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Patterns in procellariiform diversity as a test of species-energy theory in marine systems

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ABSTRACT

Biological diversity varies systematically in space with levels of primary productivity. Within regions, the relationship is hump-shaped, but across larger areas it tends to be monotonic and positive. However, the generality of this latter pattern, particularly within marine systems, is not clear. Here a global analysis across regions shows that the relationship between species richness of Procellariiformes (albatrosses, petrels, storm-petrels, diving-petrels) and remotely sensed chlorophyll concentrations, a surrogate for primary productivity, is hump-shaped with a single mode. The decline in richness at higher productivities is associated with an increase in the temporal variability in levels of productivity and a decline in the areal extent of these productivities. It appears that the relationship between the areal extent of productivity classes and species richness is, in part, a function of a positive relationship between local (grid cell) and regional (productivity class) procellariiform species richness. We argue that the relationship between the temporal mean and variance in levels of productivity may be of general importance in explaining differences in the response of species to increasing productivity. Wherever the relationship between productivity and its variance is negative, a positive monotonic species richness response may be expected, whereas a unimodal response may be expected where the productivity mean–variance relationship is positive. In the southern oceans, the relationship between productivity and species richness results in coincidence between areas of high procellariiform species richness and high resource harvesting by humans, to the detriment of the birds.

Keywords: geographic area, pelagic systems, productivity, seabirds, species richness.

INTRODUCTION

Biological diversity, as expressed by species richness, varies systematically in space with levels of primary productivity (Rosenzweig and Abramsky, 1993; Wright *et al.*, 1993; Rosenzweig, 1995). Within regions, the relationship is unimodal, with richness peaking at intermediate productivities (Abramsky and Rosenzweig, 1984; Rosenzweig and Abramsky, 1993). Across larger areas, the relationship is monotonic and positive for various land groups (Currie and Paquin, 1987; Adams and Woodward, 1989; Currie, 1991; Eggleton, 1994; Gaston and Blackburn, 1995; Blackburn and Gaston, 1996; Kerr and Packer, 1997).

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However, the generality of this latter pattern remains unclear (Wright *et al.*, 1993, Rosenzweig, 1995), particularly with regard to marine systems. Here, such relationships have scarcely been explored, and impressions of underlying patterns may be obscured by the restricted distributions of some taxa (Fraser and Currie, 1996), sampling constraints (May, 1992) and the application of untested surrogates for productivity (Rosenzweig and Abramsky, 1993).

In this paper, we examine the relationship between the species richness of Procellariiformes (albatrosses, petrels, storm-petrels, diving-petrels) and remotely sensed chlorophyll concentrations (Hovis *et al.*, 1980; Platt and Sathyendranath, 1988). The Procellariiformes are a monophyletic group (Sibley and Ahlquist, 1990) of birds which return to land mostly only to breed (Jouventin and Weimerskirch, 1990; Warham, 1990). They may be considered intensely pelagic organisms (Warham, 1990), whose species distributions are better known than those of most other marine taxa (although a great deal of work remains to be done). Hence they embody a number of advantages for a global scale analysis of the relationship between productivity and species richness in marine systems.

METHODS

Spatial variation in the regional species richness of procellariiforms was determined using a working list of 108 species (del Hoyo *et al.*, 1992), the geographic distributions (breeding and foraging) of which were plotted, from distribution maps in del Hoyo *et al.* (1992), onto a cylindrical equal area (Peter's) projection map, overlaid by the WORLDMAP grid for intervals of 10° longitude [each approximately 611,000 km^2 (Williams, 1993), hence standardizing the data for area]. The mean and standard deviation of chlorophyll concentration (mg chlorophyll per m^3) obtained by the Coastal Zone Colour Scanner [global composite, level 3 data, for pixels over full measurement period, thus incorporating both annual and seasonal variation (Hovis *et al.*, 1980; CZCS, 1996)], and reduced for the WORLDMAP grid, were used as measures of primary productivity and its seasonality, respectively. Primary production by phytoplankton and chlorophyll concentration are closely related (Longhurst, 1995; Strong *et al.*, 1995; Antoine *et al.*, 1996), and zooplankton biomass appears also to be a function of these (Daly and Smith, 1993). At mesoscales, seabird abundance and distribution correlate with resource abundance (Hunt, 1991; Croxall, 1992; Croxall and Prince, 1996). We excluded grid cells including continental land prior to analysis. There were two reasons for this: first, we were concerned with pelagic relationships and, secondly, chlorophyll concentrations and estimations thereof are biased in coastal regions by the presence of land and by turbidity (Platt and Sathyendranath, 1988; Antoine *et al.*, 1996).

We then assigned the pelagic grid cells to one of ten $\log_{10}$ scale chlorophyll concentration classes. For each of these classes, mean and total procellariiform species richness, mean standard deviation of chlorophyll concentration per grid cell, and total area (number of grid cells) and total range size (number of occupied grid cells) of the procellariiform species with the smallest range size were calculated.

RESULTS AND DISCUSSION

Unlike the relationship between productivity and diversity in various terrestrial groups determined at large spatial resolutions (plants: Currie and Paquin, 1987; Adams and Woodward, 1989; termites: Eggleton, 1994; vertebrates: Currie, 1991; Gaston and Blackburn, 1995; Blackburn and Gaston, 1996; Kerr and Packer, 1997), procellariiform regional species richness showed a marked hump-shaped relationship with chlorophyll concentration, with peak richness at intermediate concentrations (Fig. 1). It is widely accepted that the increase phase of the relationship has a straightforward explanation. Procellariiform species richness increases with productivity because of the positive relationship between energy supply and species abundances (Rosenzweig and Abramsky, 1993; Wright *et al.*, 1993).

A number of hypotheses have been proposed to explain the decline phase of species richness–productivity relationships observed within regions (Rosenzweig and Abramsky, 1993; Tilman and Pacala, 1993; Huston, 1994; Rosenzweig, 1995). Two are pertinent to procellariiform richness across regions. The decline may result from (1) a positive species–area relationship, with intermediate productivity levels having the largest geographic extent and harbouring the most species, or (2) a negative relationship between species richness and temporal environmental heterogeneity, with intermediate productivity levels being more stable than high ones and thus available to be exploited for longer periods and accruing more species as a result. Although it has been argued, particularly for terrestrial systems, that high temporal variability can enhance richness, in this system this seems unlikely. High variability in productivity in the oceans tends to be associated with the lack of available production to procellariiforms for periods in the annual production cycle.

In these data, we found some support for the first hypothesis. When we divided chlorophyll concentration into classes, those with intermediate values tended to have a larger geographic extent than those with either high or low concentrations. That is, although we controlled for species–area relationships at one spatial scale, by measuring richness in equal area grid cells (i.e. within-province), they are also operating at a larger scale

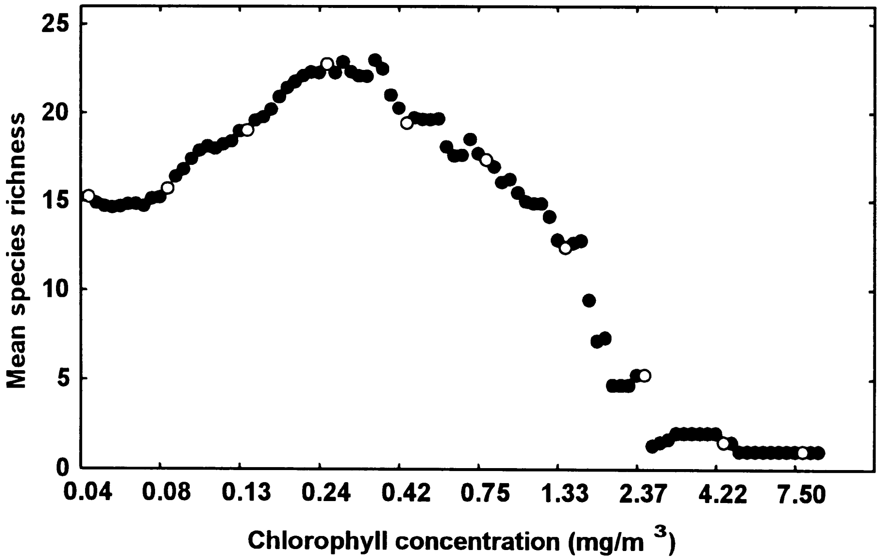


Fig. 1. The mean number of procellariiform species per grid cell in different $\log_{10}$ chlorophyll concentration classes, using a moving window on the x-axis of width 0.25, shifted in units of 0.025 (both figures in $\log_{10}$ units). The open circles correspond to the 10 classes on which the analyses were based.

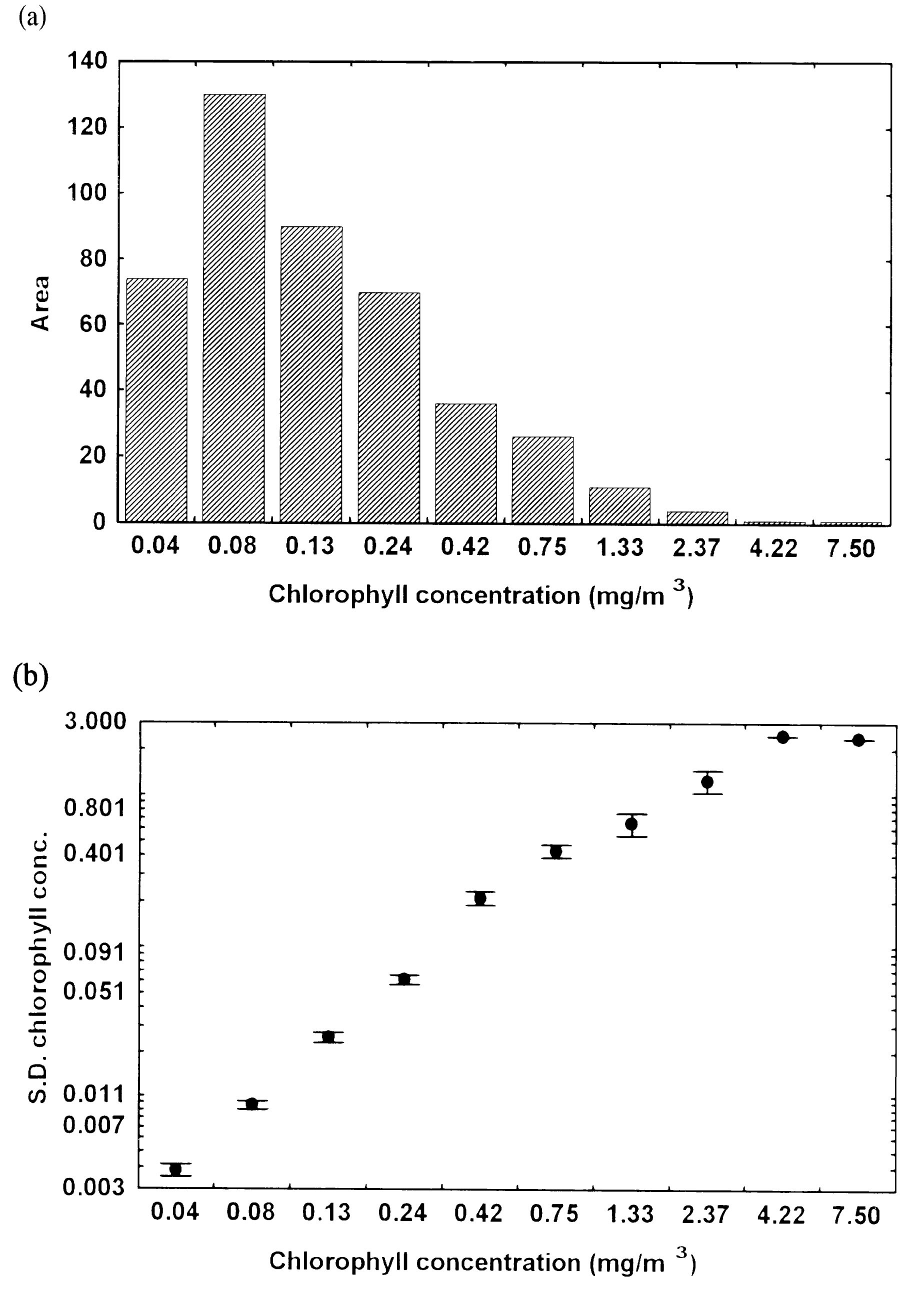
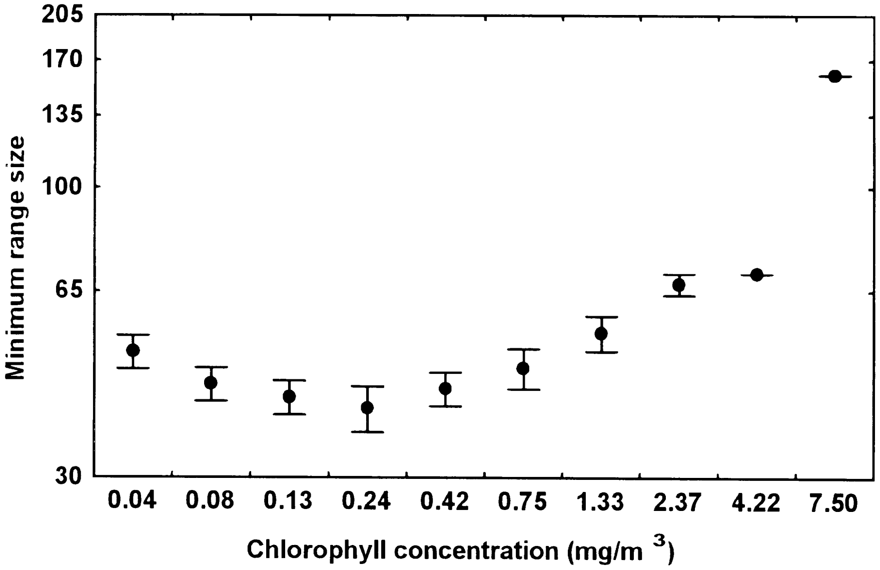


Fig. 2. (a) The geographic extent, expressed as the number of grid cells, of each of ten $\log_{10}$ chlorophyll concentration classes. (b) The $\log_{10}$-transformed mean (±1 s.e.) standard deviation of the chlorophyll concentration in each grid cell, for each of ten $\log_{10}$ chlorophyll concentration classes. (c) The mean (±1 s.e.) minimum geographic range size (expressed as the number of occupied grid cells) of species occurring in each grid cell, for each of ten $\log_{10}$ chlorophyll concentration classes.

(c)



(i.e. between-province). However, peaks in species richness and the extent of each chlorophyll concentration class did not coincide (Fig. 2a), suggesting that another variable may also be involved in determining species richness. Grid cells in the different chlorophyll concentration classes tended to be aggregated, and across classes mean procellariiform species richness and $\log_{10}$ area were strongly positively correlated ($r^2 = 0.85$, $P < 0.0001$). This pattern could be generated if local (grid cell) and regional (productivity class) procellariiform species richness are positively related (Cornell and Lawton, 1992), which was the case (Fig. 3; $r^2 = 0.84$, $P < 0.001$).

The data also support the second hypothesis. The $\log_{10}$ standard deviation of chlorophyll concentration (a measure of temporal variation in productivity) was strongly positively correlated with mean chlorophyll concentration (Fig. 2b; $r^2 = 0.97$, $P < 0.0001$). So, variation in productivity exhibited a hump-shaped relationship with procellariiform species richness similar to that exhibited by mean chlorophyll concentration (the peaks are coincident). High productivity loses its grip on richness, because it is associated with a level of seasonality in productivity which prevents effective exploitation of areas of the ocean for periods of the annual cycle.

The second hypothesis predicts that areas with high temporal variation in chlorophyll concentration should be less likely to be occupied by procellariiform species with smaller range sizes and abundances, because they are less likely to sustain individual species all year round, and species with smaller ranges are less likely to be able to exploit them for brief periods. Indeed, $\log_{10}$ minimum geographic range size was lowest at intermediate chlorophyll concentrations and increased markedly towards higher chlorophyll concentrations (Fig. 2c), as temporal variation in chlorophyll concentration also increased (Fig. 2b). Procellariiform species richness and minimum range size were negatively correlated (Spearman's rank correlation $r = -0.976$, $P < 0.0001$).

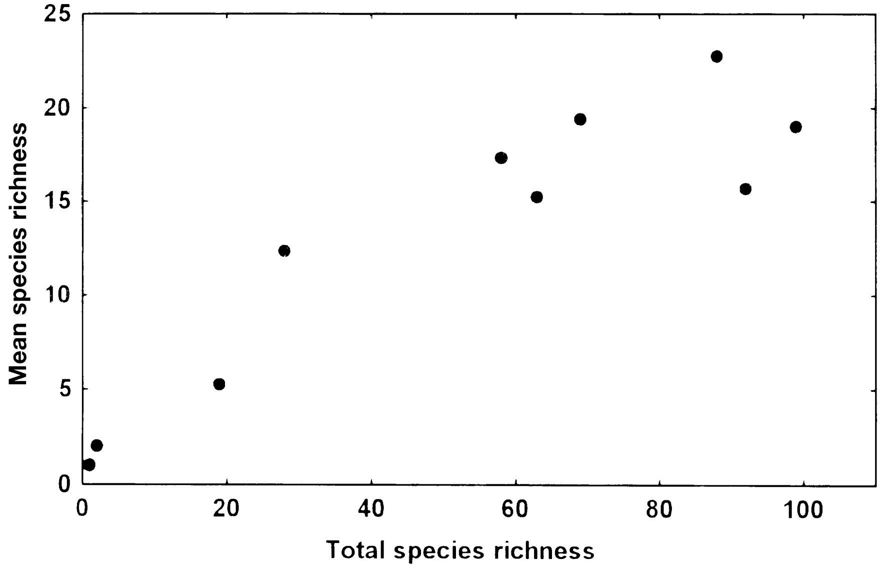


Fig. 3. The relationship between mean species richness per grid cell in each of ten $\log_{10}$ chlorophyll concentration classes and the total number of species occurring in cells in those classes.

What are the relative contributions of the between-province species–area relationship and the mean–variance productivity relationship to the determination of within-province species richness? We tentatively tested this using a multiple regression, acknowledging that some of the bivariate relationships we have discussed are plainly, and importantly, not linear. Treating productivity classes as the data points, and with mean species richness as a dependent variable and mean productivity, area and variance in productivity as 'independent' variables, only the last of these entered significantly ($r^2 = 0.88$, $n = 10$, $P < 0.001$). This results in large part because the peak in species richness occurs at relatively low values of variance in productivity, and the relationship beyond this point is approximately linear. This provides some very limited support for the argument that variance in productivity is of particular significance in determining levels of procellariiform species richness.

The relationship between the temporal mean and variance in levels of productivity may be of more general importance in explaining differences between the unimodal response of species richness to increasing productivity for the procellariiforms, and the positive monotonic response exhibited by terrestrial groups (Currie and Paquin, 1987; Adams and Woodward, 1989; Currie, 1991; Eggleton, 1994; Gaston and Blackburn, 1995; Blackburn and Gaston, 1996; Kerr and Packer, 1997) at large scales. Unlike the oceans, terrestrial systems tend to have negative mean–variance relationships, with areas of high productivity being more stable (Willmott *et al.*, 1985; Hughes *et al.*, 1996). Thus, in terrestrial systems, areas of high productivity can maintain large numbers of species consistently through time. Wherever the relationship between productivity and its variance is negative, we should expect a positive monotonic species richness response.

In summary, productivity and its variation seem likely to be an important determinant of procellariiform species richness across the oceans at coarse resolutions. Other factors, however, doubtless also play a role at this scale and at smaller ones. Sea surface temperature, in particular, is thought to be significant (Abrams, 1985; Ainley *et al.*, 1994). In addition, although any relationship between productivity and species richness must ultimately be attributable to patterns of speciation and extinction, extinctions resulting from human activity also shape observed patterns of species richness. Thus, the breeding ranges (and possibly foraging ranges) of many petrel species have been reduced in the Pacific as a consequence of prehistoric human activities (Steadman, 1995). Although only a few species are thought to have been extirpated by these activities (Milberg and Tyrberg, 1993), many local extinctions have taken place. Determining the impact of these extinctions on the breeding ranges of procellariiforms can be achieved through a straightforward comparison of current and subfossil distributions. But ascertaining the influence of extinctions on the size and nature of foraging ranges remains problematic.

The peak in procellariiform richness at intermediate levels of productivity and its temporal variability coincides, in the southern hemisphere at least, with areas of intense resource harvesting by humans, particularly through long-line fishing (e.g. Brothers, 1991; Weimerskirch *et al.*, 1997). It is thus no surprise that incidental mortality due to fishing poses serious threats to some southern procellariiforms, especially albatrosses (Murray *et al.*, 1993; Cherel *et al.*, 1996). Here, as elsewhere, the conservation of biological diversity conflicts with present patterns of human activity.

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