

Effects of annual changes in primary productivity and ocean indices on the breeding performance of tropical roseate terns in the western Indian Ocean

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ABSTRACT: We assessed the influence of inter-annual changes in primary productivity and local, regional and large scale ocean indices on the breeding parameters of roseate terns *S. dougallii* on Aride Island, Seychelles, western Indian Ocean. Productivity (chicks/breeding pair), timing of breeding, clutch and egg sizes were monitored annually for 8 years and correlated with local ocean productivity (denoted by SeaWiFS estimates of chlorophyll concentration, CC), sea surface temperature and indices recording the status of the Indian Ocean Dipole and of El Niño. The rate of increase in CC (between mean laying date and CC peak value) was positively related to roseate tern productivity and mean clutch size over the 1998-2005 study period. Colony productivity seemed also to be influenced by the Multivariate El Niño Index. In most years, the breeding phenology of roseate terns corresponded to the local increase in CC around Aride, and failure to adjust timing of reproduction to the timing of the phytoplankton bloom decreased the probability of breeding success. This is the first study showing that a tropical seabird species is sensitive to inter-annual variations in the intensity and timing of the phytoplankton bloom, which should be connected to annual variations in the availability of its main fish prey (juvenile goatfish). Overall, these patterns indicate that the reproduction of this top marine predator is dictated by the temporal variability in oceanographic conditions. We suggest that CC data available over the world's oceans may be a useful tool to develop models predicting the fate of colonies of inshore feeding seabirds when other, more conventional monitoring methods cannot be used.

KEY WORDS: *Sterna dougallii*, breeding, inter-annual variation, ocean productivity, El Niño, SeaWiFS, seabird ecology, Indian Ocean

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INTRODUCTION

The availability of food for seabirds is a major factor influencing reproductive success and is primarily affected by environmental determinants such as weather and physical oceanographic factors (Dunn 1975, Smithers et al. 2003, White 2004). To date, however, few studies have been able to relate seabird reproductive output with a direct measure of prey availability. This relationship has been established for temperate regions (Safina et al. 1988, Aebischer et al. 1990, Frederiksen et al. 2006) but has proven to be more difficult for tropical areas because seasonal patterns in marine productivity appear to be less regular and data on marine food stocks are relatively scarce (see Ballance et al. 2006). Nevertheless, ocean and climatic indices have been used to explain inter-annual variations in the breeding performance of tropical seabirds. El Niño Southern Oscillation (ENSO) is an atmosphere-ocean phenomenon occurring roughly every 3-7 years, with its main centre of action in the tropical Pacific Ocean, but with effects much further afield. ENSO events are known to affect marine food stocks throughout the tropics, and its index, the Multivariate El Niño Index (MEI), has been used to explain year-to-year fluctuations in productivity of tropical seabird species in the Pacific and Indian Oceans (Ramos et al. 2002, 2005, 2006, Vargas et al. 2006). Inter-annual climate variability in the Indian Ocean is also influenced by the Indian Ocean Dipole (IOD), which can cause anomalous sea surface temperatures (SST), winds and precipitations in some years (Saji et al. 1999). To date, however, the IOD and its index, the Dipole Mode Index (DMI), have not been invoked to explain annual changes in the breeding performance of tropical seabird species breeding in the Indian Ocean.

Measurements of the chlorophyll-a concentration (CC) in surface waters provide an indicator of the standing stock of phytoplankton which reflects primary productivity. The spatial

variations in CC in the western Indian Ocean are the product of a number of factors — the higher nutrient content of Arabian Sea Waters, the upwelling of deeper waters near the coast, and the later development of stably stratified conditions keeping the phytoplankton in the photic zone. These various mechanisms for augmenting the nutrient content of near-surface waters are important because they help stimulate greater primary productivity, which supports the food webs leading to higher trophic levels. Large inter-annual variations in zooplankton abundance have been noted around the Seychelles, western Indian Ocean (Gallienne & Smythe-Wright 2005), although insufficient data exist to relate this to inter-annual changes in the physical forcing. Satellite-borne sensors such as SeaWiFS (Sea-viewing Wide Field-of-view Sensor) can give a reasonable record of primary productivity, although they only 'see' the CC in the top 10 m or so of the water column. Phytoplankton forms the bottom of the oceanic food chain and their abundance is directly related to that of seabird prey, usually pelagic schooling fish, at higher trophic levels (Aebischer et al. 1990, Piontkovki & Williams 1995, Platt et al. 2003). Recently, satellite-based CC data have been successfully used to explain foraging strategies and spatial distribution of tropical seabirds during the breeding season (Baduini & Hyrenbach 2003), and their timing of breeding (Jaquemet et al. 2007). However, CC has not been used to explain temporal variations in tropical seabird productivity, and other reproductive parameters indicative of timing and breeding effort.

Aride (4°10'S, 55°40'E), a small island in the Central Seychelles, is a common breeding ground for many seabird species (Bowler et al. 2002), including the roseate tern (*Sterna dougallii*). During the breeding season (May-July), roseate terns feed mainly on goatfish (Mullidae) which are plankton-feeders during their larval stage (Krajewski & Bonaldo 2006), and benefit greatly from the presence of schools of tuna that force their prey to the near-surface waters (Ramos 2000). Although roseate terns can migrate large distances seasonally, when breeding and rearing young they forage in the direct vicinity of the colonies within a foraging radius that should not exceed 50 km (Surman & Wooler 2003), and so they require plentiful food supply within that range.

In this paper, we used eight years of data (1998-2005) to study the effects of annual changes in oceanic primary productivity and other ocean indices on the breeding performance of roseate terns on Aride. Productivity (number of chicks fledged per breeding pair) and other breeding parameters (timing of laying, clutch size, egg size) were monitored annually to study year-to-year variations. We investigated in particular whether (1) annual variations in roseate tern productivity could be predicted from CC recorded in the vicinity of Aride Island during the breeding season (May-July), (2) oceanic conditions at various scales (ranging from local SST to the basin scales of the IOD and ENSO) would be more or less efficient than local CC data at predicting colony productivity, and (3) inter-annual variations in CC would explain other breeding parameters (clutch size, egg volume). We hypothesized that years with higher oceanic productivity should be reflected in higher reproductive success and positively affect other reproductive parameters such as clutch size and/or egg volume. According to life-history theory, adults should time their laying season in order to have young in the nest when food is most abundant, thereby maximizing the number of offspring produced (Perrins 1970, Pettifor et al. 1988). Assuming that the main phytoplankton bloom represents the period of maximum food availability we predicted that roseate terns should adjust their laying date to track inter-annual changes in the timing of the chlorophyll peak. By addressing these points, we sought to explore the adaptive response of a tropical seabird species to temporal changes of food abundance in its nearby oceanic environment.

METHODS

Oceanography of the study area

To the south of the equator there are strong easterlies, with the winds being more intense and located slightly further north during July than in January (Schott & McCreary 2001). These trade winds lead to a westward-flowing South Equatorial Current (SEC) in the broad latitude range 10°-20°S (Fig. 1). Upon reaching Madagascar, part of the flow is forced north as the North Madagascar Current (NMC), which on reaching the northern tip of the island continues westward to the coast of mainland Africa. There it bifurcates, with the southern portion looping anticlockwise within the northern end of the Mozambique Channel, and the northern part feeding into the East African Coastal Current (EACC). The flow to the north of the equator shows significant seasonality

due to the influence of the reversing monsoonal winds. The most pronounced changes in currents are in the direction of the Somali Current and the latitude of the eastward-flowing South Equatorial Countercurrent (SECC; Fig. 1a,b).

There is also a marked seasonal change in the wind stress curl (WSC, Schott & McCreary 2001). Around Aride (4°10'S, 55°40'E), the WSC is positive at the start of the year, implying a net convergence of the Ekman transport and thus downwelling near the island; by April the WSC has changed sign and the resulting divergence leads to upwelling. This raises the thermocline locally during April-November and brings more nutrients into the near-surface waters of the photic zone.

The spatial variations in chlorophyll concentration (CC) are shown in Fig. 1a,b. Of particular interest in this paper (given the relatively short foraging radius of the terns) is the local CC maximum around 5°S. The eastward-flowing SECC brings nutrient-rich Arabian Sea Water to the area, whilst the SEC acts as a barrier to prevent the nutrients permeating further south. The shoaling of isopycnals across the SEC also allows the deeper nutrients of the south Indian Ocean to migrate to shallower depths (New et al. 2005). Thirdly, the presence of the Mascarene Plateau leads to enhanced vertical mixing (New et al. 2007). Added to all this is the seasonal movement of the shallow thermocline in response to the WSC changes alluded to earlier.

Inter-annual variability in the Indian Ocean

The monsoon causes strong seasonal changes at least north of the 10°S (Schott & McCreary 2001), whilst the most pronounced inter-annual variations are described by two large-scale phenomena: El Niño Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD)(Schott & McCreary 2001, Yu et al. 2005). The effects of ENSO in the tropical Indian Ocean may be caused by changes to the intensity and position of the atmospheric Walker circulation, or by sea level via the Indonesian throughflow leading to the creation of westward-propagating Rossby waves. Xie et al. (2002) shows how sea level changes at Indonesia in November-December can generate downwelling waves that reach the longitude of Aride roughly seven months later. The IOD is characterised by a difference in SST between the western and eastern areas of the equatorial Indian Ocean. The change in SST impacts the wind field, producing easterly anomalies along the equator (particularly during September-November) and causing moisture convergence and enhanced precipitation in the western equatorial Indian Ocean (Saji et al. 1999). These atmospheric changes act to support the already existing SST dipole. The change in wind field leads to a reduction in the WSC, and a consequent increase in sea surface height just south of the equator (Webster et al. 1999).

The effects of ENSO and IOD are inter-related, with ENSO signals in the Indian Ocean being stronger if coinciding with a positive IOD phase. Baquero-Bernal et al. (2002) suggested that many findings attributed to IOD were due to imperfect statistical analyses. A recent paper by Yu et al. (2005) attempts to disentangle the two phenomena using partial correlations. They ascribe the reduction and reversal of equatorial winds in the east as part of IOD; however, in their analysis, neither phenomenon shows a significant impact in the region of the Seychelles.

Roseate Tern productivity and breeding parameters

The breeding biology of the roseate tern was studied between 1998 and 2005 (8 years) in two long-established colonies located on Aride Island where 600-1200 pairs breed annually during May - July under a canopy of Mapou (*Pisonia grandis*) trees (Ramos et al. 2002). The number of nests was counted annually by a team of observers traversing the whole nesting area in marked sections, 18 days after the first egg was laid (Ramos et al. 2002). Clutch size was recorded for each nest (as either one or two eggs per clutch) to provide an overall mean value for the breeding population. Throughout the season, data on specific breeding parameters were collected daily in two study quadrats established with corner posts and string within the colonies (Ramos et al. 2002). Additional data from nests observed every 1-3 days from a permanent hide were also added to increase sample sizes. Overall, the total number of nests monitored annually varied between a low of 50 (2000) and a high of 183 (2002).

During incubation, we measured egg-length (L, cm) and breadth (B, cm) with calipers to the nearest 0.1 mm, calculated the volume ($V, \text{cm}^3 = 0.512 * L * B^2$), and recorded hatching dates

during daily visits of up to 45 min to the colonies. In most years, laying dates were calculated from hatching dates by subtracting an incubation period of 22 days (Gochfeld et al. 1998), except in 1999, a year with a virtually complete hatching failure when we used exact laying dates recorded for nests viewed from the permanent hide. We used only laying dates and egg volumes from first-hatched chicks (*a*-chicks) during data analyses. Hatching order (*a*- or *b*-chick) and hatching mass were recorded at marked nests, and chicks were ringed to allow subsequent recapture during the rearing period. Mass measurements were subsequently obtained from those chicks whenever encountered during daily visits to the study quadrats, which lasted throughout the season. Most surviving chicks were monitored until they fledged (25-35 days old; Milton et al. 1996, Gochfeld et al. 1998) or until they could no longer be observed. This latter situation happened generally around 2 to 3 weeks post-hatching (i.e., 15-20 days old) when large chicks frequently wandered out of the nesting territory to hide under nearby rocks or herbaceous cover. Chicks with positive mass increments during the linear growth period (4-14 days old) were considered to have fledged within the usual period reported for the species provided that food conditions did not deteriorate shortly (about 2 weeks) after it was last encountered. Colony productivity (number of chicks fledged per breeding pair) was estimated annually as the mean clutch size x hatching success (probability of eggs hatched) x fledging success (probability of chicks fledged from hatched eggs).

Measurements of CC and ocean indices

To characterise the conditions close to Aride we noted the local SST and CC values within 50 km radius around the island, and to record climatic conditions at a larger scale we used well-established indices of IOD (regional scale of Indian Ocean) and ENSO (large scale of Indian and Pacific Oceans). The details of these four measures are described here.

SST values were extracted from an optimal interpolation analysis based on *in situ* and satellite measurements (Reynolds et al. 2002). The dataset (<http://ingrid.ldeo.columbia.edu/SOURCES/IGOSS>) is produced weekly on a one-degree grid, so only the pixel containing Aride is of interest. In order to investigate some of the correlations discussed in the results section, we also accessed monthly one-degree resolution records of wind speed and wind stress curl from a blended model-observations dataset held by NOAA (http://las.pfeg.noaa.gov/las6_5/servlets/dataset?catitem=48).

Satellite observations of ocean colour can be used to infer the CC of surface waters. A potential problem is that changes in community composition may change the quantities of chlorophyll recorded, without corresponding to an actual increase in the mass of phytoplankton present. However, using a hydrographic section terminating at the Seychelles, Zubkov & Quartly (2003) showed that in this region there is a strong correlation between satellite estimates of CC and the abundance of both eukaryotic algae and heterotrophic bacteria. Hence, year-to-year changes in satellite data are likely to reflect real variations in phytoplankton biomass. Here, we use the data recorded by the SeaWiFS instrument, which has been providing data since September 1997. We acquired daily version 5 data from NASA/GSFC on a regular grid of 0.0879° in longitude and latitude; 82 such pixels lie within the terns' maximum foraging radius (50 km) from Aride (Fig. 1c). Because of cloud cover and a limited swath width of the instrument, there is not complete coverage on every day. We therefore formed composites corresponding to each fifth of a month. For each pixel, the 5 or 6 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 (Quartly & Srokosz 2004). We then considered the 82 pixels nearest Aride, and calculated the 90th percentile, as this provides a robust estimate of the peak productivity within this radius. This assumes that the birds optimise their feeding strategy to spend most of their time over the most productive waters. As most roseate terns on Aride forage within sight of the island (Ramos 2000) we also considered measures within smaller scales (9 km and 25 km around Aride). However, the sample sizes were smaller, and the derived values highly correlated with the values for 50 km (Pearson $r_{50-9} = 0.66$, $p < 0.001$, $n = 389$; Pearson $r_{50-25} = 0.73$, $p < 0.001$, $n = 425$); therefore all analyses reported here are for the 50 km radius.

We characterise the phase of ENSO by using the Multivariate ENSO Index (MEI), which integrates six physical components measured over the Pacific Ocean between 30°N and 30°S : sea-

level pressure, zonal and meridional components of the surface wind, SST, air temperature and cloudiness. We obtained bimonthly values of the MEI (<http://www.cdc.noaa.gov/people/klaus.wolter/MEI/table.html>) for each of twelve overlapping periods (Dec/Jan, Jan/Feb and so on). Positive values of the MEI indicate the El Niño phase while negative values represent the cold El Niño phase, i.e. La Niña (Wolter & Timlin 1993). For the IOD, we use the Dipole Mode Index (DMI), recommended by Suryachandra A. Rao of the Frontier Research Center for Global Change, Japan (<http://www.jamstec.go.jp/frsgc/research/d1/iod/>). A positive DMI is associated with higher SST in the west and lower SST in the east (Saji et al. 1999).

Data analyses

Phytoplankton bloom, ocean indices and reproductive parameters

Analyses of variance (one-way ANOVAs) were performed to study inter-annual variations in reproductive parameters (laying date, egg volume) followed by Neuman-Keuls multiple comparison tests. Pearson product-moment correlations were used to check for a linear association with environmental factors whenever appropriate (Zar 1999). To investigate the effect of inter-annual variations in chlorophyll abundance on roseate tern productivity, we used three measures for each year: (1) $\log_{10}\text{CC}$ May-July: the mean $\log_{10}\text{CC}$ value over the roseate tern breeding period, obtained by averaging the 6-day composites over May- June- July, (2) $\log_{10}\text{CC}$ peak: the peak $\log_{10}\text{CC}$ value of the 6-day composites during the May-August bloom, and (3) $\log_{10}\text{CC}$ rate of increase: the rate of increase of $\log_{10}\text{CC}$ during the roseate tern breeding period, defined as the slope of the regression line from the birds' mean laying date to the date of $\log_{10}\text{CC}$ peak value. For years with two dates of $\log_{10}\text{CC}$ peak, we used the mid-point date to perform the regression. Differences between significant slopes were tested using a Tukey multiple comparison test (Zar 1999). We used these three chlorophyll abundance variables and mean May-July values of MEI, DMI, and SST to model annual roseate tern productivity using simple linear regressions. To further investigate the mechanisms by which ocean productivity around Aride may affect breeding roseate terns, clutch size and egg volume were also used as dependent variables.

A multiple regression analysis was performed to predict variations in productivity and clutch size, but due to the relatively small number of years spanned by this study ($n = 8$ years), we restricted our models to four predictors: the three ocean indices (MEI, DMI, and SST) and the CC variable with the highest explanatory power in the univariate analysis. A stepwise selection of predictors was avoided in favour of a full model approach (i.e. model containing all four predictors), since the former procedure may result in bias in parameter estimation (Whittingham et al. 2006). The multiple regression was performed on standardized predictors (mean = 0, SD = 1) to understand their relative contribution in the prediction of the dependent variable (beta coefficients; Zar 1999).

Phytoplankton bloom and timing of breeding

We correlated monthly DMI, MEI and SST means in May and June with mean laying date. The weekly SST time-series showed a consistent decrease between May and mid June during each of the eight years spanned by this study (all regression $r < 0.01$), so the slope of the regression line fitting this decrease was calculated for each year and used as a variable to check for a correlation with laying date. We compared also the mean rate of decrease in SST between years of early (18-28 May) and late (> 28 May) egg-laying using a t-test. Records of laying dates were also used to quantify variations in the timing of breeding of roseate terns in relation to the timing and duration of the main phytoplankton bloom. For each roseate tern nest monitored, we calculated a 'peak-bloom lag' value as the difference (in number of days) between the laying date (*a*-egg) and the date of $\log_{10}\text{CC}$ peak for that year. Mean peak-bloom lag values were compared between years using ANOVA.

A linear modeling approach was used to further assess the predictive effect of the peak bloom lag variable on roseate tern productivity. Since most of the fluctuation in productivity on Aride is shaped by the probability of successfully raising a single chick (*a*-chick), with the fledging success of *b*-chicks being usually close to zero (Ramos et al. 2002), we developed a logistic regression model (binomial logit-linear) with the success of *a*-chicks (0= not fledged, 1= fledged; n

= 511) as the dependent variable. For each nest monitored during the 6 years of non-zero productivity spanned by this study (1998 & 2001-2005), peak-bloom lag and other biologically significant predictors such as laying date, clutch size and egg volume were included in the model. Except for clutch size, observations were divided for each predictor into quartiles of the distribution with the estimate (slope) for the first (lower) quartile (reference level) set to 0 while those of the remaining quartiles were allowed to vary (Hosmer & Lemeshow 2000). This method was justified because the probability of fledging a chick was not thought to be necessarily linear among quartiles.

The relative contribution of each variable to fledging success was assessed using odds ratios (OR) comparing for each quartile the probability of successfully raising a chick with the reference level (first quartile). Significant differences were assessed with Wald χ^2 tests, and 95% Wald's confidence limits for each odds ratio (Hosmer & Lemeshow 2000). When the confidence limits span the value of one, this indicates that there is no significant difference between the odds of successfully raising a chick at the level considered and the reference level. We checked model fitness with the Hosmer-Lemeshow goodness-of-fit statistic (χ^2 test) and the area under the ROC (receiver operating characteristic) curve (Hosmer & Lemeshow 2000). The area under the ROC curve ranges from zero to one, and as a general rule, a ROC \sim 0.7, 0.8, or 0.9 suggests acceptable, excellent, or outstanding discrimination, respectively (Hosmer & Lemeshow 2000). Data were analysed using SPSS statistical package, release 13.0.

RESULTS

Year-to-year variations in breeding performance

Complete breeding failures were recorded in 1999 and 2000 due to chick starvation and nest abandonment by parents (fledging success = 0), whereas productivity was low in 2001 and 2005 with few *a*-chicks fledging (and no *b*-chicks) in those years (Table 1). During the remaining 4 years, fledging success of *a*-chicks increased, but that of *b*-chicks remained very low (0.01 in 2002, 0.06 in 1998 and 2003, and 0.11 in 2004), resulting in an average productivity of *ca.* 0.5 chicks per breeding pair (Table 1). Clutch size ranged from 1.03 and 1.06 eggs/clutch in 2000 and 2005 respectively, to 1.42 in 2004 (Table 1). Overall, differences in mean egg volumes were slight, with those laid in 2005 being on average 6% smaller than those in 2001 (One-way ANOVA $F_{6, 562} = 3.44$, $p < 0.001$). There was also a negative correlation between laying date and productivity (Fig. 2).

CC, ocean indices and breeding performance

Chlorophyll abundance. The 8 years of SeaWiFS data showed that the waters around Aride experienced two seasonal blooms in phytoplankton productivity (Fig. 3a,b). The first, a moderate phytoplankton bloom in December-February (austral summer), with the main bloom in May-August (austral winter) overlapping with the roseate tern breeding season (May-July).

The May-August phytoplankton bloom varied from year to year in the date of the annual maximum (Fig. 4), with values ranging from 22 June in 2000 (julian day 174) and 2002 (julian day 173), to 16 August in 1999 and 2003 (julian day 228). There were also variations in amplitude and rate of increase (Table 2, Fig. 4). Among the most important features were the weak annual CC peak values observed in 1999 and 2000, when breeding success was virtually zero, contrasting with the peaks of 2003 and 2004, when roseate tern productivity reached the highest values (Fig. 4). In the poorest years, the rate of increase (slope) of the CC during the breeding season was virtually zero (1999 and 2000, Table 2), whereas the largest slope was in 2004, suggesting the most favourable conditions in that year (Table 2, Fig. 4).

Regression model (Table 3). Both the annual CC peak value and the rate of increase of CC during the phytoplankton bloom were correlated (Pearson $r = 0.91$, $p = 0.001$, $n = 8$ years), and explained respectively 51% (simple regression: $F_{1,6} = 6.3$; $p = 0.045$) and 60% ($F_{1,6} = 9.0$; $p = 0.023$, Table 3) of the inter-annual variation in roseate tern productivity. The rate of increase in CC was the only explanatory variable which influenced positively clutch size ($F_{1,6} = 14.3$; $p = 0.009$, Table 3, Fig. 5), but no such association (response) was found with egg volume ($F_{1,5} = 1.7$; $p = 0.23$).

The yearly mean CC in May-July was negatively correlated with local SST averaged over the same period (Pearson $r = -0.83$, $p = 0.01$, $n = 8$), but no other correlations were found between ocean indices (Table 2). The mean CC and SST averaged over May-July did not predict roseate tern productivity. The MEI during May-July explained 64% of the variation in roseate tern productivity (simple regression: $F_{1,6} = 10.7$; $p = 0.016$), but there was no significant relationship with the DMI. Together, the MEI and the rate of increase in CC explained more than 90% of the variation in roseate tern productivity (multiple regression $F_{4,3} = 13.1$, $p = 0.03$ with MEI coeff.: 0.76 ± 0.19 , $p = 0.03$ and CC coeff.: 0.48 ± 0.16 , $p = 0.05$).

Duration of the CC bloom, ocean indices and timing of breeding

Inter-year variation. Mean laying date of roseate terns varied between years (One-way ANOVA $F_{7, 746} = 230.05$, $p < 0.001$). The birds laid on average one month earlier in 2004 compared with 1999 (18 May vs. 20 June), and during half of the years spanned by this study, egg-laying occurred within the same week (26-30 May; Table 1). The mean peak-bloom lag was *ca.* 2 months (53-71 days) during six of the eight years studied (Table 2, Fig. 4). Mean laying dates compared between the same six years differed by *ca.* one month (18 May in 2004 to 20 June in 1999, Table 1), suggesting that roseate terns have adjusted this parameter to coincide with the timing of the phytoplankton bloom. However, this adjustment was less apparent in 2000 (a poor year in terms of productivity) and 2002 (Table 2).

Ocean indices. No significant correlations were found between mean laying date and monthly values of MEI, DMI, and SST in May or June ($p > 0.05$ for all r). Seasonal factors cause SST to decrease between 1 May (3 weeks prior to laying; Table 1) and mid June during all eight years of this study. We correlated the rate of decrease in SST with mean laying date, but found no significant relationship ($r = 0.434$, $p = 0.28$, $n = 8$ years). However, a simple division into years with the earlier mean laying date (18 -28 May) and the later ones does reveal a significant difference in the mean rate of decrease between the two groups (-0.469 vs -0.389 ; $t_6 = 2.99$, $p = 0.024$, $n = 8$).

Logistic regression model (Table 4). The importance of the peak-bloom lag in explaining reproductive success was assessed with logistic regression performed also with clutch size, egg volume and laying date. Both laying date and the peak-bloom lag variable, expressed as the difference between laying and CC peak dates, were significant in the model, but not clutch size and egg volume. The constant was not significant ($p = 0.68$), suggesting that no other variables were important in explaining fledging success. The model fitted the data (Hosmer-Lemeshow goodness-of-fit $\chi^2_{(8)} = 11.61$, $p = 0.17$) with the ROC area indicating acceptable discrimination. The odds ratios (OR) revealed that with increasing time-lag between laying date and peak-bloom date, the probability of successfully raising a chick was higher: for instance, there was almost a 150% increase in fledging success probability when the peak-bloom lag was 61-69 days compared with the reference category (10-48 days). Laying date was also an important predictor irrespective of the chlorophyll bloom; the latest birds to lay (4 June – 3 July) having a smaller probability to fledge their chicks than those laying earlier (13 – 21 May).

DISCUSSION

In this paper, we used 8 years of SeaWiFs data at a temporal resolution of 5-6 days (composite images) and at a spatial scale of 50 km around the island (maximum foraging range of roseate terns) to characterise the evolution of the phytoplankton bloom around Aride. A marked seasonal variation in CC was detected, each year being consistently characterised by 2 phytoplankton blooms. A small bloom was observed in December-February (northeast monsoon), and a main bloom in May-August (southwest monsoon). The breeding season of most seabirds on Aride coincides with the main bloom, but some species also breed during the northeast monsoon (e.g., lesser noddy *Anous tenuirostris* and brown noddy *A. stolidus*; Bowler et al. 2002), suggesting that breeding in the tropical Indian Ocean is dictated by the seasonality of food resources (Le Corre et al. 2003).

We found year-to-year differences in the main phytoplankton bloom with respect to its average value over May-July (mean chlorophyll concentration (CC)), peak amplitude (maximum CC), timing of the peak, and rate of increase ('CC growth rate') (Table 2). Both timing (Platt et al. 2003) and intensity (Robinson 2004) of the phytoplankton bloom have been related to the survival and density of phytoplankton-feeding fishes. On Aride, roseate terns feed primarily on young (0 year group) goatfishes (Mullidae; Ramos 2000), which are plankton-feeders during their larval-stage (Krajewski & Bonaldo 2006). Observations of east African reef fish species suggest that adults mostly spawn in October-November, and March-May (Nzioka 1979), corresponding to the onset of the phytoplankton blooms observed in this study and raising the possibility of a major recruitment during the peak of the bloom. Therefore, we speculate that the abundance of fish schools preyed upon by the birds may, at least in part, be connected to chlorophyll concentrations recorded in the surrounding waters. Such a relationship was suggested for the northern anchovy (*Engraulis mordax*; Robinson 2004) but cannot be validated for goatfish around Aride without direct *in situ* measurements of fish stocks. In particular, the observation of a lagged response between peaks of abundance at both trophic levels would be particularly helpful to support a 'bottom-up control' hypothesis (Aebischer et al. 1990), which has been demonstrated for several fish species in the Atlantic Ocean (Platt et al. 2003, Beaugrand et al. 2003, Frederiksen et al. 2006). Nevertheless, the similarities reported hereafter between various measures of CC and roseate tern reproductive parameters support the existence of a strong causal relationship between CC levels off Aride Island during the roseate tern breeding season and prey availability.

Effects of annual changes in phytoplankton abundance

During the roseate tern breeding season, inter-annual variations in CC (rate of increase and peak value) were correlated with productivity: in years of rapid phytoplankton growth, resulting in an intense bloom, roseate terns were more successful than in years when the phytoplankton bloom was less apparent. This was particularly obvious in 1999-2000 when only a weak phytoplankton bloom occurred, resulting in a complete breeding failure due to chick starvation and nest abandonment by parents. In contrast, the rapid growth of the 2004 bloom, associated with the highest peak value recorded during the study, led to the most successful breeding season (highest colony productivity). Such differences may be ascribed to significant year-to-year fluctuations in the availability of prey for roseate terns, particularly young goatfish (Mullidae) during the breeding season. In fact, tropical roseate terns feed on schooling fish which are made readily available in the upper layer of the water column by subsurface predators such as dolphins and tunas (Ramos 2000). Although the association between roseate terns and subsurface predators was not examined in this study, Ballance et al. (1997) showed that large flocks of boobies found over surface waters of highest chlorophyll concentrations were also those most often associated with subsurface predators. Thus, we further speculate that subsurface predators may also concentrate in oceanic areas with higher productivity that attracts zooplankton and marine fishes, thereby providing a functional link between roseate terns feeding around Aride and their main prey.

We found a significant increase in clutch size in years of higher CC, which is consistent with previous studies suggesting that food is the primary factor affecting egg formation in larids (Sydeman et al. 1991, Suddaby & Ratcliffe 1997). There was, however, no apparent correlation between CC fluctuations and egg size. These results are similar to those reported for common and roseate terns in the North Atlantic where Safina et al. (1988) found that in years of higher food supply, terns had a tendency to lay larger clutches, but not larger eggs. This finding suggests that when food conditions are favourable, it may be more advantageous for tropical roseate terns to allocate somatic reserves to the formation of supplementary, rather than larger, eggs, although our data showed that the larger clutches found in 2004 also contained the larger eggs (Table 1). Roseate terns may maximize clutch/egg size in relation to the prevalent food conditions at the time of egg-laying, but clutch size is probably a better proxy measure reflecting food availability (CC) around Aride. Rapidly increasing food conditions encountered by females upon arrival at the breeding quarters several weeks prior to laying may be important cues to later plentiful food supply during the season. Females may lay as many eggs as somatic reserves allow, and later regulate their breeding effort by a reduction of brood size or clutch desertion if food is scarce (Monaghan et al.

1992). This seems to be the situation on Aride where parents are usually unable to raise more than a single chick except in years of apparent highest food supply conditions (Ramos et al. 2002, this study).

Effects of laying date and timing of phytoplankton bloom

During the eight years spanned by this study, a negative correlation between laying date and roseate tern productivity was observed, hence suggesting the importance of food availability in shaping breeding parameters. When environmental conditions were poor such as in 1999-2000 (i.e., two years of very low roseate tern productivity), birds initiated laying much later, with an overall mean laying date for the whole colony delayed by up to one month compared to 2004 (i.e., year of highest colony productivity), when food supply conditions were presumably very good (greater CC peak and oceanic productivity). Because food is often seasonally declining, optimal breeding theory predicts that laying should be timed to allow a match between the chick-rearing period (i.e., the period of peak food demand during breeding) and the period of maximum food availability (Perrins 1970). Thus assuming that the peak date of the phytoplankton bloom around Aride Island reflected the period of maximum food availability, roseate terns were, on average, expected to lay at least *ca.* 50-60 days prior to this date in order to have a reasonable chance to fledge their chicks before food conditions started to deteriorate. This time-lag (peak-bloom lag) corresponded to an incubation period of 22-24 days (Gochfeld et al. 1998) and a chick-rearing period of 25-35 days (Milton et al. 1996, Gochfeld et al. 1998), and was found in 6 out of 8 years spanned by this study (except in 2000 [a poor year] and 2002). When removing the two years of poor food availability (1999-2000), such a strategy was found to be important in explaining fledging success on Aride. Therefore, the inter-annual variations in mean laying dates (Table 1) suggested that roseate terns may have adjusted their breeding phenology, so that in most years the chick-rearing period of the majority of birds corresponded to the maximum availability of food around Aride. Optimal adjustment in response to environmental fluctuations may, however, not always be achieved (see Safina & Burger 1988) which may perhaps account for the mismatch observed in 2000 and 2002 (Table 2). Thus, extrinsic factors such as the peak-bloom lag and the laying date appear to be important in shaping breeding success on Aride when compared with intrinsic factors (clutch/egg size, Table 4). Overall, this pattern suggests that in years with a marked seasonal phytoplankton bloom, there is a strong selection to lay early in the season, and the lag between laying and the CC peak is adjusted by the most productive birds to match the chick-rearing period with the period of maximum food availability. Conversely, in years when oceanic productivity is low or fails to show a marked seasonal bloom, terns may have difficulty with determining the appropriate time to lay eggs (e.g., 2000) and may fail completely.

Which cues roseate terns use to predict the peak in phytoplankton bloom remain to be closely investigated. In passerines, laying date is fine-tuned following both photoperiod and ambient temperature, which are good indicators of when food resources will be large enough to raise chicks (Nager & van Noordwijk 1995). In this study, we found a negative correlation between mean CC and SST around Aride during the breeding season (May-July) which is consistent with greater upwelling or mixing bringing cooler nutrient-laden waters to the surface. Thus a stronger decrease in SST from early May onwards is likely to be associated with favourable oceanic conditions earlier in the season, which may be invoked to explain the tendency for roseate terns to lay earlier in years of stronger decrease in SST from May to June. However, once there has been an injection of nutrients into the photic zone, subsequent stratified conditions allowing a warm surface may be best for encouraging phytoplankton growth. In Cassin's auklet breeding in the Pacific, laying date is positively correlated with SST and adjusted to respond to inter-annual variations in oceanographic conditions affecting the availability of their main prey, namely euphausiids (Abraham & Sydeman 2004). Jaquemet et al. (2007) previously found a match between a decrease in local SST corresponding to locally enhanced CC, and egg-laying of sooty terns (*S. fuscata*) in the western Indian Ocean. Altogether, this suggests that SST may be the cue used by the birds to predict the timing of fish abundance, and adjust egg-laying accordingly.

Effect of ocean indices

In a previous study, Ramos et al. (2002) found a significant influence of local (SST) and large-scale (MEI) oceanographic events on, respectively, the number of roseate terns that attempt to breed and on their timing of breeding. Here, we found that MEI during the breeding season (May-July) may also play a significant role in explaining inter-annual fluctuations in colony productivity, while we did not detect any effect of the DMI. Both the MEI and local CC explained a fairly similar fraction of the total variance observed, and overall the combination of local CC and large-scale climatic conditions (MEI) accounted for most of the variation observed over the study period (>90%). Our results also suggest that negative values of the MEI had a detrimental effect on roseate tern productivity. Breeding failures of brown noddies during La Niña years have been previously reported for Aride (Ramos et al. 2006).

The IOD has its largest climatic effect during September-November (Saji et al. 1999), and little coherent atmospheric or oceanic variability can be discerned unless analysis is segregated into specific calendar months (Baquero-Bernal et al. 2002). The key times for roseate terns laying and breeding are well before IOD has any appreciable effect. On the other hand, ENSO is a large-scale phenomenon that persists for many months, with a peak response in the tropical Indian Ocean lagging that in the Pacific, and consequently still having a basin-scale impact at the time of breeding and laying activity.

A possible mechanism involves the interaction of ENSO-related Rossby waves triggered off Sumatra reaching the Seychelles in the early to middle part of the year, with the associated downwelling (Xie et al. 2002) deepening the otherwise shallow nutricline found just to the north of the SEC and modifying the seasonal reduction in SST. According to this hypothesis, the effect at the Seychelles should lag the Pacific-based signals recorded by the MEI by ~7 months; however, a repeat of our analysis using lagged MEI values explained no more of the variance than the standard correlation analysis. An alternative hypothesis is that increased storminess in the La Niña phase could affect the birds' ability to forage successfully; however, an examination of monthly wind speeds showed no significant effect of ENSO on wind speeds at this location (unpublished data). Ramos et al. (2002) showed that daily variations in wind speed did not influence roseate tern chick provisioning on Aride. Finally, we also considered the interannual variations in wind stress curl (WSC), which should modulate the degree of upwelling. However, the WSC for the one-degree box containing Aride showed no significant correlation with MEI or the local rate of increase of CC.

Conclusion

To our knowledge, this is the first study showing that a tropical seabird species is sensitive to inter-annual variations in timing and intensity of the phytoplankton bloom around the colonies, which may be connected to year-to-year variations in the availability of prey. In particular, clutch size appears to be a sensitive reproductive parameter reflecting the food conditions prevalent in the surrounding waters. We also hypothesize that roseate tern females may rely on SST conditions early in the season to anticipate the local increase in food supply coinciding with the seasonal phytoplankton bloom, and time their egg-laying accordingly. Overall, these patterns indicate that the reproduction of this top marine predator is dictated by the temporal variability in oceanographic conditions. Interestingly, this study suggests that CC data available over the world's oceans (SeaWiFS sensor) may be a useful tool to develop models predicting the fate of colonies of inshore feeding seabirds when other, more conventional monitoring methods cannot be used.

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TABLES

Table 1. *Sterna dougallii*. Comparison of breeding parameters and productivity (no. chicks fledged per breeding pair) of the roseate tern population on Aride Island, Seychelles, from 1998 to 2005. Values presented as mean \pm SD, except for clutch size (sample sizes in parenthesis).

Year	Laying date ¹	Clutch size	Egg volume (cm ³) ¹	Productivity
1998	30 May \pm 6d (152) ^c	1.27 (962)	17.6 \pm 1.4 (132) ^{b,c}	0.55 (132)
1999	20 June \pm 3d (104) ^f	1.16 (1112)	17.5 \pm 1.3 (58) ^{b,c}	0.00 (58)
2000	11 June \pm 4d (50) ^e	1.03 (607)	no data	0.02 (50)
2001	26 May \pm 6d (68) ^b	1.13 (733)	18.3 \pm 1.3 (54) ^a	0.21 (140)
2002	27 May \pm 10d (183) ^b	1.11 (1046)	17.7 \pm 1.4 (154) ^{b,d}	0.53 (214)
2003	9 June \pm 3d (69) ^d	1.33 (705)	17.9 \pm 1.4 (65) ^{a,c,d}	0.47 (119)
2004	18 May \pm 4d (75) ^a	1.42 (528)	17.9 \pm 1.5 (60) ^{a,c,d}	0.57 (122)
2005	28 May \pm 6d (53) ^b	1.06 (686)	17.2 \pm 1.4 (46) ^b	0.35 (96)

¹ Superscripts having at least one letter in common indicate no significant difference Neuman-Keuls test $p > 0.05$

Table 2. Ocean indices (MEI= Multivariate El Niño Index, DMI= Dipole Mode Index), sea surface temperature (SST) and variables derived from time-series of chlorophyll concentration (log₁₀CC) around Aride (1998 to 2005) during the main annual phytoplankton bloom coinciding with the roseate tern breeding season. Log₁₀CC rate of increase per day and mean peak-bloom lag were compared between years. Superscripts having at least one letter in common indicate no significant difference between years (Multiple comparison test $p > 0.05$)

Year	MEI	DMI	SST (°C)	Log ₁₀ CC May-July (mg/m ³)	Log ₁₀ CC rate of increase per day ¹ (n) (p <)	Mean peak-bloom lag (no of days \pm SD) ^{2,3}
1998	1.158	-0.347	27.98	-0.471	0.059 ^{a,b} (10) 0.01	65.9 \pm 6.4 ^e
1999	-0.522	-0.326	27.29	-0.463	0.009 (9) 0.59	56.4 \pm 2.6 ^d
2000	-0.158	-0.075	27.40	-0.397	0.011 (5) 0.77	10.7 \pm 3.7 ^a
2001	0.100	-0.363	27.34	-0.411	0.059 ^{a,b} (14) 0.01	70.7 \pm 5.2 ^f
2002	0.757	-0.472	26.88	-0.279	0.041 ^b (8) 0.03	41.9 \pm 10.5 ^b
2003	0.018	0.388	27.70	-0.407	0.088 ^{a,b} (8) 0.01	68.4 \pm 3.3 ^{e,f}
2004	0.389	-0.515	27.04	-0.246	0.105 ^a (8) 0.01	53.2 \pm 3.4 ^c
2005	0.536	-0.275	28.00	-0.505	0.041 ^b (10) 0.01	68.3 \pm 6.3 ^{e,f}

¹ Log₁₀CC rate of increase is the linear regression coefficient of log₁₀CC six-day composites taken from mean laying date (Table 1) to the date of annual CC peak (Fig.4); 1999 & 2000 not included in the multiple comparison test

² Peak-bloom lag calculated as no. of days between mean laying date (*a*-egg) and date of log₁₀CC peak (see laying date in table 1 for sample sizes). For years with 2 peak dates, we considered the mid-point to calculate the peak-bloom lag

³ ANOVA $F_{7, 746} = 545.71$, $p < 0.0001$ (with data square-root transformed)

Table 3. *Sterna dougallii*. Percentages of variation in annual mean clutch size (no. of eggs/clutch) and productivity (chicks fledged per pair) explained by selected environmental variables between 1998 and 2005 (Simple regression models with df = 1 and 6, n = 8 years).

Covariate	Clutch size			Productivity		
	R ² (%)	Regression coefficient ± SE	p	R ² (%)	Regression coefficient ± SE	p
Log ₁₀ CC rate of increase	65.5	3.11 ± 0.82	0.009	60.0	5.41 ± 1.80	0.023
Log ₁₀ CC peak	34.3	-	0.074	51.3	0.72 ± 0.28	0.045
Log ₁₀ CC May-July	12.0	-	0.401	18.0	-	0.295
MEI (May-July)	3.9	-	0.638	64.1	0.35 ± 0.11	0.016
DMI (May-July)	1.1	-	0.803	1.6	-	0.763
SST (May-July)	0.1	-	0.981	0.2	-	0.919

Table 4. *Sterna dougallii*. Results of logistic model (binomial logit-linear) predicting probability of fledging success for *a*-chicks raised between 1998-2005 (1999-2000 excluded; n = 511 nests) on Aride Island. The peak-bloom lag refers to the number of days between the laying of the first egg and the date that chlorophyll concentration peaks. Model goodness of fit (ROC¹) = 0.68.

Term	Level ²	Regression coefficient ± SE	Effect size ³		
			Odds ratio	LCI	UCI
Terms in the model					
Peak-bloom lag (days)	10 – 48	0.00	1.00	1.00	1.00
	49 – 60	-	1.82	0.95	3.50
	61 – 69	0.90 ± 0.31*	2.46	1.33	4.55
	70 – 79	0.96 ± 0.30*	2.60	1.44	4.69
Laying date (1 May = 1)	13 – 21	0.00	1.00	1.00	1.00
	22 – 26	-	1.83	0.91	3.68
	27 – 34	-	1.32	0.62	2.81
	35 – 64	-1.00 ± 0.30*	0.37	0.20	0.66
Rejected terms					
Clutch size	1-egg	0.00	1.00	1.00	1.00
	2-eggs	-	0.97	0.53	1.66
Egg volume (cm ³)	12.8 – 16.8	0.00	1.00	1.00	1.00
	16.8 – 17.7	-	1.25	0.73	2.15
	17.7 – 18.7	-	1.03	0.60	1.75
	18.7 – 21.4	-	1.44	0.83	2.48

¹ Receiver operating characteristic (0.7 = acceptable, 0.8 = excellent, 0.9 = outstanding)

² Quartiles (4 levels) of the distribution for each predictor variable, except for clutch size (2 levels)

³ Odds of successfully raising a chick when compared to the reference level (lower value) categorised as 0.

* Wald χ^2 test p < 0.01

FIGURES

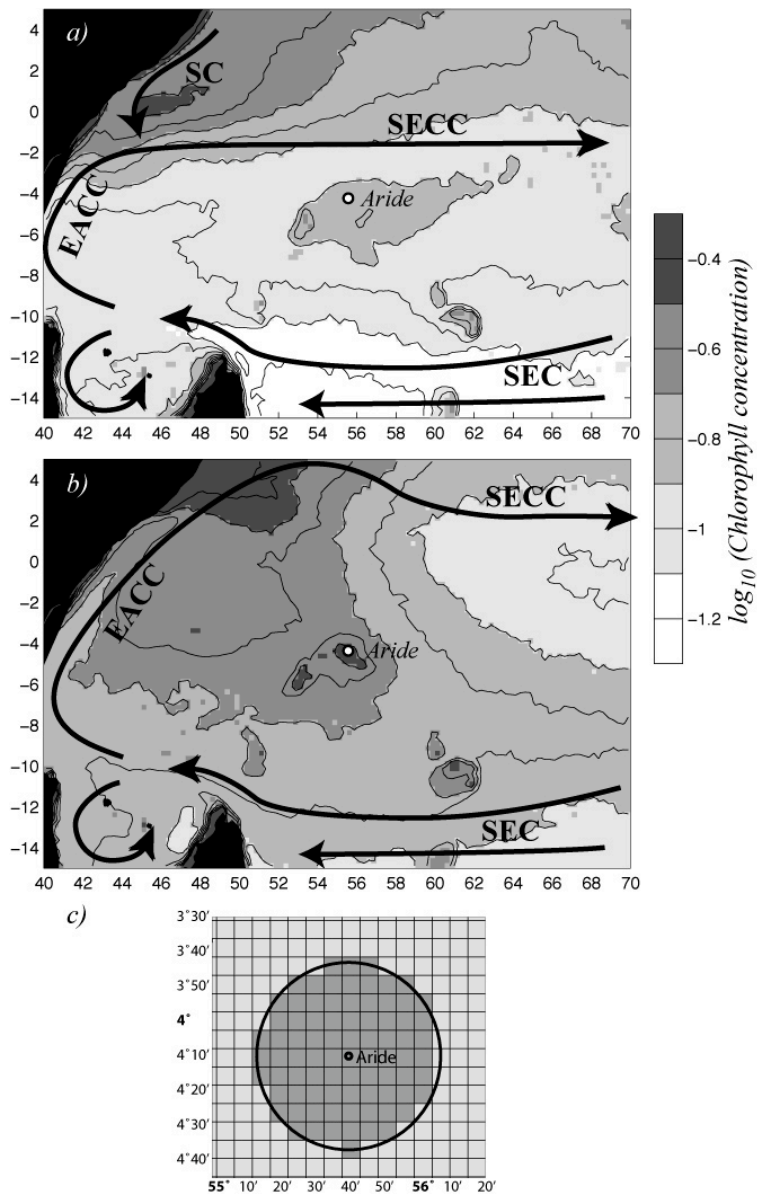


Fig 1. Seasonal variation of SeaWiFS-derived chlorophyll concentration (averaged over 1998-2005), with schematic of main currents overlaid. SEC - South Equatorial Current, NMC - North Madagascar Current, EACC - East African Coastal Current, SC - Somali Current, SECC - South Equatorial Countercurrent. a) January-February, b) July-August, c) Detail of SeaWiFS data grid, showing those pixels whose centres are within 50 km of Aride

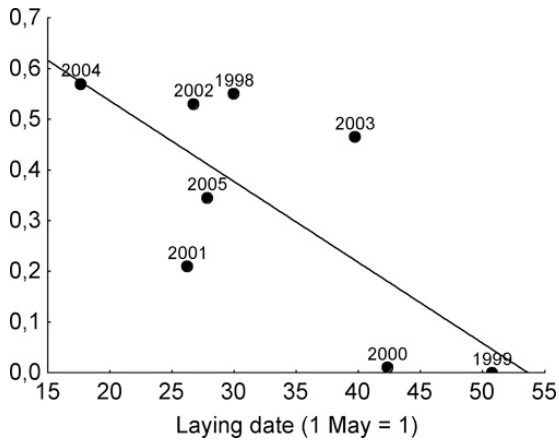


Fig 2. *Sterna dougallii*. Pearson product-moment correlation between colony productivity (no of chicks fledged per pair) and laying date for the period 1998-2005 ($r = -0.72$, $p = 0.04$)

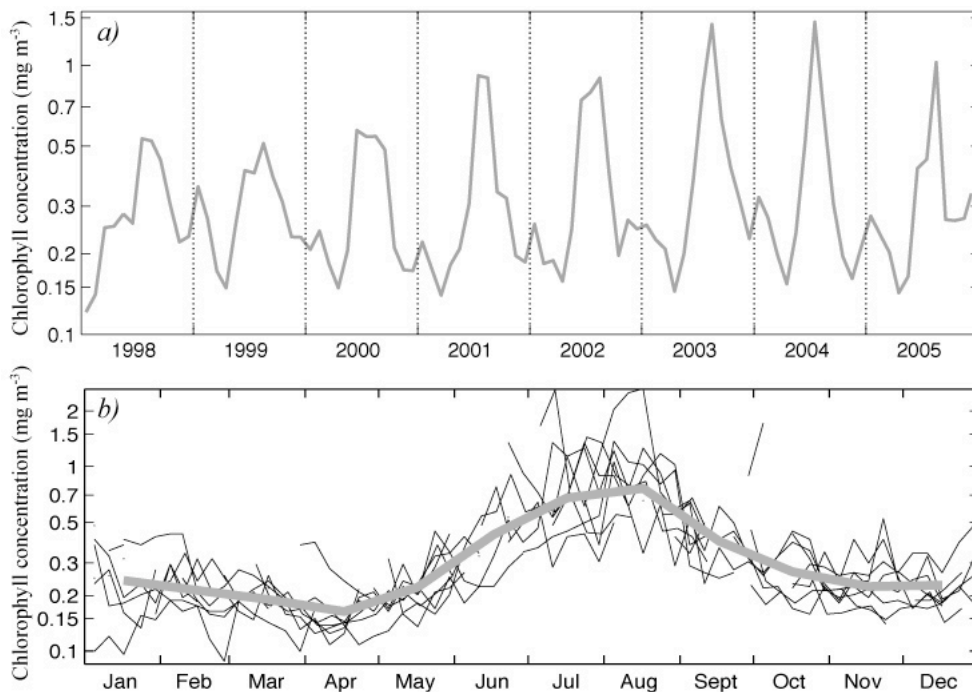


Fig 3. a) Monthly mean chlorophyll concentrations within 50 km radius around Aride Island. Monthly data plotted from January 1998 to December 2005, but labelled every 2 months. b) Thin lines show chlorophyll records for the 8 individual years at fifth of a month resolution, and the thick grey line gives the monthly averages

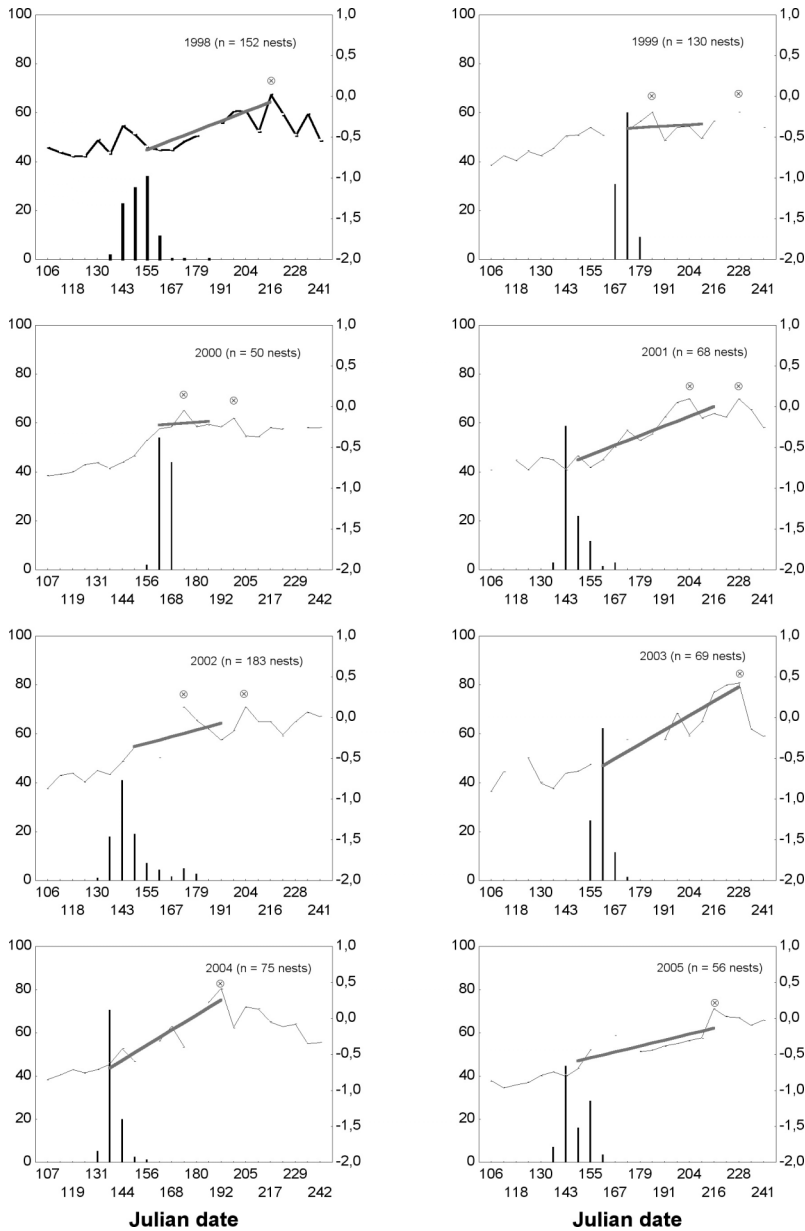


Fig 4. *Sterna dougallii*. Annual distribution of egg-laying dates (left axis), and $\log_{10}CC$ within 50 km radius around Aride Island plotted from mid April to end August (right axis). The grey line represents the linear regression of $\log_{10}CC$ values starting from mean laying date (Table 1) to the date of $\log_{10}CC$ peak value during the May-August bloom (⊗). In years with two dates of $\log_{10}CC$ peak, the regression was performed using the mid-point between these two dates

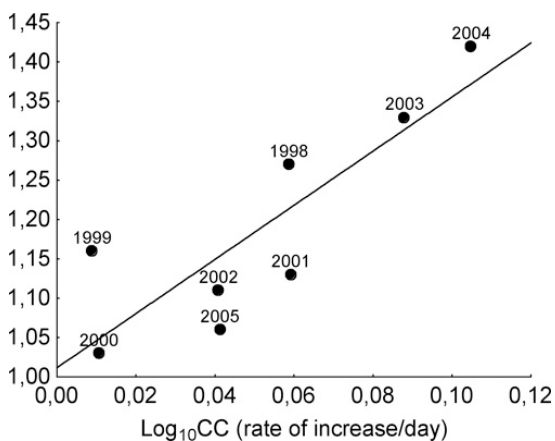


Fig 5. *Sterna dougallii*. Linear relationship between clutch size (no of eggs per nest) and $\log_{10}CC$ rate of increase per day for the period 1998-2005 (Clutch size = $1.023 + 3.11' \times \log_{10}CC$ rate of increase, $r = 0.839$, $F_{1,6} = 14.3$, $p = 0.009$)