Geographic isolation and physiological mechanisms underpinning species distributions at the range limit hotspot of South Georgia

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Abstract

In order to allocate quotas for sustainable harvests that account for climate warming, it is important to incorporate species vulnerabilities that will underlie likely changes in population dynamics. Hotspots, regions with rapidly changing climate, are important locations for rapid advances in mechanistic understanding of the factors driving these changes, particularly if they coincide with regions with a high incidence of range limits, such as the sub-Antarctic Island of South Georgia. This archipelago is at the Northern limit of the Southern Ocean and therefore the northern distribution limit for many Southern Ocean shallow water marine species, which are amongst the most sensitive fauna to increasing temperature. At range limits species may either be living close to their physiological limits, or they may have more resistant phenotypes. In case studies, the northern range limit population of the gastropod limpet, *Nacella concinna*, has greater physiological plasticity at South Georgia than those from further south, allowing them to cope better with the warmer and more variable seasonal temperatures. Bivalve species, however, alter their depth distributions at South Georgia, to avoid the warmer water masses, indicating that they may not be able to cope with the warmer temperatures. Mackerel icefish, *Champsocephalus gunnari*, has a unique Antarctic trait, the loss of haemoglobin. A combination of temperature driven change in food web structure, and this extreme physiological cold adaptation, may explain why rapid warming at its northern range limit of South Georgia, has prevented stocks fully recovering from over fishing in the 1980’s, despite highly conservative management strategies.

Keywords: warming hotspots; physiological limits; range shifts; range edge; Antarctic; evolutionary history

Introduction

In response to climate warming, species ranges are consistently moving towards cooler latitudes, terrestrial species are moving to higher elevations (Perry et al. 2005; Chen et al. 2011), whilst marine species are moving to deeper, cooler depths (Dulvey et al. 2008). The rate of surface warming is not even across latitudes (Burrows et al., 2011) and the distributions of terrestrial species are shifting faster in more rapidly warming environments (Chen et al. 2011). In order to make rapid advances in understanding, warming “hotspots” have been identified as regions for focussed research investigating the mechanisms underlying range limits (this volume). Whilst climate envelope models can identify regions that are warming rapidly, the sensitivity of faunal assemblages to warming is not uniform across these regions. The variability and predictability of environmental temperature has a strong influence on geographic patterns of physiological tolerance and plasticity (e.g. Gaston et al. 2009; Clusella-Trullas et al. 2011). Marine fauna from high and low latitude regions that have experienced stable shallow seawater temperatures over evolutionary time scales have limited ability to respond to variation in their thermal environment, which makes them particularly vulnerable to the effects of climate warming (Peck 2005; Deutsch et al. 2008; Peck et al. 2009; Richard et al. 2011; Nguyen et al. 2011).

The Western Antarctic Peninsula (WAP) and Scotia Arc region (Fig. 1) are amongst the fastest warming marine environments (Meredith and King 2005, Hansen et al. 2010). Sea surface temperatures in the WAP are warming faster than the global average (1°C in 50 years; Meredith and King 2005) but more importantly, temperature is increasing at a rate which is biologically significant to the physiology of the resident marine fauna (e.g. Peck 2005; Peck et al. 2009). Situated at the northern edge of the Southern Ocean, South Georgia is an isolated sub-Antarctic Island with a rich fauna, which has been isolated for long enough (~45ma; Livermore et al. 2007) to have developed a high degree of endemism (Hogg et al. 2011). Due to its position in the sub-Antarctic it is potentially supplied with a mix of larvae and adults from two sources: Antarctica, one of the most stenothermal faunal assemblages, and from more eurythermal species living in cool temperate regions north of the polar front. Both these fauna must overcome substantial barriers to reach South Georgia, which results in South Georgia having many more species at their geographic and physiological limits than is usual, making it a hotspot in this respect. It therefore presents the ideal location to study the mechanisms underpinning marine species distributions. In this paper we use the example of South Georgia to highlight how incorporating the knowledge of physiological sensitivity of species, populations and individuals, into the management of fish stocks, can increase the robustness of exploitation models. This will help predict shifting interactions between species (Poloczanska et al. 2008) and improve the ecosystems approach to fisheries management.

South Georgia fauna

South Georgia is a range limit hotspot, which, despite its geographic (~1800km) and environmental (polar front) isolation, has a diverse marine fauna and anomalously high levels of endemic and range-edge species (Barnes et al. 2009; Hogg et al. 2011; Table 1). The richness of South Georgia marine fauna has also been linked to its large shelf sea area and the rich nutrients created from mixing of shelf waters by eddies from the Antarctic circumpolar current (Hogg et al. 2011).

Whilst the shallow water marine fauna at South Georgia is characteristic of an Antarctic assemblage (Barnes et al. 2005), with up to 52% of some groups reaching their northern distribution limit at South Georgia, there are other species for which South Georgia is the southern range limit (up to 13%; Table 1). Some hints regarding the adaptive potential of the South Georgian marine assemblage may be found in the physical and evolutionary history of the region. The Scotia Sea has a complex history spanning 20 - 30 million years (Thomson 2004; Eagles 2010). Prior to this point the shallow water marine faunas were largely shared between the continental shelves of Antarctica and South America (Crame 1999). Since then the complex interaction of drift, selection, migration and extinction has resulted in a highly endemic Antarctic fauna (Dell 1972; Clarke and Johnston 1999).

The origin of the South Georgia fauna depends on how the South Georgian microplate was associated with Gondwana before breakup. Current theory suggests it was associated with the southern tip of Tierra del Fuego (Mukasa and Dalziel 1996), although Eagles (2010) places it further east which may indicate it had an impoverished fauna compared to that of the Gondwanan continental shelf. Either way, the uniqueness of the current composition of the South Georgian shallow water benthos is a product of its historical and adaptive diversity. The complex geological, oceanographic and glaciological history of South Georgia indicates large changes of physical environment leading to diverse selection pressures on the fauna. One of the best explored examples of this is the clade of notothenioid fish, in which the adaptation to cold environments by evolution of antifreeze glycoproteins triggered an explosive radiation south of the Polar Front soon after its formation (Matschiner et al. 2011). There is evidence for more recent or recurrent gene flow between South Georgia and the West Antarctic Peninsula, as well as with the Patagonian shelf (e.g. the bivalve *Gaimardia trapesina* Helmuth et al. 1994, and the gastropod *Nacella concinna* Hoffman et al. 2011). Given the difficulties of stenothermal organisms overcoming a new temperature regime, the ability of these migrants to survive is dependent on their physiological plasticity and subsequent adaptive potential. The ability of a species or populations to adapt is intrinsically tied to the genetic diversity of the source population, which, in turn, is largely a function of the effective population size (Hartl and Clark 1997).

Species physiologies are expected to vary across their range with optimal fitness at the centre of a species range and limited fitness at range edges when they encounter conditions that are beyond species tolerance (Spicer and Gaston 1999; Lee et al. 2009). This would result in species at range edges having the same or even reduced thermal plasticity than from their range centre and therefore being more sensitive to climate warming. However, if there is a restriction in gene flow across a species geographic range, adaptation, either through mutation or via natural selection of specific traits (Barret and Schlutter 2008), may lead to populations at range edges having different thermal optima and tolerances, more suited to their environment (Kirkpatrick and Barton 1997; Gaston et al. 2009). These two situations could clearly have very different implications for the survival of species exposed to environmental change. *Nacella concinna* has been shown to have different thermal tolerances across its distribution range that correlates with its regional thermal environment and restricted gene flow has lead to population level genetic differences between limpets from the WAP and South Georgia (Hoffman et al. 2011).

South Georgia as a physiological limit

Studies of environmental variability and its correlation with the physiological plasticity of species have led to a wide range of hypotheses correlating distributions with physiological tolerances (Gaston et al. 2009). In particular the magnitude and variability of habitat temperature is strongly correlated with the tolerance of species and populations. One extreme example of this is the Southern Ocean, which has the planets coldest and most thermally stable surface waters; Antarctic ectotherms have subsequently evolved to be amongst the most sensitive to increased temperature (Peck et al. 2004). However, within the Southern Ocean there are still biologically significant differences in temperature across the latitudinal gradient from McMurdo Sound to South Georgia. McMurdo Sound is the highest latitude seasonal open water environment at 76°S (Fig.1). Recent studies have shown that despite the very small differences in thermal regime, both invertebrate and fish species from higher Southern Ocean latitudes are less temperature tolerant than those from warmer, lower latitudes (Bilyk and DeVries 2011; Morley et al. 2012).

South Georgia has the warmest summer and the highest annual variability of surface seawater temperatures within the Southern Ocean and maximum summer temperatures regularly exceed the measured thermal limits for species further south on the WAP, despite many of the same species occurring at South Georgia (Morley et al. 2010). Long term physiological limits for survival of an array of marine ectotherms from Marguerite Bay on the WAP have been measured at between 1 and 6°C (Peck et al. 2009), with limits for key behavioural escape responses between 1 and 3°C (Peck et al. 2004), indicating that the summer maximum temperature in the shallow water at South Georgia may be above the temperature tolerance of some of these species. These co-occurring species may need to avoid the warmest water masses or have greater physiological flexibility at South Georgia; both of these strategies have been found at South Georgia (see below).

The Southern Ocean is not only characterised by a latitudinal temperature gradient but also by a strongly vertically stratified water column with shelf water masses of different temperature (summer temperature depth profiles shown in Fig. 2). The intermediate layer of cold water, the winter water (WW), is formed during winter when strong mixing creates a thick mixed layer with cold temperatures and high salinity. This mixed layer is capped by the surface layer which heats up during the austral summer forming the surface Antarctic water (SAW; Brandon et al. 2004). The water mass below the winter water is the circumpolar deep water (CDW) but the temperature of all three water masses also varies with latitude across the Southern Ocean (Fig. 2), a temperature variation which is of biological significance.

All co-occurring bivalve species had depth distributions that were shifted at South Georgia (Table 2), compared to those along the WAP. Species with both deeper and shallower distributions on the WAP were all centred within the cooler, intermediate depth, winter water, at South Georgia, avoiding the warmest surface Antarctic water and the warm upper layer of circumpolar deep water (Morley et al. 2010), which are potentially beyond the physiological limits of the WAP population (e.g. Peck et al. 2004, 2009).

This pattern was not seen in the co-occurring gastropods (Table 2), and in the only comparative study of gastropod physiology to date, the widely distributed Antarctic limpet, *N. concinna*, actually had a lower acute temperature limit at South Georgia than at the WAP (Morley et al. 2009a) but a higher physiological plasticity (Morley et al. 2009b). A high physiological plasticity should enable the South Georgia population to better cope with the seasonal fluctuations in temperature at South Georgia, and is thought to be a key trait that will help species cope with rapid rates of climate change (Stillman 2003).

Impacts on fisheries

Fisheries catch statistics provide one of the longest records of shifts in species distributions through time. Recently shifts in distribution have been recorded for many fish stocks, to cooler latitudes (Perry et al. 2005) and deeper depths (Dulvey et al. 2008). Fish stocks in the North Sea (such as cod, *Gadus morhua*; Pörtner et al. 2001) and British Columbia's Fraser River (Sockeye salmon, *Oncorhynchus nerka*; Eliason et al. 2011) have been shown to have different thermal limits that can be explained by differences in experienced temperature and subsequent physiological differences, particularly in aerobic scope. This provides a mechanistic framework that has been used to explain physiological limits underlying species distributions (Pörtner and Knust 2007; Pörtner and Farrell 2008) that can potentially be applied across all marine fauna.

South Georgia is the focus of a number of valuable commercial fisheries including Patagonian toothfish (*Dissostichus eleginoides*), mackerel icefish (*Champsocephalus gunnari*) and Antarctic krill (*Euphausia superba*). The historical over-exploitation of South Georgia's finfish resources, as elsewhere in the Southern Ocean, resulted in dramatic stock crashes in the 1970s and 1980s that have only partially recovered despite the implementation of highly conservative management regimes (Kock 1992; Agnew 2004). Antarctic marine ectotherms are typified by slow growth rates and long generation times, traits which also slows the rate of stock recovery (Denney et al. 2002; Hutchings and Reynolds 2004). The current fisheries are managed using CCAMLR's (Commission for the Conservation of Antarctic Marine Living Resources) ecosystem based fisheries management principles in order to prevent the fisheries having detrimental impacts on the large populations of dependent vertebrate predators in the region.

Antarctic marine fish also show a range of adaptations to life in the constant cold from very low temperature tolerances (Somero and DeVries 1967), elevated mitochondrial densities in fish red muscle (Johnston et al. 1998), antifreeze proteins in their blood (Chen et al. 1997) to the loss of haemoglobin in the blood of some Channicthydae, or icefish, (Verde et al. 2011). However, with an enlarged heart and capillaries, the increased oxygen concentration of the cold waters of the Southern Ocean and low metabolic rate at low temperatures, some fish species including mackerel icefish, are still pelagic predators, feeding predominantly on krill in the water column (Main et al 2009). However, increasing temperature is predicted to rapidly reduce the tissue oxygen partial pressure in icefish (Egginton et al. 2002). Recent studies have demonstrated that the thermal tolerance of icefishes (those lacking haemoglobin) is severely compromised when compared to sympatric, red-blooded notothenioid fishes (Beer and Sidell 2011). Mackerel icefish is at its northern distributional limit at South Georgia and Shag Rocks and the unique adaptations of icefish may lead to the population being extremely sensitive to even a small amount of warming. Indeed, despite a highly conservative management policy the population of mackerel icefish has never recovered to a population size sufficient to support catches at the levels that occurred in the 1980's (Fig. 3).

The impact of rapid warming on mackerel icefish is not restricted to their physiology but has wider ecosystem effects, affecting both food availability and predation pressure. There is considerable oceanographically-driven interannual variability in krill abundance at South Georgia.

Sea surface temperature (SST) anomalies arising in the pacific sector of the Southern Ocean are propagated via the Antarctic Circumpolar Current (ACC) to the Atlantic sector and South Georgia on timescales > 1 year. SST anomalies and related fluctuations in winter sea ice extent affect the recruitment and dispersal of krill (Murphy et al. 2007). Over a longer timescale a reduction in winter sea ice has been linked to a steady reduction in krill numbers (one of the main prey species of icefish) over the last 70 years (Atkinson et al. 2004). At South Georgia there is a clear reduction in krill numbers in warm years (Whitehouse et al. 2008) and this results in an ecosystem shift as their predators switch to other prey (Fig. 4).

In poor krill years mackerel icefish move to a diet of hyperiid amphipods (*Themisto gaudichaudi*) (Main et al. 2009). The Antarctic fur seal (*Arctocephalus gazella*) also switches its diet to consume a higher proportion of *C. gunnari* (Everson et al. 1999). The negative impacts of the warming on *C. gunnari* could, therefore, easily explain the lack of stock recovery to historical levels and suggest that further warming is likely to increase the pressure on this northern range limit population.

In another commercially exploited species, Patagonian toothfish (*Dissostichus eleginoides*) variability in recruitment at South Georgia has also been linked to climatically driven fluctuations in regional SST with peaks in recruitment associated with years in which SST is below average in the period leading up to spawning (Belchier and Collins 2008). It is suggested that increase in SST could have a negative impact on this highly valuable fishery at South Georgia.

Studies of species in the rapidly warming shallow waters around South Georgia, with their complex faunal origins; genetic structure and physiological tolerance provide an ideal “natural laboratory” which has already provided some plausible mechanisms underlying recent fluctuations in species distributions. There is a good prospect that further, similar, studies will be highly valuable in furthering understanding changes at this range limit hotspot.

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Figure Legends

Figure 1. Average summer sea surface temperatures in the South Atlantic, Scotia Sea and Southern Ocean. SSt data compiled from the NASA Aqua satellite for mid-December to mid-March between 2002 and 2012 (Feldman et al. 2012).

Fig. 2. Water masses inhabited by bivalves and gastropods common to the Western Antarctic Peninsula (WAP) and South Georgia (SG). A, The depths of surface Antarctic water (SAW 0-90m), winter water (WW, 90-150m) and circumpolar deep water (CDW, >150m) delimited by the depth of 1°C water at South Georgia, are shown (separated by dashed lines). B, Mean depth distributions of the same species of bivalves (open squares) and gastropods (crosses) found in the three vertical water masses at the WAP and their corresponding mean depth at SG. Example depth temperature profiles from summer CTD casts in Marguerite Bay (15/02/10, Rothera Time Series) on the Western

Antarctic Peninsula (dotted line) and an average profile for South Georgia (solid line; between 11/01/06-29/01/06, Collins et al. 2006). Modified from Morley et al (2010).

Figure 3. Reported catches (dotted line) and estimated stock sizes (solid line) of Mackerel icefish, *Champsocephalus gunnari*, at South Georgia. Data from CCAMLR statistical Bulletin, CCAMLR, Hobart.

Figure 4. Food train relationships involving *Champsocephalus gunnari*, krill and fur seals at South Georgia. Modified from Everson et al. 1999

Tables

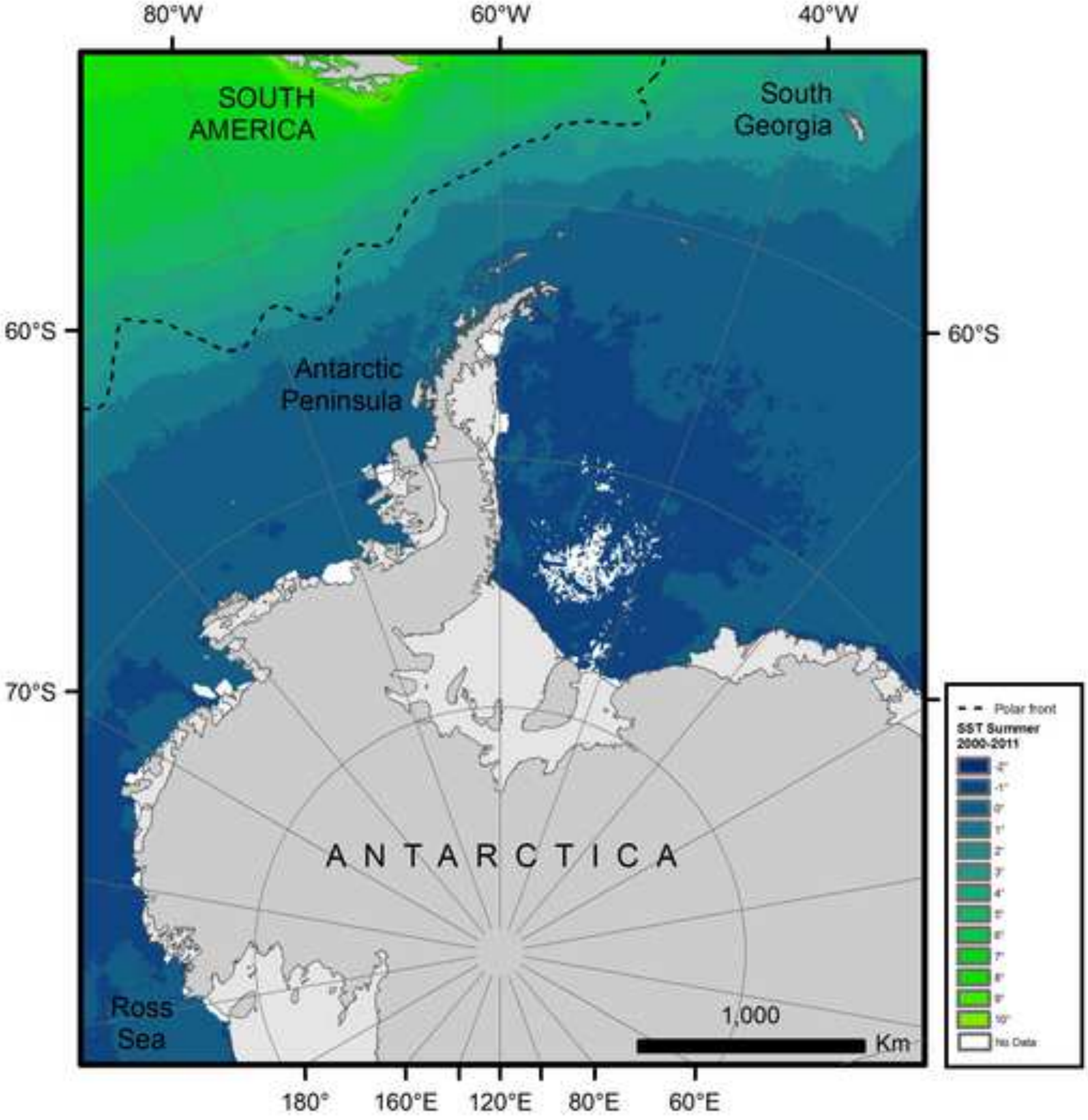
Table 1. Levels of endemism, and the proportion of species occurring at their northern and southern range limits at South Georgia (Hogg et al. 2011).

Phylum	% Endemism	% Northern Limit	% Southern Limit
Bryozoans	55.6	21.3	8.3
Cnidarians	44.2	51.9	3.9
Molluscs	45.9	40.0	13.3
Crustaceans	23.7	29.0	7.2
Chordates	8.5	8.5	12.8
Sponges	2.7	17.6	4.0

Table 2. Mean depths (metres ±1 se) for bivalve and gastropod species that co-occur at both the Western Antarctic Peninsula and South Georgia. Species separated into three groups based on the 1°C isotherm that separates the different water masses found at South Georgia; SAW = surface Antarctic water >90m; WW = winter water 90-150m; CDW = Circumpolar deep water >150m (modified from Morley et al. 2010).

		Western Antarctic Peninsula		South Georgia				
Taxon	Water Mass	Mean Depth (m)	s.e.	Mean Depth (m)	s.e.	T	d.f.	P
Bivalves	SAW	42	7	180	45	1	5	<0.05
	WW	127	14	167	19	0	2	<0.05
	CDW	300	38	164	11	-4	12	<0.01
Gastropods	SAW	22	9	21	4	8	5	NS
	WW	136	5	273	149	-7	3	NS
	CDW	232	24	142	43	-6	6	NS

Figure1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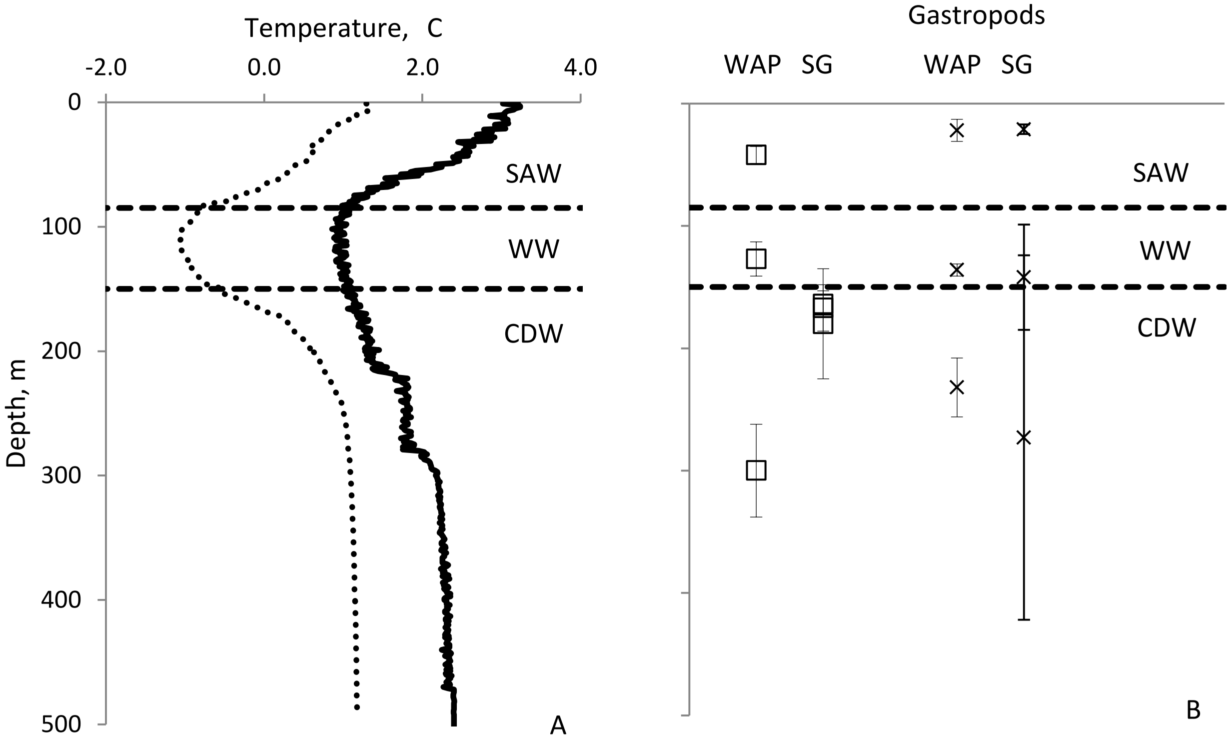
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Figure3

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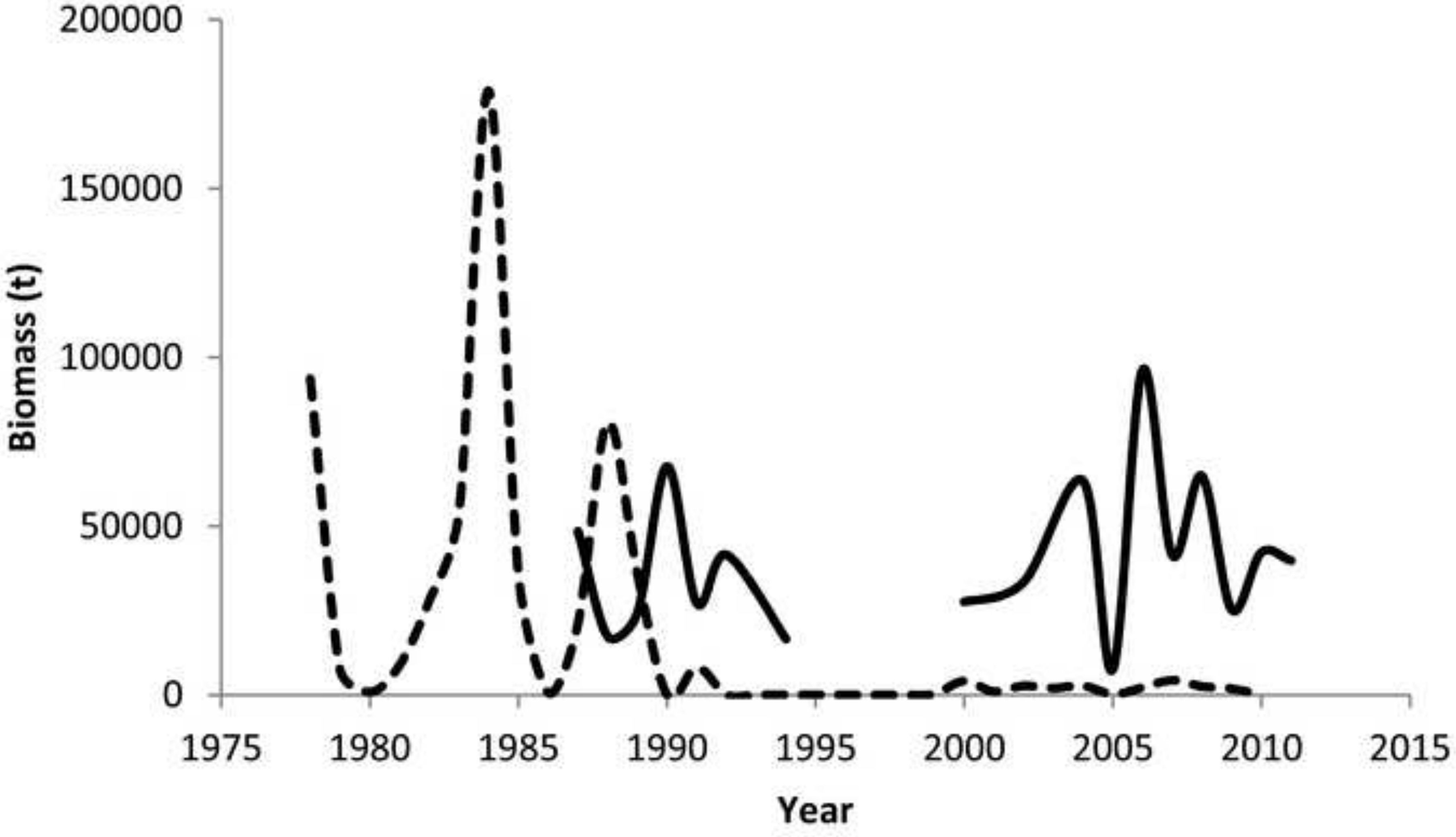

Figure4

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