THE POPULATION DYNAMICS OF TROPICAL SEABIRDS ESTABLISHING FRONTIER COLONIES ON ISLANDS OFF SOUTH-WESTERN AUSTRALIA

J.N. DUNLOP

Conservation Council (WA), 2 Delhi Street, West Perth, Australia, 6005
nic.dunlop@conservationwa.asn.au

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SUMMARY

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Significant changes have been observed since 1900 in the distribution and abundance of populations of at least eight tropical seabird species off south-western Australia, south of the Houtman Abrolhos Islands. The observed changes have involved a southward shift in breeding distribution or the rapid growth of colonies located on or beyond previous limits. The rate of change appears to have accelerated over the last three decades.

A study that encompassed the entire establishment period of one "frontier colony" was used as a framework for a demographic transition model extrapolated to other frontier colonies. A wide range of historical observations, together with more detailed recent studies, are brought together to propose a general hypothesis to explain the observed changes in tropical seabird population dynamics in the region.

Key words: Population dynamics, seabird colonies, demographic transition, Leeuwin Current, south-western Australia

INTRODUCTION

The present paper reviews the trends observed in the population dynamics of a group of tropical seabird species breeding on islands around south-western Australia. It proposes a general model for the establishment and growth of frontier colonies that now occur south of the historical breeding range of these species populations.

The marine environment of south-western Australia

The continental islands along the coast of south-western Australia, between 26°S and 34°S latitude, provide breeding stations for a range of tropical-, temperate- and cool-water, and cosmopolitan seabird species. Tropical- and cool-water species often occupy the same islands whilst foraging over different water masses (Serventy *et al.* 1971, Dunlop & Wooller 1990, Wooller *et al.* 1991).

The biophysical processes of continental shelf and slope waters in this region are strongly influenced by the Leeuwin Current. This relatively warm, low-salinity current can be distinguished against cooler background waters meandering southwards along the outer shelf from North-West Cape (22°S) to Cape Leeuwin (34°S) and then eastwards along the south coast of Australia towards the west coast of Tasmania (Waite *et al.* 2007).

The Leeuwin Current blankets the cold, northward-flowing Westralia Current, preventing the deeper nutrient-bearing waters entering the photic zone along the continental slope. The upwelling associated with other eastern boundaries is suppressed, and clear-water oligotrophic conditions prevail. Phytoplankton production is relatively low, as is pelagic consumer–fish biomass. The dominant food chains and fisheries in the littoral waters of the region are based on primary production from species-rich communities of benthic macroalgae, seagrasses and corals (Waite *et al.* 2007).

The relatively warm, lower-salinity waters of the Leeuwin Current enable southward dispersal of many tropical marine organisms and the establishment of some populations at relatively high latitudes, at least for an eastern boundary. For example, substantial hard coral reefs occur at the Houtman Abrolhos (at 28°S) and many scleratine coral species establish long-lived colonies within sheltered limestone reef habitats as far south as 34°S (Pearce & Walker 1991, Waite *et al.* 2007).

There are marked interannual variations in the velocity and extent of the Leeuwin Current and in the behaviour of its eddy structures (Waite *et al.* 2007). Because this Indian Ocean current sources much of its flow from the Pacific, via the Indonesian Through-flow, its behaviour is strongly influenced by the El Niño Southern Oscillation (ENSO). In El Niño years, the Through-flow decreases, weakening the Leeuwin Current and reducing the recruitment of Western Rock Lobsters *Panulirus cygnus* (Pearce & Phillips 1988; Feng *et al.* 2003, 2004). It is currently postulated that marine productivity in the region may depend in part on the cross-shelf transport of nutrients by eddies from littoral to oceanic waters (Waite *et al.* 2007). If that is the case, then prey resources for pelagic marine consumers would be more limited during ENSO events.

The frequency of ENSO events has increased over the last century and particularly in the last three to four decades. The trend towards a much higher frequency, duration and magnitude of El Niño events is predicted to continue as a result of anthropogenic climate change (Pattiaratchi & Buchan 1991). Given the equatorial origin of part of the Leeuwin Current flow, mean sea temperature might be expected to decline off south-western Australia with increasing El Niño frequency. However sea temperatures on the continental shelf between the Houtman Abrolhos and Fremantle have risen between 0.6°C and 1°C over the last 50 years (Pearce & Ming Feng 2007) indicating that other factors are influencing background oceanographic conditions.

RESULTS

Observed changes in tropical seabird distribution and population size in south-western Australia

During the colonial period in Western Australia (*c.* 1900), colonies of tropical terns (Sooty Terns *Sterna fuscata,* Bridled Terns *S. anaethetus,* Roseate Terns *S. dougalli,* Brown Noddies *Anous stolidus,* Lesser Noddies *A. tenuirostris*) bred as far south as the Pelsaert Group in the Houtman Abrolhos at 26°S (Fig. 1). Small numbers of Red-tailed Tropicbirds *Phaethon rubricauda* also nested there, although somewhat episodically, around that time. The tropical Wedge-tailed Shearwater *Puffinus pacificus* bred in small numbers as far south as Rottnest Island (32°S) in 1889 (Storr 1964, Ford 1965, Serventy *et al.* 1971 Storr *et al.* 1986). Since then, tropical seabird species and populations have apparently expanded south of the Houtman Abrolhos, particularly in the region below 30°S. The observed changes have involved incursions of seabirds outside their former ranges, the growth of colonies near the southern limit of their range, the establishment of frontier breeding colonies south of the original limits, and the expansion and consolidation of populations in colonized areas (e.g. Storr 1959, Dunlop & Wooller 1986, Dunlop & Wooller 1990, Dunlop & Goldberg 1999, Dunlop & Mitchell 2001). The documented observations involving six species are summarized in the subsections that follow.

Wedge-tailed Shearwater Puffinus pacificus

Rottnest Island (at 32°S) lies at the southern edge of the breeding distribution of the Wedge-tailed Shearwater off Western Australia. The burrows of the species were first recorded at Cape Vlaming on the island's western tip in 1889 and may have been absent in 1840 (Storr 1964). A small number of burrows were present in 1904, nearly 600 in 1956, 2570 in 1982, 5865 in 1993 and 11 745 in 2002 (Bancroft 2004).

Shearwaters experience delayed maturity and variable breeding success, raise only a single chick when successful, and defer breeding in years when foraging conditions are adverse (Dunlop *et al.* 2002, Brooke 2004).

An exponential growth curve can be fitted to the time series for shearwater burrows on Rottnest Island using immature survival of 0.85 to 0.89, adult survival of 0.92, and breeding success at 0.5. This curve would yield an innate capacity for increase (r) of 0.06

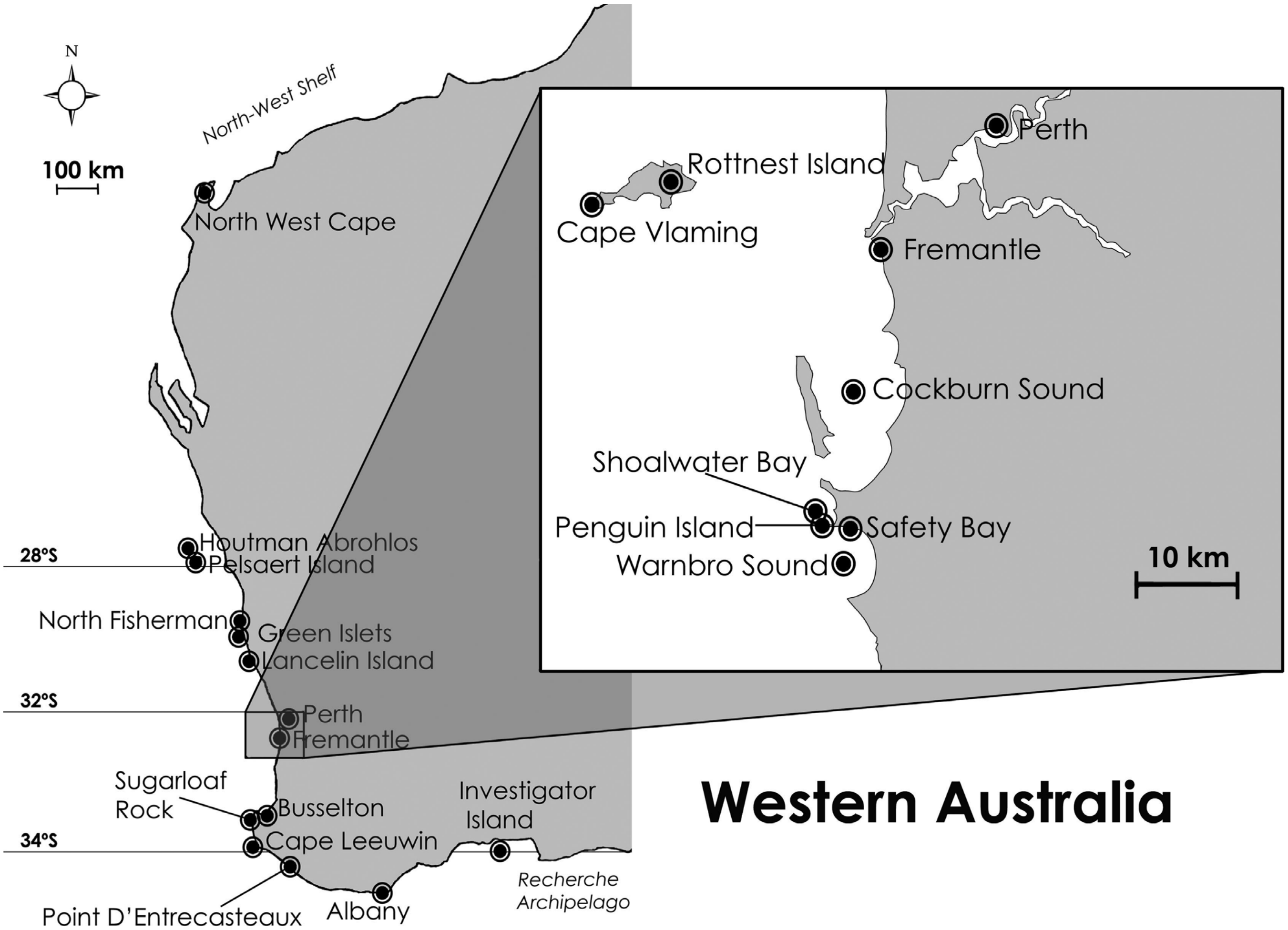

Fig. 1. Map of Western Australia showing localities mentioned in the review.

and an annual growth increment rate of 1.06 (anon. referee): high for a Procellariiforme, but not unrealistic, assuming a consistently high reproductive output. Under these circumstances, immigration need not have been a significant driver beyond the earliest establishment years.

The reproductive performance of Wedge-tailed Shearwaters breeding off the coast of Western Australia has been shown to be highly variable and generally poor over a vast geographic area during ENSO events (Dunlop *et al.* 2002, Surman & Nicholson 2009). At three colonies on the North West Shelf, fledging success per occupied burrow ranged from around 50% to a low as 5% in El Niño years between 1994 and 2000. Much of this variation was a result of the participation rate—that is, the number of birds with excavated burrows that ultimately laid an egg. Over the period, the participation rate varied (depending on the colony and season) from nearly 80% to below 20%.

At the Abrolhos Islands during the 1997/98 El Niño, laying was negligible, with around 2% of excavated burrows having eggs (Dunlop *et al.* 2002). Between 1991 and 2007 shearwater mean breeding success (as chicks reared per egg laid) ranged from 21.6% in four years when food availability was poor to 46.9% in seven years where food was less limiting (Surman & Nicholson 2009).

Breeding performance was observed at the Rottnest Island colony in the 1991/92 season (Garkaklis 1992, Garkaklis *et al.* 1998), during the extended El Niño period of the early 1990s. Breeding success per egg laid was 45.9%, but the relevant measure for a population being estimated by active burrow counts is breeding success per burrow. This works out at 15.1% because of the low participation rate in that year.

These studies suggest that, over the latter period of rapid population growth on Rottnest Island, the breeding performance of Wedge-tailed Shearwaters on the coast of Western Australia has varied from moderate to very low, with poor performance during the increasingly frequent El Niño years.

The Rottnest population has in fact been growing over a period of declining breeding performance in the region attributable to the increasing ENSO frequency (Surman & Nicholson 2009). Breeding success was unlikely to approach the 50% assumed in the model, and frequent difficult breeding conditions were likely to have reduced the post-fledging fitness of progeny in some years. It is highly probable therefore that the rapid growth in the Rottnest colony has been largely driven by immigration caused by the displacement of recruits from colonies further north.

Red-tailed Tropicbird Phaethon rubricauda

Red-tailed Tropicbirds have nested, somewhat intermittently, on the Abrolhos Islands over the period of historical record. Pairs attempted to breed at Busselton in 1939 and on Rottnest Island between 1957 and 1959. A group became established at Sugarloaf Rock (Cape Naturaliste 33°34′S) in 1966/67, and this colony grew to 34 pairs by 1969/70 (Tarburton 1977, Dunlop & Wooller 1990).

Between 1987 and 1997, 15 to 18 pairs nested each season with individuals and pairs apparently missing some seasons. Breeding success was low, with up to four chicks fledging in the better seasons. Squid were an important component of the diet in the better years. No natal recruitment was recorded from about 100 marked chicks. By 2007 only one breeding pair remained (K. Williams, Department of Environment and Conservation, WA, pers. comm.).

Roseate Tern Sterna dougallii

Roseate Terns have autumn/winter and spring/summer breeding populations. The former are believed to have colonized the Abrolhos in the 1890s, were breeding as far south as Green Islets (30°41′S) by the 1950s and in Warnbo Sound (32°18′S) and around Rottnest Island (31°59′S) in the early 1980s. An irruption of nuptial-plumaged birds was recorded in the Cockburn Sound region in the autumn of 1958, although this event apparently did not lead to the establishment of new colonies at the time (Storr 1959, Ford 1965). Spring breeders were already present at the Abrolhos in 1843 and had reached Green Islets by the 1950s, Lancelin Island (31°00′S) by the mid-1970s and Shoalwater Bay (Seal Island 32°18′S) by the mid 1990s (Dunlop & Wooller 1986, 1990).

Crested Tern Sterna bergii

Spring/summer breeding colonies of Crested Terns occur in most island groups around mid- and south-western Australia. Autumn/winter colonies dominate in northern waters and have been reported from a few localities along the western and southern coasts. An autumn/winter breeding population of Crested Terns became established in the vicinity of Rottnest Island around 1978 and persisted alongside the spring breeding population until sometime in the 1990s (Dunlop 1985, Dunlop 1987, Dunlop & Wooller 1990).

The autumn/winter breeding component of the Crested Tern population in the Fremantle area post 1978 disappeared sometime in the 1990s (pers. obs.). The precise timing of this change is unknown, because the species was not being monitored at the time. The demise of this breeding subpopulation in the area was probably the result of two catastrophic Pilchard *Sardinops sagax* fish kills in 1995 and 1997 that removed their preferred prey resources.

Bridled Tern Sterna anaethetus

Bridled Terns were observed breeding in the Abrolhos in 1843, but were not recorded further south until 1889, by which time the species was observed around Rottnest Island. It was recorded from the Safety Bay area in 1901, where breeding on the smaller islands in Shoalwater Bay (32°18′S) was observed by 1921. The species had reached the islands around Cape Leeuwin (34°23′S) by 1956 (Dunlop & Wooller 1990).

The Bridled Tern was the earliest species to shift distribution southwards. Recent decades have seen remarkable growth in the size of some colonies south of the Abrolhos (e.g. North Fishermen, Lancelin, Penguin and Rottnest islands) and a general infilling of the southern breeding areas (Dunlop & Wooller 1990; Dunlop & Jenkins 1992, 1994). There are unpublished reports of the species breeding along the western south coast of Western Australia near Point d'Entrecasteaux in the late 1990s. In January 2008, a small group was recorded on Haul Out Rock (34°42′S, 118°39′E) near Albany, and in December 2007, Bridled Terns were observed on Investigator Island (34°05′S, 120°52′E) on the eastern south coast, suggesting that the species had nearly reached the Recherche Archipelago (J. Pridham & R. Campbell, pers.comm.). An expedition to Investigator Island on 23 January 2008 confirmed a successful breeding colony of around 400 pairs that could have been present for at least a decade (JND, in prep.).

Brown Noddy Anous stolidus

Prior to 1991/92, Brown Noddies had not been recorded breeding south of Pelsaert Island in the Houtman Abrolhos (28°54′S) (Surman & Wooller 2003). In that year, five pairs were discovered nesting on Lancelin Island (31°00′S). The Lancelin colony grew exponentially between 1994/95 and 1997/98 and had reached around 900 pairs in 1998/99 (Dunlop & Mitchell 2001).

Dunlop (2005) analysed the demographic changes that occurred in this colony from 1991/92 until 2003/04. A demographic transition model based on that study is proposed in this paper and extrapolated to some of the other frontier colonies documented off south-western Australia. By the 2007/08 season, the Lancelin Brown Noddy colony was estimated to be around 1200 pairs (pers. obs.).

In the 2003/04 season, Brown Noddies began prospecting Penguin Island (32°S); they continued to do so during late December and January in 2004/05, 2005/06 and 2006/07 (pers. obs.). However no prospecting noddies were observed in the 2007/08 season.

Sooty Tern Sterna fuscata

Until recently, Sooty Terns had not been reported breeding south of Pelsaert Island (28°54′S) in the Houtman Abrolhos (Surman & Wooller 2003), although non-breeding birds were recorded as far south as the Fisherman Islands (30°08′S). Prospecting Sooty Terns were observed over Lancelin Island during the 1996/97 and 1997/98 seasons. Six pairs nested on that island in the 1998/99 season (Dunlop & Mitchell 2001), and the colony expanded to 16 pairs in 2003/04 and 30 pairs in 2006/07.

Sooty Terns began prospecting Penguin Island (32°S) in the 2003/04 season and continued to do so during late December and January in 2004/05, 2005/06 and 2006/07 (pers. obs.). However no prospecting Sooty Terns were observed in the 2007/08 season.

Demographic changes in frontier colonies

The observed southward shift in tropical seabird species and populations has occurred in species with both high and low colony or nest-site fidelity. Roseate and Crested Terns both nest in dense, synchronous clusters where the geographic locations of colonies and the relative positions of nest sites are determined by pre-laying interactions between pairs in a prospecting flock (e.g. Dunlop 1987). Terns that adopt this breeding strategy can establish closer to prey concentrations by moving between islands within a natal area (e.g. Dunlop 1987), or in the context of a long-term broad-scale decline in prey availability, even shift between regions (e.g. Crawford 2003).

Colour-banding confirmed the interseasonal movement of Crested Tern breeding adults and pairs between islands and colonies in the Fremantle region (Dunlop 1985). Breeding adult Crested Terns marked in South Australia showed both patterns of dispersal with birds marked in the Gulfs being exchanged between colonies within the region, whilst some birds breeding elsewhere moved to colonies up to 2000 km away from their original location (Waterman *et al.* 2003). No banding data are available on the movements of Western Australian Roseate Terns. Experienced adults are likely to be amongst the founders of frontier colonies outside former distributions in seabirds that adopt this flexible strategy.

Few tropical seabirds have been banded as nestlings or fledglings at the Abrolhos or at other colonies further north. Consequently, the probability of encountering the emigration of recruits from these colonies at frontier colonies was extremely remote. However, Wedge-tailed Shearwaters (Dunlop *et al.* 2002), Red-tailed Tropicbirds (Fleet 1974), Bridled Terns (Dunlop & Jenkins 1994, Dunlop & Rippey 2006), Sooty Terns (Harrington 1974, Feare & Lesperance 2002, Feare & Doherty 2004) and Brown Noddies (Morris & Chardine 1992,Dunlop 2005) are all species in which established breeders retain nest sites within colonies between years, although local shifts (generally within a few metres) may be forced by physical changes to the habitat, by divorce or by breeding failure. The young are philopatric, with the majority recruiting to their natal colony, as was the case in this region for the Bridled Tern on Penguin Island (Dunlop & Jenkins 1994) and the Brown Noddy on Lancelin Island (Dunlop 2005), where nesting habitat and foraging conditions remained conducive to successful breeding.

The seabird species that establish long-term breeding colonies at particular locations should provide the best information on the marine environment as their population dynamics must integrate the trends in prey availability within foraging range (Hamer *et al.* 2006). The demographic changes occurring within frontier colonies are potentially a window into both the intrinsic socio-biology of colonial breeding and into the shifts occurring in marine ecosystems.

In the 1991/92 spring/summer season, five pairs of the Brown Noddy were discovered on Lancelin Island (31°S). These were the founders of a frontier colony 275 km south of the probable source or core population, on Pelsaert Island in the Houtman Abrolhos Group (28°S). The growth and demographic structure of this colony has been studied since 1994/95 and documented up to the 2003/04 season by Dunlop (2005).

Over its first 13 years, the Brown Noddy colony on Lancelin Island moved from a small founder group to a period of slow early growth with the arrival of more colonists (1992–1994), to a period of exponential growth driven by rapid immigration (1995–1997), to a period of continued immigration augmented by natal recruitment (1998–2000) and finally to a period of slowing growth supplied primarily by natal recruitment (2001–2003). It was calculated that net immigration ceased to contribute to population increase by the 2003/04 season. It was predicted that the colony would continue to grow based on natal recruitment whilst nesting habitat space was readily available (Dunlop 2005). Between 2003/04 and 2007/08, the colony grew from just over 900 pairs to around 1200 pairs, broadly consistent with the prediction. The habitat used by Brown Noddies and Sooty Terns on Lancelin Island is widespread and is not currently (2008) limiting the spatial extent of those colonies.

The Brown Noddy colony on Lancelin Island is the only one that has been followed through its entire establishment period, from initial settlement to self maintenance. The other colonies have been studied during various stages of a proposed demographic transition. The model diagram (Fig. 2) shows the various stages in the transition and allocates some studied frontier colonies to their current stage.

The Red-tailed Tropicbird colony on Sugarloaf Rock has evidently failed because of insufficient natal recruitment—despite the persistence of some marked colonists for nearly five decades (K. Williams pers. comm.). By contrast, the Wedge-tailed Shearwater colony on Rottnest Island is still in its exponential growth and rapid immigration phase after nearly a century. Given that the Brown Noddy on Lancelin Island completed the transition in only 13 years, it is clear that the time scale for the demographic transition can vary significantly because of a range of factors. These probably include the age of first breeding and the number of non-breeding years at the frontier location (all of which influence natal recruitment) and the supply of immigrants from source colonies. It is interesting that the highly pelagic Sooty Terns appear to be only just on the threshold of the rapid immigration phase after 11 years on Lancelin Island.

The Bridled Terns on Penguin Island have expanded across all habitats through the peripheral establishment of natal recruits, a process that has been happening since at least the early 1990s (Dunlop & Jenkins 1994). Today, all available cover on the island is occupied by Bridled Terns, and it is likely this relatively large colony is a source of colonists for new colonies.

Processes underlying the redistribution of tropical seabirds off southwestern Australia

The tropical seabirds establishing frontier colonies are normally philopatric, indicating that in these species the probability of a high lifetime reproductive output is usually enhanced by recruitment to the natal colony or natal area. Philopatric behaviour may, however, break down in response to a decline in colony habitat quality (Kildaw *et al.* 2005), excessive predation on breeding islands (Feare & Lesperance 2002), high ectoparasite concentrations (Feare 1976) or reduced prey availability within foraging range of the breeding station (e.g. Crawford 2003). Because the establishment of frontier colonies in south-western Australia involves a range of species populations from a variety of potential sources, the driver is likely to be related to broad-scale changes in prey availability or marine productivity.

The ENSO is known to produce major shifts in tropical seabird breeding performance and even survival in the Pacific Ocean because of collapses in marine productivity (Schreiber 2002). These impacts have also been observed in the Indian Ocean (e.g. Reville *et al.* 1987, Ramos *et al.* 2006). Wedge-tailed Shearwaters breeding on islands on the North West Shelf of Western Australia (Dunlop *et al.* 2002) had very poor breeding participation and fledging success in El Niño years (e.g. 1997, 2002) compared with other years, and a lag relationship was observed between the number of burrows excavated at the start of each season and the Southern Oscillation Index (SOI). In the 1997 event, there was also almost complete breeding failure in Wedge-tailed Shearwaters on the Houtman Abrolhos Islands (Dunlop *et al.* 2002).

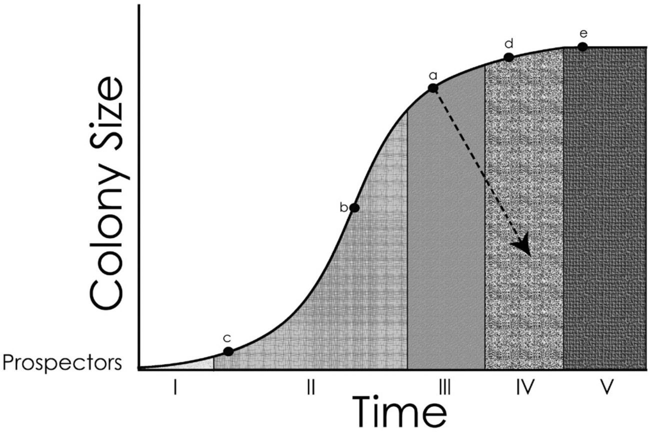

Fig. 2. Model diagram showing the different stages in the demographic transition allocating some studied frontier colonies to their current stage.

The Brown Noddy and Sooty Tern colonies at Houtman Abrolhos and Lancelin Island were monitored simultaneously between 1994 and 2002. Breeding in both species failed on the Abrolhos in 1997 and again in 2002 (C. Surman pers. comm.)—that is, during the strong El Niño years. By contrast, the establishing frontier Brown Noddy colony at Lancelin Island continued to expand in both of those years with moderate chick survival to fledging (Dunlop 2005, pers. obs.). The Sooty Tern colony on Lancelin Island was very small at this stage, but in both years during which laying failed at the Abrolhos, the Lancelin birds were incubating—although fledging success was not known (pers. obs.).

A compilation both of recent observations and of published historical records indicates that prospecting or nesting events in tropical seabirds outside their former breeding distribution generally occurred during El Niño periods (i.e. when the SOI was low; Fig. 3). Collectively, these observations suggest that failures in marine productivity associated with ENSO events around core (northern) colonies may force the dispersal of pre-breeders (in philopatric species) away from foraging areas near their natal colonies during the breeding season. The displacement of these birds, and the discovery of new productive foraging areas, probably underlies their appearance at seabird breeding islands further south.

The frequency and intensity of El Niño events have both been increasing over the last century, but particularly over the last three

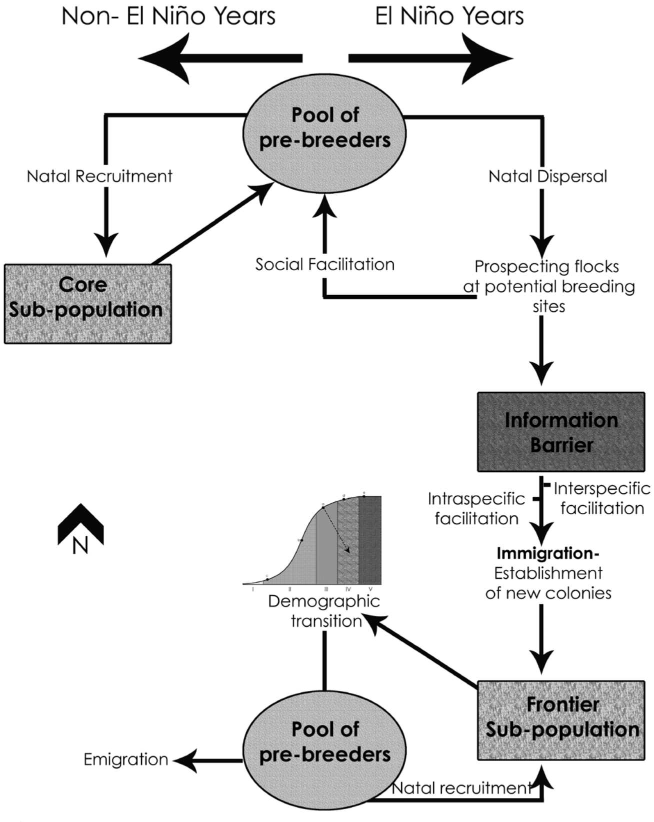

Fig. 3. Schematic representation of the current model for tropical seabird re-distribution in south-western Australia.

to four decades [Timmermann *et al.* 1999, Bureau of Meteorology SOI data (www.bom.gov.au/climate/current/soi2.shtml)]. This trend is consistent with climate change modelling (Pattiaratchi & Buchan 1991) and will presumably continue to drive changes in tropical seabird population dynamics in the eastern Indian Ocean. The relatively successful breeding performance under El Niño conditions recorded at some frontier colonies (e.g. Lancelin Island) compared with the large established colonies further north (i.e. the Houtman Abrolhos) may be the result of reduced competition or may indicate the appearance of new pockets of productivity. A weaker Leeuwin Current reduces the cross-shelf transport of nutrients from the littoral zone to oceanic waters, but may also allow some minor upwelling at the shelf edge, at least in areas with a favourable bathymetry. However, there is nothing to indicate that these productive zones are comparable in scale to those that normally support hundreds of thousands of breeding Brown Noddies and Sooty Terns at the Abrolhos (Gaughan *et al.* 2002).

Although the increasing frequency and intensity of the El Niño may be an important driver of tropical seabird dislocation, other factors, such as the background rise in sea temperature, may allow tropical seabird prey and most frontier subcolonies to persist at higher latitudes.

Fig. 3 is a schematic representation of the current model for tropical seabird re-distribution in south-western Australia. The model applies to seabird species with high adult site fidelity and natal philopatry. The displacement of pre-breeders from foraging areas around core or source colonies does not necessarily lead to the settlement of potential colonists. The lack of nesting conspecifics presents an "information barrier" to prospectors with no experience of a potential breeding site with respect to predator security or the reliability of marine prey resources (Kildaw *et al.* 2005). For example, Brown Noddies and Sooty Terns prospected Penguin Island during December and January from 2003/04 to 2006/07 without settling (pers. obs.).

Ultimately, the information barrier may be overcome by the advanced breeding and nutritional condition of some prospectors, by the increasing size of prospecting flocks (critical mass) or by the stimulus provided by similar "associated" species that may have shared the natal habitat. Following settlement, the eventual establishment of frontier colonies will depend on the ability of the colonist pairs, and later immigrants, to replace themselves in the new environment.

DISCUSSION

Interactions of environmental change and demographic processes in frontier colonies

Seabird colonization events are rare apparently because prospective breeders are reluctant to start new colonies despite the high costs of recruitment to well established ones (Tims *et al.* 2004, Kildaw *et al.* 2005). When they are observed, such events provide an opportunity to investigate the role of colonial breeding and environmental change in seabird population dynamics.

The frontier colonies of tropical seabirds in south-western Australia share many of the characteristics observed in new colonies elsewhere. New colonies were formed at times where there was evidence of habitat decline (in this case marine) around the established colonies. In the pioneering of new colonies, factors such as island or marine habitat quality at the original (core) colonies were more likely than the quality of individuals to be more important (Kildaw *et al.* 2005).

Once initiated, the frontier colonies are strongly attractive to prospectors, and at least during periods of food stress, may be more productive than core colonies (Tims *et al.* 2004). Rapid immigration dominated the early growth of new colonies. The age of first breeding at frontier colonies was significantly younger, as presumably was the overall age structure because of the accession of inexperienced immigrants [Brown Noddy (Dunlop 2005), Common Tern *S. hirundo* (Tims *et al.* 2004)].

Of particular interest was the decline in the immigration and growth rate of the frontier colony with the increasing availability and influence of natal recruits (Dunlop 2005, Fig. 2). In the Brown Noddies on Lancelin Island, the immigration rate declined long before breeding habitat became a limiting factor or before competition for prey (for an oceanic species) was plausible. This suggests that natal recruits, with experience and familiarity with the colony's structure and its foraging area, may have a competitive advantage over immigrants and negate further recruitment from other colonies.

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