

Dispersal and metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries

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Summary

1. We measured for the first time in a pelagic seabird the dispersal rate of wandering albatrosses and show that while adults are highly philopatric to breeding sites the dispersal rate of young birds is not negligible, even at large distances. We show that the wandering albatross has metapopulation dynamics, i.e. migration events are sufficient to influence the dynamics of populations at other islands.

2. The spatial dynamics of wandering albatross has important consequences when analysing and making projections of the effects that incidental by-catch related to long-line fishery activities at different spatial scales can have on the persistence of local populations of wandering albatross.

Key-words: by-catch, colonial birds, conservation, pelagic birds, long-line fisheries, migration.

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Introduction

The wandering albatross (*Diomedea exulans chionoptera*) illustrates the extreme adaptations of seabird species to forage resources that are distributed patchily and unpredictably over wide areas of the Southern Oceans, with breeding in highly fragmented habitat patches (oceanic islands) scattered from South America to Australia. This species, like most pelagic seabirds, typically has high philopatry and low reproductive rates (e.g. Warham 1990), although its actual dispersal rate among colonies or islands is poorly known.

Due to recent decline in numbers of many of its populations, all of which seemed to be associated with fishing activities, this species is listed currently as Vulnerable by the IUCN (2000) and by Birdlife International (Collar, Crosby & Stattersfield 1994). The wandering albatross is one of seabird species attending fishery vessels and is very susceptible to being drowned after striking at baited hooks (Croxall *et al.* 1998; Brothers 1991). Being a diurnal feeder that forages close to the nesting grounds (breeding birds typically spend 65% of their foraging time within 200–300 km of the island), the wandering albatross has a high risk of encountering fishing ships operating close to

nesting islands during the breeding season (Cherel, Weimerskirch & Duhamel 1996; Klaer & Polacheck 1997; Weimerskirch & Jouventin 1997; Croxall *et al.* 1998).

In this paper we provide the first results on the dispersal rate of a large pelagic seabird, and use these results to address two issues. First, whether the wandering albatross functions as a metapopulation, i.e. whether the dispersal events can influence the dynamics and degree of persistence of other island populations; secondly, the impact that long-line fisheries operating at different spatial scales can have on the persistence at both the local and metapopulation levels.

Methods

We built an age-structured, stochastic metapopulation model with three post-breeding transition matrices that correspond to the main areas (Crozet: Indian Ocean, South Georgia: Atlantic Ocean and Macquarie: Pacific Ocean) where the wandering albatross currently breeds. The spatially explicit metapopulation model considers 10 populations (Cochons, Possession, Apotres, Ile de l'Est, Kerguelen, Heard, Marion, Prince Edward, South Georgia, Macquarie; Fig. 1) for which long-term population counts were available (Croxall, Rothery & Pickering 1990; DelaMare & Kerry 1994; Weimerskirch, Brothers & Jouventin 1997). Due to the restricted exchange of breeding

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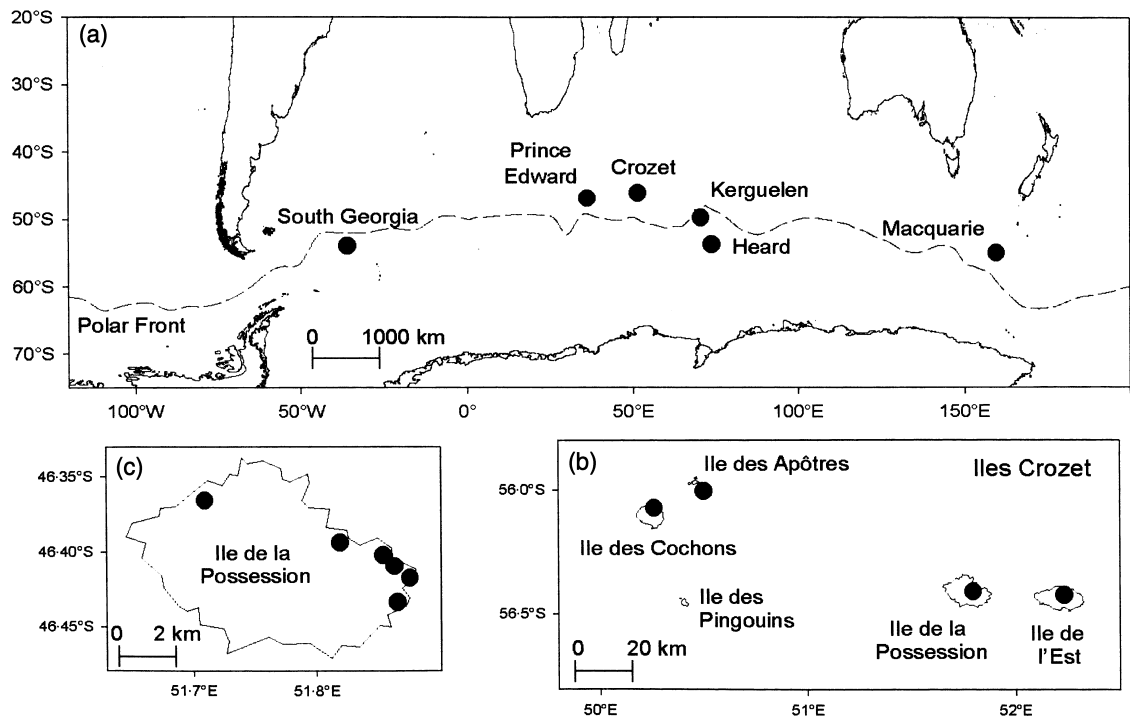


Fig. 1. Map of the Southern Ocean showing the breeding sites of wandering albatrosses at different scales (a) in the Southern Ocean (b) in the Crozet Islands and (c) on Ile de la Possession where the banding of adult and juvenile birds has been carried out over the last 40 years.

adults between colonies (see below) all colonies of an island were considered part of a single breeding population, and thus the model describes the population dynamics at the island level. Lacking estimates of demographic data for Marion and Prince Edward islands, we assumed that these two islands had the same demographic rates of the Crozet group (Cochons, Possession, Apotres, Ile de l'Est, Kerguelen, Heard). The assumption was based on the fact that the number of breeding pairs in the two island groups has changed roughly in parallel since the 1980s (Weimerskirch *et al.* 1997; Nel, Ryan & Crawford 2002).

The life cycle of the wandering albatross was subdivided into 14 age classes: chicks, juveniles (2–5-year-olds), immatures (6–8-year-olds) and adults (9 years and older). As with other southern oceanic birds, juvenile wandering albatross disperse after fledging and remain scattered over extensive areas in the oceans (Robertson & Gale 1998). Each transition matrix had 14 age classes and reproduction started at the age of 9 years; we accounted for the observed longevity of Procelariiformes (Robertson & Gale 1998), by allowing individuals to have a non-zero probability of remaining at the last age class. The latter, however, should not be construed with assuming that the birds are immortal, because the chances of remaining in the last age class diminishes each year at a rate of $(1 - S_{adults})$.

PARAMETER ESTIMATION

The extensive, on-going census and mark–recapture programme of the wandering albatross at Ile de la

Possession (Crozet) over the last 40 years provided yearly estimates of adult survival. Details of the field methodology can be found in (Weimerskirch *et al.* 1997). Since juveniles remain at sea and hence cannot be surveyed, annual juvenile survival was estimated retrospectively from the cumulative survival from fledging until breeding assuming that the annual survival of juvenile and immature age classes was equal (Weimerskirch 1992). The estimates of the annual survival rates for Macquarie and South Georgia were obtained from (Croxall *et al.* 1990; DelaMare & Kerry 1994).

Fecundity rates were calculated as the product of breeding frequency (proportion of breeding adults), breeding success (proportion of eggs resulting in chicks), clutch size (equal to one) and the sex ratio (a 1 : 1 sex ratio was assumed). Age-specific fecundity rates were obtained as the proportion of breeding adults in each age class (data obtained from Weimerskirch *et al.* 1997) and the estimate of fecundity obtained as explained above. Breeding frequency was estimated to be 0.563 in Crozet and assumed to be constant over time for all populations, because data on breeding frequency over time for all populations was unavailable to us. However, even if data on the temporal variability of the breeding frequency had been available, it has been shown (Inchausti & Weimerskirch 2001) that it had a very small effect on the modelling of the population growth rate of a closely related species of albatross.

Dispersal rates were based on recapture of 6037 chicks banded prior to fledging at Ile de la Possession, Crozet Islands between 1966 and 1996 (Fig. 2). On each

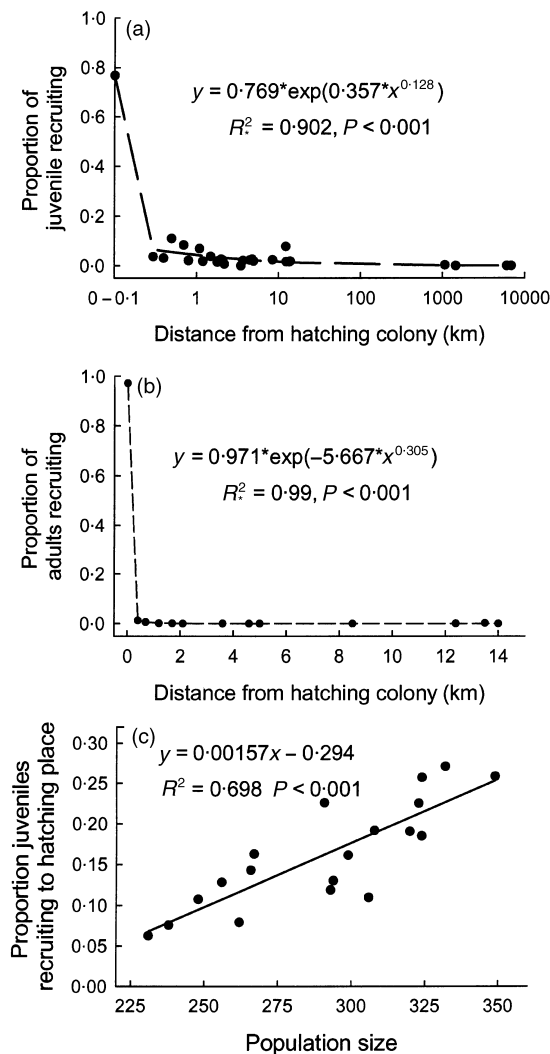


Fig. 2. Dispersal rate (expressed as percentage of individuals recruiting) of juvenile (a) and (b) adult wandering albatross in relation to the distance from the hatching place, and (c) of juveniles in relation to the size of the breeding population at Ile de la Possession. The parameter estimates for each regression equation and the regression statistics are shown in each panel.

colony of this island, all breeding birds were recaptured during incubation for identification (Weimerskirch, Jouventin & Mougin 1985). Outside Crozet Islands, the breeding population of at least one island is monitored regularly and breeding birds controlled for band reading, providing the recapture as breeding adults of seven chicks banded on Ile de la Possession (Weimerskirch, Brothers & Jouventin 1997). We estimated the dispersal rates of juveniles and adults separately. In the case of juveniles, inter-island dispersal rates (expressed as the proportion of juveniles migrating) was estimated using the non-linear function: $\text{proportion migrating} = a \cdot \exp(b \cdot \text{distance}^c)$ where a , b and c are the proportion of individuals remaining on site, the rate of decay of migration proportion with the distance between islands, and a parameter indicating whether migration rates decreased exponentially ($c = 1$) or faster than exponentially ($c < 1$) with the dis-

tance between islands (see Akcakaya 1998 for details). Having the estimates of this function and knowing the geographical distance between the islands, we calculated the (symmetric) migration rate of juveniles between all pairs of islands and entered the set of migration rates into the metapopulation model. Juvenile dispersal rate was related to the size of the source population, a feature that was incorporated into the metapopulation model. In the case of adults, we also estimated the dispersal rate of adults as a function of distance from the hatching colony but given that all dispersal events of adults occurred between colonies of the same island (see below), adult dispersal was not incorporated into the metapopulation model.

Environmental stochasticity was modelled by drawing the values of the age-specific survival and fecundity rates of each population from a set of log-normal distributions whose parameters (means and standard deviations) reflect the average value and the temporal variability of each demographic rate of each population. The means and standard deviation of each demographic rate were estimated using the time series of annual estimates of Crozet (Weimerskirch *et al.* 1997), Macquarie (DelaMare & Kerry 1994) and South Georgia (Croxall *et al.* 1990). The long chick-rearing period of wandering albatross makes it likely that breeding success and adult survival be correlated, and hence we assumed that the values of fecundity and adult survival of a population for a given year were perfectly correlated. Environmental correlations (i.e. the synchronicity of the temporal variation of demographic rates between pairs of islands) were assumed to be equal to one within an island group due to the geographical proximity of the islands. Among island groups, environmental correlations were estimated by the Spearman correlation of adult survival rates, the demographic rate that has the largest influence on the population growth rate (Weimerskirch *et al.* 1997). The set of environmental correlations thus calculated were Crozet–South Georgia = -0.279 , Crozet–Macquarie = 0.185 and South Georgia–Macquarie = 0.354 . These values of environmental correlations were used to generate correlated values of the age-specific survival and fecundity rates at each time step for each island. Demographic stochasticity was incorporated by independently drawing the number of surviving individuals of each age class and the actual number of chicks produced in each island at each year from binomial distributions.

Because wandering albatrosses aged 1–5 years remain at sea, the precise initial age distribution of each population is essentially unknown. In addition, only counts of breeding pairs are available for several of the islands considered here (Croxall *et al.* 1990; DelaMare & Kerry 1994; Weimerskirch *et al.* 1997; Nel *et al.* 2002). In the absence of precise censuses for all age classes in each island, we assumed the initial age structure of all populations to be in proportion to their expected stable age distribution.

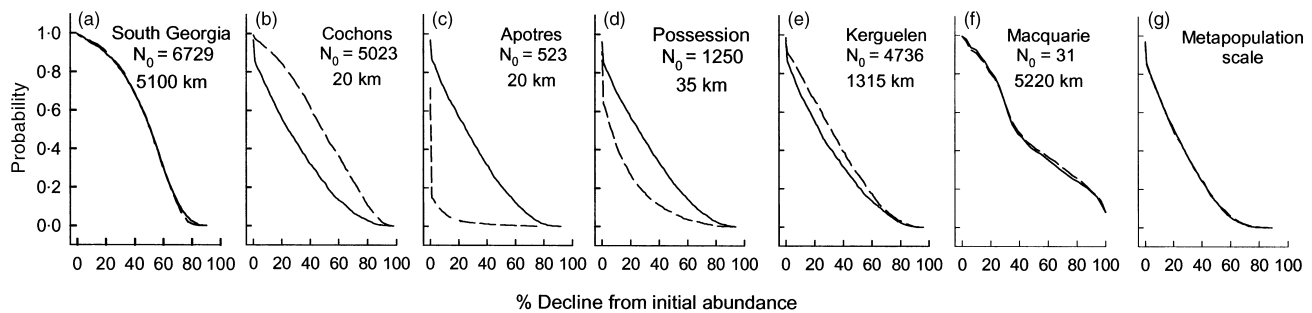


Fig. 3. Effect of juvenile dispersal on the probability of decline (expressed as a percentage of the initial abundance) shown for the populations of six islands (a–f) and for the entire metapopulation (g). The lines in each panel refer to the results of metapopulation models without dispersal (continuous line) and with dispersal (dotted line). The distance to the closest island and the initial population size of each island are indicated above each panel.

EFFECT OF LONG-LINE FISHERIES

The impact of long-line fishery on the wandering albatross was obtained by regressing the adult survival rate on the extent of the fishery as measured by the proportion of $5^\circ \times 5^\circ$ squares of ocean with long-line ships in the Crozet area, yielding adult survival = $97.1 - 28.0 \times$ extent of the fishery (SE of slope = 11.00; $n = 22$; $P = 0.02$) (Inchausti & Weimerskirch 2001). Long-line fisheries for Southern Bluefin Tuna *Thunnus maccoyi* have been shown to overlap with foraging wandering albatrosses from Crozet during the 1970s until the early 1980s. Using this regression equation and the minimum extent of the long-line fisheries in the Crozet sector (Weimerskirch *et al.* 1997), we calculated a separate transition matrix whose average adult survival values were decreased by 5.5% that was used in all simulations involving the effect of long-line fisheries. We considered a systematic (as opposed to random) effect of long-line fisheries whose intensity remained constant over time and was compared with the baseline model not involving fisheries. Two spatial scales were considered for the impact of fisheries: a local scale focused only on Apotres, and a regional scale on all islands of the Crozet archipelago. Apotres was chosen because its population has intermediate size and it is surrounded by nearby islands with larger populations that could serve as the source of migrants to the impacted population.

IMPLEMENTATION OF THE MODELS

All metapopulation models simulated the dynamics of the ensemble of 10 populations by projecting the number of individuals in each age class of each population for a time horizon of 200 years (corresponding roughly to 6–8 generations of the species). The model was analysed by Monte Carlo simulation using RAMAS/METAPOP (Akçakaya 1998) using 2000 replications for each set of parameter values. The results of the simulations are summarized in terms of probability of decline (within the time horizon of 200 years) as a function of amount of decline at the level of each island and at the level of the metapopulation.

Results

Trends in population size of the wandering albatross have been similar for the three major nesting island groups (Crozet, Kerguelen and Prince Edward islands) in the Indian Ocean: all populations decreased during the 1970s and have been recovering since the mid-1980s (Woehler 1991; Weimerskirch *et al.* 1997; Nel *et al.* 2002). The population at South Georgia has been decreasing continuously since the 1980s (Croxall *et al.* 1990), whereas at Macquarie the population is currently stable (De La Mare & Kerry 1994). Although almost 77% of the juveniles individuals returned to their hatching place and most of the remaining ones to neighbouring colonies, the remaining fraction (23%) dispersed to breed in colonies of other island groups up to 1450 km away (Fig. 3a). The probability of dispersing to the farthest colonies at 6050 km was 0.0001. Once birds start breeding in a colony 97.1% of adults return to the same colony, while the remaining 2.9% of adults stay in colonies of the same island located up to within 1 km away: no wandering albatross has ever been found breeding outside the island where it bred before (Fig. 3b). The dispersal rate of juveniles from the hatching colony was related positively and significantly to the size of the source population (Fig. 3c). There was no significant change in the dispersal rate of adult breeding birds over time or in relationship with the size of the source population (slope = -0.006 ; SE = 0.006; $P = 0.350$; $n = 21$).

Our modelling results show that the dispersal of juvenile wandering albatross may alter the dynamics and the persistence of populations in other islands. Dispersal had a diversity of effects of migration on the risk of decline of an island's population depending on the distance to neighbouring islands and on their relative population size (Fig. 3). For very distant large or small populations, migration has little effect on their risk of decline (Fig. 3a,f). However, migration had a positive effect, i.e. it decreased the probability of decline in abundance, for small- or medium-sized populations with close larger populations that function as a source of migrants (Fig. 3d,e). Finally, migration increased the risk of decline for large populations having either

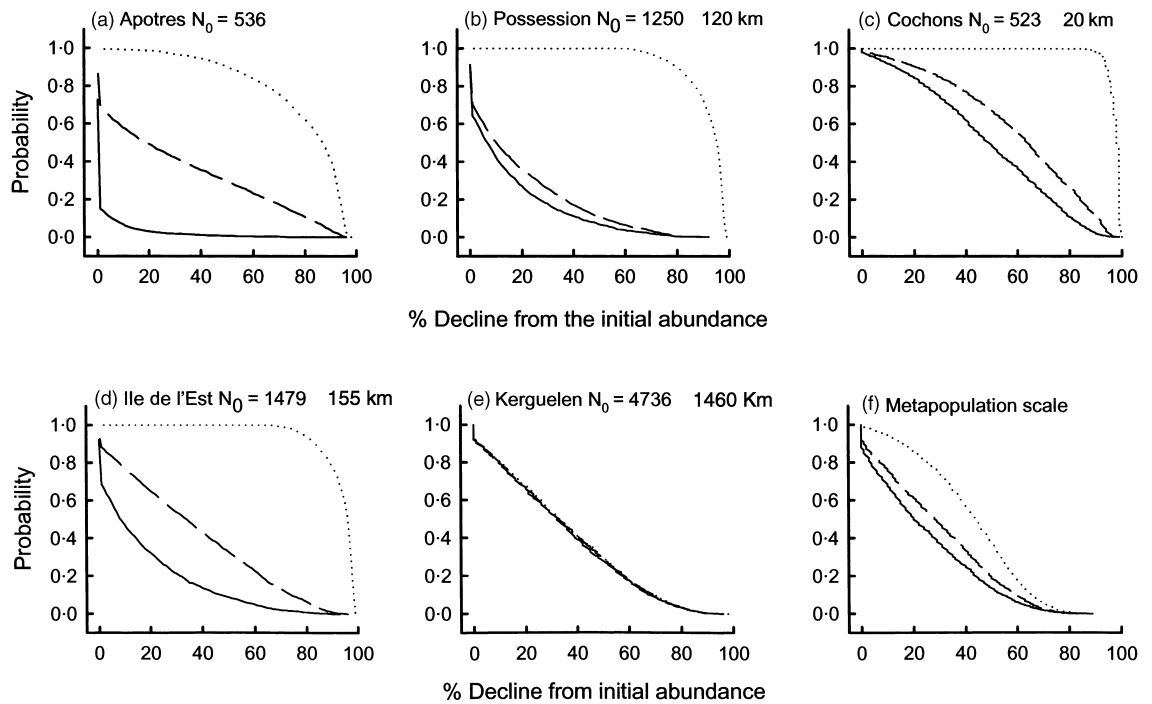


Fig. 4. Effect of the occurrence and spatial extent of long-line fisheries on the probability of decline (expressed as a percentage of the initial abundance) for the populations of six islands (a–e) and for the entire metapopulation (f). The lines in each panel indicate without long-line fishery (continuous line), with fishery affecting only Apotres (dashed line) and with fishery affecting all Crozet Islands (dotted line). The distance to Apotres and the initial population size of each island are indicated above each panel.

small populations (Fig. 3c) or isolated medium-sized populations (Fig. 3b). At the level of the entire metapopulation, the compounding of these different effects at the island level shows that dispersal has a small effect of the risk of overall decline of the metapopulation (Fig. 3g).

Long-line fisheries had the expected effect of increasing the probability of population decline both at the level of single populations (Fig. 4a–e) and at the level of the metapopulation (Fig. 4f). Interestingly, the effects of a localized action of long-line fisheries in Apotres would increase the risk of decline of other populations of the Crozet archipelago that were not affected by fisheries (Fig. 4b–d). Because the indirect effect of localized action of long-line fisheries is mediated by migration, it is not surprising that it would not affect the risk of decline of populations located much farther away (Fig. 4e). When long-line fisheries operate at a regional scale (e.g. all Crozet islands), its overall effects consist of the direct effects on a given population, plus the impact on other populations to which the local population is connected by migration. This can be seen in Fig. 4a by comparing the curves of risk of decline of Apotres when fisheries affect this island only (direct effects) and when they affect all islands of the Crozet archipelago (direct and indirect effects).

Discussion

Our results have shown that the populations of wandering albatross in the Southern oceans have a metapopulation dynamics since the migration of juvenile

birds can alter the dynamics and the degree of persistence of populations of other islands. We have presented the first estimation of interpopulation dispersal in a pelagic seabird and shown that while adult wandering albatrosses are highly philopatric to breeding sites the dispersal rate of young birds is not negligible, even at large distances. These findings counter the thus far widely held view that albatrosses are the quintessential example of a philopatric bird species.

An important feature in the metapopulation functioning of the wandering albatross was that juveniles were more philopatric to the hatching island when local population density was lower. It is this feature that largely determines whether a local population functions as either a sink or a source of juvenile migrants in the metapopulation. This type of source–sink metapopulation dynamics does not result from habitat heterogeneity on the breeding sites (as it may be the case for terrestrial animals, e.g. Holt 1985; Pulliam 1988). The dynamics of pelagic seabird populations is determined largely by the quality of their feeding habitats at sea and by their interaction with long-line fisheries (Robertson & Gale 1998) and essentially independent from the nesting habitats, i.e. oceanic islands, provided that the latter are free of ice or of land predators. Rather, it is the specific characteristics of the wandering albatross whose populations have a discrete spatial distribution with density- and distance-dependent dispersal that results in the asymmetric dispersal between islands, thus producing the observed source–sink metapopulation dynamics.

The metapopulation functioning of wandering albatross has important consequences when analysing and make projections of the effects that incidental by-catch related to long-line fishery activities can have on the persistence of local populations of wandering albatross. Although long-line fisheries have affected wandering albatross throughout the southern ocean its impact was not even, as some populations were more impacted than others and fishing effort has had extensive variation over time and space (Brothers 1991; Croxall *et al.* 1998). Japanese fishing for the Southern Bluefin Tuna has been linked to the decrease of the Indian Ocean populations of the wandering albatross (Weimerskirch *et al.* 1997) and in Australian waters (DelaMare & Kerry 1994). Other fisheries such as those for the Patagonian toothfish (*Dissostichus eleginoides*) around Kerguelen and South Georgia (Cherel *et al.* 1996; Klaer & Polacheck 1997; Croxall *et al.* 1998) and for Antarctic squid in New Zealand (Bartle 1991) have also induced heavy mortality on the wandering albatross populations. The interrelated dynamics of local populations mediated by distance- and density-dependent juvenile migration produces a source-sink type of metapopulation that permits the occurrence and propagation of a diversity of effects through the network of island populations. On one hand, migration would allow that the localized impacted of long-line fisheries be ameliorated partly by the exchange of individuals from populations of nearby islands. The magnitude of this 'rescue effect' would depend on the distance between the islands and on their relative local population abundances. On the other hand, a local decrease in population abundance caused by long-line fisheries may impact negatively the persistence of other island populations that were not affected directly by the fishery activities. This is because the localized impact of long-line fisheries can shift the sink-source relation between pairs of populations in nearby islands dictated by positive density-dependent migration. When operating at a regional level (i.e. affecting population of more than one island), long-line fishery activities would have an augmented negative effect: a direct negative impact on local populations, and indirect regional effect through enhancing local philopatry, thereby decreasing the potential of 'rescue' from nearby populations.

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