THE GOOD, THE BAD AND THE UGLY: ENSO-DRIVEN OCEANOGRAPHIC VARIABILITY AND ITS INFLUENCE ON SEABIRD DIET AND REPRODUCTIVE PERFORMANCE AT THE HOUTMAN ABROLHOS, EASTERN INDIAN OCEAN

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SUMMARY

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Each spring/summer more than a million pairs of seabirds breed at the Houtman Abrolhos, Western Australia, the most significant seabird breeding site in the Eastern Indian Ocean. The southward-flowing Leeuwin Current is the dominant oceanographic feature influencing the region, in conjunction with the northward-flowing Leeuwin Undercurrent and the Capes Current. Seabirds at the Houtman Abrolhos are reliant wholly upon marine sources of food, and several species feed predominately upon larval ichthyoplankton species, the availability of which has been found to play a pivotal role in their reproduction. We conducted a comparative study of the timing of breeding, breeding participation and reproductive success over a 17-year period of four tropical pelagic seabird species in relation to the regional oceanographic conditions affecting the Leeuwin Current. Three tern species, the Lesser Noddy *Anous tenuirostris,* Brown Noddy *A. stolidus* and Sooty Tern *Sterna fuscata,* and the Wedge-tailed Shearwater *Puffinus pacificus* comprised our study species at the Houtman Abrolhos between 1991 and 2007. The diet of these species was also investigated between 1991 and 2000. Life-history traits determined the response of these seabirds to fluctuations in marine resources caused by variation in the flow of the Leeuwin Current. During El Niño Southern Oscillation (ENSO) events, reproductive effort and output were severely reduced in all species, which coincided with reduced volumes of key prey species in regurgitates. Between 1991 and 2000, ENSO driven changes in the Leeuwin Current resulted in lower participation rates and reduced breeding success or catastrophic breeding failure for all four seabird species and delayed timing of breeding for the tern species. Between 2000 and 2007, the relationship between each ENSO event and a subsequent poor reproductive season was not as strong. Increasing years of poor breeding performance were recorded outside El Niño periods, accompanied by a significant seasonal delay in the onset of breeding in the three tern species. Based on our seabird observations, we postulate that in recent years the high number of ENSO events have resulted in a regime shift in offshore and oceanic planktonic food chains off central Western Australia. The use of seabirds as an upper-trophic-level indicator of change in marine productivity as a result of variability in the Leeuwin Current system is discussed. The possibility that tropical seabirds in the region are adapting to a new suite of prey, dictated by a Leeuwin Current system which is influenced by more frequent ENSO events, is also discussed.

Key words: ENSO, Leeuwin Current, Seabirds, Houtman Abrolhos, Diet, Reproductive Performance

INTRODUCTION

The effects of prey availability on the reproductive performance of seabirds has been well documented for seasonal climates (Monaghan *et al.* 1992, Kitaysky *et al.* 1999, Rindorf *et al.* 2000, Furness & Tasker 2000); the effects of less predictable patterns of prey availability upon tropical seabirds are still being explored (Ramos 2000, Ramos *et al.* 2002, Surman & Wooller 2003, Jaquemet *et al.* 2007, Monticelli *et al.* 2007). Seabirds respond negatively to reduced prey availability, and this effect is compounded in surface feeders (as compared with pursuit divers) and in seabirds with low diet diversity (Gaughan *et al.* 2002). Typical responses are reduced breeding success (Ramos 2000, Rindorf *et al.* 2000) and reduced breeding attempts (Crawford & Dyer 1995). The localised and regional environmental factors that affect prey availability, as measured by changes to local seabird breeding phenology and effort, are just beginning to be identified and understood (Ashmole & Ashmole 1968, Diamond 1983, Schreiber & Schreiber 1986, Gaughan *et al.* 2002, Ramos *et al.* 2002, Frederiksen *et al.* 2004, Jaquemet *et al.* 2007, Monticelli *et al.* 2007).

The influence of the El Niño Southern Oscillation (ENSO) on ocean currents, sea levels and fisheries off the Western Australian coast has been well documented (Pearce & Walker 1991, Pearce 1997). There is evidence that the ENSO profoundly influences the availability of prey to the region's tropical pelagic seabirds, resulting in reduced breeding participation and reduced breeding success, probably by inducing changes in the oceanographic conditions that drive marine productivity (Surman 1998, Dunlop *et al.* 2002, Gaughan *et al.* 2002, Nicholson 2002).

The Houtman Abrolhos is located at 28°S and contains one of the southernmost extensions of tropical marine flora and fauna in the Indian Ocean, principally because of the flow of the Leeuwin

Current, which is a body of warm (>24°C), low-salinity (<35‰) water that flows southward along the continental shelf of Western Australia in a broad and shallow band (200 km wide by 50 m depth) at speeds of up to 2 km h^{-1} (Cresswell 1990, Pearce & Walker 1991). The strength of the flow of the Leeuwin Current varies both annually in its cycle and seasonally. It flows principally in winter, between April and July, and its strength and temperature are affected by ENSO events. In ENSO years, the Leeuwin Current is weaker, resulting in cooler, more saline water along the outer continental shelf (Pearce & Walker 1991). Higher sea levels and warmer sea temperatures occur along the Western Australian coastline during non-ENSO years, resulting in the Leeuwin Current having a stronger southward flow (Cresswell *et al.* 1989). Associated with the Leeuwin Current are the northward-flowing Leeuwin Undercurrent at the subsurface, and the northward-flowing Capes Current on the continental shelf during the summer months (Pattiaratchi 2005). The dynamics of the Leeuwin Current system in the delivery and distribution of seabird ichthyoplankton prey at the Houtman Abrolhos is not clearly understood.

Most studies agree that seabird breeding is specifically timed to coincide with maximal food supply (Ashmole & Ashmole 1968, Diamond 1983, Ainley *et al.* 1986, Ramos *et al.* 2002, Frederiksen *et al.* 2004, Jaquemet *et al.* 2007, Monticelli *et al.* 2007). This timing varies with latitude, with high-latitude species having a narrower period of opportunity to breed because of climate and seasonal food availability, resulting in predictable breeding times, high synchrony and relatively short breeding seasons. At lower latitudes, however, breeding at some locations may commence at any time, and timing is determined only by the availability of food in reach of the colony. Because of the influence of the Leeuwin Current system, the waters surrounding the Houtman Abrolhos provide breeding seabirds with a mixture of tropical and temperate prey sources (Surman & Wooller 2003) and a breeding timetable that is highly synchronous but that, for many species, can shift in timing from year to year. The seabirds that breed at the Houtman Abrolhos are considered predominantly tropical, and they breed annually during the austral spring/summer (Surman 1998). This location is the central breeding area for the eastern Indian Ocean metapopulations of the Lesser Noddy *Anous tenuirostris,* Brown Noddy *A. stolidus,* Sooty Tern *Sterna fuscata* and Wedge-tailed Shearwater *Puffinus pacificus* (Surman 1997). The terns species share breeding times of between 75 and 85 days (Surman 1998); the Wedge-tailed Shearwater has a much longer breeding time of 120 days (Serventy *et al.* 1971) and, as a consequence, has the least ability to shift timing of breeding. The Lesser Noddy is a resident species at this location; the other three species migrate or disperse northwards during the austral winter (Surman 1997).

This paper aims to determine the influence of ENSO-induced variability in the Leeuwin Current system upon the reproductive performance of four seabird species breeding at the Houtman Abrolhos, and the relationship between current flow, food supply and reproductive performance. We hypothesized that, at the Houtman Abrolhos, seabirds were breeding later and were being less successful as time progressed during the 17-year study.

STUDY AREA AND METHODS

The study was conducted on Pelsaert Island (28°56′S, 113°58′30″E), the southernmost and third largest of an archipelago of 192 islands, islets and rocks (the Houtman Abrolhos), 60 km off the mid-western coast of Australia (Fig. 1). Pelsaert Island (120 ha) is 12 km long, only 50–500 m wide and very low (<3 m Above High Water Springs), comprising coral rubble, limestone and sand.

Study species

On Pelsaert Island, the Lesser Noddy (35 000 pairs) nests in White Mangrove *Avicennia marina* trees, the Brown Noddy (130 000 pairs) nests on low Nitre *Nitraria billardierei* and Samphire *Halosarcia halocnemoides* bushes, the Sooty Tern (260 000 pairs) nests on bare ground below herbaceous *Atriplex cinerea* and Nitre bushes, and the Wedge-tailed Shearwater (75 000 pairs) digs burrows up to one metre long in sandy areas throughout the southern portion of the island (Surman & Wooller 1995, 2000). All four species breed during the austral spring/summer. At the Houtman Abrolhos, Pelsaert Island contains 99% of Brown Noddies and 70% of Lesser Noddies breeding along the Western Australian coastline. It also contains the largest colony of Sooty Terns in the Eastern Indian Ocean and significant colonies of Wedge-tailed Shearwaters.

Breeding phenology, participation and success

Nest sites of each species were selected at random and permanently marked. Nest contents were recorded weekly over the spring/

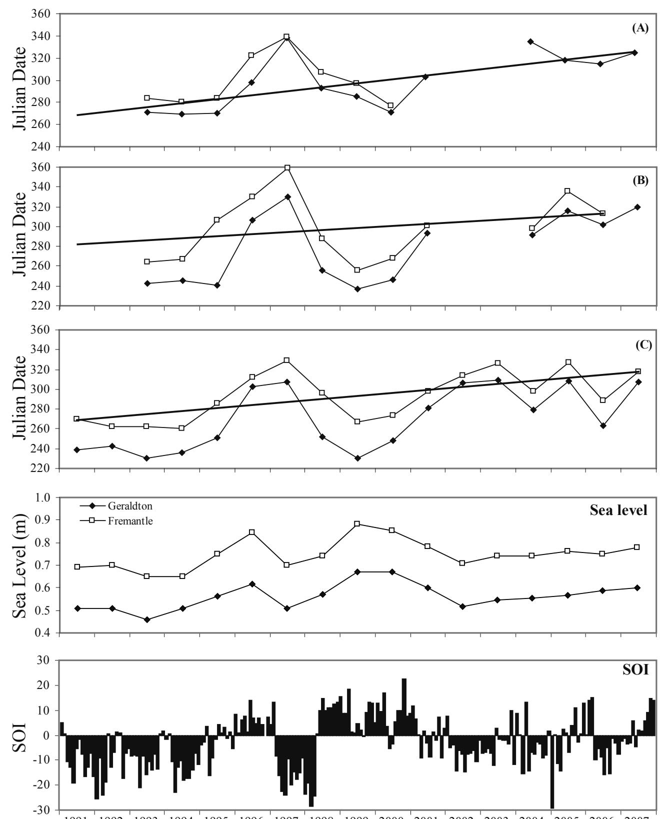

Fig. 1. Timing of breeding (Julian date, where 27 October = 300) as represented by the date of first egg (closed diamonds) and mean lay date (open squares) in the (A) Sooty Tern *Sterna fuscata*, (B) Brown Noddy *Anous stolidus* and (C) Lesser Noddy *A. tenuirostris*, with trend line for the mean lay date for Lesser and Brown Noddies and date of first egg for Sooty Terns. The sea levels at Geraldton (open squares) and Fremantle (closed squares) and at the bottom the Southern Oscillation Index (SOI) are shown for the same period. El Niño–Southern Oscillation events are associated with negative SOI values and lower sea levels.

summer period (September to May) between 1991 and 2001, and in more recent years (2002–2007) during several shorter visits between October and January of each year. There are some data gaps in these latter years, which were excluded from analyses. The burrow contents of the Wedge-tailed Shearwater were determined using an electronic burrowscope. Breeding participation was recorded as the percentage of all nest sites or burrows that contained an active breeding attempt during the breeding season.

Laying chronology was determined using lay dates of known-age eggs; the laying dates of other eggs was estimated by backdating, using egg water-loss techniques (Wooller & Dunlop 1980, Surman & Wooller 1995). Eggs known to be re-laid were excluded from calculations of the mean date of laying for each species. Chick age was estimated from growth curves described in Surman (1997).

As a measure of reproductive performance, we used breeding success or the proportion of all active breeding attempts that survived to produce a fledgling. We arbitrarily assigned those seasons when breeding success was less than 15% overall for each study species as "bad," and those above 15% as "good."

In more recent years, we have noticed that the commencement of breeding was later for the three terns studied. To test the hypothesis that, at the Houtman Abrolhos, seabirds were breeding later and were being less successful as time progressed, we divided our data into the periods 1991–1999 inclusive and 2000–2007 inclusive.

Environmental parameters

We measured ENSO events using the Southern Oscillation Index (SOI), which is based on the difference in atmospheric pressure between Tahiti, in the Pacific, and Darwin in northern Australia. The SOI is expressed as positive values (La Niña) or negative values (El Niño) (Pearce & Walker 1991). The mean monthly SOI was obtained from the Australian Bureau of Meteorology (www.bom.gov.au/).

The strength of flow of the Leeuwin Current was determined by using the mean monthly sea level at Fremantle and Geraldton, Western Australia, and these data were obtained from the National Tidal Facility, Flinders University, Australia. Sea level is measured by remote tidal gauges in centimetres and is presented in units of metres. Mean monthly Sea Surface Temperature (SST, in degrees Celsius) was obtained using the Reynold's SST database for the latitude band at 28.5°S, between 113.5°E and 114.5°E. Data were kindly provided by Alan Pearce.

Dietary samples

Adult birds recently returned from a foraging trip were captured at the nest-site by hand or using a small net, whereupon most would spontaneously regurgitate. They were marked individually with leg bands to ensure that no individual was sampled more than once during any single breeding season. A minimum of 10–20 regurgitations were collected from each tern species in each sampling month, corresponding to the incubation, small nestling and large nestling stages in their breeding cycle. Regurgitations were collected from shearwaters during the nestling stages of their breeding cycle only, because earlier in the season, they were less likely to spontaneously regurgitate. Sampling was not undertaken in the period 2002–2007.

Regurgitates were preserved in 70% ethanol, then rinsed and vacuum filtered to allow the percentage volumes of identifiable material to be estimated before obtaining the wet mass of each sample. We used a volumetric estimate that determined the surface area of a 14-cm diameter Petri dish covered by each prey type. Prey items were identified using keys (Last *et al.* 1983, Leis & Rennis 1983, Smith & Heemstra 1986, Leis & Trnski 1989, Gommon *et al.* 1994) and from reference specimens in the Western Australian Museum. The detailed methodology is described in Surman and Wooller (2003).

Statistical analysis

Data was analysed using the Statistica statistical software package (StatSoft, Tulsa, OK, USA) and was based on statistical methods described in Zar (1996). We arcsine-transformed data expressed as percentages before undertaking analysis. Long-term trends were investigated by pooling data from the study years 1991–1999 and 2000–2007 inclusive.

RESULTS

Timing of breeding

Wedge-tailed Shearwaters commenced breeding on or near 17 November each year, with no discernable variability. The mean lay date for this species varied by a single day around 23 November in each year studied. The commencement of breeding was much more variable for the three tern species.

Fig. 1 shows the date of first eggs and the mean lay date for Sooty Terns, Lesser Noddies and Brown Noddies at Pelsaert Island. Later breeding coincided with stronger ENSO events (negative SOI values) and lower sea levels. All three tern species were delayed significantly during the 1996/97 and 1997/98 austral summers, with mean lay dates 60 days later (Sooty Tern), 65 days later (Lesser Noddy) and 98 days later (Brown Noddy) than in the preceding years. This change was not significantly related to Fremantle sea levels between 1991 and 1998 ($F_{1,6}$ = 3.55, P = 0.11); however, between 1991 and 1998, the mean lay dates for both the Lesser (y = 0.02x + 18.05, R^2 = 0.67, $F_{1,6}$ = 12.18, P = 0.012) and the Brown Noddy (y = 0.02x + 19.02, R^2 = 0.74, $F_{1,6}$ = 11.73, P = 0.026) were correlated with the SST in January and March of the breeding year. These species returned to early breeding during the1999/00 and 2000/01 seasons, which coincided with the SOI becoming positive once again. The data suggest that the commencement of breeding in the three tern species had become later over the past 17 years (Fig. 1). The variability in the onset of breeding was greatest in Brown Noddies, with a range of 103 days. In years when breeding was delayed until November, there was a shorter period between the first egg laid and the mean lay date for Lesser and Brown Noddies alike.

Between 1991 and 1999, the mean dates of the first egg laid on Pelsaert Island for Lesser and Brown Noddies were 11 September and 22 September respectively; for the Sooty Tern, the mean date was 16 October. Between 2001 and 2007, this date was delayed to 15 October for Lesser Noddies, 28 October for Brown Noddies, and 7 November for Sooty Terns. The differences were significantly for the two noddy species (Lesser: t_{15} = –2.52, P = 0.01; Brown: t = –1.99, df = 12, P = 0.03), but not for the Sooty Tern (t_{11} = –1.68, P = 0.06). The mean lay date had also increased by 24 and 30 days in Lesser and Brown Noddies respectively, which was significantly later for the Lesser Noddy ($t = -2.17$, df = 15, $P = 0.02$), but not for the Brown Noddy ($t_{13} = -1.31$, $P = 0.11$, Table 1).

Breeding participation

From 1991 to 2007, delayed breeding was accompanied by a decline in the proportion of birds participating in that year for all tern species (Fig. 2). Poor breeding participation was most evident during the lead-up to, and continuing into, the 1997/98 and 2002/03 ENSO events for all four species. Wedge-tailed Shearwaters did not attempt to breed at all during the 1997/98 ENSO event. The Lesser Noddy appeared to be the least affected of the four species by these events (Fig. 2) and, overall, had the least fluctuation in breeding participation (from 39.6% to 54.7%) when the mean participation rates for bad years and good years were compared (Table 2). Mean Sooty Tern breeding participation varied the most between bad and good years, from 0.3% to 49.5% ($t_9 = 4.82$, $P < 0.001$). Mean Brown Noddy breeding participation also varied significantly ($t_9 = -3.16$, $P = 0.008$), but mean breeding participation in both Lesser Noddies ($t_{12} = -1.49$, $P = 0.10$) and Wedge-tailed Shearwaters ($t_7 = 2.02$, $P = 0.07$) was not significantly lower in "bad" years, even though it was reduced (Table 2). Brown Noddy, Sooty Tern and Wedge-tailed Shearwater participation was not significantly correlated with sea level or SST; however, the number of participating Lesser Noddies was significantly related to the SST between January and March of the breeding year during 1991–1998 ($y = -0.02x + 24.14$, $R^2 = 0.78$, $P = 0.004$). There was also a significant linear relationship between Lesser Noddy participation and Fremantle sea levels ($y = 0.002x + 0.786$, $R^2 = 0.47$, $P = 0.03$).

Breeding success

Reproductive success was greatly reduced during ENSO years (Fig. 3). The mean SOI in reproductively bad years was –48.4, compared with 45.6 in reproductively good years. The sea level in Geraldton was 0.55 m and 0.58 m respectively (Table 3). In the Wedge-tailed Shearwater, reproductive output was zero for both the 1997/98 and 2007/08 austral summers on Pelsaert Island. For the two noddy species, success was very low in the 1996/97, 1997/98, 2002/03 and 2004/05 seasons, coinciding with ENSO events. In the 2007/08 season, the Brown Noddy fared poorly, although the Lesser Noddy had more than 40% breeding success in the same year. A robust indicator of breeding success was not obtained for the Sooty Tern, because it was difficult to follow young to fledging age; however, no young were raised in the 1996/97, 1997/98, 2002/03 and 2004/05 breeding seasons, which coincided with ENSO events. The Lesser and Brown Noddy both showed significant differences in mean reproductive output between bad years and good years. Lesser Noddies had a mean breeding success rate of 9.6% in poor years, compared with 40.2% in good years ($t_{11} = 4.36$, $P = 0.001$); Brown Noddies had a mean rate of <1% in poor years compared with 18.0% in good years ($t_{10} = 3.18$, $P = 0.009$, Table 2). Similarly, Wedge-tailed Shearwaters had a significantly lower mean breeding success rate of 9.4% in "bad" years, compared with 58.8% in "good" years ($t_7 = 6.63$, $P < 0.001$, Table 2).

TABLE 1
The mean lay date and the date of first eggs for the three tern species studied on Pelsaert Island, Houtman Abrolhos

Species	1991–1999	2000–2007
Lesser Noddy *Anous tenuirostris*		
First egg	11 Sep	15 Oct
Mean lay date	9 Oct	2 Nov
Brown Noddy *A. stolidus*		
First egg	22 Sep	28 Oct
Mean lay date	12 Oct	11 Nov
Sooty Tern *Sterna fuscata*		
First egg	16 Oct	7 Nov
Mean lay date	24 Oct	—

Diet and reproductive performance

Dietary analysis of 3500 regurgitations (48 000 items) revealed that Lesser Noddies consumed 37 species of prey, but with three main ichthyoplankton species being in the majority, namely, Beaked Salmon *Gonorynchus greyi,* Hawaiian Bellowfish *Macroramphosus scolopax* and Black-spotted Goatfish *Parupeneus signatus* (Table 4; for details, see Surman & Wooller 2003). Brown Noddies were found to consume slightly fewer species (n = 32) and relied predominately on Beaked Salmon and cephalopods. Similarly, Sooty Terns consumed 34 species, predominately cephalopods, larval goatfish, Beaked Salmon and lanternfishes (Myctophidae). The Wedge-tailed Shearwater fed on 15 species, mainly cephalopods, adult Scaly Mackerel *Sardinella lemuru* and small quantities of larval Beaked Salmon (Table 4).

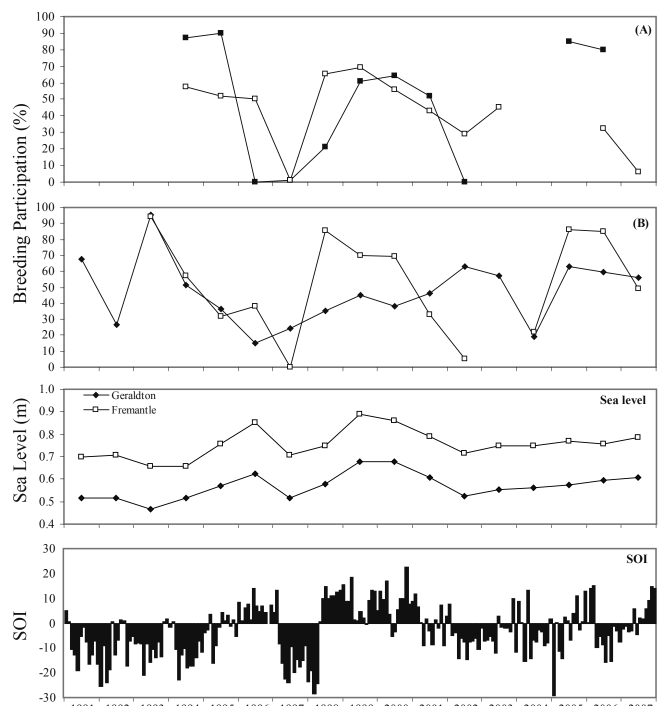

Fig. 2. Breeding participation (percentage) for (A) Sooty Terns *Sterna fuscata* (solid squares) and Wedge-tailed Shearwaters *Puffinus pacificus* (open squares) and (B) Lesser Noddies *Anous tenuirostris* (solid diamonds) and Brown Noddies *A. stolidus* (open squares). The sea levels at Geraldton (open squares) and Fremantle (closed squares) and at the bottom the Southern Oscillation Index (SOI) for the same period are shown. El Niño–Southern Oscillation events are associated with negative SOI values and lower sea levels.

Low availability of Beaked Salmon later in the breeding season, measured by volume in the diets of Brown and Lesser Noddies, appeared to occur during strong ENSO years. Fig. 4 shows the relationship between the volume of Beaked Salmon in regurgitates of Lesser and Brown Noddies compared with their breeding success in the seasons 1991 to 2000. Both noddy species displayed lower volumes of Beaked Salmon during the severe 1997/98 ENSO event; however, the Lesser Noddy appeared to be less reliant upon this prey item, because it had higher breeding success than the Brown Noddy did over the same period. Despite this trend, the volume of Beaked Salmon was significantly correlated with breeding success in the Lesser Noddy (y = 0.54x +26.41, R^2 = 0.44, P = 0.03), but there was not such a clear relationship in the Brown Noddy.

The Brown Noddy population suffered a complete reproductive failure in those years when the proportion of Beaked Salmon fell below 50% by volume (Fig. 4). In general, Lesser Noddy regurgitates were nearly always characterized by Black-spotted Goatfish and Beaked Salmon, whilst Brown Noddy regurgitates were dominated by Beaked Salmon and cephalopods. The volume of Beaked Salmon was lower during most "bad" seasons than in "good" seasons for both noddy species, although this difference was significant only in the Lesser Noddy (t_7 = 3.83, P = 0.003). Conversely, the volume of Black-spotted Goatfish was significantly higher in "bad" years in the Lesser Noddy (t_5 = 3.11, P = 0.01, Table 2, Fig. 5).

Seasonal prey availability, ENSO and breeding success for Lesser and Brown Noddies

Because the diet and foraging grounds of the two noddy species exhibited substantial overlap (Surman & Wooller 2003), and because both exhibited some reliance upon the same prey item, ten years of dietary data were pooled for Brown and Lesser Noddies on Pelsaert Island. "Good" breeding success for the noddy species appeared to be linked to the availability of large volumes of Beaked

TABLE 2
The breakdown of timing, performance and diet for those years with sufficient data for each species studied on Pelsaert Island, Houtman Abrolhos

Species	Season[a] Bad (n=4)	Season[a] Good (n=7)
Lesser Noddy		
Participation (%)	39.6	54.7
First egg date (day)	306	255
Mean lay date (day)	318	284
Breeding success (%)	9.6	40.2
Beaked Salmon *Gonorynchus greyi* (% volume)	34.7	53.9
Black-spotted Goatfish *Parupeneus signatus* (% volume)	46.5	20.4
Brown Noddy		
Participation (%)	22.9	66.9
First egg date (day)	319	266
Mean lay date (day)	344	275
Breeding success (%)	0.9	18.0
Beaked Salmon *G. greyi* (% volume)	48.0	73.2
Black-spotted Goatfish *Parupeneus signatus* (% volume)	2.9	0.9
Sooty Tern *Sterna fuscata*		
Participation (%)	0.3	67.5
First egg date (day)	318	280
Mean lay date (day)	330	291
Wedge-tailed Shearwater *Puffinus pacificus*		
Participation (%)	21.6	46.9
First egg date (day)	322	322
Breeding success (%)	9.4	58.8

[a] Years were pooled into reproductively bad or good years to illustrate the other breeding characteristics for each species in those years. We assigned seasons as "bad" when breeding success was less than 15%.

Salmon during the early (September/October) portion of the breeding season (Fig. 5). In reproductively good seasons, the volume of Beaked Salmon collected from regurgitates in the early portion of the breeding season was very high (70%), dropping off later to about 50%. During bad seasons, the volume of Beaked Salmon was very low (18%) early in the breeding season, rising gradually to 40% in the latter months (November–February, Fig. 5).

The proportion of Black-spotted Goatfish was higher in poorer years for both noddy species (Table 2, Fig. 5), with the volume in regurgitates increasing as the season progressed in both "good" and "bad" years. The occurrence of other major prey species remained proportionately the same in both "good" and "bad" years, which would suggest that their delivery to the Houtman Abrolhos region was independent of ENSO events.

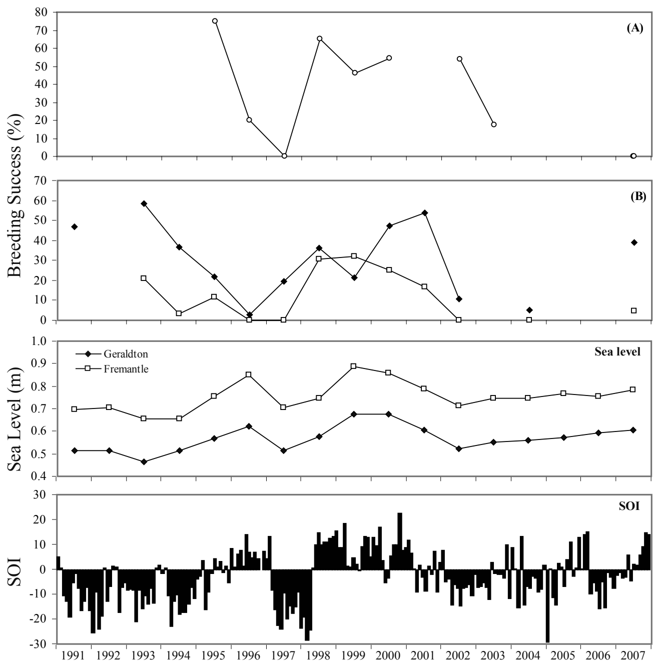

Fig. 3. Breeding success (percentage) in the (A) Wedge-tailed Shearwater *Puffinus pacificus* and the (B) Lesser Noddy *Anous tenuirostris* (solid diamonds) and Brown Noddy (open squares). A robust measure was not obtained for the Sooty Tern *Sterna fuscata*. The sea levels at Geraldton (open squares) and Fremantle (closed squares) and at the bottom the Southern Oscillation Index (SOI) for the same period are shown. El Niño–Southern Oscillation events are associated with negative SOI values and lower sea levels.

DISCUSSION

Our data suggest that the reproductive performance of the four tropical pelagic seabird species studied was affected by large-scale (ENSO) and regional variation in the Leeuwin Current system. During the 17 years of this study, ENSO-driven changes in oceanographic conditions (as measured by SOI and sea-level changes) were correlated with lowered breeding participation and success for all species, and delayed breeding phenology in the three tern species. For the Lesser and Brown Noddy, initiation of breeding was significantly later in years 2000–2007 as compared with the earlier period of this study (1991–1999). In the later years of this study, as the frequency of ENSO events increased, poorer reproductive performance began to occur for all four species in non-ENSO years also. The Wedge-tailed Shearwater's timing of breeding remained unaffected, which reflects its life-history strategy of a long breeding schedule and dispersal during the non-breeding season, precluding delayed breeding as a strategy when faced with a limited window of opportunity (Nicholson 2002)

TABLE 3
The breakdown of oceanographic parameters in bad and good seasons

Measure	Season	
	Bad	Good
Total annual Southern Oscillation Index	–48.3	45.6
Sea level Geraldton (m)	0.55	0.58
Sea level Fremantle (m)	0.75	0.76
SST @ 114.5E (°C)	22.2	22.4

[a] Years were pooled into reproductively bad or good years to illustrate the other breeding characteristics for each species in those years.

TABLE 4
A summary of the main prey items identified in regurgitates from the Lesser Noddy *Anous tenuirostris*, Brown Noddy *A. stolidus*, Sooty Tern *Sterna fuscata* and Wedge-tailed Shearwater *Puffinus pacificus* from Pelsaert Island, Houtman Abrolhos between 1991 and 2001 (after Surman and Wooller 2003)

Prey	Lesser Noddy	Brown Noddy	Sooty Tern	Wedge-tailed Shearwater
Beaked Salmon *Gonorynchus greyi* (% by vol.)	45.5	68.8	6.4	3.1
Black-spotted Goatfish *Parupeneus signatus* (% by vol.)	27.4	1.2	7.3	0.5
Hawaiian Bellowfish *Macroramphosus scolopax* (% by vol.)	7.7	7.6	2.8	0.1
Lanternfish (Myctophidae) (% by vol.)	1.4	2.5	5.4	2.9
Scaly Mackerel *Sardinella lemuru* (% by vol.)	0.0	0.0	0.0	11.1
Squid (% by vol.)	2.4	11.5	65.4	59.8
Total items (n)	1303	768	449	?

ENSO events also had a strong influence on the reproduction of the Brown Noddy breeding at the Seychelles, Western Indian Ocean, with the years of poorest breeding success occurring in El Niño and La Niña years (Ramos *et al.* 2006). Roseate Terns *Sterna dougallii* at the same location experienced delayed onset of breeding and decreased hatching success as a result of ENSO events (Ramos *et al.* 2002) and were affected by temporal variability in oceanographic conditions (Monticelli *et al.* 2007).

It has been suggested that seabird breeding phenology is adjusted to the timing of emergence of a species' main prey, which is anticipated through localized changes in SST during the pre-breeding phase (Frederiksen *et al.* 2004, Monticelli *et al.* 2007). There was a relationship of the mean SST between January and March and the mean lay date for Brown and Lesser Noddies in the following season at the Houtman Abrolhos during the earlier years of this study. In addition, the breeding participation for Lesser Noddies was also significantly related to the SST and to Fremantle sea levels in the same years. The Lesser Noddy is the only resident species in this study, and so it would be expected that Lesser Noddies may rely on more local environmental cues than do the other migratory species. In a study of seabird breeding phenology in the North Sea, it was found that widely dispersing species showed responses to large-scale environmental cues, whereas a resident species responded to more local oceanographic cues, including SST (Frederiksen *et al.* 2004). Another study found that individual environmental cues in the western Indian Ocean would mediate different responses in Roseate Tern reproduction, with large-scale climatic fluctuations (such as ENSO) affecting timing of breeding, and local SST affecting breeding participation (Ramos *et al.* 2002).

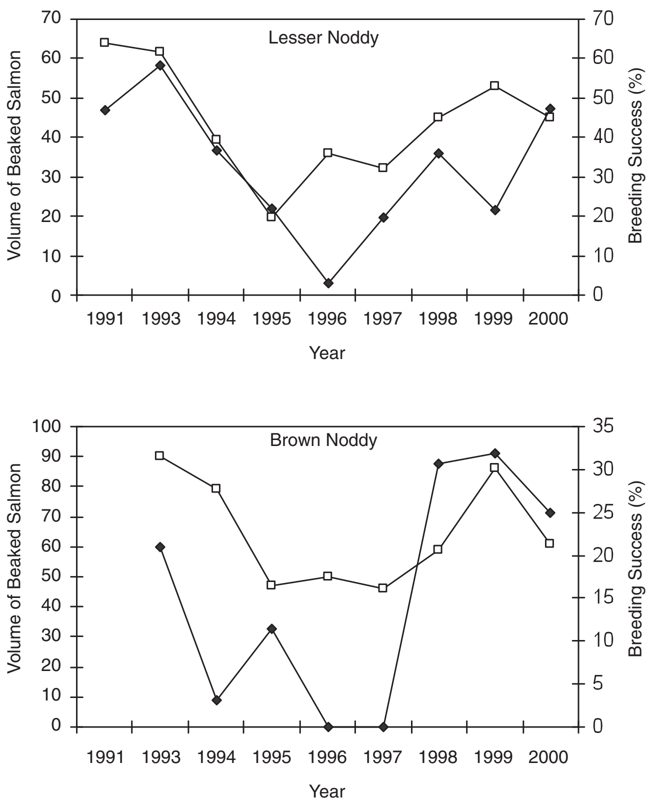

Fig. 4. The volume of Beaked Salmon *Gonorynchus greyi* found in regurgitates (open squares, left axis) and the breeding success (closed diamonds, right axis) of the Lesser Noddy and Brown Noddy over nine years that dietary data was collected at Pelsaert Island, Houtman Abrolhos.

It would seem that residential knowledge of the pre-breeding environment at the Houtman Abrolhos conferred the advantage of higher breeding success to Lesser Noddies, even in years affected by ENSO events. Variation in the strength of flow of the Leeuwin Current appeared to influence the timing of delivery of Beaked Salmon larvae to within the seabird foraging ranges at the Houtman Abrolhos. The reduced volume of Beaked Salmon in regurgitates of the two noddy species during ENSO years suggested that there was a reduction in the availability of this prey.

The Lesser Noddy was far less reliant upon larval Beaked Salmon than was the migratory Brown Noddy, which consumed the highest proportion of this prey of all the species studied. The Lesser Noddy was buffered by its ability to take advantage of the smaller larval Black-spotted Goatfish later in the season; the Brown Noddy required a much higher proportion of Beaked Salmon throughout the season and, on average, faired worst in ENSO years when this prey was less available. The Brown Noddy population suffered a complete reproductive failure in those years when the proportion of Beaked Salmon fell below 50% by volume, which coincided with low SOI values (ENSO years). Surman and Wooller (2003) found that whilst this prey occurred in a similar proportion of samples from both noddy species, Brown Noddy regurgitates contained significantly more Beaked Salmon in reproductively "good" years, both in terms of number and volume consumed. The Brown Noddy was the species most affected by the lower availability of Beaked Salmon during ENSO years, and it may be that Brown Noddies are less able to switch prey. Given that the two noddy species have overlap in their foraging range and prey composition, it is possible that the cost–benefit of capturing and feeding on the smaller goatfish was not advantageous to the larger Brown Noddy (Gaughan *et al.* 2002).

Importantly, Beaked Salmon appeared to be a requirement at high volumes in the diet of Brown Noddies during the pre-laying period of the season in September/October. Overall, Beaked Salmon comprised 73% of the diet in good years, but 48% in bad years, although the poorer years were skewed by the appearance of Beaked Salmon in the regurgitates of Brown Noddies later in the year than would normally be expected. Similarly, Crawford and Dyer (1995) observed changes in the numbers of breeding attempts, and the numbers of chicks that were raised, of four seabird species in relation to changes in the abundance of the Cape Anchovy *Engraulis capensis* in their diet. In addition, Ramos (2000) observed a reduction in the volume of the principal prey, goatfish, in the diet of Roseate Terns breeding in the western Indian Ocean during reproductively poor years. Interestingly, at this eastern Indian Ocean breeding site, there were higher volumes of goatfish in regurgitates of both the Lesser Noddy and Brown Noddy in reproductively poor years, perhaps supplementing the decline in the presence of Beaked Salmon.

Although both Sooty Terns and Wedge-tailed Shearwaters fed predominately on adult squid, a significant portion of their dietary intake also included Beaked Salmon and Black-spotted Goatfish. The Sooty Tern and Wedge-tailed Shearwater also experienced breeding failures in ENSO years, even though Beaked Salmon was not their main prey. The oceanographic factors that may have led to a change in the distribution or abundance of Beaked Salmon near to the Houtman Abrolhos in these years could represent a general reduction in marine productivity across the region.

Beaked Salmon is a southwestern benthic species (Hutchins & Swainston 1986), and the delivery of its larvae appeared to be higher when the Leeuwin Current was stronger, during non-ENSO years. This cause and effect is counterintuitive, because the larvae were then being delivered northwards against a stronger-flowing southwards current. However, mixing of the Leeuwin Current and the Capes Current at the Geelvink Channel may have facilitated the delivery of Beaked Salmon larvae within range of the two species south and west of the Abrolhos, where previously-identified foraging "hotspots" of both noddy species occurred, at least to the shelf edge (Surman & Wooller 2003). The two species have seldom been observed foraging in the Geelvink Channel itself (Surman pers. obs.). The Capes Current flows most strongly between October and February, principally along inshore shelf waters of Western Australia, at a time that the Leeuwin Current flows most weakly and during the breeding season of the four study species. The long (3 months) larval duration of Beaked Salmon may facilitate its northward delivery via the Capes Current. During ENSO years, there is less potential for upwelling in the area, which may reduce the distribution of Beaked Salmon larvae. The orientation of eddies regularly observed west of the Houtman Abrolhos may also play a role in defining the distribution of Beaked Salmon larvae during ENSO years.

Whilst the Leeuwin Current has likely facilitated the seabird colonisation of the Houtman Abrolhos by tropical seabirds, the dynamics of how the current delivers prey or suppresses or enhances the arrival of prey from southern regions remains unclear and, from the data presented here, appears to be changing. Oceanographic productivity data is still inadequate in the region off south-western Australia, but the observations reported here suggest that there is zonal shift in productivity on the shelf edge during ENSO conditions. A similar phenomenon has been reported on Australia's eastern boundary (Prince 2001, Ramos *et al.* 2002, Ramos *et al.* 2006, Monticelli *et al.* 2007). Further studies of seabird productivity at the Houtman Abrolhos could benefit from assessments of the influence of other environmental indices upon breeding performance. Measurements of the Indian Ocean Dipole, which affects SST, winds

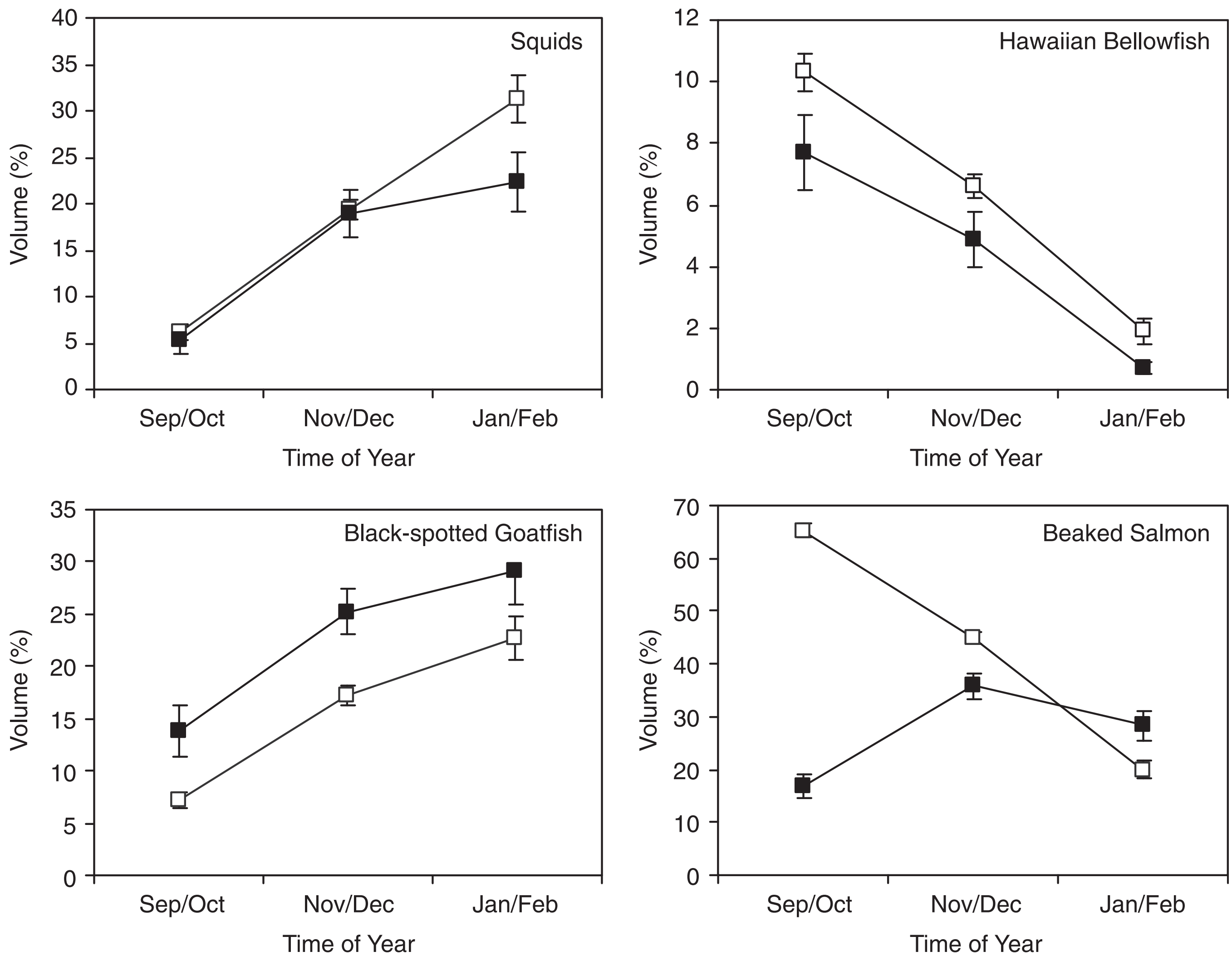

Fig. 5. Pooled seasonal dietary data (open squares = reproductively successful years; closed squares = reproductively poor years) for Lesser *Anous tenuirostris* and Brown Noddies *A. stolidus* at Pelsaert Island, Houtman Abrolhos, for the four key prey items consumed by these species: (A) squids, (B) Hawaiian Bellowfish *Macroramphosus scolopax*, (C) Black-spotted Goatfish *Parupeneus signatus* and (D) Beaked Salmon *Gonorynchus greyi*. Dietary data was pooled into early season (September–October, n = 782), mid-season (November–December, n = 1226), and late season (January–February, n = 394).

and precipitation in the Indian Ocean, and estimates of chlorophyll-*a* concentration (utilizing Sea-viewing Wide Field-of-view Sensor) to assess changes in primary productivity around the Houtman Abrolhos (as described and utilized in Monticelli *et al.* 2007 could provide further information about the dynamics of prey delivery in this region of the Indian Ocean.

The long-term distribution of these tern metapopulations may be driven by the increasing frequency of the ENSO (Allan *et al.* 1996). The data presented in this study on the timing of breeding of the Lesser Noddy, Brown Noddy and Sooty Tern illustrate that the breeding season of these species at the Houtman Abrolhos is undergoing a gradual seasonal shift. During a study of seabirds in the North Sea, Frederiksen *et al.* (2004) have highlighted the likelihood that global climate change will cause shifts in the timing of peak food availability, with successful adaptation of animals requiring that they be able to adjust the time at which they initiate breeding. With the increasing likelihood of later commencement of breeding continuing for tern species at the Houtman Abrolhos, unless a concurrent shift in peak marine productivity occurs, reproductive output is likely to continue to be poor. Later breeding often correlates with lower breeding success (Dunlop & Jenkins 1994, Gaughan *et al.* 2002, Ramos *et al.* 2002, Ramos *et al.* 2006, Monticelli *et al.* 2007). The implications for the core breeding populations of seabirds at the Houtman Abrolhos are severe. One response to poor food availability is to relocate elsewhere. The establishment of recent seabird colonies southwards along the Western Australian coastline has been well documented (Dunlop & Wooller 1990, Dunlop 2009). Little suitable island habitat exists south of the Houtman Abrolhos to continue to support the southern range extension in tropical seabirds (Dunlop 2009). Global climate change is likely to present some severe challenges for seabirds at the Houtman Abrolhos. Coupled with the effects of increasing sea levels upon island habitats, seabirds at the Abrolhos must adapt to what appears to be shifting levels of prey availability as a result of changes in productivity in the oceanic region adjacent to the Houtman Abrolhos.

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