El Niño Southern Oscillation and the Leeuwin Current influence on seabird reproductive performance and diet at the Houtman Abrolhos

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Abstract

Each spring/summer over a million pairs of seabirds breed at the Houtman Abrolhos, Western Australia, Eastern Indian Ocean. The southward flowing Leeuwin Current is the main oceanographic feature influencing this location. Seabirds 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 reproductive parameters. The timing of breeding, breeding participation and reproductive success were investigated in two tern species, the Lesser Noddy and Brown Noddy, at the Houtman Abrolhos between 1991 and 2006. The diet of these two species was investigated from 1991–2000. Life history traits determined the response of these seabirds to fluctuations in marine resources through variation in the flow of the Leeuwin Current. During ENSO events, when the Leeuwin Current flowed more weakly and the Southern Oscillation Index had been low, reproductive effort and output was severely reduced for these two tern species. These conditions appeared to result in low prey availability, which delayed the commencement of seabird breeding by up to two months and caused catastrophic breeding failures. The long-term data set would indicate that the interaction of other oceanographic factors at the Houtman Abrolhos, such as eddies, the Cresswell and Capes Currents, in conjunction with the Leeuwin Current, may influence seabird prey availability, however the dynamics of these interactions are not yet understood. The use of seabirds as an upper trophic- level indicator of changes in marine productivity, as a result of variability in the Leeuwin Current and other oceanographic factors, is discussed.

Introduction

The main oceanographic feature of the Western Australian coastline is the Leeuwin Current. This is a body of warm (>24°C), low-salinity (<35‰) water which flows southward along the continental shelf of Western Australia, in a broad and shallow band (200km wide by 50m depth) at speeds of up to 2 km.h^{-1} (Cresswell 1990; Pearce 1991). The strength of the flow of the Leeuwin Current varies both annually in its cycle as well as seasonally. The greatest flow occurs in winter, between April and July, and its strength and temperature is affected by El Nino Southern Oscillation (ENSO) events. ENSO events are measured 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 (Pearce 1991). In ENSO years the Leeuwin Current is weaker, resulting in cooler, more saline water along the outer continental shelf (Pearce 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). Reduced breeding participation and reduced breeding success has been observed in seabird colonies along the WA coastline, ranging between 19°S and 32°S, during seasons influenced by ENSO events (Dunlop *et al*. 2002; Nicholson 2002; Surman 1997).

The Houtman Abrolhos is located at 28°S (Figure 1) and contains one of the southernmost extensions of tropical marine flora and fauna in the Indian Ocean principally due to the influence of the Leeuwin Current. The Leeuwin Current transports pelagic larvae of corals, fishes, crustaceans and molluscs from tropical northern waters to the surrounding waters of the Houtman Abrolhos and further south to Rottnest Island (32°S), and in response to this influx, there has been a corresponding southwards shift in tropical seabird breeding populations to new higher latitude colonies in the past 50 years (Dunlop & Wooller 1990). This has included the colonisation of Rottnest Island by Wedge-tailed Shearwaters *Puffinus pacificus* in the 1940's (Serventy *et al*. 1971), the continued expansion of a Bridled Tern *Sterna anaethetus* colony on Penguin Island (Dunlop & Jenkins 1994), the discovery of Bridled Terns foraging offshore of the Recherche Archipelago in 1993 (Surman & Wooller 2000) and their consequent colonisation (Dunlop pers. comm.), and the establishment of a new colony of Brown Noddies *Anous stolidus* and Sooty Terns *Sterna fuscata* on Lancelin Island (Dunlop & Mitchell 2001). The role of the Leeuwin Current in the delivery and distribution of seabird ichthyoplankton prey at the Houtman Abrolhos remains unclear but well-established relationships exist between Leeuwin current strength and

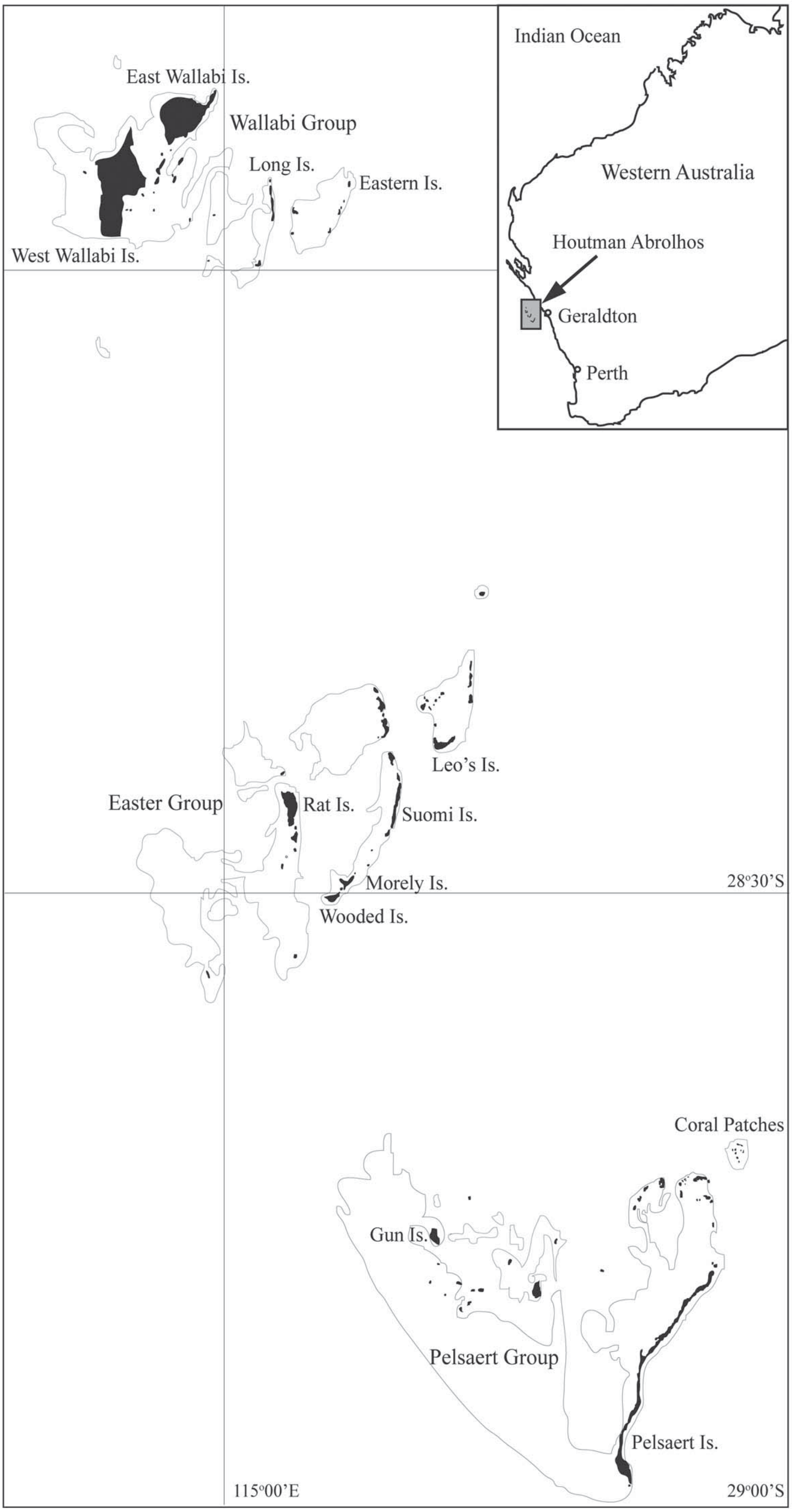

Figure 1. Location map of the Houtman Abrolhos, Western Australia.

western rock lobster (*Panulinus cygnus*) recruitment (Caputi *et al.* 2001; Caputi 2008).

Many of the seabirds which breed at the Houtman Abrolhos are considered predominantly tropical and breed annually during the austral spring-summer (Surman 1998). Most studies agree that seabird breeding is specifically timed to coincide with maximal food supply (Ashmole & Ashmole 1968; Diamond 1983; Ainley & Boekelheide 1990). This timing varies with latitude, with high-latitude species having a narrower period of opportunity to breed due to strong seasonality in climate and food availability and so are characterized by predictable breeding times, high synchrony and relatively short breeding seasons (considered here from the time of laying to fledging of young, excluding prelaying and postfledging periods). At lower latitudes, however, breeding at some locations may commence at any time, and timing is only determined by the availability of food in reach of the colony (Ashmole & Ashmole 1968; Diamond 1983). At the Houtman Abrolhos seabirds breed annually and commence during the spring/summer period (Surman 1998). The Houtman Abrolhos can be considered a sub-tropical location due to the influence of the Leeuwin Current, and as such provides breeding seabirds with a mixture of tropical and temperate prey sources (Surman & Wooller 2003). Two terns which breed at the Houtman Abrolhos, the Lesser Noddy *Anous tenuirostris* and Brown Noddy, share breeding times of between 75–85 days. The former is a resident species of the Houtman Abrolhos for most of the year, while the larger Brown Noddy is a migratory species, returning to the region in August of each year from northern parts of the Eastern Indian Ocean.

This paper investigates inter annual variability in the breeding performance and phenology of the Lesser and Brown Noddy, and the influence that regional oceanography may have upon the diet of these species, in relation to the Leeuwin Current dynamics.

Methods

Study area and species

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 (Figure 1). Pelsaert Island (120 ha) is 12 km long, 50–500 m wide, up to 2 m above sealevel, comprising coral rubble, limestone and sand. The Lesser Noddy (35,000 pairs) nests mainly in branches of the White Mangrove *Avicennia marina* on the island and the Brown Noddy (130,000 pairs) nests on low Nitre *Nitraria billardierei* and Samphire *Halosarcia halocnemoides* bushes (Surman & Wooller 1995, 2000; Surman & Nicholson 2008). At the Houtman Abrolhos, Pelsaert Island contains 100% of Brown Noddies and 70 % of Lesser Noddies breeding along the Western Australian coastline.

Nest sites of the Lesser Noddy and Brown Noddy were selected at random and permanently marked in 1991 and 1993 respectively, for each species. Their contents were recorded weekly over the spring summer period (September–May) between 1991–2001, and in more recent years (2002–2006) during several shorter visits between October and January of each year.

Timing of Breeding and Reproductive Performance

Laying chronology was determined using lay dates of known age eggs, and the estimated laying dates of other eggs was determined by backdating, using the egg water loss techniques (Wooller & Dunlop 1980; Surman & Wooller 1995). Eggs known to be "re-lays" (a second egg laid in the same nest after the first has been damaged or predated) were excluded from calculations for the mean date of laying of each species. In years limited to shorter duration field visits, we were able to determine the timing of breeding from measurement of chicks or eggs at the permanently marked nest sites of the two noddy species.

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 above 15% as "good".

Environmental parameters

Measures of oceanographic factors between 1991–2006 were obtained from the National Tidal Facility, Flinders University. The strength of flow of the Leeuwin Current was determined by using the mean monthly sealevel at Fremantle and Geraldton, Western Australia. Sealevel is considered a proxy for determining the strength of the Leeuwin Current (Pattiaratchi 2005). Mean monthly Sea Surface Temperature (SST) was obtained from the Reynold's database for the degree squares centred at 28.5°S and 113.5°E and 114°E. The mean monthly Southern Oscillation Index (SOI), an indicator of El Nino activity, was obtained from the Bureau of Meteorology.

Dietary samples

Lesser Noddies and Brown Noddies were induced to regurgitate without the use of emetics or stomach flushing. Although spontaneous regurgitations may not always empty the proventriculus (Duffy & Jackson 1986), this method was judged minimally intrusive and is commonly used to determine seabird diet (Cooper & Klages 1995; Croxall *et al*. 1997; Shealer 1998). Adult birds recently returned from a foraging trip were captured at the nest-site by hand or using a small net, whereupon most regurgitated. 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 species in each sampling month, corresponding to the incubation, small nestling and large nestling stages in their breeding cycle.

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. The total number of individuals of each prey type in each sample was recorded. 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.

Head parts were poorly preserved in most samples and tails were the most effective method of identifying and counting each species. Of the three main prey species, Beaked Salmon *Gonorhynchus greyii* resisted digestion better than the more fragile Black-spotted Goatfish *Parupeneus spirulata*; Hawaiian Bellowfish *Macrorhamphosus scolopax* remained more intact than either. Fortunately, the tails of these three species proved particularly distinctive.

Results

Timing of Breeding

Figure 2 shows the date (Julian, where 300 = 27 Oct) of first eggs laid and the mean lay date in the Lesser Noddy (A) and Brown Noddy (B), in comparison with the SOI (C), sea level at Geraldton and Fremantle (D) and SST of south-western waters (E) over a 16 year period, from

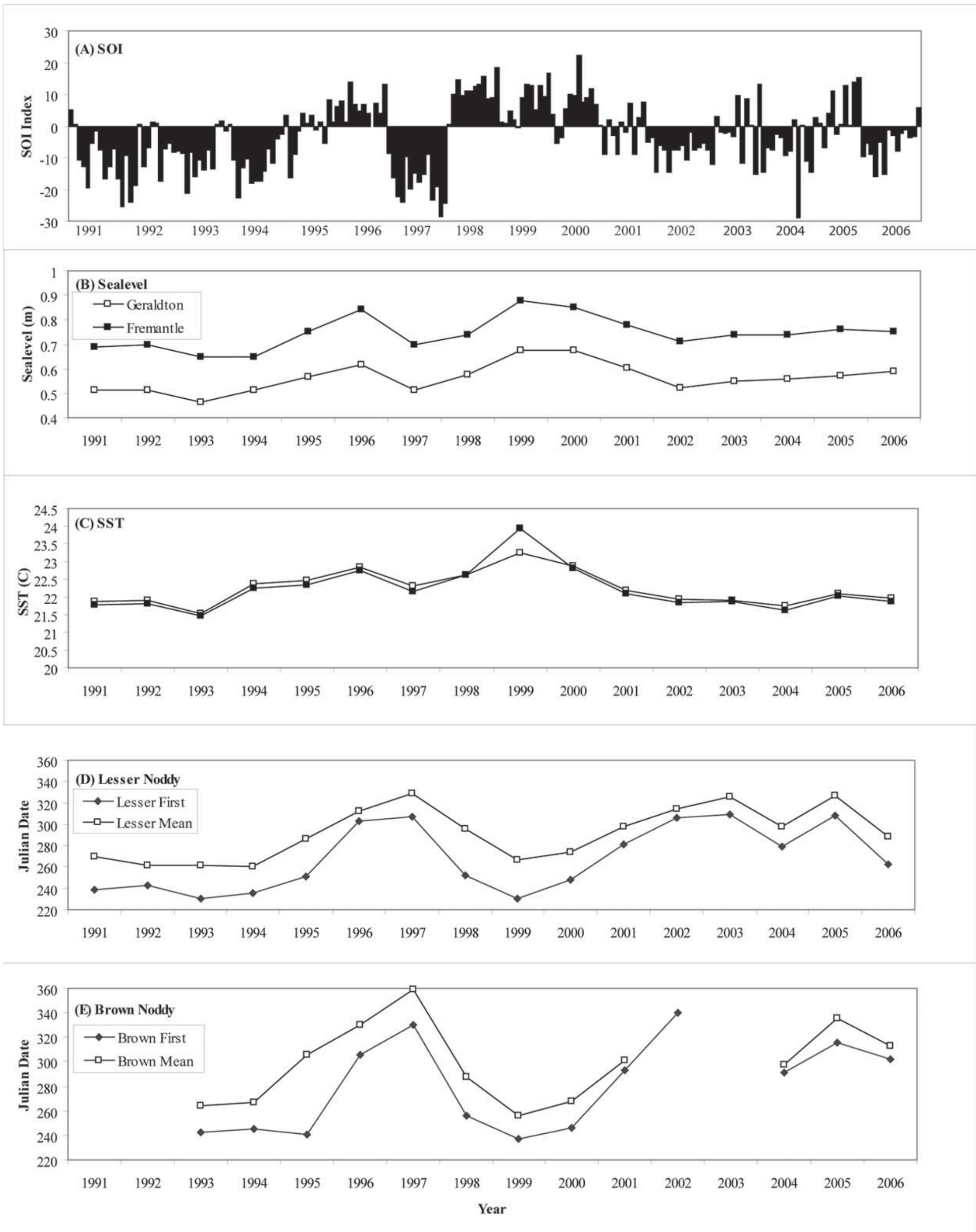

Figure 2. Timing of breeding (Julian Date, where 27 October = 300) as represented by the date of first egg (closed diamonds) and mean lay date (open squares) in the Lesser Noddy (D) and Brown Noddy (E). The Southern Oscillation Index (A) and sealevel (B) at Geraldton (open squares) and Fremantle (closed squares), and the Sea Surface Temperature (C – °C) centred at 28.5°S and 113.5°E (open squares) and 114.5°E (closed squares). Negative SOI values indicate ENSO conditions.

1991–2006. Later breeding coincided with stronger ENSO (negative SOI values) events, lower sea levels and cooler SST. The timing of egg laying in the two noddy species was increasingly delayed until the 1997 ENSO event, after which it returned to an earlier start. This coincided with the SOI becoming positive once again.

During this 16 year period, delayed breeding was accompanied by a decline in the proportion of birds participating in that year (Table 2). The commencement of breeding ranged from late August (in those years when the SOI was positive) to late December (in those years when the SOI was negative).

Diet

Analysis of over 3500 regurgitations (48 000 items) revealed that both the Lesser Noddy and Brown Noddy favoured Beaked Salmon *Gonorynchus greyii* (Table 1, for details see Surman & Wooller 2003), which appeared to be predominately available earlier in the breeding season, particularly during ENSO years. In general, Lesser Noddy regurgitates consisted mostly of Black-spotted Goatfish and Beaked Salmon, whilst Brown Noddy regurgitates were dominated by Beaked Salmon and cephalopods.

Figure 3 shows the relationship between the proportion of beaked salmon and black-spotted goatfish items in the diet during reproductively successful and unsuccessful years. Figure 4 shows pooled data for the ten years of dietary data collected from Brown and Lesser Noddies from the Pelsaert Island colonies. In reproductively good years, the volume of beaked salmon collected from regurgitates in the early portion of the season was very high (70%), dropping off later in the season to about 50%. During poor years, the volume was very low (18%) rising gradually to 40% in the latter part of the breeding season.

Table 1

Main prey items identified in regurgitates from the Lesser Noddy and Brown Noddy from Pelsaert Island, Houtman Abrolhos between 1991 and 2001.

Prey (% Volume)	Lesser Noddy	Brown Noddy
Beaked Salmon	46	69
Black-spotted Goatfish	27	1
Hawaiian Bellowfish	8	8
Squid	3	10

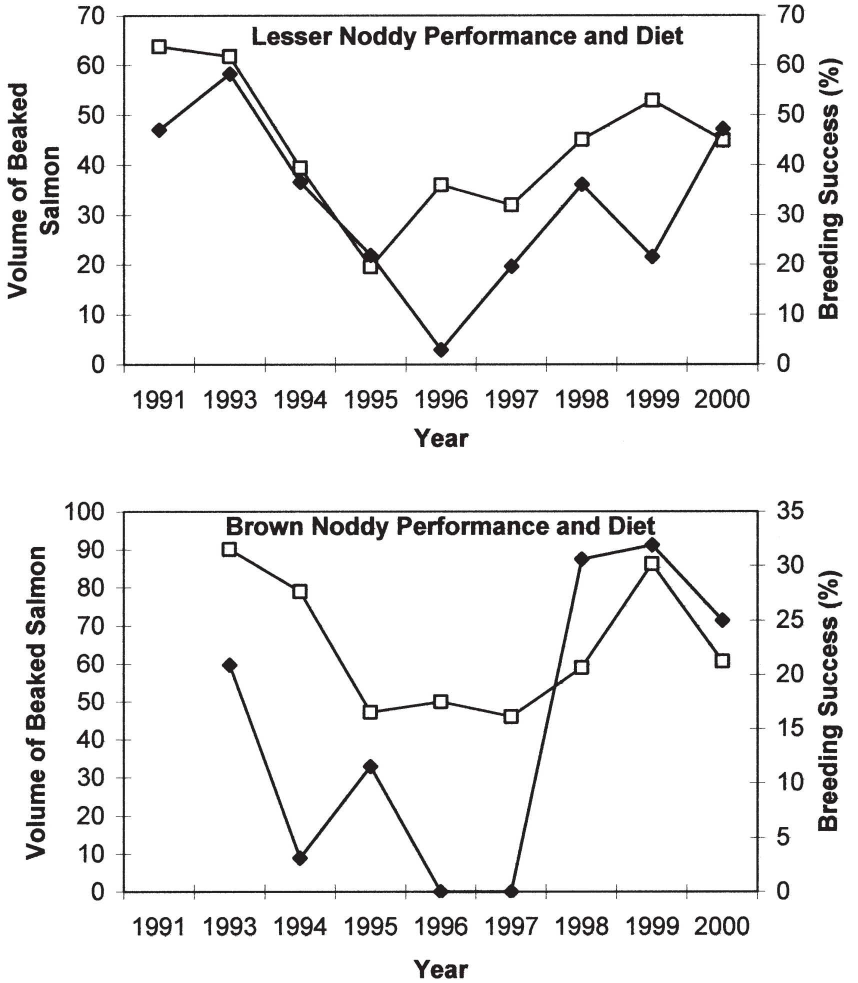

Figure 3. The volume of beaked salmon found in regurgitates (left hand side-open squares) and the breeding success (right hand side-closed diamonds) of the Lesser Noddy (top) and Brown Noddy (bottom) over nine years that dietary data was collected at Pelsaert Island, Houtman Abrolhos.

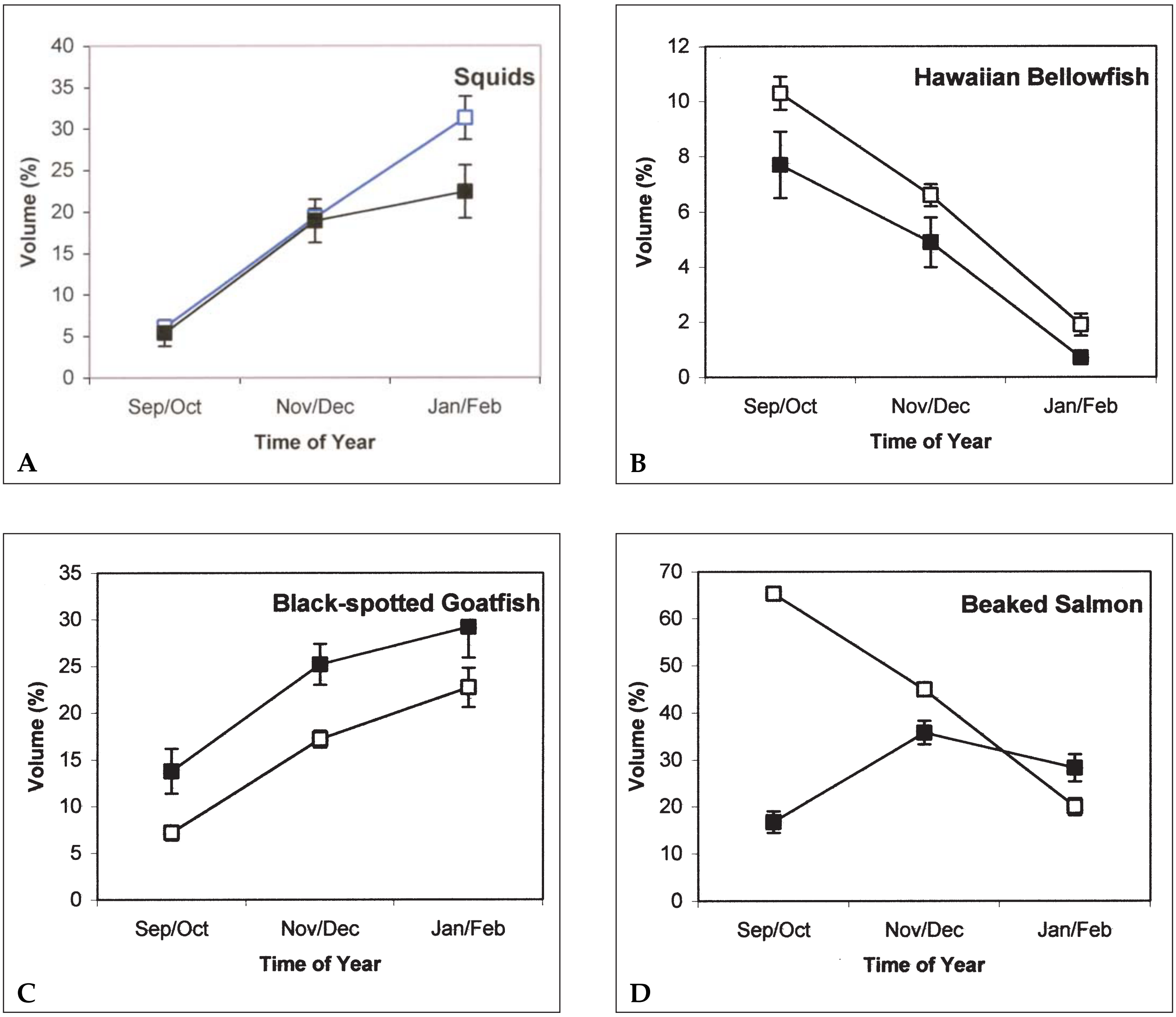

Figure 4. Pooled seasonal dietary data for Lesser and Brown Noddies at Pelsaert Island, Houtman Abrolhos between 1993–2001. The figures represent the four key prey items consumed by these species, (A) Squids, (B) Hawaiian Bellowfish, (C) Black-spotted Goatfish and (D) Beaked Salmon. Open squares represent dietary data from reproductively successful years and closed squares from reproductively poor years.

The residential Lesser Noddy was less reliant upon Beaked Salmon than the migratory Brown Noddy. This was reflected in the reproductive performance of the two species in ENSO years, as the Lesser Noddy was buffered by its ability to take advantage of the small larval Black-spotted Goatfish later in the season, whereas the Brown Noddy required a much higher proportion of Beaked Salmon throughout the season, and on average faired worst (Table 2, Figure 3). For Brown Noddies the population suffered a complete reproductive failure in those years when the proportion of Beaked Salmon in diet fell below 50 % by volume (Figure 3).

Breeding Success

Breeding success, defined as the proportion of young raised to fledging age, was dramatically reduced in years of strong ENSO events (Figure 3). The delayed commencement of breeding in these years resulted in chicks being reared very late in the season when prey availability was already declining (Table 2). In 1997, 2002 and 2004 this resulted in total breeding failure for the 125 000 pairs of Brown Noddies breeding on Pelsaert Island. In contrast, the residential Lesser Noddy still had a breeding success of 19.6 % (1997), 10.8 % (2002) and 5.0 % (2004) during these reproductively poor years.

Discussion

The gradual delay in the onset of breeding over successive years until 1997, and reduced breeding success, indicated that some outside influence was having a negative impact upon reproductive performance of the two noddy species at the Houtman Abrolhos. The breeding success of the noddies at the

Table 2

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

Species	Measure	Bad Seasons	Good Seasons
Lesser Noddy	Participation (%)	30.3	52.1
	First Egg Date (Day)	306	255
	Mean Lay Date (Day)	318	284
	Breeding Success (%)	9.6	40.2
	Beaked Salmon (% volume)	34.7	53.9
	Black-spotted goatfish (% volume)	46.5	20.4
Brown Noddy	Participation (%)	16.2	66.1
	First Egg Date (Day)	319	266
	Mean Lay Date (Day)	344	275
	Breeding Success (%)	0.0	18.0
	Beaked Salmon (% volume)	48.0	73.2
	Black-spotted goatfish (% volume)	2.9	0.9
N		**4**	**7**

Abrolhos appeared to be linked to the availability of large volumes of Beaked Salmon during the early (September–October) portion of the breeding season (Surman 1997; Surman & Wooller 2003; Gaughan *et al*. 2002). 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. Crawford & 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. Similarly, 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, in reproductively poor years there was higher volumes of goatfish in regurgitates of both the Lesser Noddy and Brown Noddy, perhaps supplementing the decline in the presence of Beaked Salmon.

During ENSO years, reduced marine productivity may impact upon noddies at the Houtman Abrolhos through a reduction in the abundance and availability of a critical prey, the Beaked Salmon. Other major dietary components followed similar trends whether it was a good or poor year, although the proportion of Black-spotted Goatfish was higher in poorer years (Table 2). During 'poor' years the regurgitates of Brown Noddies and Lesser Noddies contained 2.9% and 46.5% Black-spotted Goatfish respectively. In contrast, during the 'good' years this percentage fell to 0.9% in Brown Noddies and 20.4% for Lesser Noddies. Lesser Noddies appeared to be better able to substitute Beaked Salmon with Black-spotted Goatfish during 'poor' years, and this may have buffered them from the severe effects of ENSO events exhibited by the Brown Noddy. The Brown Noddies inability to switch prey was likely linked to body size, foraging techniques and foraging grounds. Lesser Noddies are hoverers, dipping for minute prey just from the surface, and they consume prey of an average length of 33.5mm (N=16 559, see Surman & Wooller 2003). Brown Noddies, on the other hand, consumed prey of an average 51.3 mm (N=8 291). The small size of the larval Black-spotted goatfish (<35mm SL) may make them difficult to handle or catch for the larger Brown Noddy.

It appeared that the breeding success of the noddies at the Abrolhos was linked to the availability of large volumes of Beaked Salmon during the early (September–October) portion of the breeding season. For Brown Noddies the population suffered a complete reproductive failure in those years when the proportion of Beaked Salmon fell below 50 % by volume, and those years coincided with negative SOI values (ENSO years). 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 90% of the diet in good years, but 70% 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. The breeding success of other seabird species have similarly been linked to prey availability at critical periods during the breeding season. For example, breeding success of kittiwake *Rissa tridactyla* colonies in the NE Atlantic have been linked to the availability and quality of their main prey, sandeels *Ammodytes marinus*, during the breeding season (Lewis *et al*. 2001; Rindorf *et al*. 2000). Crawford & Dyer (1995) also observed changes in the performance of seabirds in relation to changes in the abundance of the Cape Anchovy *Engraulis capensis*. They found the effects of the abundance of anchovies influenced the numbers of breeding attempts, the occurrence of anchovies in the diet and the numbers of chicks that were raised by four seabird species heavily dependent upon this prey.

The strength of flow of the Leeuwin Current appeared to influence the timing of delivery of Beaked Salmon larvae (sub 75mm SL) to within the foraging ranges of the noddy species at the Houtman Abrolhos. Beaked Salmon are a benthic species found in south-western waters (Hutchins & Swainston 1986), and the availability of its larvae appeared to be greater when the Leeuwin current was stronger – during non-ENSO years. This cause and effect is counter-intuitive, as the larvae are being delivered northwards against a stronger flowing southwards current. Associated with the Leeuwin Current are the northward flowing Leeuwin Undercurrent at the sub-surface, and the northward flowing Capes Current on the continental shelf during the summer months (Pattiaratchi 2005). Mixing of the Leeuwin Current and Capes Current at the Geelvink Channel may facilitate the delivery of Beaked Salmon larvae within range of the two species south and west of the Abrolhos where foraging "hotspots" of noddies occur (Surman & Wooller 2003). Since the ENSO weakens the potential for upwelling in the area, it may also affect the distribution of Beaked Salmon larvae. 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. The long (3 month) larval duration of Beaked Salmon may allow their northward delivery via the Capes Current.

The precise role of the Leeuwin Current upon the diet and performance of the two noddies at the Houtman Abrolhos remains unclear. Whilst the Leeuwin Current has likely facilitated the colonisation of the Houtman Abrolhos by tropical seabirds, the dynamics of how the current delivers prey and suppresses/enhances the arrival of prey from southern regions is unknown. However, ENSO events impact severely upon the timing of breeding, the numbers of participants and ultimately the reproductive output of the two noddy species. It was evident that during poorer years, Beaked Salmon were less abundant in regurgitates of the noddies, and presumably less available within the foraging range of these species. Foraging areas of the two noddies occur south and west of the islands, at least to the shelf edge (Surman & Wooller 2003), however they are rarely observed foraging in the Geelvink Channel (Surman pers. obs.). It may be that the orientation of eddies regularly observed west of the Houtman Abrolhos may play a role in defining the distribution of Beaked Salmon larvae during ENSO years.

It would appear from the long-term data presented in this paper that the timing of breeding of Lesser and Brown Noddies is undergoing a gradual seasonal shift, more frequently commencing later in the year with an associated decrease in reproductive success. From the dietary data presented it can be surmised that this shift is likely caused by oceanographic driven changes in productivity in the waters adjacent to the Houtman Abrolhos. The noddy species will need to adapt to shifting levels of prey availability, coupled with the expected effects of increasing sealevels upon these low-lying island habitats. The long-term implications of this shift for the noddy populations, and most likely other core breeding populations of seabirds at the Houtman Abrolhos, are potentially severe.

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References

Ainley D G & Boekelheide R J 1990 Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community. Stanford University Press, California.

Ashmole M J & Ashmole N P 1968 The use of food samples from seabirds in the study of seasonal variation in the surface fauna of tropical oceanic areas. Pacific Science 22: 1–10.

Caputi N 2008 Impact of the Leeuwin Current on the spatial distribution of the peurulus settlement of the western rock lobster (*Panulirus cygnus*) and implications for the fishery of western Australia. Fisheries Oceanography 17: 147–152.

Caputi N, Chubb C & Pearce A 2001 Environmental effects on recruitment of the western rock lobster, *Panulirus cygnus*. Marine & Freshwater Research 52: 1167–1174.

Cooper J & Klages N T W 1995 The diets and dietary segregation of Sooty Albatrosses (*Phoebetria* spp.) at sub-Antarctic Marion Island. Antarctic Science 7: 15–23.

Crawford R J M & Dyer B M 1995 Responses by four seabird species to a fluctuating availability of Cape Anchovy *Engraulis capensis* off South Africa. Ibis 137 : 329–339.

Cresswell G 1990 The Leeuwin Current. Corella 14: 113–118.

Cresswell G R, Boland F M, Peterson J L & Wells G S 1989 Continental shelf currents near the Abrolhos Islands, Western Australia. Australian Journal of Marine & Freshwater Research 40: 113–128.

Croxall J P, Prince P A & Reid K 1997 Dietary segregation of krill-eating South Georgia seabirds. Biological Journal of the Linnean Society 814: 103–131.

Diamond A W 1983 Feeding overlap in some tropical and temperate seabird communities. Studies in Avian Biology 8: 24–46.

Duffy D C & Jackson S 1986 Diet studies of seabirds: a review of methods. Colonial Waterbirds 9: 1–17.

Dunlop J N, Long P, Stejskal I & C A Surman 2002 Inter-annual variations in breeding participation at four western Australian colonies of the Wedge-tailed Shearwater *Puffinus pacificus*. Marine Ornithology 30 (1): 13–18.

Dunlop J N & Jenkins J 1994 Population dynamics of the Bridled Tern *Sterna anaethetus* colony on Penguin Island, south-western Australia. Corella 18: 33–36.

Dunlop J N & Mitchell D 2001 Further changes to the breeding seabirds of Lancelin Island, Western Australia. Corella 25: 1–4.

Dunlop J N & R D Wooller 1990 The breeding seabirds of south-western Australia. Trends in species, populations and colonies. Corella 34: 107–112.

Gaughan D, Surman C A, Moran M & Burbidge A (2002) Feeding ecology of seabirds nesting at the Abrolhos Islands, Western Australia. Project 1998/203. FRDC. 140pp.

Gommon M F, Glover J C M & Kuiter R H (eds) 1994 The Fishes of Australia's South Coast. State Print, Adelaide.

Hutchins B & Swainston R 1986 Sea Fishes of Southern Australia. Swainston Publishing, Perth.

Last P R, Scott C O G & Talbot P H 1983 Fishes of Tasmania. Tasmanian Fisheries Authority, Hobart.

Leis J M & Rennis D S 1983 The Larvae of Indo-Pacific Coral Reef Fishes. New South Wales University Press, Sydney.

Leis J M & Trnski T 1989 The Larvae of Indo-Pacific Shorefishes. New South Wales University Press, Sydney.

Lewis S, Wanless S, Wright P J, Harris M P, Bull J & Elston D A 2001 Diet and breeding performance of black-legged kittiwakes Rissa tridactyla at a North Sea colony. Marine Ecology Progress Series 221: 277–284.

Nicholson L W 2002 Breeding strategies and community structure of tropical seabirds on the Lowendal Islands, Western Australia. Ph.D Thesis, Murdoch University, 327pp.

Pattiaratchi C 2005 Variability in the Leeuwin Current. Climate Note 10/05 in Indian Ocean Climate I.

Pearce A F 1991 Eastern boundary currents of the southern hemisphere. Journal of the Royal Society of Western Australia 74: 35–45.

Ramos J A (2000). Characteristics of foraging habitats and chick food provisioning by tropical roseate terns. The Condor 102:795–803.

Rindorf A, Wanless S & Harris M P 2000 Effects of changes in sandeel availability on the reproductive output of seabirds. Marine Ecology Progress Series 202: 241–252

Serventy D L, Serventy V N & Warham J 1971 The handbook of Australian Sea-birds. Reed, Sydney, 255pp.

Shealer D A 1998 Differences in diet and chick provisioning between adult Roseate and Sandwich Terns in Puerto-Rico. Condor 100: 131–140.

Smith M M & Heemstra P C 1986 Smith's Sea Fishes. Macmillan South Africa, Johannesburg.

Surman C A 1997 A comparative study of the breeding and feeding ecology of three sympatric tropical terns on the Houtman Abrolhos, Western Australia. Ph.D Thesis, Murdoch University, 224pp.

Surman C A 1998 Seabird breeding schedules at the Pelsaert group of islands, Houtman Abrolhos, Western Australia between 1993 and 1998. Records of the Western Australian Museum. 19: 209–215.

Surman C A & L W Nicholson 2008 Trends in Population and Habitat Status in the Threatened Lesser Noddy *Anous tenuirostris melanops* at the Houtman Abrolhos. Unpublished report prepared for the DEC, Geraldton by Halfmoon Biosciences, 47pp.

Surman C A & Wooller R D 1995 The breeding biology of the Lesser Noddy on Pelsaert Island, Western Australia. Emu 95: 47–53.

Surman C A & Wooller R D 2000 Nestling escape behaviour in tree, bush and ground-nesting tropical terns. Ibis 142: 320–322.

Surman C A & Wooller R D 2003 Comparative foraging ecology of five sympatric terns at a sub-tropical island in the Eastern Indian Ocean. Journal of Zoology, London 259:219–230.

Wooller R D & Dunlop J N 1980 The use of simple measurements to determine the age of Silver Gull eggs. Australian Wildlife Research 7: 113–115.