

Reproductive parameters of tropical lesser noddies respond to local variations in oceanographic conditions and weather



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ABSTRACT

Most attempts to link seabirds and climate/oceanographic effects have concerned the Atlantic and Pacific Oceans with comparatively few studies in the tropical Indian Ocean. This paper examines the reproductive response of the lesser noddy *Anous tenuirostris* to temporal fluctuations in oceanographic and climatic conditions using 8 years of monitoring data from Aride Island (Seychelles), tropical Western Indian Ocean. We tested the hypothesis that breeding parameters (mean hatching date, mean egg size, hatching and fledging successes) and chick growth are influenced by local, seasonal oceanographic conditions as expressed by ocean primary productivity (surface chlorophyll-*a* concentrations; CC), sea surface temperature (SST) and wind speed. We also examined the relationship between lesser noddy breeding parameters and climate conditions recorded at the basin-wide scale of the Indian Ocean (Indian Ocean Dipole Mode Index, DMI). Our findings suggest that birds had a tendency to lay slightly larger eggs during breeding seasons (years) with higher CC during April–June (pre-laying, laying and incubation periods). Hatching date was positively related to SST in April–June, with the regression parameters suggesting that each 0.5 °C increase in SST meant a delay of approx.10 days in hatching date. A negative linear relationship was also apparent between hatching success and SST in June–August (hatching and chick-rearing periods), while the quadratic regression models detected a significant effect of wind speed in June–August on fledging success. Body mass increments of growing chicks averaged over 7-day periods were positively related with (2-week) lagged CC values and negatively related with (2-week) lagged SST values. No significant relationship between DMI and lesser noddy breeding parameters was found, but DMI indices were strongly correlated with local SST. Altogether, our results indicate that the reproduction of this top marine predator is dictated by fluctuations in local environmental conditions around the colony, while the effects of large-scale oceanographic processes (DMI) on our study population might be mediated by an effect on local SST.

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1. Introduction

Apex predators such as piscivorous seabirds have been long suggested as indicators of both spatial and temporal fluctuations in prey abundance (Furness and Camphuysen, 1997; Le Corre and Jaquemet, 2005). Due to the logistical difficulty when sampling prey stocks at sea continuously in space and time, however, the association of prey-predator is often examined indirectly. For instance, remotely-sensed sea-surface temperatures and chlorophyll-*a* concentrations have been successfully used as surrogates of oceanic primary productivity (phytoplankton

abundance) and food stocks at higher trophic levels from zooplankton to larval and adult fishes (Pinaud and Weimerskirch, 2007; Weimerskirch et al., 2010). Recent seabird studies suggest that foraging individuals maximise their daily food intake by feeding over the most profitable patches and, to a certain extent, are capable of adapting their foraging behaviour during the course of the annual cycle to track seasonal changes in the location and abundance of prey (Weimerskirch et al., 2002; Weimerskirch, 2007).

In order to further understand how seabird population dynamics may be influenced by oceanographic processes, long-term studies have also examined whether or not the fate of breeding colonies can be used to monitor temporal changes in marine food webs. In most cases, inter-annual and seasonal variations in climate indices, biophysical oceanographic variables and fishery landings

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have been correlated to various output measures of seabird colonies such as breeding participation (Devney et al., 2009), phenology (Abraham and Sydeman, 2004; Jaquemet et al., 2007), average clutch size (Monticelli et al., 2007), chick growth (Quillfeldt et al., 2007; Ancona et al., 2011), and colony productivity (Thompson and Ollason, 2001; Le Corre and Jaquemet, 2005; Surman et al., 2012). These variations in demographic parameters of apex predators are often induced by changes in plankton composition and biomass (Frederiksen et al., 2006), which are known to occur at multiple time scales ranging from annual/seasonal to weekly and daily variations (Madariaga, 2002; Winder and Cloern, 2010). Few studies, however, have examined the differential response of seabird reproductive performance to fluctuations in oceanic productivity measured within multiple time frames, including both inter-annual and short-term temporal scales (i.e. on a seasonal, weekly and daily basis; but see Erwin and Congdon, 2007; Devney et al., 2010). Understanding the response of seabird populations to environmental fluctuations measured at various spatial and temporal scales is nevertheless crucial to fully evaluate their potential as biological indicators and to address conservation issues (Piatt et al., 2007 and references therein).

In addition, there has been increasing interest in recent decades to examining the relationship between local environmental factors driving seabird population dynamics and large-scale oceanic climate indices, such as the North Atlantic Oscillation (NAO; Frederiksen et al., 2006) and El Niño Southern Oscillation (ENSO; Devney et al., 2009; Ancona et al., 2011 and references therein). Most of these attempts to link seabirds and climate effects, however, have been focused on the Atlantic and Pacific Oceans with comparatively few studies currently available for the Indian Ocean, particularly its tropical region (but see e.g. Catry et al., 2013).

Our main aim here was to examine the reproductive response of the lesser noddy *Anous tenuirostris* – an abundant colonial seabird in the tropical western Indian Ocean – to fluctuations in both local and large-scale oceanographic variables over multiple time frames. For this, we analysed a dataset comprising 8 years of breeding parameters and chick growth monitoring data from Aride Island (Seychelles) and the corresponding ocean indices extracted in the vicinity of the island and at the basin-wide scale of the Indian Ocean. We tested the hypothesis that weekly fluctuations in food intake by growing chicks are controlled by primary productivity (surface chlorophyll-*a* concentrations; CC), sea surface temperatures (SST) and wind speed conditions occurring at a similar temporal scale (i.e. on a weekly basis) within the presumed foraging range (~100 km) of breeding adults around the colony. We also examined whether other seasonal breeding parameters reflecting the fate of the studied population as a whole (mean hatching date, mean egg size, hatching and fledging successes) reflected inter-annual variations in both local (SST, CC, wind speed) and large-scale oceanic conditions in the tropical Indian Ocean (Indian Ocean Dipole; Saji et al., 1999). Specifically, we expected chick growth and breeding performance to be depressed by warmer SST (Ancona et al., 2011; Catry et al., 2013), lower CC (Peck and Congdon, 2005) and at high wind speed (Dunn, 1973).

2. Material and methods

2.1. Study site, study species and sampling survey

Fieldwork was conducted intensively on Aride Island (4°10'S, 55°40'E) during 8 breeding seasons spanning the 2001–2011 period. This island hosts a large seabird community of international importance, including the largest known breeding population of the lesser noddy *Anous tenuirostris* (approx.100,000–200,000 breeding pairs annually; Bowler et al., 2002). The oceanography of

the study area and the nesting biology and monitoring methods of the lesser noddy population have been described in detail in Monticelli et al. (2007) and Ramos et al. (2004), respectively. The waters around Aride Island experience two annual blooms in primary productivity, a moderate bloom in December–February (austral summer) and a main bloom in April–August (austral winter; see Fig. 3B in Monticelli et al., 2007). Few noddies breed during the austral summer, most breeding during a protracted period of 5 months in April–August, presumably taking advantage of enhanced food availability around the island at that time. Lesser noddy nests are constructed from leaves and seaweed, and are placed on tree branches; one egg is laid, usually in May, with chick-rearing in June–August, rarely through September for late breeders (Ramos et al., 2004). Adults forage in multi-species flocks over schooling fishes and have a highly specialized diet throughout their breeding cycle with chicks being mostly fed 0-age group class goatfishes (fam Mullidae: >85% of all deliveries on Aride Island and >27% in Australia, see Surman and Wooller, 2003; Catry et al., 2009).

During each survey year (8 years), nests were marked in study plots at the time of egg laying. Egg width and breadth were measured with vernier callipers to the nearest 0.1 mm, except in 2002. During incubation, our sample of marked nests was monitored at intervals of 1–3 days to record egg fate (egg lost, egg in the nest, egg hatched). Monitoring was increasing to daily level around predicted hatching times in order to record exact hatching dates. The fate of growing chicks (alive in nest, alive but fell from nest, disappeared from nest, dead in nest) was recorded from hatching up to the fledging stage (approx. 45 days old). To estimate fledging success, we considered that those chicks that fell down or had disappeared from the nest before the usual fledging age of 45 days died; the rationale behind this being that lesser noddy parents do not feed chicks outside the nest (Surman and Wooller, 2000).

Mass measurements were obtained annually during the early and linear growth periods of chicks (age 0–19 days) while in some years, mass data were collected up to the asymptotic mass phase (>30 days of age). The sample of weighed chicks varied substantially between study years due to large variations in the number of nests present in the study plots. The weighing procedure consisted in routinely weighing a sample of 15–63 chicks daily at the same hour (usually around midday). Each bird was placed in a clean, tared bag attached to a Pesola spring balance and weighed to the nearest 0.5 g. Recently-fed and/or incorrectly-handled chicks during the weighing procedure may regurgitate part of their last meal in the bag; whenever they did so this was recorded and the meal was fed back to the chick.

2.2. Oceanographic variables

To characterise the oceanographic conditions close to Aride Island we obtained the local Chlorophyll-*a* concentration (CC), sea surface temperature (SST), and wind speed values, and to record climatic conditions at the regional scale of the Indian Ocean we used the Indian Ocean Dipole Mode Index (DMI).

2.2.1. CC, SST and wind speed

Daily values of (CC) as provided by the SeaWiFS instrument were obtained from OceanColor website (<http://oceancolor.gsfc.nasa.gov>) at a scale of 0.09° in longitude and latitude, whereas daily values of sea surface temperature (SST) and wind speed were obtained from NOAA website (<http://www.nodc.noaa.gov>) at a scale of 0.04°. Both SST and CC daily values were downloaded for the April–August (i.e. breeding season of the study species) periods from 2001 to 2011, and combined into weekly composites (see below) to overcome the problem of missing values due to

incomplete coverage by the satellites on some days (e.g. due to cloud cover). For SST and wind speed, the weekly composites were the arithmetic means of all daily values, while for CC, we computed a value corresponding to a 'peak' productivity following the method described by Monticelli et al. (2007). For each pixel, the 7 days of data were combined by taking the arithmetic mean of the logarithms of the chlorophyll concentration ($\log_{10}CC$ in mg m^{-3}), as this measure is more robust to occasional extreme values (Quarty and Srokosz, 2004). We then considered the 164 pixels (100 km radius) near Aride Island and calculated the 90th percentile, as this provides a robust estimate of the peak productivity within this radius. This assumes that while at sea, lesser noddy parents will target and forage over the most productive (i.e. higher CC values) waters. All computations were carried out within the R environment (v2.15.0; R Development Core Team, 2012).

2.2.2. DMI

The Indian Ocean Dipole (IOD) is a coupled ocean-atmosphere phenomenon reflecting the climatic state of the tropical Indian Ocean. The intensity of the IOD is represented by the Dipole Mode Index (DMI), which is the difference in sea-surface temperature anomaly between the western equatorial ($50^{\circ}\text{E}-70^{\circ}\text{E}$, $10^{\circ}\text{S}-10^{\circ}\text{N}$) and south-eastern equatorial ($90^{\circ}\text{E}-110^{\circ}\text{E}$, $10^{\circ}\text{S}-\text{Equator}$) Indian Ocean. A positive DMI is associated with higher sea-surface temperatures (SST) in the west and lower SST in the east (Saji et al., 1999). Monthly values of the DMI were downloaded from the Frontier Research Centre for Global Change website (<http://www.jamstec.go.jp/frsgc/research/d1/iod/>).

2.3. Statistical analyses

2.3.1. General population indices

Estimates of seasonal hatching success (% of hatched eggs from marked nests), fledging success (% of chicks fledged from hatched eggs) and colony productivity (hatching success \times fledging success) were derived from the nest monitoring data (8 breeding seasons). Egg size was calculated as $[0.512 \times (\text{length} \times \text{breadth}^2)]/1000$ in order to give a seasonal mean value.

Due to large variations in annual sampling effort (see Appendix 1 for sample sizes), weighted sample means and variances were used in further calculations. For each of the breeding parameters, we estimated the temporal (process) variance after removal of sampling variance from the total observed variance and subsequently computed a coefficient of variation as $\text{CV} (\%) = [(\text{temporal variance})^{1/2}/\text{weighted mean}] * 100$ (see methods in e.g. Akçakaya, 2002). This approach was justified by the fact that variation due to demographic stochasticity and measurement error may account for a substantial proportion of the observed variance (Gould and Nichols, 1998).

Trends in breeding parameters over time were examined with Pearson's correlation coefficients. Our set of breeding parameters was tested against environmental predictors using regression models. We fitted linear curves with all predictors, except wind speed for which a quadratic regression model was preferred (Dunn, 1973). The values entered in the regression analysis with egg size and hatching date as dependent (response) variables corresponded to the arithmetic mean of all weekly composites of SST, CC and DMI during the pre-laying, laying and incubation periods (i.e. April–June), while for the remaining reproductive parameters, we used the weekly composites of SST, CC, wind speed and DMI averaged over the 3-monthly interval overlapping with the hatching and chick-rearing periods (i.e. June–August).

2.3.2. Chick mass increments

To evaluate whether growth rates of lesser noddy chicks reflected variations in food availability over short time scales (as expressed by weekly composites of local oceanographic conditions), weekly averages of daily mass increments (*DM*) were calculated in order to match the time scale at which ocean indices were computed. Mass data of very young chicks aged 0–4 days were not used in subsequent calculations as variations in mass increments during the early part of the growth period depends more on the age of the chick than on variation in food availability (Shea and Ricklefs, 1996). The weekly averages of chick growth were defined as $\text{mean } DM = [M(5) - M(1) + M(6) - M(2) + M(7) - M(3) + M(8) - M(4)]/16$, where $M(d)$ refers to mass (g) from day 1 to day 8 (8 consecutive data points per chick). Chick age was used to normalize *DM* with respect to structural size in order to remove the contribution of size itself to this measurement. Accordingly, we calculated a quadratic regression between weekly averages of *DM* and chick age and used the residuals about the regression line (*RDM*) for subsequent analysis. The regression equation was $DM = 3.721 + 0.114 (\text{age}) - 0.011 (\text{age}^2)$; $F_{2,465} = 134.5$, $R^2 = 0.37$, $p < 0.001$ (Fig. 1).

Co-variation between weekly composites of CC, SST and wind speed data series (see Appendix 2) were examined with Pearson's correlation coefficients. Least-square regression analyses were used to examine the predictive effects of weekly composites of our environmental predictors (SST, CC, wind speed) on date-matched *RDM* (weekly averages in June–August). A least-square regression analysis might not be appropriate when there is a high degree of temporal autocorrelation in time-series data (Kutner et al., 2005). Thus, a Durbin–Watson statistic was calculated in all regressions to test for serial autocorrelation in the residuals (Kutner et al., 2005). Previous studies identified that seabird foraging distribution may be uncoupled from current oceanographic conditions measured by productivity proxies such as SST and CC (Grémillet et al., 2008) due to time lags between oceanographic variables that can be measured and the factors (prey availability) that actually attract seabirds (Mann and Lazier, 2006; Wakefield et al., 2009). Thus, to test for a lagged effect of local SST and CC conditions on lesser noddy chick growth, a second set of regression analyses was conducted between the weekly averages of *RDM* and date-lagged composites of SST and CC. To determine the most likely time lag, we followed a previous life history and growth study of *Upeneus* goatfishes (one of the main prey items fed to lesser noddy chicks; Monticelli et al., 2008) from the Great Barrier Reef (Australia) in which McCormick (1994) reported that pelagic goatfish larvae gather into large schools from approx. 7.5 mm in size (standard length) and subsequently grow at

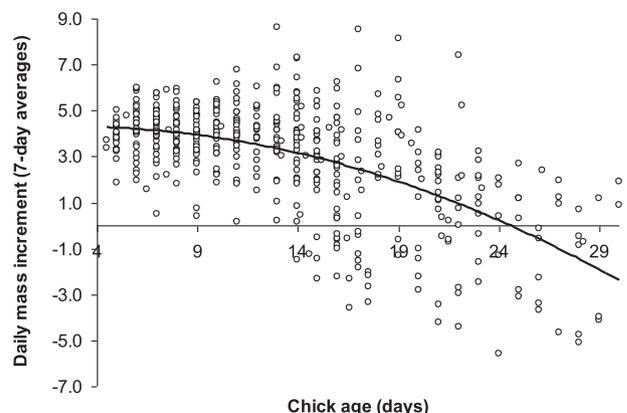


Fig. 1. Daily mass increment (7-day averages; g) in relation to age (days) of lesser noddy chicks on Aride Island, 2001–2011 (8 breeding seasons).

a daily rate ranging from 0.5 to 1.0 mm. Because lesser noddy parents on Aride Island feed their chicks with schooling goatfishes ranging from 21 to 85 mm in size (Catry et al., 2009), we used a minimum time lag of two weeks (14 days).

3. Results

3.1. Lesser noddy breeding parameters

Statistics of egg size, hatch date, hatching success, fledging success, and colony productivity are summarized in Table 1 (all years pooled) and Appendix 1 (seasonal estimates). None of the five breeding parameters monitored from 2001 to 2011 (8 breeding seasons) showed a systematic trend over time ($r_{\text{egg size}} = -0.006$, $p = 0.99$; $r_{\text{hatch date}} = 0.619$, $p = 0.10$; $r_{\text{hatch success}} = -0.708$, $p = 0.05$; $r_{\text{fledging success}} = -0.221$, $p = 0.59$; $r_{\text{productivity}} = -0.372$, $p = 0.36$). Temporal variation over the study period was very low in both egg size and hatching success (CV = 1.4 and 13.6%, respectively), intermediate for hatching date (CV = 30.8%), and high for fledging success and colonial productivity (CV = 63.9 and 68.5%, respectively). The large CV value obtained for colony productivity should be connected, at least in part, to contrasting conditions in offspring survival observed between breeding seasons, including, for instance, a very high fledging success in 2001 (>90% of chicks fledged) but a near-complete breeding failure recorded in 2002 (i.e. 1.7% of chicks fledged; Appendix 1).

3.2. Relationship with seasonal variations in oceanographic conditions

The monthly values of local sea-surface temperatures (SST) revealed a consistent pattern of higher SST in April–June (pre-laying and incubation periods) compared to lower SST in June–August (chick-rearing period) (Fig. 2). During the present study, this decrease in SST as the breeding season progressed was accompanied by a strong increase in (log₁₀CC peak) Chlorophyll-*a* values (phytoplankton bloom) between the same periods (April–June vs. June–August; Fig. 3). Local SST was positively correlated to the

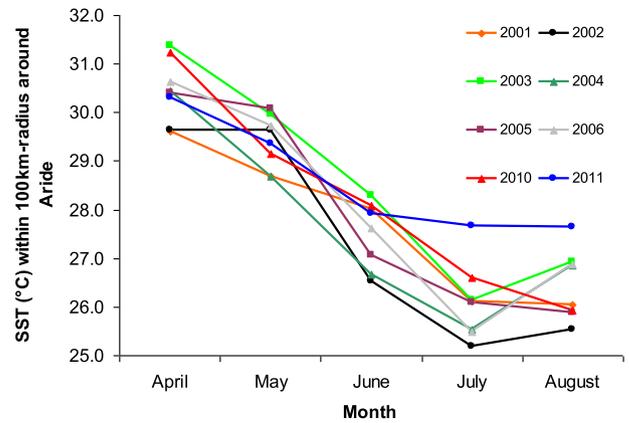


Fig. 2. Monthly sea-surface temperatures (SST; °C) recorded within a 100 km-radius around Aride Island in April–August, 2001–2011 (8 breeding seasons).

Dipole Mode Index (April–June: $r_{\text{SST-DMI}} = 0.853$, $p = 0.001$ and June–August: $r_{\text{SST-DMI}} = 0.624$, $p = 0.04$). In addition, SSTs in both April–June and June–August were correlated ($r_{\text{SST-SST}} = 0.728$, $p = 0.011$) and a significant association between SST in June–August and average wind speed during the same period was detected ($r_{\text{SST-WIND}} = 0.630$, $p = 0.038$).

The linear regression models (Table 1) found that birds had a tendency to lay slightly larger eggs during breeding seasons with higher CC during April–June (Fig. 4a). Hatching date was also positively related to SST in April–June (Fig. 4b), with the regression parameters suggesting that each 0.5 °C increase in SST meant a delay of approx.10 days in hatching date. A negative relationship was also apparent between hatching success and SST in June–August (Fig. 4c) and there was a tendency, albeit non-significant ($p = 0.08$), for a positive linear relationship between hatching success and CC in June–August (Table 1).

Fledging success and colony productivity were not related to SST or CC in June–August (all linear models with $p > 0.05$; Table 1). However, the quadratic models suggested a significant effect of

Table 1

Regression models examining the relationship between sea-surface temperature (SST), log₁₀CC peak Chlorophyll-*a* concentration, wind speed or the Dipole Mode Index (DMI) and breeding parameters of the lesser noddy population on Aride Island, Seychelles, 2001–2011. Wind speed, SST and CC are locally estimated within a 100 km-radius around the island. Oceanographic predictors are averaged over April–June and June–August in order to reflect the prevailing conditions during the pre-laying/incubation and chick-rearing periods, respectively. For each breeding parameter, sample sizes are detailed by total number of years available and total number of nests monitored. Means and variances are weighed according to annual sampling effort (i.e. differing sample sizes each year; see Appendix 1) and the coefficients of variation are based on temporal process variances (i.e. after removal of variation due to sampling). Significant ($p < 0.05$) and marginally significant ($p < 0.06$) predictors are highlighted in bold.

Breeding parameter	No. of years (sample size)	Mean	Range	Coefficient of variation (%)	Oceanographic predictor	Model fitting	R ²	p	Slope ± SE
Egg size (cm ³)	7 (571)	21.66	21.01–22.24	1.4	DMI (April–June)	Linear	0.004	0.888	
					CC (April–June)	Linear	0.626	0.034	1.0 ± 0.3
Hatching date (1 June = 1) (days)	8 (217)	35	23–57	30.8	SST (April–June)	Linear	0.251	0.252	
					DMI (April–June)	Linear	0.291	0.167	
Hatching success (%)	8 (627)	76.4	54.2–91.0	13.6	CC (April–June)	Linear	0.271	0.186	
					SST (April–June)	Linear	0.641	0.017	21.5 ± 6.6
Fledging success (%)	8 (627)	54.9	1.7–92.2	63.9	DMI (June–August)	Linear	0.001	0.993	
					CC (June–August)	Linear	0.409	0.088	
					SST (June–August)	Linear	0.602	0.024	–15.3 ± 5.1
					Wind speed (June–August)	Quadratic	0.022	0.946	
Colony productivity (No. of fledglings. pair ⁻¹)	8 (627)	0.43	0.01–0.76	68.5	DMI (June–August)	Linear	0.004	0.877	
					CC (June–August)	Linear	0.011	0.809	
					SST (June–August)	Linear	0.001	0.931	
					Wind speed (June–August)	Quadratic	0.814	0.015	(34.5 ± 10.9)x – (2.2 ± 0.7)x²
Colony productivity (No. of fledglings. pair ⁻¹)	8 (627)	0.43	0.01–0.76	68.5	DMI (June–August)	Linear	0.005	0.873	
					CC (June–August)	Linear	0.113	0.415	
					SST (June–August)	Linear	0.075	0.512	
					Wind speed (June–August)	Quadratic	0.683	0.057	(27.5 ± 12.3)x – (1.8 ± 0.8)x²

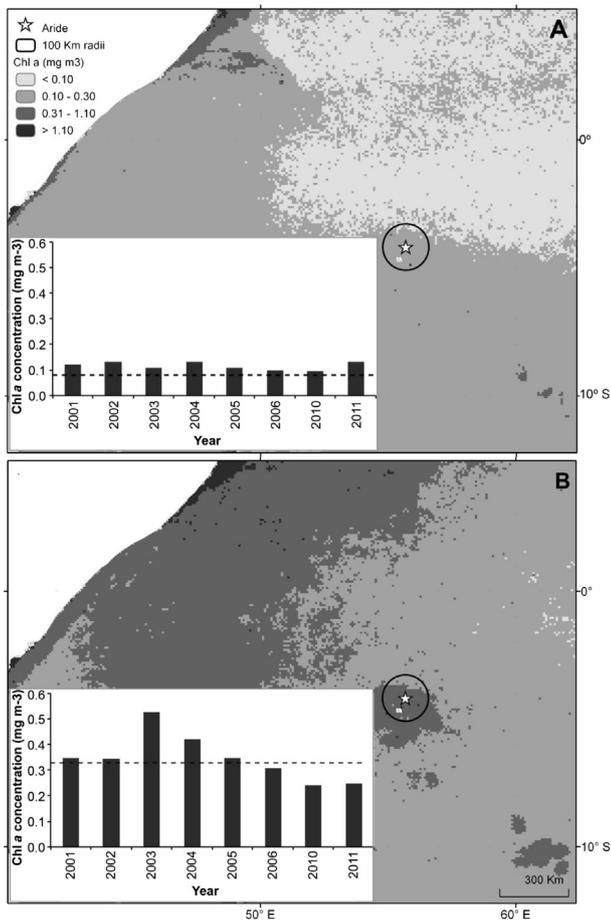


Fig. 3. Spatial representation of mean Chlorophyll-*a* values recorded in (A) April–June and (B) June–August during the 2001–2011 study period (8 breeding seasons).

wind speed in June–August on fledging success, and a near-significant relationship with colony productivity (Table 1). In particular, intermediate wind-speed conditions prevailed during half of the study years and promoted high fledging success, while during the four remaining years of more “extreme” values (i.e. wind speed conditions above 8 m/s or below 7.5 m/s), fledging success was depressed (Fig. 4d).

3.3. Relationship with weekly variations in oceanographic conditions

The weekly composites of local ocean indices ($n = 23$ weeks; see Appendix 2) were extracted for the period matching our growth measurements of chicks (date-matched SST, CC, wind speed), except for one week in early August 2006 due to missing Chlorophyll-*a* data (i.e. presumably due to intense cloud cover over Aride Is.). The correlation analysis performed between paired data series included date-lagged sea-surface temperatures (lagged SST) and date-lagged \log_{10} CC peak Chlorophyll-*a* concentrations (lagged CC) corresponding to weekly composite-values recorded two weeks prior to the dates of chick mass measurement. A positive correlation between the two SST data series (lagged vs. date-matched: $r = 0.702$, $p = 0.0001$) but not between the two CC data series was detected (lagged vs. date-matched: $r = 0.235$, $p = 0.279$). A negative correlation between CC-SST weekly composites ($r = -0.589$, $p = 0.003$) and between lagged CC-lagged SST weekly composites ($r = -0.596$, $p = 0.003$) was also apparent. Wind speed was not correlated with either SST or CC data series (all $p > 0.05$).

Chick mass data were used to compute 7-day (weekly) averages of daily mass increments ($n = 23$ weeks; see Appendix 2). Daily mass gain (*DM*) un-corrected for chick age was very variable with a mean *DM* ranging from approx. 5 g/day in “good” weeks (e.g. in 2005, 2006, 2010) to < 2.5 g/day during “poor” weeks (e.g. in 2004, 2005, 2011). No significant trend was detected when testing for the effect of date-matched CC, SST or wind speed values on weekly averages of mass increment residuals (*RDM* corrected for chick age) (all 3 models with p -level > 0.05). No association was found between (2-week) lagged wind speed and *RDM* data series. However, there was a marginally significant and positive relationship between mass increment residuals and (2-week) lagged CC values (Fig. 5a; $F_{1-21} = 4.09$, $p = 0.056$, $R^2 = 0.163$), while a negative relationship was also apparent between mass increment residuals and (2-week) lagged SST values (Fig. 5b; $F_{1-21} = 4.336$, $p = 0.050$, $R^2 = 0.171$). No autocorrelation was observed in either of these two regressions using the Durbin–Watson test (Durbin–Watson statistic $D \sim 2.17$, $n = 23$, $p > 0.05$).

4. Discussion

Compared to temperate and polar systems, tropical waters show weaker seasonal cycles in primary production (Pennington et al., 2006; Quarty et al., 2008). Nonetheless, predictable oceanographic events such as up-welling and phytoplankton blooms occur in tropical oceanic environments (Pennington et al., 2006), resulting in a seasonally-enhanced biomass at higher trophic levels from zooplankton to larval and adult fishes (Thompson et al., 2012). Indeed, several decades of monitoring seabird breeding parameters on Aride Island indicate a fairly marked seasonality of biophysical processes, with annual breeding of most seabird species coinciding with the seasonal cooling of surrounding waters, usually from April onwards, and the subsequent annual peak in primary production (phytoplankton bloom) that takes place in June–August (Monticelli et al., 2007; this study).

As adults are constrained to forage near the colony during most of the breeding season, local (temporal) fluctuations in food availability are important proximate factors shaping seabird reproductive parameters and breeding success (Aebischer et al., 1990; Frederiksen et al., 2006). In the present study, the differential sensitivity of lesser noddy breeding parameters to several surrogate measures of food supply conditions around Aride Island was explored at various temporal scales. We suggest that offspring growth responds to short-term (weekly) variations in prey availability, as expressed by weekly chlorophyll-*a* concentration (CC) and sea-surface temperature (SST) estimates. This significant relationship was obtained when using a time lag of 2 weeks between CC (and SST) measurements and their effects on prey availability and chick growth. Furthermore, we found that breeding parameters recorded at the population level are shaped by inter-annual variations in local oceanographic conditions: SST conditions influence timing of breeding, hatching success and chick growth, CC is positively related to egg size and chick growth, and wind speed conditions predict fledging success. The influence of the Indian Ocean Dipole on lesser noddy reproductive parameters was only (indirectly) apparent through an effect on local SST.

4.1. Oceanographic conditions and chick growth

Temporal variations in the growth of both temperate and polar-zone seabird chicks have been related to both inter- and intra-seasonal variations in prey abundance, either ‘directly’, through direct comparison with available prey stocks at sea (Safina and Burger, 1988; Abraham and Sydeman, 2004), or ‘indirectly’, by relying on oceanographic and weather surrogates, which correlate

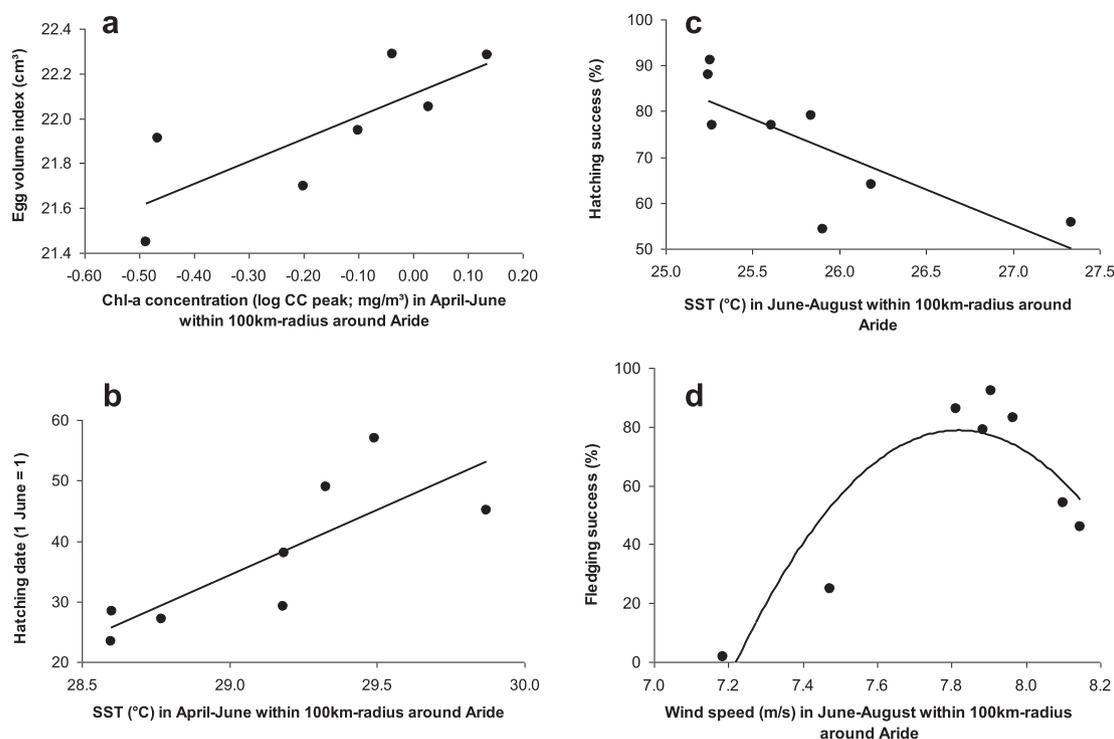


Fig. 4. Relationships between breeding parameters and local oceanographic conditions within a 100 km-radius around Aride Island: (a) log₁₀CC peak Chlorophyll-*a* values recorded annually in April–June and size of lesser noddy eggs (7 breeding seasons). Egg size (cm³) is indexed as $[0.512 \times (\text{length} \times \text{breadth}^2)]/1000$; (b) sea-surface temperatures recorded annually in April–June and hatching date (coded with 1 June = 1) of lesser noddy chicks (8 breeding seasons); (c) sea-surface temperatures recorded annually in June–August and hatching success (proportion of marked eggs that hatched; %) at lesser noddy nests (8 breeding seasons); (d) wind speed (m s⁻¹) recorded annually in June–August and fledging success (proportion of hatched chicks that fledged; %) at lesser noddy nests (8 breeding seasons).

with prey biomass and availability (e.g. Dunn, 1975; Ricklefs et al., 1984; Ritz et al., 2005). In the tropical Pacific Ocean, recent studies of sooty terns *Sterna fuscata*, black noddies *Anous minutus* and blue-footed boobies *Sula nebouxi* found a negative impact of SST on the foraging success of adults (Erwin and Congdon, 2007), chick provisioning rates (Devney et al., 2010) and growth (Ancona et al., 2011). Similarly, our findings suggest that lesser noddy chick growth is a sensitive indicator of oceanographic conditions recorded at a fine temporal scale (i.e. on a weekly basis), with chicks gaining more mass and growing faster when cooler SST and higher CC were recorded off Aride Island. Conversely, mass gain is reduced following weeks of warmer SST and lower CC. Several hypothesis may be advanced to explain this relationship and these are not mutually exclusive.

The physical forcing and chemical mechanisms leading to seasonal and weekly fluctuations in sea-surface temperature and primary production off Aride Island are not fully understood, although our correlation analysis shows that SST and CC are inversely related. SST is closely linked with the depth of the oceanic mixed layer, which determines the nutrient up-welling and consequently controls primary production (Sarmiento et al., 2004). Thus, the progressive seasonal cooling of SST recorded between April–August off Aride Island (Fig. 2) raises the thermocline locally and brings more nutrients into the near-surface waters of the photic zone, hence resulting in seasonally enhanced CC levels (primary productivity) and biomass at higher trophic levels (Monticelli et al., 2007). The effect of SST on chick growth may not be exclusively mediated by CC and fish abundance, but may arise directly from the influence of SST on fish accessibility to foraging adults (see e.g. Ancona et al., 2011). Changes in SST on a short-term basis (e.g. weekly variations) can promote the disruption of the thermocline, which in turn causes shifts in the vertical distribution of prey in the water column (Hsieh

et al., 2009), modifying their availability near the water surface to aerial predators.

Both intra and inter-seasonal shifts in SST may not only affect chick growth by impacting food availability and abundance, but also through a change in diet regime and/or quality. For instance, rising ocean temperature can modify plankton composition, which, in turn, may affect the composition of fish stocks, the body condition of fish prey and their energetic content (Österblom et al., 2008). Those climate-related changes may force seabird parents to feed their offspring with sub-optimal prey items of lower energy content, with negative consequences on growth rates and breeding performance (Wanless et al., 2005; Sorensen et al., 2009). On Aride Island, where lesser noddy chicks are predominantly fed with young goatfishes, chicks displayed lower growth rates and had higher mortality rates during years of warmer SST (e.g. 2006) despite receiving larger meals (Table 2 in Catry et al., 2013). An increasing proportion of fish larvae – a probable less energetic prey than juvenile (0-age group class) goatfish – was also reported in the diet of lesser noddy chicks in years with strong SST anomalies around the study colony (see Catry et al., 2009). Overall, this pattern may be indicative of a reduction in diet quality during years of poor growth rates and high breeding failure, though this topic warrants further analysis.

Previous studies examining prey–predator relationships have pointed out that failure to account for time-lags between oceanographic processes (e.g. SST shifts, phytoplankton blooming) and their effects up the food chain would probably result in a mismatch between the biophysical predictor and seabird response variables (e.g. Mann and Lazier, 2006; Grémillet et al., 2008). Changes in zooplankton and fish biomasses may lag primary production by weeks or months (Thompson et al., 2012), depending on the rate at which primary production is transmitted up the food chain which, in

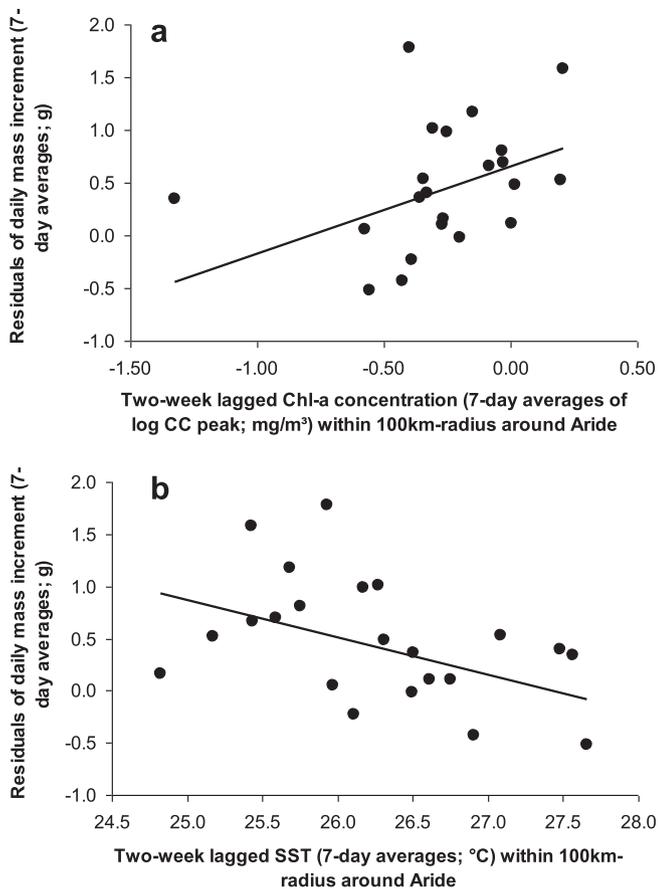


Fig. 5. Relationship between daily mass increment residuals (7-day averages) of lesser nobby chicks aged 5–36 days (23 study weeks across 8 breeding seasons) and 2-week lagged weekly composites of (a) Chlorophyll-*a* concentrations, and (b) sea-surface temperatures recorded in a 100 km radius around Aride Island.

turn, is a function of the characteristics of the ecosystem and species involved (Clarke, 2003). The appropriate determination of the relationships between trophic levels normally requires calibration (Thompson et al., 2012), although in many cases, likely time-lags can be estimated from *a priori* knowledge of life-history traits, trophic position, and movement capabilities of the study species (Wakefield et al., 2009 and references therein). On Aride Island, lesser noddies feed mostly on small juvenile goatfish which are plankton feeders and thus occupy a relatively low position in the food chain (Krajewski and Bonaldo, 2006). Consequently, a short time-lag of 2 weeks was considered in this study, based on published growth rates of larval goatfish (McCormick, 1994). Our significant regression models obtained between chick growth (response parameter) and lagged SST and CC estimates – but not with date-matched CC and SST – further highlight the need to account for appropriate temporal lags between the measurement of biophysical processes and their expected effects at higher trophic levels.

4.2. Oceanographic conditions, weather and breeding parameters

4.2.1. Sea-surface temperature

The large inter-annual variation in hatching dates of lesser nobby chicks ($CV \approx 30\%$) may be ascribed to variations in incubation periods; however, the magnitude of the inter-annual differences (one month) suggest that mean laying date is fairly variable in this population (Ramos et al., 2004). In seasonal environments, adults are expected to adjust laying to match the chick-rearing phase with the peak period in food availability (Perrins,

1970). Thus, early in the breeding season, seabirds must rely on one or more environmental cues to anticipate the timing and intensity of the seasonal peak in food conditions and time their breeding (laying) season and effort (e.g. clutch size) optimally. SST in June–July is strongly correlated with SST in April–June around Aride Island, which supports the assumption that food supply conditions later in the breeding season are “connected” with SST conditions that prevailed earlier (pre-laying and incubation periods). Therefore, our significant relationship between SST during April–June and hatch-date may indicate that surface temperature is used by lesser noddies to adjust laying: warmer temperatures in April–June may delay the annual peak of the phytoplankton bloom, and, accordingly, birds may postpone the egg laying season in those years “to allow” the further cooling of surface waters which should trigger the blooming of primary production and subsequent seasonal peak in goatfish availability. This idea that local SST is an important cue used by birds to adjust laying date is, however, not new and has been previously proposed in a number of temperate (e.g. Frederiksen et al., 2004) and tropical (e.g. Jaquemet et al., 2007; Surman et al., 2012) seabird species.

Warmer than average SST early in the breeding season (April–June) is also connected to poorer hatching success in this population, a pattern previously reported for tropical blue-footed boobies (Ancona et al., 2011). The mechanism by which SST affects hatching success is not clear, although a plausible explanation involves a negative effect of warmer SST on food availability to adults (both sexes incubate in this species) and/or a reduction in thermoregulatory capabilities of breeding adults resulting in nest abandonment and failure at an early seasonal stage. Hatching success may be also depressed by nest predation events, whose frequency increases usually during years of poor food supply conditions because incubating parents need to spend longer-than-average time at sea to maintain their own condition and hence may leave their sole egg unattended for longer periods. Despite a significant effect of SST on hatching success, our regression analysis did not find any effect of SST (and CC) in June–August on colony productivity. Presumably, by using fledging success to compute colony productivity (colony productivity = hatching success \times fledging success), any potential impact of prey abundance (as expressed by proxies such as SST, CC) on colony productivity was not shown as fledging success in this species is affected by additional factors acting at the level of the breeding habitat (see below), and, overall, exhibits a relatively large inter-annual (stochastic) variation. This suggests that chick survival (fledging success) and colony productivity for the Aride population may not be sensitive indicators to monitor changes in local oceanographic conditions, at least within the range of values (SST, CC) and time scales considered in the present study.

4.2.2. Chlorophyll-*a* concentration

An accurate relationship was detected between egg volume (a proxy of egg size/mass) and CC in April–June, which suggests that during years of higher primary production (and prey availability) recorded during the early part of the breeding season, lesser nobby females responded by allocating more somatic reserves to egg formation. The influence of prevailing food supply conditions during the laying period on clutch and egg sizes has been examined in a number of seabirds (see e.g. Sydeman et al., 1991; Suddaby and Ratcliffe, 1997; Ancona et al., 2011). In terns (*Sterna* spp.), both temperate (Safina et al., 1988) and tropical-zone (Monticelli et al., 2007) studies have reported that in years of higher food supply, females have a tendency to increase breeding effort and lay larger clutches, but not larger eggs. In tropical noddies, which are sister-species to terns (Baker et al., 2007), females only lay a single egg per clutch and are therefore ‘constrained’ to allocate supplementary resources, whenever available, to increasing egg mass (rather

than clutch size). To lay larger eggs during years of more favourable food conditions may be advantageous in our study species because egg mass is usually positively related to hatchling mass and chick survival in terns (Arnold et al., 2006). Embryo survival and hatching probability are also positively influenced by egg size (D'Alba and Torres, 2007), hence by promoting larger eggs, higher levels of CC around Aride Island may also increase hatching success, a pattern which was almost apparent in our analyses (see Table 1).

4.2.3. Wind speed

Climatic effects on oceanic food chains are driven primarily by local surface temperatures and wind conditions (Stenseth et al., 2002). In temperate species, particularly small terns, wind speed and sea surface condition influences the fishing ability of foraging adults: prey capture rate is usually depressed at low and high wind speeds but is maximum under intermediate wind conditions (Dunn, 1973). Thus, wind speed has measurable implications on food provisioning of seabird chicks and therefore on reproductive success (Dunn, 1975). Our significant relationship observed between fledging success and wind speed (Table 1) could have resulted from an effect on lesser noddy adult foraging success as described for some temperate tern species, although no effect on chick mass increments and growth was apparent in our analyses. In addition, the range of variation in mean seasonal wind speeds was relatively small in the present study (from 7.2 to 8.2 m/s; Fig. 4d), suggesting that other mechanisms might be involved. A peculiar trait in the biology of lesser noddies is their nest construction in trees, which is advantageous on Aride Island so that ticks, a major problem for ground-nesting species (Monticelli and Ramos, 2012), do not parasitize their chicks. Field observations, however, reveal that intense rainfall and higher-than-average wind speed sustained during a few consecutive days may result in the collapsing of tree branches and nests. Chicks falling on the ground are abandoned by their parents and starve to death, even in years of plentiful food conditions. This pattern was particularly evident in 2011 (unpubl. obs.) when average wind speed exceeded 8 m/s. Altogether, our data demonstrate that wind speed may affect fledging success of tropical lesser noddies in complex ways, involving a mixture of direct (nest collapsing) and indirect (adult's foraging efficiency) pathways.

4.2.4. Indian Ocean Dipole

Environmental conditions close to oceanic island seabird breeding colonies are influenced by larger scale oceanic/climatic events (Stenseth et al., 2002; Ancona et al., 2011). The ecological effects of ENSO conditions on marine environments have been measured far from its main centre of action in the Pacific Ocean, including in the Indian Ocean (Ramos et al., 2002; Surman et al., 2012). ENSO events are strongly interrelated to rainfall and SST changes in the Indian Ocean (Terray and Dominiak, 2005) and to the Indian Ocean Dipole (IOD; Cai et al., 2011). In the present study, we only considered the potential influence of the IOD and its index, the Dipole Mode Index because it describes a coupled ocean-atmosphere phenomenon within the tropical Indian Ocean, and thus is likely to impact the Aride Island population more directly than ENSO (see also Van de Pol et al., 2013). Our analyses provided no direct evidence of any impact of the DMI on lesser noddy breeding parameters. Despite this, mean DMI indices in April–June and June–August were strongly correlated with local SST during the same periods, suggesting that DMI effects on our study population might be mediated by an effect on local SST. The influence of climate index such as ENSO on seabird reproductive data is more easy to detect when extreme events occur (e.g. Shea and Ricklefs, 1996), but no strong DMI events were recorded during the study period. Several authors have also considered temporal lags between climate indices and their potential impacts on their study

species (e.g. Lewis et al., 2009). Moreover, the IOD is known to have its largest climatic effect during September to November (Saji et al., 1999) but a repeat of our analyses with DMI conditions averaged over the previous winter (Sept–Feb) did not improve the results of the regression analysis with concurrent datasets.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.ecss.2013.12.026>

References

- Abraham, C.L., Sydeman, W.J., 2004. Ocean climate, euphausiids and auklet nesting: inter-annual trends and variation in phenology, diet and growth of a planktivorous seabird, *Ptychoramphus aleuticus*. *Mar. Ecol. Prog. Ser.* 274, 235–250.
- Aebischer, N.J., Coulson, J.C., Colebrook, J.M., 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* 347, 753–755.
- Akçakaya, H.R., 2002. Estimating the variance of survival rates and fecundities. *Anim. Conserv.* 5, 333–336.
- Ancona, S., Sanchez-Colon, S., Rodriguez, C., Drummond, H., 2011. El Niño in the warm tropics: local sea temperature predicts breeding parameters and growth of blue-footed boobies. *J. Animal Ecol.* 80, 799–808.
- Arnold, J.M., Hatch, J.J., Nisbet, I.C.T., 2006. Effects of egg size, parental quality and hatch-date on growth and survival of Common Tern *Sterna hirundo* chicks. *Ibis* 148, 98–105.
- Baker, A.J., Pereira, S.L., Paton, T.A., 2007. Phylogenetic relationships and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of at least 14 clades of shorebirds. *Biol. Lett.* 3, 205–207.
- Bowler, J., Betts, M., Bullock, I., Ramos, J.A., 2002. Trends in seabird numbers on Aride Island Nature Reserve, Seychelles 1988–2000. *Waterbirds* 25, 26–38.
- Cai, W., van Rensch, P., Cowan, T., Hendon, H.H., 2011. Teleconnection pathways of ENSO and the IOD and the mechanisms for impacts on Australian rainfall. *J. Clim.* 24, 3910–3929.
- Catry, T., Ramos, J.A., Catry, I., Monticelli, D., Granadeiro, J.P., 2013. Inter-annual variability in the breeding performance of six tropical seabird species: influence of life-history traits and relationship with oceanographic parameters. *Mar. Biol.* <http://dx.doi.org/10.1007/s00227-013-2171-2>.
- Catry, T., Ramos, J.A., Jaquemet, S., Faulquier, L., Berlincourt, M., Hauselmann, A., Pinet, P., Le Corre, M., 2009. Comparative foraging ecology of a tropical seabird community of the Seychelles, western Indian Ocean. *Mar. Ecol. Prog. Ser.* 374, 259–272.
- Clarke, A., 2003. Costs and consequences of evolutionary temperature adaptation. *Trends Ecol. Evol.* 18, 573–581.
- D'Alba, L., Torres, R., 2007. Seasonal egg-mass variation and laying sequence in a bird with facultative brood reduction. *The Auk* 124, 643–652.
- Devney, C.A., Caley, M.J., Congdon, B.C., 2010. Plasticity of Noddy parents and offspring to sea-surface temperature anomalies. *PLoS One* 5, e11891. <http://dx.doi.org/10.1371/journal.pone.0011891>.
- Devney, C.A., Short, M., Congdon, B.C., 2009. Sensitivity of tropical seabirds to El Niño precursors. *Ecology* 90, 1175–1183.
- Dunn, E.K., 1975. The role of environmental factors in the growth of tern chicks. *J. Animal Ecol.* 44, 743–754.
- Dunn, E.K., 1973. Change in fishing ability of terns associated with wind speed and sea surface conditions. *Nature* 224, 520–521.
- Erwin, C.A., Congdon, B.C., 2007. Day-to-day variation in sea-surface temperature reduces sooty tern *Sterna fuscata* foraging success on the Great Barrier Reef, Australia. *Mar. Ecol. Prog. Ser.* 331, 255–266.
- Furness, R.W., Camphuysen, K.C.J., 1997. Seabirds as monitors of the marine environment. *ICES J. Mar. Sci.* 54, 726–737.
- Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C., Wanless, S., 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *J. Animal Ecol.* 75, 1259–1268.

- Frederiksen, M., Harris, M.P., Daunt, F., Rothery, P., Wanless, S., 2004. Scale-dependent climate signals drive breeding phenology of three seabird species. *Glob. Change Biol.* 10, 1214–1221.
- Gould, W.R., Nichols, J.D., 1998. Estimation of temporal variability of survival in animal populations. *Ecology* 79, 2531–2538.
- Grémillet, D., Lewis, S., Drapeau, L., van Der Lingen, C.D., Huggett, J.A., Coetzee, J.C., Verheye, H.M., Daunt, F., Wanless, S., Ryan, P.G., 2008. Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *J. Appl. Ecol.* 45, 610–621.
- Hsieh, C.H., Kim, H.J., Watson, W., Di Lorenzo, E., Sugihara, G., 2009. Climate-driven changes in abundance and distribution of larvae of oceanic fishes in the southern California region. *Glob. Change Biol.* 15, 2137–2152.
- Jaquemet, S., Le Corre, M., Quartly, G.D., 2007. Ocean control of the breeding regime of the sooty terns in the South-West Indian Ocean. *Deep-Sea Res.* 54, 130–142.
- Krajewski, J.P., Bonaldo, R.M., 2006. Plankton-picking by the goatfish *Pseudupeneus maculatus* (Mullidae), a specialized bottom forager. *J. Fish. Biol.* 68, 925–930.
- Kutner, M.H., Nachtsheim, C.J., Neter, J., Li, W., 2005. *Applied Linear Statistical Models*, fifth ed. McGraw-Hill/Irwin Ed, New York.
- Le Corre, M., Jaquemet, S., 2005. Assessment of the seabird community of the Mozambique Channel and its potential use as an indicator of tuna abundance. *Estuar. Coast. Shelf Sci.* 63, 421–428.
- Lewis, S., Elston, D.A., Daunt, F., Cheney, B., Thompson, P.M., 2009. Effects of extrinsic and intrinsic factors on breeding success in a long lived seabird. *Oikos* 118, 521–528.
- McCormick, M.I., 1994. Variability in age and size at settlement of the tropical goatfish *Upeneus tragula* (Mullidae) in the northern Great Barrier Reef lagoon. *Mar. Ecol. Prog. Ser.* 104, 1–15.
- Madariaga, I., 2002. Short-term variations in the physiological state of phytoplankton in a shallow temperate estuary. *Hydrobiologia* 475/476, 345–358.
- Mann, K.H., Lazier, J.R.N., 2006. *Dynamics of Marine Ecosystems*. Blackwell Publishing, Malden, MA.
- Monticelli, D., Ramos, J.A., 2012. Laying date, body mass and tick infestation of nestling tropical Roseate Terns *Sterna dougallii* predict fledging success, first-year survival and age at first return to the natal colony. *Ibis* 154, 825–837.
- Monticelli, D., Ramos, J.A., Tavares, P.C., Bataille, B., Lepoint, G., Devillers, P., 2008. Diet and foraging ecology of roseate terns and lesser noddies breeding sympatrically on Aride Island, Seychelles. *Waterbirds* 31, 239–248.
- Monticelli, D., Ramos, J.A., Quartly, G.D., 2007. Effects of annual changes in primary productivity and ocean indices on breeding performance of tropical roseate terns in the western Indian Ocean. *Mar. Ecol. Prog. Ser.* 351, 273–286.
- Österblom, H., Olsson, O., Blenckner, T., Furness, R.W., 2008. Junk-food in marine ecosystems. *Oikos* 117, 967–977.
- Peck, D.R., Congdon, B.C., 2005. Colony-specific foraging behaviour and co-ordinated divergence of chick development in the wedge-tailed shearwater *Puffinus pacificus*. *Mar. Ecol. Prog. Ser.* 299, 289–296.
- Pennington, J.T., Mahoney, K.L., Kuwahara, V.S., Kolber, D.D., Calienes, R., Chavez, F.P., 2006. Primary production in the eastern tropical Pacific: a review. *Prog. Oceanogr.* 69, 285–317.
- Perrins, C.M., 1970. The timing of bird's breeding seasons. *Ibis* 112, 243–255.
- Piatt, J.F., Sydeman, W.J., Wiese, F., 2007. Introduction: a modern role for seabirds as indicators. *Mar. Ecol. Prog. Ser.* 352, 199–204.
- Pinaud, D., Weimerskirch, H., 2007. At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *J. Animal Ecol.* 76, 9–19.
- Quartly, G.D., Jaquemet, S., Le Corre, M., Monticelli, D., Ramos, J.A., 2008. Climatological effects on the breeding of terns. In: *Proceedings of the 2008 IEEE International Geo-science & Remote Sensing Symposium (IGARSS)*, Boston, USA, pp. 918–921.
- Quartly, G.D., Srokosz, M.A., 2004. Eddies in the southern Mozambique Channel. *Deep-Sea Res.* II 51, 69–83.
- Quillfeldt, P., Strange, I.J., Masello, J.F., 2007. Sea surface temperatures and behavioural buffering capacity in thin-billed prions *Pachyptila belcheri*: breeding success, provisioning and chick begging. *J. Avian Biol.* 38, 298–308.
- R Development Core Team, 2012. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>.
- Ramos, J.A., Maul, A.M., Bowler, J., Monticelli, D., Pacheco, C., 2004. Laying date, chick provisioning, and breeding success of Lesser Noddies on Aride Island, Seychelles. *Condor* 106, 888–896.
- Ramos, J.A., Maul, A.M., Ayrton, V., Bullock, I., Hunter, J., Bowler, J., Castle, G., Mileto, R., Pacheco, C., 2002. Influence of local and large-scale weather events and timing of breeding on tropical roseate tern reproductive parameters. *Mar. Ecol. Prog. Ser.* 243, 271–279.
- Ricklefs, R.E., Duffy, D., Coulter, M., 1984. Weight gain of Blue-footed Booby chicks: an indicator of marine resources. *Ornis Scand.* 15, 162–166.
- Ritz, M.S., Hahn, S., Peter, H.-U., 2005. Factors affecting chick growth in the South Polar Skua (*Catharacta maccormicki*): food supply, weather and hatching date. *Polar Biol.* 29, 53–60.
- Saji, N.H., Goswami, B.N., Vinayachandran, P.N., Yamagata, T., 1999. A dipole mode in the tropical Indian Ocean. *Nature* 401, 360–363.
- Safina, C., Burger, J., 1988. Prey dynamics and the breeding phenology of Common Terns (*Sterna hirundo*). *Auk* 105, 720–726.
- Safina, C., Burger, J., Gochfeld, M., Wagner, R.H., 1988. Evidence for prey limitation of Common and Roseate Tern reproduction. *Condor* 90, 852–859.
- Sarmiento, J.L., Gruber, N., Brzezinski, M.A., Dunne, J.P., 2004. High latitude controls of thermocline nutrients and low latitude biological productivity. *Nature* 427, 56–60.
- Shea, R.E., Ricklefs, R.E., 1996. Temporal variation in growth performance in six species of tropical, pelagic seabirds. *J. Animal Ecol.* 65, 29–42.
- Sorensen, M.C., Hipfner, J.M., Kyser, T.K., Norris, D.R., 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. *J. Animal Ecol.* 78, 460–467.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S., Lima, M., 2002. Ecological effects of climate fluctuations. *Science* 297, 1292–1296.
- Suddaby, D., Ratcliffe, N., 1997. The effects of fluctuating food availability on breeding Arctic Terns (*Sterna paradisaea*). *The Auk* 114, 524–530.
- Surman, C.A., Nicholson, L.W., Santora, J.A., 2012. Effects of climate variability on breeding phenology and performance of tropical seabirds in the eastern Indian Ocean. *Mar. Ecol. Prog. Ser.* 454, 147–157.
- Surman, C.A., Wooller, R.D., 2003. Comparative foraging ecology of five sympatric terns at a sub-tropical island in the eastern Indian Ocean. *J. Zool.* 259, 219–230.
- Surman, C.A., Wooller, R.D., 2000. Nestling escape behaviour in tree, bush and ground nesting tropical terns. *Ibis* 142, 320–322.
- Sydeman, W.J., Penniman, J.F., Penniman, T.M., Pyle, P., Ainley, D.G., 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding and year in relation to food availability. *J. Animal Ecol.* 60, 135–149.
- Terray, P., Dominiak, S., 2005. Indian ocean sea surface temperature and El Niño–Southern Oscillation: a new perspective. *J. Clim.* 18, 1351–1368.
- Thompson, P.M., Ollason, J.C., 2001. Lagged effects of ocean climate change on fulmar population dynamics. *Nature* 413, 417–420.
- Thompson, S.A., Sydeman, W.J., Santora, J.A., Black, B.A., Suryan, R.M., Calambokidis, J., Peterson, W.T., Bograd, S.J., 2012. Linking predators to seasonality of upwelling: using food web indicators and path analysis to infer trophic connections. *Prog. Oceanogr.* 101, 106–120.
- Van de Pol, M., Brouwer, L., Brooker, L.C., Brooker, M.G., Colombelli-Négrel, D., Hall, M.L., Langmore, N.E., Peters, A., Pruett-Jones, S., Russell, E.M., Webster, M.S., Cockburn, A., 2013. Problems with using large-scale oceanic climate indices to compare climatic sensitivities across populations and species. *Ecography* 36, 249–255.
- Wakefield, E.D., Phillips, R.A., Matthiopoulos, J., 2009. Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Mar. Ecol. Prog. Ser.* 391, 165–182.
- Wanless, S., Harris, M.P., Redman, P., Speakman, J.R., 2005. Low energy value of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar. Ecol. Prog. Ser.* 294, 1–8.
- Weimerskirch, H., Bonadonna, F., Bailleul, F., Mabile, G., Dell'Omo, G., Lipp, H.-P., 2002. GPS tracking of foraging albatrosses. *Science* 295, 1259.
- Weimerskirch, H., 2007. Are seabirds foraging for unpredictable resources? *Deep-Sea Res.* II 54, 211–223.
- Weimerskirch, H., Le Corre, M., Tew Kai, E., Marsac, F., 2010. Foraging movements of great frigatebirds from Aldabra Island: relationship with environmental variables and interactions with fisheries. *Prog. Oceanogr.* 86, 204–213.
- Winder, M., Cloern, J.E., 2010. The annual cycles of phytoplankton biomass. *Philos. Transact. Royal Soc. B* 365, 3215–3226.