Spatial distribution of predator/prey interactions in the Scotia Sea: implications for measuring predator/ fisheries overlap.

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Abstract

The measurement of spatial overlap between predators and fisheries exploiting a common prey source is dependent upon the measurement scale used and the use of inappropriate scales may provide misleading results. Previous assessments of the level of overlap between predators and fisheries for Antarctic krill *Euphausia superba* in the South Shetland Islands have used different measurement scales and arrives at contradictory conclusions. At-sea data from observations of krill predators during the CCAMLR 2000 krill survey were used to identify the areas of potential overlap with fisheries in the Scotia Sea and to determine the scale at which such overlap should be measured. The relationship between auto-correlation and sampling distance was used to identify the characteristic scales of the distribution of predators, krill and krill fisheries and an effort-corrected index of relative abundance as a function of distance from land was used to identify the characteristics of areas of high potential for overlap. Despite distinct differences in foraging ecology a group of krill-dependent species including chinstrap penguin *Pygoscelis antarctica*, (Antarctic) fur seal *Arctocephalus* sp. (*gazella*) and white-chinned petrel *Procellaria aequinoctialis* showed similar patterns of distribution; the relative abundances were highest at 60 - 120 and decreased sharply t distances greater than 150 km from land. There was more inter-specific differences in the characteristic scales which were of the order of 50 - 100 km. Antarctic krill had a characteristic scale of c 200 km and the relationship with distance from land showed a log-linear decline. Krill fisheries operated at a scale of 150 km and almost all of this operation took place within 100 km of land. The requirement of land for breeding and the biological and oceanographic conditions that produce high concentrations of krill associated with those islands produce a system in which the demand for Antarctic krill from fisheries and predators is essentially co-extensive. The areas of greatest potential overlap are within 150 - 200 km of land and the extent of any such overlap in these areas should be assessed at scales of 70 - 100 km to accommodate the scales of operation of the predators involved.

Keywords

Antarctic krill Euphausia superba , Fisheries/predator overlap, Auto-correlation, Spatial scale.

Introduction

The measurement of the spatial overlap between predators and their prey in marine systems is highly dependent upon the measurement scale used. The measurements of such interactions at inappropriate spatial scales has the potential to produce unexpected and often misleading results (Rose & Leggett, 1990). In general, the spatial correlation between predators and prey increases with increasing scale of measurement, thus at large measurement scales the spatial correlation may be high whereas at smaller scales it may be low or even negative (Fauchald et al., 2000). Clearly, however, at a very small scales the spatial overlap between predators and their prey must be very high since they must be in the same place at the same time in order that the predator actually captures its prey. It therefore follows that in order to evaluate the extent of spatial overlap between predators and prey, or between fisheries and predators exploiting a common prey source, it is essential to use an appropriate scale of measurement.

Where attempts have been made to assess the potential impact of commercial fisheries for Antarctic krill *Euphausia superba* (hereafter referred to as krill) on krill-dependent predators, by examining the spatial overlap in the region of the South Shetland Islands, the results have generally reflected the differences in measurement scales used. The spatial scales used range from several 100s of km (Croll & Tershy, 1998) to 100 km (Agnew 1992), c 50 km (Agnew and Phegan 1995) to c 20 km (Ichii et al., 1996). At the largest scale Croll and Tershy (1998) concluded that there was a high degree of overlap and high potential for competition, in and contradiction to the conclusions of Ichii et al. (1996) who concluded that there was little overlap. Where the overlap between a fisheries and predators exploiting a common resource is to be measured (and potentially used in a management context) it is clearly essential to define a measurement scale which is appropriate to the processes that determine the distribution of the exploited resource, the predators and fisheries; rather than simply using some geographically convenient scale. This is especially important in the case of the fisheries for Antarctic krill where a single species fishery is operating in an area where the target species is also the dominant prey species of a range of vertebrate predators (Croxall et al., 1988, 1997). In addition, the management system for krill fisheries in the Antarctic has as its central theme the need to maintain ecological relationships and to minimise the impacts on dependent species of fishing for krill (see Constable et al. 2000).

Existing studies of the potential for overlap between predators and krill fisheries have considered only the distribution of predators during the breeding season based on the location of land-based colonies. Although the conditions encountered by adults during the breeding season will undoubtedly be important in their ability to raise offspring to independence, the conditions encountered by other demographic components of the population and at other times of year may be the equally important in determining the long-term survival and hence population sizes. In order to consider the potential overlap between krill fisheries and predators there is a need to consider the foraging distribution of all components of the predator populations, rather than simply the distribution of breeding colonies. By restricting the consideration of overlap to those individuals currently involved in breeding, critical periods for other components of the population may well be overlooked.

Determining the actual foraging distribution of predators has been addressed using satellite telemetry and although this approach is often restricted to a small number of individuals at particular stages of the life-cycle it has shown great utility in highlighting the locations of potential predator/fisheries interactions in this region (Prince et al., 1998). A complement to satellite tracking, that has the potential to provide information on all components of the population of predator species, is direct at-sea observations of predators. These direct observations, mainly for seabirds, have been successfully used to assess the geographical distribution of potential interaction between predators and fisheries (Camphuysen and Garthe 1997). One advantage of direct ship-board observations is the ability to relate the distribution of predators to simultaneous measurement of prey distribution (Hunt et al., 1992, Fauchald et al., 2000). The production of detailed maps of the distribution of predators, which inevitably have a high level of spatial and temporal variability, requires replicate surveys and this is often not compatible or possible within the estimating prey abundance. Producing 'snapshot' maps of species distribution might provide relatively limited information on the distribution of the demand for prey and potential for overlap with fisheries. Therefore, rather than attempt to produce such maps, it may be more appropriate to consider the general patterns of the distribution of predators in order to provide a more general framework in which to consider the processes underlying the distribution of predators and prey .

Analysis of the spatial distribution, using autocorrelation analysis, is frequently used to detect and provide a description of the spatial structure in distributional data (Legendre & Legendre, 1998). Examination of the level of autocorrelation as a function of distance between sampling points can be used to define a characteristic scale or zone of influence of the dominant ecological factor shaping the pattern of distribution. At scales smaller than this 'characteristic scale' the distribution is driven by stochastic processes and hence attempts to measure the overlap will provide misleading results that do not relate to the biological processes underlying the distribution. By examining the scales of distribution of krill, krill predators and krill fisheries it may be possible to determine the characteristic scales of operation (the zone of influence) and to use these to develop biologically appropriate scales at which to evaluate the overlap between krill predators and krill fisheries.

The aim of this paper is to use at-sea observation data on the spatial distribution of krill predators collected during the CCAMLR 2000 krill survey in the Scotia Sea to,

(i) examine the scales of distribution of krill predators in the Scotia Sea,

(ii) assess spatial scales of distribution of krill and the potential for spatial overlap of predators and krill;

and (by using historical data on the distribution of krill fisheries),

(iii) consider approaches to defining areas fo potential overlap between predators and fisherie and to determine the spatial scales at which such overlap should be measured.

Methods

i. Data collection

Predators.

Predator observations were conducted from *RRS James Clark Ross* (20 m above sea-level) during January and February 2000 as part of the CCAMLR 2000 krill survey (for details see Watkins et al. this volume). All birds and mammals recorded on the water in a 300 m transect ahead and to one side of the vessel were recorded during observation periods. In addition to this strip transect all flying birds were sampled using snapshot counts every 5 minutes; for details of the methods for recording predators see Tasker et al. (1984) and White et al. (1999). Observations were conducted as frequently as possible depending on weather conditions (i.e with visibility up to 300 m and winds of Beaufort 6 or less) with the aim of providing uniform coverage over the survey area (Figure 1). The distance from land was estimated for each predator observation as the distance between the observation location and nearest point of land; no attempt was made to estimate distance to the nearest known colony/breeding site. Where the specific identification of individuals at-sea is not practicable the most probable species is given in parentheses in Table 1. This approach avoids artificially dividing individuals of the same species into 2 groups depending on whether they were identified to species level, especially where the most likely alternative species are ecologically very similar (eg prions, diving petrels, fur seals). Contour plots of predator distributions were constructed using a linear spline interpolation of the count data in Matlab (www.mathworks.com). These contour plots are not effort corrected, however, as effort was equal for all species they are appropriate for the comparison of distributions between species.

Krill

The methods for the assessment of krill biomass and distribution are presented in detail by (Trathan et al., 2001) and Hewitt et al. (this volume). Krill fisheries data were taken from the CCAMLR Statistical summaries for Area 48 in the years 1990 to 2000. In this set of data the values for krill catches are presented in 1 degree latitude by 0.5 degree longitude rectangles and the minimum distance between a pair of sampling locations was taken as the distance between the lower left-hand corner of adjacent grid squares.

ii. Spatial structure

Autocorrelation Analysis

To identify the characteristic spatial scales of krill and its predators (Addicott et al., 1987, Deroos et al., 1991) we measured the spatial autocorrelation of ln(x + 1) transformed abundance values using Moran's I statistic (Moran, 1950). Only those observation periods where a species occurred were used in the calculation of Moran's I statistic; inclusion of large numbers of locations with zero abundance would increase the level of autocorrelation between locations where the species did not occur. Correlograms were produced showing Moran's I as a function of distance between sampling locations. A maximum distance was set to 400km for the spatial data on krill and either 50km or 200km for the predator data sets. We used Sturge's rule to determine the number of distance classes following the approach of Legendre & Legendre (1998), with the exception of the krill fisheries data which was already aggregated.

The statistical significance of the Moran's I values was tested using the progressive Bonferroni correction (α=0.05) (Hewitt et al., 1997). A significant Moran's I value indicates significant autocorrelation. Positive autocorrelation suggests that abundance at the sampling locations was more similar than average. Negative autocorrelation indicates these sampling locations have less similar abundance values than average. The scale of spatial pattern, i.e. the characteristic spatial scale, is defined as the point at which the correlogram first crosses the x-axis(denoted by L_0) (Epperson, 1990) or the shortest distance at which the correlogram is not significantly different from zero (and denoted by I_0) (Bjornstad & Falck 2001, Sokal and Wartenburg, 1983). We estimated the characteristic spatial scale using both measures.

Distance from land

For each predator species an index of relative abundance for the *i*th distance class, denoted as RA_i was calculated as

$$RA_i = \ln\left(\frac{(x_i + 1)}{z_i}\right) \qquad \text{Equation 1.}$$

where x_i is the predator count and z_i is the number of observation periods in distance class i. This approach was then extended to the data on krill biomass (using the total biomass and the number of acoustic integration periods in each distance class) and the distribution of the commercial krill fisheries (using the catch and the number of reported catches in each distance class). For the predators and krill, 30 km distance classes were used from 0 - 600 km, whereas to accommodate the different scale at which the data are available the fisheries data, 60km size distance classes were used.

Results

Predators

A total of 4777 predator records (15036 individuals) were made during 208 hours of observations. Ten of the 38 bird species and 1 of the 11 marine mammal species were recorded on more than 100 occasions (Table 1) and there was a positive correlation between the number of records and number of individuals recorded ($r_{47} = 0.94$ $P < 0.001$). The most frequently recorded and most abundant species were (Antarctic) prions *Pachyptila* sp (*desolata*), chinstrap penguins *Pygoscelis antarctica*, Antarctic fulmar *Fulmarus glacialoides* and (Antarctic) fur seals *Arctocephalus* sp.(*gazella*) (Table 1). These four species showed quite different distributions with (Antarctic) prions recorded over the entire survey area with highest concentrations near South Georgia (Fig 2a); in contrast the highest densities of Antarctic fulmar was in the region of the Bransfield Strait (Fig 2b). The the main concentrations of chinstrap penguins were to the north of the South Shetland Islands and the Antarctic Peninsula (Fig 2c) whilst Antarctic fur seals were found in the greatest abundance to the northwest of South Georgia (Fig 2d).

The L_0 values for the 11 most frequently encountered species ranged from 11 km for black-bellied storm petrel to 168 km for white-chinned petrel and fell into 2 groups with Antarctic fulmar, Wilson's and black-bellied storm petrel and macaroni penguin between 37 and 11km and (Antarctic) prions, chinstrap penguins,(Antarctic) fur seals and white-chinned petrels all between 74 and 168 km (Table 2). Both blue petrel and cape petrel showed no significant spatial auto-correlation. The I_0 index produced a smaller range of values (8 - 74 km)and whereas (Antarctic) prions had the same L_0 and I_0 there were substantial reductions in the characteristic scales of (Antarctic) fur seals, white-chinned petrel and chinstrap penguin (Figure 3).

There was a significant negative correlation between RA and distance from land for chinstrap penguins, Antarctic fulmar, Antarctic fur seal and Wilson's storm petrel and a significant positive relationship for blue petrel (Figure 4a). Of the other species macaroni penguin, black-browed albatross and white-chinned petrel all showed a very similar relationship between RA and distance from land with high values up to 100 km and a large reduction at distances greater than 100 km (Fig 4b).

Krill

There was a significant spatial auto-correlation in the krill data and the characteristic scale for the krill biomass over the entire survey area was between 210 km (I_0) and 230 km L_0 (Figure 5). The krill biomass from those areas in which there were predator observations had the same I_0 and L_0 values with characteristic scale of 213 km. There was a significant positive relationship between the abundance of krill and distance from land, the linear form of which suggests an exponential decrease in krill abundance with increasing distance from land (Fig 6).

Fisheries

The L_0 value for the fine-scale catch data was 175 km and there was a very distinct relationship with distance from land which showed a step function since almost all of the fisheries occurred with 100 km of land (Figure 7).

Discussion

The high level of spatial and temporal variability in the distribution of marine predators over an area as large as the Scotia Sea means that using a single survey to produce ‘maps’ of their distribution and hence maps of the distribution of predator impact on krill may not be appropriate. Hence the aim in the approach taken in this analysis was to examine the general patterns and scales of distribution of marine predators in order to provide information not simply on their geographical distribution but to develop a framework within which to consider the spatial scales at which predators, krill and commercial fisheries might interact. The relationship with distance from land provides an indication of where the greatest abundances of predators, krill or fisheries tend to occur and the characteristic spatial scale reveals the extent of the those aggregations.

The form of the decline in covariance with distance reveals important information about the processes that create the spatial structure in biological systems. A system in which the component parts are randomly distributed would generate a ‘flat’ correlogram centred on zero and containing no significant values of Moran’s I. This was the case with blue petrel and cape petrel in this study, two species rarely encountered in large aggregations, in marked contrast to species such as prions and white-chinned petrels which are often found in large single and multi-species flocks (Harrison et al., 1991; Veit, 1988, KR & RW pers obs). The form of the correlogram will also depend on the relationship between the scale of the survey area relative to the characteristic scale of the component parts. However, while biases may arise across a multi-species study, the uniform sampling protocol should mean that comparison between these spatial scales of these species should be relatively robust (Bjornstad & Falck, 2001).

Taking account of the limitations associated with attempting to map large-scale distribution from a single survey it is still possible to gain inferences about the distribution of key predators. For example the largest numbers of Antarctic fur seal and macaroni penguins were recorded in the region of South Georgia, whereas the largest numbers of chinstrap penguins were recorded the area to the north of the South Shetland Islands. Despite the differences in geographical locations the similarity in the characteristic scales and relationship with *RA* and distance from land indicates that the spatial distributions of these species, which are predominantly krill predators (Lishman, 1985; Reid & Arnould, 1996, Croxall et al., 1997) are driven by similar ecological processes.

The relationship between predator abundance and distance from land might be expected to show a log-linear decline assuming a uniform prey distribution. However, since there is an exponential decrease in krill abundance operating over the same spatial scale as the foraging ranges of breeding predators there is likely to be a strong interaction between these two processes.   The interaction of these two non-linear functions has the potential to produce a step function. Such a response is shown by a number of the predator species with the location of the break-point presumably dependent upon the species-specific nature of the response of difference predators to krill abundance. Despite quite distinct differences in their foraging and feeding ecologies (Antarctic) fur seal, chinstrap penguin, black-browed albatross and white-chinned petrel showed similarities in the scales of aggregation and the relationship with distance from land. The similarity in the relationship in scales of operation within this group of krill predators contrasted with that of the more pelagic smaller petrels including (Antarctic) prion, black-bellied storm petrel and especially blue petrel.

There is also evidence from both the krill and predator abundance that the peak demand for krill occurs at some distance from land, indicating that predators are moving rapidly offshore before beginning to forage. The distance from land of these areas is consistent with predators targeting high krill densities associated with oceanographic fronts occurring in shelf-break or shelf slope areas. The general form of the spatial impact of predators as a function of distance from land is very similar to that suggested by the modelling approaches (e.g. Murphy, 1995) in which the greatest krill retention was between 50 - 150 km from land. Although this model did not include Antarctic fur seals the similarity in characteristic scale with other species used in the model suggest that its inclusion would serve to increase the level of krill consumption but not to substantially change the location of that consumption.

The spatial scales of operation of the krill centred ecosystem of the Scotia Sea means that there are high numbers of krill-dependent predators that obtain the vast majority of their krill from a relatively small proportion of the area. A combination of the requirement for land to breed and the oceanographic conditions which produce concentrations of krill biomass mean that the breeding sites for predators tend to be located near areas of particularly high krill abundance. In the absence of such association between breeding sites and prey abundance the overlap of predators and fisheries could be minimised by directing fishing operations away from areas where predators abundances are greatest. However, since predators are restricted to the area within which the highest proportion of krill occurs, and hence this is where the fisheries mainly operate, the spatial structure of the krill centred ecosystem in the Scotia Sea region would appear to predisposed to a high level of spatial overlap between dependent species and krill fisheries.

In the study by Croll & Tershy (1998) the analysis was restricted to the krill demand from breeding adult penguins and Antarctic fur seals, although they recognised the potential importance of the non-breeding components of these populations. Based on the population demographics of the predator species involved there is likely to be a substantial component of the population of most species which are not currently engaged in breeding; either failed breeders or those that are not yet mature enough to breed. This component of the population is not constrained to central place foraging and might be expected to operate in a similar fashion to pelagic predators such as baleen whales. However, it is clear from Reilly et al. (this volume) that the most of the records of baleen whales were recorded at similar distances from land as the majority of the other krill predators, suggesting that much of the krill demand from the non-breeding components of other predators is likely to be similarly spatially distributed.

The results of this analysis indicate that the potential for spatial overlap between predators and fisheries for krill is likely to be concentrated in relatively small areas of the Scotia Sea. It is likely that these areas will be in the vicinity of land-based predator breeding colonies but they are also the areas used by predators that are not restricted in their foraging ranges by the need to return to land-based colonies. That this overlap is so concentrated underlies the importance of using a measurement scale appropriate to the scales of operation of the component processes. We can now appreciate that the approach of Ichii et al (1996), using a scale of less than 20 km to measure the level of overlap between processes where the characteristic scales of the predators involved are of the order of 60 - 70 km, will result in measures of overlap heavily influenced by stochastic processes rather than by the scales of operation of the predators or the fisheries. The model developed by Agnew and Phegan (1995) used a normal density function to describe the distribution of predators foraging from a colony that approximates more closely to the distribution of foraging intensity as a function of distance from land. However, the scale at which the overlap is measured is based upon a geographically convenient unit (1^{o} latitude by $0.5\ ^{o}$ longitude) and this scale, approximately 50 x 50 km, is somewhat smaller than the characteristic scale of chinstrap penguins, the species that has the greatest potential for overlap with fisheries in the South Shetland Islands region.

In addition to defining the area in which there is the greatest potential for overlap between fisheries and predators this analysis has provided an empirical basis upon which to determine the spatial scale at which any such overlap should be assessed. We have reaffirmed the view that key krill-dependent predators and krill fisheries are essentially co-extensive within the Scotia Sea. Furthermore, by using the at-sea distribution data, we have indicated that those krill predators whose foraging ranges are not restricted by breeding location also forage in the same general areas as those involved in breeding; but not necessarily the specific areas that would be identified by the extrapolation of foraging intensity from land-based colonies. Since the vast majority of predator demand for krill, and almost all krill fishing, occurs within150 - 200 km of land this has important implications for management of krill fisheries. Where quantification of the level of spatial overlap between predators and fisheries is to be used in managing krill fisheries it should be assessed at scales of 70-100 km, consistent with the scales of operation of the species involved.

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References

Agnew D.J. (1992) Distribution of krill *Euphausia superba* Dana catches in the South Shetland Islands and South Orkneys. In: Selected Scientific Papers, 1992 (SC-CAMLR-SSP/9). CCAMLR, Hobart Australia. 287-303.

Agnew, D.J. & Phegan, G. (1995) A fine-scale model of the overlap between penguin foraging demands and the krill fishery in the South Shetland Islands and Antarctic Peninsula. CCAMLR Science 2:99-110.

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S., & Soluk, D.A. (1987) Ecological neighbourhoods - scaling environmental patterns. Oikos, 49, 340-346.

Bjornstad, O.N. & Falck, W. (2001) Nonparametric spatial covariance functions: Estimation and testing. Environmental and Ecological Statistics, 8, 53-70.

Camphuysen, C.J. & Garthe, S. (1997) An evaluation of the distribution and scavenging habits of northern fulmars (Fulmarus glacialis) in the North Sea. ICES Journal of Maine Science 54:654-683.

Constable, A. J., W. K. de la Mare, D. J. Agnew, I. Everson, and D. Miller. 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). ICES Journal of Marine Science **57**:778-791.

Croll, D.A. & Tershy, B.R. (1998) Penguins, fur seals, and fishing: prey requirements and potential competition in the South Shetland Islands, Antarctica. Polar Biology, 19, 365-374.

Croxall, J.P., McCann, T.S., Prince, P.A., & Rothery, P. (1988). Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976-1987:

implications for Southern Ocean monitoring studies. In Antarctic Ocean and resources variability (ed D. Sahrhage), pp. 261-285. Springer-Verlag, Berlin.

Croxall, J.P., Prince, P.A., & Reid, K. (1997) Dietary segregation of krill-eating South Georgia seabirds. Journal of Zoology, London, 242, 531-556.

Deroos, A.M., McCauley, E., & Wilson, W.G. (1991) Mobility versus density-limited predator prey dynamics on different spatial scales. Proceedings of the Royal Society of London Series B-Biological Sciences, 246, 117-122.

Epperson, B.K. (1990) Spatial autocorrelation of genotypes under directional selection. Genetics, 124, 757-771.

Fauchald, P., Erikstad, K.E., & Skarsfjord, H. (2000) Scale-dependent predator-prey interactions: The hierarchical spatial distribution of seabirds and prey. Ecology, 81, 773-783.

Harrison, N.M., Whitehouse, M.J., Heinemann, D., Prince, P.A., Hunt, G.L., & Veit, R.R. (1991) Observations of multispecies seabird flocks around South Georgia. The Auk, 108, 801-810.

Hewitt, J.E., Legendre, P., McArdle, B.H., Thrush, S.F., Bellehumeur, C., & Lawrie, S.M. (1997) Identifying relationships between adult and juvenile bivalves at different spatial scales. Journal of Experimental Marine Biology and Ecology, 216, 77-98.

Hunt, G.L., Heinemann, D., & Everson, I. (1992) Distributions and predator-prey interactions of macaroni penguins, Antarctic fur seals, and Antarctic krill near Bird Island, South Georgia. Marine Ecology Progress Series, 86, 15-30.

Ichii, T., Naganobu, M., & Ogishima, T. (1996) Competition between the krill fishery and penguins in the South Shetland Islands. Polar Biology, 16, 63-70.

Legendre, P. & Legendre, I. (1998) Numerical Ecology. Elsevier Science, Amsterdam.

Lishman, G.S. (1985) The food and feeding ecology of Adelie penguins (*Pygoscelis adeliae*) and Chinstrap penguins (*P. antarctica*) at Signy Island, South Orkney Islands. Journal of Zoology, 205, 245-263.

Moran, P.A.P. (1950) Notes on continuous stochastic phenomenon. Biometrika, 27, 17-23.

Murphy, E.J. (1995) Spatial structure of the Southern Ocean ecosystem: predator-prey linkages in Southern Ocean food webs. Journal of Animal Ecology, 64, 333-347.

Prince, P.A., Croxall, J.P., Trathan, P.N., & Wood, A.G. (1997). The pelagic distribution of South Georgia albatrosses and their relationships with fisheries. In Albatross Biology and Conservation (eds G. Robertson & R. Gales), pp. 137-167. Surrey Beatty & Sons, Chipping Norton, Australia.

Reid, K. & Arnould, J.P.Y. (1996) The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. Polar Biology, 16, 105-114.

Rose, G.A. & Leggett, W.C. (1990) The importance of scale to predator-prey spatial correlations: an example of Atlantic fishes. Ecology, 71, 33-43.

Sokal, R.R. & Wartenburg, D.E. (1983) A test for spatial autocorrelation analysis using isolation-by-distance model. Genetics, 105, 219-237.

Tasker, M.L., Jones, P.H., Dixon, T., & Blake, B.F. (1984) Counting seabirds at sea from ships - a review of methods employed and a suggestion for a standardized approach. Auk, 101, 567-577.

Trathan, P.N., Watkins, J.L., Murray, A.W.A., Brierley, A.S., Everson, I., Goss, C., Priddle, J., Reid, K., & Ward, P. (2001) The CCAMLR-2000 Krill Synoptic Survey: A description of the rationale and design. CCAMLR Science, 8, 1-23.

Veit, R.R. (1988) Spatial dispersion patterns of Antarctic seabirds. Dissertation, University of California, Irvine.

White, R.W., Reid, J.B., Black, A.D., & Gillon, K.W. (1999) Seabird and marine mammal dispersion in the waters around the Falklands Islands 1998-1999 JNCC, Peterborough, UK.

Figure Legends

Figure 1. Location of predator observations from the *RRS James Clark Ross.*

Figure 2. Distribution of a. (Antarctic) prions, b. Antarctic fulmar, c. chinstrap penguin and d. (Antarctic) fur seal during the CCAMLR Synoptic survey.

Figure 3. Spatial autocorrelation function for a. (Antarctic) prions, b. Antarctic fulmar, c. chinstrap penguin and d. (Antarctic) fur seal during the CCAMLR Synoptic survey. Open circles indicate Moran's I not significantly different to zero.

Figure 4. Relationship between relative abundance (RA) and distance from land for the most abundance species recorded. The lines are fitted using a locally weighted least squares regression fitted using the Minitab LOWESS routine (Minitab Inc).

Figure 5. Spatial autocorrelation function for Antarctic krill biomass during the CCAMLR Synoptic survey. Open circles indicate Moran's I not significantly different to zero.

Figure 6. Relationship between relative abundance (RA) and distance from land for Antarctic krill biomass. The line is fitted using a locally weighted least squares regression fitted using the Minitab LOWESS routine (Minitab Inc).

Figure 7. Relationship between relative abundance (RA) and distance from land for Antarctic krill fisheries. The line is fitted using a locally weighted least squares regression fitted using the Minitab LOWESS routine (Minitab Inc).

Table 1. Species, number of records (N) and total number of individuals (n) recorded during the CCAMLR 2000 survey from RRS James Clark Ross during routine predator observation periods. See methods for species details of species in parentheses

Species	**N**	**n**
(Antarctic) Prion *Pachyptila* sp. (*desolata*)	1164	5588
Chinstrap Penguin *Pygoscelis antarctica*	523	1906
Antarctic Fulmar *Fulmarus glacialoides*	392	978
(Antarctic) fur seal *Arctocephalus* sp. (*gazella*)	361	1208
Wilson's storm petrel *Oceanites oceanicus*	354	515
Black-bellied Storm-petrel *Fregetta tropica*	323	373
White-chinned Petrel *Procellaria aequinoctislis*	270	437
Nil records	263	-
Black-browed Albatross *Thalassarche melanophris*	158	239
Unidentified Diving-petrel *Pelecanoides* sp.	122	583
Cape Petrel *Daption capense*	111	159
Macaroni Penguin *Eudyptes chrysolophus*	110	579
Blue Petrel *Halobaena caerulea*	107	117
Gentoo Penguin *Pygoscelis papua*	82	271
Soft-plumaged Petrel *Pterodroma mollis*	74	138
Grey-headed Albatross *Thalassarche chrysostoma*	74	89
Kerguelen Petrel *Pterodroma brevirostris*	50	215
King Penguin *Aptenodytes patagonicus*	44	57
Grey-backed Storm-petrel *Garrodia nereis*	43	107
Penguin Sp. *Pygoscelis/Eudyptes* sp	42	76
Snow Petrel *Pagodroma nivea*	34	38
Southern Giant Petrel *Macronectes giganteus*	30	36
Great Shearwater *Puffinus gravis*	24	36
Antarctic Petrel *Pterodroma incerta*	23	32
Magellanic Penguin *Spheniscus magellanicus*	22	77
Imperial Shag *Phalocrocorax atriceps*	21	23
Wandering Albatross *Diomedea exulans*	20	21
Rockhopper/macaroni Penguin *Eudyptes* sp	19	58
Northern Giant Petrel *Macronectes halli*	19	22
Minke Whale *Balaenoptera acutorostrata*	18	25
Hourglass Dolphin *Lagenorynchyus cruciger*	16	47
Sooty Shearwater *Puffinus griseus*	14	814
Giant Petrel sp *Macronectes* sp	12	15
Light-mantled Albatross *Phoebetria palpebrata*	12	13
South Polar Skua *Catharacta maccormicki*	11	11
Brown Skua *Catharacta lonnbergi*	11	11
White-bellied Storm-petrel *Fregetta grallaria*	11	11

Table 1 cont.

	N	**n**
Rockhopper Penguin *Eudytes chrysocome*	9	40
Adelie Penguin *Pygoscelis adelie*	6	17
Humpback Whale *Megaptera novaeangliae*	6	9
Antarctic Tern *Sterna vittata*	6	7
South Georgia Shag *Phalocrocorax georgianus*	5	5
Fin Whale *Balaenoptera physalus*	3	7
Sei Whale *Baleanoptera borealis*	3	4
Southern Right Whale *Eubalaena australis*	3	3
Southern Bottlenose Whale *Hyperoodon*	2	5
Leopard Seal *Hydrurga leptonyx*	2	2
Fairy Prion *Pachyptila turtur*	2	2
Southern Elephant Seal *Mirounga leonina*	2	2
Unidentified seal	2	2
Peale's Dolphin *Lagenorynchyus australis*	1	2
Grey Phalarope *Phalaropus lobatus*	1	1
Catharacta skua sp. *Catharacta* sp.	1	1
Southern Royal Albatross *Diomedea epomophora*	1	1

Table 2. The characteristic spatial scales of krill, krill fisheries and predators obtained form spatial correlograms

Species/ group	n	Maximum dist (km)	Class width (km)	Characteristic scale (km)[a]
Antarctic krill [b]	2454	400	20	230 (210)
Antarctic krill [c]	898	400	24	213 (213)
Fisheries	186	-	60	152 (152)
(Antarctic) prion	879	200	13	74 (74)
chinstrap penguin	309	200	14	82 (63)
Antarctic fulmar	275	200	14	37 (35)
(Antarctic) fur seal	279	200	13	131 (72)
Wilson’s storm petrel	281	200	15	24 (24)
white-chinned petrel	219	200	14	168 (50)
black-bellied storm petrel	303	50	5	11 (11)
black-browed albatross	138	50	5	13 (12)
macaroni penguin	71	50	5	20 (8)
cape petrel	100	50	6	*
blue petrel	101	50	5	*

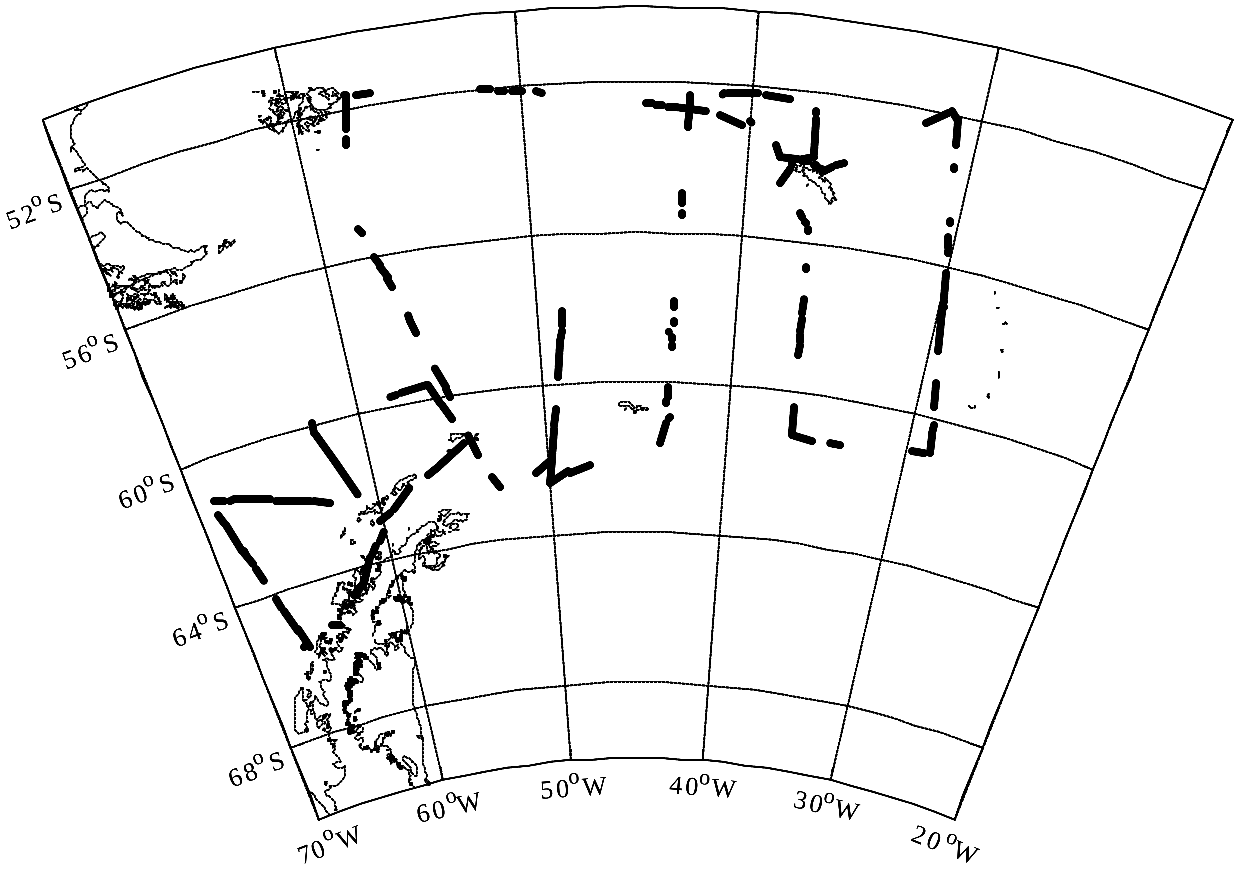
The first column gives the number of sampling locations (n) used in the computations.

[a] The spatial scale defined by Sokal and Wartenberg (1983) and Epperson (1993) with the estimate obtained using the definition from Bjornstad and Falck (2001) given in parenthesis.

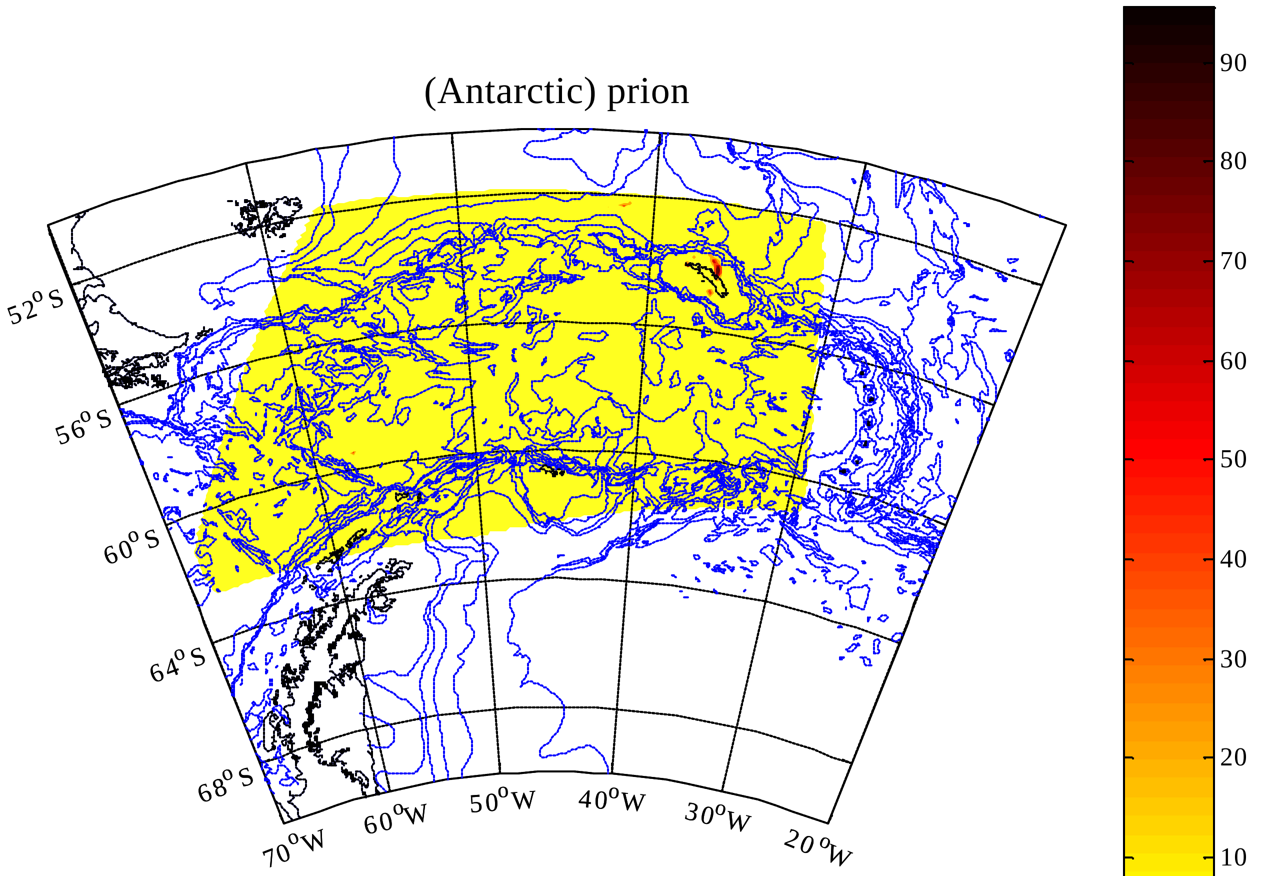
[b] Using all krill sampling locations.

[c] Using only sampling locations where there are records of both krill and predator abundance.

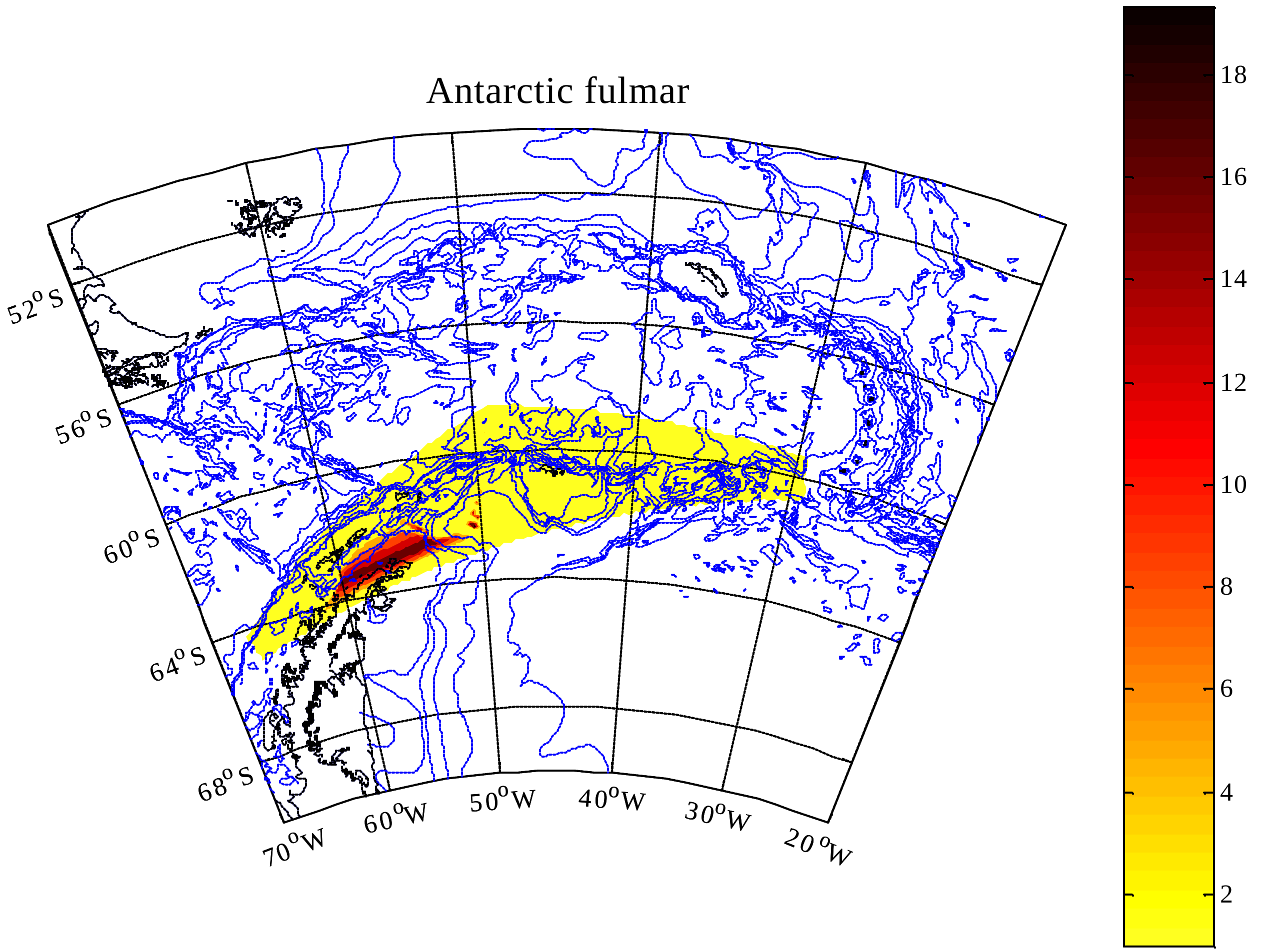
*No distance class showed significant autocorrelation.



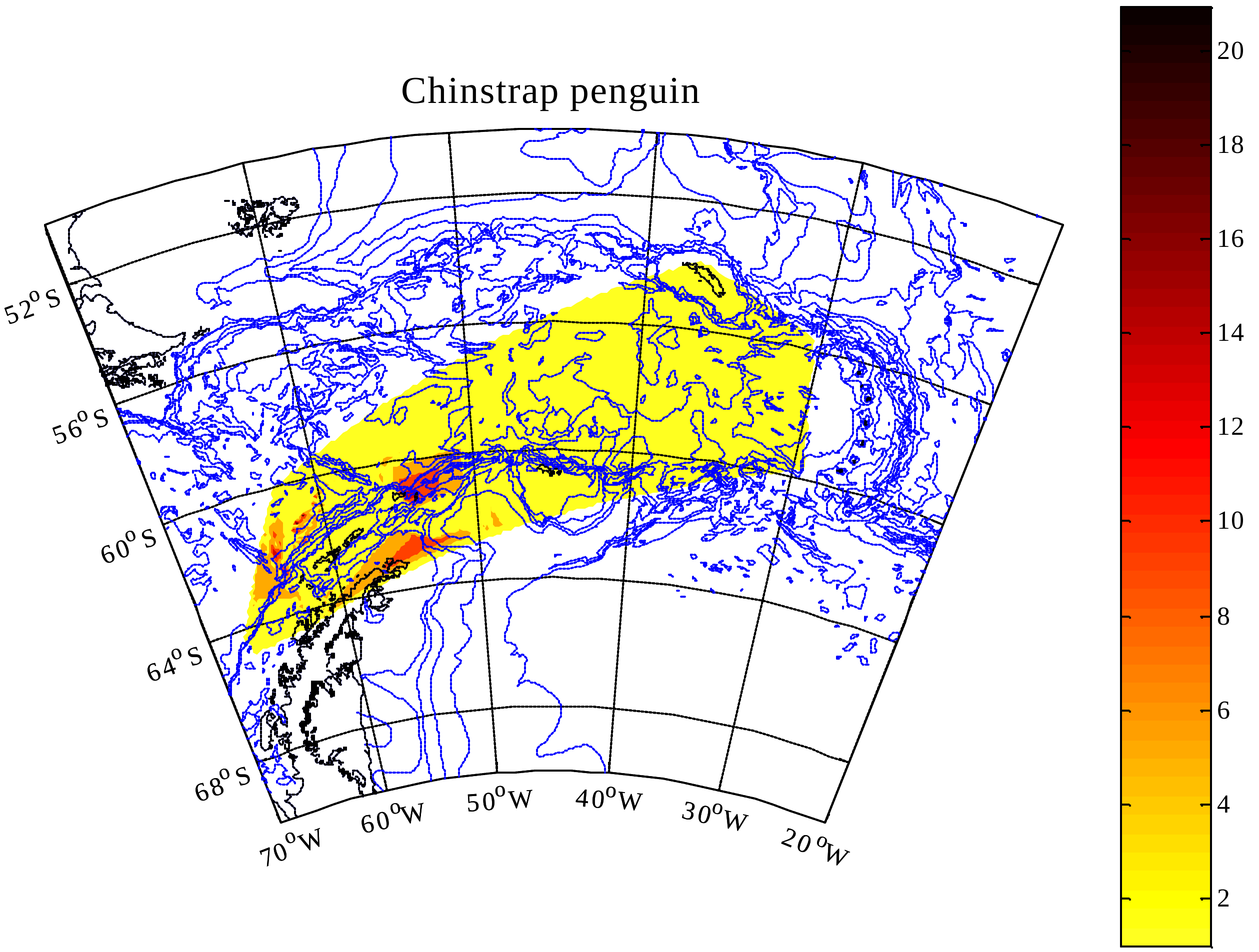
Reid et al. Figure 1



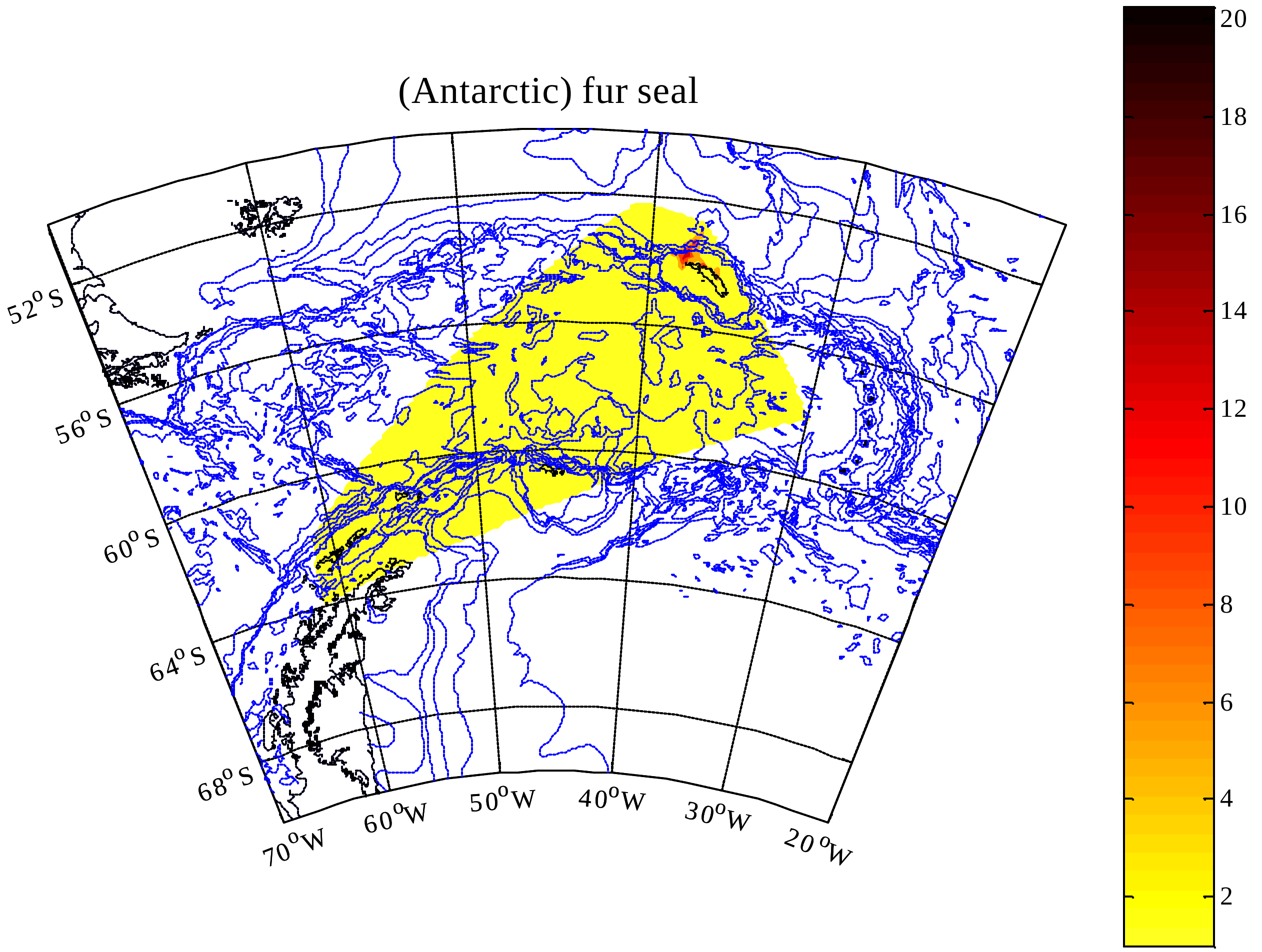
Reid et al. Figure 2a



Reid et al. Figure 2b



Reid et al. Figure 2c



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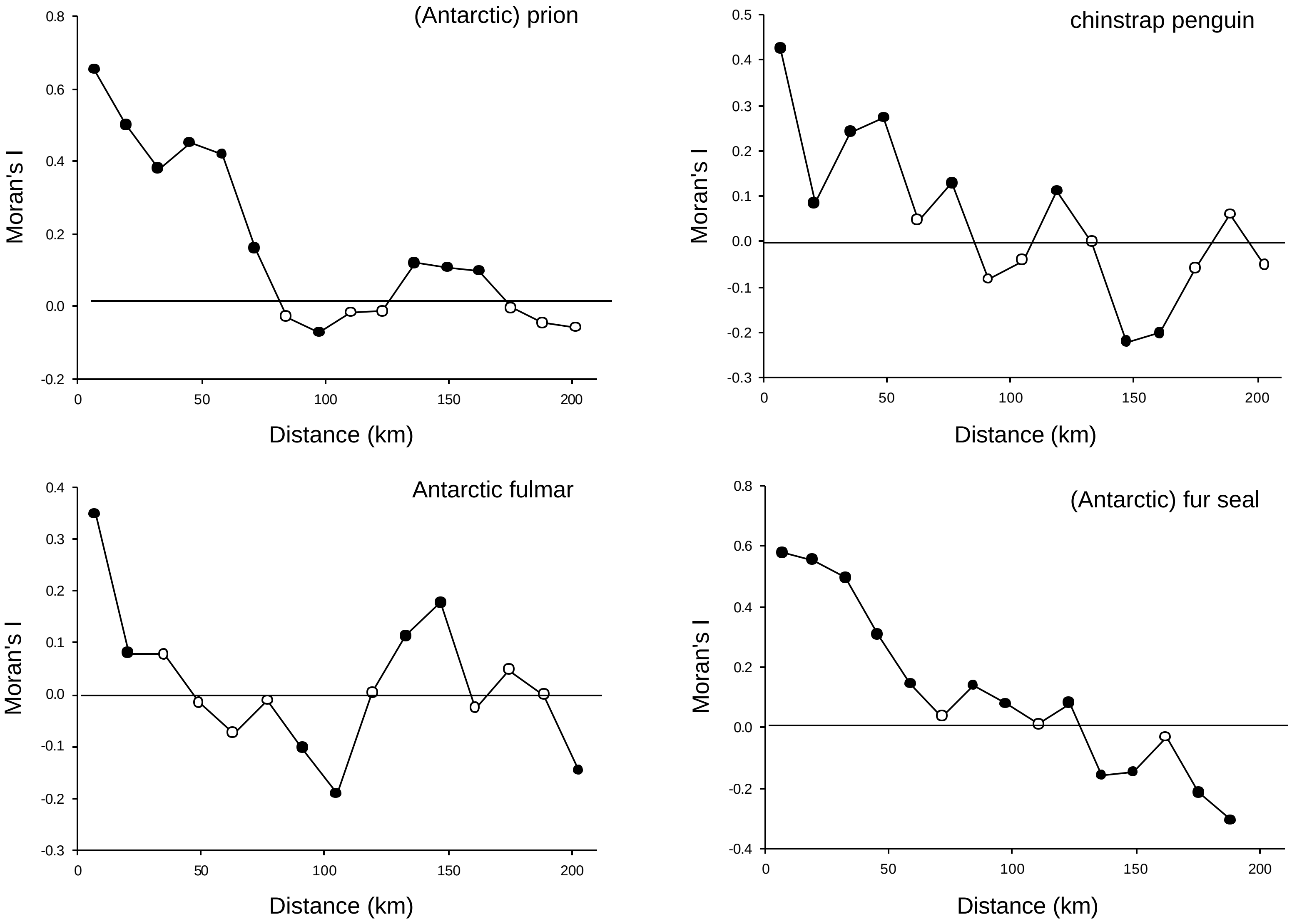
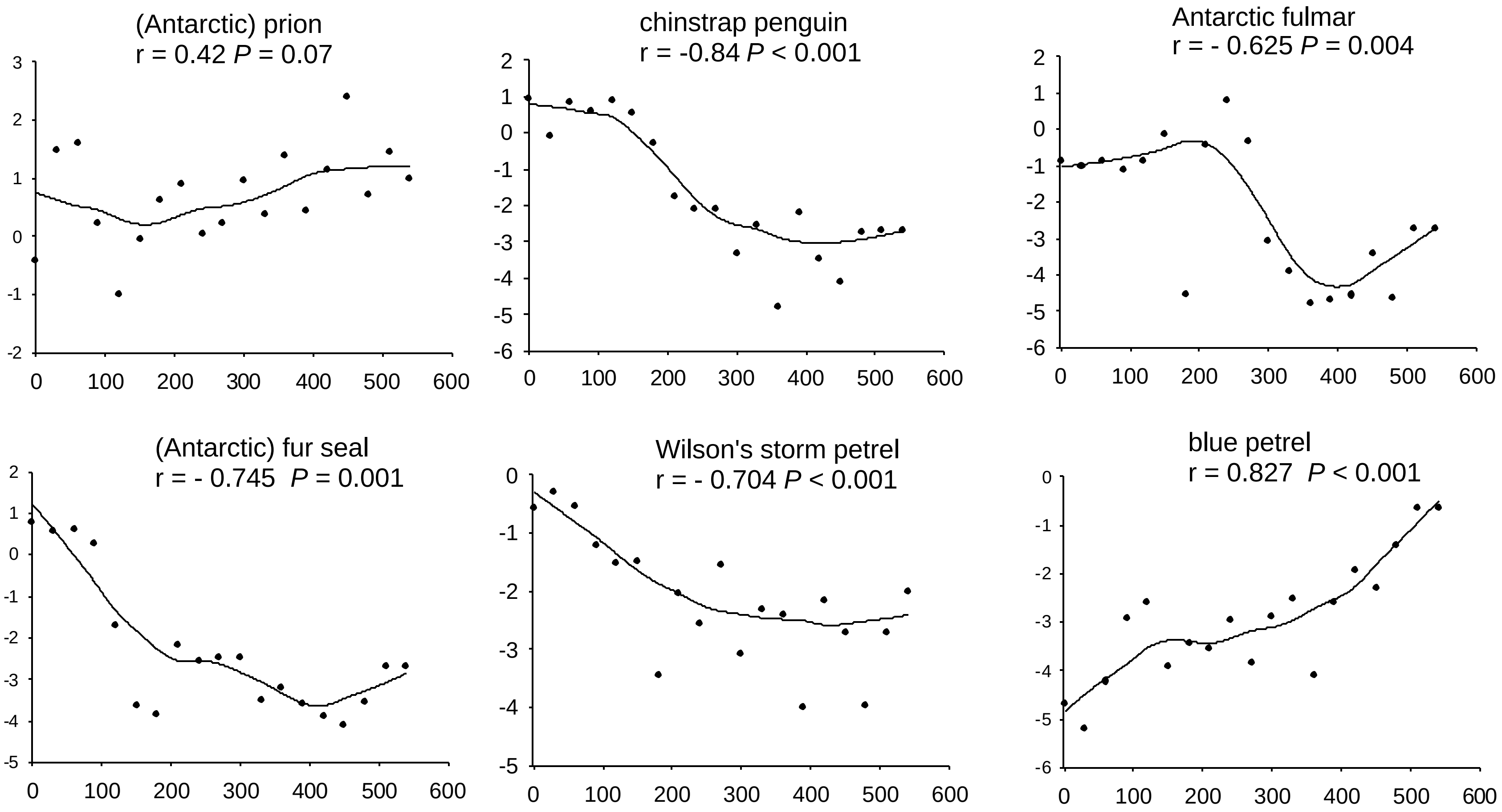
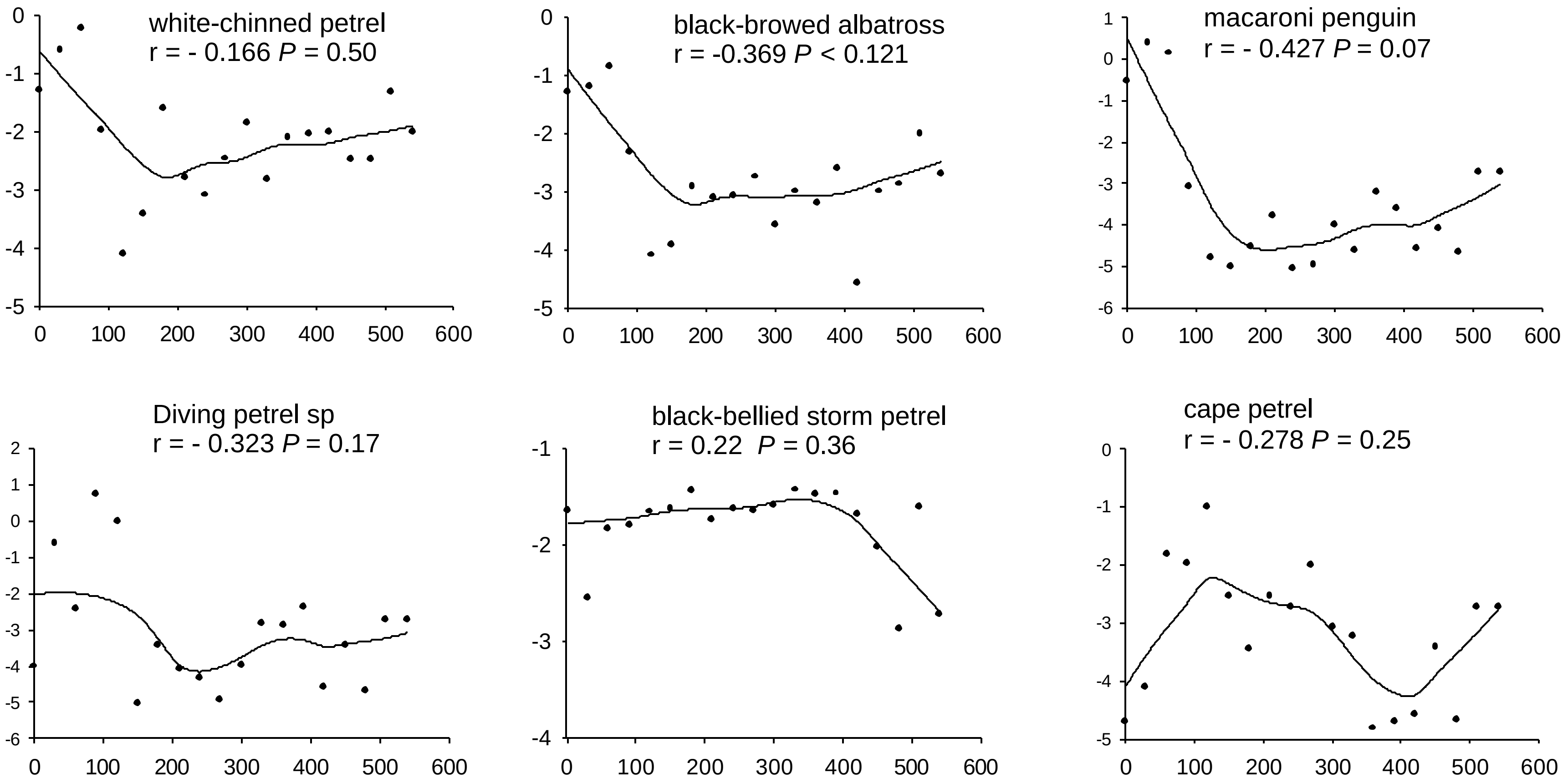


Reid et al. Figure 3



Reid et al. Figure 4a



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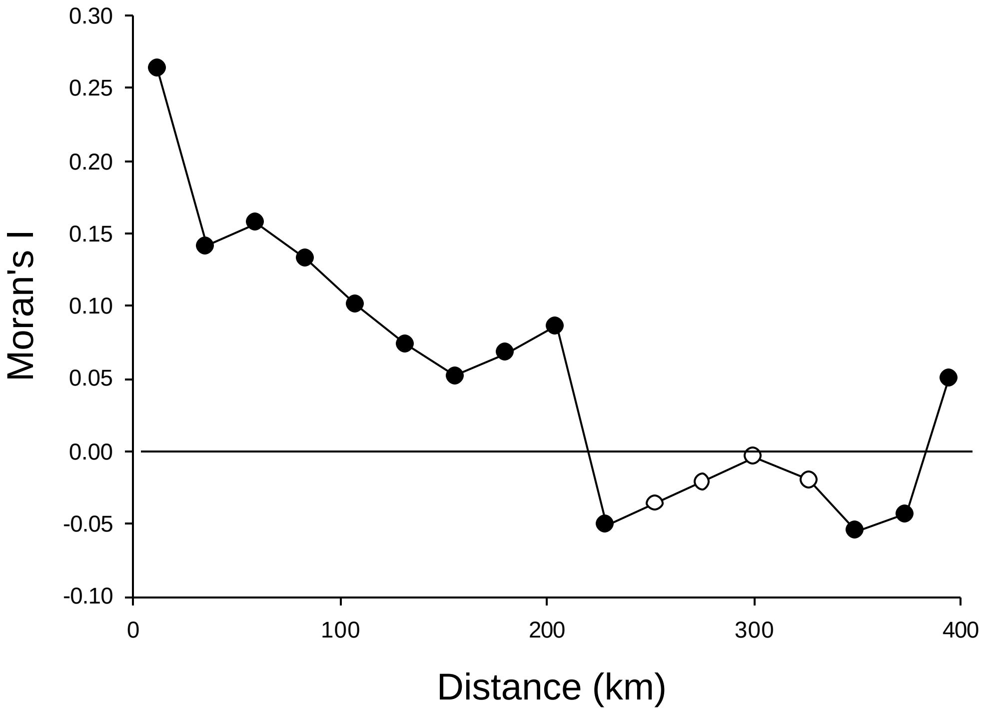
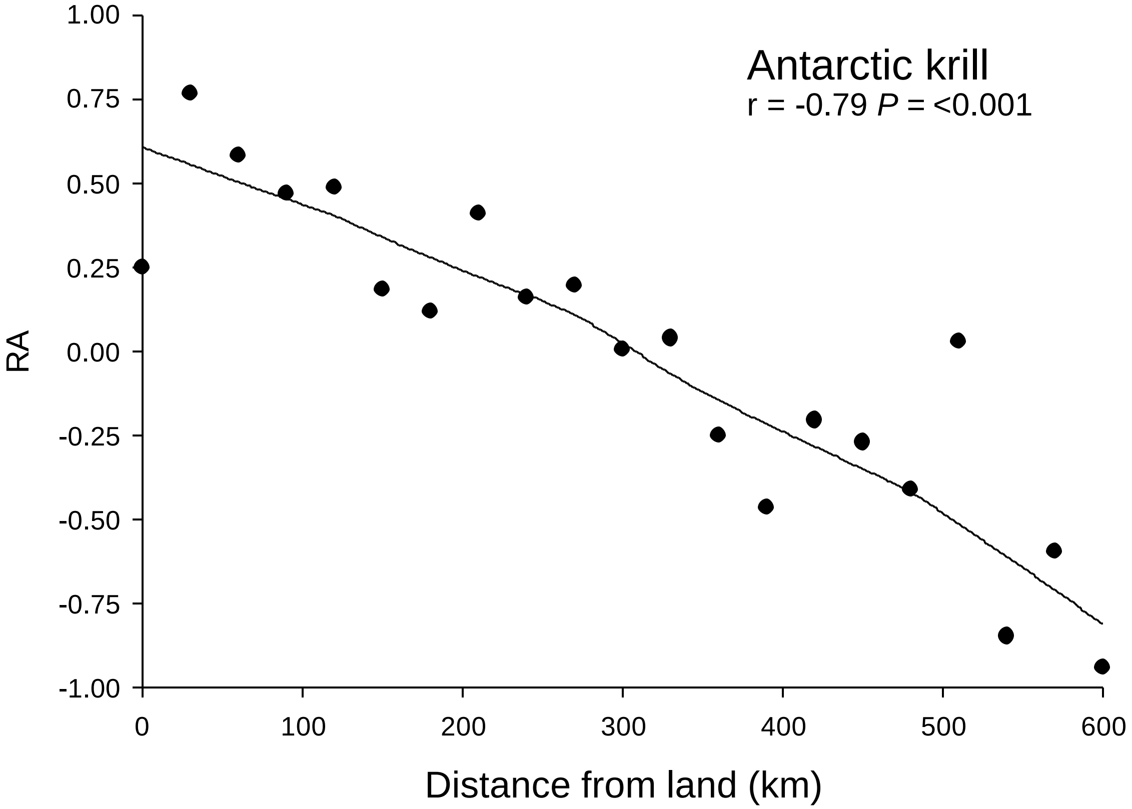
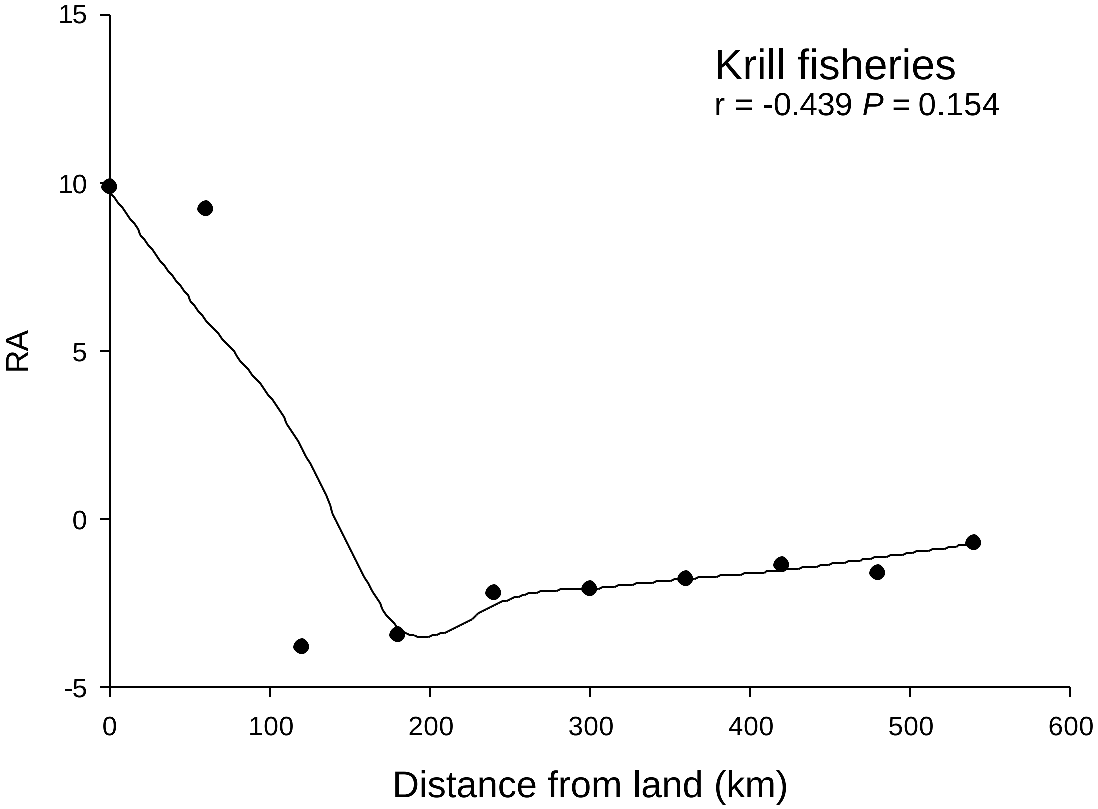


Reid et al. Figure 5



Reid et al. Figure 6



Reid et al. Figure 7