

Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill

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The utility of upper-trophic-level species as ecosystem indicators is determined by our ability to relate changes in indices of their performance to changes at lower trophic levels. Such relationships were assessed using indices of predator performance (response vectors) for four predator species, together with independent ship-based acoustic estimates of abundance of their main prey, Antarctic krill (*Euphausia superba*), from South Georgia in the South Atlantic Ocean. Out of 32 response vectors investigated, 13 showed a significant non-linear relationship, based on a Holling Type II response, to krill abundance, and just five showed a significant linear relationship. Predator responses reflecting the processes during summer, when prey surveys were undertaken, showed the closest relationship with prey abundance. Distinct relationships existed between the variability of indices and the biological processes they measured. Body mass variables had the lowest variability (CVs < 10%), whereas those measuring breeding success showed the greatest variability (CVs > 50%). Multivariate indices, produced by combining response vectors from all four predator species into a single combined index, provided a better fit with krill data than any of the individual vectors. Whereas population size parameters for individual species showed no relationship with annual estimates of krill abundance, a combined, multispecies population size index did show a significant response. Understanding the form of the relationship between concurrent indicators of prey abundance and key ecosystem metrics/reference points, such as population size, is crucial to the application of monitoring data to management action.

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Introduction

The importance of adopting ecosystem-based approaches to fisheries management has been increasingly recognized in the last decade (Garcia and Cochrane, 2005). The inclusion in management procedures of the effects of fishing on the host ecosystem depends on an ability to monitor the exploited ecosystem and to detect such effects. The monitoring objectives may be to assess the performance of management measures that seek to maintain a specified ecosystem condition, based on reference points for key components of the system, or simply to detect any changes in the ecosystem that may result from fishing. For either scenario, ecosystem status needs to be characterized in sufficient detail to provide useful information for management.

The ability to characterize ecosystem status generally relies on describing the status of a limited range of key

species or processes. The choice of these proxies depends upon a range of factors, including their functional or structural importance, their amenability to measurement, and the extent to which they integrate variability at other levels in the ecosystem. In many cases, upper-trophic-level species fulfil these criteria, so indices of their diet, reproductive performance, and population size are frequently chosen as ecosystem indicators on the assumption that they will vary in relation to conditions at lower trophic levels. Seabirds and land-based marine mammals have been used in a range of situations, either as part of formal monitoring schemes or where changes in their reproductive performance have indicated larger-scale ecosystem changes (Ainley *et al.*, 1992, 1995; Vanfraneker, 1992; Bost and LeMaho, 1993; Furness and Greenwood, 1993; Monaghan, 1996; Furness and Camphuysen, 1997; Regehr and Montevecchi, 1997; Reid and Croxall, 2001; Weimerskirch *et al.*, 2003).

In complex ecosystems, the causes of changes at upper trophic levels may be difficult to ascribe. However, ecosystems dominated by a single, mid-trophic-level species at the centre of the foodweb may present a more tractable situation to quantify the response of indicator species. Such an ecosystem exists in the Southern Ocean, where Antarctic krill (*Euphausia superba*) is the major prey resource for a range of top predators, and fluctuations in its abundance are reflected in the reproductive performance and diet of those species (Croxall *et al.*, 1988, 1999).

Antarctic krill is also the target of a commercial fishery, and although exploitation is currently restricted, the fishery has potential for considerable expansion (Nicol and Foster, 2003). The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has adopted an ecosystem-based approach to management, in which the impact of fishing on dependent species is a major consideration (Constable *et al.*, 2000). An important component of this approach is the CCAMLR Ecosystem Monitoring Programme (CEMP), established in 1989 to detect changes, particularly with respect to krill-dependent predators, and to evaluate whether observed changes are due to krill fishing or environmental factors (Agnew, 1997).

The long-term monitoring of population size, diet, and reproductive performance of land-breeding, krill-dependent predators at Bird Island, South Georgia, conducted by the British Antarctic Survey (BAS), was a forerunner to, and then an important component of, CEMP (Croxall and Prince, 1979; Croxall *et al.*, 1988, 1999). In addition, the BAS monitoring programme also includes independent, ship-based acoustic estimates of krill abundance from within the foraging range of those predators.

We use the combined data from the predators and their prey to examine the characteristics of a suite of predator response variables to changes in krill abundance and to select the most appropriate indicators of ecosystem status. To evaluate the utility of these predator responses as indicators, the hypotheses examined are listed below:

- (i) A change in krill abundance produces a predictable change in the value of the predator response.
- (ii) Predator responses are non-linear given the expectation of a functional relationship.
- (iii) Vectors exhibiting the greatest variability are the most sensitive indicators of change in krill abundance.
- (iv) A multivariate index is more sensitive to changes in krill than a single-response vector, assuming a high degree of correlation among response vectors (de la Mare and Constable, 2000).

Methods

For clarity, we refer to the individual time-series of reproductive performance, diet, and population size of

predators as response vectors. Sets of these response vectors were collected at Bird Island between 1973 and 2002 for Antarctic fur seals (*Arctocephalus gazella*), gentoo penguins (*Pygoscelis papua*), macaroni penguins (*Eudyptes chrysolophus*), and black-browed albatrosses *Thalassarche melanophris* (Table 1; for detailed description see Croxall *et al.*, 1988, 1999; Boyd and Murray, 2001; Reid and Croxall, 2001). A logit transformation was applied to all rate vectors, i.e. those expressed as proportions, to obtain approximately normal distributions. In addition, the sign (positive or negative) of predator response values was made consistent across vectors such that, in our opinion, positive values reflected “better” environmental conditions.

Krill density was measured with shipboard acoustics (Brierley *et al.*, 1999). If multiple estimates were available for a given year, the estimate temporally closest to 1 January, and geographically closest to Bird Island, was used (Table 2).

Because response-vector values were expected to increase as a function of krill abundance, their relationship was examined using linear models. However, given the potential for no effect on response vectors beyond a certain level of krill abundance, an asymptotic exponential function (i.e. a Holling Type II functional response) was also fitted.

In considering the most appropriate formulation of a multivariate index, response vectors were grouped by species and by the time scales over which they reflect environmental conditions. Thus, vectors pertaining to conditions prior to the onset of and during the breeding season are referred to as winter and summer vectors, respectively. Population size vectors reflect conditions over a longer time frame and are referred to as multi-year vectors. Response vectors were then aggregated according to these groupings and by species to produce combined standardized indices (CSI; de la Mare and Constable, 2000; Boyd and Murray, 2001).

A least-squares approach was used to fit both linear and non-linear relationships. The strength of the relationship between krill abundance and response vectors, as well as the CSI, was assessed using the r^2 value from regression, the statistical significance of which was determined using the F-statistic from ANOVA.

Results

Linear and Type II functional relationships with krill abundance were significant for five and 13 of the 32 response vectors, respectively (with three in common; Table 3). Hence, further considerations are largely confined to results for non-linear relationships. Of the 20 vectors relating to the summer period, 11 (55%) were significantly correlated with krill abundance (Table 3). In contrast, only two of six vectors relating to the winter period (Table 3), and none of the six multi-year vectors, showed a significant

Table 1. Predator response variables collected at Bird Island, South Georgia, including information on temporal (T – Wi, winter; Su, summer; My, multi-year) and spatial (S; in km) scales and description.

ID	Predator response variable	T	S	Description
Antarctic fur seal				
1	Median pupping date	Wi	1 000	Date before 31 December on which 50% of pups born
2	Pup production	My	1 000	Number born in study colony
3	Male birth mass	Wi	100	Mean mass (kg) of males on day of birth
4	Female birth mass	Wi	100	Mean mass (kg) of females on day of birth
5	Frequency of fish	Su	100	Proportion of scats containing fish (December–March)
6	Pup survival	Su	100	Proportion surviving to end of pupping period
7	Foraging trip duration	Su	100	Mean of first six foraging trips during lactation
8	Male growth deviate	Su	100	Long-term anomaly of mean male pup mass (January–March)
9	Female growth deviate	Su	100	Long-term anomaly of mean female pup mass (January–March)
10	Male weaning mass	Su	100	Mean mass of male pups at 3 months of age
11	Female weaning mass	Su	100	Mean mass of female pups at 3 months of age
Gentoo penguin				
12	Population size	My	100	Number of breeding pairs in study colony
13	Median laying date	Wi	10	Date before 30 November when 50% of eggs were laid
14	Breeding success	Su	10	Proportion of chicks fledged per pair
15	Fledging mass	Su	10	Mean chick mass 90 days after median egg laying date
16	Meal mass	Su	10	Mean stomach contents of adults returning to feed chicks
17	% krill mass	Su	10	Proportion of krill mass in meal mass
Macaroni penguin (FP and GP refer to Fairy Point and Goldcrest Point colonies, respectively)				
18	Population size (FP)	My	1 000	Number of breeding pairs FP
19	Population size (GP)	My	1 000	Number of breeding pairs GP
20	Male arrival mass	Wi	100	Mean mass of males on first arrival in colony
21	Female arrival mass	Wi	100	Mean mass of females on first arrival in colony
22	Breeding success	Su	100	As for gentoo penguin
23	Fledging mass	Su	100	As for gentoo penguin
24	Meal mass	Su	100	As for gentoo penguin
25	% krill mass	Su	100	As for gentoo penguin
Black-browed albatross (H and J refer to colonies)				
26	Population size (H)	My	10 000	Number of breeding pairs H
27	Population size (J)	My	10 000	Number of breeding pairs J
28	Peak mass	Su	100	Mean chick mass 100 days after mean hatching date
29	Hatching success (H)	Su	1 000	Proportion of chicks hatched per egg laid H
30	Fledging success (H)	Su	100	Proportion of chicks fledged per chick hatched H
31	Breeding success (H)	Su	100	Proportion of chicks fledged per egg laid H
32	Breeding success (J)	Su	100	Proportion of chicks fledged per egg laid J

relationship (Table 3). The mean r^2 values differed significantly among the three temporal groups (ANOVA $F_{(2,28)} = 3.8$; $p = 0.04$), those for summer vectors being highest (Table 4). Among species, differences were not significant (ANOVA $F_{(3,28)} = 1.5$; $p = 0.24$).

Mean CV for individual response vectors was 28.7% (range 2.6–72.4%), but marked contrasts existed among different types of parameters: eight of nine vectors with a CV < 10% were measures of body mass, whereas vectors measuring breeding success showed the greatest variability, with four of six having a CV > 50% (Figure 1). There was no relationship between sensitivity to krill abundance (as

measured by r^2) and the level of variability (as measured by CV) either for the total data set ($r_{30} = -0.01$; $p = 0.96$), or for summer response vectors only ($r_{18} = -0.17$; $p = 0.50$).

Values of r^2 for CSI by temporal group and by species were always higher than the means of individual relationships for the component response vectors in each CSI (Table 5). The relationship between CSI and krill abundance showed significant linear (with the exception of black-browed albatross and multi-year indices) and non-linear relationships for summer response vectors. With the exception of winter CSI, r^2 for the non-linear relationship was greater than that for the corresponding linear model

Table 2. Estimates of krill density at South Georgia, 1981–2002 (classification of location follows Brierley *et al.*, 1999, with West being closest to Bird Island).

Year	Location	Time	Density (g m ⁻²)	Reference
1981	North	25 February–7 March	59.7	Brierley <i>et al.</i> (1999)
1982	All	24 November–19 December	11.7	Brierley <i>et al.</i> (1999)
1986	West	6–12 December	29.7	Brierley <i>et al.</i> (1999)
1990	West	5–18 January	45.1	Brierley <i>et al.</i> (1999)
1991	North	19 January	6.4	Brierley <i>et al.</i> (1999)
1992	All	8–27 January	95.0	Brierley <i>et al.</i> (1999)
1993	North	6–7 January	65.8	Brierley <i>et al.</i> (1999)
1994	West	9–10 January	7.4	Brierley <i>et al.</i> (1999)
1996	West	18–22 January	26.7	Brierley <i>et al.</i> (1999)
1997	West	29 December–2 January	25.2	Brierley <i>et al.</i> (1999)
1998	West	24–28 December	21.4	Brierley <i>et al.</i> (1999)
1999	West	2–6 January	12.0	BAS, unpublished data
2000	West	5–8 January	12.3	BAS/AtlantNIRO, unpublished data
2001	West	2–5 January	34.7	Brierley <i>et al.</i> (2002)
2002	West	13–27 January	59.7	BAS, unpublished data

(Table 5). The highest values of r^2 were obtained for the non-linear relationship between krill and Antarctic fur seal ($r^2 = 0.61$), and for summer vectors ($r^2 = 0.60$).

The relationship between krill and the CSI based on all response vectors (species and time scales) that were individually correlated with krill had a lower r^2 than did the summer CSI ($r^2 = 0.54$). Similarly, the summer CSI had a greater r^2 than a CSI that included only those summer vectors that were individually correlated with krill ($r^2 = 0.49$). Inspection of the covariance matrix (Table 6) for the summer response vectors indicates that >70% of vector pairs were positively correlated, 50% having a correlation coefficient $r > 0.3$ (i.e. were at least moderately correlated, following de la Mare and Constable, 2000).

Discussion

To have confidence in an ecosystem-monitoring programme, any results should broadly reflect knowledge of the underlying biological processes. Because our choice of parameters was based on the expectation of a particular response to changes in Antarctic krill abundance, it is important to assess how well the suite of indicators selected met those expectations. More than 50% of the response vectors chosen showed a response to changes in the abundance of krill. When grouped by species, response vectors for Antarctic fur seals and gentoo penguins showed a similar fit to the krill data, which was higher than for macaroni penguins, while the fit for black-browed albatrosses was lowest. This accords with biological understanding, particularly in respect of trophic and spatial dynamics. The diets of Antarctic fur seals and gentoo

penguins are dominated by krill and krill-eating fish (Williams, 1991; Reid, 1995; Reid and Arnould, 1996; Croxall *et al.*, 1997). In contrast, macaroni penguins are capable of changing prey to small zooplankton and maintaining a fairly consistent level of breeding success in periods when krill abundance is low (Croxall *et al.*, 1997, 1999). Black-browed albatrosses have a much greater foraging range than penguins and seals (Prince *et al.*, 1997; Barlow *et al.*, 2002), and a consistently lower proportion of krill in their diet (Reid *et al.*, 1996; Xavier *et al.*, 2003). Grouping the response vectors according to the temporal scales over which they operate identified the summer variables as best fitting the krill abundance data; this is perhaps not surprising, because all krill surveys were made during summer.

There was at least one response vector for each species that did not appear to fulfil the expectation of a positive relationship with krill abundance during summer (Table 3). Two are measures of offspring mass at or near independence (for gentoo penguins and black-browed albatrosses), that may have been confounded by differential offspring survival, which puts limits on the size range of individuals available for sampling (Williams and Croxall, 1990; Gray *et al.*, 2003). There was no relationship between krill abundance and the frequency of occurrence of fish (the main alternative prey) in the diet of Antarctic fur seals. This, however, may be a reflection of the relative insensitivity of frequency of occurrence as an indicator of dietary change (because the occurrence of a single fish in a sample is of equivalent value to a diet solely of fish). The difference in sensitivities of qualitative and quantitative diet measures is emphasized by the much better relationship between krill abundance and the proportion of krill by mass in the diet of both penguin species. Unfortunately, it is

Table 3. Relationship between response vector and krill abundance according to temporal grouping (* = significant; n.s. = not significant).

ID	n	Linear			Holling Type II		
		r ²	F	p	r ²	F	p
Summer							
5	11	0.38	5.6	*	0.18	1.9	n.s.
6	15	0.18	2.9	n.s.	0.11	1.6	n.s.
7	15	0.12	1.7	n.s.	0.48	12.1	*
8	12	0.26	3.6	n.s.	0.51	10.5	*
9	12	0.27	3.8	n.s.	0.50	10.1	*
10	14	0.23	3.6	n.s.	0.40	8.1	*
11	14	0.05	0.6	n.s.	0.57	15.9	*
14	14	0.29	4.8	*	0.00	0.0	n.s.
15	12	0.26	3.5	n.s.	0.32	4.7	
16	13	0.07	0.9	n.s.	0.31	4.9	*
17	13	0.20	2.7	n.s.	0.40	7.3	*
22	15	0.00	0.0	n.s.	0.05	0.7	n.s.
23	12	0.34	5.1	*	0.42	7.2	*
24	13	0.23	3.3	n.s.	0.34	5.8	*
25	13	0.22	3.1	n.s.	0.46	9.3	*
28	13	0.00	0.0	n.s.	0.00	0.0	n.s.
29	15	0.13	2.0	n.s.	0.00	0.0	n.s.
30	15	0.03	0.5	n.s.	0.20	3.2	n.s.
31	15	0.10	1.4	n.s.	0.46	11.2	*
32	12	0.04	0.4	n.s.	0.06	0.6	n.s.
Winter							
1	13	0.01	0.1	n.s.	0.00	0.0	n.s.
3	13	0.31	4.9	*	0.00	0.0	n.s.
4	13	0.48	10.0	*	0.33	5.4	*
13	13	0.06	0.7	n.s.	0.31	4.9	*
20	12	0.30	4.2	n.s.	0.32	4.6	n.s.
21	12	0.05	0.5	n.s.	0.00	0.0	n.s.
Multi-year							
2	15	0.13	1.9	n.s.	0.17	2.6	n.s.
12	14	0.23	3.6	n.s.	0.13	1.8	n.s.
18	15	0.02	0.3	n.s.	0.00	0.0	n.s.
19	15	0.07	1.0	n.s.	0.00	0.1	n.s.
27	12	0.02	0.2	n.s.	0.00	0.0	n.s.
2	15	0.13	1.9	n.s.	0.17	2.6	n.s.

unrealistic to try to use analogous sampling methods for Antarctic fur seals (stomach lavage), to obtain routine quantitative estimates of krill in their diet as part of a monitoring programme.

The lack of a relationship between krill abundance and breeding success of both penguin species, or Antarctic fur seal pup survival (the closest analogue to penguin breeding success), presents a good example of the potential for interaction among different processes to influence the apparent response of a single indicator of environmental conditions. In the case of Antarctic fur seals, the general expectation would be that pup survival is dictated by the effects of changes in prey abundance on the ability of females to provision their offspring. Local density-dependent

Table 4. Mean r² and s.d. for the relationship between response vectors and krill abundance by temporal group and species.

Response vector group	n	Linear		Holling Type II	
		Mean	s.d.	Mean	s.d.
Summer	20	0.17	0.12	0.29	0.20
Winter	6	0.20	0.19	0.16	0.17
Multi-year	6	0.10	0.09	0.06	0.08
Antarctic fur seal	11	0.22	0.14	0.30	0.21
Gentoo penguin	6	0.18	0.10	0.24	0.15
Macaroni penguin	8	0.15	0.13	0.20	0.20
Black-browed albatross	7	0.05	0.05	0.10	0.17

mortality on the study beach, however, may also have an effect, such that in years with high pup density, a relatively greater proportion die from traumatic injuries (Doidge *et al.*, 1984). Also, the proportion of primiparous animals may increase in years of good food availability, potentially resulting in greater pup mortality during the first few weeks after parturition. Similar confounding effects of local density-dependence and demographic shifts are likely to affect the breeding success of penguins. That more than one process may influence a particular index is not in itself a problem, as long as the respective responses to changes in krill abundance are similar. It is, however, particularly important to identify situations where variations in signal (e.g. pup survival) to noise (e.g. effect of maternal experience, or risk of traumatic injury) ratio has a systematic component, because this has the potential to produce apparently counter-intuitive results (Reid, 2002).

As expected, more response vectors showed a significant non-linear than a significant linear relationship with krill abundance. Although the form of the non-linear relationship fitted was similar to a Type II functional feeding relationship (Holling, 1959), this function does not necessarily reflect the rate of prey ingestion as a function

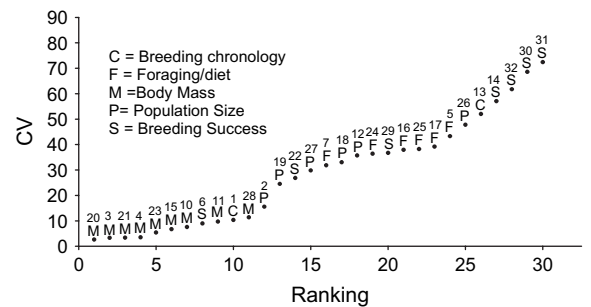


Figure 1. Ranked coefficients of variation (CV) of the response vectors (labelled according to whether they measure: C – breeding chronology, F – foraging/diet, M – body mass, P – population size, or S – breeding success; numerical labels refer to Table 1).

Table 5. Relationship between combined standardized indices (CSI) and krill abundance according to temporal groups and species (* = significant; n.s. = not significant).

CSI	n	Linear			Holling Type II		
		r ²	F	p	r ²	F	p
Summer	15	0.35	6.9	*	0.60	19.8	*
Winter	13	0.48	11.9	*	0.43	9.9	*
Multi-year	15	0.12	1.9	n.s.	0.37	7.7	*
Antarctic fur seal	15	0.51	13.4	*	0.61	20.7	*
Gentoo penguin	14	0.23	4.0	*	0.58	17.9	*
Macaroni penguin	15	0.31	5.8	*	0.34	6.8	*
Black-browed albatross	15	0.11	1.7	n.s.	0.32	6.2	n.s.

of prey density. In the functional feeding relationship, the asymptote is reached at a point where the predator is not capable of capturing more prey, even if prey becomes more abundant. In the non-linear predator response functions examined here however, the response vectors may reach an asymptote at a point at which there is sufficient prey to support predator demand, and any further increase in prey abundance does not result in a measurable increase in the performance indicators available.

There was a relationship between the variability shown by individual predator response vectors and the characteristics of the biological process they are supposed to measure. Thus, breeding success may have a mean of 0.5, but occasionally reach values close to zero in years of reproductive failure. In contrast, measures of body mass are likely to be tightly constrained by physical and metabolic controls that limit the range of values that this index can take relative to the mean. This highlights the need to recognize the underlying assumptions about the biological processes being measured, and how these processes are represented numerically when comparing the properties of

different response vectors. Nevertheless, the lack of a relationship between CV and sensitivity to changes in krill abundance indicates that the vectors showing the greatest variability do not necessarily provide the best response indicators.

The highly synchronous breeding season of krill-dependent predators suggests that there is relatively little interspecific difference in the periods over which different response vectors integrate krill availability. In contrast, interspecific variability in the spatial scales over which krill availability is integrated by the same vectors is high, ranging from 1–100 km in gentoo penguins, to 10–10 000 km in black-browed albatrosses (Figure 2). Despite these scale differences, the general pattern, whereby processes that take place over longer temporal scales also occur over greater spatial scales, is consistent among species. This interspecific consistency in temporal scales means that, while it may be biologically appropriate to group response vectors across species within the same temporal scale, it may not be appropriate to do the same within spatial scales.

Results of monitoring programmes are often represented in a matrix of *m* years of data from *n* response vectors. Such matrices may contain a large amount of information but are rarely amenable to direct interpretation in that form (de la Mare and Constable, 2000; Boyd and Murray, 2001). It is therefore important to provide a more tractable basis for analysis and interpretation and, ultimately, for facilitating input to management procedures. The CSI method may be viewed as a simple extension of the same concepts underlying the original selection of response vectors. For example, the tactical operational decisions made by a predator during a single foraging trip are too many and too complex to be measured in any currently feasible monitoring system. Nevertheless, recording key outputs of a foraging trip, such as the frequency and amount of energy delivered to offspring, provides appropriate measures of foraging performance. However, the time and effort

Table 6. Covariance matrix for summer response variables (ID numbers refer to Table 1).

ID	5	6	7	8	9	10	11	14	15	16	17	22	23	24	25	28	29	30	31
6	0.32																		
7	-0.14	0.38																	
8	0.12	0.14	0.47																
9	0.46	0.17	0.70	0.72															
10	0.43	0.27	0.74	0.65	0.95														
11	0.15	0.06	0.68	0.57	0.88	0.81													
14	-0.12	-0.09	0.00	0.45	0.39	0.32	0.29												
15	0.22	0.01	0.47	0.48	0.91	0.76	0.68	0.47											
16	0.26	0.10	0.44	0.75	0.71	0.58	0.62	0.29	0.81										
17	0.29	0.03	0.40	0.65	0.81	0.78	0.58	0.07	0.53	0.69									
22	0.09	-0.39	-0.35	-0.12	-0.16	-0.25	-0.22	0.01	-0.23	-0.18	-0.20								
23	0.42	0.03	-0.25	-0.24	0.01	0.05	-0.43	-0.22	-0.14	0.06	0.04	-0.45							
24	0.51	0.30	0.42	0.32	0.67	0.81	0.55	0.12	0.28	0.37	0.59	-0.15	0.03						
25	0.19	-0.09	0.12	0.39	0.43	0.44	0.35	0.30	0.37	0.48	0.64	-0.14	0.12	0.53					
28	0.56	0.09	-0.39	-0.21	-0.18	-0.19	-0.10	-0.18	-0.30	0.06	-0.27	0.36	0.05	0.15	0.07				
29	-0.22	0.04	0.25	-0.15	-0.10	-0.12	0.25	-0.36	-0.08	-0.06	-0.40	-0.06	-0.66	-0.03	-0.24	0.13			
30	-0.15	-0.10	-0.02	0.05	0.18	0.18	0.08	0.53	0.23	0.21	-0.13	0.25	-0.26	0.24	0.10	0.36	-0.11		
31	0.02	-0.50	-0.07	0.36	0.50	0.55	0.22	0.53	0.28	0.52	0.30	-0.18	0.02	0.50	0.53	-0.17	0.02	0.16	
32	0.04	0.07	0.18	0.51	0.67	0.70	0.34	0.69	0.36	0.61	0.28	-0.22	-0.07	0.58	0.43	0.00	-0.04	0.54	0.73

Negative values are shown in grey and values where $r > |0.3|$ are shown in bold.

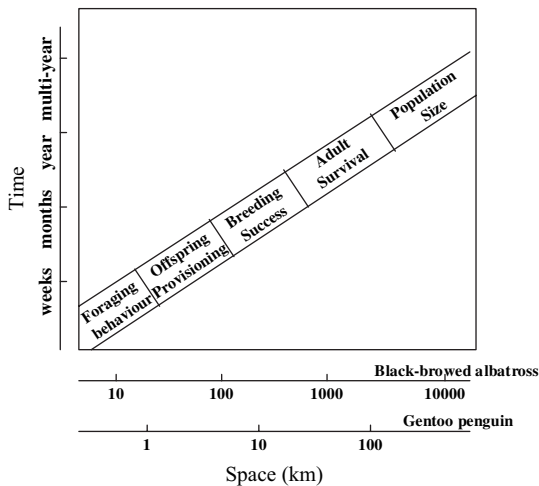


Figure 2. Relationship between temporal and spatial scales over which indices of predator performance reflect krill abundance for black-browed albatross and gentoo penguin, the two extremes within the group of predators investigated (developed from Murphy *et al.*, 1988).

required to measure these variables throughout the offspring-rearing period is considerable, even where practicable. Measuring the mass of offspring just before attainment of independence potentially provides a simpler alternative, or complementary, approach that has the potential to integrate over all provisioning events. This example of using mass at independence as a suitable proxy for the sum of all foraging decisions made by a parent highlights the importance of understanding the underlying biological processes. Similarly, in selecting response vectors to be included in the CSI, it is important that they reflect homogeneity in the underlying biological processes involved, the spatial and temporal scales in particular.

The multivariate approach using CSI not only has the advantage of reducing the dimensionality of the data to a more readily interpretable form, but also provides a better fit to the functional response model than any of the individual vectors. The relationship between krill abundance and population size (multi-year vectors) is a good example of the utility of the multivariate approach. None of the individual multi-year vectors showed a relationship with krill, yet the associated CSI did show a significant response. This suggests that the multivariate index is able to capture some element of the response to krill abundance that individual vectors cannot. Population size, measured as the number of adults making a breeding attempt in a given year (a function of adult survival and juvenile recruitment, as well as breeding deferral) has shown a reduction in some years of low krill abundance (Croxall *et al.*, 1997). This suggests that some component of population size is influenced by the krill abundance in that year. Considering breeding deferral in this context, the effect of krill abundance may make a very small contribution to the

variation in population size of individual species, so no correlation is detected. In a multivariate index, however, similar patterns of breeding deferral across species may become reinforced, and be reflected in a detectable relationship. Such an amplification of a common response signal in a CSI (while averaging out independent stochastic processes/errors) might allow detection of signals that would remain effectively hidden in the noise of individual response vectors.

The simulation work of de la Mare and Constable (2000) highlighted the need to choose response vectors that are highly correlated both with krill abundance and with each other to produce an indicator that was robust to missing data. Our analysis suggests that choosing vectors that share common biological attributes, in particular relating to their temporal scales, may also be important. Nevertheless, the degree of positive correlation shown between the summer response vectors would suggest that the derived CSI should be relatively robust to effects of missing data (as long as the reason why data are missing is independent of krill abundance).

We have shown that the characteristics of different predator response vectors depend upon a combination of both numerical and biological properties. Combining these indices, with due regard for their inherent biological characteristics (particularly the scale over which indicator species operate), provides a means of reducing the dimensionality and clarifying the general form of the relationship with prey abundance. Using a multispecies response approach, including species with different levels of dietary dependence, the observed relationship reflects the broader ecosystem response to changes in krill abundance, rather than the direct effect on obligate krill predators. Identifying the form of the functional relationship is crucial in determining to what extent dependent predators can be used as indicators of krill abundance and what level of fisheries-induced change these might detect, based on the results of a monitoring programme.

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