

BUT FIRST, ARE YOU EXPERIENCED? THE CONSEQUENCES OF TIMING, AGE, AND ADULT CONDITION ON REPRODUCTIVE PERFORMANCE IN GREATER CRESTED TERNS *THALASSEUS BERGII*

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Received 17 February 2017, accepted 30 June 2017

ABSTRACT

McLEAY, L.J., PAGE, B.P. & GOLDSWORTHY, S.D. 2017. But first, are you experienced? The consequences of timing, age, and adult condition on reproductive performance in Greater Crested Terns *Thalasseus bergii*. *Marine Ornithology* 45: 205–215.

Among bird species with defined breeding seasons, rates of reproductive success are higher among individuals that breed earlier in the season and decrease as the season progresses. Seasonal decreases in breeding success have been explained by decreases in prey availability or by variations in parental “quality,” mediated by age-related experience or phenotype. We examined seasonal patterns of primary production, as an indicator of prey availability, in relation to the breeding phenology of three Greater Crested Tern *Thalasseus bergii* colonies in gulf waters of South Australia. We then determined the influence of reproductive timing on the reproductive performance (chick growth and survival) of Greater Crested Terns and the role of parental “quality” in reproductive success by measuring reproductive timing in relation to parental age and body condition. In contrast to expectations, increased primary production was observed in winter months, long after the chick fledging period. High production in winter may benefit newly fledged juvenile terns that have relatively less skill and experience than adults. Chick hatching was synchronised among colonies located 250 km apart, and the timing of breeding had a significant effect on reproductive performance. Chicks reared by older adults hatched earlier in the breeding season than younger adults, and exhibited better growth and body condition (hatch mass, linear growth rate, and asymptotic mass) and higher rates of survival. There was less support for the effects of body condition, measured by a body condition index (BCI), on reproductive timing, and no significant relationship between adult age and body condition. However, individuals less than seven years old had significantly poorer body condition than those that were older. The seasonal patterns in age-related breeding success we observed may be explained by parents’ age-related improvements in breeding and foraging proficiency, shaped through their need to provision their chicks with a single prey item that is small enough for the chick to swallow.

Key words: Greater Crested Tern, body condition, chick growth, demography, reproductive success, reproductive timing, seabird, South Australia

INTRODUCTION

The premise that relatively few individuals within a population contribute the most recruits to subsequent generations is well accepted in ecological theory as a key factor influencing natural selection (Clutton Brock 1988, Lewis *et al.* 2006). Among bird species with defined breeding seasons, rates of reproductive success are typically higher for individuals that breed earlier in the season compared with those that breed later (Lack 1950, Forslund & Part 1995, Arnold *et al.* 2004). This may be explained by the “timing hypothesis,” which predicts that reproduction will coincide with peaks in prey availability (Lack 1954; Perrins 1970; Arnold *et al.* 2004). In temperate marine ecosystems, the summer breeding seasons of seabirds are often associated with peak periods of prey availability, and availability declines as winter approaches (Hamer *et al.* 2002, Schreiber 2002; Regular *et al.* 2014). For individuals that reproduce later in the breeding season, reproductive performance is expected to be relatively poorer because their offspring do not benefit from the hypothesised peak in prey availability.

A second and well-supported hypothesis explains seasonal decreases in reproductive success as a function of parental age, with older

parents breeding earlier (Forslund & Part 1995, Mauck *et al.* 2004, Limmer & Becker 2009, 2010, Zhang *et al.* 2015). According to this hypothesis, the reasons for improved reproductive success with age are 1) improvements in breeding proficiency, or other learned behaviours, such as foraging or predator avoidance, that liberate time and energy for reproduction; 2) “the selection hypothesis,” where reproductive success improves with age as a function of the progressive disappearance of poorer-quality phenotypes over time; and/or 3) older individuals allocating more resources to reproduction before senescence.

A third hypothesis to explain seasonal decreases in reproductive success links reproductive performance to phenotypic traits, where reproductive success would decrease seasonally independent of age (Drent & Dann 1980, Wendeln & Becker 1999, Blums *et al.* 2005). For instance, individuals in better condition may simply be more proficient in acquiring and allocating resources towards reproduction (Richner 1989a, Gebhardt-Henrich & Richner 1998, Cam *et al.* 2003). These three hypotheses, currently believed to explain observed seasonal decreases in reproductive success, are not mutually exclusive, but few studies have concurrently measured seasonal patterns of

production and reproductive performance in seabirds of known age or phenotype (but see Dunn & Winkler 2010).

Greater Crested Terns *Thalasseus bergii* are a small, plunge-diving seabird common in the Indo-Pacific region, including coastal Australia. During the breeding season, adults have one clutch consisting of one egg, which they incubate for approximately 28 d (Langham & Hulsman 1986). After hatching, chicks are provisioned with a single prey item. Adults are long-lived (maximum recorded 32 years; Australian Bird and Bat Banding Scheme [ABBBS] data) and highly philopatric. Breeding is highly synchronous in South Australia (McLeay *et al.* 2009a) over the Austral summer. This breeding phenology contrasts with that recorded for colonies in other parts of Australia, where breeding seasons may be asynchronous, protracted, or occur year round (Dunlop 1985, Smith 1993, Walker 1992).

In this study, we measured the influence of reproductive timing on aspects of reproductive performance (chick growth and survival) for Greater Crested Terns at three colonies (Fig. 1). To assess the links between reproductive performance and seasonal changes in food availability, we measured monthly patterns of chlorophyll-*a*, obtained from satellites, as a surrogate of prey availability near to colonies. The use of chlorophyll-*a* data as an indicator of prey availability is common in marine predator studies due to the difficulty of obtaining reliable measures of prey distribution and abundance (Polovina *et al.* 2004, Page *et al.* 2006, Suryan *et al.* 2006; Pinaud & Weimerskirch 2007; Afan *et al.* 2015). Chlorophyll-*a* was also chosen in this study based on previous research findings that indicated high summer levels of secondary production within frontal systems close to Greater Crested Tern colonies (Bruce & Short 1990), and spatial correlation of this secondary production with areas of spawning sardines *Sardinops sagax*, which are a key prey item of Greater Crested Terns in South Australia (McLeay *et al.* 2009a,b; Ward & Staunton-Smith 2002). Chlorophyll-*a* has also been linked to areas of concentrated foraging by Greater Crested Terns breeding at Troubridge Island (McLeay *et al.* 2010), but the seasonal patterns of chlorophyll-*a* and any spatio-temporal link to their breeding phenology in the region have not previously been determined.

We examined the role of parental age in reproductive performance by measuring the timing of reproduction in relation to the age of breeding adults. Reproductive timing in relation to the body condition of adult Greater Crested Terns was also quantified to examine the role of phenotype as a factor influencing reproductive performance. Body condition is a commonly used indicator of phenotypic quality in avian studies and has been linked to survival (Blums *et al.* 2005, Golet *et al.* 1998, Lamb *et al.* 2016), decisions to breed (Weimerskirch 1992), and parameters of reproductive success (chick growth and reproductive success; Wendeln & Becker 1999). To assess the relative importance of phenotype and age in determining reproductive success, we also measured body condition as a function of age in breeding adults.

STUDY AREAS AND METHODS

Colonies

This study was undertaken between November and February in 2006/07 at Troubridge Island (35°4'S, 137°49'E) and Lipson Island (34°15'S, 136°15'E), and November and February 2007/08 at

Troubridge Island and Rocky Island (34°29'S, 137°25'E), South Australia (Fig. 1). The Greater Crested Tern colony at Troubridge Island is the largest in South Australia, consisting of approximately 3000 pairs (McLeay *et al.* 2009a). Colonies at Lipson and Rocky islands have approximately 2000 and 1300 breeding pairs, respectively. In this paper, we further refer to seasons as belonging to the year that breeding began (e.g., 2006/07 is referred to as 2006).

Measures of primary production

Chlorophyll-*a* data were obtained from the Integrated Marine Observing System (AODN Open access to ocean data). IMOS collates chlorophyll-*a* data, measured daily, at 0.6×0.6 nm (1.12×1.12 km) resolution by a moderate resolution imaging spectroradiometer (MODIS) instrument onboard the NASA Aqua satellite. Data were processed by applying the Garver–Siegel–Maritorena (GSM) algorithm implemented in SeaDAS processing software (Maritorena *et al.* 2002). The GSM algorithm is a semi-analytical algorithm used in shallow areas, such as Gulf St. Vincent and Spencer Gulf (Fig. 1), that takes into account the interaction of bottom reflectance with coloured dissolved organic matter (Maritorena *et al.* 2002). Data were downloaded for each month between October 2006 and September 2007 to assess changes in primary production through incubation (October/November), chick provisioning (November to February), and post fledging (March to September).

Measures of reproductive performance

Hatching success was monitored in a sample of 83–118 marked nests distributed randomly at each colony during the incubation period (Table 1). Colonies were visited at least every six days, for periods of one to four days. Nests were checked daily for signs of hatching, and hatch dates were recorded. Eggs that did not hatch after 35 d were considered dead (Langham & Hulsman 1986). Hatching success was calculated as the proportion of eggs that hatched from eggs laid. Greater Crested Tern chicks are mobile within 5 d of hatching. To enable measurements of chick growth and survival (fledging success) from the same individuals throughout the season, we constructed enclosures 30–45 cm high from 5 mm wire mesh to surround a further sample of 50–87 nests

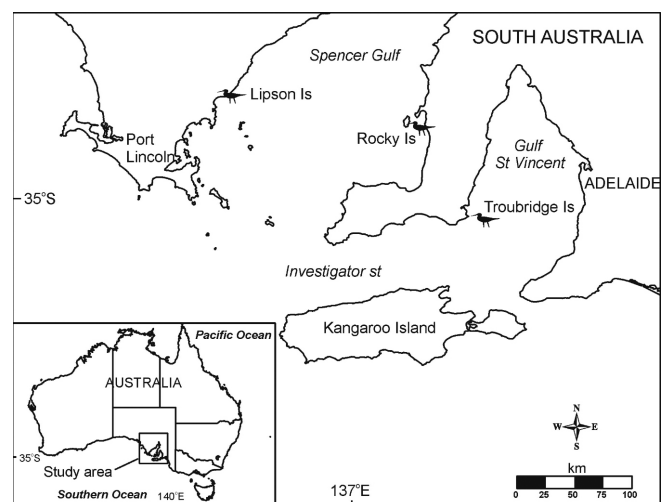


Fig. 1. Map of Gulf St. Vincent and Spencer Gulf, South Australia, showing the location of the study colonies (bird symbol).

at each colony (Table 1). Enclosures have been observed to affect chick growth and survival responses in other tern species by increasing relative rates of kleptoparasitism and predation (Stienen & Brenninkmeijer 1999). These effects were reduced by making the enclosures large enough to surround a large number of chicks (~10 m radius). This enabled them to form crèches once mobile and also allowed easy access to parents. As a further guard against observer impacts, a band of green shade-cloth 15 cm high was attached to the bottom of each enclosure to prevent injury to chicks. The enclosures had vegetation to afford chicks shade and protection from predators. Field observations indicated that rates of kleptoparasitism and predation by Silver Gulls *Chroicocephalus novaehollandiae* were low, and were similar both inside and outside the enclosures (L. McLeay, unpubl. data).

Nests within each enclosure were individually marked and monitored on each colony visit until all chicks hatched, at which point each was banded and weighed (± 2 g) with a Pesola spring balance. After the hatching period, colonies were visited once per week for a total of seven times during the season; chick mass was recorded once each visit. Chick survival was monitored within each fence over 60 d, including the period from hatching until the time all chicks had either left the fenced areas, at which time they were considered to have fledged and survived, or until they died. The hatch dates of all marked nests were recorded and compared with the date that the first egg in the colony was recorded as hatched. To ensure hatch dates were assigned correctly, only chicks that were observed to have hatched were included in the analyses.

Adult recaptures

Banding of Greater Crested Tern chicks at Troubridge Island commenced in 1966 (Waterman *et al.* 2003), and since 1985 an average of 1348 chicks (range 640–2350) have been banded annually. At Troubridge Island in 2007, we captured 778 adults with bands from their nests with a handheld net, recorded their band number, and measured their culmen length, bill depth, head length (± 0.01 mm), and body mass (± 5 g) before they were released. Disturbance to the colony was minimised by transferring captured adults from their nests to a mobile measuring station at least 15 m from the colony perimeter, and by regularly changing the areas in the colony where adults were captured. The presence of an egg or chick was recorded from each nest where adults were captured. Adult ages were subsequently determined from banding records (ABBBS data).

Data analyses

Chlorophyll-a

Chlorophyll-*a* data (mg/m^3) were filtered to exclude erroneous values $>20 \text{ mg}/\text{m}^3$ and applied to a grid of cells 3.75×3.75 nautical miles (6.94×6.94 km) in Mapinfo Professional (v12.5). Data within each cell were averaged and assigned to a central node. To assess seasonal patterns of primary production near colonies of Greater Crested Terns while breeding, we extracted data from the grid at two spatial scales: 10 and 40 km radii of each colony. Within-season trends in chlorophyll-*a* at 10 and 40 km distances were found to be the same at each colony, so data are presented for the 40 km surrounding each colony, as this distance represents known maximum foraging distances of breeding adults in South Australia (McLeay *et al.* 2010).

Chick growth and survival

To estimate parameters of chick growth at each colony, we fitted logistic curves using Curve Expert to mass measurements from chicks with five measurements or less taken over the course of the breeding season. Estimates included at least two measurements taken during the linear phase of growth (days 11–25) and two measurements taken during the asymptotic phase of growth (>30 d of age). Logistic curves were of the form:

$$W = A/(1 + e^{-K(t-I)}) \quad (\text{eq. 1})$$

where W represents mass at time t (days), A is the asymptote, I is the inflection point (time) at which 50% of growth in body mass is achieved, and K is a constant proportional to the overall growth rate (Ricklefs 1968). We also estimated hatch mass (M_0) and linear growth rate (LGR, 11–25 d) using the logistic growth equation derived for individual chicks. Overall differences in growth parameters among colonies were tested using Mann–Whitney tests. Breeding success for each colony was calculated as the product of hatching success and fledging success, respectively (i.e., breeding success = hatching success \times fledging success).

Generalised linear modelling (GLM) in SPSS (v24) was used to fit and compare a series of models of the effects of site, hatch date, M_0 , LGR, and their interactions, on relevant chick growth response parameters: M_0 , LGR, and A . Similarly, GLM was used to fit and compare a series of models of the effects of site, hatch date, M_0 , LGR, and their interactions, on chick survival (fledging success). Absence of strong co-linearity between and among predictor variables is an important assumption of GLM procedures, so we investigated correlation between all variables using collinearity diagnostics (Variance Inflation Factors [VIF]) obtained through regression analysis in SPSS (v24). Collinearity between all variables in GLMs relating to growth and chick survival was negligible (all VIF less than three). Year and site were initially included as categorical variables in GLMs, but GLM parameter estimates for year and site indicated that variation in the models was explained mainly by site (i.e., colony). Year was subsequently removed from further analyses. Akaike's information criterion (AIC) was used to select the best models from the set of candidate models developed *a priori*. AIC is useful as to compare candidate models derived from the same dataset; models with smaller AIC values are preferred and models with changes in AIC (ΔAIC) greater than two have less support (Burnham & Anderson 2002).

Adult body condition

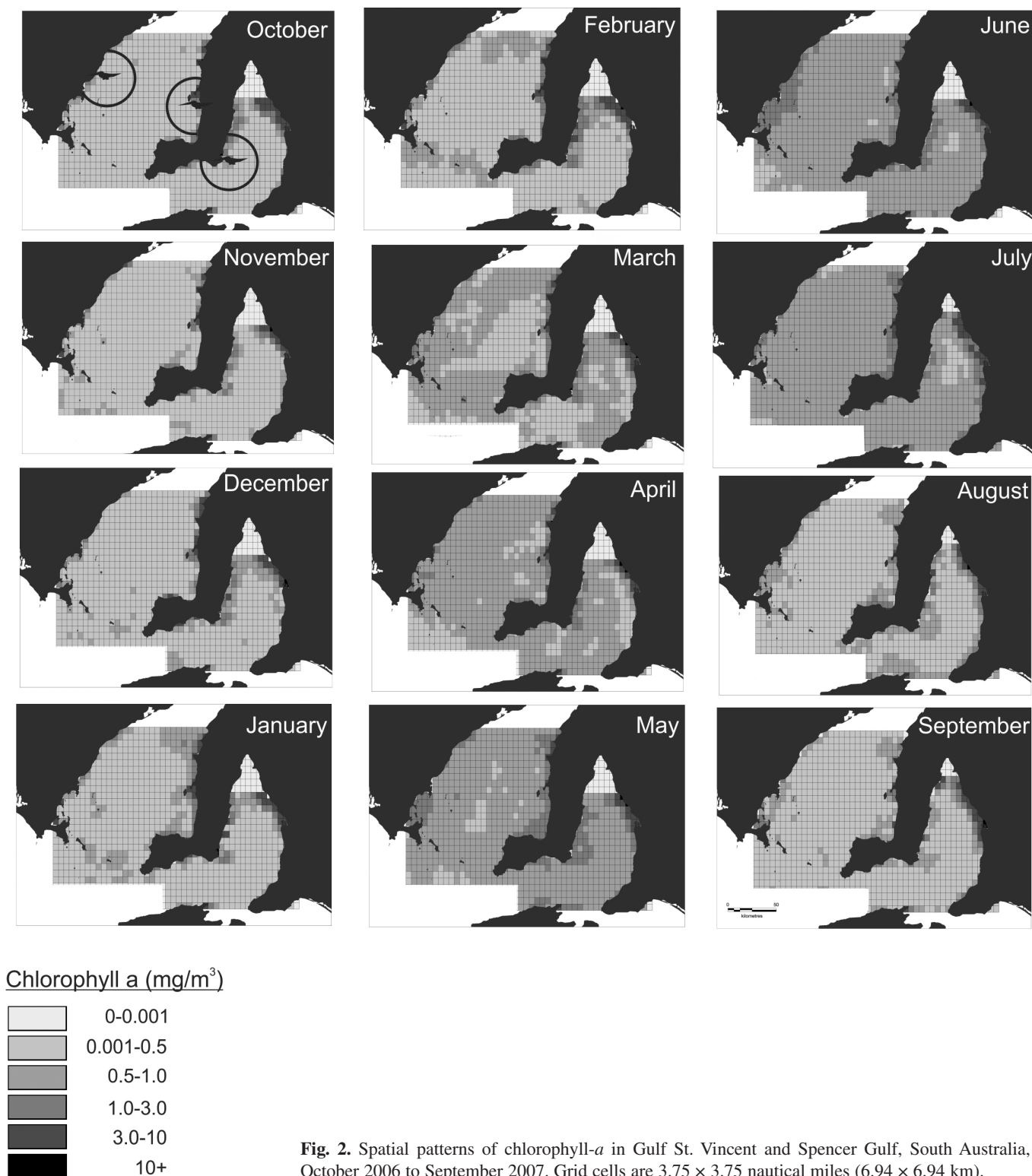
Adult body condition was measured by constructing a body condition index (BCI) separately for male and female adults captured from nests at Troubridge Island in 2007. Sex was assigned by a previously developed discriminant function that combined measurements of head length, culmen length, bill depth, and body mass (McLeay *et al.* 2009a). BCI estimation was adapted from the methods of Le Corre *et al.* (2003):

$$\text{BCI} = 1 - ([\text{TM} - \text{OM}]/\text{TM}) \quad (\text{eq. 2})$$

where TM is the theoretical body mass (g) calculated from the regression between mass and overall structural size determined from the first principal component (PC1) obtained through factor analyses (SPSS v24) of measurements relating to culmen length,

bill depth, and head length, and OM is the observed body mass (g) (female mass = $12.30PC1 + 334.3$, $F = 123.1$, $r^2 = 0.23$, $P \leq 0.001$; $n = 409$; male mass = $12.67PC1 + 338.9$, $F = 120.8$, $r^2 = 0.23$, $P \leq 0.001$; $n = 369$). In studies of animal body condition, PC1 is considered a more reliable indicator of structural size than individual measures alone (Green 2001). For BCI less than one, adult body mass is lower than expected. Conversely, for a BCI greater than one, adult body mass is greater than expected.

To assess the influence of age and body condition (BCI) on the timing of breeding, we used logistic regression analyses with a binomial distribution and a logit link function within GLM (SPSS v24) to fit and compare a series of models relating to the effects of age and BCI on timing of breeding, where timing of breeding was estimated from the absence/presence (coded 0,1) of chicks from nests of adults captured at Troubridge Island during the peak time of hatching between 16 and 28 November 2007. We also tested for the



effect of age on BCI using linear regression. The earliest recorded breeding age for Greater Crested Terns at Troubridge Island is 3 years (L. McLeay, unpubl. data). We hypothesised that young adults (aged less than seven years) may have less breeding and/or foraging experience and lower BCI than older adults (aged seven years or older), so we also tested for differences in BCI between young and older adults using Mann–Whitney *U*-tests. Variation in BCI within and between cohorts (annual age classes) was compared using nonparametric analysis of similarity (ANOSIM), on a Bray–Curtis similarity matrix (PRIMER version 5.1.2, PRIMER-E Ltd., Plymouth, UK). ANOSIM is a hypothesis-testing procedure that generates a probability value and a test statistic (*R*), which lies between 1 and –1. High positive *R*-values indicate greater variation between groups than within groups, and negative values indicate high levels of within-group variation compared with that between groups. Values of *R* equal to zero represent the null hypothesis of no significant difference between groups. All data were tested for assumptions of normality and homoscedasticity using Kolmogorov–Smirnov/Shapiro–Wilks’ tests and Levene’s tests.

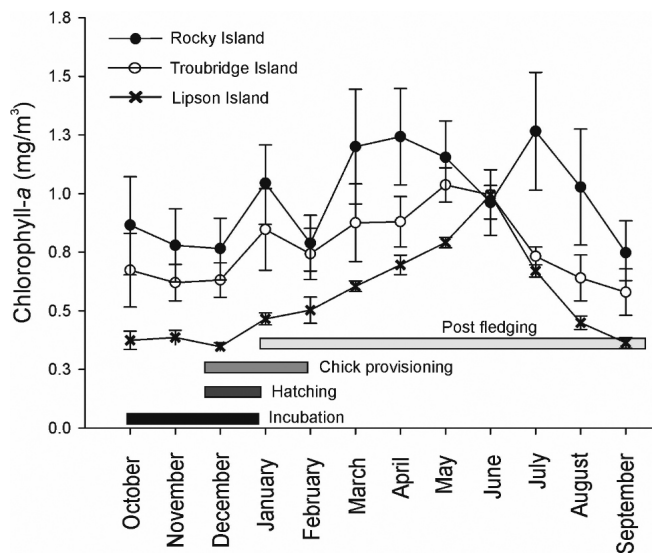


Fig. 3. Average chlorophyll-*a* measured within a 40 km radius of Rocky Island (Spencer Gulf), Lipson Island (Spencer Gulf), and Troubridge Island (Gulf St. Vincent), October 2006 to September 2007.

RESULTS

Seasonal patterns in primary production

Seasonal patterns of chlorophyll-*a* in Gulf St. Vincent and Spencer Gulf between October 2006 and September 2007 were similar, with relatively low concentrations (0.001–0.5 mg/m³) recorded throughout both gulfs between October and February (Fig. 2). From March, concentrations of chlorophyll-*a* in both gulfs increased, reaching 1.0–3.0 mg/m³ in July before decreasing again through August and September to 0.001–0.5 mg/m³ (Fig. 2). Seasonal patterns of chlorophyll-*a* recorded within 40 km radii of each colony between October 2006 and September 2007 reflected the patterns observed throughout both gulfs (Fig. 3). Relatively low average concentrations of chlorophyll-*a* were recorded between October and December near colonies during the incubation and early chick-provisioning periods (range: 0.35–0.87 mg/m³; Fig. 3). From January, chlorophyll-*a* increased near all colonies with average concentrations peaking in May at Troubridge Island, in June at Lipson Island, and in July at Rocky Island (range: 1.00–1.27 mg/m³; Fig. 3). Chlorophyll-*a* generally decreased after these months, reaching lows in September of 0.58 mg/m³ and 0.75 mg/m³ near Troubridge Island and Rocky Island, respectively, and lows in September and December of 0.36 mg/m³ and 0.35 mg/m³ near Lipson Island (Fig. 3).

Reproductive performance

Chick hatching was highly synchronous within each colony and between colonies in each season, with hatching occurring between 15 November and 18 December (Table 1). Mean hatch mass (*M*₀) showed some variation among colonies, ranging 37.6–41.3 g. Hatchlings were significantly larger at Troubridge Island in 2006 compared with Troubridge and Rocky Island in 2007 (Mann–Whitney *U*-test *M*₀ *P* ≤ 0.05; Table 1). Overall chick growth rates (*K*) did not vary significantly among colonies (Mann–Whitney *U*-tests all *P* ≥ 0.05, Table 1). Chicks reached 50% of asymptotic mass (*I*) (eq. 1) at 13.5–15.3 d (Table 1). Chicks at Troubridge Island in 2007 exhibited significantly higher LGR (11–25 d after hatching) (8.1 g ± 0.2 SE g/d) compared with those at the other colonies (Mann–Whitney *U*-test: *P* ≤ 0.05; Table 1). Conversely, chicks at Troubridge Island in 2006 had lower LGR (6.8 g ± 0.2 g/d) compared with chicks at all other colonies (Mann–Whitney *U*-tests all *P* ≤ 0.05; Table 1). Colony differences in LGR were reflected

TABLE 1
Parameters of growth and breeding success for Crested Tern chicks during 2006–2007^a

Location and date	Hatching period	Median hatch date	<i>M</i> ₀ (g) ± SE	LGR (g/d) ± SE	<i>K</i> ± SE	<i>I</i> (d) ± SE	<i>A</i> (g) ± SE	Hatching success (<i>n</i>)	Fledging success (<i>n</i>)	Breeding success
Lipson Island 2006	18 Nov–16 Dec	23 Nov 2006	40.8 ± 1.5	7.3 ± 0.2	0.12 ± 0.00	15.3 ± 1.6	285.5 ± 4.1	0.946 (112)	0.767 (60)	0.726
Troubridge Island 2006	21 Nov–17 Dec	26 Nov 2006	41.3 ± 0.7	6.8 ± 0.2	0.13 ± 0.00	13.5 ± 0.5	259.2 ± 3.9	0.983 (118)	0.943 (87)	0.927
Rocky Island 2007	26 Nov–9 Dec	1 Dec 2007	37.7 ± 0.8	7.3 ± 0.1	0.12 ± 0.00	14.5 ± 0.5	277.7 ± 3.4	0.964 (83)	0.949 (59)	0.915
Troubridge Island 2007	15 Nov–18 Dec	21 Nov 2007	37.6 ± 1.1	8.1 ± 0.2	0.13 ± 0.00	14.7 ± 0.7	295.8 ± 3.6	0.967 (92)	0.940 (50)	0.909

^a Symbols: *M*₀, chick mass at hatching; LGR, linear growth rate (11–25 d); *K*, logistic growth equation constant proportional to the overall growth rate; *I*, time to reach 50% of asymptotic mass; *A*, asymptotic mass). Breeding success = hatching success × fledging success.

in measures of asymptotic mass (A) (Mann–Whitney U -test all $P \leq 0.05$; Table 1). Hatching success was high at all colonies, ranging 0.95–0.98 per egg laid (Table 1). Fledging success varied among colonies but was also high, ranging from 0.77 at Lipson Island in 2006 to 0.95 at Rocky Island in 2007 (Table 1). Estimates of breeding success at colonies in 2006 and 2007 ranged from 0.73 at Lipson Island in 2006 to 0.93 at Troubridge Island in 2006 (Table 1). At Lipson Island, chick mortality was highest at the end of the linear growth phase (>20 d) (Fig. 4).

Factors affecting reproductive performance—chick growth and survival

Residual plots and AIC values indicated that the most suitable GLMs to model the effects of site, hatch date, M_0 , LGR, and their interactions on relevant chick growth responses (M_0 , LGR, and A) incorporated a Gaussian error structure and identity link function. The top candidate sets of models for each growth response, including the “null” model, are presented in Tables 2, 3, and 4, respectively.

The most well-supported model for M_0 included site (colony), hatch date, and the interaction between site and hatch date. This model explained 27.2% of the deviance from the null model (i.e., $100 \times (16322.7 - 11882.3)/16322.7$) (Table 3), and there was strong support for the effects of site (Wald chi-square 35.3, $df = 3$, $P < 0.001$), hatch date (Wald chi-square 13.8, $df = 1$, $P < 0.001$), and the interaction between site and hatch date (Wald chi-square 38.3, $df = 3$, $P < 0.001$). Hatch mass (M_0) was also negatively correlated

with hatch date, indicating that chicks that hatched later in the season had lower hatch mass.

The most well supported GLM for LGR included site, hatch date, M_0 , and the interaction between site and hatch date (Table 3). This model explained 27.2% of the deviance from the null model, and there was strong support for the effects of site (Wald chi-square 8.7,

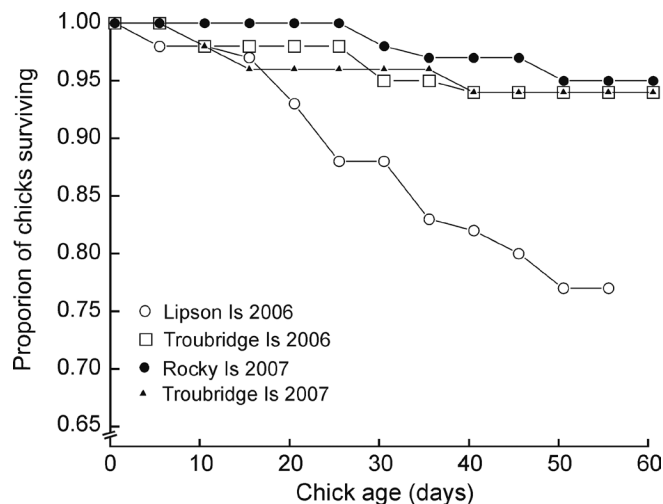


Fig. 4. Proportion of Crested Tern chicks surviving between hatching and fledging at all colonies (1.00 represents all chicks alive).

TABLE 2
Results of generalised linear modelling for the effects of site and hatch date on hatch mass (M_0)^a

Model	N	k	Dev	LL	AIC	Δ AIC
$M_0 \sim \text{site} + \text{hatchdate} + \text{site}*\text{hatchdate}$	219	7	11 882.3	-748.1	1 514.1	0.0
$M_0 \sim \text{site} + \text{hatchdate}$	219	6	13 959.5	-765.7	1 543.4	29.3
$M_0 \sim \text{site}$	219	5	15 077.8	-774.1	1 558.3	44.2
$M_0 \sim \text{hatchdate}$	219	2	15 863.8	-779.7	1 565.4	51.3
$M_0 \sim 1$ (null)	219	1	16 322.7	-782.8	1 569.7	55.5

^a Abbreviations: k = number of parameters; Dev = deviance; LL = log-likelihood; AIC = Akaike's information criterion; Δ AIC is the change in Akaike's information criterion between the best and candidate model.

TABLE 3
Results of generalised linear modelling for the effects of site, hatch date, and hatch mass (M_0) on linear growth rate (LGR)^a

Model	N	k	Dev	LL	AIC	Δ AIC
$\text{LGR} \sim \text{site} + \text{hatchdate} + M_0 + \text{site}*\text{hatchdate}$	219	8	240.0	-320.8	661.5	0.0
$\text{LGR} \sim \text{site} + \text{hatchdate} + M_0$	219	7	256.2	-327.9	669.9	8.4
$\text{LGR} \sim \text{site} + M_0$	219	6	261.7	-330.3	672.5	11.0
$\text{LGR} \sim \text{site}$	219	5	278.9	-337.2	684.5	22.9
$\text{LGR} \sim \text{site} + \text{hatchdate}$	219	6	277.6	-336.7	685.4	23.9
$\text{LGR} \sim M_0$	219	2	301.0	-345.6	697.2	35.6
$\text{LGR} \sim \text{hatchdate} + M_0$	219	3	300.7	-345.5	698.9	37.4
$\text{LGR} \sim 1$ (null)	219	1	329.8	-355.6	715.1	53.6
$\text{LGR} \sim \text{hatchdate}$	219	2	327.6	-354.9	715.7	54.2

^a Abbreviations: k = number of parameters; Dev = deviance; LL = log-likelihood; AIC = Akaike's information criterion; Δ AIC is the change in Akaike's information criterion between the best and candidate model.

df = 3, $P = 0.034$), M_0 (Wald chi-square 15.1, df = 1, $P < 0.001$) and the interaction between site and hatch date (Wald Chi-square 14.8, df = 3, $P = 0.002$). These results indicate that growth rates (LGR) were influenced by site, M_0 , and the timing of hatching at each site. The most well-supported model for A included site, hatch date, LGR, M_0 , and the interaction between site and hatch date (Table 4). This model explained 57.7% of the deviance from the null model, and there was strong support for the effects of site (Wald chi-square 25.2, df = 3, $P < 0.001$), M_0 (Wald chi-square 37.9, df = 1, $P < 0.001$), LGR (Wald chi-square 165.1, df = 1, $P < 0.001$), and the interaction between site and hatch date (Wald chi-square 13.4, df = 3, $P = 0.004$). These results indicate that A is influenced by site, M_0 , LGR, and the timing of hatching at each site.

Logistic regression analyses with a binomial distribution and a logit link function were used to fit and compare a series of GLMs relating to the effects of site, hatch date, M_0 , LGR, and their interactions on chick survival (fledging success) (Table 5). Values of AIC indicated that survival was best predicted by site alone (AIC 21.5, Table 5) and is explained by the relatively lower chick survival recorded

at Lipson Island in 2006. The next best-supported model was that including hatch date alone, with strong support for the effects of hatch date on survival (Wald chi-square 14.1, df = 3, $P = 0.003$). This model explained 81.5% of the deviance from the null model with the negative GLM β coefficient of -0.07 for hatch date, consistent with the hypothesis that chicks that hatch later in the season have a lower probability of survival than chicks that hatch early (Table 5).

Age, phenotype, and reproductive timing

Logistic regression analyses with a binomial distribution and a logit link function were used to fit and compare GLMs relating to the effects of age and body condition (BCI) on reproductive timing. Values of AIC indicated that age alone was the best predictor of reproductive timing (AIC 171.9, Table 6). This model explained 4.2% of the deviance from the null model. Tests of model effects also indicated strong support for the effects of age on reproductive timing (Wald chi-square 7.2, df = 3, $P = 0.007$). The next two best-supported models included 1) age and BCI and 2) age and BCI with

TABLE 4
Results of generalised linear modelling for the effects of site, hatch date, hatch mass (M_0), and linear growth rate on A (asymptotic mass)^a

Model	N	k	Dev	LL	AIC	Δ AIC
A ~ site + hatchdate + M_0 + LGR + site*hatchdate	219	9	93 750.9	-974.2	1 970.5	0.0
A ~ site + hatchdate + M_0 + LGR + hatchdate*LGR	219	9	97 713.6	-978.8	1 975.6	5.1
A ~ site + hatchdate + M_0 + LGR	219	8	99 501.8	-980.8	1 977.5	7.0
A ~ site + M_0 + LGR	219	7	100 502.5	-981.9	1 977.7	7.2
A ~ M_0 + LGR	219	3	115 036.9	-996.6	2 001.3	30.8
A ~ hatchdate + M_0 + LGR	219	4	115 029.9	-996.6	2 003.3	32.8
A ~ site + hatchdate + LGR	219	7	114 307.1	-996.0	2 005.9	35.4
A ~ site + LGR	219	6	119 391.2	-1 000.7	2 013.4	42.9
A ~ LGR	219	2	132 038.2	-1 011.7	2 029.5	59.0
A ~ hatchdate + LGR	219	3	131 745.6	-1 011.5	2 031.0	60.5
A ~ 1 (null)	219	1	221 777.9	-1 068.5	2 141.1	170.6

^a Abbreviations: k = number of parameters; Dev = deviance; LL = log-likelihood; AIC = Akaike's information criterion; Δ AIC is the change in Akaike's information criterion between the best and candidate model.

TABLE 5
Results of generalised linear modelling for the effects of site, hatch date, and hatch mass (M_0) on chick survival (fledging success)^a

Model	N	k	Dev	LL	AIC	Δ AIC
Survival ~ site	256	5	0.0	-6.8	21.5	0.0
Survival ~ hatchdate	256	2	27.3	-29.9	63.8	42.3
Survival ~ site + hatchdate	256	6	33.4	-33.8	77.6	56.1
Survival ~ M_0	256	2	100.9	-58.9	121.8	100.3
Survival ~ site + M_0	256	6	109.6	-61.9	133.8	112.3
Survival ~ site + hatchdate + M_0	256	7	128.1	-67.8	147.5	126.0
Survival ~ hatchdate + M_0	256	3	137.1	-72.2	150.5	128.9
Survival ~ 1 (null)	256	1	147.8	-77.6	157.2	135.7

^a Abbreviations: k = number of parameters; Dev = deviance; LL = log-likelihood; AIC = Akaike's information criterion; Δ AIC is the change in Akaike's information criterion between the best and candidate model.

an interaction between age and BCI. However, tests of model effects indicated no support for the effects of BCI or an age/BCI interaction on reproductive timing (all $P > 0.05$).

There was no significant relationship between age and BCI (ANOVA, $F = 2.0$, $r^2 = 0.003$, $P > 0.05$). However, comparison of BCI between young (less than seven years) and older adults (seven years or older) indicated that young individuals had significantly lower BCI than older individuals (Mann–Whitney U -test: $Z = 2.573$, $P = 0.010$). Comparison of levels of variation in BCI within and between cohorts via ANOSIM supports these results. Within-cohort variation in BCI was not different from between-cohort variation (ANOSIM, $R = 0.003$, $P = 0.353$) indicating that body condition was not influenced by age alone (Fig. 5). Of note was also the finding that males and females reared in 1995 (aged 12 years), during a sardine mass mortality event, had similar BCI to individuals less than years of age (Fig. 5).

DISCUSSION

Seasonal timing

While seasonal patterns in primary production were evident in both gulfs, with increases recorded between April and July, chlorophyll-*a* data do not provide direct support for the “timing hypothesis” that predicts that reproduction of Greater Crested Terns will coincide with peaks in prey availability (Lack 1954, Perrins 1970). The possibility of a lag between the April to July peak in primary production and subsequent increases in prey availability during the breeding season of Greater Crested Terns in both gulfs cannot be discounted. It is also possible that breeding decisions are related to environmental and biological cues from a wider spatial scale than investigated in this study. Such spatio-temporal mismatches have been recorded among different trophic levels in other temperate marine ecosystems (Gremillet *et al.* 2008; Afan *et al.* 2015).

Alternatively, if the April and July peaks in chlorophyll-*a* observed in the gulfs are closely matched to peaks in prey availability, this winter period of elevated production may benefit newly fledged juvenile terns that would have relatively less foraging skill and experience than adults. It is also possible that adult terns would benefit from any increases in prey availability at this time by increasing the body reserves needed for reproduction before the next breeding season starting in October. A closer spatio-temporal match between primary production and prey availability in the gulfs is supported by high commercial catches of Australian sardine,

which are a key prey item of Greater Crested Terns, between March and June, as well as the high abundance of juvenile sardine in the gulfs following the peak spawning period of sardine in February (Ward *et al.* 2015).

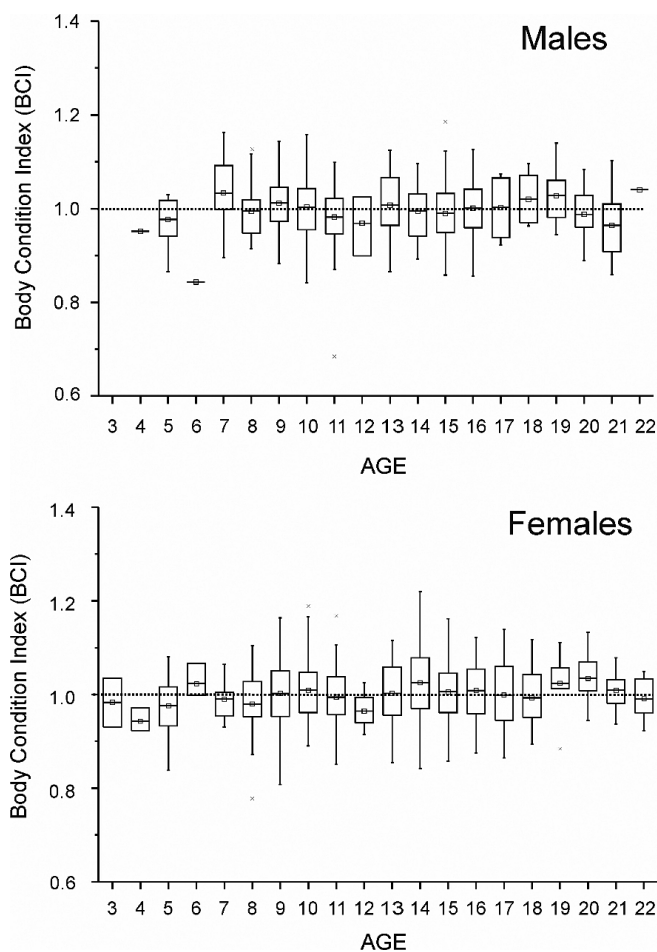


Fig. 5. Box-and-whisker plot showing variation of male and female adult body condition (BCI) with age (years) in 2007 at Troubridge Island. Line indicates a BCI of 1, where an adult's expected mass is determined according to its structural size from the first principal component (PC1) obtained through factor analyses (see Methods). Confidence limits: box limits = 25th and 75th percentiles, whisker limits = 5th and 95th percentiles. (Total adults $n = 742$; sample size range per cohort: $n = 2$ (three years) to 140 (10 years).

TABLE 6
Results of generalised linear modelling for the effects of age and body condition on reproductive timing^a

Model	N	k	Dev	LL	AIC	ΔAIC
Timing ~ Age	220	2.0	167.9	-84.0	171.9	0.0
Timing ~ Age +BCI	220	3.0	167.1	-83.6	173.1	1.2
Timing ~ Age + BCI + BCI*Age	220	4.0	165.4	-82.7	173.4	1.5
Timing ~ null	220	1.0	175.3	-87.6	177.3	5.3
Timing ~ BCI	220	2.0	175.1	-87.5	179.1	7.1

^a Abbreviations: k = number of parameters; Dev = deviance; LL = log-likelihood; AIC = Akaike's information criterion; ΔAIC is the change in Akaike's information criterion between the best and candidate model.

Reproductive performance

Our GLM results indicate that the timing of breeding is a key factor influencing the reproductive performance of Greater Crested Terns. Chicks that hatched earlier in the season attained greater hatch mass (M_0), higher rates of linear growth (LGR), larger asymptotic mass (A) and also had higher survival. These results indicate a distinct selective advantage for Greater Crested Terns that breed early in South Australia and corroborate findings for other bird species with well defined breeding seasons (Lack 1950, Perrins 1970, Arnold *et al.* 2004, Regular *et al.* 2014).

Despite reproductive timing among colonies being synchronised, our study also recorded significant differences in reproductive performance among colonies. Many factors can influence reproductive success in tern colonies, including predation, colony disturbance, weather conditions, availability of nest sites, or prey conditions (Nisbet & Welton 1984, Fracasso & Branco 2012, Newell *et al.* 2015). No extreme weather conditions or invasive rodent predators were recorded at any of the colonies in 2006 and 2007, and researcher disturbance was minimised during each colony visit (see Methods). Rates of disturbance from human visitation are unknown but are likely to be minimal, considering the isolated location of each colony and the distance of each colony from major population centres. The lower survival rates of chicks at Lipson Island were likely related to prey availability. Prey conditions are a key factor influencing inter-annual reproductive success in seabirds (Monaghan *et al.* 1992, Ainley *et al.* 2003, Furness & Tasker 2000). Adults at Lipson Island delivered a relatively lower total mass of prey during the mid-to-late chick provisioning period (chicks >11 d of age) compared with other colonies (McLeay 2010). This supports the hypothesis that lower prey availability may have contributed to the decreased survival rates observed.

Age, phenotype, and reproductive timing

When comparing age and body condition factors in GLMs, adult age alone was the best predictor of reproductive timing, indicating that chicks reared by older adults hatched earlier in the breeding season than chicks reared by younger adults. Age-related breeding experience is well documented as a factor enhancing breeding success in long-lived seabirds (Sydeman *et al.* 1991, Weimerskirch 1992, Pyle *et al.* 2001).

Mate fidelity in Greater Crested Terns is indicated by the presence of monogamous breeding pairs at Troubridge Island (McLeay, unpubl. data) and may also drive age-related breeding proficiency. Age-related foraging experience likely also plays a role in enhancing their breeding success. As single-prey loaders, adult Greater Crested Terns are constrained during breeding by the need to provision their offspring with single prey items of suitable size for physical ingestion (McLeay *et al.* 2009b). Consequently, increased foraging skills learned while breeding are likely to enable efficient location of suitable size prey, thereby improving prey delivery rates and enhancing chick growth and reproductive success. Such age-related patterns have been observed in Common Terns *Sterna hirundo* (Limmer & Becker 2009).

The influence of the selection hypothesis on the observed patterns of age-related breeding success is unknown, and any effect of older-aged individuals increasing reproductive effort before senescence is also unquantified, if present. Future longitudinal analyses that measure the survival, phenotypic traits, and reproductive effort and performance of known-age individuals over many years may help

elucidate the influence of these factors on the age-related patterns in reproduction we observed.

One of the key mechanisms regulating whether parents devote time to self-feeding or provisioning is adult body condition (Drent & Dann 1980, Wendeln & Becker 1999). There was less support in GLM for the effects of body condition on reproductive timing, and no significant relationship was observed between adult age and body condition. Comparison of variation in BCI within and between cohorts using ANOSIM indicated that within-cohort BCI was not different from between-cohort BCI, which also indicates that body condition was not influenced by age. These results support Wendeln & Becker (1999), who found high inter- and low intra-individual variation in the body condition of adult Common Terns. However, our analyses of BCI between cohorts also indicated that adults less than seven years of age had significantly lower BCI than those seven years and older. The relatively low BCIs recorded for younger adults likely indicates that these cohorts, as newly recruited breeders, may be less proficient at obtaining the energy required for egg development and for provisioning themselves and their offspring during the breeding season.

All adults aged 12 years exhibited relatively poor body condition compared with other cohorts aged seven years and older. This cohort, reared during 1995, experienced high chick mortality and retarded growth when approximately 70% of the biomass of their primary prey (sardine) was killed by a herpesvirus introduced from anthropogenic sources (Gaughan *et al.* 2000, Ward *et al.* 2001, McLeay *et al.* 2009a). Our data do not permit analysis of age-specific reproductive rates, but the relatively poor body condition of 12 year-old birds indicates that the prey conditions experienced by chicks during the breeding season not only affect their survival as chicks, but also their body condition as adults.

Adult morphological and fitness consequences arising from poor prey conditions during chick growth have been well studied in passerines (Cooch 2002, and see Gebhardt-Henrich & Richner 1998 for a review) and less studied in seabirds (but see Cam *et al.* 2003). Passerine research indicates that retardation during early somatic growth can have long-term fitness consequences (Gebhardt-Henrich & Richner 1998, Schew & Ricklefs 1998, Cooch 2002). For instance, Carrion Crow *Corvus corone* chicks reared under good food conditions attain larger adult body size and have better reproductive success than chicks reared under a poor food supply (Richner 1989b, Richner *et al.* 1989). Future longitudinal studies of individual Greater Crested Tern breeding histories at Troubridge Island, where many cohorts are already banded, may help to elucidate the potential interaction of past prey conditions, adult body condition, and future reproductive success in Greater Crested Tern populations.

In conclusion, our study found no evidence to link seasonal patterns in breeding success to elevated levels of primary production in the summer. However, the winter timing of peaks in marine productivity in the gulfs may benefit both juvenile Greater Crested Terns learning new foraging skills and adults before the next breeding season. We found that adult age plays a significant role in mediating reproductive success. Chicks reared by older adults hatched earlier in the breeding season, were in better condition, and had higher rates of survival. There was no relationship between adult body condition and reproductive timing, but adults less than seven years of age had poorer body condition than adults seven years or older, indicating that newly recruited breeders may be less proficient at obtaining the energy required for both themselves and their offspring during breeding. The

observed seasonal patterns of age-related breeding success may be explained by age-related improvements in foraging and/or breeding proficiency. One of the key selective pressures likely shaping this pattern is the need for adult Greater Crested Terns to provision their chick with a single prey item that the chick can swallow. This strategy results in older, more experienced Greater Crested Terns having higher reproductive rates compared with younger, less experienced adults.

ACKNOWLEDGEMENTS

This study was principally supported through the Australian Government's Fisheries Research and Development Corporation (FRDC) Grants Scheme (PN 2005/031), co-funded by the South Australian Sardine Fishery. We also thank the South Australian Department for Environment, Water and Natural Resources for financial assistance through the Wildlife Conservation Fund. Banding was undertaken under the Australian Bird and Bat Banding Scheme (ABBBS) banding authority 2695, and we thank the ABBBS for managing and supplying information relating to banded Greater Crested Terns. All bird-handling procedures were carried out under South Australian scientific research permit A24684. We thank A. Baylis, G. French, T. Kemper, J. McKenzie, R. Mayo, G. McLeay, H. McLeay, L.K. McLeay, M. McLeay, A. Newman, J. Nichols, C. Platt, P. Rogers, M. Waterman, and A. Wiebkin for their assistance in field operations, and Ana Redondo Rodriguez for her advice on downloading and processing MODIS data. Many thanks go to Chris and Judy Johnson for providing logistical support and accommodation on Troubridge Island. We are also grateful to all reviewers for useful comments that greatly improved the manuscript.

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