

[Click here to view linked References](#)

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

3

4 Morley, S.A.\*, Belchier, M., Sands C., Barnes, D.K.A., Peck, L.S.

5

6 British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road,

7 Cambridge, Cambridgeshire, CB30ET. UK.

8

9 \*Corresponding author: [smor@bas.ac.uk](mailto:smor@bas.ac.uk) Tel: 01223 221 554. Fax 012223 221 559

10

11 Abstract

12

13 In order to allocate quotas for sustainable harvests that account for climate warming, it is important  
14 to incorporate species vulnerabilities that will underlie likely changes in population dynamics.

15 Hotspots, regions with rapidly changing climate, are important locations for rapid advances in

16 mechanistic understanding of the factors driving these changes, particularly if they coincide with

17 regions with a high incidence of range limits, such as the sub-Antarctic Island of South Georgia. This

18 archipelago is at the Northern limit of the Southern Ocean and therefore the northern distribution

19 limit for many Southern Ocean shallow water marine species, which are amongst the most sensitive

20 fauna to increasing temperature. At range limits species may either be living close to their

21 physiological limits, or they may have more resistant phenotypes. In case studies, the northern range

22 limit population of the gastropod limpet, *Nacella concinna*, has greater physiological plasticity at

23 South Georgia than those from further south, allowing them to cope better with the warmer and

24 more variable seasonal temperatures. Bivalve species, however, alter their depth distributions at

25 South Georgia, to avoid the warmer water masses, indicating that they may not be able to cope with

26 the warmer temperatures. Mackerel icefish, *Champsocephalus gunnari*, has a unique Antarctic trait,

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

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).

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52           The Western Antarctic Peninsula (WAP) and Scotia Arc region (Fig. 1) are amongst the fastest  
53 warming marine environments (Meredith and King 2005, Hansen et al. 2010). Sea surface  
54 temperatures in the WAP are warming faster than the global average (1°C in 50 years; Meredith and  
55 King 2005) but more importantly, temperature is increasing at a rate which is biologically significant  
56 to the physiology of the resident marine fauna (e.g. Peck 2005; Peck et al. 2009). Situated at the  
57 northern edge of the Southern Ocean, South Georgia is an isolated sub-Antarctic Island with a rich  
58 fauna, which has been isolated for long enough (~45ma; Livermore et al. 2007) to have developed a  
59 high degree of endemism (Hogg et al. 2011). Due to its position in the sub-Antarctic it is potentially  
60 supplied with a mix of larvae and adults from two sources: Antarctica, one of the most stenothermal  
61 faunal assemblages, and from more eurythermal species living in cool temperate regions north of  
62 the polar front. Both these fauna must overcome substantial barriers to reach South Georgia, which  
63 results in South Georgia having many more species at their geographic and physiological limits than  
64 is usual, making it a hotspot in this respect. It therefore presents the ideal location to study the  
65 mechanisms underpinning marine species distributions. In this paper we use the example of South  
66 Georgia to highlight how incorporating the knowledge of physiological sensitivity of species,  
67 populations and individuals, into the management of fish stocks, can increase the robustness of  
68 exploitation models. This will help predict shifting interactions between species (Poloczanska et al.  
69 2008) and improve the ecosystems approach to fisheries management.

## 70 71 South Georgia fauna

72  
73 South Georgia is a range limit hotspot, which, despite its geographic (~1800km) and environmental  
74 (polar front) isolation, has a diverse marine fauna and anomalously high levels of endemic and  
75 range-edge species (Barnes et al. 2009; Hogg et al. 2011; Table 1). The richness of South Georgia  
76 marine fauna has also been linked to its large shelf sea area and the rich nutrients created from  
77 mixing of shelf waters by eddies from the Antarctic circumpolar current (Hogg et al. 2011).

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

78 Whilst the shallow water marine fauna at South Georgia is characteristic of an Antarctic  
79 assemblage (Barnes et al. 2005), with up to 52% of some groups reaching their northern distribution  
80 limit at South Georgia, there are other species for which South Georgia is the southern range limit  
81 (up to 13%; Table 1). Some hints regarding the adaptive potential of the South Georgian marine  
82 assemblage may be found in the physical and evolutionary history of the region. The Scotia Sea has  
83 a complex history spanning 20 - 30 million years (Thomson 2004; Eagles 2010). Prior to this point  
84 the shallow water marine faunas were largely shared between the continental shelves of Antarctica  
85 and South America (Crame 1999). Since then the complex interaction of drift, selection, migration  
86 and extinction has resulted in a highly endemic Antarctic fauna (Dell 1972; Clarke and Johnston  
87 1999).

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

104 diversity of the source population, which, in turn, is largely a function of the effective population size  
105 (Hartl and Clark 1997).

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

119  
120 South Georgia as a physiological limit

121  
122 Studies of environmental variability and its correlation with the physiological plasticity of  
123 species have led to a wide range of hypotheses correlating distributions with physiological  
124 tolerances (Gaston et al. 2009). In particular the magnitude and variability of habitat temperature is  
125 strongly correlated with the tolerance of species and populations. One extreme example of this is  
126 the Southern Ocean, which has the planets coldest and most thermally stable surface waters;  
127 Antarctic ectotherms have subsequently evolved to be amongst the most sensitive to increased  
128 temperature (Peck et al. 2004). However, within the Southern Ocean there are still biologically

129 significant differences in temperature across the latitudinal gradient from McMurdo Sound to South  
1 Georgia. McMurdo Sound is the highest latitude seasonal open water environment at 76°S (Fig.1).  
2  
3  
4  
5 131 Recent studies have shown that despite the very small differences in thermal regime, both  
6  
7 132 invertebrate and fish species from higher Southern Ocean latitudes are less temperature tolerant  
8  
9 133 than those from warmer, lower latitudes (Bilyk and DeVries 2011; Morley et al. 2012).

11 134 South Georgia has the warmest summer and the highest annual variability of surface  
12  
13  
14 135 seawater temperatures within the Southern Ocean and maximum summer temperatures regularly  
15  
16 136 exceed the measured thermal limits for species further south on the WAP, despite many of the same  
17  
18 137 species occurring at South Georgia (Morley et al. 2010). Long term physiological limits for survival of  
19  
20  
21 138 an array of marine ectotherms from Marguerite Bay on the WAP have been measured at between 1  
22  
23 139 and 6°C (Peck et al. 2009), with limits for key behavioural escape responses between 1 and 3°C (Peck  
24  
25 140 et al. 2004), indicating that the summer maximum temperature in the shallow water at South  
26  
27 141 Georgia may be above the temperature tolerance of some of these species. These co-occurring  
28  
29 142 species may need to avoid the warmest water masses or have greater physiological flexibility at  
30  
31 143 South Georgia; both of these strategies have been found at South Georgia (see below).

35 144 The Southern Ocean is not only characterised by a latitudinal temperature gradient but also  
36  
37  
38 145 by a strongly vertically stratified water column with shelf water masses of different temperature  
39  
40 146 (summer temperature depth profiles shown in Fig. 2). The intermediate layer of cold water, the  
41  
42 147 winter water (WW), is formed during winter when strong mixing creates a thick mixed layer with  
43  
44 148 cold temperatures and high salinity. This mixed layer is capped by the surface layer which heats up  
45  
46 149 during the austral summer forming the surface Antarctic water (SAW; Brandon et al. 2004). The  
47  
48 150 water mass below the winter water is the circumpolar deep water (CDW) but the temperature of all  
49  
50 151 three water masses also varies with latitude across the Southern Ocean (Fig. 2), a temperature  
51  
52 152 variation which is of biological significance.

56 153 All co-occurring bivalve species had depth distributions that were shifted at South Georgia  
57  
58  
59 154 (Table 2), compared to those along the WAP. Species with both deeper and shallower distributions

155 on the WAP were all centred within the cooler, intermediate depth, winter water, at South Georgia,  
156 avoiding the warmest surface Antarctic water and the warm upper layer of circumpolar deep water  
157 (Morley et al. 2010), which are potentially beyond the physiological limits of the WAP population  
158 (e.g. Peck et al. 2004, 2009).

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

#### 167 Impacts on fisheries

168  
169 Fisheries catch statistics provide one of the longest records of shifts in species distributions through  
170 time. Recently shifts in distribution have been recorded for many fish stocks, to cooler latitudes  
171 (Perry et al. 2005) and deeper depths (Dulvey et al. 2008). Fish stocks in the North Sea (such as cod,  
172 *Gadus morhua*; Pörtner et al. 2001) and British Columbia's Fraser River (Sockeye salmon,  
173 *Oncorhynchus nerka*; Eliason et al. 2011) have been shown to have different thermal limits that can  
174 be explained by differences in experienced temperature and subsequent physiological differences,  
175 particularly in aerobic scope. This provides a mechanistic framework that has been used to explain  
176 physiological limits underlying species distributions (Pörtner and Knust 2007; Pörtner and Farrell  
177 2008) that can potentially be applied across all marine fauna.

178 South Georgia is the focus of a number of valuable commercial fisheries including  
179 Patagonian toothfish (*Dissostichus eleginoides*), mackerel icefish (*Champsocephalus gunnari*) and  
180 Antarctic krill (*Euphausia superba*). The historical over-exploitation of South Georgia's finfish

181 resources, as elsewhere in the Southern Ocean, resulted in dramatic stock crashes in the 1970s and  
182 1980s that have only partially recovered despite the implementation of highly conservative  
183 management regimes (Kock 1992; Agnew 2004). Antarctic marine ectotherms are typified by slow  
184 growth rates and long generation times, traits which also slows the rate of stock recovery (Denney et  
185 al. 2002; Hutchings and Reynolds 2004). The current fisheries are managed using CCAMLR's  
186 (Commission for the Conservation of Antarctic Marine Living Resources) ecosystem based fisheries  
187 management principles in order to prevent the fisheries having detrimental impacts on the large  
188 populations of dependent vertebrate predators in the region.

189 Antarctic marine fish also show a range of adaptations to life in the constant cold from very  
190 low temperature tolerances (Somero and DeVries 1967), elevated mitochondrial densities in fish red  
191 muscle (Johnston et al. 1998), antifreeze proteins in their blood (Chen et al. 1997) to the loss of  
192 haemoglobin in the blood of some Channichthyidae, or icefish, (Verde et al. 2011). However, with an  
193 enlarged heart and capillaries, the increased oxygen concentration of the cold waters of the  
194 Southern Ocean and low metabolic rate at low temperatures, some fish species including mackerel  
195 icefish, are still pelagic predators, feeding predominantly on krill in the water column (Main et al  
196 2009). However, increasing temperature is predicted to rapidly reduce the tissue oxygen partial  
197 pressure in icefish (Egginton et al. 2002). Recent studies have demonstrated that the thermal  
198 tolerance of icefishes (those lacking haemoglobin) is severely compromised when compared to  
199 sympatric, red-blooded notothenioid fishes (Beer and Sidell 2011). Mackerel icefish is at its northern  
200 distributional limit at South Georgia and Shag Rocks and the unique adaptations of icefish may lead  
201 to the population being extremely sensitive to even a small amount of warming. Indeed, despite a  
202 highly conservative management policy the population of mackerel icefish has never recovered to a  
203 population size sufficient to support catches at the levels that occurred in the 1980's (Fig. 3).

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



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

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

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

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

231  
232 References

233  
1  
2 234 Agnew DJ (2004) Fishing South. The history and management of South Georgia fisheries. St. Albans:  
3  
4 235 Penna Press.  
5  
6  
7 236  
8  
9 237 Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in  
10  
11 238 salps within the Southern Ocean. Nature 432: 100-103.  
12  
13  
14 239  
15  
16 240 Barrett RDH, Schlutter D (2008) Adaptation from standing genetic variation. TREE 23: 38-44.  
17  
18  
19 241  
20  
21 242 Barnes DKA, Linse K, Waller C et al. (2005) Shallow benthic communities of South Georgia Island. Pol  
22  
23 243 Biol 29: 223-228.  
24  
25  
26 244  
27  
28 245 Barnes DKA, Kaiser S, Griffiths HJ, Linse K (2009) Marine, intertidal, freshwater and terrestrial  
29  
30 246 biodiversity of an isolated polar archipelago. J Biogeogr 36: 756–769.  
31  
32  
33 247  
34  
35 248 Beers JM, Sidell BD (2011) Thermal Tolerance of Antarctic Notothenioid Fishes Correlates with Level  
36  
37 249 of Circulating Hemoglobin. Physiol Biochem Zool 84, 353-362.  
38  
39  
40 250  
41  
42 251 Belchier M, Collins MA (2008) Recruitment and body size in relation to temperature in juvenile  
43  
44 252 Patagonian toothfish (*Dissostichus eleginoides*) at South Georgia. Mar Biol 155 (5):493-503.  
45  
46 253 doi:10.1007/s00227-008-1047-3  
47  
48  
49 254  
50  
51 255 Bilyk KT, DeVries AL (2011). Heat tolerance and its plasticity in Antarctic fishes. Comp Biochem  
52  
53 256 Physiol A 158:382-290  
54  
55  
56 257  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

258 Brandon MA, Naganobu M, Demer DA, et al. (2004) Physical oceanography in the Scotia Sea during  
259 the CCAMLR 2000 survey, austral summer 2000. *Deep-Sea Res II*, 51: 1301-1321.  
260  
261 Burrows MT, Schoeman DS, Buckley LB et al. (2011) The pace of shifting climate in marine and  
262 terrestrial ecosystems. *Science* 334. 652-655.  
263  
264 Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated  
265 with high levels of climate warming. *Science* 333: 1024-1026.  
266  
267 Chen L, DeVries AL, Cheng CH (1997). Convergent evolution of antifreeze glycoproteins in Antarctic  
268 notothenioid fish and Arctic cod. *Proc Nat Acad Sci* 94: 3817–22.  
269  
270 Clarke AC, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost  
271 fish. *J Animal Ecol*, 68: 893-905.  
272  
273 Clusella-Trullas S, Blackburn TM, Chown SL (2011) Climatic predictors of temperature performance  
274 curve parameters in ectotherms imply complex responses to climate change. *Am Nat* 177:738-751.  
275  
276 Collins MA, Jones C, Clark J, Fielding S, Slakowski J, North T, Reid W, Watts J (2006). Report of the  
277 South Georgia groundfish survey (Subarea 48.3) in January 2006. SC-CCAMLR-WG-FSA06.51.  
278  
279 Crame JA (1999) An evolutionary perspective on marine faunal connections between southernmost  
280 South America and Antarctica. *Sci Mar* 63: 1-14.  
281  
282 Dell RK, 1972. Antarctic benthos. *Adv Mar Biol* 10: 1–216.

1 283 Denney NH, Jennings S, Reynolds JD (2002) Life-history correlates of maximum population growth  
2 284 rates in marine fishes. Proc Roy Soc B 269: 2229-2237.  
3  
4 285  
5  
6  
7 286 Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts  
8  
9 287 of climate warming on terrestrial ectotherms across latitude. Proc Nat Acad Sci 105: 6668-6672.  
10  
11 288  
12  
13  
14 289 Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR (2008) Climate change and  
15  
16 290 deepening of the North Sea fish assemblage: a biotic indicator of warming seas. J App Ecol 45: 1029-  
17  
18 291 1039.  
19  
20  
21 292  
22  
23 293 Eagles G, 2010. The age and origin of the central Scotia Sea. Geophys J Int 183: 587–600.  
24  
25  
26 294  
27  
28 295 Egginton S, Silbeck C, Hoofd L, Calvo J, Johnston IA (2002) Peripheral oxygen transport in skeletal  
29  
30 296 muscle of Antarctic and sub-Antarctic notothenioid fish. J Exp Biol 205: 769-779.  
31  
32  
33 297  
34  
35  
36 298 Eliason EJ, Clark TD, Hague MJ et al. (2011) Differences in thermal tolerance among sockeye salmon  
37  
38 299 populations. Science 332: 109-112.  
39  
40  
41 300  
42  
43  
44 301 Everson I, Parkes G, Kock KH, Boyd IL (1999) Variation in standing stock of the mackerel icefish  
45  
46 302 *Champscephalus gunnari* at South Georgia. J Applied Ecol 36: 591-603.  
47  
48  
49 303  
50  
51  
52 304 Feldman GC, McClain CR (2012) Ocean Color Web, MODIS Reprocessing 2012, NASA Goddard Space  
53  
54 305 Flight Center. (ed) Kuring N, Bailey SW <http://oceancolor.gsfc.nasa.gov/>  
55  
56  
57 306  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7 310 Gaston KJ, Chown SL, Calosi P et al. (2009) Macrophysiology: a conceptual reunification. *Am Nat* 174:  
8  
9 311 595–612.  
10  
11  
12 312  
13  
14 313 Hansen J, Ruedy R, Sato M, Lo K (2010) Global surface temperature change. *Rev Geophys* 48:  
15  
16 314 RG4004.  
17  
18  
19 315 Hartl D, Clark AG (1997) *Principles of Population Genetics*. (third ed.) Sinauer Associates, Sunderland.  
20  
21 316  
22  
23  
24 317  
25  
26  
27 318 Helmuth B, Veit RR, Holberton R (1994) Long-distance dispersal of a subantarctic brooding bivalve  
28  
29 319 *Gaimardia trapesina* by kelp-rafting. *Mar Biol* 120: 421–426.  
30  
31 320  
32  
33  
34 321 Hoffman JI, Peck LS, Linse K, Clarke A (2011) Strong population genetic structure in a broadcast-  
35  
36 322 spawning Antarctic marine invertebrate. *J Heredity* 102: 55-66.  
37  
38  
39 323  
40  
41 324  
42  
43  
44 325 Hogg OT, Barnes DKA, Griffiths HJ (2011) Highly diverse, poorly studied and uniquely threatened by  
45  
46 326 climate change: An assessment of marine biodiversity on South Georgia’s continental shelf. *PLoS*  
47  
48 327 *One* 6: e19795  
49  
50  
51 328  
52  
53 329 Hutchings J A, Reynolds JD (2004) Marine fish population collapses: Consequences for recovery and  
54  
55 330 extinction risk. *Bioscience* 54: 297-309.  
56  
57  
58 331  
59  
60 332 Johnston IA, Calvo J, Guderley H, Fernandez D, Palmer L (1998) Latitudinal variation in the  
61  
62 abundance and oxidative capacities of muscle mitochondria in perciform fishes. *J Exp Biol* 201: 1-12.  
63  
64  
65

333  
1  
2 334 Kock, K. H. 1992. Antarctic Fish and Fisheries. Cambridge University Press: Cambridge.  
3  
4  
5 335  
6  
7 336 Lee JE, Janion C, Marais E, van Vuuren BJ, Chown SL (2009) Physiological tolerances account for  
8  
9 337 range limits and abundance in an invasive slug. Proc Roy Soc B 276: 1459-1468.  
10  
11 338  
12  
13  
14 339 Livermore R, Hillenbrand C-D, Meredith M, Eagles G (2007) Drake passage and cenozoic climate: an  
15  
16 340 open and shut case? *Geochem Geophys Geosyst* 8: Q01005.  
17  
18  
19 341  
20  
21 342 Main CE, Collins MA, Mitchell R, Belchier M (2009) Identifying patterns in the diet of mackerel icefish  
22  
23 343 (*Champscephalus gunnari*) at South Georgia using bootstrapped confidence intervals of a dietary  
24  
25 344 index. *Polar Biol* 32 (4):569-581.  
26  
27 345  
28  
29 346 Matschiner M, Hanel R, Salzburger W (2011) On the origin and trigger of the Notothenioid adaptive  
30  
31 347 radiation. *PLoS ONE* 6: e18911.  
32  
33  
34 348  
35  
36  
37 349 Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula  
38  
39 350 during the second half of the 20th century. *Geophys Res Lett* 32: L19604.  
40  
41 351  
42  
43  
44 352 Morley SA, Hirse T, Pörtner HO, Peck LS (2009a). Geographical variation in thermal tolerance within  
45  
46 353 Southern Ocean marine ectotherms. *Comp Biochem Physiol A* 153: 154-161.  
47  
48  
49 354  
50  
51  
52 355 Morley SA, Lurmann GL, Skepper J, Pörtner HO, Peck LS (2009b) Thermal plasticity of mitochondria: a  
53  
54 356 latitudinal comparison between Southern Ocean molluscs. *Comp Biochem Physiol A* 152: 423-430.  
55  
56  
57  
58 357  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

358 Morley SA, Clark MS, Peck LS (2010) Depth gradients in shell morphology correlate with thermal  
359 limits for activity and ice disturbance in Antarctic limpets. *J Exp Mar Biol Ecol* 390: 1-5.  
360  
361 Mukasa SB, Dalziel IWD (1996) Southernmost Andes and South Georgia Island, North Scotia Ridge:  
362 Zircon U-Pb and muscovite <sup>40</sup>Ar/<sup>39</sup>Ar age constraints on tectonic evolution of Southwestern  
363 Gondwanaland. *J S Am Earth Sci* 9: 349–365.  
364  
365 Murphy EJ, Trathan PN, Watkins JL, Reid K, Meredith MP, Forcada J, Thorpe SE, Johnston NM,  
366 Rothery P (2007) Climatically driven fluctuations in Southern Ocean ecosystems. *Proc Roy Soc B* 274,  
367 3057–3067  
368  
369 Nguyen KDT, Morley SA, Lai C-H, Clark MS, Tan KS, Bates A, Peck LS (2011) Upper Temperature Limits  
370 of Tropical Marine Ectotherms: Global Warming Implications. *PLoS ONE* 6: e29340.  
371  
372 Peck LS (2005) Prospects for survival in the Southern Ocean: vulnerability of benthic species to  
373 temperature change. *Ant Sci* 17: 497-507  
374  
375 Peck LS, Webb KE, Bailey DM (2004) Extreme sensitivity of biological function to temperature in  
376 Antarctic species. *Funct Ecol* 18: 625-630  
377  
378 Peck LS, Clark MS, Morley SA, Massey A, Rossetti H (2009) Animal temperature limits and ecological  
379 relevance: effects of size, activity and rates of change. *Funct Ecol* 23: 248-256.  
380

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

381 Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes.  
382 Science 308: 1912-1915  
383  
384 Poloczanska ES, Hawkins SJ, Southward AJ, Burrows MT (2008) Modelling the response of  
385 populations of competing species to climate change. Ecology 89: 3138-3149  
386  
387 Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of  
388 thermal tolerance. Science 315: 95-97  
389  
390 Portner HO, Farrell AP (2008) Physiology and climate change. Science 322: 690-692.  
391  
392 Richard J, Morley SA, Peck LS (2012) Upper temperature limits in temperate marine species: a  
393 macrophysiological view. PloS One. 7: e34655.  
394  
395 Somero GN, DeVries AL (1967) Temperature tolerance of some Antarctic fishes. Science 156: 257-  
396 258.  
397  
398 Spicer JJ, Gaston KJ (1999) Amphipod gigantism dictated by oxygen availability? Eco Lett 2: 397-401.  
399  
400 Stillman JH (2003) Acclimation capacity underlies susceptibility to climate change. Science 301: 65  
401  
402 Thomson MRA (2004) Geological and palaeoenvironmental history of the Scotia Sea region as a basis  
403 for biological interpretation. Deep Sea Res II 51: 1467–1487.



404

1

2

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27

28

29

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

48

49

50

51

52

53

54

55

56

57

58

59

60

61

62

63

64

65

405 Verde C, Giordano D, Russo R, Riccio A, Coppola D, di Prisco G (2011) Adaptations in Antarctic fish:  
406 the oxygen-transport system. *Oecologia Australis* 15: 40-50.

407

408

Whitehouse MJ, Meredith MP, Rothery P, Atkinson A, Ward P, Korb RE (2008) Rapid warming of the  
ocean around South Georgia, Southern Ocean, during the 20th century: forcings, characteristics and  
implications for lower trophic levels. *Deep-Sea Res I* 55: 1218-1228.

411

412 Acknowledgements

413

414 This contribution to the hotspots symposium was funded by the UK Natural Environment Research  
Council's British Antarctic Survey, Adaptations and physiology program.

416

417 Figure Legends

418 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).

421

422 Fig. 2. Water masses inhabited by bivalves and gastropods common to the Western Antarctic

423 Peninsula (WAP) and South Georgia (SG). A, The depths of surface Antarctic water (SAW 0-90m),

424 winter water (WW, 90-150m) and circumpolar deep water (CDW, >150m) delimited by the depth of

425 1°C water at South Georgia, are shown (separated by dashed lines). B, Mean depth distributions of

426 the same species of bivalves (open squares) and gastropods (crosses) found in the three vertical

427 water masses at the WAP and their corresponding mean depth at SG. Example depth temperature

428 profiles from summer CTD casts in Marguerite Bay (15/02/10, Rothera Time Series) on the Western

429 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).

431  
432 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.

435  
436 Figure 4. Food train relationships involving *Champsocephalus gunnari*, krill and fur seals at South  
Georgia. Modified from Everson et al. 1999

#### 438 439 Tables

440  
441 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      | %<br>Endemism | %<br>Northern<br>Limit | %<br>Southern<br>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                    |

444

445 Table 2. Mean depths (metres  $\pm 1$  se) for bivalve and gastropod species that co-occur at both the  
 446 Western Antarctic Peninsula and South Georgia. Species separated into three groups based on the  
 447 1°C isotherm that separates the different water masses found at South Georgia; SAW = surface  
 448 Antarctic water >90m; WW = winter water 90-150m; CDW = Circumpolar deep water >150m  
 449 (modified from Morley et al. 2010).

450

|            |            | 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    |

451

Figure1

[Click here to download high resolution image](#)

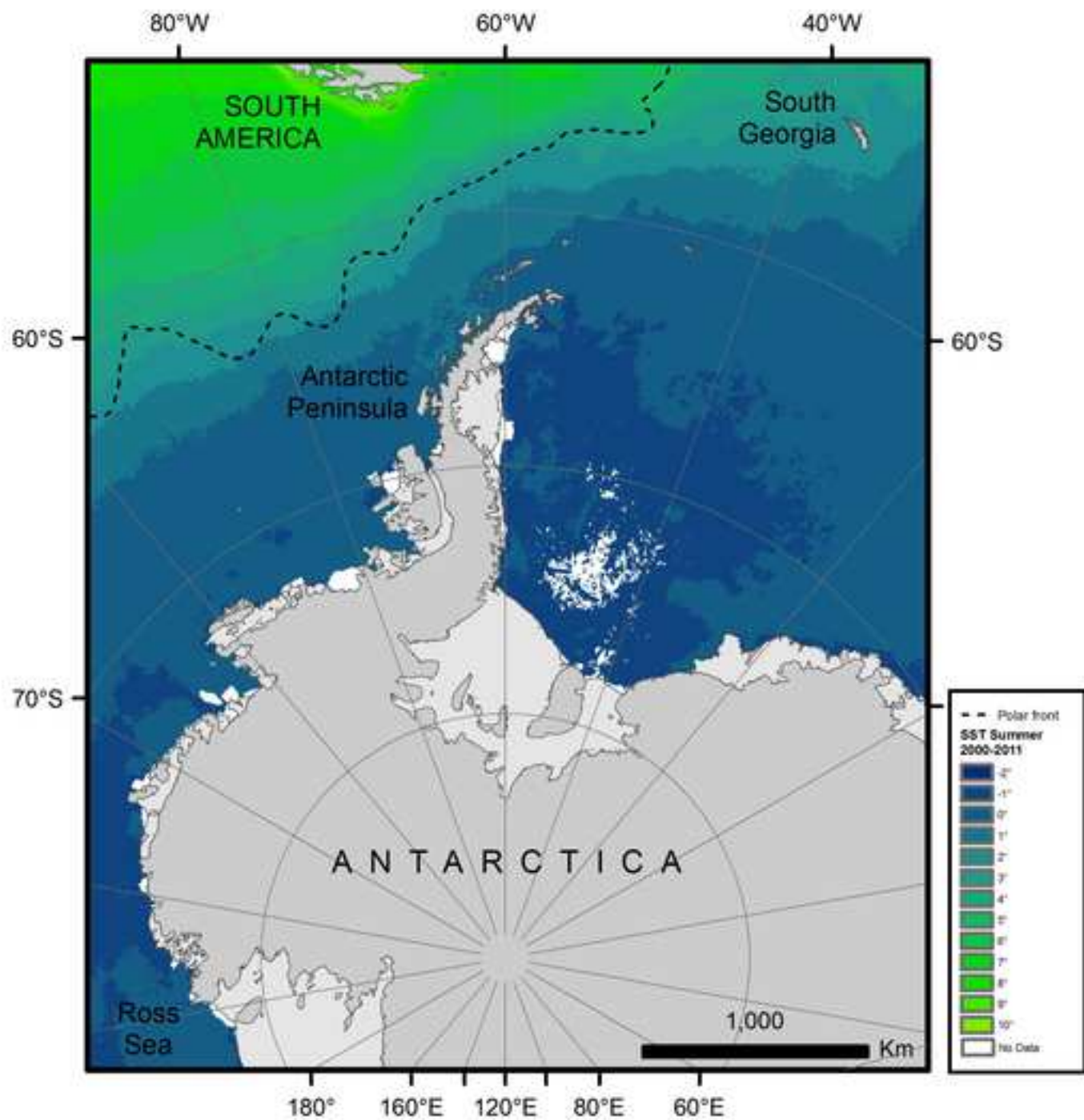


Figure2

[Click here to download Figure: figure2.xls](#)

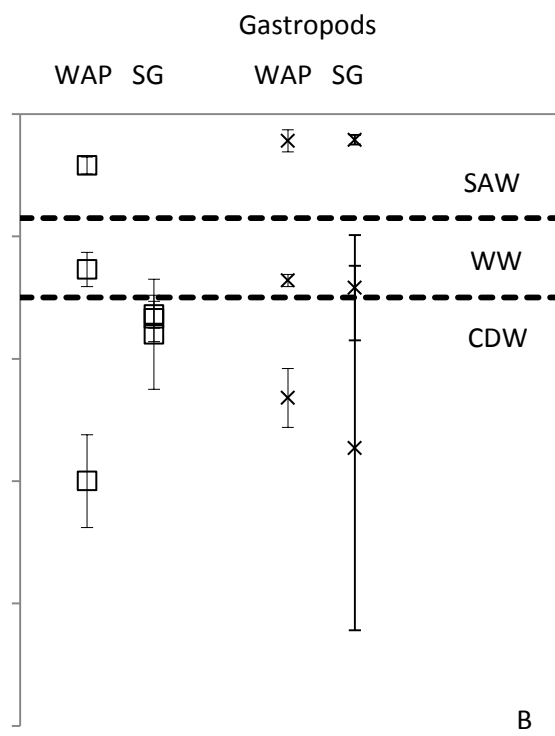
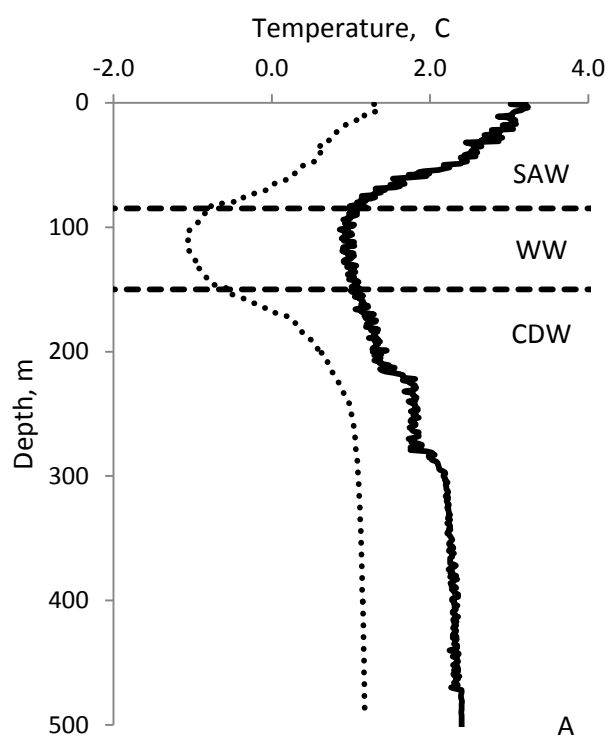


Figure3  
[Click here to download high resolution image](#)

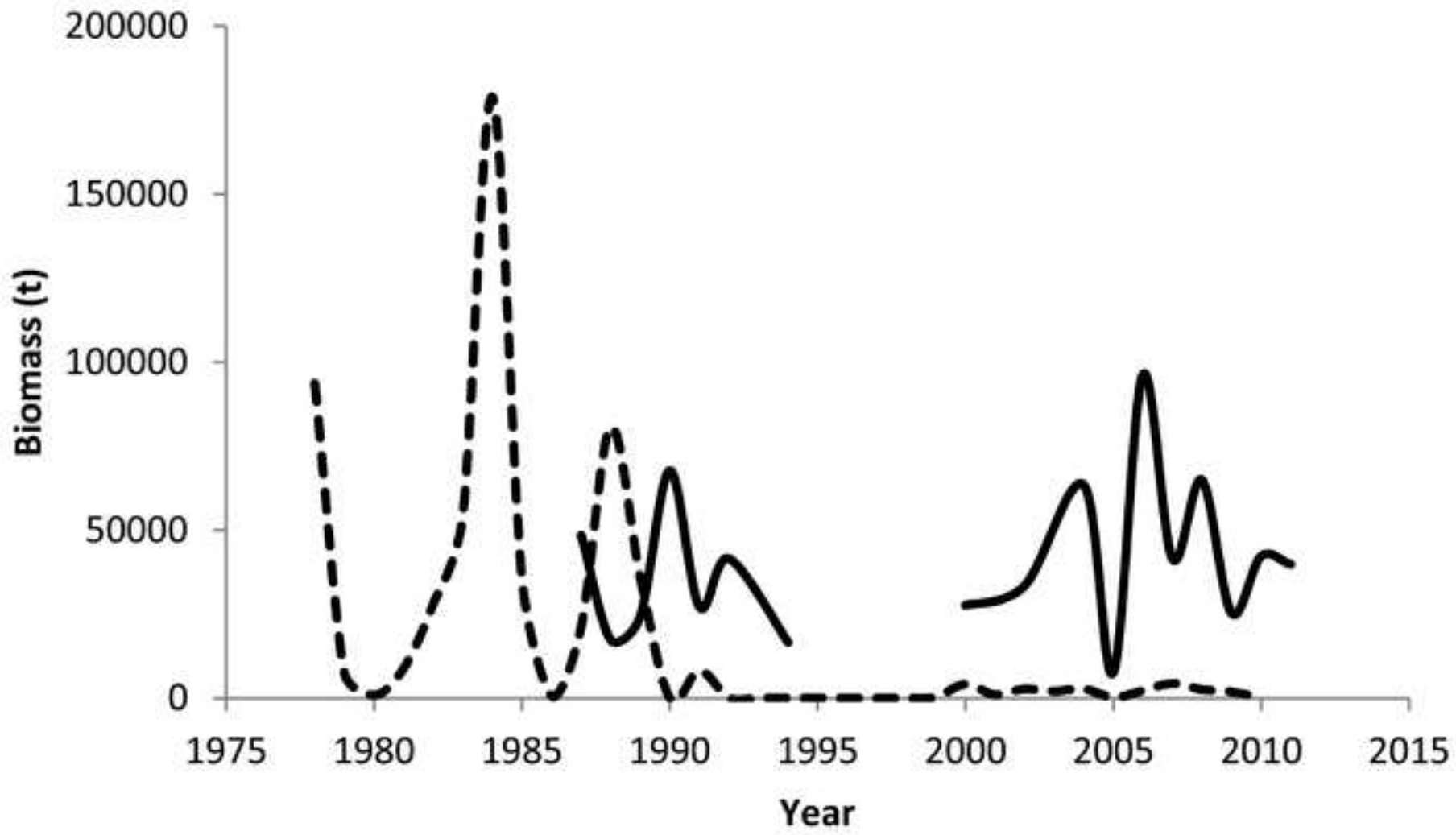


Figure4  
[Click here to download high resolution image](#)

