3	S	SMHN	*Chorismus antarcticus*	-77.8319	166.5769	19.45	104.73	103
4	S	SMHN	*Chorismus antarcticus*	-77.8508	166.6219	14.9	78.65	51
5	S	SMHN	*Chorismus antarcticus*	-84.4183	167	9.56	57.71	732
6	S	SMHN	*Chorismus antarcticus*	-64.8203	243.5025	12.59	69.74	20
7	S	SMHN	*Chorismus antarcticus*	-64.8203	243.5025	12.78	64.5	20
8	S	SMHN	*Chorismus antarcticus*	-64.8203	243.5025	12.52	66.17	20
9	S	SMHN	*Chorismus antarcticus*	-64.8203	243.5025	11.85	67.18	20
10	S	SMHN	*Chorismus antarcticus*	-61.3367	224.425	15.08	80.46	274
11	S	SMHN	*Chorismus antarcticus*	-61.3367	224.425	16.9	85.4	274
12	S	SMHN	*Chorismus antarcticus*	-60.925	224.685	15.08	81.43	236
13	S	SMHN	*Chorismus antarcticus*	-60.4267	226.4217	15.22	52.29	97
14	S	SMHN	*Chorismus antarcticus*	-60.4267	226.4217	12.98	78.02	97
15	S	SMHN	*Chorismus antarcticus*	-77.6567	166.27	15.57	83.61	
16	S	SMHN	*Chorismus antarcticus*	-77.6567	166.27	17.11	77.25	
17	S	SMHN	*Chorismus antarcticus*	-77.6567	166.27	17.04	88.51	
18	S	NMHN	*Chorismus antarcticus*	-66.3343	142.3041	36	101	217
19	S	NMHN	*Chorismus antarcticus*	-66.3343	142.3041	20	57	217
20	S	NMHN	*Chorismus antarcticus*	-66.3343	142.3041	22	59	217
21	S	NMHN	*Chorismus antarcticus*	-66.3392	142.5591		78	391
22	S	NMHN	*Chorismus antarcticus*	-66.3392	142.5591	21	60	391
23	S	NMHN	*Chorismus antarcticus*	-66.3392	142.5591	19	54	391
24	S	NMHN	*Chorismus antarcticus*	-66.3392	142.5591	20	61	391
25	S	NMHN	*Chorismus antarcticus*	-66.5582	140.8446	30	79	361
26	S	NMHN	*Chorismus antarcticus*	-66.5582	140.8446	27	66	361
27	S	NMHN	*Chorismus antarcticus*	-66.5582	140.8446	23	64	361
28	S	NMHN	*Chorismus antarcticus*	-66.7499	144.0697	26	65	641

29	S	NMHN	*Chorismus antarcticus*	-66.7499	144.0697	31	84	641
30	S	NMHN	*Chorismus antarcticus*	-66.7499	144.0697	24	65	641
31	S	NMHN	*Chorismus antarcticus*	-66.1691	139.9321	26	66	150
32	S	NMHN	*Chorismus antarcticus*	-66.1691	139.9321	26	67	150
33	S	NMHN	*Chorismus antarcticus*	-66.1691	139.9321	30	86	150
34	S	NMHN	*Chorismus antarcticus*	-66.1762	143.3458	34	85	534
35	S	NMHN	*Chorismus antarcticus*	-66.1762	143.3458	28	68	534
36	S	NMHN	*Chorismus antarcticus*	-66.1762	143.3458	20	58	534
37	S	NMHN	*Chorismus antarcticus*	-65.9766	143.3876	30	77	479
38	S	NMHN	*Chorismus antarcticus*	-65.9766	143.3876	32	80	479
39	S	NMHN	*Chorismus antarcticus*	-65.9766	143.3876	30	73	479
40	S	NMHN	*Chorismus antarcticus*	-65.9766	143.3876	24	66	479
41	S	NMHN	*Chorismus antarcticus*	-65.9766	143.3876	26	63	479
42	S	NMHN	*Chorismus antarcticus*	-65.9155	144.0765	25	70	370
43	S	NMHN	*Chorismus antarcticus*	-65.9155	144.0765	28	68	370
44	S	NMHN	*Chorismus antarcticus*	-66.3419	141.3392	28	76	230
45	S	NMHN	*Chorismus antarcticus*	-66.3419	141.3392	28	74	230
46	S	NMHN	*Chorismus antarcticus*	-66.3419	141.3392	28	78	230
47	S	NMHN	*Chorismus antarcticus*	-66.3419	141.3392	22	57	230
48	S	NMHN	*Chorismus antarcticus*	-66.5321	140.0464	25	64	176
49	S	NMHN	*Chorismus antarcticus*	-66.5321	140.0464	21	66	176
50	S	NMHN	*Chorismus antarcticus*	-66.5321	140.0464	19	49	176
51	S	NMHN	*Chorismus antarcticus*	-66.564	141.338	31	81	170
52	S	NMHN	*Chorismus antarcticus*	-66.564	141.338	23	52	170
53	S	NIWA	*Chorismus antarcticus*	-74.5887	170.2692	8.5	39	283
54	S	NIWA	*Chorismus antarcticus*	-74.5887	170.2692	16	70	283
55	S	NIWA	*Chorismus antarcticus*	-74.5805	170.293	11	47	285
56	S	NIWA	*Chorismus antarcticus*	-76.205	176.2439	15	69	447
57	S	NIWA	*Chorismus antarcticus*	-76.204	176.241	17	76	451
58	S	NIWA	*Chorismus antarcticus*	-76.819	179.97	10.5	49	664
59	I	NIWA	*Chorismus antarcticus*	-75.633	169.7816		76.16	529.5
60	I	NIWA	*Chorismus antarcticus*	-75.6334	169.7854		61.51	528.3
61	I	NIWA	*Chorismus antarcticus*	-75.6341	169.7891		54.49	531
62	I	NIWA	*Chorismus antarcticus*	-75.6341	169.7898		69.68	531.6

63	I	NIWA	*Chorismus antarcticus*	-75.628	167.3448	70.33	
64	I	NIWA	*Chorismus antarcticus*	-75.6275	167.3441	76.53	
65	I	NIWA	*Chorismus antarcticus*	-75.6277	167.3449	85.32	
66	I	NIWA	*Chorismus antarcticus*	-75.6272	167.3446	78	
67	I	NIWA	*Chorismus antarcticus*	-76.8335	359.9576	76.79	662.7
68	I	NIWA	*Chorismus antarcticus*	-76.6061	176.7625	62.2	367
69	I	NIWA	*Chorismus antarcticus*	-76.606	176.762	60.42	366.8
70	I	NIWA	*Chorismus antarcticus*	-76.6054	176.764	53.72	367.4
71	I	NIWA	*Chorismus antarcticus*	-76.6043	176.7667	80.51	369.3
72	I	NIWA	*Chorismus antarcticus*	-76.6042	176.7671	73.24	369.2
73	I	NIWA	*Chorismus antarcticus*	-76.6038	176.7682	65.49	369.3
74	I	NIWA	*Chorismus antarcticus*	-76.6036	176.769	68.66	368.6
75	I	NIWA	*Chorismus antarcticus*	-76.6036	176.7686	66.02	369
76	I	NIWA	*Chorismus antarcticus*	-76.6035	176.7688	70.3	368.6
77	I	NIWA	*Chorismus antarcticus*	-76.6034	176.769	64.09	368.7
78	I	NIWA	*Chorismus antarcticus*	-76.6017	176.7757	65.06	368.5
79	I	NIWA	*Chorismus antarcticus*	-76.6015	176.7759	62.97	368.6
80	I	NIWA	*Chorismus antarcticus*	-76.6013	176.776	74.12	368.5
81	I	NIWA	*Chorismus antarcticus*	-76.6009	176.7778	72	367.4
82	I	NIWA	*Chorismus antarcticus*	-76.5999	176.7819	70.93	367.3
83	I	NIWA	*Chorismus antarcticus*	-76.5996	176.7838	61.74	367
84	I	NIWA	*Chorismus antarcticus*	-76.599	176.785	58.38	367.2
85	I	NIWA	*Chorismus antarcticus*	-76.599	176.785	56.45	367.2
86	I	NIWA	*Chorismus antarcticus*	-76.599	176.7861	74.21	366.3
87	I	NIWA	*Chorismus antarcticus*	-76.5988	176.786	75.24	366.9
88	I	NIWA	*Chorismus antarcticus*	-76.5988	176.786	79.42	366.9
89	I	NIWA	*Chorismus antarcticus*	-76.5987	176.7888	82.25	367.3
90	I	NIWA	*Chorismus antarcticus*	-76.5987	176.7892	67.84	368
91	I	NIWA	*Chorismus antarcticus*	-76.5987	176.7892	76.89	368
92	I	NIWA	*Chorismus antarcticus*	-76.5987	176.7892	81.3	367.4
93	I	NIWA	*Chorismus antarcticus*	-76.5985	176.7911	67.49	367.7
94	I	NIWA	*Chorismus antarcticus*	-76.198	176.2798	56.69	451
95	I	NIWA	*Chorismus antarcticus*	-76.1979	176.2797	64.63	451
96	I	NIWA	*Chorismus antarcticus*	-76.198	176.2801	60.38	450.9
97	I	NIWA	*Chorismus antarcticus*	-76.1978	176.2804	61.7	451

98	I	NIWA	*Chorismus antarcticus*	-76.1977	176.2804		62.65	451
99	I	NIWA	*Chorismus antarcticus*	-76.1976	176.2808		73.78	451
100	I	NIWA	*Chorismus antarcticus*	-76.1975	176.281		68.26	451.3
101	I	NIWA	*Chorismus antarcticus*	-76.1974	176.2814		63.66	450.4
102	I	NIWA	*Chorismus antarcticus*	-76.1972	176.2816	29.03	75.53	450.4
103	I	NIWA	*Chorismus antarcticus*	-76.1973	176.2817		64.35	450.2
104	I	NIWA	*Chorismus antarcticus*	-76.197	176.2821		80.1	449.8
105	I	NIWA	*Chorismus antarcticus*	-76.1969	176.2821		73.5	449.6
106	I	NIWA	*Chorismus antarcticus*	-76.1968	176.2825		72.89	449.3
107	I	NIWA	*Chorismus antarcticus*	-76.1967	176.2834		25.65	448.8
108	I	NIWA	*Chorismus antarcticus*	-76.1966	176.2837		59.75	448.6
109	I	NIWA	*Chorismus antarcticus*	-76.1966	176.2837		67.5	448.6
110	I	NIWA	*Chorismus antarcticus*	-76.1963	176.2845		64.24	449.2
111	I	NIWA	*Chorismus antarcticus*	-76.1963	176.2846		71.09	449.7
112	I	NIWA	*Chorismus antarcticus*	-76.1962	176.2852		26.4	451
113	I	NIWA	*Chorismus antarcticus*	-76.1958	176.287		79	451.2
114	I	NIWA	*Chorismus antarcticus*	-76.1957	176.2873		63.33	450.7
115	I	NIWA	*Chorismus antarcticus*	-76.1957	176.2873		73.77	450.7
116	I	NIWA	*Chorismus antarcticus*	-76.1949	176.2891		74.63	450
117	I	NIWA	*Chorismus antarcticus*	-76.1949	176.2891		63.86	450
118	I	NIWA	*Chorismus antarcticus*	-76.1952	176.2892		62.62	449.8
119	I	NIWA	*Chorismus antarcticus*	-76.1951	176.2894	32.64	76.18	449.9
120	I	NIWA	*Chorismus antarcticus*	-76.195	176.2903		70.45	449.5
121	I	NIWA	*Chorismus antarcticus*	-76.1948	176.2912		88.99	449.9
122	I	NIWA	*Chorismus antarcticus*	-76.1947	176.2911		65.96	450.3
123	I	NIWA	*Chorismus antarcticus*	-76.1947	176.2911		68.54	450.3
124	I	NIWA	*Chorismus antarcticus*	-76.1948	176.2914		69.11	450.6
125	I	NIWA	*Chorismus antarcticus*	-76.1946	176.2917		63.08	450.9
126	I	NIWA	*Chorismus antarcticus*	-76.1946	176.2918		50.23	450.7
127	I	NIWA	*Chorismus antarcticus*	-76.1946	176.2919		53.01	451.1
128	I	NIWA	*Chorismus antarcticus*	-76.1945	176.2923		60.18	450.4
129	I	NIWA	*Chorismus antarcticus*	-76.1935	176.2967		62.44	448.6
130	I	NIWA	*Chorismus antarcticus*	-76.1929	176.3001		59.53	449
131	I	NIWA	*Chorismus antarcticus*	-76.1929	176.3001		63.43	449

132	I	NIWA	*Chorismus antarcticus*	-76.1925	176.3007		68.36	449
133	I	NIWA	*Chorismus antarcticus*	-76.1921	176.304		63.4	449.8
134	I	NIWA	*Chorismus antarcticus*	-76.1917	176.3043		68.44	449.6
135	S	NSMT	*Chorismus antarcticus*	-70.1517	24.03167	12.6		295
136	S	NSMT	*Chorismus antarcticus*	-70.1417	24.28	13		270
137	S	NSMT	*Chorismus antarcticus*	-70.2283	24.42833	11.4		276
138	S	NSMT	*Chorismus antarcticus*	-68.3917	34.125	16.2		281
139	S	CBM	*Chorismus antarcticus*	-67.985	41.92667	14.2		342
140	S	CBM	*Chorismus antarcticus*	-67.9883	41.93333	11		342
141	S	NMHN	*Nematocarcinus lanceopes*	-59.3167	82.03333	27	89	1740
142	S	NMHN	*Nematocarcinus lanceopes*	-59.3833	76.9	25	93	1160
143	S	SMHN	*Nematocarcinus lanceopes*	-62.1883	222.7217	35.6	129.11	1228
144	S	SMHN	*Nematocarcinus lanceopes*	-62.1883	222.7217	25.39	106.83	1228
145	S	SMHN	*Nematocarcinus lanceopes*	-62.1883	222.7217	25.89	100.9	1228
146	S	SMHN	*Nematocarcinus lanceopes*	-62.1883	222.7217	29.12	114.83	1228
147	S	SMHN	*Nematocarcinus lanceopes*	-62.1883	222.7217	20.75	74.98	1228
148	S	SMHN	*Nematocarcinus lanceopes*	-62.1883	222.7217	32.09	82.56	1228
149	S	NIWA	*Nematocarcinus lanceopes*	-68.0837	359.3058	27	106	780
150	S	NIWA	*Nematocarcinus lanceopes*	-68.1273	359.256	30	104	855
151	S	NIWA	*Nematocarcinus lanceopes*	-72.7947	177.2358	29	121	1403
152	S	NIWA	*Nematocarcinus lanceopes*	-72.0852	175.5942	29	126	1567
153	S	NIWA	*Nematocarcinus lanceopes*	-71.3842	174.7368	29	104	2281
154	S	NIWA	*Nematocarcinus lanceopes*	-72.7947	177.2358	43.1	120.44	1403
155	S	NIWA	*Nematocarcinus lanceopes*	-72.7947	177.2358	63.19	131.44	1403
156	S	NIWA	*Nematocarcinus lanceopes*	-72.7947	177.2358	49.7	104.07	1403
157	S	NIWA	*Nematocarcinus lanceopes*	-72.7947	177.2358	29.48	83.6	1403
158	S	NIWA	*Nematocarcinus lanceopes*	-72.7947	177.2358	53.37	122.08	1403
159	S	NIWA	*Nematocarcinus lanceopes*	-72.0865	175.5538	52.3	133.18	1620
160	S	NIWA	*Nematocarcinus lanceopes*	-72.0865	175.5538	58.74	137.5	1620
161	S	NIWA	*Nematocarcinus lanceopes*	-72.0865	175.5538	52.27	132.63	1620
162	S	NIWA	*Nematocarcinus lanceopes*	-72.0865	175.5538	28.69	71.79	1620
163	S	NIWA	*Nematocarcinus lanceopes*	-71.89	174.1098	63.64	163.44	1990
164	S	NIWA	*Nematocarcinus lanceopes*	-71.89	174.1098	71.81	170.87	1990
165	S	NIWA	*Nematocarcinus lanceopes*	-71.89	174.1098	53.1	127.42	1990
166	S	NIWA	*Nematocarcinus lanceopes*	-68.0917	359.2463	22.46	87.19	640

167	S	NIWA	*Nematocarcinus lanceopes*	-68.1153	359.2387	53.46	118.7	879
168	S	NIWA	*Nematocarcinus lanceopes*	-68.1153	359.2387	34.54	93.98	879
169	S	NIWA	*Nematocarcinus lanceopes*	-68.1153	359.2387	25.48	88.64	879
170	S	NIWA	*Nematocarcinus lanceopes*	-68.1153	359.2387	37.76	102.6	879
171	S	NIWA	*Nematocarcinus lanceopes*	-68.1123	359.285	54.72	125.62	602
172	S	NIWA	*Nematocarcinus lanceopes*	-68.1123	359.285	53.81	118.93	602
173	S	NIWA	*Nematocarcinus lanceopes*	-67.7297	359.7163	32.2	100.02	1145
174	S	NIWA	*Nematocarcinus lanceopes*	-67.7297	359.7163	40.89	128.36	1145
175	S	NIWA	*Nematocarcinus lanceopes*	-67.7303	359.6323	23.1	69.73	732
176	S	NIWA	*Nematocarcinus lanceopes*	-67.4055	359.8047	26.99	84.12	1520
177	S	NIWA	*Nematocarcinus lanceopes*	-67.3778	179.9782	43.84	115.5	1450
178	S	NIWA	*Nematocarcinus lanceopes*	-67.3778	179.9782	41.72	120.57	1450
179	S	NIWA	*Nematocarcinus lanceopes*	-67.1383	171.154	59.52	131.38	897
180	S	NIWA	*Nematocarcinus lanceopes*	-67.1258	170.886	40.71	93.39	696
181	S	NIWA	*Nematocarcinus lanceopes*	-67.1258	170.886	17.31	56.16	696
182	S	NIWA	*Nematocarcinus lanceopes*	-67.1258	170.886	19.66	67.53	696
183	I	NIWA	*Nematocarcinus lanceopes*	-72.8235	177.131	53.44	138.4	
184	I	NIWA	*Nematocarcinus lanceopes*	-72.8238	177.132		75.16	
185	I	NIWA	*Nematocarcinus lanceopes*	-72.8238	177.1321		125.67	
186	I	NIWA	*Nematocarcinus lanceopes*	-72.8239	177.1325	45.67	128	
187	I	NIWA	*Nematocarcinus lanceopes*	-72.8239	177.1325		89.84	
188	I	NIWA	*Nematocarcinus lanceopes*	-72.824	177.1328	42.8	126.27	
189	I	NIWA	*Nematocarcinus lanceopes*	-72.8242	177.1333		116.33	
190	I	NIWA	*Nematocarcinus lanceopes*	-72.8242	177.1333		108.1	
191	I	NIWA	*Nematocarcinus lanceopes*	-72.8244	177.1348		88.34	
192	I	NIWA	*Nematocarcinus lanceopes*	-72.8251	177.1365		98.28	
193	I	NIWA	*Nematocarcinus lanceopes*	-72.8254	177.1366		133.33	
194	I	NIWA	*Nematocarcinus lanceopes*	-72.8255	177.1367		96.97	
195	I	NIWA	*Nematocarcinus lanceopes*	-72.8256	177.1367		76.38	
196	I	NIWA	*Nematocarcinus lanceopes*	-72.8256	177.1367		19.08	
197	I	NIWA	*Nematocarcinus lanceopes*	-72.8258	177.1371		108.59	
198	I	NIWA	*Nematocarcinus lanceopes*	-72.826	177.1391		123.4	
199	I	NIWA	*Nematocarcinus lanceopes*	-72.8258	177.1401	54.25	122.63	
200	I	NIWA	*Nematocarcinus lanceopes*	-72.8258	177.1403		135.62	

201	I	NIWA	*Nematocarcinus lanceopes*	-72.8257	177.1405		87.61
202	I	NIWA	*Nematocarcinus lanceopes*	-72.8257	177.1406		105.98
203	I	NIWA	*Nematocarcinus lanceopes*	-72.8257	177.1407		103.24
204	I	NIWA	*Nematocarcinus lanceopes*	-72.8256	177.1409		120.02
205	I	NIWA	*Nematocarcinus lanceopes*	-72.8256	177.1411		52.29
206	I	NIWA	*Nematocarcinus lanceopes*	-72.8255	177.1412		89.31
207	I	NIWA	*Nematocarcinus lanceopes*	-72.8255	177.1413		83.37
208	I	NIWA	*Nematocarcinus lanceopes*	-72.8254	177.1416	35.71	95.18
209	I	NIWA	*Nematocarcinus lanceopes*	-72.8254	177.1417	29.02	74.71
210	I	NIWA	*Nematocarcinus lanceopes*	-72.8253	177.1418		96.29
211	I	NIWA	*Nematocarcinus lanceopes*	-72.8253	177.142		97.55
212	I	NIWA	*Nematocarcinus lanceopes*	-72.8252	177.1422		103.63
213	I	NIWA	*Nematocarcinus lanceopes*	-72.8252	177.1423		126.7
214	I	NIWA	*Nematocarcinus lanceopes*	-72.8251	177.1425	52.56	137.72
215	I	NIWA	*Nematocarcinus lanceopes*	-72.8251	177.1426		97.1
216	I	NIWA	*Nematocarcinus lanceopes*	-72.825	177.1428		59.73
217	I	NIWA	*Nematocarcinus lanceopes*	-72.825	177.143		86.05
218	I	NIWA	*Nematocarcinus lanceopes*	-72.825	177.1431	36.46	99.05
219	I	NIWA	*Nematocarcinus lanceopes*	-72.8249	177.1433		80.53
220	I	NIWA	*Nematocarcinus lanceopes*	-72.8249	177.1435		79.12
221	I	NIWA	*Nematocarcinus lanceopes*	-72.8249	177.1438		59.8
222	I	NIWA	*Nematocarcinus lanceopes*	-72.0914	175.5488	55.84	151.64
223	I	NIWA	*Nematocarcinus lanceopes*	-72.0909	175.5487		134
224	I	NIWA	*Nematocarcinus lanceopes*	-72.0902	175.5492		151.58
225	I	NIWA	*Nematocarcinus lanceopes*	-72.0899	175.5495	51.26	145.07
226	I	NIWA	*Nematocarcinus lanceopes*	-72.0898	175.5496		119.94
227	I	NIWA	*Nematocarcinus lanceopes*	-72.0895	175.5495		99.05
228	I	NIWA	*Nematocarcinus lanceopes*	-72.0891	175.5491		129.08
229	I	NIWA	*Nematocarcinus lanceopes*	-72.089	175.5491		102.02
230	I	NIWA	*Nematocarcinus lanceopes*	-72.0885	175.5493		95.85
231	I	NIWA	*Nematocarcinus lanceopes*	-72.0882	175.5497		129.75
232	I	NIWA	*Nematocarcinus lanceopes*	-72.0881	175.5501	56.09	151.65
233	I	NIWA	*Nematocarcinus lanceopes*	-72.088	175.5502		107.27
234	I	NIWA	*Nematocarcinus lanceopes*	-72.0879	175.5508		86.89
235	I	NIWA	*Nematocarcinus lanceopes*	-72.0875	175.5512		119.09

236	I	NIWA	*Nematocarcinus lanceopes*	-72.0873	175.5511	53.48	139.17	
237	I	NIWA	*Nematocarcinus lanceopes*	-72.0873	175.551		122.68	
238	I	NIWA	*Nematocarcinus lanceopes*	-72.0868	175.5508		114.53	
239	I	NIWA	*Nematocarcinus lanceopes*	-72.086	175.5511		188.54	
240	I	NIWA	*Nematocarcinus lanceopes*	-72.0859	175.5512		89.49	
241	I	NIWA	*Nematocarcinus lanceopes*	-72.085	175.5518		127.87	
242	I	NIWA	*Nematocarcinus lanceopes*	-72.085	175.5519		101.01	
243	I	NIWA	*Nematocarcinus lanceopes*	-72.0848	175.5523		103.54	
244	I	NIWA	*Nematocarcinus lanceopes*	-72.0843	175.5536		140.32	
245	I	NIWA	*Nematocarcinus lanceopes*	-72.0842	175.5538	51.35	131.02	
246	I	NIWA	*Nematocarcinus lanceopes*	-72.084	175.554		103.91	
247	I	NIWA	*Nematocarcinus lanceopes*	-72.0838	175.5538		150.89	
248	I	NIWA	*Nematocarcinus lanceopes*	-72.0828	175.5536	54.49	144.9	
249	I	NIWA	*Nematocarcinus lanceopes*	-71.8372	173.991		138.42	1919.6
250	I	NIWA	*Nematocarcinus lanceopes*	-71.838	173.9969		130.1	1918.5
251	I	NIWA	*Nematocarcinus lanceopes*	-71.838	173.9954		105.97	1918
252	I	NIWA	*Nematocarcinus lanceopes*	-71.8386	173.9976	51.21	137.71	1917.8
253	I	NIWA	*Nematocarcinus lanceopes*	-71.8387	173.9981		136.34	1917.4
254	I	NIWA	*Nematocarcinus lanceopes*	-71.8398	174.0001	42.46	110.33	1917
255	I	NIWA	*Nematocarcinus lanceopes*	-71.84	174.002		136.57	1917.1
256	I	NIWA	*Nematocarcinus lanceopes*	-71.8401	174.0038	51.04	130.56	1916.8
257	I	NIWA	*Nematocarcinus lanceopes*	-71.841	174.0045	46.04	115.68	1916.7
258	I	NIWA	*Nematocarcinus lanceopes*	-71.841	174.0059	51.3	132.19	1916.8
259	I	NIWA	*Nematocarcinus lanceopes*	-71.8413	174.0073	52.25	136.52	1916.1
260	I	NIWA	*Nematocarcinus lanceopes*	-71.8419	174.0087	53.6	147.46	1915.8
261	I	NIWA	*Nematocarcinus lanceopes*	-71.8423	174.0105		118.75	1914.6
262	I	NIWA	*Nematocarcinus lanceopes*	-71.8422	174.0111		91.74	1914.6
263	I	NIWA	*Nematocarcinus lanceopes*	-71.8429	174.011	48.51	136.22	1914.1
264	I	NIWA	*Nematocarcinus lanceopes*	-71.8432	174.013		153.13	1913.3
265	I	NIWA	*Nematocarcinus lanceopes*	-71.3827	174.7311		117.13	2205.8
266	I	NIWA	*Nematocarcinus lanceopes*	-71.3838	174.7333	55.82	154.15	2209
267	I	NIWA	*Nematocarcinus lanceopes*	-71.3838	174.7345	52.74	136.47	2209.2
268	I	NIWA	*Nematocarcinus lanceopes*	-71.3851	174.7356		32.37	2209.6
269	I	NIWA	*Nematocarcinus lanceopes*	-71.3851	174.736	46.52	125.43	2209.5

270	I	NIWA	*Nematocarcinus lanceopes*	-71.3845	174.7375	50.09	133.63	2209.2
271	I	NIWA	*Nematocarcinus lanceopes*	-71.3856	174.7375		112.78	2211.7
272	I	NIWA	*Nematocarcinus lanceopes*	-71.3853	174.7385	46.67	125.63	2213.3
273	I	NIWA	*Nematocarcinus lanceopes*	-71.386	174.7407	44.24	123.88	2215.4
274	I	NIWA	*Nematocarcinus lanceopes*	-71.3861	174.7408		118.43	2215.7
275	I	NIWA	*Nematocarcinus lanceopes*	-71.3866	174.7414	50.14	133.9	2217
276	I	NIWA	*Nematocarcinus lanceopes*	-71.3864	174.7414		111.94	2216.6
277	I	NIWA	*Nematocarcinus lanceopes*	-71.3865	174.7424	40.5	114.75	2216.7
278	I	NIWA	*Nematocarcinus lanceopes*	-71.3864	174.7432	49.44	123.73	2217.7
279	I	NIWA	*Nematocarcinus lanceopes*	-68.0796	359.3107		134.85	1243.5
280	I	NIWA	*Nematocarcinus lanceopes*	-68.0792	359.3115		47.56	1244.3
281	I	NIWA	*Nematocarcinus lanceopes*	-68.0788	359.3113		120.9	1243.3
282	I	NIWA	*Nematocarcinus lanceopes*	-68.0786	359.312	34.53	97.8	1233.4
283	I	NIWA	*Nematocarcinus lanceopes*	-68.0779	359.3132		112.53	1222.7
284	I	NIWA	*Nematocarcinus lanceopes*	-68.0775	359.3138		117.56	1207.9
285	I	NIWA	*Nematocarcinus lanceopes*	-68.0765	359.3155		76.32	1161.2
286	I	NIWA	*Nematocarcinus lanceopes*	-68.0764	359.3162	45.64	129.97	1171.2
287	I	NIWA	*Nematocarcinus lanceopes*	-68.0764	359.3163		128.49	1155.3
288	I	NIWA	*Nematocarcinus lanceopes*	-68.0759	359.3169	44.58	125.3	1144.2
289	I	NIWA	*Nematocarcinus lanceopes*	-68.0743	359.3201		118.33	1109.8
290	I	NIWA	*Nematocarcinus lanceopes*	-68.0741	359.3202		129.2	1116.4
291	I	NIWA	*Nematocarcinus lanceopes*	-68.0739	359.3204		104.36	1109.8
292	I	NIWA	*Nematocarcinus lanceopes*	-68.0737	359.321		139.25	1106.1
293	I	NIWA	*Nematocarcinus lanceopes*	-68.0735	359.3213		132.06	1098.7
294	I	NIWA	*Nematocarcinus lanceopes*	-68.073	359.3218		143.74	1080.9
295	I	NIWA	*Nematocarcinus lanceopes*	-68.0731	359.322		129.38	1094.5
296	I	NIWA	*Nematocarcinus lanceopes*	-68.0727	359.3224		148.93	1069.4
297	I	NIWA	*Nematocarcinus lanceopes*	-68.0718	359.3244		143.2	1065.7
298	I	NIWA	*Nematocarcinus lanceopes*	-68.0717	359.3244		99.91	1061.3
299	I	NIWA	*Nematocarcinus lanceopes*	-68.0714	359.325		111.86	1059.2
300	I	NIWA	*Nematocarcinus lanceopes*	-68.1076	359.2353		159.07	854.5
301	I	NIWA	*Nematocarcinus lanceopes*	-68.1078	359.2363		73.48	855.4
302	I	NIWA	*Nematocarcinus lanceopes*	-68.1083	359.2368		131.67	855.6
303	I	NIWA	*Nematocarcinus lanceopes*	-68.1085	359.237		74.08	856.1
304	I	NIWA	*Nematocarcinus lanceopes*	-68.1092	359.2384		114.06	857.2

305	I	NIWA	*Nematocarcinus lanceopes*	-68.1095	359.2386		87.85	857.6
306	I	NIWA	*Nematocarcinus lanceopes*	-68.11	359.2396		117.34	858.8
307	I	NIWA	*Nematocarcinus lanceopes*	-68.1106	359.2405		96.54	860.6
308	I	NIWA	*Nematocarcinus lanceopes*	-68.1128	359.2424		72.85	864.3
309	I	NIWA	*Nematocarcinus lanceopes*	-68.1143	359.2437	46.86	128.26	867.2
310	I	NIWA	*Nematocarcinus lanceopes*	-68.1152	359.2441	44.81	126.22	868.3
311	I	NIWA	*Nematocarcinus lanceopes*	-68.1169	359.246		133.73	870.5
312	I	NIWA	*Nematocarcinus lanceopes*	-68.117	359.246		104.25	870.7
313	I	NIWA	*Nematocarcinus lanceopes*	-68.1404	359.2108		54.9	1133.8
314	I	NIWA	*Nematocarcinus lanceopes*	-68.1403	359.2107		104.72	1145.1
315	I	NIWA	*Nematocarcinus lanceopes*	-68.1404	359.2106		100.66	1141.5
316	I	NIWA	*Nematocarcinus lanceopes*	-68.1404	359.2106		55.9	1141.5
317	I	NIWA	*Nematocarcinus lanceopes*	-68.1406	359.2099	37.01	100.82	1143.8
318	I	NIWA	*Nematocarcinus lanceopes*	-68.1413	359.2105		61.1	1151.6
319	I	NIWA	*Nematocarcinus lanceopes*	-68.1414	359.2105		155.11	1150.9
320	I	NIWA	*Nematocarcinus lanceopes*	-68.1416	359.2105		50.8	1161.6
321	I	NIWA	*Nematocarcinus lanceopes*	-68.1417	359.211	44.8	111.97	1164.6
322	I	NIWA	*Nematocarcinus lanceopes*	-68.1423	359.2106	48.47	122.35	1170.9
323	I	NIWA	*Nematocarcinus lanceopes*	-68.1428	359.2113	50.97	131.41	1186
324	I	NIWA	*Nematocarcinus lanceopes*	-68.1431	359.211	46.89	119.79	1200.2
325	I	NIWA	*Nematocarcinus lanceopes*	-68.1431	359.211		92.21	1209.5
326	I	NIWA	*Nematocarcinus lanceopes*	-68.1435	359.2108	54.07	134.07	1213.8
327	I	NIWA	*Nematocarcinus lanceopes*	-68.1439	359.2106	36.19	96.18	1242.2
328	I	NIWA	*Nematocarcinus lanceopes*	-68.1438	359.2107		154.03	1236
329	I	NIWA	*Nematocarcinus lanceopes*	-68.1438	359.2106		117.58	1227.5
330	I	NIWA	*Nematocarcinus lanceopes*	-68.1439	359.2106	50.04	135.06	1241.6
331	I	NIWA	*Nematocarcinus lanceopes*	-68.144	359.2108		66.39	1246.8
332	I	NIWA	*Nematocarcinus lanceopes*	-68.1442	359.2106		133.14	1243.8
333	I	NIWA	*Nematocarcinus lanceopes*	-68.1442	359.2107	47.1	118.05	1245.4
334	I	NIWA	*Nematocarcinus lanceopes*	-68.1442	359.2099		37.42	1247.9
335	I	NIWA	*Nematocarcinus lanceopes*	-68.1444	359.2106		78.13	1247.5
336	I	NIWA	*Nematocarcinus lanceopes*	-68.1449	359.2096	38.22	106.06	1292.2
337	I	NIWA	*Nematocarcinus lanceopes*	-67.7874	359.7616		145.46	1096.5
338	I	NIWA	*Nematocarcinus lanceopes*	-67.7871	359.7645		82.94	1128.3

339	I	NIWA	*Nematocarcinus lanceopes*	-67.7814	359.7802		108.92	1133.5
340	I	NIWA	*Nematocarcinus lanceopes*	-67.7895	359.7703		112.67	1194.9
341	I	NIWA	*Nematocarcinus lanceopes*	-67.7895	359.7703		87.28	1194.9
342	I	NIWA	*Nematocarcinus lanceopes*	-67.7897	359.7735	43.01	107.72	1229
343	I	NIWA	*Nematocarcinus lanceopes*	-67.7901	359.7764	44.45	117.85	1232.7
344	I	NIWA	*Nematocarcinus lanceopes*	-67.7895	359.7756		120.45	1233.8
345	I	NIWA	*Nematocarcinus lanceopes*	-67.3857	359.8457		113.24	771.4
346	I	NIWA	*Nematocarcinus lanceopes*	-67.3857	359.8457	55.53	134.79	771.4
347	I	NIWA	*Nematocarcinus lanceopes*	-67.3857	359.8457		95.81	771.4
348	I	NIWA	*Nematocarcinus lanceopes*	-67.3847	359.8445	55.15	140.4	772.2
349	I	NIWA	*Nematocarcinus lanceopes*	-67.3847	359.8445		114.74	772.2
350	I	NIWA	*Nematocarcinus lanceopes*	-67.3847	359.8445	40.76	104.6	772.2
351	I	NIWA	*Nematocarcinus lanceopes*	-67.3851	359.8436		86.43	770.7
352	I	NIWA	*Nematocarcinus lanceopes*	-67.385	359.845	43.73	112.01	769.2
353	I	NIWA	*Nematocarcinus lanceopes*	-67.385	359.845	36.81	87.77	769.2
354	I	NIWA	*Nematocarcinus lanceopes*	-67.3849	359.8451	45.92	114.07	772.1
355	I	NIWA	*Nematocarcinus lanceopes*	-67.3847	359.8446	49.87	131.18	776.2
356	I	NIWA	*Nematocarcinus lanceopes*	-67.3838	359.8449		77.64	771.4
357	I	NIWA	*Nematocarcinus lanceopes*	-67.3848	359.8452	45.3	117.19	776.6
358	I	NIWA	*Nematocarcinus lanceopes*	-67.3849	359.8448	50.82	138.78	773.7
359	I	NIWA	*Nematocarcinus lanceopes*	-67.3849	359.8448	40.94	101.38	773.7
360	I	NIWA	*Nematocarcinus lanceopes*	-67.3851	359.8445		132.89	769.2
361	I	NIWA	*Nematocarcinus lanceopes*	-67.3851	359.8445		109.31	769.2
362	I	NIWA	*Nematocarcinus lanceopes*	-67.3851	359.8445		109.03	769.2
363	I	NIWA	*Nematocarcinus lanceopes*	-67.3848	359.8436	40.37	115.37	767.4
364	I	NIWA	*Nematocarcinus lanceopes*	-67.3855	359.8462		146.99	765.6
365	I	NIWA	*Nematocarcinus lanceopes*	-67.3853	359.8449	43.02	117.55	762.6
366	I	NIWA	*Nematocarcinus lanceopes*	-67.3853	359.8449	34.88	93.64	762.6
367	I	NIWA	*Nematocarcinus lanceopes*	-67.3848	359.8452	52.69	141.64	764.7
368	I	NIWA	*Nematocarcinus lanceopes*	-67.3847	359.845	57.52	148.08	758
369	I	NIWA	*Nematocarcinus lanceopes*	-67.3847	359.8447		119.58	761.8
370	I	NIWA	*Nematocarcinus lanceopes*	-67.3847	359.8447	40.56	108.37	761.6
371	I	NIWA	*Nematocarcinus lanceopes*	-67.3847	359.8447		59.67	761.6
372	I	NIWA	*Nematocarcinus lanceopes*	-67.3845	359.8456	51.5	141.7	761.5
373	I	NIWA	*Nematocarcinus lanceopes*	-67.385	359.845		95.88	757.8

374	I	NIWA	*Nematocarcinus lanceopes*	-67.385	359.845	42.23	113.49	757.8
375	I	NIWA	*Nematocarcinus lanceopes*	-67.3845	359.8446	46.25	115.68	761.2
376	I	NIWA	*Nematocarcinus lanceopes*	-67.3842	359.8443	47.4	127.27	757.4
377	I	NIWA	*Nematocarcinus lanceopes*	-67.3842	359.8443		72.56	757.4
378	I	NIWA	*Nematocarcinus lanceopes*	-67.3843	359.845	49.86	130.67	758.2
379	I	NIWA	*Nematocarcinus lanceopes*	-67.3844	359.8444	35.95	95.94	757.2
380	I	NIWA	*Nematocarcinus lanceopes*	-67.3844	359.8444	54	140.61	757.2
381	I	NIWA	*Nematocarcinus lanceopes*	-67.3841	359.8446		131.48	756
382	I	NIWA	*Nematocarcinus lanceopes*	-67.3843	359.845		75.57	753.5
383	I	NIWA	*Nematocarcinus lanceopes*	-67.3843	359.845		26.62	753.5
384	I	NIWA	*Nematocarcinus lanceopes*	-67.3838	359.8433	47.57	124.97	748.6
385	I	NIWA	*Nematocarcinus lanceopes*	-67.3834	359.843		91.43	742.6
386	I	NIWA	*Nematocarcinus lanceopes*	-67.3788	359.8467	43.71	116.73	730.8
387	I	NIWA	*Nematocarcinus lanceopes*	-67.3834	359.8434	47.26	121.25	711.5
388	I	NIWA	*Nematocarcinus lanceopes*	-67.3832	359.8437	48.03	122.18	707.6
389	I	NIWA	*Nematocarcinus lanceopes*	-67.3831	359.8437	47.48	124.74	732.6
390	I	NIWA	*Nematocarcinus lanceopes*	-67.3837	359.8435	49.79	128.37	708
391	I	NIWA	*Nematocarcinus lanceopes*	-67.383	359.8433	45.85	121.58	707
392	I	NIWA	*Nematocarcinus lanceopes*	-67.3833	359.8437		108.4	707.8
393	I	NIWA	*Nematocarcinus lanceopes*	-67.3827	359.8436		113.66	715.2
394	I	NIWA	*Nematocarcinus lanceopes*	-67.3842	359.8437	32.98	97.71	707
395	I	NIWA	*Nematocarcinus lanceopes*	-67.3836	359.8442	45.67	125.98	706.3
396	I	NIWA	*Nematocarcinus lanceopes*	-67.3828	359.8427	35.54	90.78	703.9
397	I	NIWA	*Nematocarcinus lanceopes*	-67.3826	359.8417		104.62	709.9
398	I	NIWA	*Nematocarcinus lanceopes*	-67.3824	359.842	42.94	120.01	718.9
399	I	NIWA	*Nematocarcinus lanceopes*	-67.3816	359.8411	52.92	138.36	716.7
400	I	NIWA	*Nematocarcinus lanceopes*	-67.3821	359.8409	45.66	128.06	715.2
401	I	NIWA	*Nematocarcinus lanceopes*	-67.3821	359.8409		138.87	715.2
402	I	NIWA	*Nematocarcinus lanceopes*	-67.3821	359.8409		104.08	715.2
403	I	NIWA	*Nematocarcinus lanceopes*	-67.3819	359.843	38.3	102.85	708.5
404	I	NIWA	*Nematocarcinus lanceopes*	-67.3818	359.8409	59.84	153.11	708.5
405	I	NIWA	*Nematocarcinus lanceopes*	-67.3823	359.8421	54.85	146.82	712.1
406	I	NIWA	*Nematocarcinus lanceopes*	-67.3817	359.842		158.12	696.8
407	I	NIWA	*Nematocarcinus lanceopes*	-67.3815	359.8412		119.5	701.5

408	I	NIWA	*Nematocarcinus lanceopes*	-67.381	359.8411	51.36	135.94	697.3
409	I	NIWA	*Nematocarcinus lanceopes*	-67.3812	359.841		121.96	703.4
410	I	NIWA	*Nematocarcinus lanceopes*	-67.3807	359.8411	39.83	109.57	700.4
411	I	NIWA	*Nematocarcinus lanceopes*	-67.3815	359.8422	50.89	134.97	690.2
412	I	NIWA	*Nematocarcinus lanceopes*	-67.3811	359.8419	50.4	131.25	697.1
413	I	NIWA	*Nematocarcinus lanceopes*	-67.381	359.8417	52.4	144.11	706.3
414	I	NIWA	*Nematocarcinus lanceopes*	-67.3807	359.8409	49.54	133.17	695.9
415	I	NIWA	*Nematocarcinus lanceopes*	-67.3811	359.8411		132.04	698
416	I	NIWA	*Nematocarcinus lanceopes*	-67.3807	359.8408		129.12	687.2
417	I	NIWA	*Nematocarcinus lanceopes*	-67.3807	359.8408		78.22	687.2
418	I	NIWA	*Nematocarcinus lanceopes*	-67.3801	359.8407	57.07	147.4	638.2
419	I	NIWA	*Nematocarcinus lanceopes*	-67.3801	359.8392		114.17	621.6
420	I	NIWA	*Nematocarcinus lanceopes*	-67.3801	359.8407		93.04	571.6
421	I	NIWA	*Nematocarcinus lanceopes*	-67.3802	359.8407		119.8	595.2
422	I	NIWA	*Nematocarcinus lanceopes*	-67.3798	359.8409		95.27	604.5
423	I	NIWA	*Nematocarcinus lanceopes*	-67.3801	359.8416	57.38	149.14	598.2
424	I	NIWA	*Nematocarcinus lanceopes*	-67.3799	359.8409	54.46	135.57	593.8
425	I	NIWA	*Nematocarcinus lanceopes*	-67.3793	359.8397	53.49	132.96	607
426	I	NIWA	*Nematocarcinus lanceopes*	-67.3772	179.9706		110.56	1467.4
427	I	NIWA	*Nematocarcinus lanceopes*	-67.377	179.9696		105.01	1477.7
428	I	NIWA	*Nematocarcinus lanceopes*	-67.3773	179.9721		108.38	1488.1
429	I	NIWA	*Nematocarcinus lanceopes*	-67.3775	179.9652	38.64	111.55	1497
430	I	NIWA	*Nematocarcinus lanceopes*	-67.3773	179.9639	54.58	149.65	
431	I	NIWA	*Nematocarcinus lanceopes*	-67.3753	179.9616	53.87	149.27	
432	I	NIWA	*Nematocarcinus lanceopes*	-67.3749	179.9558		120.53	
433	I	NIWA	*Nematocarcinus lanceopes*	-67.3772	179.9542	37.06	105.27	
434	I	NIWA	*Nematocarcinus lanceopes*	-67.3772	179.9542		49.6	
435	I	NIWA	*Nematocarcinus lanceopes*	-67.3751	179.9522		86.91	
436	I	NIWA	*Nematocarcinus lanceopes*	-67.3748	179.9476		126.76	
437	I	NIWA	*Nematocarcinus lanceopes*	-67.3753	179.9492		113.32	
438	I	NIWA	*Nematocarcinus lanceopes*	-67.3758	179.9508		105.57	
439	I	NIWA	*Nematocarcinus lanceopes*	-67.375	179.9503		53.48	
440	I	NIWA	*Nematocarcinus lanceopes*	-67.3396	359.9348	41.57	116.06	968.4
441	I	NIWA	*Nematocarcinus lanceopes*	-67.3397	359.9347		98.08	964.7
442	I	NIWA	*Nematocarcinus lanceopes*	-67.34	359.9357		115.27	976.5

443	I	NIWA	*Nematocarcinus lanceopes*	-67.3408	359.9376		99.58	967.2
444	I	NIWA	*Nematocarcinus lanceopes*	-67.3407	359.9387		137.99	955
445	I	NIWA	*Nematocarcinus lanceopes*	-67.3407	359.9387		122.28	955
446	I	NIWA	*Nematocarcinus lanceopes*	-67.3406	359.9387		113.5	956
447	I	NIWA	*Nematocarcinus lanceopes*	-67.3411	359.9403	32.37	95.74	953
448	I	NIWA	*Nematocarcinus lanceopes*	-67.3428	359.9419		88.45	850.4
449	I	NIWA	*Nematocarcinus lanceopes*	-67.3443	359.9405		109.83	1807.6
450	I	NIWA	*Nematocarcinus lanceopes*	-67.3442	359.9402		119.27	1807.4
451	I	NIWA	*Nematocarcinus lanceopes*	-67.3445	359.9394	41.22	126.95	1807.5
452	I	NIWA	*Nematocarcinus lanceopes*	-67.3447	359.9399		144.28	1807.4
453	I	NIWA	*Nematocarcinus lanceopes*	-67.3453	359.94		106.39	1807.5
454	I	NIWA	*Nematocarcinus lanceopes*	-67.3448	359.9406		138.64	1807.5
455	I	NIWA	*Nematocarcinus lanceopes*	-67.3448	359.9406		106.14	1807.5
456	I	NIWA	*Nematocarcinus lanceopes*	-67.3454	359.9408		112.52	1807.4
457	I	NIWA	*Nematocarcinus lanceopes*	-67.3455	359.9417		141.63	738.5
458	I	NIWA	*Nematocarcinus lanceopes*	-67.3466	359.9417		101.58	697.8
459	I	NIWA	*Nematocarcinus lanceopes*	-67.0182	171.0747		76.94	754.5
460	I	NIWA	*Nematocarcinus lanceopes*	-67.0186	171.0732		88.05	725.8
461	I	NIWA	*Nematocarcinus lanceopes*	-67.0187	171.0734		79.63	714.4
462	I	NIWA	*Nematocarcinus lanceopes*	-67.0281	171.0624	33.2	93.6	604.9
463	I	NIWA	*Nematocarcinus lanceopes*	-67.0103	171.0802		70.31	772.5
464	I	NIWA	*Nematocarcinus lanceopes*	-67.0124	171.0777		90.6	774
465	I	NIWA	*Nematocarcinus lanceopes*	-67.0137	171.0762		87.2	770.7
466	I	NIWA	*Nematocarcinus lanceopes*	-67.015	171.0743		107.12	775.9
467	I	NIWA	*Nematocarcinus lanceopes*	-66.919	170.9903		49.07	1955.3
468	I	NIWA	*Nematocarcinus lanceopes*	-66.9185	170.9921	41.04	127.45	1979
469	I	NIWA	*Nematocarcinus lanceopes*	-66.9142	171.0032		52.49	2114.4
470	I	NIWA	*Nematocarcinus lanceopes*	-67.1405	171.1704		88.06	1070.4
471	I	NIWA	*Nematocarcinus lanceopes*	-67.1411	171.1674		73.24	1063.6
472	I	NIWA	*Nematocarcinus lanceopes*	-67.141	171.1669	38.71	106.92	1051.8
473	I	NIWA	*Nematocarcinus lanceopes*	-67.1399	171.1637		109.45	1024.6
474	I	NIWA	*Nematocarcinus lanceopes*	-67.1395	171.1602		80.94	1004.9
475	I	NIWA	*Nematocarcinus lanceopes*	-67.1392	171.1585		118.79	996.7
476	I	NIWA	*Nematocarcinus lanceopes*	-67.1383	171.1548		103.32	957.2

477	I	NIWA	*Nematocarcinus lanceopes*	-67.1694	171.2013		82.21	814.4
478	I	NIWA	*Nematocarcinus lanceopes*	-67.1689	171.1965		83.93	718.8
479	S	NMHN	*Notocrangon antarcticus*	-66.358	143.6949	27	93	570
480	S	NMHN	*Notocrangon antarcticus*	-65.9766	143.3876	28	96	479
481	S	NMHN	*Notocrangon antarcticus*	-66.5571	142.2773	25	86	384
482	S	NMHN	*Notocrangon antarcticus*	-65.8412	142.976	17	62	430
483	S	NMHN	*Notocrangon antarcticus*	-65.9766	143.3876	27	90	479
484	S	NMHN	*Notocrangon antarcticus*	-66.5842	144.6998	25	90	575
485	S	NMHN	*Notocrangon antarcticus*	-66.5751	145.0207	28	98	441
486	S	NMHN	*Notocrangon antarcticus*	-66.7477	145.4443	30	107	526
487	S	NMHN	*Notocrangon antarcticus*	-66.1762	143.3458	28	100	534
488	S	NMHN	*Notocrangon antarcticus*	-66.358	143.6949	26	88	570
489	S	NMHN	*Notocrangon antarcticus*	-66.7524	145.3345	30	91	597
490	S	NMHN	*Notocrangon antarcticus*	-66.0129	139.3271	30	107	472
491	S	NMHN	*Notocrangon antarcticus*	-66.3468	139.9591	26	92	510
492	S	NMHN	*Notocrangon antarcticus*	-66.3631	139.8098	34	102	903
493	S	NMHN	*Notocrangon antarcticus*	-66.3179	143.1895	31	104	702
494	S	NMHN	*Notocrangon antarcticus*	-66.1668	139.6902	25	86	414
495	S	NMHN	*Notocrangon antarcticus*	-66.3402	140.5241	23	83	444
496	S	NMHN	*Notocrangon antarcticus*	-66.778	144.7186	30	102	846
497	S	NMHN	*Notocrangon antarcticus*	-66.3179	143.1895	28	107	702
498	S	NMHN	*Notocrangon antarcticus*	-65.8412	142.976	33	105	430
499	S	NMHN	*Notocrangon antarcticus*	-66.3179	143.1895	26	90	702
500	S	SMHN	*Notocrangon antarcticus*	-74.4183	167.005	14.23	57.25	732
501	S	SMHN	*Notocrangon antarcticus*	-74.4183	167.005	28.7	87.73	732
502	S	SMHN	*Notocrangon antarcticus*	-74.4183	167.005	17.92	69.54	732
503	S	SMHN	*Notocrangon antarcticus*	-75.5	165.73	30	98.76	631
504	S	SMHN	*Notocrangon antarcticus*	-75.5	165.73	22.54	76.59	631
505	S	SMHN	*Notocrangon antarcticus*	-75.5	165.73	32.91	108.55	631
506	S	SMHN	*Notocrangon antarcticus*	-75.5	165.73	17.93	70	631
507	S	SMHN	*Notocrangon antarcticus*	-75.5	165.73	17.99	62.98	631
508	S	SMHN	*Notocrangon antarcticus*	-75.06	165.52	27.23	92.69	832
509	S	SMHN	*Notocrangon antarcticus*	-75.06	165.52	21.08	71.75	832
510	S	SMHN	*Notocrangon antarcticus*	-75.06	165.52	21.1	72.97	832
511	S	SMHN	*Notocrangon antarcticus*	-75.7733	165.25	27.31	94.53	860

512	S	SMHN	*Notocrangon antarcticus*	-75.7733	165.25	26.72	89.32	860
513	S	SMHN	*Notocrangon antarcticus*	-75.7733	165.25	14.95	56.51	860
514	S	SMHN	*Notocrangon antarcticus*	-76.7733	164.5833	17.56	76.39	587
515	S	SMHN	*Notocrangon antarcticus*	-76.7733	164.5833	24.56	83.39	587
516	S	SMHN	*Notocrangon antarcticus*	-76.7733	164.5833	24.12	82.64	587
517	S	SMHN	*Notocrangon antarcticus*	-76.7789	164.15	13.4	47.54	836
518	S	SMHN	*Notocrangon antarcticus*	-76.7789	164.15	8.9	31.69	836
519	S	SMHN	*Notocrangon antarcticus*	-76.7789	164.15	11.1	37.67	836
520	S	SMHN	*Notocrangon antarcticus*	-77.53	166.44	15.91	58.34	565
521	S	NIWA	*Notocrangon antarcticus*	-74.5887	170.2692	16	59	283
522	S	NIWA	*Notocrangon antarcticus*	-76.205	176.2439	22	96	447
523	S	NIWA	*Notocrangon antarcticus*	-74.1198	170.7952	19	87	632
524	S	NIWA	*Notocrangon antarcticus*	-74.7105	167.025	23	101	930
525	S	NIWA	*Notocrangon antarcticus*	-74.7105	167.025	30.17	106.02	930
526	S	NIWA	*Notocrangon antarcticus*	-74.7105	167.025	20.63	106.66	930
527	S	NIWA	*Notocrangon antarcticus*	-75.6085	167.3117	27.98	98.34	474
528	S	NIWA	*Notocrangon antarcticus*	-75.6085	167.3117	25.27	70.37	474
529	S	NIWA	*Notocrangon antarcticus*	-75.6085	167.3117	19.79	71.22	474
530	S	NIWA	*Notocrangon antarcticus*	-76.759	167.8223	29.9	108.74	738
531	S	NIWA	*Notocrangon antarcticus*	-76.759	167.8223	28.03	102.24	738
532	S	NIWA	*Notocrangon antarcticus*	-76.759	167.8223	22.56	81.78	738
533	S	NIWA	*Notocrangon antarcticus*	-76.599	176.755	28.62	106.39	369
534	S	NIWA	*Notocrangon antarcticus*	-76.599	176.755	25.72	84.04	369
535	S	NIWA	*Notocrangon antarcticus*	-76.599	176.755	18.13	68.23	369
536	I	NIWA	*Notocrangon antarcticus*	-74.7332	167.0116		22.24	900.8
537	I	NIWA	*Notocrangon antarcticus*	-74.7349	167.0102		19.76	899.9
538	I	NIWA	*Notocrangon antarcticus*	-74.7355	167.0101		76.77	899.7
539	I	NIWA	*Notocrangon antarcticus*	-74.7359	167.0091		76.36	899.5
540	I	NIWA	*Notocrangon antarcticus*	-74.7361	167.009		43.51	899.5
541	I	NIWA	*Notocrangon antarcticus*	-74.7371	167.0091		48.92	899.1
542	I	NIWA	*Notocrangon antarcticus*	-74.7376	167.0101		93.62	895
543	I	NIWA	*Notocrangon antarcticus*	-74.7384	167.0121		68.12	892.3
544	I	NIWA	*Notocrangon antarcticus*	-74.7392	167.0138	30.14	87.39	891.4
545	I	NIWA	*Notocrangon antarcticus*	-75.6317	169.7792		91.8	529.6

546	I	NIWA	*Notocrangon antarcticus*	-75.6318	169.7792		69.09	529
547	I	NIWA	*Notocrangon antarcticus*	-75.6318	169.7792		41.76	529
548	I	NIWA	*Notocrangon antarcticus*	-75.632	169.7788		61.09	528.4
549	I	NIWA	*Notocrangon antarcticus*	-75.632	169.7792		78.42	529.2
550	I	NIWA	*Notocrangon antarcticus*	-75.6321	169.7788		77.9	527.8
551	I	NIWA	*Notocrangon antarcticus*	-75.6322	169.7791		77.95	527.8
552	I	NIWA	*Notocrangon antarcticus*	-75.6326	169.7796		45.88	526.7
553	I	NIWA	*Notocrangon antarcticus*	-75.6325	169.7804		69.49	527.2
554	I	NIWA	*Notocrangon antarcticus*	-75.6324	169.7804	27.88	90.26	526.8
555	I	NIWA	*Notocrangon antarcticus*	-75.6325	169.7812		43.87	527.2
556	I	NIWA	*Notocrangon antarcticus*	-75.6329	169.7823		67.99	528.3
557	I	NIWA	*Notocrangon antarcticus*	-75.6329	169.7823		41.73	528.3
558	I	NIWA	*Notocrangon antarcticus*	-75.6328	169.7816		56.72	529.5
559	I	NIWA	*Notocrangon antarcticus*	-75.6328	169.7816		26.46	529.5
560	I	NIWA	*Notocrangon antarcticus*	-75.6331	169.7833		42.2	528.7
561	I	NIWA	*Notocrangon antarcticus*	-75.6333	169.7823	30.71	96.02	528.3
562	I	NIWA	*Notocrangon antarcticus*	-75.6332	169.7829		68.5	528.7
563	I	NIWA	*Notocrangon antarcticus*	-75.6332	169.7835	29.92	96.07	529.2
564	I	NIWA	*Notocrangon antarcticus*	-75.6332	169.7835		56.98	529.2
565	I	NIWA	*Notocrangon antarcticus*	-75.6332	169.7831		65.74	528.7
566	I	NIWA	*Notocrangon antarcticus*	-75.6332	169.7844		81.42	529.2
567	I	NIWA	*Notocrangon antarcticus*	-75.6336	169.7845		32.09	528
568	I	NIWA	*Notocrangon antarcticus*	-75.6332	169.7848		47.32	528.7
569	I	NIWA	*Notocrangon antarcticus*	-75.6332	169.7856		101.89	529.4
570	I	NIWA	*Notocrangon antarcticus*	-75.6335	169.786		85.27	529
571	I	NIWA	*Notocrangon antarcticus*	-75.6333	169.7858		105.24	531.8
572	I	NIWA	*Notocrangon antarcticus*	-75.6333	169.7858		91.23	531.8
573	I	NIWA	*Notocrangon antarcticus*	-75.6337	169.7863		133.79	530.1
574	I	NIWA	*Notocrangon antarcticus*	-75.6337	169.7863		96.5	530.1
575	I	NIWA	*Notocrangon antarcticus*	-75.6336	169.786		41.15	530.8
576	I	NIWA	*Notocrangon antarcticus*	-75.6336	169.7861		50.12	530.2
577	I	NIWA	*Notocrangon antarcticus*	-75.6338	169.787		45.47	530.2
578	I	NIWA	*Notocrangon antarcticus*	-75.6337	169.7876		81.94	532
579	I	NIWA	*Notocrangon antarcticus*	-75.6337	169.7876	25.9	78.11	532
580	I	NIWA	*Notocrangon antarcticus*	-75.6337	169.7876		67.45	532

581	I	NIWA	*Notocrangon antarcticus*	-75.6339	169.7881		83.57	531.4
582	I	NIWA	*Notocrangon antarcticus*	-75.6341	169.7886	31.81	100.67	530.9
583	I	NIWA	*Notocrangon antarcticus*	-75.6341	169.7888		43.61	530.8
584	I	NIWA	*Notocrangon antarcticus*	-75.6341	169.7898		46.44	531.6
585	I	NIWA	*Notocrangon antarcticus*	-75.6342	169.7899		46.09	530.9
586	I	NIWA	*Notocrangon antarcticus*	-75.6342	169.7899		40.04	530.9
587	I	NIWA	*Notocrangon antarcticus*	-75.634	169.7901		40.34	531.3
588	I	NIWA	*Notocrangon antarcticus*	-75.6341	169.7901		74.42	532
589	I	NIWA	*Notocrangon antarcticus*	-75.6341	169.7901		47.08	532
590	I	NIWA	*Notocrangon antarcticus*	-75.634	169.7905		69.38	530.9
591	I	NIWA	*Notocrangon antarcticus*	-75.634	169.7905		53.81	530.9
592	I	NIWA	*Notocrangon antarcticus*	-75.634	169.7905		40.5	530.9
593	I	NIWA	*Notocrangon antarcticus*	-75.6341	169.7908		61.17	531.3
594	I	NIWA	*Notocrangon antarcticus*	-75.6341	169.7908		78.15	531.3
595	I	NIWA	*Notocrangon antarcticus*	-75.6341	169.7908		27.43	531.3
596	I	NIWA	*Notocrangon antarcticus*	-75.634	169.7915		70.22	531.3
597	I	NIWA	*Notocrangon antarcticus*	-75.6338	169.7916		55.32	531.9
598	I	NIWA	*Notocrangon antarcticus*	-75.6338	169.7915		61.17	530.5
599	I	NIWA	*Notocrangon antarcticus*	-75.634	169.7922		100.5	531.3
600	I	NIWA	*Notocrangon antarcticus*	-75.6345	169.794		73.34	531.4
601	I	NIWA	*Notocrangon antarcticus*	-75.6345	169.794		49.36	531.4
602	I	NIWA	*Notocrangon antarcticus*	-75.6343	169.7934		59.41	530.5
603	I	NIWA	*Notocrangon antarcticus*	-75.6349	169.7933		45.63	532.2
604	I	NIWA	*Notocrangon antarcticus*	-75.6349	169.7933		69.67	532.2
605	I	NIWA	*Notocrangon antarcticus*	-75.6349	169.7933		50.35	532.2
606	I	NIWA	*Notocrangon antarcticus*	-75.6349	169.7933		54.2	532.2
607	I	NIWA	*Notocrangon antarcticus*	-75.635	169.7931		88.27	531.3
608	I	NIWA	*Notocrangon antarcticus*	-75.6352	169.7933		55.9	531.8
609	I	NIWA	*Notocrangon antarcticus*	-75.6352	169.7933		54.14	531.8
610	I	NIWA	*Notocrangon antarcticus*	-75.6353	169.7937		46.94	532.2
611	I	NIWA	*Notocrangon antarcticus*	-75.6353	169.7926		70.71	530.6
612	I	NIWA	*Notocrangon antarcticus*	-75.6353	169.7926		24.59	530.6
613	I	NIWA	*Notocrangon antarcticus*	-75.6356	169.7928	30.26	100.5	531
614	I	NIWA	*Notocrangon antarcticus*	-75.6356	169.7928	33.35	102.18	531

615	I	NIWA	*Notocrangon antarcticus*	-75.6358	169.793		73.04	529.9
616	I	NIWA	*Notocrangon antarcticus*	-75.6366	169.7928		38.61	530.6
617	I	NIWA	*Notocrangon antarcticus*	-75.6366	169.7928		56.17	530.6
618	I	NIWA	*Notocrangon antarcticus*	-75.6368	169.7933	31.71	94.85	530.6
619	I	NIWA	*Notocrangon antarcticus*	-75.6368	169.7933		47.13	530.6
620	I	NIWA	*Notocrangon antarcticus*	-75.628	167.3429		90.06	
621	I	NIWA	*Notocrangon antarcticus*	-75.628	167.3448		71.68	
622	I	NIWA	*Notocrangon antarcticus*	-75.6282	167.3442		57.74	
623	I	NIWA	*Notocrangon antarcticus*	-76.8037	167.8702		86.23	696.9
624	I	NIWA	*Notocrangon antarcticus*	-76.8037	167.8702	23.84	84.5	696.9
625	I	NIWA	*Notocrangon antarcticus*	-76.8037	167.8705	35.44	113.54	698.1
626	I	NIWA	*Notocrangon antarcticus*	-76.8031	167.8701	33.28	104.77	699
627	I	NIWA	*Notocrangon antarcticus*	-76.8031	167.8684	28.21	91.23	699.7
628	I	NIWA	*Notocrangon antarcticus*	-76.8024	167.8697		83.37	702
629	I	NIWA	*Notocrangon antarcticus*	-76.8023	167.8702		83.28	701.9
630	I	NIWA	*Notocrangon antarcticus*	-76.802	167.8703		50.54	701.4
631	I	NIWA	*Notocrangon antarcticus*	-76.8016	167.8707		88.48	702.2
632	I	NIWA	*Notocrangon antarcticus*	-76.8011	167.8704		51.2	703.1
633	I	NIWA	*Notocrangon antarcticus*	-76.8008	167.8701		102.61	703.2
634	I	NIWA	*Notocrangon antarcticus*	-76.8008	167.8708		104.4	704.2
635	I	NIWA	*Notocrangon antarcticus*	-76.8	167.8711		87.09	707.2
636	I	NIWA	*Notocrangon antarcticus*	-76.7995	167.8709		47.57	709.2
637	I	NIWA	*Notocrangon antarcticus*	-76.7987	167.8715	21.5	97.71	711.3
638	I	NIWA	*Notocrangon antarcticus*	-76.7986	167.8717		101.65	711.9
639	I	NIWA	*Notocrangon antarcticus*	-76.7982	167.8714		52.16	713.3
640	I	NIWA	*Notocrangon antarcticus*	-76.798	167.8726	26.39	90.09	713.5
641	I	NIWA	*Notocrangon antarcticus*	-76.7976	167.8728		101.74	713.5
642	I	NIWA	*Notocrangon antarcticus*	-76.7954	167.8754		87.89	715.3
643	I	NIWA	*Notocrangon antarcticus*	-76.8312	359.9528		73.54	663.1
644	I	NIWA	*Notocrangon antarcticus*	-76.8334	359.9574		67.07	662.9
645	I	NIWA	*Notocrangon antarcticus*	-76.8359	359.9464		92.96	665.7
646	I	NIWA	*Notocrangon antarcticus*	-76.6063	176.7607		82.58	368.7
647	I	NIWA	*Notocrangon antarcticus*	-76.6063	176.7613		86.83	369.4
648	I	NIWA	*Notocrangon antarcticus*	-76.6061	176.7625		87.69	367
649	I	NIWA	*Notocrangon antarcticus*	-76.606	176.7628		70.76	366.1

650	I	NIWA	*Notocrangon antarcticus*	-76.606	176.7628		97.85	366.1
651	I	NIWA	*Notocrangon antarcticus*	-76.6058	176.7634		95.76	366.7
652	I	NIWA	*Notocrangon antarcticus*	-76.6054	176.764		99.13	367.4
653	I	NIWA	*Notocrangon antarcticus*	-76.6054	176.7644		59.46	367.2
654	I	NIWA	*Notocrangon antarcticus*	-76.6053	176.7647		61.6	368.1
655	I	NIWA	*Notocrangon antarcticus*	-76.6053	176.7647		62.78	368.1
656	I	NIWA	*Notocrangon antarcticus*	-76.6043	176.7669		71.44	368.9
657	I	NIWA	*Notocrangon antarcticus*	-76.6043	176.7669		47.49	368.9
658	I	NIWA	*Notocrangon antarcticus*	-76.6043	176.7669		67.33	368.9
659	I	NIWA	*Notocrangon antarcticus*	-76.6037	176.7686	28.46	93.5	369.1
660	I	NIWA	*Notocrangon antarcticus*	-76.6035	176.7688	25.54	86.08	368.6
661	I	NIWA	*Notocrangon antarcticus*	-76.6034	176.7688		79.03	369.4
662	I	NIWA	*Notocrangon antarcticus*	-76.6033	176.7692		68.77	368.7
663	I	NIWA	*Notocrangon antarcticus*	-76.6032	176.7697		29.67	369
664	I	NIWA	*Notocrangon antarcticus*	-76.6032	176.7697		44.35	369
665	I	NIWA	*Notocrangon antarcticus*	-76.6031	176.7697		62.78	369.1
666	I	NIWA	*Notocrangon antarcticus*	-76.6031	176.7696		45.37	369.8
667	I	NIWA	*Notocrangon antarcticus*	-76.603	176.7711		42.38	368.9
668	I	NIWA	*Notocrangon antarcticus*	-76.6028	176.7716	32.04	104.69	369.5
669	I	NIWA	*Notocrangon antarcticus*	-76.6027	176.7719		83.6	369.2
670	I	NIWA	*Notocrangon antarcticus*	-76.6027	176.7729		73.17	368.7
671	I	NIWA	*Notocrangon antarcticus*	-76.6026	176.7725		83.11	369.4
672	I	NIWA	*Notocrangon antarcticus*	-76.6022	176.7742		58.42	368.9
673	I	NIWA	*Notocrangon antarcticus*	-76.6019	176.7754		61.47	368.2
674	I	NIWA	*Notocrangon antarcticus*	-76.6018	176.7756		66.46	368
675	I	NIWA	*Notocrangon antarcticus*	-76.6018	176.7756		65.89	368
676	I	NIWA	*Notocrangon antarcticus*	-76.6017	176.7757		74.89	368.5
677	I	NIWA	*Notocrangon antarcticus*	-76.6013	176.776		95.12	368.5
678	I	NIWA	*Notocrangon antarcticus*	-76.6013	176.7761		91.5	368.8
679	I	NIWA	*Notocrangon antarcticus*	-76.6013	176.7767		82.08	368.6
680	I	NIWA	*Notocrangon antarcticus*	-76.6009	176.7778		69.61	367.4
681	I	NIWA	*Notocrangon antarcticus*	-76.6003	176.7808		62.35	367
682	I	NIWA	*Notocrangon antarcticus*	-76.6003	176.7808		64.48	367
683	I	NIWA	*Notocrangon antarcticus*	-76.6002	176.781		83.09	367.5

684	I	NIWA	*Notocrangon antarcticus*	-76.6001	176.7818		101.35	367.7
685	I	NIWA	*Notocrangon antarcticus*	-76.6001	176.7819	26.2	78.59	367.5
686	I	NIWA	*Notocrangon antarcticus*	-76.5999	176.7819		69.34	367.3
687	I	NIWA	*Notocrangon antarcticus*	-76.5999	176.7825		88.7	367.4
688	I	NIWA	*Notocrangon antarcticus*	-76.5999	176.7819		87.27	367.3
689	I	NIWA	*Notocrangon antarcticus*	-76.5999	176.7819		101.4	367.3
690	I	NIWA	*Notocrangon antarcticus*	-76.5995	176.7841		69.9	366.9
691	I	NIWA	*Notocrangon antarcticus*	-76.5994	176.7842		47.34	367
692	I	NIWA	*Notocrangon antarcticus*	-76.5994	176.7842		33.71	367
693	I	NIWA	*Notocrangon antarcticus*	-76.5993	176.7848		63.69	366.8
694	I	NIWA	*Notocrangon antarcticus*	-76.5991	176.7854		64.15	366.7
695	I	NIWA	*Notocrangon antarcticus*	-76.5991	176.7854		49.83	366.7
696	I	NIWA	*Notocrangon antarcticus*	-76.5988	176.786		62.32	366.9
697	I	NIWA	*Notocrangon antarcticus*	-76.5988	176.786		71.27	366.9
698	I	NIWA	*Notocrangon antarcticus*	-76.5989	176.7862		70.9	367.1
699	I	NIWA	*Notocrangon antarcticus*	-76.5987	176.7874		91.4	367
700	I	NIWA	*Notocrangon antarcticus*	-76.5987	176.7874		84.45	367
701	I	NIWA	*Notocrangon antarcticus*	-76.5988	176.7872		72.14	367
702	I	NIWA	*Notocrangon antarcticus*	-76.5988	176.7877		53.37	367.3
703	I	NIWA	*Notocrangon antarcticus*	-76.5988	176.7877		74.42	367.3
704	I	NIWA	*Notocrangon antarcticus*	-76.5987	176.7884		82.31	366.6
705	I	NIWA	*Notocrangon antarcticus*	-76.5986	176.7884		83.27	367.5
706	I	NIWA	*Notocrangon antarcticus*	-76.5986	176.7899		63.93	367.1
707	I	NIWA	*Notocrangon antarcticus*	-76.5985	176.7907		72.52	367.4
708	I	NIWA	*Notocrangon antarcticus*	-76.5985	176.7907		45.89	367.4
709	I	NIWA	*Notocrangon antarcticus*	-76.5985	176.7907		54.62	368.2
710	I	NIWA	*Notocrangon antarcticus*	-76.5985	176.7911		63.44	367.7
711	I	NIWA	*Notocrangon antarcticus*	-76.1971	176.2818		105.52	449.9
712	I	NIWA	*Notocrangon antarcticus*	-76.1971	176.2817		45.21	449.9
713	I	NIWA	*Notocrangon antarcticus*	-76.197	176.2821		63.18	449.8
714	I	NIWA	*Notocrangon antarcticus*	-76.197	176.2821		69.53	449.8
715	I	NIWA	*Notocrangon antarcticus*	-76.197	176.282		48.5	449.4
716	I	NIWA	*Notocrangon antarcticus*	-76.1969	176.2821		69.83	449.6
717	I	NIWA	*Notocrangon antarcticus*	-76.1968	176.2825		64.56	449.3
718	I	NIWA	*Notocrangon antarcticus*	-76.1968	176.2825		49.41	449.3

719	I	NIWA	*Notocrangon antarcticus*	-76.1968	176.2825		84.02	449.3
720	I	NIWA	*Notocrangon antarcticus*	-76.1968	176.2827	17.72	59.88	449
721	I	NIWA	*Notocrangon antarcticus*	-76.1967	176.2834		52.39	448.8
722	I	NIWA	*Notocrangon antarcticus*	-76.1966	176.2834		75.69	448.8
723	I	NIWA	*Notocrangon antarcticus*	-76.1965	176.2837	28.58	99.15	449.1
724	I	NIWA	*Notocrangon antarcticus*	-76.1962	176.2852	20.27	62.69	451
725	I	NIWA	*Notocrangon antarcticus*	-76.1961	176.2858		75.07	451.7
726	I	NIWA	*Notocrangon antarcticus*	-76.1957	176.2873		72.73	450.7
727	I	NIWA	*Notocrangon antarcticus*	-76.1957	176.2873		61.7	450.7
728	I	NIWA	*Notocrangon antarcticus*	-76.1956	176.2876		68.55	450.8
729	I	NIWA	*Notocrangon antarcticus*	-76.1954	176.2883		73.73	450.6
730	I	NIWA	*Notocrangon antarcticus*	-76.1952	176.2892	24.74	77.08	449.8
731	I	NIWA	*Notocrangon antarcticus*	-76.1948	176.2914	36.66	106.76	450.6
732	I	NIWA	*Notocrangon antarcticus*	-76.1944	176.2931		39.87	450
733	I	NIWA	*Notocrangon antarcticus*	-76.1943	176.2931		67.69	449.6
734	I	NIWA	*Notocrangon antarcticus*	-76.1942	176.2931		65.74	449.8
735	I	NIWA	*Notocrangon antarcticus*	-76.1942	176.2943		81.65	449.4
736	I	NIWA	*Notocrangon antarcticus*	-76.1941	176.2944	30.11	92.18	449.4
737	I	NIWA	*Notocrangon antarcticus*	-76.1935	176.2969		86.13	448.3
738	I	NIWA	*Notocrangon antarcticus*	-76.193	176.2977		79.17	448.1
739	I	NIWA	*Notocrangon antarcticus*	-76.1931	176.2978		75.83	448.1
740	I	NIWA	*Notocrangon antarcticus*	-76.1929	176.2978		46.02	448.2
741	I	NIWA	*Notocrangon antarcticus*	-76.1928	176.2988		70.32	447.9
742	I	NIWA	*Notocrangon antarcticus*	-76.1929	176.2994	28.74	98.9	448.2
743	I	NIWA	*Notocrangon antarcticus*	-76.1927	176.3005		70.37	449.1
744	I	NIWA	*Notocrangon antarcticus*	-76.1927	176.3005		53.22	449.1
745	I	NIWA	*Notocrangon antarcticus*	-76.1923	176.3015		70.12	450
746	I	NIWA	*Notocrangon antarcticus*	-76.1921	176.303		72.65	449.7
747	I	NIWA	*Notocrangon antarcticus*	-76.192	176.3033		73.55	449.7
748	I	NIWA	*Notocrangon antarcticus*	-76.1916	176.3047		99.44	448.9
749	I	NIWA	*Notocrangon antarcticus*	-76.1913	176.3063	19.45	55.2	448.5
750	I	NIWA	*Notocrangon antarcticus*	-76.1913	176.3063		103.57	448.2
751	I	NIWA	*Notocrangon antarcticus*	-76.1911	176.3079	18.98	67.79	448.6
752	I	NIWA	*Notocrangon antarcticus*	-76.1909	176.309	32.22	111.31	449.9

753	S	NSMT	*Notocrangon antarcticus*	-70.2283	24.42833	13.7	282.5
754	S	NSMT	*Notocrangon antarcticus*	-68.3917	34.125	15.8	281.5
755	S	CBM	*Notocrangon antarcticus*	-67.985	41.92667	19.2	352.5
756	S	CBM	*Notocrangon antarcticus*	-69.1967	75.49167	15.6	592

Appendix V

SIMER analysis based on a Bray-Curtis distance matrix on Presence Absence Transformed faunal abundance for comparison of samples in four regions: Shelf, Slope, Seamount (Scott) and SeamountA (Admiralty). Second SIMPER result is based on Bray-Curtis Distance matrix on non-transformed faunal abundance for comparison of samples with three common shrimps. Av. Abun= average abundance, Av.Sim= average similarity, Sim/SD= average similarity contribution divided by the standard deviation, Contrib%= %Contribution, Cum%= cumulative %contribution, Av.Diss= average dissimilarity, Diss/SD = average dissimilarity contribution divided by the standard deviation.

Ross Sea Shelf (Average similarity: 29.74)

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
ophiuroid	28.71	8.77	1.24	29.51	29.51
bryozoan	29.71	8.18	1.13	27.5	57.01
sponge	17.43	4.1	0.87	13.77	70.78
worms	17.14	3.29	0.91	11.07	81.85
holothurian	5.57	1.74	0.83	5.84	87.69
anemone	9.29	1.6	0.7	5.4	93.08

Ross Sea Slope (Average similarity: 26.36)

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
sponge	9.33	11.39	0.87	43.2	43.2
ophiuroid	8.33	5.85	0.83	22.18	65.39
asteroid	1.17	2.92	0.4	11.09	76.48
mollusc	1.83	1.89	0.72	7.18	83.66
brachiopod	4	1.65	0.29	6.26	89.92
seleractinia	5.83	1.57	0.48	5.95	95.87

Seamount (Average similarity: 42.57)

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
sponge	21.57	19	1.87	44.62	44.62
anemone	18	14.83	1.62	34.83	79.45
bryozoan	15.29	3.1	0.96	7.27	86.72
ophiuroid	11.86	2.63	0.67	6.17	92.9

SeamountA (Average similarity: 31.27)

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
sponge	7	12	1.21	38.36	38.36
ophiuroid	4.71	11.12	0.74	35.55	73.91
brachiopod	7.14	3.95	0.71	12.63	86.54
anemone	6.86	1.65	0.44	5.28	91.83

Ross Sea Shelf & Ross Sea Slope (Average dissimilarity = 80.65)

	Shelf	**Slope**				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
ophiuroid	28.71	8.33	14.85	2.08	18.42	18.42
bryozoan	29.71	0.17	14.38	1.88	17.83	36.25
sponge	17.43	9.33	12.5	1.35	15.5	51.75
worms	17.14	0.5	7.66	1.49	9.5	61.25
seleractinia	0	5.83	4.91	0.64	6.09	67.34
anemone	9.29	2.5	4.76	1.54	5.9	73.25
crinoid	10.57	0.67	4.49	1.11	5.57	78.82
brachiopod	0	4	3.92	0.56	4.86	83.69
holothurian	5.57	0.17	3.61	0.99	4.48	88.16
asteroid	2.14	1.17	3.01	0.58	3.73	91.89

Ross Sea Shelf & Seamount (Average dissimilarity = 73.70)

	Shelf	**Seamount**				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
sponge	17.43	21.57	13.25	1.29	17.98	17.98
bryozoan	29.71	15.29	11.97	1.64	16.25	34.23
ophiuroid	28.71	11.86	11.46	1.72	15.55	49.78
anemone	9.29	18	10.67	1.15	14.48	64.26
worms	17.14	0.29	6.31	1.28	8.57	72.83
seleractinia	0	12.43	3.86	0.7	5.24	78.07
mollusc	0.86	6.43	3.81	0.61	5.16	83.23
crinoid	10.57	0	3.41	0.91	4.62	87.86
holothurian	5.57	0	2.85	1.01	3.87	91.73

Ross Sea Slope & Seamount (Average dissimilarity = 69.77)

	Slope	**Seamount**				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
anemone	2.5	18	14.09	1.52	20.19	20.19
sponge	9.33	21.57	13.88	1.26	19.9	40.09
ophiuroid	8.33	11.86	9.63	1.44	13.81	53.9
seleractinia	5.83	12.43	7.85	1.11	11.25	65.15
bryozoan	0.17	15.29	7.28	1.1	10.44	75.59
mollusc	1.83	6.43	5.43	0.83	7.79	83.38
brachiopod	4	0.43	4.25	0.71	6.09	89.48
asteroid	1.17	3.57	2.85	1.11	4.08	93.55

Ross Sea Shelf & SeamountA (Average dissimilarity = 78.19)

	Shelf	**SeamountA**				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
bryozoan	29.71	1.86	14.85	1.9	18.99	18.99
ophiuroid	28.71	4.71	13.98	1.86	17.88	36.87
sponge	17.43	7	10.59	1.79	13.55	50.42
worms	17.14	0	8.31	1.61	10.63	61.05
anemone	9.29	6.86	6.98	1.17	8.93	69.98
brachiopod	0	7.14	6.07	0.84	7.77	77.75
crinoid	10.57	2.43	5.22	1.18	6.67	84.42
holothurian	5.57	0	4.03	1.01	5.16	89.58
pycnogonid	3.43	0	1.76	1.14	2.25	91.83

Ross Sea Slope & SeamountA (Average dissimilarity = 73.93)

	Slope	**SeamountA**				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
sponge	9.33	7	15.84	1.62	21.42	21.42
ophiuroid	8.33	4.71	12.48	1.41	16.88	38.31
brachiopod	4	7.14	10.89	1.29	14.73	53.04
anemone	2.5	6.86	7.64	1.09	10.33	63.37
seleractinia	5.83	0.29	7.21	0.78	9.75	73.13
asteroid	1.17	0.86	4.61	0.69	6.24	79.37
mollusc	1.83	0.43	3.85	0.84	5.21	84.58
crinoid	0.67	2.43	3.09	0.68	4.19	88.77
bryozoan	0.17	1.86	2.45	0.86	3.32	92.08

Seamount & SeamountA (Average dissimilarity = 73.60)

	Seamount	**SeamountA**				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
sponge	21.57	7	17.22	1.67	23.39	23.39
anemone	18	6.86	16.59	1.89	22.54	45.93
bryozoan	15.29	1.86	7.73	1.18	10.5	56.43
ophiuroid	11.86	4.71	7.55	1.46	10.26	66.69
brachiopod	0.43	7.14	5.86	0.96	7.97	74.66
mollusc	6.43	0.43	5.23	0.67	7.11	81.77
seleractinia	12.43	0.29	5.06	0.82	6.87	88.65
asteroid	3.57	0.86	2.26	1	3.08	91.72

Appendix VI

SIMPER result is based on Bray-Curtis Distance matrix on non-transformed faunal abundance for comparison of samples found next to three common shrimps *C. antarcticus, N. antarcticus and N. lanceopes*. Av. Abun= average abundance, Av.Sim= average similarity, Sim/SD= average similarity contribution divided by the standard deviation, Contrib%= %Contribution, Cum%= cumulative %contribution, Av.Diss= average dissimilarity, Diss/SD = average dissimilarity contribution divided by the standard deviation.

Notocrangon antarcticus (Average similarity: 36.33)

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
bryozoan	0.69	12.83	0.97	35.32	35.32
ophiuroid	0.68	12.02	0.93	33.09	68.4
sponge	0.41	4.14	0.46	11.41	79.81
worms	0.4	3.89	0.44	10.72	90.53

Chorismus antarcticus (Average similarity: 37.80)

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
bryozoan	0.74	13.87	1.11	36.69	36.69
ophiuroid	0.7	12.22	0.98	32.33	69.03
worms	0.43	4.42	0.49	11.7	80.72
sponge	0.42	4.01	0.47	10.61	91.33

Nematocarcinus lanceopes (Average similarity: 37.05)

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
sponge	0.71	16.32	0.89	44.06	44.06
ophiuroid	0.48	6.4	0.52	17.27	61.33
anemone	0.47	6.09	0.51	16.43	77.76
seleractinia	0.39	3.66	0.42	9.89	87.65
bryozoan	0.35	2.92	0.37	7.88	95.53

Notocrangon antarcticus & Chorismus antarcticus (Average dissimilarity = 62.68)

Species	***N. antarcticus* Av.Abund**	***C. antarcticus* Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum.%**
ophiuroid	0.68	0.7	10.64	0.78	16.97	16.97
bryozoan	0.69	0.74	10.5	0.78	16.75	33.72
worms	0.4	0.43	8.92	0.89	14.23	47.95
sponge	0.41	0.42	8.81	0.89	14.06	62.02
crinoid	0.25	0.26	6.53	0.71	10.42	72.43
anemone	0.22	0.22	5.77	0.67	9.21	81.64
holothurian	0.16	0.07	3.4	0.46	5.42	87.06
pycnogonid	0.09	0.07	2.09	0.37	3.33	90.39

Notocrangon antarcticus & Nematocarcinus lanceopes (Average dissimilarity = 73.97)

Species	***N. antarcticus* Av.Abund**	***N. lanceopes* Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
sponge	0.41	0.71	12.78	0.75	17.28	17.28
ophiuroid	0.68	0.48	10.85	0.82	14.67	31.95
bryozoan	0.69	0.35	10.8	0.95	14.6	46.55
anemone	0.22	0.47	9.13	0.77	12.34	58.89
seleractinia	0	0.39	6.24	0.69	8.44	67.32
worms	0.4	0.02	6.24	0.76	8.43	75.76
crinoid	0.25	0.02	3.86	0.55	5.22	80.98
mollusc	0.02	0.19	3.7	0.41	5	85.99
holothurian	0.16	0	2.43	0.41	3.28	89.27
brachiopod	0	0.12	2.26	0.31	3.05	92.32

Chorismus antarcticus & Nematocarcinus lanceopes (Average dissimilarity = 73.70)

Species	***C. antarcticus* Av.Abund**	***N. lanceopes* Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
sponge	0.42	0.71	12.45	0.74	16.89	16.89
bryozoan	0.74	0.35	10.8	0.99	14.65	31.54
ophiuroid	0.7	0.48	10.65	0.81	14.46	46
anemone	0.22	0.47	8.9	0.77	12.07	58.07
worms	0.43	0.02	6.62	0.82	8.98	67.05
seleractinia	0	0.39	6.13	0.69	8.31	75.36
crinoid	0.26	0.02	4.33	0.56	5.88	81.24
mollusc	0.03	0.19	3.68	0.41	4.99	86.23
brachiopod	0	0.12	2.21	0.31	3	89.23
asteroid	0.07	0.09	2.09	0.39	2.84	92.07

Appendix VII

Locations and source of *Nematocarcinus lanceopes* records used for the model training and validation.

Type/Collection	**Institute Code**	**Locations**	**Source** (See below)
Database		6	a
	AAD	18	a
	AADC	10	a
	AWI	6	a
	BAS	2	a
	SAMC	2	a
	SMF	1	a
Journal Article	-	32	b
	AWI	44	c
	UoI	1	d
	CBM	1	e
	BAS	6	f
	AWI	1	g
	MNHN	3	h
	NIWA	30*	i
Museum	USNM	1	j
Expedition Report	NIWA	8	k

* Records used for independent model validation.

Citations:

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(b) Dambach, J., Thatje, S., Rödder, D., Basher, Z., Raupach, M.J. 2012. Effects of Late-Cenozoic glaciation on habitat availability in Antarctic benthic shrimps (Crustacea: Decapoda: Caridea). PLoS ONE, 7(9), e46283. doi:10.1371/journal.pone.0046283.;

(c) Gorny, M. 1999. On the biogeography and ecology of the Southern Ocean decapod fauna. Scientia Marina 63 (Supl. 1): 367-382.;

(d) Guzmán, G., Quiroga, E. 2005. New records of shrimps (Decapoda: Caridea and Dendrobranchiata) in deep waters of Chile. Gayana (Concepcin), 69(2), 285-29;

(e) Komai T. & Segonzac M. 2005. — Two new species of Nematocarcinus A. Milne-Edwards,1881 (Crustacea, Decapoda, Caridea, Nematocarcinidae) from hydrothermal vents on the North and South East Pacific Rise. Zoosystema 27 (2): 343-364.;

(f) Linse, K., Griffiths, H.J., Barnes, D.K.A., Brandt, A., Davey, N., David, B., De Grave, S., D′Udekem D′Acoz, C., Eléaume, M., Glover, A.G., Hemery, L.G., Mah, C., Martín-Ledo, R., Munilla, T., O′Loughlin, M., Pierrat, B., Saucède, T., Sands, C.J., Strugnell, J.M., Enderlein, P. 2013. The macro- and megabenthic fauna on the continental shelf of the eastern Amundsen Sea, Antarctica. Continental Shelf Research, 68(0), 80–90. doi:10.1016/j.csr.2013.08.012.;

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(h) Basher, Z., & Costello, M. J. (2014). Crustacea: Decapoda: shrimps. In K. P. De Broyer C., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', Van de Putte A.P., Danis B., David B., Grant S., Gutt J., Held C., Hosie G., Huettmann F., Post A., Ropert-Coudert Y. (Ed.), Biogeographic Atlas of the Southern Ocean (in press). Cambridge: Scientific Committee on Antarctic Research;

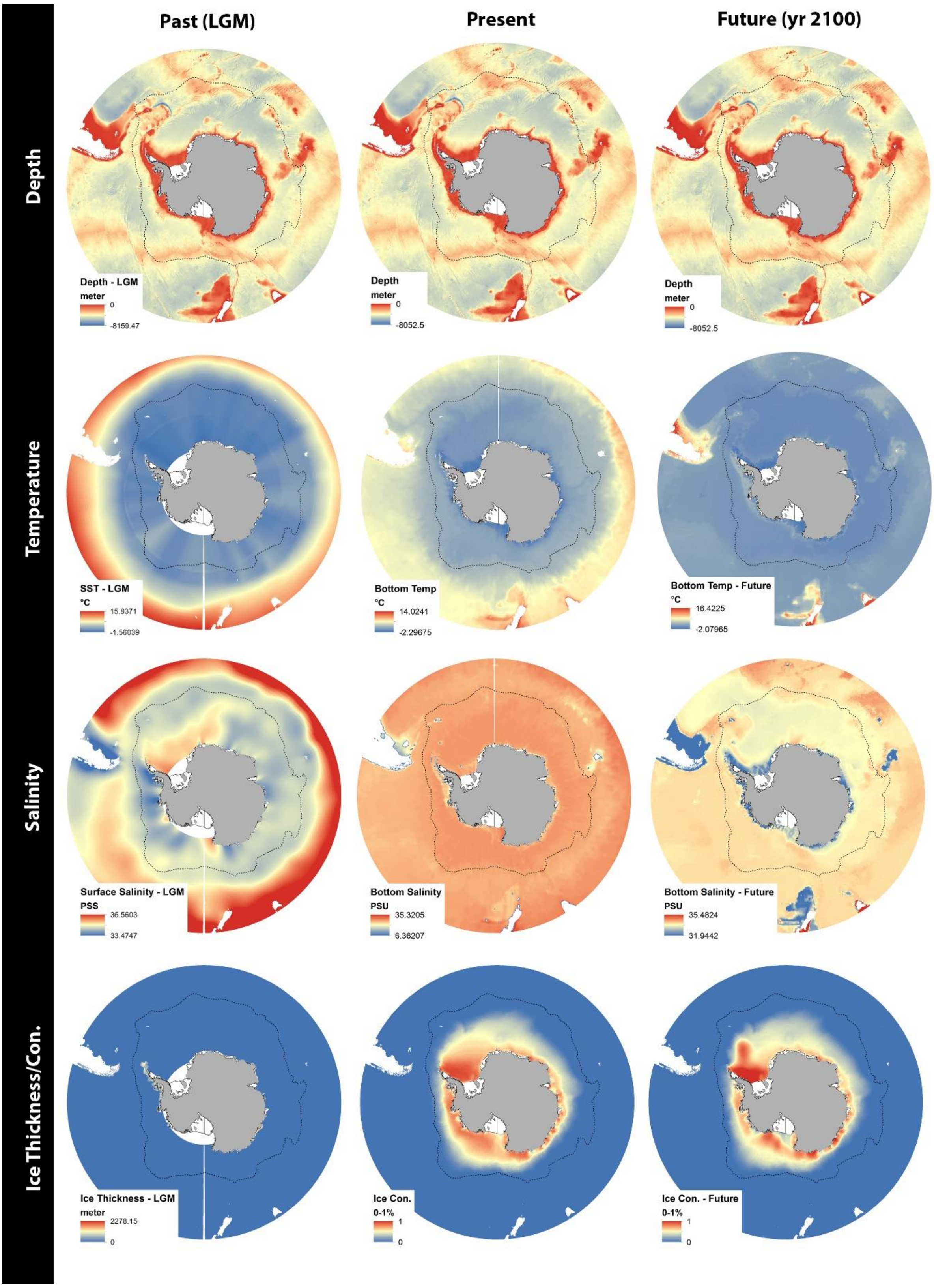
(i) Basher, Z., Bowden, D. A., & Costello, M. J. (2014). Diversity and distribution of deep-sea shrimps in the Ross Sea region of Antarctica. PLoS ONE, (doi:10.1371/journal.pone.0103195);

(j) Department of Invertebrate Zoology, Research and Collections Information System, NMNH, Smithsonian Institution. See: http://www.mnh.si.edu/rc/db/collection_db_policy1.html, 05-14-2010;

(k) NIWA OBIS; Available at nzobis.niwa.co.nz

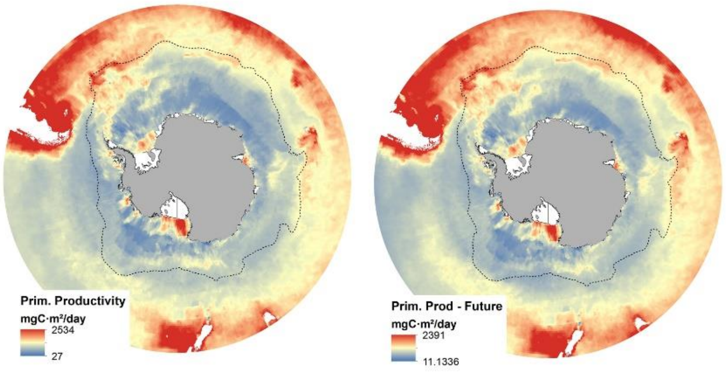
Appendix VIII

Environmental layers used for modelling in this study.


Past (LGM)
Present
Future (yr 2100)
Depth
Temperature
Salinity
Ice Thickness/Con.
Depth - LGM
meter
0
-8159.47
Depth
meter
0
-8052.5
Depth
meter
0
-8052.5
SST - LGM
°C
15.8371
-1.56039
Bottom Temp
°C
14.0241
-2.29675
Bottom Temp - Future
°C
16.4225
-2.07965
Surface Salinity - LGM
PSS
36.5603
33.4747
Bottom Salinity
PSU
35.3205
6.36207
Bottom Salinity - Future
PSU
35.4824
31.9442
Ice Thickness - LGM
meter
2278.15
0
Ice Con.
0-1%
1
0
Ice Con. - Future
0-1%
1
0

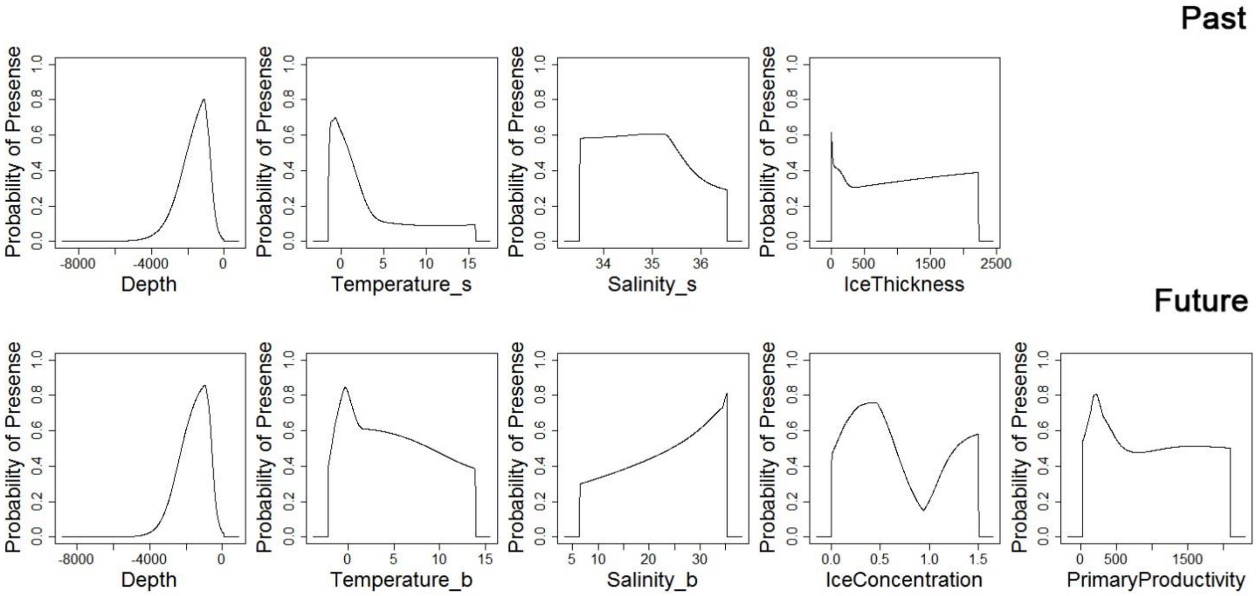
Primary Productivity

Past (LGM) **Present** **Future (yr 2100)**



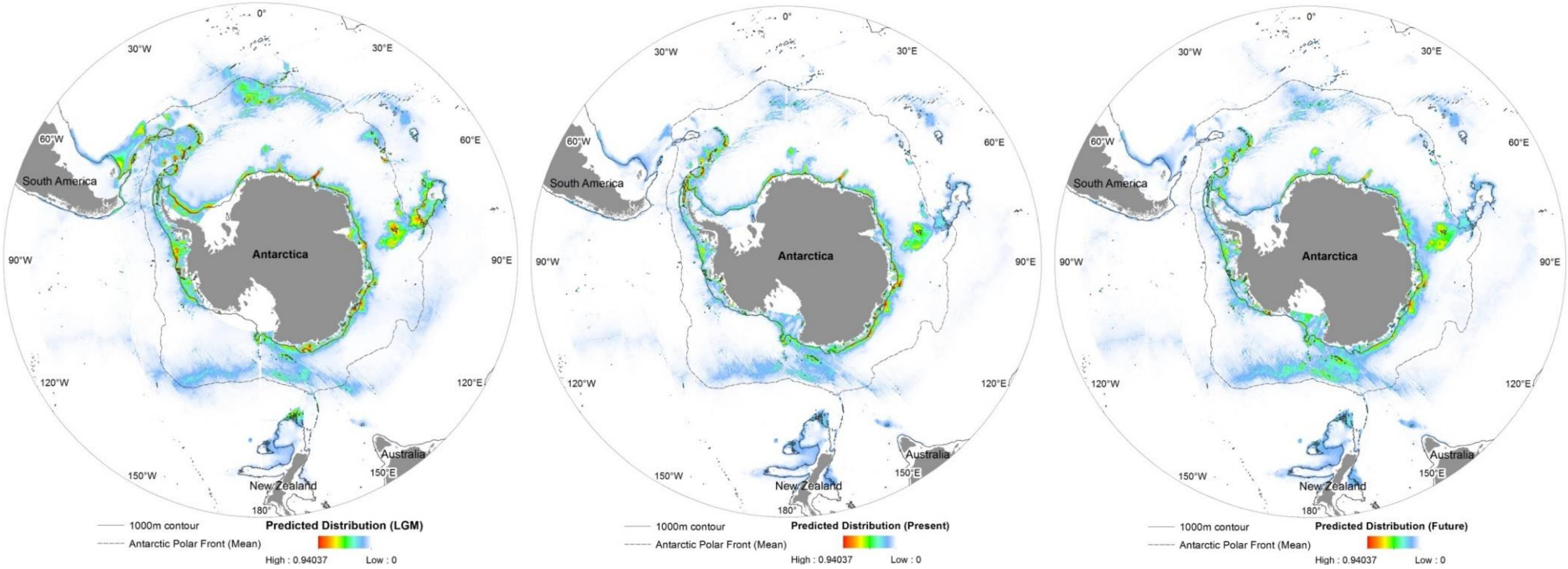
Appendix IX

Influence of environmental variables in the model prediction performance.



Appendix X

Unclassified MaxEnt prediction maps of past, present and future distribution of *N. lanceopes* (left to right)



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