Postnatal dispersal of wandering albatrosses *Diomedea exulans*: implications for the conservation of the species

Henri Weimerskirch, Susanne Åkesson and David Pinaud

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Many large marine vertebrates are today threatened by human activities and it is therefore crucial to obtain information on their distribution and behaviour at sea. In particular little is known about the time necessary for juveniles to acquire the foraging skills of adults. We tracked 13 juvenile wandering albatrosses *Diomedea exulans* by satellite telemetry during their first year at sea. They covered an average distance of 184 000 km during the first year and restricted their dispersal to the unproductive waters of the subtropical Indian Ocean and Tasman Sea. This region of low wind velocities does not overlap with the foraging areas used by adults. After an innate phase of rapid dispersal with a fixed flight direction, young birds progressively increased their daily flight distances and attained adult flight efficiency within their first six months at sea. The complete overlap of the juveniles' foraging ranges with major long-line fisheries in the subtropical waters constitutes a major threat that could jeopardize the long term recovery ability of populations of the endangered wandering albatross in the Indian Ocean.

H. Weimerskirch (correspondence) and D. Pinaud, Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, 79360 Villiers en Bois, France. S. Åkesson, Department of Animal Ecology, Ecology Building, SE-223 62 Lund, Sweden. E-mail: henriw@cebc.cnrs.fr

Many species of large marine vertebrates are today threatened by human activities, especially from incidental capture by long-line fishing operations (e.g. Tuck et al. 2001, Baum et al. 2003, Lewison et al. 2004). Although there is an urgent need to improve our understanding of the movements and distribution of such species to allow the implementation of conservation measures, most currently available information for taxa such as sea turtles, tunas or seabirds (Block et al. 2001, Croxall et al. 2005, James et al. 2005) is typically both patchy in its geographic coverage and limited to a small part of the population, e.g. the adults or breeding animals (Birdlife International 2004, Croxall et al. 2005). In particular, there is a complete lack of information on immature animals that can represent up to half of the total population of long-lived species (e.g. Weimerskirch et al. 2005), and that may have higher susceptibility to increased by-catch mortality related to long-line fisheries because of their naïve behaviour.

After becoming independent from their parents, young animals have to forage and disperse on their own by using a series of learnt and/or genetically fixed behaviours (Berthold 1996, Alerstam et al. 2003). During this period in which naïve animals acquire the skills of efficient locomotion and foraging (Burger 1980, Yoda et al. 2004), they may not only have high mortality rates through natural causes (Clutton-Brock 1988), but also may be more susceptible to incidental by-catch mortality (Gales et al. 1998). Little information is however available on this critical period when young individuals generally disperse from their birthplace (Drent and Daan 1980), often at long distances. The proximate cause of juvenile dispersal from birthplace related to environmental conditions, could for example be a result of competition for suitable resources with adults around the breeding grounds (Clobert et al. 2001). These ecological proximate factors can lead to the fixation of genetic dispersal mechanisms that enable birds to find

their way to safe and suitable foraging sites (Berthold 1996, Dingle 1996, Clobert et al. 2001, Alerstam et al. 2003).

The duration of immaturity in many seabird species such as albatrosses is particularly long (5–10 years; Warham 1990) and it is assumed to result from a long period of learning of foraging skills (Lack 1954). The most critical stage, with a high risk of mortality, occurs during the first year when juveniles disperse over long distances across completely unknown ocean areas and have to acquire foraging skills (Warham 1990). The behaviour of seabirds during this phase of dispersal is almost unknown because of the difficulty to track the movements of these animals over long periods, especially in the pelagic marine environment (Kooyman et al. 1996). This is the case even for albatrosses in which the movements and behaviour of adults are now well documented for most species, but unknown for juvenile birds, particularly during their first months of independence.

The endangered wandering albatross *Diomedea exulans* is well known for its ability to forage over wide areas of ocean when breeding (Weimerskirch et al. 2000a). Long-line fisheries especially threaten the species because birds are drowned when taking baits on the baited lines (Weimerskirch et al. 1997, Gales et al. 1998). Modelling indicates that tuna long-line fisheries may be the major cause of the decline of its populations (Tuck et al. 2001). The recovery of some populations is currently impeded by a decline in their recruitment rate due to poor survival during the first years at sea (Weimerskirch et al. 1997, unpubl. data). Knowledge of the distribution and movements of juvenile birds is therefore essential for predicting how different threats could impact this species. Upon leaving the colony, juvenile wandering albatrosses have an entirely brown plumage that contrasts with the white plumage of adults, and will progressively whiten during the period of immaturity (Weimerskirch et al. 1989). This is in sharp contrast to most albatross species whose juvenile plumage differs little from that of adults, suggesting that in wandering albatrosses the dark plumage may have evolutionary significance, and in particular be an adaptation to a different environment (Bretagnolle 1993).

The aim of this study was to examine for the first time the foraging movements and behaviour during the first year at sea of a marine bird (see also Kooyman et al. 1996). We used satellite telemetry to track the movements of juvenile wandering albatrosses during the critical period of postnatal dispersal. In this paper we address five questions of major interest not only with respect to wandering albatrosses but to marine vertebrates in general: 1) How do juvenile animals move during their first year at sea? 2) Do they disperse through a fixed behaviour, or do they disperse randomly over the open ocean? 3) Where do juveniles forage during their first year at sea? 4) Do they use zones with a different environment from that of adults, which, for wandering albatrosses, might explain their different plumage pattern? 5) Is there an overlap with long-line fisheries and, if so, what are the conservation implications?

Methods

To record the movements of juvenile wandering albatrosses we attached satellite transmitters (PTT 100, Microwave Telemetry, Columbia USA) to 13 (6 males and 7 females) fully feathered juveniles in mid November 2001 (7 individuals) and 2002 (6) at the Crozet Islands, south-western Indian Ocean. Chicks were measured and weighed prior to fledging, and a body condition index was calculated (Weimerskirch et al. 2000b). They were sexed by measurements taken at fledging using a discriminant analysis (Weimerskirch et al. 2000b); sex was confirmed in 2002 using a molecular sexing method (Weimerskirch et al. 2005). We used six solar panel-powered 35–50 g satellite transmitters with a duty cycle of 10 h on and 24 h off, and seven 35–45 g battery-powered satellite transmitters with a duty cycle of 10–18 h on and 24–54 h off fitted with adhesive tape on the back feathers. With this attachment method the PTTs were expected to be lost during the first moult of the back feathers that starts progressively 12–24 months after fledging (Weimerskirch et al. 1989). According to the producer's specifications, the battery-powered transmitters were expected to last 8–14 months. The location of transmitters was determined using the Argos system (http://www.argosinc.com/). Following Weimerskirch et al. (1993), we filtered the locations obtained (all classes) and removed those that necessitated a speed of travel of >90 km h^{-1}, and locations that were obtained at less than 10 minute intervals because the distance that a bird could travel during this short time is that of the inherent error of the locations. To estimate the daily distance covered, we only used speeds calculated between two locations (all classes) at intervals less than 5 hours, i.e. for the periods when the transmitter was working continuously (average time between 2 locations 1.5 ± 0.4 h). The total distance travelled during the year by each individual was estimated from the cumulative distance covered during periods of transmission and taking into account the proportion of time when the transmitter was not on duty cycle. This allowed us to compensate for the underestimation that would result from estimating distance covered between locations separated by long periods of time, and to compare with previous data (Salamolard and Weimerskirch 1993, Weimerskirch et al. 1993) obtained on adults where transmitters were working continuously. We used the fixed kernel method (Worton 1995) with least squares algorithm (Seaman and Powell 1996) and a smoothing

factor of 1° to calculate contours including 95% of locations (Wood et al. 2000) for breeding adults of the Crozet, Kerguelen and Marion Islands (Nel et al. 2002), and for the Crozet juvenile birds. Monthly wind data were obtained from CERSAT, at IFREMER, Plouzané, France (http://www.ifremer.fr/cersat/fr/data/). The position of fronts is taken from Belkin and Gordon (1996). We used ringing recoveries to investigate to which region of the ocean the young wandering albatrosses were dispersing. A total of 6,570 wandering albatross chicks were banded between 1966 and 2003 on Possession Island. We have considered here the recapture of birds aged 1–5 years, i.e. before birds started to return to the breeding colonies (Weimerskirch et al. 1997).

Results

The thirteen individuals were tracked for 66 to 389 days (168.8±93.6 days). The transmitters of three birds stopped transmitting prematurely after 66, 69 and 83 days, possibly as a result of the death of the bird. These individuals were not in a poorer condition when they left the colony (Mann Whitney U=16, P=0.866), or of a particular sex, compared to the birds transmitting longer. Remarkably, all individuals showed similar dispersal behaviour: after leaving the island, they immediately landed on the water, drifted away from the birthplace for 1–15 days (mean 4.9±5.0), waited until southerly winds started to blow before starting a rapid directional movement towards north-north-east, until they crossed the subtropical convergence 600 km to the north of the Crozet Islands (Fig. 1). They then engaged in continuous movement in the sub-tropical waters (Fig. 2a). During the first six months, the average

distance covered daily by each individual increased progressively from 300 to 600 km (repeated measures ANOVA $F_{5,30}$=10.3, P<0.001), and stabilised later at a high level (Fig. 3). Although there was no sex-specific difference in the dispersal zones used, females had consistently higher movement rates than males (repeated measures MANOVA, sex effect $F_{1,11}$=5.03, P=0.042, interaction of time and sex, $F_{5,44}$=0.3, P=0.814).

The prevailing winds dictated the initial flight direction and changes in flight direction were always associated with changes in wind direction, with birds remaining strictly north of the sub-tropical convergence in the Indian Ocean and Tasman Sea (Fig. 2b). Importantly, the overall foraging zone of the Crozet Island juveniles had little overlap with that of breeding adults from the major breeding sites (Fig. 2b). After six months at-sea, birds seemed to restrict their range to a more specific sector, generally south of Australia (Fig. 2c). The estimated average distance covered by a juvenile wandering albatross during its first year at sea was 183,800 ± 34,100 km (range 127 020 – 267 000 km). Recoveries of wandering albatrosses banded as chicks on Possession Island (Crozet) were made along the coasts and in open waters (for birds caught by fisheries) of the Indian Ocean and Tasman Sea (Fig. 2b).

The oceanic areas used by juvenile birds as foraging zones during their first year overlapped extensively with the major fishing zones of long-liners in the Indian Ocean, whereas the overlap between these fisheries and the foraging ranges adults is more limited (Fig. 2).

Discussion

The dispersal of juvenile albatrosses is most likely the result of both innate and learned behaviour (Dingle 1996, Clobert et al. 2001). Their ability to always return to their birthplace after years of immaturity on the open ocean (Inchausti and Weimerskirch 2002) indicates an innate mechanism for navigation over long distances of open waters. Much like many terrestrial birds (Berthold 1996), the movements of juvenile albatrosses during the initial dispersal phase seemed to be partly innate with a first step encoded as a fixed flight direction. Indeed all birds had a directed flight towards north, favoured by southerly winds that they waited for before starting their northward movement. The limited overlap between foraging zones of breeding adults and of juveniles may not be the result of direct interactions with adults forcing juveniles to leave the proximity of the breeding grounds. Rather it may suggest the existence of a genetically encoded behaviour that has been selected for in the past to avoid competition (Clobert et al. 2001). This is also suggested by the strict foraging of young birds in waters that are much less productive than those exploited by adults.
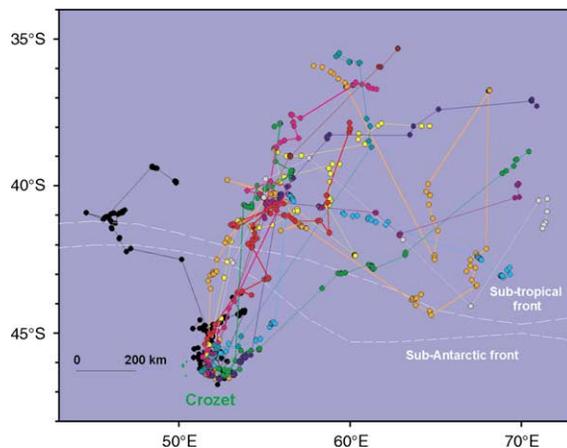

Fig. 1. Post-natal movements of 13 juvenile wandering albatrosses during the first weeks after leaving their birthplace at Crozet, showing the north-northeast route taken by almost all the birds from their birthplace on the Crozet islands to subtropical waters.
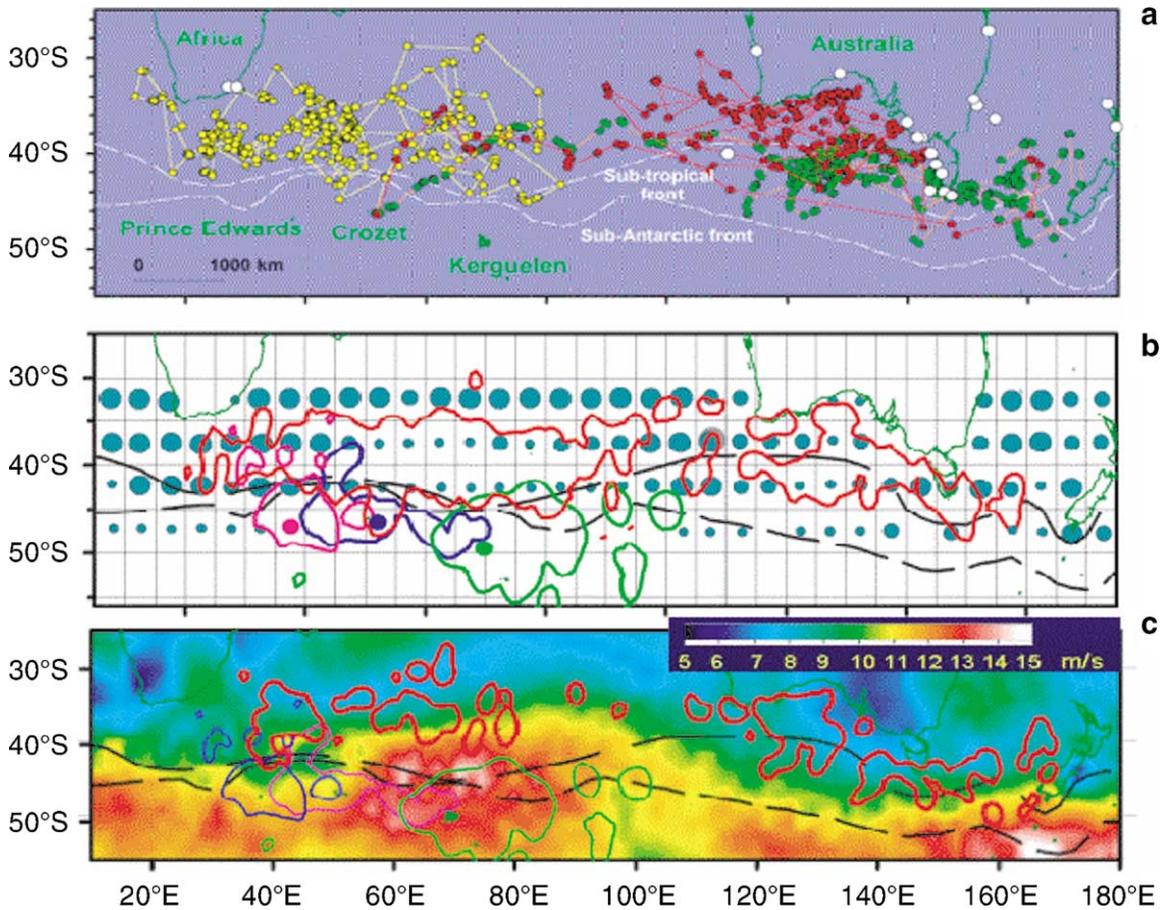
Fig. 2. Movements and foraging zones of 13 juvenile wandering albatrosses. a. Tracks of three individuals during trips of 6–13 months. White dots indicate recaptures of banded immature birds (aged 1–5) from Crozet Island, with no band return from the Atlantic and Pacific Oceans. b. Foraging ranges (95% kernel contours) of juveniles (contours in red, all locations November–October) and of breeding adults from the three major nesting grounds of the species in the area (pink: Prince Edward Islands (from Nel et al. 2002), blue: Crozet Islands, green Kerguelen Islands). Also shown is the distribution of reported long-line fisheries south of 30°S: the diameter of circles increases according to hook ranges, 1–250 000, 250 000–1 million, >1 million hooks set by five-degree squared averages over 1990–1998 (from Tuck et al. 2003). c. Foraging range of juvenile (contours in red, May–June) and adult wandering albatrosses in relation to average wind speed in May–June 2002 and 2003.
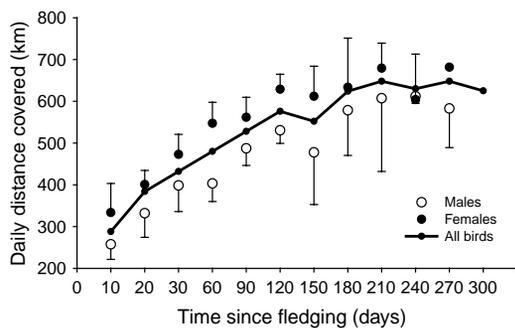

Fig. 3. Change over time since departure from birthplace in the average distance travelled daily by juvenile wandering albatrosses. The birds appear to attain a maximum value of 600 km per day after 6 months, i.e. a flight efficiency similar to that of adults. Females have higher travelling rates than males from the departure from the colony (mean±one SE).

The second and more mobile phase of dispersal probably corresponds to the period of learning when birds disperse in several directions, with their movement being strongly influenced by wind conditions. The foraging success of wandering albatrosses is strongly influenced by the distance covered daily (Salamolard and Weimerskirch 1993). Juveniles progressively increased this distance during the first months at sea. Distances showed a tendency to reach a plateau at 600 km per day which roughly corresponds to the daily distance covered by adults (Salamolard and Weimerskirch 1993), indicating that juveniles attained the flight efficiency of adults after six months. Interestingly, there were sex-specific differences in mobility during the early stages of the learning phase, with females covering longer distances per day than males, a

phenomenon that also occurs in adults (Salamolard and Weimerskirch 1993). After the first six months of independence when flight skills comparable to those of adults have been acquired, juvenile birds still have to improve their foraging efficiency and settled in more restricted geographical sectors of the ocean, noticeably in the Australian region (Fig. 2c). This may represent the first step in establishing an area to which a bird will return during future sabbatical years between breeding events (Weimerskirch and Wilson 2000).

During their first year at sea, in contrast to adults, juvenile wandering albatrosses are not constrained in their movements by the necessity to return regularly to their breeding grounds. Yet, contrary to what might be expected for a species with extreme wide-ranging capacities (Weimerskirch et al. 1993, 2000a), juvenile wandering albatrosses restricted their foraging range to a single oceanic basin, the southern Indian Ocean and the Tasman Sea. This is confirmed by the lack of band recoveries of 1–5 year olds in the Pacific or Atlantic Oceans (Fig. 2a). Similarly, during their sabbatical year when they are not constrained by central place foraging, adult wandering albatrosses remain in specific sectors of the Indian Ocean and the Tasman Sea (Weimerskirch et al. 1985, Weimerskirch and Wilson 2000). The foraging zones of juveniles during their first six months differ from those of adults for being restricted to the subtropical part of the Indian Ocean, a zone that is overall much less productive than the sub-Antarctic waters favoured by adults (Moore and Abbott 2000).

In contrast to other petrels and albatross species, when leaving the colony, juvenile wandering albatrosses have a dark plumage different from that of adults (Weimerskirch et al. 1989) and their flight feathers are also longer than those of adults (Weimerskirch et al. 2000b), two features that are probably adaptive for foraging in sub-tropical waters (Bretagnolle 1993). While adults rely on strong, consistent winds in the sub-Antarctic waters for foraging (Weimerskirch et al. 2000a), the comparatively longer wings and lower wing loading of young birds should give them a better ability to exploit the lighter wind conditions of the subtropics (Fig. 2c, Weimerskirch et al. 2000a, Shaffer et al. 2001). The remarkable changes in morphology and plumage of juvenile wandering albatrosses suggest that these are progressive adaptive changes to a transition from foraging in subtropical waters during the first years at sea to the areas of colder waters and higher wind speeds used by adults. This idea is supported by the fact that Amsterdam albatrosses *Diomedea amsterdamensis*, a closely related species that forages solely in sub-tropical waters (Waugh and Weimerskirch 2003), retains a dark plumage throughout its life.

The extensive use of a subtropical foraging zone by naïve wandering albatrosses has important implications for the conservation of the species, which is considered endangered due to the incidental mortality induced by long-line fisheries in the Southern Ocean (Croxall and Gales 1998), and particularly given that 70% of the world population occurs in the Indian Ocean . Whereas adult breeding birds in the Indian Ocean have limited contact with fisheries, the juvenile ranges overlap extensively with the areas used by long-line fisheries (Fig. 2b). Although a significant overlap occurs in the Australian Exclusive Economic Zone where measures are taken to reduce seabird mortality, the overlap between the foraging areas of wandering albatross and areas exploited by fisheries is large in international subtropical waters where no protective regulations currently exist (Tuck et al. 2003). The recovery of the Crozet wandering albatross is currently hindered by a decline in the recruitment rate caused by low survival of juvenile and immature birds (Weimerskirch et al. 1997, unpubl. data). Interestingly juvenile wandering albatrosses forage in pelagic subtropical waters where a large tuna fishery has expanded recently (Tuck et al. 2003). Remarkably, these birds show similar environmental preferences to those of albacore tunas *Thunnus alalunga* in the Indian Ocean (Chen et al. 2005), a species increasingly targeted by a developing Taiwanese tuna fishery. Being naïve, young albatrosses are probably also more susceptible to being caught than adult birds, and selection must therefore be very strong during the first year of learning. The results of our study highlight the importance of considering the movements and distribution of all age classes and genders of a population to fully understand the conservation status of this seabird species. In particular, the recovery of the Crozet wandering albatross population is likely to be due in a large extent by recruitment of young birds. Future efforts to protect wandering albatross populations should therefore focus on the tuna fisheries operating in international sub-tropical waters where these birds spend their first years of life.

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