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TITLE PAGE

Climate variation and population dynamics in tropical seabirds

Thesis submitted by

Carol Ann DEVNEY nee ERWIN

Gr Dip Rsch Mths (Wildlife Biology & Mgmt) ***James Cook University, Qld***

BSc (Environmental Chemistry) ***Colorado School of Mines, USA***

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within the School of Marine & Tropical Biology
James Cook University

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DEDICATION

This book is dedicated to my family, which came together amidst this protracted PhD journey. Four special people are more important to me than all other things: my husband and my three children. My first two have had to put up with me pottering away at the computer whilst they quickly grew from infants to a toddler and a little lady. New baby will be here just in time for my graduation. Thanks for all your support, love, keyboard crunching and for keeping it in perspective for me.

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Chapter 3

Devney, C.A., Short, M. and Congdon, B.C. 2009. Sensitivity of tropical seabirds to El Niño precursors. *Ecology* 90(5), 1175-1183.

Chapter 4

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Chapter 5

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Chapter 6

Devney, C.A., Short, M. and Congdon, B.C. 2009. Cyclonic and anthropogenic influences on terns of the Great Barrier Reef, Australia. *Wildlife Research* 36, 368-378.

Chapter 7

Devney, C. A., and Congdon, B.C. 2009. Testing the efficacy of a boundary fence on an important tropical seabird breeding colony and key tourist destination. *Wildlife Research* 36, 353-360.

SUMMARY

Impacts from variation in climate associated with global warming are often difficult to discern in natural ecosystems. The effects of climate fluctuations appear to manifest differently both temporally and spatially depending on the prevailing environmental conditions to which species are exposed throughout the course of their reproductive and/or life cycles. This may be particularly prevalent in tropical systems where food availability is temporally and spatially more variable compared to higher latitudes. To examine current and potential future impacts of environmental variability on tropical seabirds, I examined the population and reproductive dynamics of multiple sympatric species using different foraging guilds and breeding at northern and southern breeding sites on the Great Barrier Reef, Australia.

Sooty terns (*Onychoprion fuscata*), Common noddies (*Anous stolidus*) and Black noddies (*A. minutus*) share the life-history traits of pelagic/offshore foraging regimes, suspected breeding-site fidelity, clutch size of one and protracted post-natal growth. Crested terns (*Sterna bergii*) breed at similar locations and adhere to an inshore foraging regime, a brood size of one, variation in colony sites between and within breeding seasons and rapid post-natal growth.

The population dynamics of Sooty terns, Common noddies and Crested terns breeding at Michaelmas Cay, northern Great Barrier Reef were examined over 18 years relative to a broad range of environmental and anthropogenic covariates. I also used several seasons of fieldwork to compare foraging success and chick growth of Sooty terns at Michaelmas Cay and Black noddies breeding at Heron Island, southern Great Barrier Reef, to fine-scale variation in sea-surface temperature. Next, the potential for Black noddies to respond to

predicted future changes in climate through behavioural and developmental flexibility was assessed using variation in natural and artificial feeding conditions over two breeding seasons. Trophic mechanisms underlying these relationships were also examined, thereby identifying the potential for these same processes to both operate within the Great Barrier Reef and affect taxa at other trophic levels. Finally, while I primarily focussed on determining the relative role of large-scale oceanographic variation on seabird biology, I could not ignore potential confounding influences not related to major oceanography, such as catastrophic events (cyclones), direct (tourism) or indirect (fisheries) human pressure.

Results from the long-term monitoring component of this research suggest that breeding Sooty terns and Common noddies are sensitive to changes in both surface chlorophyll concentration and thermocline depth that occur well in advance of El Niño generated sea-surface temperature anomalies. The most likely explanation for this finding is that these relationships are mediated through a strict reliance by these tropical pelagic piscivorous seabird species on underwater predators, such as tuna and mackerel, to push prey to the surface where it becomes available to these aerial predators. In contrast, Crested tern breeding is not correlated with any environmental/biological parameters investigated. Inshore foraging species such as Crested terns depend on more localised and a larger variety of prey types and do not rely on underwater predators to capture food. These findings demonstrate that El Niño related phenomena do not affect seabird prey dynamics solely via productivity shifts at seasonal scales, nor in similar ways across different foraging guilds. The findings also suggest that population declines observed at multiple colonies of a variety of pelagic/offshore foraging species in western tropical Pacific may be directly related to the frequency and intensity of El Niño anomalies over the study period.

Direct analyses of the influence of fine-scale variation in sea-surface temperature on foraging success and chick growth of Sooty terns at Michaelmas Cay and Black noddies at Heron Island confirmed within-season variation in sea-surface temperature as another important determinant of foraging success at a reef-wide scale for these two similar tropical seabird species. Consistent patterns were observed on the northern reef with significant negative relationships between day-to-day variation in sea-surface temperature and both the amount of food fed to Sooty tern chicks and the feeding frequency in both years. For Black noddies on the southern reef, sea-surface temperature was negatively related to meal sizes and feeding frequency in a season of extremely high sea-surface temperatures but not when sea-surface temperatures were average. Considering forecasts for increases in extreme temperature events associated with global warming, as well as similar recent findings from the southern reef on a separate species, these results suggest that sea-surface temperature variation commonly does and will continue to influence the foraging success of multiple tropical seabird species across the Great Barrier Reef and implies a significant negative effect of forecasted climatic changes on seabirds breeding in the region.

Next, my assessment of Black noddy flexibility in provisioning behaviour and development of offspring suggests limited plasticity in both life-history characteristics and that the potential capacity of this species to resist future environmental variation associated with climate change is low. Results garnered from the four food treatment groups (two natural and two artificially supplemented) demonstrated that during periods of low prey abundance, parents brought back smaller meals but at the same rate as chicks exposed to normal conditions. Super-abundance of food through food supplementation, also resulted in delivery of smaller meals by adults, but again did not influence feeding frequency. Evidence from this study suggests that smaller meals fed to artificially supplemented chicks resulted from a decrease in chick demands associated with satiation, rather than adult behavioural responses to chick condition. Chicks maintained structural growth while sacrificing body condition during periods of low prey abundance, and chicks were unable to take advantage of periods of high prey abundance by increasing growth rates, suggesting chick development is driven by an obligate rather than facultative mechanism. Combined these results suggest that future changes in sea-surface temperature and other environmental variation may require evolutionary responses to natural selection in these birds. The long generation time and low fecundity of this taxon make such responses over short periods unlikely. If so, this, and possibly similar, species may be at high risk from climate change.

The potential complication of other anthropogenic stressors in the system influencing the main findings of this thesis is effectively negated. The 18 year dataset on population trends for Sooty terns, Common noddies and Crested terns breeding at Michaelmas Cay was assessed relative to two potential threatening processes: anthropogenic disturbance (as either tourism of commercial fishing) and cyclone activity. Longer-term trends in population sizes of all species remained unaffected by direct human pressure through tourism. Long-term population trends were also not closely related to indirect pressure through competition for resources via commercial fishing. Nor were long-term population trends in any species threatened by localised disturbance from cyclones or associated changes in cay size and/or nesting habitat. Field studies into the immediate influence of tourism on foraging success and chick growth of Sooty terns at Michaelmas Cay support these results, with only minor, short-term impacts on breeding success observed as a result of the proximity of nesting sites to tourists.

Combined, the results from this study have defined climatic variation at multiple temporal and spatial scales as the primary driver of population dynamics in pelagic/offshore foraging tropical seabird species across the Great Barrier Reef. The findings significantly enhance our mechanistic understanding of how El Niño-related phenomena impact biological processes in tropical marine systems by substantially increasing knowledge of the potential effects of climate change on trophic dynamics and by elucidating how these impacts vary by taxa. Affected species have life-history characteristics in common which made them particularly sensitive to ENSO-associated fluctuations in food availability, while the single unaffected species has life-history characteristics which naturally buffered it to climate variability. These patterns are similar to comparative findings from elsewhere. The information compiled in this thesis can be used to guide enlightened management decisions, on a species by species and/or regional basis, that protect Australia’s marine biodiversity and allow the long-term sustainable use of the Great Barrier Reef and other tropical ecosystems.

CHAPTER 1

1.0. GENERAL INTRODUCTION

1.1. Large-scale oceanographic processes

The biology of marine fauna is generally dominated by large-scale oceanographic processes such as the El Niño Southern Oscillation (ENSO) (Stenseth et al., 2002). Seabirds are key upper trophic level predators in marine ecosystems which are impacted heavily by oceanographic processes (Ramos et al., 2002, Veit et al., 1997, Guinet et al., 1998, Pinaud and Weimerskirch, 2002, Jenouvrier et al., 2003). Although airborne and land bound when breeding, seabirds spend most of their lives at sea, feed primarily or exclusively at sea, and many forage over large distances to obtain sufficient food to breed. These characteristics mean that seabird demographics and reproductive parameters are strongly impacted by, and closely reflect, changing oceanographic and trophic conditions (Schreiber, 2002).

Large-scale oceanographic processes which can influence seabird foraging and breeding biology, and future survival (Kitaysky and Goluvova, 2000, Durant et al., 2003, Weimerskirch et al., 2001, Sandvik et al., 2005, Ramos et al., 2002) include global processes such as the ENSO, changes in sea-surface temperature (SST), and changes in thermocline depth. The published literature is rife with documented impacts of the ENSO and climate change-associated seasonal shifts in SST for seabirds living in temperate regions (reviewed by Congdon et al., 2007, Chambers et al., 2011). Less documented are impacts to foraging and reproduction from within-season shifts in oceanographic conditions such as SST

(Gjerdrum et al., 2003, Peck et al., 2004) and changes to thermocline depth (Spear et al., 2001, Ballance et al., 2006).

Similarly, while the temperate region is well covered for documented impacts of climate variation on seabirds (Ainley and Divoky, 2001, Grémillet and Boulinier, 2009), seabirds living in tropical regions of the world may be similarly affected by large-scale oceanographic processes, but generally there is less information available for fewer species (reviewed by Congdon et al., 2007).

1.1.1. El Niño Southern Oscillation

The ENSO is a major driver of large-scale patterns of climate variability with marked ecological impacts on interannual or longer scales (Fiedler, 2002). A large body of literature documents the impact of climate on seabirds as seasonal or longer-term correlations between reproductive demographics and large-scale oceanographic processes such as the ENSO. Specifically, this work suggests that ENSO-type phenomena impact important demographic parameters, such as breeding chronology, breeding participation and hatching success on an annual or longer term basis and adult survival (Ramos et al., 2006, Bertram et al., 2005, Dunlop et al., 2002, Schreiber and Schreiber, 1984, Veit et al., 1997, Croxall et al., 2002). The ENSO may elicit both beneficial and detrimental seasonal or longer-term impacts in temperate regions (Barbraud et al., 2011, Sandvik et al., 2008), but to date only detrimental impacts have been documented in tropical ecosystems (Congdon et al., 2007).

1.1.2. Seasonal shifts in SST

Seasonal shifts in SST, either associated with phenomena such as the ENSO or driven by other interannual variations in oceanographic characteristics, have been correlated with changes in food availability, provisioning, breeding success, timing of breeding, adult mass and survival for seabirds (Weimerskirch et al., 2001, Pinaud and Weimerskirch, 2002, Durant et al., 2003, Peck et al., 2004, Ramos et al., 2002). In general, these large-scale upper trophic level impacts of SST variability on seabird demography have been attributed to interrelated seasonal-scale decreases in productivity or prey species abundance at lower trophic levels (Stenseth and Mysterud, 2002), where unfavourable SSTs disrupt or block nutrient rich upwelling zones, thereby disrupting phytoplankton distribution and abundance (McGowan et al., 1998, Kaplan et al., 2003, Wilson et al., 2003).

1.1.3. Thermocline depth

Thermocline depth changes are integral oceanographic processes which regulate the appearance of cool, nutrient-rich oceanic waters at the surface (Steinberg, 2007). Altered thermocline depths are also well documented precursors to changes in the ENSO (Harrison and Vecchi, 2001, McPhaden and Yu, 1999). Thermocline depth and gradient characteristics strongly influence piscivorous seabird foraging behaviour in the eastern tropical Pacific through their association with pelagic underwater predators such as tuna and mackerel (Spear et al., 2001, Ballance et al., 2006). The density and distribution of foraging temperate seabirds is also influenced by thermocline depth and associated upwelling characteristics (Oedekoven et al., 2001).

1.2. Small-scale oceanographic processes

Most evidence of potential climate change impacts on seabirds comes from the large-scale correlations between reproductive biology and ENSO-type activity. As well as larger-scale longer-term impacts, there is also recent evidence that SST variation at smaller within-season and day-to-day time scales significantly impacts seabird foraging success, growth patterns and reproductive output (Gjerdrum et al., 2003, Peck et al., 2004). Significant decreases in prey availability have been seen to track changes in SST over short time scales while not remaining depressed over entire breeding seasons. Trophic mechanisms identified to explain these short-term impacts include (Peck et al., 2004): SST fluctuations impact the short-term vertical and/or horizontal distribution of prey via physiological (Castillo et al., 1996, Yang et al., 1995), ecological (Kaplan et al., 2003, McIlwain, 2003) or behavioural (Spear et al., 2001) factors; and SST directly influences the abundance of subsurface predators which drive prey to the surface making them available to seabirds (Le Corre, 2001).

1.3. Other threatening processes

In addition to climatic threats posed to seabird productivity and longevity, seabirds are exposed to a number of physical disturbances and anthropogenic threats, including major weather events, overexploitation of fish stocks by industrial fisheries; and human disturbance at seabird colonies (Schreiber and Burger, 2002). Intense storms, strong winds and cyclones and hurricanes in tropical regions can impact on foraging and nesting habitats, sometimes causing catastrophic destruction to breeding colonies and high mortality (Ropert-Coudert et al., 2009, King et al., 1992). The negative effects from climate variation or localised weather events may be exacerbated if seabirds are subject to anthropogenic disturbance (Votier et al., 2005, Hulsman et al., 1996). For example, tourism-associated repeated human intrusion into or near breeding colonies (Anderson and Keith, 1980) or competition with fisheries and the associated changes to ecosystems dynamics (Blaber et al., 1995, Lewison et al., 2004) may drive seabird foraging and breeding characteristics.

1.4. Physical description of GBR & study areas

The Great Barrier Reef (GBR) borders the northeast coast of Australia, spanning 14^{o} of latitude (10^{o} S to 24^{o} S) and is located along 2100 km of the coastline of Queensland. The GBR supports an important and varied seabird community, comprising 20 species and approximately 1.7 million individuals (Hulsman et al., 1996). Most major seabird colonies are located in the far northern, northern or far southern regions of the GBR.

The GBR's ecology is heavily influenced by the East Australia Current, a complex and energetic western boundary system that is weaker than other western boundary currents and is dominated by a series of mesoscale eddies that produce highly variable patterns of current strength and direction (Ridgway and Hill, 2009). Intrusions from a variety of processes cause cooler, deeper water to encroach on the outer GBR shelf, mixing waters around the coral reefs (Steinberg, 2007). The GBR shelf is considered to be well mixed during most of the year, except during summer warming events (Steinberg, 2007). The continental shelf in the far northern and northern GBR is relatively narrow (50-70 km) for most of its length. In the central region, the shelf gradually widens and is widest at latitude 21^{o} S at around 250 km. There is a sudden narrowing of the continental shelf south of the Swain Reefs (21^{o} 40'S) to approximately 60 km width (Steinberg, 2007).

The ENSO is a major contributor to Australia's climate, and is observed as a relatively weak signal in the southward-flowing East Australian Current (Lough, 2009), which strengthens during El Niño events (Steinberg, 2007). SSTs in the waters surrounding Australia have significantly increased since the early 20th century (+0.7°C) and six of the 10 warmest years have occurred in the most recent 10 years (based on data since 1910)(Lough, 2009).

This thesis examines the breeding, foraging and population dynamics of multiple species of seabirds breeding on the GBR breeding at two similar locations, one on the northern GBR and one on the southern GBR. Michaelmas Cay, on the northern GBR (13-16 ºS & 146-149 ºE)(Fig. 7, Chapter 4), is a sand covered coral cay 1.8 ha in size situated 40 km from the Queensland coast, and is rated as the second most significant bird nesting site on the GBR (GBRMPA, 2002). The vegetated area on Michaelmas Cay supports a community of a few, low growing (0.3 – 0.5 m) plant species, including Beach spinifex (*Spinifex sericeus*), Stalky grass (*Lepturus repens*), Goats foot (*Ipomoea pes-caprae*), Bulls head vine (*Tribulus cistoides*), Sea purslane (*Sesuvium portulacastrum*) and Tar vine (*Boerhavia diffusa*)(DERM, 2011). The vegetation on Michaelmas Cay is more characteristic of the cays found on the outer barrier reef. Occasionally seeds from trees such as *Barringtonia* sp. and mangroves wash ashore and germinate but die due to a lack of suitable stable substrate.

The size and vegetative composition of Michaelmas Cay are influenced by winds and currents and the available breeding habitat can be heavily impacted by major storms (Chapter 6). Ten seabird species have been recorded as breeding on Michaelmas Cay, but breeding on the cay is dominated by three species: the Sooty tern (*Onychoprion fuscata*), the Common noddy (*Anous stolidus*) and the Crested tern (*Thalasseus bergii*) (King, 1985, King et al., 1992). A description of the life history characteristics of these species can be found in Chapter 2.

On the southern GBR, Heron Island (23° 26’ S, 151° 51’ E)(Fig. 7, Chapter 4) is part of the Capricorn-Bunker group of islands, which contain nationally and internationally significant seabird breeding populations (Stokes et al., 1997). Heron Island is a much larger coral cay (19 ha) compared to Michaelmas Cay on the northern GBR, is situated 80 km off the Queensland coast and has a broader vegetative composition including mature *Pisonia grandis* trees, Octopus bush (*Argusia argentea*), *Pandanus tectorius* trees, She oak (*Casuarina equisetifolia*), Native mulberry (*Pipturus argenteus*), and Native elm (*Celtis paniculata*). Wedge-tailed shearwaters (*Ardenna pacifica*) and Black noddies (*Anous minutus*) dominate the seabird fauna of the island (Dyer et al., 2005). Black noddies have similar life history characteristics to that of the Sooty tern and the Common noddy (Chapter 2).

Michaelmas Cay and Heron Island both have large seabird breeding populations with similar life history characteristics (Chapter 2), are exposed to cyclonic storms (Ogden, 1993a, King et al., 1992), and are subject to heavy tourist visitation and other anthropogenic threats (Ogden, 1993b, Edwards, 1997). The geographical and ecological similarities between these two locations foster productive reef-wide comparisons on the relative influences of ENSO-related oceanographic processes and SST variation on seabird reproductive biology and population dynamics. The species compositions and locations also allow for data analyses on multiple sympatric species using different foraging guilds.

CHAPTER 2

2.1. Study locations and experimental design

Details regarding the experimental design for the behavioural component of this project (foraging behaviour, chick begging behaviour) are found in the relevant chapters. In all cases, a generalised template for sample/data collection was used, with minor variation depending on permitted access to study species and/or flightiness of the adults. Similarly, the acquisition and application of climatic and oceanographic data, as well as the statistical analyses, are detailed in the appropriate chapters.

In order to examine the potential impacts of climate variation on seabirds of the Great Barrier Reef (GBR), multiple species breeding at two distant locations were chosen for assessments during each species' breeding season. As described in Chapter 1, Michaelmas Cay, on the northern GBR (Fig. 7, Chapter 4) is home to a large breeding colony dominated primarily by Sooty terns (*Onychoprion fuscata*), Common noddies (*Anous stolidus*) and Crested terns (*Thalasseus bergii*). Heron Island, on the southern GBR (Fig. 7, Chapter 4) contains a large breeding colony of Black noddies (*A. minutus*).

2.2. Study species

2.2.2. Sooty tern (Onychoprion fuscata) and Common noddy (Anous stolidus)

The Sooty tern and the Common noddy are pelagic species from the tern family (Sternidae), breeding in tropical and subtropical regions of Indian, Pacific and Atlantic Oceans. Around

Australia, these species are common from the GBR near Cairns, around northern Australia to the Abrolhos Islands (Higgins and Davies, 1996). Stragglers are reported further south. Sooty terns and Common noddies mix indiscriminately with each other and Black noddies when breeding, and show marked fidelity to their natal colony.

Sooty terns, in particular, are well known for their ability to stay airborne for years at a time between fledging and first breeding, never coming to land during non-breeding season and essentially never resting on water. Breeding adults return to vicinity of colony $\geq$ 2 months prior to land and laying eggs. Young Sooty terns and Common noddies remain at sea 2-5 years before returning to breed. Adult Sooty terns rear a single chick over a 40-60 day nestling period, and adult Common noddies rear one or two (less common) chicks over a 50 day nestling period. Adults feed young regurgitated food 1-2 times daily. Adults of these species forage up to 250 km from breeding sites, mostly feeding by dipping or shallow-plunging into the surface of the water but rarely submerging. These species are thought to be completely reliant on large migratory tuna and mackerel to obtain prey.

2.2.3. Black noddy (Anous minutus)

The Black noddy is an offshore foraging tropical seabird which resembles the closely related Common noddy. The Black noddy has a worldwide distribution in tropical and subtropical seas, with colonies widespread in the Pacific Ocean and more scattered across the Caribbean, central Atlantic and in the northeast Indian Ocean (Gauger, 1999). Most populations are sedentary and resident throughout the year on nesting islands. This species has been recorded breeding at 2 years of age on Tern Island, GBR although first breeding at 3 years of age may be more common. Adult Black noddies rear a single chick over a 45 day nestling period, feeding chicks regurgitated meals 3-4 times each day. Adults may forage up to 80 km from breeding sites but are common found foraging in nearby lagoons. Prey are obtained from the ocean surface, usually in association with subsurface predators.

2.2.4. Crested tern (Thalasseus bergii)

The Crested tern is an inshore foraging seabird distributed throughout the IndoPacific and on all coasts of Australia (Higgins and Davies, 1996). This is an adaptable species capable of feeding on a large range of prey (McLeay et al., 2009) and switching breeding islands within and between seasons. Crested tern colonies are smaller than the other species investigated. Adults forage in and around reefs adjacent to colonies (up to 10 km from breeding islands) on reef fish and shoaling pelagic fish, and carry whole fish in their bills to feed young. A single chick is reared over a 38-40 day nestling period and fed 6-8 meals per day. Prey is captured via plunge diving up to a depth of 1 m, or by dipping from the surface. Crested terns are known to actively follow fishing trawlers to forage on bycatch.

CHAPTER 3

Publication arisen:
Devney, C.A., Short, M. and Congdon, B.C. 2009. Sensitivity of tropical seabirds to El Niño precursors. *Ecology* 90(5), 1175-1183.

3.0. INTRODUCTION

The El Niño Southern Oscillation (ENSO) is a major driver of both global climate and associated variation in sea-surface temperature (SST) (Fiedler, 2002). Intense El Niño events have been linked to severe negative impacts on both temperate and tropical seabird populations (Schreiber and Schreiber, 1984, Bertram et al., 2005). In general these impacts are attributed to seasonal-scale crashes in productivity at lower tropic levels linked to deepening of the nutricline (remotely forced by Kelvin waves (Barber and Chavez, 1983)) and an associated lack of nutrient upwelling. Such seasonal-scale decreases in nutrient availability are clearly evident in large-scale temperate upwelling systems (Cane, 1983, Norton and McLain, 1994) and in cold tropical regions (Cronin and Kessler, 2002), but evidence of similar scale processes in warm tropical systems is limited. Similarly, the magnitude and even direction of ecological responses to ENSO-related variation in tropical marine environments appears to differ by region (Roemmich and McGowan 1995; Lavaniegos, Gómez-Gutierrez et al. 1998; Dandonneau, Deschamps et al. 2004), or species (Edwards and Richardson, 2004), with these differences being attributable to complex regional upwelling dynamics and/or other physical processes (Messié and Radenac, 2006). In fact, variance in ecological responses to this type of phenomenon is not exclusive to the ENSO. Impacts of the North Atlantic Oscillation on seabird breeding demographics are also strongly geographically patterned (Sandvik et al., 2008). In addition, recent data further suggest that detrimental impacts may also involve fine-scale (day-to-day) trophic stresses not linked to seasonal-scale declines in productivity (Peck et al., 2004, Chapter 4). Clearly, a more regionally-specific and comprehensive mechanistic understanding of how El Niño related phenomena impact biological processes in tropical marine systems is needed in order to clarify current inconsistencies in the available data. Such clarification is also essential if predicted climate change impacts in these systems are to be successfully managed into the future (Congdon et al., 2007).

Oceanographic data suggest that there are significant precursors to El Niño events that can vary in intensity and direction both spatially and temporally (Garcés-Vargas et al. 2005, Terray and Dominiak 2005, Ruiz et al. 2006). The most well documented of these precursors is changes in the depth of the 20 $^{\circ}$C Pacific Ocean thermocline (Harrison and Vecchi, 2001, McPhaden and Yu, 1999). Changes in thermocline characteristics are known to effect biological productivity and hence prey availability directly (Sarmiento et al., 2004), but they are also known to significantly influence the distribution and abundance of marine fish (Kitagawa et al., 2004, Brill et al., 1999, Schaefer et al., 2007) and zooplankton (Fernández-Álamo and Färber-Lorda, 2006) via processes that do not necessarily involve productivity changes. For example, during foraging, fish-eating seabirds in the eastern tropical Pacific are sensitive to changes in both the depth and the gradient of the thermocline via their association with pelagic underwater predators (Spear et al., 2001, Ballance et al., 2006). However, the influence of thermocline depth on reproductive success in these same taxa has not been examined. Similarly, in the western tropical Pacific, where the thermocline is considerably deeper (Fiedler and Talley, 2006), nothing is known of its influence on seabird reproductive biology and the mechanisms by which these effects are manifest.

I investigated 18 years of data on the population dynamics of three tropical seabirds breeding in the western Pacific to determine how breeding participation related to ENSO intensity, associated SST changes and/or precursive depth changes in the 20 °C Pacific Ocean thermocline. I was specifically interested in whether the effects of thermocline depth changes could be consistently identified and if so, whether they could be related to either productivity decreases and/or to changes in the accessibility of prey independent of background changes in productivity.

3.1. METHODS

3.1.1. Location and data collection

Michaelmas Cay (16º 36’ S, 145º 59’ E), in the far-northern Great Barrier Reef, Australia, is an important tropical seabird nesting site that supports populations of some of the most abundant species in tropical regions (Sibley and Monroe, 1990). Approximately monthly counts of all breeding seabirds present on Michaelmas Cay were made between 1984 and 2001. The breeding population present each month was estimated using the number of nest sites observed (King et al., 1992, Chapter 6). Based on these data I calculated an index of breeding participation for each year of the study period for three species, the Sooty tern (*Onychprion fuscata*), Common noddy (*Anous stolidus*), and Crested tern (*Thalasseus bergii*). The pelagic foraging Sooty tern and Common noddy are the most common species breeding at Michaelmas Cay. These two species are also among the most abundant seabird taxa in tropical regions (Sibley and Monroe, 1990). The inshore foraging Crested tern is the third most abundant seabird breeding on the cay and is also the most common tern species in Australia (Serventy et al., 1971). Crested terns breed all along the Australian coastline in tropical, subtropical and temperate habitats, as well as throughout the tropical Indo and western Pacific Oceans (Blakers et al., 1984). The importance of Michaelmas Cay as a breeding site for these three common and widespread species identifies this location as a good model system for examining the potential influence of these same processes elsewhere.

3.1.2. Environmental descriptors

To explore how breeding participation for each species was influenced by ENSO associated environmental variation and/or potential ENSO precursors, the mean number of breeding pairs in each year was regressed against the Multivariate ENSO Index (MEI) (Wolter and Timlin, 1993, Wolter and Timlin, 1998), SST and the depth of the 20 °C thermocline at a range of different spatial and temporal scales (Fig. 1).

Bimonthly MEI values (in 0.001 of standard deviations) were downloaded from the National Oceanic and Atmospheric Administration (http://www.cdc.noaa.gov/people/klaus.wolter/MEI/table.html; downloaded 17 Feb 2006). Monthly satellite SST data were available for the entire study period from the Reynolds/National Centers for Environmental Prediction Satellite (http://poet.jpl.nasa.gov) for an area between 14 and 18 °S latitude and 144 and 148 °E longitude. Data for the depth of the 20 °C isotherm, which represents the thermocline, or depth where the temperature gradient is a maximum (Pickard and Emergy, 1990), were provided by the Australian Bureau of Meteorology Research Centre. Data were extracted monthly for the region between 0 to 30 °S latitude and 140 °E to 140 °W longitude. The data has a 1x2 latitude-longitude grid resolution and is created using an optimal interpolation technique that combines hydrographic measurements with moored temperature measurements from the tropical ocean and atmosphere observation program (Smith, 1995). Average annual thermocline depths were calculated for two subregions in the western tropical Pacific: the West Pacific Warm Pool (0-3 ºS & 140-159 ºE) and the Coral Sea region near Michaelmas Cay (13-16 ºS & 146-149 ºE).

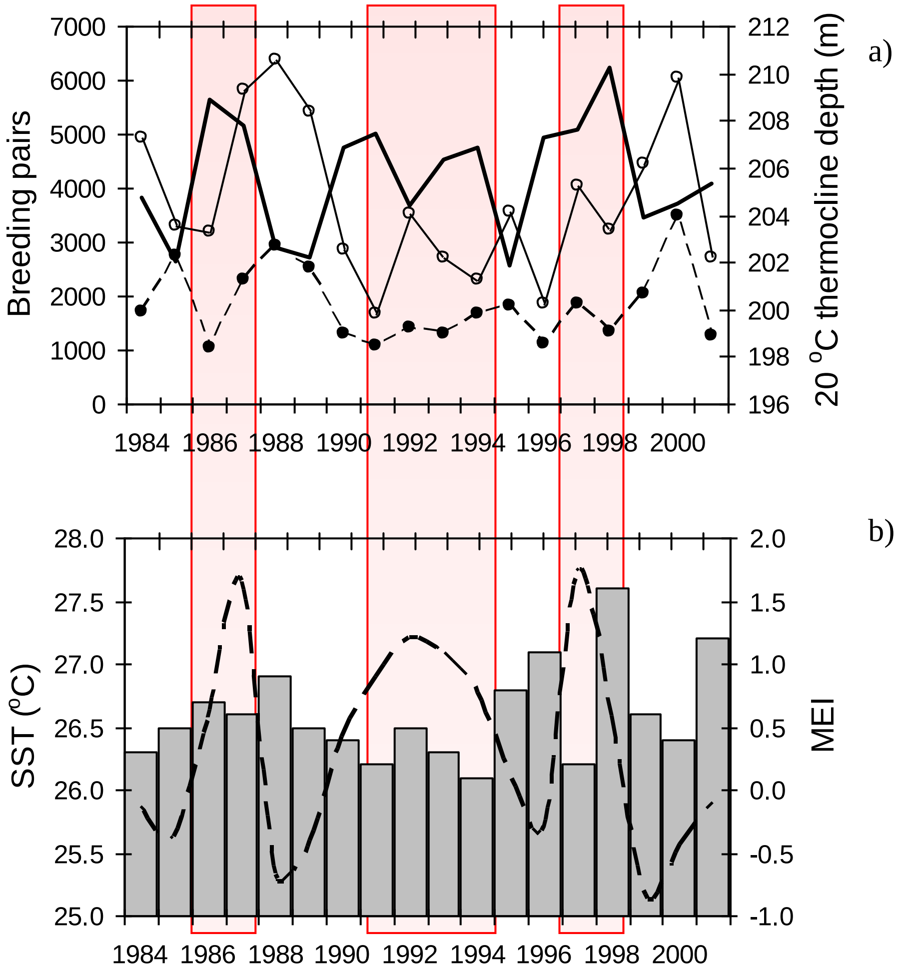


Figure 1. Top panel shows time series of mean annual number of breeding pairs of Sooty terns and Common noddies (full and dashed lines, respectively, left vertical axes) and the 20 °C thermocline depth averaged annually within 13-16 °S & 146-149 °E (bold line, right vertical axes, units are in metres). The bottom panel shows time series of SST averaged within 14-18 °S & 144-148 °E (shaded bars, left vertical axes, units are in °C) and MEI (dashed bold line, right vertical axes). The data are relative to the 1984-2001 time period, with El Niño events identified by red shaded bars.

3.1.3. Productivity

Both coastal upwelling, driven by localised tidal and wind forcing, and oceanic upwelling, occur in the Coral Sea region near Michaelmas Cay (Andrews and Gentien, 1982). The ENSO appears to drive interannual variation in both these upwelling dynamics (Wolanski and Pickard, 1985). Large-scale variations in primary productivity, due to changes in upwelling intensity, are observable as changes in the chlorophyll-a content of the surface waters

(Lorenzen, 1970, Sacau-Cuadrado et al., 2003). Therefore, to document changes in upwelling dynamics and examine how these changes may be linked to other oceanographic and climatic phenomena, *in-situ* chlorophyll-a data were obtained from a long-term chlorophyll monitoring program (1993 – current). This program has sampling stations located in the 'Far Northern (13 °S)' and 'Cairns (16 °S)' transects of the Great Barrier Reef. Data for the period 1993 – 2001 were provided by the Australian Institute of Marine Science (http://adc.aims.gov.au:9555/chloro/do/gotoStart.do; downloaded on 5 July 2007) and were used to calculate average annual indices of surface chlorophyll concentration for each year during the sample period.

3.2. RESULTS

3.2.1. Precursor impacts of the ENSO

Sooty tern and Common noddy breeding participation in each year (*n*) was significantly negatively correlated with the MEI for the following year ($n + 1$) (Table 1) (Fig. 2), but not for the same year (*n*) or for the year prior ($n – 1$). A relationship between Crested tern breeding participation and MEI was not present at any temporal scale (Table 1). This implies significant negative associations between as yet unidentified ENSO precursors and average breeding population sizes of both pelagic species, but not the inshore foraging species.

Table 1. Results of regressions testing the influence of oceanic factors on the mean number of breeding pairs of the three main breeding species of Michaelmas Cay. The annual average Multivariate El Niño Index (MEI) and sea-surface temperature (SST) were compiled at three distinct temporal (real-time, precursor and lagged) scales and compared with the number of breeding pairs of Sooty terns (*Onychoprion fuscata*), Common noddies (*Anous stolidus*) and Crested terns (*Thalasseus bergii*). Associations are presented between the number of breeding pairs of each species in each year (*n*) and MEI/SST each year, in the year prior (*n* - 1) and in the following year (*n* + 1).

		Sooty tern			Common noddy			Crested tern		
	Year	$F_{1,16}$	*r*	*P*	$F_{1,16}$	*r*	*P*	$F_{1,16}$	*r*	*P*
Annual average MEI	*n*	1.830	0.320	0.195	3.390	0.418	0.084	2.034	0.336	0.173
	n - 1	0.006	0.019	0.941	0.229	0.119	0.639	0.486	0.172	0.496
	n + 1	**10.647**	**0.632**	**0.005**	**4.930**	**0.485**	**0.041**	0.026	0.040	0.875
Annual average SST	*n*	0.010	0.025	0.923	0.369	0.150	0.552	3.733	0.435	0.071
	n - 1	2.033	0.345	0.174	0.779	0.222	0.391	0.948	0.244	0.346
	n + 1	1.358	0.288	0.262	1.840	0.331	0.195	0.452	0.171	0.511

Note: Significant relationships are in boldface.

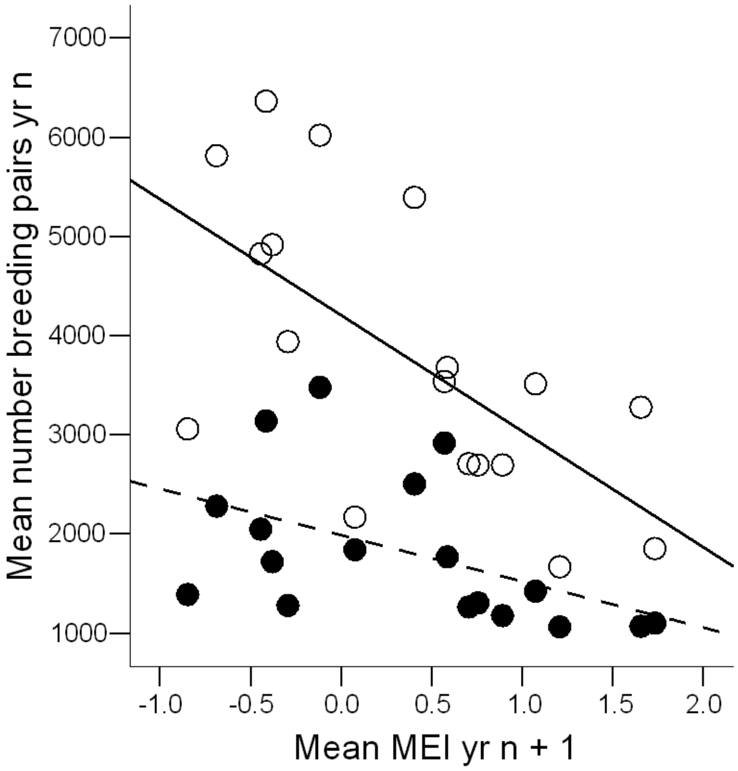


Figure 2. Annual averages of Multivariate El Niño Index (MEI) and number of breeding pairs of pelagic terns. The average annual number of breeding pairs counted on Michaelmas Cay 1984-2001 for the Sooty tern (○) and Common noddy (●) in each year (*n*) and mean annual MEI in the following year (*n + 1*).

3.2.2. Thermocline & SST changes

During the build up to an El Niño event, warm surface waters along the equatorial region are redistributed so that in general the 20 °C thermocline deepens in the eastern tropical Pacific while it shoals in the west (Meinen and McPhaden, 2000). However, my results indicate that in the western Pacific (140 – 160 °E) the direction and timing of ENSO-related thermocline change varied with latitude. My analyses show that during high positive periods of the MEI (El Niño-like conditions) significant shoaling of the thermocline occurred at the equator (0-3°S) ($r = 0.815$, $F_{1,16} = 31.699$, $P < 0.001$) as expected for the western Pacific (Meinen and McPhaden, 2000), but that in the Coral Sea region adjacent to Michaelmas Cay (13-16 °S) more intense El Niño-like conditions produced small-scale deepening of the thermocline ($r = 0.605$, $F_{1,16} = 9.249$, $P = 0.008$) (Fig. 3). These thermocline depth changes in the region around Michaelmas Cay did not occur exactly 12 months ahead of the contrasting changes in thermocline depth at the equator, but nevertheless occurred well in advance (10 months) ($r = 0.546$, $F_{1,19} = 8.086$, $P = 0.010$) (Fig. 4), making them clear ENSO procurers.

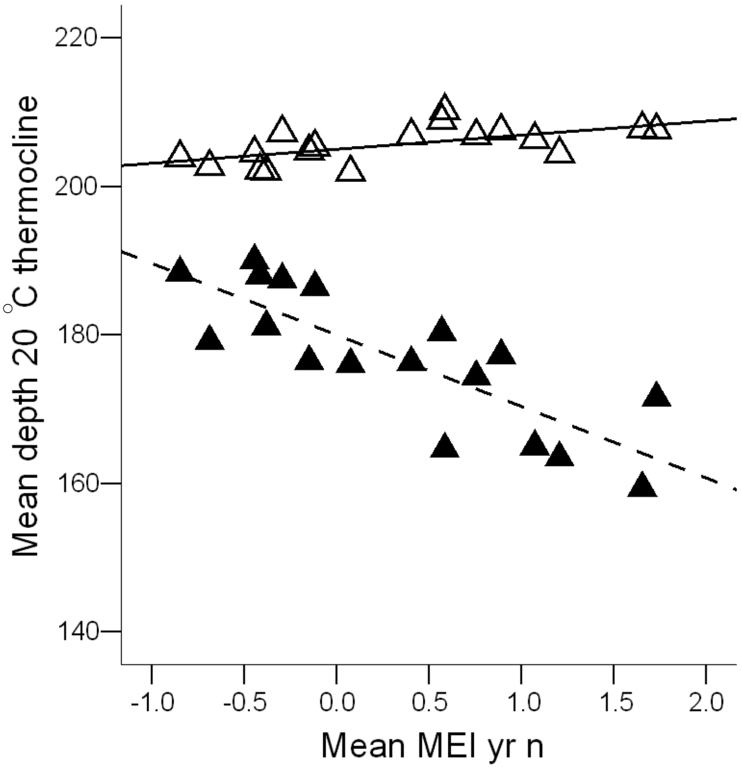


Figure 3. Depth of the 20 °C thermocline (m) relative to MEI at different latitudes. Differences in thermocline and MEI correlations between equatorial (0-3 °S & 140-160 °E, black symbols) and higher latitude tropical regions (13-16 °S & 146-149 °E, white symbols) of the western Pacific Ocean.

Localised changes in thermocline depth for the Coral Sea region correlate directly with changes in Sooty tern and Common noddy breeding participation at Michaelmas Cay. My analyses confirmed that breeding populations of both species decreased as the average thermocline depth in the vicinity of Michaelmas Cay (13-16 °S) deepened (Sooty tern: r = 0.484, $F_{1,16}$ = 4.902, P = 0.042; Common noddy: r =0.537, $F_{1,16}$ = 6.470, P = 0.022) (Fig. 5a). In contrast, there was no significant relationship between thermocline depth and the number of breeding pairs of Crested terns (r = 0.005, $F_{1,16}$ = 0.000, P = 0.983) at Michaelmas Cay.

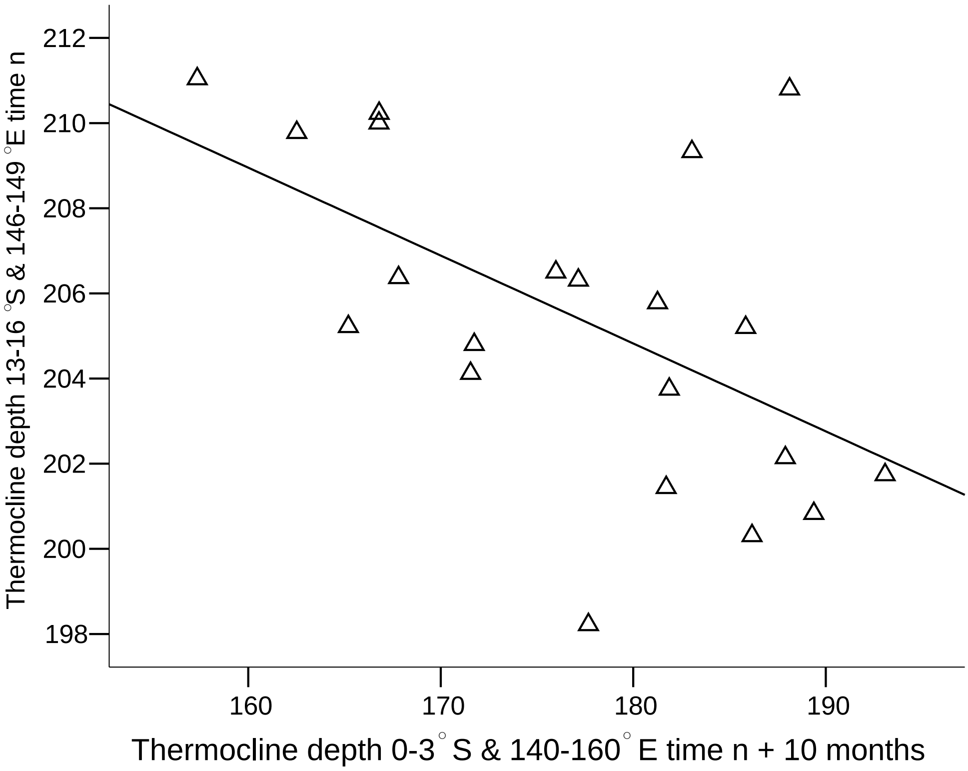
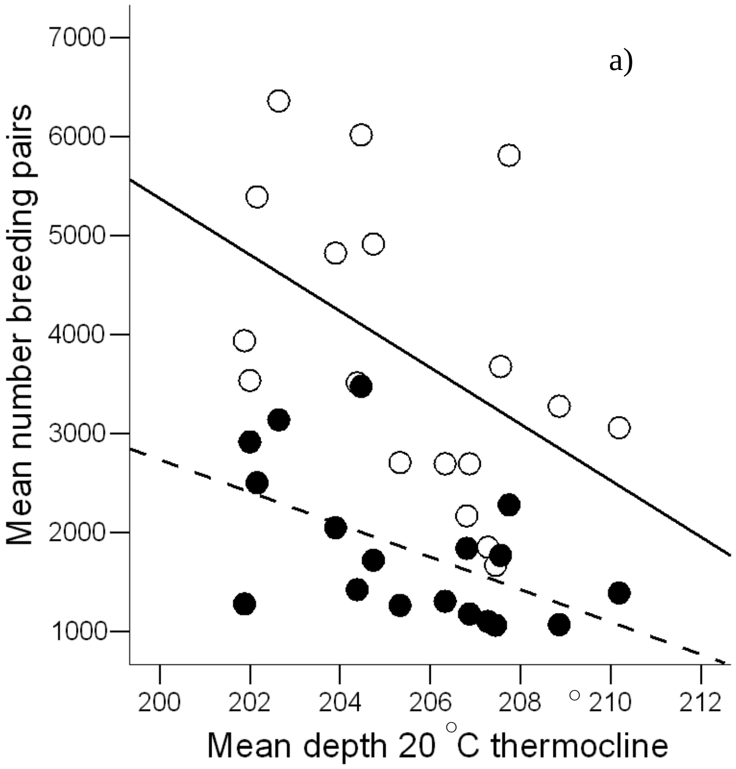


Figure 4. Precursive changes in 10-month average depths of the 20 °C thermocline (m) that occur at higher latitude tropical regions (13-16 ºS & 146-149 ºE) in advance of those at equatorial regions (0-3 ºS & 140-160 ºE).

During the development phase of El Niño, anomalous SSTs are first seen in the central equatorial Pacific, then propagate eastward to reach the South American coast several months later (Wang, 1995). However, changes in annual breeding participation of all three species at Michaelmas Cay in the western tropical Pacific were not related to localised changes in surface water temperature at any temporal scale (Table 1).



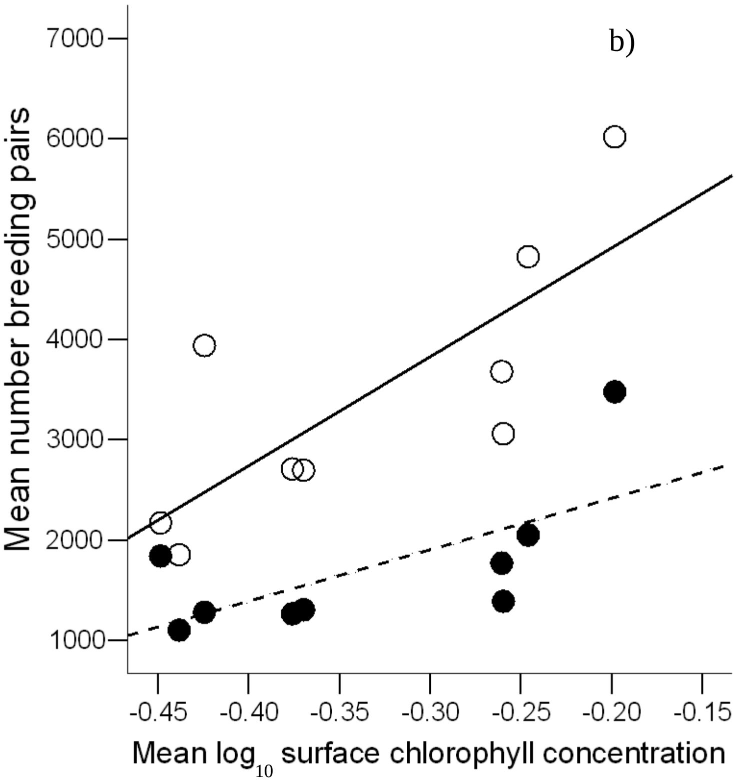


Figure 5. Number of breeding pairs of pelagic terns at Michaelmas Cay relative to mean annual a) depth of the 20 °C thermocline (m) and b) *in-situ* measurements of mean annual $\log_{10}$ surface chlorophyll-a concentration (mg/m^3) for Sooty terns (○) and Common noddies (●).

3.2.3. Productivity changes

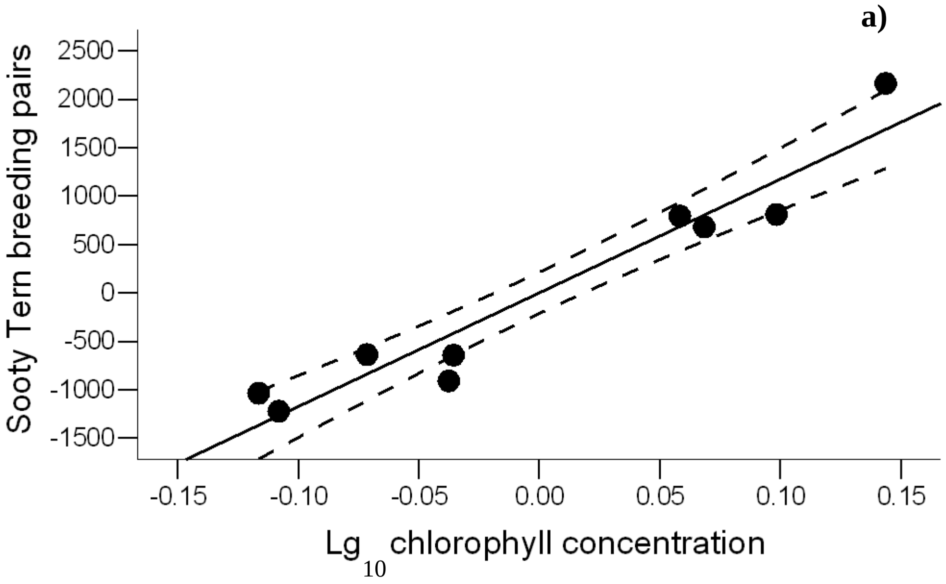
The surface chlorophyll concentration in the region 13-16 °S was significantly positively related to Sooty tern and Common noddy breeding participation at Michaelmas Cay during 1993 – 2001 (r = 0.773, $F_{1,7} = 10.400$, $P = 0.015$; r = 0.667, $F_{1,7} = 5.612$, $P = 0.050$, for Sooty terns & Common noddies respectively) (Fig. 5b) over this same period. Crested tern presence at the cay was not related to annual changes in surface chlorophyll concentration in the region (r = 0.342, $F_{1,7} = 0.925$, $P = 0.368$).

Combined, 20 °C thermocline depth and surface chlorophyll concentrations in the Coral Sea explained >95% of the observation variation in breeding participation of Sooty terns at Michaelmas Cay each year (Table 2) (Fig. 6a, b). Similar but less robust relationships were also found for Common noddy breeding participation (Table 2). Importantly, there was no direct relationship between chlorophyll concentration and thermocline depth (r = 0.057, $F_{1,7} = 0.023$, $P = 0.884$) implying that each of these factors influences breeding participation independently.

Table 2. Step-wise multiple regression analysis of breeding participation in Sooty terns and Common noddies versus the two environmental predictor variables. Variable names are Chlorophyll ($\log_{10}$ surface chlorophyll-a concentration in mg/m^3) and Thermocline (thermocline depth at 13-16 °S & 146-149 °E). r_p, refers to the partial correlation of each variable with the number of breeding pairs.

Species	Step	Variable	Cumulative *r*	Increase in *r*	r_p	Model $F_{2,6}$	*P*
Sooty tern	1	Chlorophyll	**0.773**	-	0.773	**10.400**	**0.015**
	2	Chlorophyll Thermocline	**0.972**	0.199	0.962 -0.928	**50.767**	**<0.001**
Common noddy	1	Chlorophyll Thermocline	0.737	-	0.701 -0.316	3.571	0.095
	2	Chlorophyll	**0.667**	-0.070	0.667	**5.612**	**0.050**

Note: Significant relationships are in boldface.



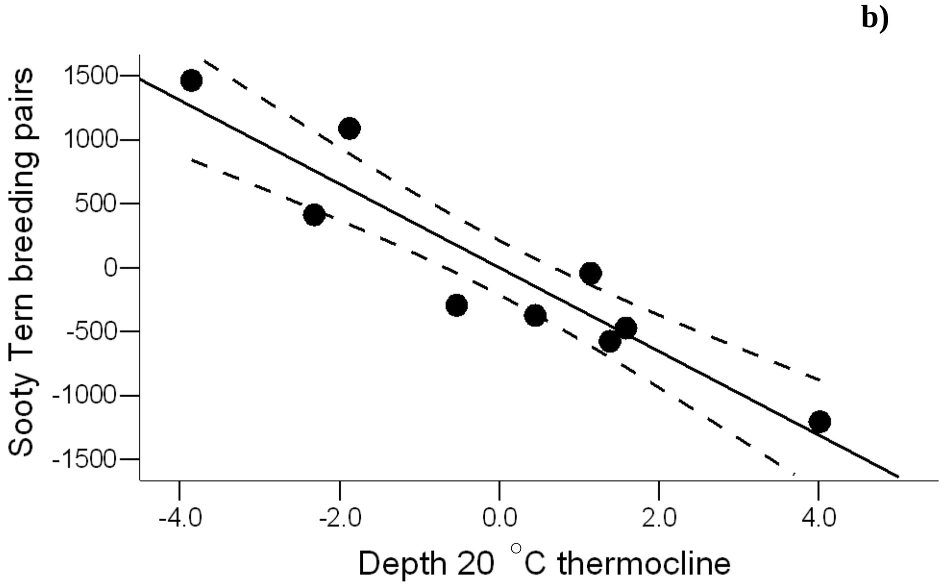


Figure 6. Partial regression plots showing residual a) $\log_{10}$ surface chlorophyll-a concentration (mg/m^3) and b) depth of the 20 °C thermocline (m) (effects of thermocline depth and chlorophyll concentration, respectively, controlled) plotted against the mean annual number of breeding pairs of Sooty terns at Michaelmas Cay.

3.3. DISCUSSION

I observed significant negative associations between two potential ENSO precursors (thermocline depth change, chlorophyll concentration) and average breeding participation of both pelagic tern species at Michaelmas Cay. Such findings imply that in the western Coral Sea region at least, pelagic species are sensitive to both these ENSO precursors up to a year in advance of ENSO indices registering a formal event.

Although unusual, observations of El Niño precursor impacts are not completely novel. Similar relationships have been documented for a southern temperate breeding shearwater species (*Ardenna griseus*) in the south-west Pacific Ocean (Lyver et al., 1999) and for multiple species breeding along the southern African coast (La Cock, 1986). Trophic mechanisms responsible for both these earlier described relationships are unknown. Untested general hypotheses previously proposed for each of these observations both implicate SST anomalies as the process responsible. Respectively, these hypotheses are (i) that SST increases in the north-west Pacific significantly alter prey abundance/availability during shearwater migration which in turn influences breeding participation and (ii) that a decline in upwelling along the African coast associated with lessening of the trade winds and a pooling of warm surface waters reduces resource availability to seabirds in this region both during an El Niño year and in the year previous.

In contrast, my analyses demonstrate that this same phenomenon in the tropical south-western Pacific is not associated with precursive changes in SST. Instead it is linked to changes in productivity and/or thermocline depth that occur independent of SST variation. Both these phenomena appear to have significant and relatively immediate impacts on the food available to birds during the pre-breeding season. I had no evidence that variation in these two phenomena is related. Instead, our analyses suggest that both phenomena independently influence Sooty tern and Common noddy breeding participation.

That productivity changes significantly influence breeding participation is consistent with previous findings for temperate systems (Durant et al., 2003, Inchausti et al., 2003, Stenseth and Mysterud, 2002) where intense El Niño events disrupt upwelling (Wilson et al., 2003, McGowan et al., 1998), or induce changes in the timing of peak productivity of seabird prey species (Hedd et al., 2002, Bertram et al., 2009). In general, and primarily excluding the cold tropical regions of the Humboldt Current, upwelling in tropical systems occurs at a much smaller and more localised scale than in temperate systems (Kessler, 2006). However, despite these substantial differences in upwelling dynamics, our data suggest that pelagic seabird breeding participation in tropical systems, ocean productivity and ENSO related changes in oceanographic and atmospheric conditions are similarly linked.

The deepening of the thermocline I observed off eastern Australia was relatively minor compared to deepening that occurs in the eastern Pacific (Fiedler and Talley, 2006), or to the level of shoaling that occurs in the western Pacific at lower latitudes (Fig. 3). Despite this, thermocline depth significantly influenced breeding participation independent of productivity changes. This finding highlights a previously unidentified trophic impact of El Niño in tropical marine systems and suggests that changes in thermocline depth may directly influence prey species distribution, abundance or accessibility to seabirds over relatively short (within-season) time periods. However, separating the two hypotheses proposed in the introduction, whether thermocline depth changes could be related to either productivity decreases and/or to changes in the accessibility of prey independent of background changes in productivity, will be difficult without detailed long-term oceanographic data obtained by research vessels on marine productivity and abundance index of small pelagic prey fish along the water column.

The mechanisms by which thermocline depth changes may influence prey accessibility are currently unknown. However, two non-mutually exclusive possibilities can be identified. First, in most tropical marine habitats, pelagic foraging seabirds feed by gleaning prey items from or just below the surface of the water, while flying (Higgins and Davies, 1996), resulting in a strong reliance on subsurface predators such as tuna and/or marine mammals to drive prey to the surface (Au and Pitman, 1986, Ballance et al., 1997, Jaquemet et al., 2004). In the early stages of an El Niño event, thermocline shoaling in the western tropical Pacific (McPhaden and Yu, 1999) causes tuna foraging resources in this region to decline as the area of highest productivity moves into the central Pacific (Lehodey, 2001). The resulting redistribution of subsurface predators presumably impacts upon prey accessibility to foraging seabirds in the region. This is because pre-breeding or breeding seabirds are central placed foragers whose movements are restricted by the need to remain in the vicinity of breeding sites (Orians and Pearson, 1979).

Second, variation in thermocline dynamics in the western tropical Pacific may directly influence the concentration of forage fish, independent of changes in the distribution or abundance of marine subsurface predators. This idea is untested (Fiedler et al., 1998) but is supported by data from the eastern tropical and equatorial Pacific (reviewed by Ballance et al., 2006), where changes in thermocline structure can induce vertically migrating prey to aggregate and become more readily available to subsurface predators (Spear et al., 2001). However it must also be remembered that in the western Pacific the thermocline is on average much deeper (150 – 200m in the west versus 15 – 50m in the east) and so structural changes at depth would not necessarily be expected to have as great an impact on prey accessibility in this region.

Breeding participation of Crested terns did not respond to precursory changes in either the depth of the 20 °C thermocline, or to variation in ocean productivity. These results are consistent with previous comparative findings among inshore and pelagic foraging species (Surman et al., 2002). Both Sooty terns and Common noddies have been shown to fare poorly throughout most of their range during periods of intense El Niño conditions (Megysei and Griffin, 1996, Ramos et al., 2006, Schreiber and Schreiber, 1984, Duffy, 1990), while sympatric populations of Crested terns have remained unaffected (Schreiber and Schreiber, 1984).

Inshore foragers such as Crested terns feed singularly or in pairs over reefs, lagoons and beaches, near breeding islands (Surman and Wooller, 2003, Le Corre and Jaquemet, 2005) and plunge dive for prey so do not rely in the same way on the presence of subsurface predators (Higgins and Davies, 1996). Inshore species also have the highest diversity of prey amongst seabird taxa, a characteristic that may buffer them against decreases in the availability of any single prey type (Diamond, 1983). In contrast, pelagic foraging species generally feed on similar prey while in large multi-species flocks (Jaquemet et al., 2004) often at vast distances from breeding colonies (Ballance and Pitman, 1999, Schreiber et al., 2002, Surman and Wooller, 2003).

My findings add to increasing evidence that El Niño conditions not only interfere with major seasonal-scale trophic processes, but that in at least some tropical marine systems, they also add multiple additional fine-scale within-season trophic stresses (Peck et al., 2004, Chapter 4) that vary by species. The trophic relationships represented by these findings have a number of significant potential implications for pelagic foraging terns in the western tropical Pacific. Firstly, they suggest that the resources required by these species for non-breeding season survival, or during the build up to breeding, are influenced by the same precursory oceanographic events that have previously only been observed to impact temperate taxa. Unfortunately, at the moment very little is known about the non-breeding distribution and resource use of tropical breeding terns that can be used to further test this idea. Secondly, they suggest that the significant population fluctuations observed for both pelagic species breeding at Michaelmas Cay over 18 years (Queensland Parks & Wildlife Service unpublished data) may be directly linked to contemporary increases in the frequency and intensity of ENSO events (Timmerman et al., 1999, Zhang et al., 2008). This possibility is significant and requires further investigation, as it suggests that similar impacts may be occurring in declining pelagic seabird populations throughout both the Great Barrier Reef (Heatwole et al., 1996, Batianoff and Cornelius, 2005, Baker et al., 2004) and greater western Pacific region (Lyver et al., 1999, Benoit and Bretagnolle, 2002).

CHAPTER 4

Publication arisen:
Erwin, C.A. and Congdon, B.C. 2007. Day-to-day variation in sea-surface temperature reduces sooty tern *Sterna fuscata* foraging success on the Great Barrier Reef, Australia. *Marine Ecology Progress Series* 331, 255-266.

4.0. INTRODUCTION

Increasingly, human-induced climate change is being identified as a major threat to seabird conservation on a global scale. Historically, and primarily in temperate regions, seabird population fluctuations and declines have been frequently associated with long-term and seasonal-scale effects of climate variation (Veit et al., 1997, Lyver et al., 1999, Dunlop et al., 2002), with individual species responding differently to temperature anomalies depending upon their diet (Kitaysky and Goluvova, 2000, Inchausti et al., 2003) and dispersal characteristics (Frederiksen et al., 2004a).

Many species threatened by climate change are found mainly or exclusively in tropical oceans (Gaston, 2001). Despite this, a scarcity of long-term datasets linking climatic variation, foraging ecology and reproductive success in these regions means that predicting the potential impact of climate change on tropical seabirds remains difficult. From data that are available for tropical systems, extreme variations in reproductive performance have been related to both seasonal-scale (Smithers et al., 2003, Ramos et al., 2002) and longer-term (Schreiber and Schreiber, 1984, Ainley et al., 1988) processes associated with the El Niño Southern Oscillation (ENSO). Recently, in addition to these inter-annual effects, intra-annual effects have been documented in a tropical seabird by directly correlating daily changes in provisioning rates, meal sizes and chick growth with day-to-day fluctuations in sea-surface temperature (SST) (Peck et al., 2004). While it is clear from these data that SST impacts tropical Procellariiform (tube-nosed) seabirds, there is currently a critical lack of information on the trophic mechanisms responsible for these impacts and on whether this is a general phenomenon affecting a range of tropical seabird taxa.

Prey abundance and seabird reproductive biology have been significantly correlated many times (Anderson et al., 1982, Burger and Piatt, 1990). In particular, growth patterns in pelagic seabirds are frequently presumed to reflect characteristics of food supply (Ashmole and Ashmole, 1967), with short-term fluctuations in resource availability being directly linked to altered growth rates (Feare, 1976, Suryan et al., 2002). Foraging seabirds have also been shown to respond rapidly to SST changes in foraging areas (Hunt et al., 1992). Similarly, prey abundance and availability have also been linked to climate-associated variation in SST, at both inter- and intra-annual temporal scales (Spear et al., 2001, Stenseth et al., 2002, McIlwain, 2003). Combined, these findings suggest that short-term reproductive success in seabirds (i.e. as measured by day-to-day variations in foraging success and/or chick growth) directly reflect prey abundance and availability at similar temporal scales and, so, can be used as an immediate indicator of food availability.

The Sooty tern (*Onychoprion fuscata*) is the most abundant seabird species in tropical regions (Schreiber et al., 2002). As measured by food consumed, it is also the principal tropical species and fourth most important species world-wide (Brooke, 2004). Sooty terns are found breeding on many of Australia’s tropical vegetated coral cays, offshore islands and stacks (Higgins and Davies, 1996). Michaelmas Cay is a highly important tropical seabird nesting site in the Great Barrier Reef (GBR) World Heritage Marine Park, Australia (GBRMPA,

2002) and constitutes a major nesting site for Sooty terns (King, 1985). Significant declines in Sooty tern populations have been recorded throughout the GBR over a 15 to 24 yr period, with marked declines occurring between about 11 and 12°S (Blaber et al., 1998). From 1984 to 1994 Sooty tern numbers declined by 26% at Michaelmas Cay (GBRMPA, 1998), and, over a 24 yr period, by 84.4% at Raine Island, another important breeding site in the far northern sector of the GBR (Batianoff and Cornelius, 2005).

Elsewhere in Australia, the Sooty tern is listed as vulnerable on the schedules of the New South Wales Threatened Species Conservation Act based on its breeding ecology, distribution and poor recovery potential (Lunney et al., 2000). In the Seychelles this species has been declining since the beginning of the century (Ridley and Percy, 1958). Although long-term declines have been attributed primarily to human consumption of eggs (Feare, 1976), more recent declines have not, to my knowledge, been investigated in the context of changing climatic regimes. Similarly, at Christmas Island in the Central Pacific, the breeding colony for this species has been reduced to approximately 1.5% of its known original size (Schreiber et al., 2002), with declines being attributed to a combination of ENSO influences and human predation.

Sooty terns have been shown to fare poorly throughout most of their range during periods of El Niño conditions (Ashmole, 1963, Schreiber and Schreiber, 1984, Duffy, 1990). In temperate Australia, almost complete reproductive failure was documented for this species at Lord Howe Island during the 2002 ENSO event (L. O’Neill pers. comm.). The response of this species to ENSO events is generally unknown in the GBR region. However, ENSO events have caused reduced provisioning and reproductive failure in other breeding seabirds on the GBR (Smithers et al., 2003, Hoegh-Guldberg, 1999). As a result of the enhanced greenhouse effect, recent SSTs on the GBR are the warmest in a century of instrumental record (Lough, 2000), with further increases predicted (IPCC, 2001). Similarly, since the 1970s, El Niño events on the GBR have apparently increased in both frequency and intensity (Hughes, 2003).

These correlated long-term trends suggest that climatic factors, including increasing SSTs, may be, in part, responsible for the previously observed population decline of Sooty terns on the GBR. If so, negative impacts may be manifested at either the long-term seasonal, or within-season temporal scale. Consistent evidence that small-scale variation in SST affects food availability, provisioning and growth on a daily basis in the southern GBR (Peck et al., 2004) suggests that there may be an important and as yet undocumented link between Sooty tern population declines at Michaelmas Cay and short-term fluctuations in SST. More importantly, findings that populations of the most abundant seabird species in the tropics are declining could indicate major changes in the structure and functioning of tropical marine ecosystems that could be affecting other species. Therefore, the primary aim of this study was to investigate the relationship between Sooty tern foraging success and intra-seasonal SST variation within near-colony foraging areas of the GBR. Specifically, I tested whether day-to-day fluctuations in SST impacted chick provisioning, resulting in changes in meal size, feeding rate and/or meal composition.

4.1. METHODS

Michaelmas Cay is a small vegetated sand cay located on Michaelmas Reef (16° 36’ S, 145° 59’ E, Fig. 7) in the Cairns section of the GBR. The cay is ~1.8 ha in size, with a vegetated area of available nesting habitat of approximately 180 m^2. Data on foraging success and SST were collected at Michaelmas Cay over the same stage of 2 independent breeding cycles: 16 d from 1 September to 3 October 2004 and 19 d from 6 May to 22 June 2005 (data were not collected every day during these 2 periods). At Michaelmas Cay, Sooty terns (*Onychoprion fuscata*) breed at irregular intervals (King et al., 1992) and exhibit a mean breeding periodicity of ~10.35 ± 0.91 mo (QPWS unpubl. data). Data collection periods in this study represent approximately the first 36 and 52% of each breeding cycle, respectively (Le Corre, 2001, QPWS unpublished data). During 2004, all data were collected remotely, i.e. no handling or banding of the chicks or adults was undertaken. During the 2005 breeding season a subset of 42 same-aged chicks were banded for individual recognition at 3 d of age.

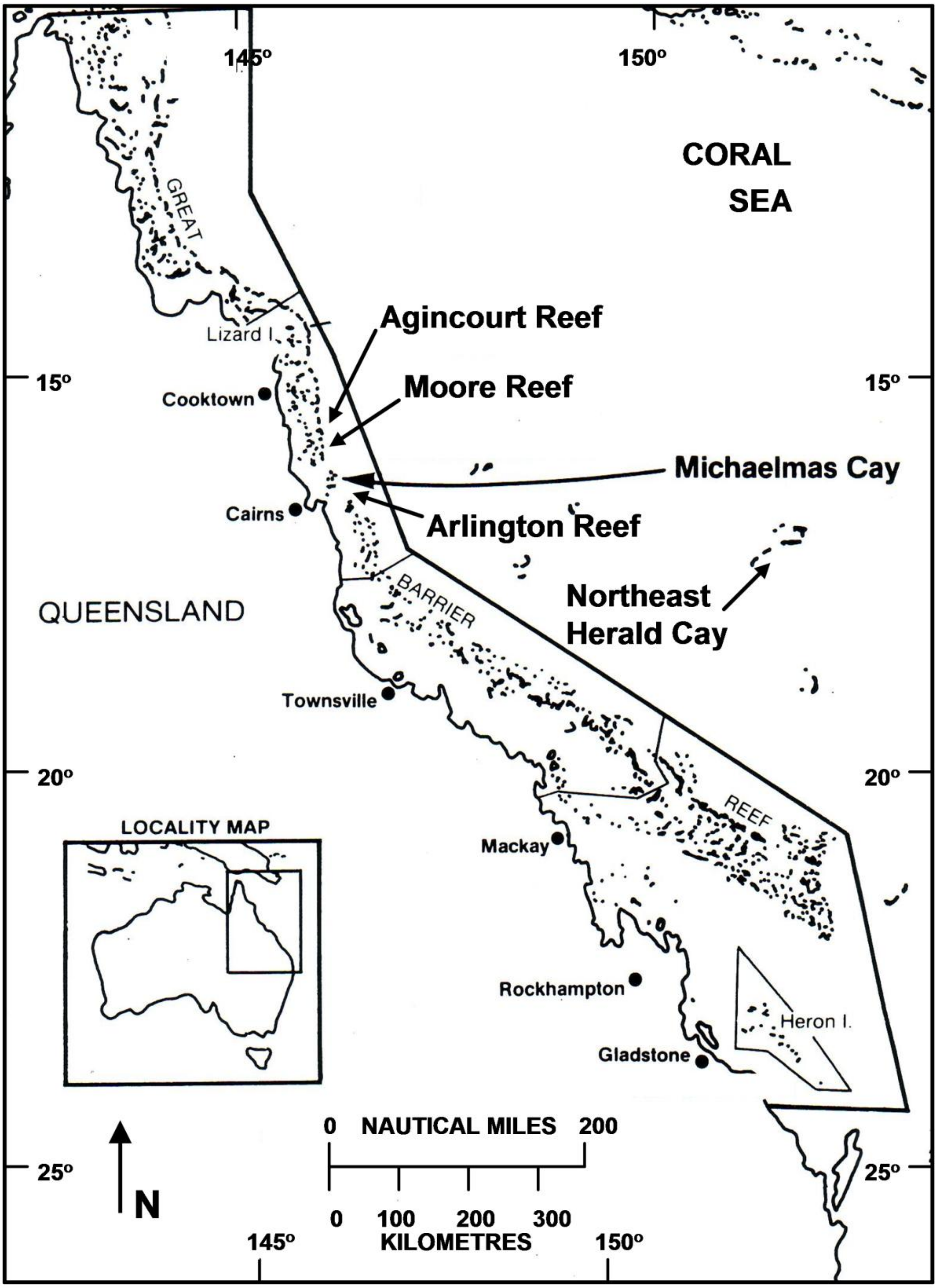


Figure 7. Map of Queensland, Australia, and the Cairns section of the Great Barrier Reef (GBR) showing locations of Michaelmas and Northeast Herald Cays and Agincourt, Arlington and Moore Reefs. Heron Island on the southern GBR is also shown (adapted from GBRMPA and QPWS, 1986).

Sooty tern chicks become mobile at an early age (<10 d), and crèche under dense shrubs where available. During each observation period, adult feeding rates in a spatially defined area of the colony containing a different but known number of either all unbanded (2004) (n = 73 to 157) or groups of both banded and unbanded (2005) (n = 20 to 65) chicks at nests (<10 d of age) and in crèches (>10 d of age) were monitored continuously using binoculars. Areas of the colony and the numbers of chicks to be monitored were redefined at the beginning of each observation period. Observations occurred for at least 1.4 h and up to 3.8 h associated with the same period each day (10:45 to 14:15 hrs). Multiple logistical constraints precluded data collection outside these hours; however, standardising observations over the same period each day serves as a relative measure of day-to-day foraging success.

4.1.1. Meal index (M_{INDEX}) and feeding frequency (F_{FREQ})

During 2004, when no chicks were banded or handled, provisioning was monitored using binoculars only. Food items delivered to chicks were quantified into a ‘meal index’ (M_{INDEX}) based on prey linear dimensions, using the size of the adult’s bill as a reference, a technique which has been used previously (Forbes and Sealy, 1990, Shealer, 1998). Food items that were approximately the same length as the adult’s bill were given a value of 1. Items that were approximately 1.5 times the length of the bill were assigned a value of 1.5, and so on. Items that were wider or taller than the bill were treated in the same manner. This technique assumes a linear relationship between prey size and volume (i.e. that prey have zero depth) and so may underestimate slightly the caloric value of larger prey items. Thus, M_{INDEX} provides an index of relative change in meal size among days, rather than absolute measure of meal size (Suryan et al., 2002). Using the bill as a ruler also assumes little variation in bill size between individual adult Sooty terns at a single breeding colony; a realistic assumption based on available data (Higgins and Davies, 1996).

For each chick that was fed in the observation group over the observation interval, a M_{INDEX} value was calculated based on the relative length × width of each prey item multiplied by the number of prey items of that size + the length × width × number of prey items for each differently sized prey item. To standardise M_{INDEX} between observation periods, a mean M_{INDEX} was computed for each observation period by dividing total food by both the number of chicks and the number of minutes per observation period.

In 2005, provisioning was monitored as in 2004. In addition, in 2005, a ‘food curve’ was generated, so that M_{INDEX} values could be converted into an index of meal mass in grams. On 3 d of data collection (12, 14 and 17 May) colour-banded chicks ($n = 23$) were weighed both in the morning, prior to their first meal (08:00 hrs), and in the afternoon, directly subsequent to 8 h of visual observations (16:00 hrs). A meal mass equivalent of M_{INDEX} was estimated by regressing the mass increment for each chick, based on the differences between the morning and afternoon weighings, against M_{INDEX} for the same chicks over the same period. Derivation of meal sizes from chick mass changes is a standard method of obtaining relative measures of adult foraging success for comparative purposes (Phillips and Hamer, 2000, Peck et al., 2004). As chicks lose mass during the day, due to digestion, respiration, defecation and evaporative cooling, the difference in mass between the morning and afternoon weights does not represent the total mass of food received (Ricklefs et al., 1985). Thus, mass meal values serve as a relative measure of mass gain per chick from the visually observed M_{INDEX}. Mass values were standardised for stage of chick growth by dividing each chick’s daily mass change by their age in days.

The average size of all prey items of known size for each day of observation was used to assign an M_{INDEX} value to prey items of unknown size (i.e. when a food item was exchanged, but the observer could not determine the size). The proportion (±SE) of prey items that had to be assigned a mean value was 0.063 ± 0.010 in 2004 and 0.052 ± 0.014 in 2005. The adult feeding frequency (F_{FREQ}) was also recorded. This variable comprised the total number of deliveries per observation period divided by the number of chicks in the observation area and the number of minutes of observation.

Squids make up the primary prey items in the diet of Sooty terns (53 to 70%), while fishes make up 33.2 to 46% (Surman et al., 2002, Harrison et al., 1983, Higgins and Davies, 1996). In this study, food items were categorised as fish, squid, or unknown. Immature fish are of only slightly higher energy density than squid (Davis et al., 1998), and M_{INDEX} values obtained in my study were consistent with previous observations that terns feed primarily on immature fishes (Shealer, 1998). Thus, each prey type was assumed to be of approximately equal calorific value per gram provided. Meal composition as a percentage of each prey type was determined for each day of the study.

4.1.2. Adjustments for chick age and changing energy demands

Analyses of M_{INDEX} or F_{FREQ} examined changes in the amount of food reaching each chick per unit time. Since adults may adjust food loads or feeding frequencies relative to the energetic demands of chicks (Feare, 1976), M_{INDEX} and F_{FREQ} were also adjusted for potential changes in energy requirements with chick age. This procedure required estimates of both chick age and of the relationship between chick energy demands and chick age.

Sooty terns breeding in different subsections of a colony nest relatively synchronously (Feare, 1976, Devney pers. obs.). This means that at any single point in time, the majority of chicks in a definable area of colony are of equivalent ages. In 2004, the chick age estimates used to adjust M_{INDEX} and F_{FREQ} data were the median values estimated for each similarly aged group of chicks observed during an observation interval. These age estimates were derived from comparison with time-series photographs taken of multiple known-age chicks.

For Sooty tern young, the growth rate and shape of the growth curve are such that chick energy demands increase more rapidly during the first week of growth, but then increase relatively uniformly throughout the developmental period (Ricklefs and White, 1981). For example, during the first 20 d, the energy requirement increases from 55 to 80% of the maximum. This suggests an approximately linear relationship between the energy requirements of Sooty tern neonates and age. If so, dividing M_{INDEX} by chick age is an appropriate adjustment for increasing energy demands.

4.1.3. SST data

Sooty terns are rarely found feeding within sight of land (Ashmole, 1963). However, the distance travelled from nesting to foraging grounds is variable among years and colonies (Ashmole and Ashmole, 1967) as well as according to reproductive status (Flint, 1991). Outside the Australian region, Sooty terns have been observed foraging 80 to 200 km from their breeding colonies (Dinsmore, 1972, Feare, 2002). In Australia, this species has been observed foraging 480 to 600 km from their colonies, on the edge of the continental shelf (Surman and Wooller, 2003).

To account for the fact that foraging adults may experience conditions different to those at the breeding colony, SST data were collected at different spatial scales from 4 independent sources. From 15 September to 3 October (the second half of the 2004 study period) and from 6 May to 22 June (the entire study period in 2005) dual IBUTTON (Maxim/Dallas Semiconductor) data loggers were fastened to a permanent mooring in Michaelmas Cay harbour at 1 m depth below the sea surface. These data loggers recorded hourly SST measurements in the waters directly adjacent to Michaelmas Cay (SST_{MC}) that were later converted to daily averages. IBUTTON data at Michaelmas Cay for 1 through 14 September 2004 were not obtained due to equipment failure.

In order to generate SST values for the first portion of the 2004 study period, as well as to determine the comparability between daily SST collected locally and more broadly, SST_{MC} 2004 data were compared with daily average SST data from Great Barrier Reef Marine Park Authority (GBRMPA) and Australian Institute of Marine Science (AIMS) monitoring stations on multiple outer reefs in the Cairns section of the GBR, as well as at a location in the Coral Sea, which is within the Sooty tern foraging range (at least 500 km in the Australian region (Surman and Wooller, 2003, Higgins and Davies, 1996)). At each monitoring station, average daily SSTs were computed from the average of SST measurements recorded every 30 min at 1 to 2 depths per station (4 to 7 m).

4.1.4. Fisheries

Daily catch and effort records from the Eastern Tuna and Billfish Fishery (ETBF) were obtained from Australian longline daily fishing logbooks (ALO5 logtypes) housed at the Australian Fisheries Management Authority (AFMA). Daily catch (kg) data were analysed for all days during each study interval. Latitudes were limited to between 13.0° S and 19.99° S and longitudes to between 142.5° E and 150.99° E. Data from this area were used to estimate the relationship between Sooty tern foraging success and the relative abundance of some of the most important obligate commensal sub-surface marine predators that forage in association with Sooty terns. Almost all tropical feeding terns, noddies and shearwaters occur where surface-feeding tunas or mammals are present (Au and Pitman, 1986, Jaquemet et al., 2004), and tonnage capture data indicate the presence and spatial abundance of these taxa.

4.1.5. Statistical analyses

All data were tested for normality and homogeneity of variance. Linear regressions were then calculated where those assumptions were met. To account for the very small values associated with M_{INDEX} and F_{FREQ} data, these variables were linearly transformed by multiplication by 1000. The standardised foraging variables (M_{INDEX}, F_{FREQ} and meal composition) were then tested against SST measurements that were recorded primarily at Michaelmas Cay in both seasons (see 'Results' for justification). To determine the influence of daily fluctuations in SST on the observed pattern of inter-annual foraging success, ANCOVA analyses were conducted with M_{INDEX} and F_{FREQ} as dependent variables, year as the fixed factor and SST as the covariate. The relationship between M_{INDEX} and chick mass change was established by regressing $\log_{10}$chick mass change and $\log_{10}$chick mass change per day of age against the M_{INDEX} values. Log_{10} transformations were required to meet the assumption of normality. Different levels of variance were observed between years for fisheries data (Levene’s *F*-test; see ‘Results’). As a consequence, the between-year comparisons were undertaken using a non-parametric test that adjusted for unequal variance among samples (Mann–Whitney *U*-test). All statistical analyses were performed using SPSS for Windows Version 11.0.1 (SPSS, 2001).

4.2. RESULTS

4.2.1. SST data

$\mathrm{SST}_{\mathrm{MC}}$ 2004 data were compared with daily SST data from the GBRMPA temperature monitoring stations at Arlington (16° 43’ S, 146° 03’ E) and Moore Reefs (16° 52’ S, 146° 12’ E) ($\mathrm{SST}_{\mathrm{Broad}}$) (Fig. 7). These monitoring stations are on outer reefs in the Cairns section of the GBR Marine Park, approximately 15 and 40 km from Michaelmas Cay, respectively. $\mathrm{SST}_{\mathrm{Broad}}$ values from 15 September to 3 October were compared with $\mathrm{SST}_{\mathrm{MC}}$ values collected during the same period. The 2 temperatures were highly correlated ($F_{1,7} = 30.364$, adjusted $r^2 = 0.786$, $P = 0.001$; $SST_{MC} = 1.236\ SST_{Broad} - 6.022$).

At the time of publication, SST data were not available from Arlington and Moore Reefs for the 2005 study period; instead SST_{MC} values were compared with SST data generated from the AIMS temperature monitoring station at Agincourt Reef (16° 02’ S, 145° 49’ E; Fig. 7). This monitoring station is also on an outer reef in the Cairns section of the GBR Marine Park, approximately 80 km from Michaelmas Cay. Daily values from Agincourt Reef were then used as a broad-scale measure of SST (SST_{Agin}) in 2005. SST_{MC} values in 2005 were compared with SST_{Agin} values collected during the same period. The 2 temperatures were highly correlated ($F_{1,19} = 116.153$, adjusted $r^2 = 0.852$, $P < 0.001$; $SST_{MC} = 1.3\ SST_{Agin} - 8.774$).

SST_{MC} data for both 2004 and 2005 were also compared with SSTs that were generated from a GBRMPA temperature monitoring station at Northeast Herald Reef (16° 56’ S, 149° 11’ E), an isolated seamount in the Coral Sea, approximately 400 km from Michaelmas Cay (Fig. 7). Daily SSTs from Northeast Herald Reef ($SST_{NEHerald}$) provided a very broad-scale measure of SST during both seasons. $SST_{NEHerald}$ values from 15 September to 3 October 2004 and 6 May to 22 June 2005 were compared with SST_{MC} values collected during the same period; again the temperatures were highly correlated ($F_{1,39} = 202.455$, adjusted $r^2 = 0.834$, $P < 0.001$; $SST_{MC} = 1.200\ SST_{NEHerald} - 5.670$).

Significant correlations were found between SST at Michaelmas Cay and SST data from all other locations, suggesting that SST_{MC} accurately reflects the variation in SST that Sooty tern adults breeding at Michaelmas Cay experience throughout their foraging range. Therefore,

SST_{MC} was used as the general measure of sea-surface temperature variation in all further analyses.

4.2.2. Foraging success in relation to SST

During both 2004 and 2005, 2 distinctly different and temporally discrete relationships were evident between SST variation and Sooty tern foraging success. Potential SST impacts were consistently observed only during the second two-thirds of the study period in each year (Fig. 8a, b).

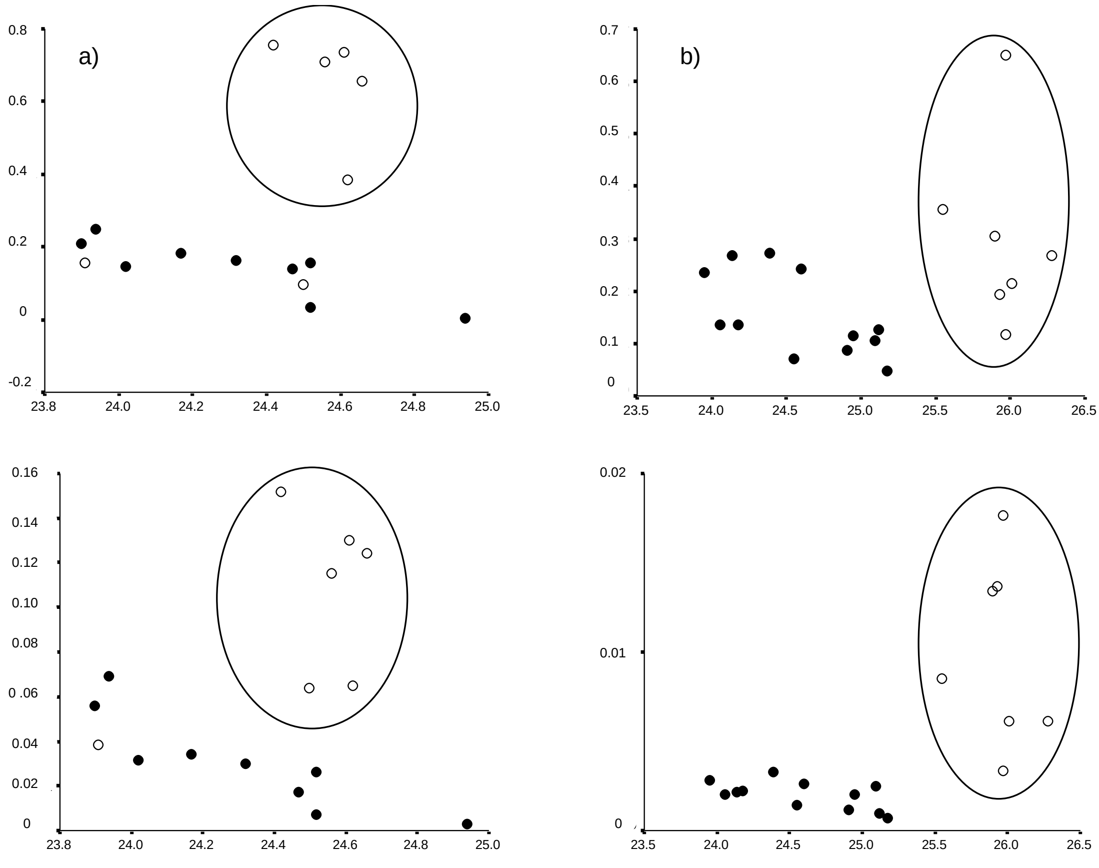


Figure 8. Effect of daily sea-surface temperature (SST) at Michaelmas Cay on day-to-day a) age-adjusted M_{INDEX} and F_{FREQ} during the first one-third (○, 1 to 13 September) and second two-thirds (●, 15 September to 3 October) of 2004 and b) age-adjusted M_{INDEX} and F_{FREQ} during the first one-third (○, 6 to 19 May) and second two-thirds (●, 23 May to 22 June) of 2005.

During the 15 September to 3 October 2004 and again during 23 May to 22 June 2005 ('Foraging Regime 2') SST_{MC} was a significant negative predictor of age-adjusted M_{INDEX} (ANCOVA: $F_{1,17} = 12.868$, adjusted $r^2 = 0.335$, $P = 0.002$; Table 3, Fig. 9a). There was also a significant difference in the intercept of each regression line ($F_{1,17} = 14.458$, $P = 0.001$), but not in the slopes of the lines between years ($F_{1,17} = 0.150$, $P = 0.704$). Thus, during both 2004 and 2005, age-adjusted M_{INDEX} declined at the same rate with increasing SST, but, for any given temperature, the M_{INDEX} was consistently lower during 2004. For each 1°C increase in SST, age-adjusted M_{INDEX} declined by 7.96% ($F_{1,19} = 9.463$, adjusted $r^2 = 0.297$, $P = 0.006$; age-adjusted $M_{INDEX} = 2.09 – 0.0796\ SST_{MC}$).

Table 3. Regression analyses results describing relationships between predictor variables (local- and broad-scale SSTs) and Sooty tern foraging success in contrasting 'regimes' and both regimes combined (entire) during 2004 and 2005, in terms of meal index (M_{INDEX}) and feeding frequency (F_{FREQ}). Bold print denotes significant relationships.

Dependent variable	Year	Regime	Predictor	F	Adjusted r^2	*P*
M_{INDEX} (chick^{-1} min^{-1})	2004	1st	SST_{Broad}	$F_{1,3} = 0.525$	–0.135	0.521
		2nd	SST_{MC}	$F_{1,7} = 2.249$	0.135	0.177
		Entire	SST_{Broad}	$F_{1,14} = 0.172$	–0.058	0.685
	2005	1st	SST_{MC}	$F_{1,5} = 0.045$	–0.189	0.840
		2nd	**SST_{MC}**	**$F_{1,10} = 7.459$**	**0.370**	**0.021**
		Entire	**SST_{MC}**	**$F_{1,17} = 6.078$**	**0.220**	**0.025**
M_{INDEX} (chick^{-1} min^{-1} d^{-1} of age)	2004	1st	SST_{Broad}	$F_{1,3} = 0.763$	–0.062	0.445
		2nd	**SST_{MC}**	**$F_{1,7} = 6.973$**	**0.427**	**0.033**
		Entire	SST_{Broad}	$F_{1,14} = 0.738$	–0.018	0.405
	2005	1st	SST_{MC}	$F_{1,5} = 0.113$	–0.173	0.750
		2nd	**SST_{MC}**	**$F_{1,10} = 6.246$**	**0.323**	**0.031**
		Entire	SST_{MC}	$F_{1,17} = 1.875$	0.046	0.189
F_{FREQ} (chick^{-1} min^{-1})	2004	1st	SST_{Broad}	$F_{1,3} = 0.893$	–0.028	0.414
		2nd	**SST_{MC}**	**$F_{1,7} = 6.525$**	**0.409**	**0.038**
		Entire	SST_{Broad}	$F_{1,14} = 0.116$	–0.063	0.739
	2005	1st	SST_{MC}	$F_{1,5} = 0.215$	–0.151	0.662
		2nd	**SST_{MC}**	**$F_{1,10} = 21.575$**	**0.652**	**0.001**
		Entire	SST_{MC}	$F_{1,17} = 4.044$	0.145	0.060
F_{FREQ} (chick^{-1} min^{-1} d^{-1} of age)	2004	1st	SST_{Broad}	$F_{1,3} = 1.339$	–0.078	0.331
		2nd	**SST_{MC}**	**$F_{1,7} = 8.388$**	**0.480**	**0.023**
		Entire	SST_{Broad}	$F_{1,14} = 0.223$	–0.055	0.644
	2005	1st	SST_{MC}	$F_{1,5} = 0.154$	–0.164	0.711
		2nd	**SST_{MC}**	**$F_{1,10} = 5.176$**	**0.275**	**0.046**
		Entire	**SST_{MC}**	**$F_{1,17} = 11.632$**	**0.371**	**0.003**

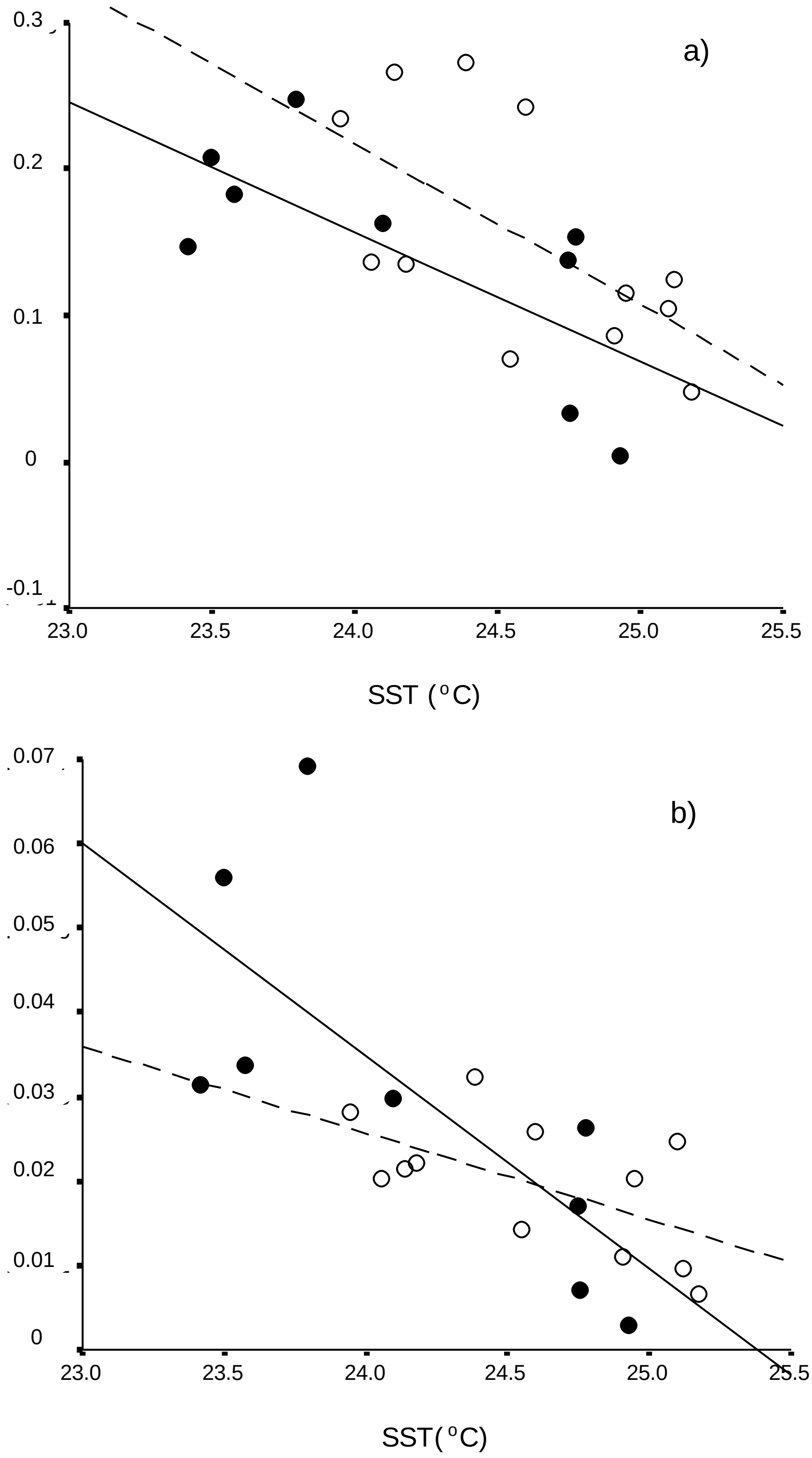


Figure 9. Effect of daily SST at Michaelmas Cay on a) age-adjusted M_{INDEX} during 'Foraging Regime 2' (●, 15 September to 3 October) of 2004 and (○, 20 May to 22 June) of 2005 and on b) age-adjusted F_{FREQ} in Foraging Regime 2 of 2004 (●) and 2005 (○).

During these same periods, age-adjusted F_{FREQ} was also significantly negatively correlated with $\mathrm{SST_{MC}}$ (ANCOVA: $F_{1,17} = 13.142$, adjusted $r^2 = 0.495$, $P = 0.002$; Table 3, Fig. 9b). Again there was a difference in the intercepts of the regression line between years ($F_{1,17} = 14.549$, $P = 0.001$), but not between the slopes ($F_{1,17} = 2.355$, $P = 0.143$). Thus, during both years, age-adjusted F_{FREQ} again declined at a similar rate with increasing SST, but, for any given temperature, F_{FREQ} was lower during 2004. For each 1°C increase in SST, age-adjusted F_{FREQ} declined by 2.00% ($F_{1,19} = 19.314$, adjusted $r^2 = 0.478$, $P < 0.001$; age-adjusted $F_{\mathrm{FREQ}} = 0.512 – 0.0200\ \mathrm{SST_{MC}}$).

Significant negative relationships were also present for the non-age-adjusted M_{INDEX} and F_{FREQ} in 2005 (Table 3) and for non-age-adjusted F_{FREQ} in 2004. However, no significant relationship was observed for M_{INDEX} in 2004 when chick age was not accounted for (Table 3).

During the later portions of both study periods in each year when SST was a significant negative predictor of foraging success, absolute meal sizes (±SE) also differed significantly between the 2 seasons, meal sizes being larger in 2005 (2004: $3.74 \pm 0.62\ M_{\mathrm{INDEX}}\ \mathrm{d}^{-1}$, 2005: $6.32 \pm 0.89\ M_{\mathrm{INDEX}}\ \mathrm{d}^{-1}$; independent samples *t*-test: $t = –2.220$, df =19, $P = 0.039$).

From 6 to 13 September 2004 and from 6 to 19 May 2005 (‘Foraging Regime 1’) no significant effects of $\mathrm{SST_{MC/Broad}}$ on M_{INDEX} or F_{FREQ} were observed (Table 3). During this period in 2004 there was on average ~5 times the age-adjusted M_{INDEX} (Regime 1: 0.646 ± 0.068 SE, Regime 2: 0.141 ± 0.024 SE) and ~3 times as many meals relative to chick requirements (Regime 1: 0.117 ± 0.014 SE, Regime 2: 0.030 ± 0.0065 SE) brought to the colony for equivalent SSTs. This equates to ~15 times as much food with no apparent temperature effect. Similarly, during this period in 2005, there was on average ~2 times the amount of food (Regime 1: 0.299 ± 0.065 SE, Regime 2: 0.152 ± 0.023 SE) and ~5 times as many meals (Regime 1: 0.979 ± 0.020 SE, Regime 2: 0.0196 ± 0.0063 SE) brought to the colony for equivalent SSTs. This equates to ~10 times as much food with no apparent temperature effect. Therefore, over a relatively short 1 to 2 d period in both years, food availability to foraging adult Sooty terns decreased by approximately 1 order of magnitude, after which it did not recover and SST effects became apparent.

4.2.3. Converting meal index (M_{INDEX}) values into meal mass

Significant positive relationships were observed between M_{INDEX}, chick mass change ($F_{1,21}$ = 12.551, adjusted $r^2 = 0.344$, $P = 0.002$; $\log_{10}$chick mass change = 0.0782 M_{INDEX} + 0.743) and age-adjusted chick mass change ($F_{1,21}$ = 15.626, adjusted $r^2 = 0.399$, $P < 0.001$; $\log_{10}$chick mass change per day of age = 0.0591 M_{INDEX} – 0.330; Fig. 10). Thus, each change of 1 meal index was equal to 0.0782 g and 0.0591 g d^{-1} of age.

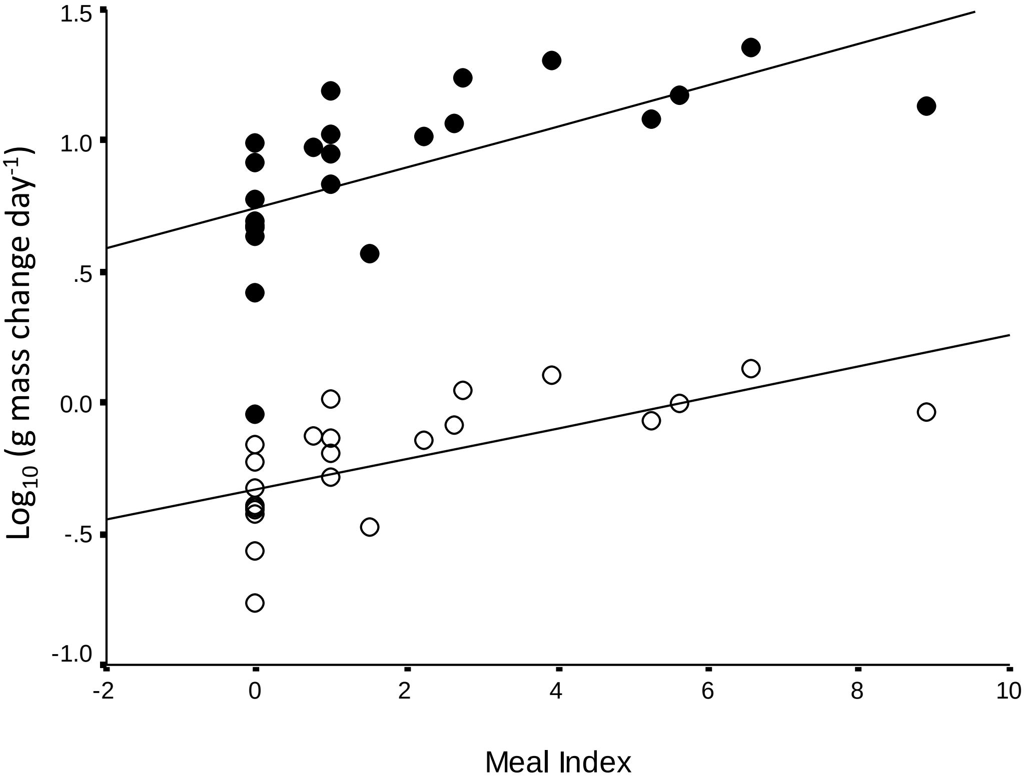


Figure 10. Relative change in chick mass in relation to M_{INDEX} (●, Log_{10} mass change g = 0.0782 M_{INDEX} + 0.743) and chick mass change per day of age relative to M_{INDEX} (○, Log_{10} mass change grams per day of age = 0.0591 $\mathrm{M}_{\mathrm{INDEX}} - 0.330$).

4.2.4. Meal composition

There was a significant negative relationship between $\mathrm{SST}_{\mathrm{MC}}$ and percent squid brought to the colony during the entire study period of 2005 ($F_{1,19} = 6.101$, adjusted $r^2 = 0.203$, $P = 0.023$; Fig. 11), implying a significant positive relationship between percent fish and $\mathrm{SST}_{\mathrm{MC}}$ over the same period. However, there were no detectable relationships between either the percent squid or fish in meals fed to chicks and $\mathrm{SST}_{\mathrm{MC/Broad}}$ during all of 2004 or during any of the sub-periods previously identified in each year (Table 4).

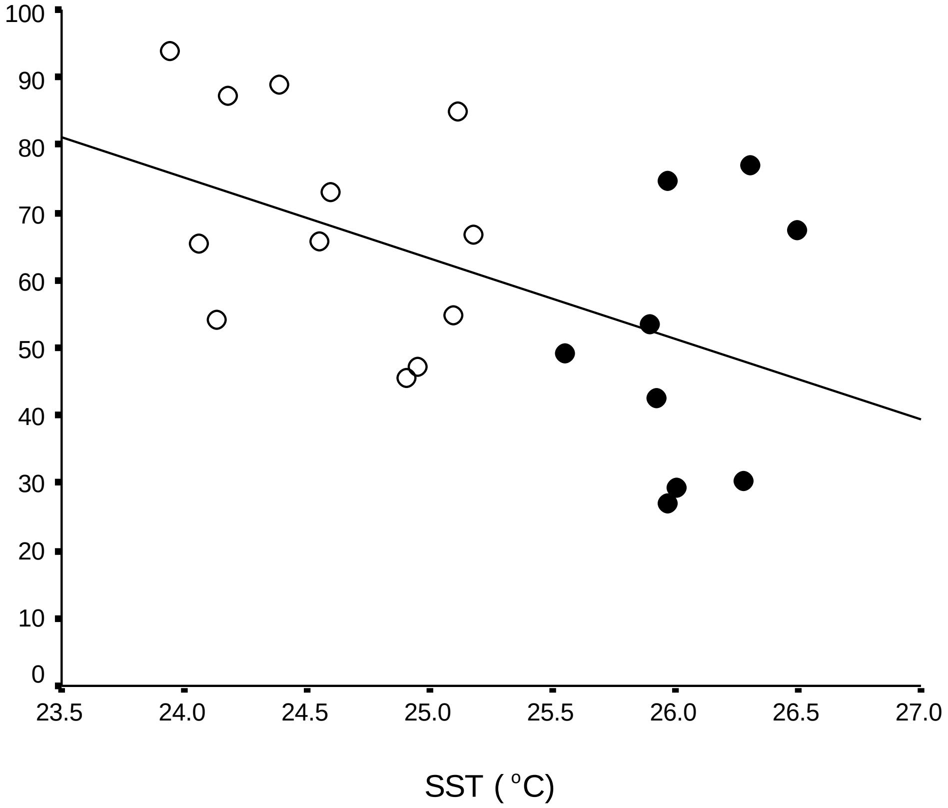


Figure 11. Significant relationship between daily SST at Michaelmas Cay and percent squid meal composition during the entire 2005 study period, where (●) and (○) represent the Foraging Regimes 1 and 2, respectively.

Table 4. Regression analysis results describing relationships between SST at Michaelmas Cay (SST_{MC}) and Sooty tern chick meal composition (percent squid and fish) at Michaelmas Cay during contrasting regimes and during both regimes combined (entire) in 2004 and 2005 breeding cycles (SST_{Broad}: SST data from Arlington and Moore Reefs).

	2004				2005			
	SST_{Broad}				SST_{MC}			
Dependent variable	Regime	F	Adjusted r^2	*P*	Regime	F	Adjusted r^2	*P*
Percent squid observed	1st	$F_{1,3}$ = 0.000	–0.333	0.998	1st	$F_{1,7}$ = 0.545	–0.060	0.484
	2nd	$F_{1,9}$ = 0.218	–0.085	0.652	2nd	$F_{1,10}$ = 2.037	0.086	0.184
	Entire	$F_{1,14}$ = 0.644	–0.024	0.436	Entire	**$F_{1,19}$ = 6.101**	**0.203**	**0.023**
Percent fish observed	1st	$F_{1,3}$ = 0.005	–0.331	0.951	1st	$F_{1,7}$ = 0.031	–0.138	0.866
	2nd	$F_{1,9}$ = 0.256	–0.080	0.625	2nd	$F_{1,10}$ = 1.968	–0.081	0.191
	Entire	$F_{1,14}$ = 0.002	–0.071	0.963	Entire	**$F_{1,19}$ = 10.247**	**0.316**	**0.005**

4.2.5. Foraging success in relation to fisheries

The mean fisheries catch for all days during the study was significantly more variable in 2004 ($F_{1,33}$ = 5.565, *P* = 0.024). Mean (±SE) daily catch rate was also significantly higher during the period when SST effects were not apparent in 2004 (Regime 1: 2453.20 ± 721.48 kg d^{-1}, Regime 2: 583.36 ± 152.56 kg d^{-1}; Mann–Whitney Z = –2.322, *P* = 0.019, n = 16), but not during 2005 (Regime 1: 387.29 ± 126.92 kg d^{-1}, Regime 2: 918.75 ± 282.96 kg d^{-1}; Mann–Whitney Z = –0.767, *P* = 0.482, n = 19).

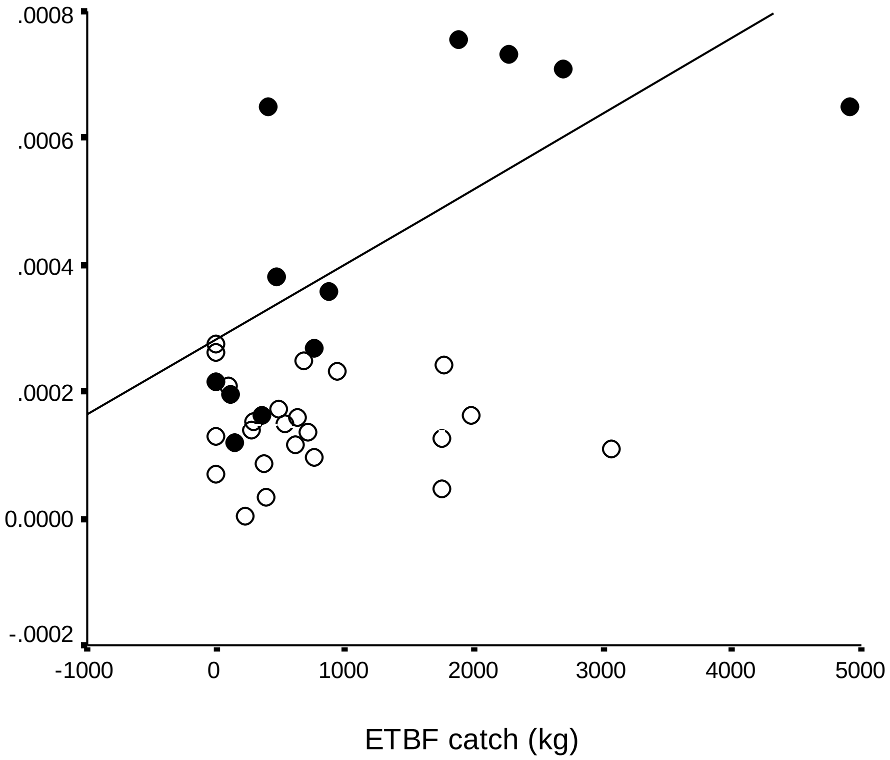


Figure 12. Significant relationship between Eastern Tuna and Billfish Fisheries (ETBF) daily mean catch (kg) and age-adjusted meal index during Foraging Regime 1 (●) of both years combined and the non-relationship between the 2 parameters in Foraging Regime 2 (○) of both years combined.

During foraging Regime 1, when SST did not influence foraging success, mean daily ETBF catch rates were a weak, but significant, positive predictor of the total and age-adjusted amount of food that came into the colony. For example, during Foraging Regime 1 for both years combined, meal daily catch rate was a significant positive predictor of both meal index ($F_{1,10} = 9.136$, adjusted $r^2 = 0.425$, $P = 0.013$) and age-adjusted meal index ($F_{1,10} = 9.755$, adjusted $r^2 = 0.443$, $P = 0.011$, Fig. 12), but not feeding frequency ($F_{1,10} = 1.086$, adjusted $r^2 = 0.008$, $p = 0.322$) or age-adjusted feeding frequency ($F_{1,10} = 1.707$, adjusted $r^2 = 0.060$, $P = 0.221$). In contrast, when SST effects were apparent in both years (Foraging Regime 2), there were no significant relationships between ETBF catch rates and any of the foraging variables (meal index: $F_{1,19} = 0.081$, adjusted $r^2 = –0.048$, $P = 0.779$; age-adjusted meal index: $F_{1,19} =$

0.111, adjusted $r^2 = –0.047$, $P = 0.743$; feeding frequency: $F_{1,19} = 0.261$, adjusted $r^2 = –0.038$, $P = 0.615$; age-adjusted feeding frequency: $F_{1,19} = 0.096$, adjusted $r^2 = –0.047$, $p = 0.761$; Fig. 12). There were also no significant effects of $SST_{MC/Broad}$ on mean daily ETBF catch rates in either year (2004: $F_{1,14} = 1.499$, adjusted $r^2 = 0.032$, $p = 0.241$; 2005: $F_{1,17} = 0.020$, adjusted $r^2 = –0.058$, $P = 0.888$) or in both years combined ($F_{1,33} = 0.086$, adjusted $r^2 = –0.028$, $P = 0.771$).

4.3. DISCUSSION

During the second two-thirds of each Sooty tern (*Onychoprion fuscata*) breeding cycle in 2004 and 2005, significant negative relationships were observed between increasing SST and both the amount of food delivered to chicks and the rate of delivery. These results were consistent for feeding frequency across years, but were uniformly significant for meal index only when meal sizes from 2004 were adjusted for chick age/energy requirements.

During 2004, total meal size suggests that food was generally less abundant. At this time my foraging data suggest that Sooty tern adults returned to the colony with relatively constant absolute food loads (i.e. possibly the minimum obtained during a successful foraging dive), but that both the time taken to obtain this load and its size relative to chick needs decreased as SST increased. By comparison, during 2005, both absolute and relative food loads decreased with increasing SST as did the time taken to obtain each meal.

Both age-adjusted feeding frequency and age-adjusted meal size responded to changes in SST in a similar manner among years. However, during 2004, both variables were consistently lower for the same SST. In 2004, SST generally increased as chick age increased. Conversely, in 2005, SST generally decreased as chick age increased. Therefore, in 2004, meal index and feeding frequency may have been more sensitive to changing SST, not only because food was generally less abundant that year, but also because both SSTs and chick age/requirements were increasing simultaneously. Consistency in the rate of change between years suggests that despite inferred differences in food availability and chick development stage, short-term variation in SST impacts Sooty tern provisioning similarly across breeding seasons and across temperature ranges of ~23 to 26°C.

While correlations do not necessarily imply direct causation, my findings combined with existing data on SST effects in other seabird species, strongly suggest that changes in prey availability associated with increasing SST reduced the ability of Sooty tern adults to provision young. These effects were observed for up to 3 wk during the mid- to late chick-rearing period in both 2004 and 2005. My results also suggest that feeding frequency is more sensitive to changes in SST than meal size. These findings are consistent with the results obtained for Wedge-tailed shearwaters (*Ardenna pacifica*) breeding in the southern GBR, where feeding frequency was also found to be more significantly affected by within-season fluctuations in SST (Peck et al., 2004).

In general, seabirds are not always able to compensate for changes in the distribution or abundance of forage-fish by increasing food loads or foraging rates (Gjerdrum et al., 2003). My results suggest that Sooty terns, like Wedge-tailed shearwaters (Peck et al. 2004), are not always able to increase foraging rates enough when prey are scarce during periods of enhanced SSTs.

Data from this study were used to determine that each 1°C SST increase results in approximately 8% decrease in the meal index brought to chicks. Thus, there is clear potential for detrimental impacts of short-term temperature variation of just a few degrees. Small increases in temperature for sustained periods of several days or weeks may lead to decreased growth and survival. For example, 2 wk of low food availability caused virtually all tropical Roseate tern (*Sterna dougallii*) chicks to die of starvation in 1997, while, in the subsequent season, chicks recovered after only 6 d of low food availability (Ramos, 2000).

No relationship between SST and foraging success was apparent during the first one-third of the study period in either year (6 to 13 September 2004/6 May to 19 May 2005) when prey availability was ~10 to 15 times greater. During both breeding seasons this period coincided with earlier stages of chick-rearing. Adult Sooty terns have been shown to forage in different areas when brooding (290 km foraging radius) and when feeding older chicks (522 km foraging radius) (Flint, 1991). Sooty terns may also feed young chicks a greater number of small meals compared to older chicks (Dinsmore, 1972, Feare, 1976); however, my observations of provisioning of young chicks over intervals of ~1 to 4 h suggest this phenomenon did not impact my results.

Alternatively, the rapid change in prey availability that occurred over a very short 2 to 3 d period in both years highlights that other potential short-term, within-season mechanisms must also significantly influence prey accessibility and foraging potential. One possibility is the distribution of subsurface predators. Intra-annual variation in Sooty tern foraging success has already been shown to be highly influenced by the distribution of underwater predators, especially tuna (Le Corre and Jaquemet, 2005). A significant positive relationship between the provisioning rates and ETBF sub-surface predator catch rates is evidence of the potential influence of this phenomenon on my data. In both seasons, the presence of sub-surface predators either mitigated the impact of SST variability on Sooty tern foraging success or predator numbers also declined in response to a rapid decrease in forage-fish availability.

Unfortunately, it is not possible to distinguish between these 2 alternatives with the current dataset. The 2005 data also suggest that at some times of year a relationship may exist between the availability of specific prey types and SST. Regardless of the mechanisms involved, my results imply that it is not just large seasonal-scale phenomena that impact reproductive success, but also short-term within-season changes in both SST and other factors. How these other potential factors interact with oceanography and whether they are also influenced by climate change is currently unknown and requires further clarification.

Results from this study show that prey availability can track SST for periods of up to 1 mo and that feeding frequency is a more sensitive indicator of how SST impacts Sooty tern foraging success. These findings when combined with those of Peck et al. (2004) suggest that SST variation may impact the foraging success of multiple tropical seabird species at a reef-wide scale. Such results further support a potentially significant negative effect of forecasted climatic changes on seabird reproduction on the GBR. As global climate change continues to increase average SSTs on the GBR at a rate of 1 to 2°C per century (Hoegh-Guldberg, 1999), my findings have significant conservation and management implications.

These results further support earlier findings that, while longer-term impacts of climate fluctuations such as ENSO are important to tropical systems (Schreiber and Schreiber, 1984), even during non-ENSO years the potential effect of short-term climate variation on seabird reproductive output cannot be ignored. Indeed, short-term declines in food availability for periods of days and weeks have resulted in reduced reproductive success (Ramos, 2000, Peck et al., 2004) and seasonal declines in nestling growth rates (Gjerdrum et al., 2003), although the severity of these impacts appears to be related to the number of days of reduced provisioning (Ramos, 2000).

The relative importance of within-season, climate-related variation in foraging success in the broader context of interannual, decadal-scale, climate-related variation is unclear and complex. For example, the number of Wedge-tailed shearwater burrows excavated each season is most related to the cumulative impact of oceanographic conditions from previous breeding seasons (Dunlop et al., 2002), while the percentage of burrows in which eggs were laid is correlated with prevailing feeding conditions during the pre-laying season, and the final breeding outcome is related to short-term environmental conditions during the chick-rearing period (Peck et al., 2004). While inter-seasonal ENSO-associated variation in environmental parameters such as SST may influence the timing and result of a breeding attempt, intra-seasonal variation in SST may be as important for the actual breeding outcome.

Information about the mechanistic links between climate, oceanography and seabird reproduction is vital if the predicted changes in climate are to be successfully managed in the future. My results highlight pelagic foraging seabirds with single egg clutches, such as Sooty terns and Wedge-tailed shearwaters, as useful for identifying broader scale trophic changes that may be occurring and as indicators of how climate change may be impacting other less abundant species within the GBR ecosystem.

CHAPTER 5

Publication arisen:
Devney, C.A., Caley, M.J. and Congdon, B.C. 2010. Plasticity of noddy parents and offspring to sea-surface temperature anomalies. *PLoS One* 5(7), e11891.

5.0. INTRODUCTION

Contemporary climate change has led to organisms encountering more extreme and variable environmental conditions (Stenseth et al., 2002, Walther et al., 2002). Organisms with greater behavioural, phenological, developmental and/or physiological plasticity are generally better able to cope with such environmental variation and extremes (e.g., Réale et al., 2003, Moe et al., 2004, Chiaradia and Nisbet, 2006)). Some studies of long-lived vertebrates with low reproductive capacity support this idea. Individuals of these species that can adjust their behaviour, morphology and/or physiology to changing environmental conditions have greater lifetime reproductive success (Gotthard and Nylin, 1995, Nussey et al., 2007, Reed et al., 2009). Greater plasticity of life-history traits, however, is not always the best strategy. For example, low behavioural plasticity might be selected in long-lived vertebrates where a fixed level of parental investment in young maximises adult survival and lifetime reproductive success (Pianka, 1976, Bókony et al., 2009). This prediction is consistent with patterns of reproductive investment in species such as seabirds where during periods of low prey abundance adults either forego breeding, or abandon young, rather than reduce their own probability of survival (Schreiber and Schreiber, 1984, Monaghan et al., 1992, Wernham and Bryant, 1998, Smithers et al., 2003). However, the generality of such responses in all long-lived species is questionable; some breeding seabirds will, to a limited degree, adjust foraging patterns to changes in environmental conditions at the expense of their future survival

(Lindén and Møller, 1989, Erikstad et al., 1998). In addition, where such plasticity occurs it is uncertain whether it is sufficient to allow species to cope with the environmental variation they face.

Offspring developmental plasticity may also buffer species against environmental variation and extremes (Shine and Brown, 2008). Here again, the optimal strategy may not always be to have the highest possible levels of plasticity during development. For example, high growth rates in the face of large and unpredictable variations in provisioning rates, or meals sizes, may compromise an offspring’s ability to maintain itself above starvation levels during periods of low provisioning (Schew and Ricklefs, 1998). In such species, developmental rates may be optimized for long-term average food availability (e.g., Robinson et al., 2002). As with adult foraging, avian developmental patterns have proven both flexible (Moe et al., 2004, Emlen et al., 1991) and inflexible (Konarzewski et al., 1996, Konarzewski and Starck, 2000) in response to temporal variations in food supply.

Therefore, in many long-lived species such as seabirds, it remains unclear how either adult provisioning behaviour or chick developmental patterns respond to environmental variation. Here we report the results of a study designed to address this uncertainty by simultaneously evaluating flexibility in adult foraging behaviour and chick development in a long-lived species of seabird characterised by a relatively low rate of adult mortality and reproduction, a single-egg clutch, and slow chick maturation, the Black noddy (*Anous minutus*). Anecdotal evidence suggests that food available to this species is related to sea-surface temperatures (SST), and that noddies fare poorly during extreme warm water events (Dyer et al., 2005, Schreiber and Schreiber, 1984). For example, mass mortality of Black noddy adults and chicks was observed on the southern Great Barrier Reef (GBR), Australia, in January 1998

(Hoegh-Guldberg, 1999) coincident with both elevated SSTs (Berkelmans and Oliver, 1999) and a severe coral bleaching event (Wilkinson, 2000). Exploiting this combination of traits, I compared adult foraging behaviour and chick developmental patterns in response to a series of supplementary feeding manipulations between 28 November 2006 and 5 January 2007. In addition, I examined the plasticity of these characteristics in response to decreases in prey availability by comparing my 2006/07 results to patterns of foraging behaviour and chick growth observed during an anomalous warm-water event in the Southern GBR the previous year (i.e. December 2005 to February 2006 (GBRMPA, 2006)). Specifically, I tested (1) the relationship between food availability and SST variation for Black noddies and (2) whether adult foraging/provisioning behaviour and/or chick growth and development responded to food availability.

5.1. METHODS

5.1.1. Study site and species

I studied Black noddies at Heron Island (23° 26’ S, 151° 51’ E), in the Capricorn Section of the GBR Marine Park, Australia, over two consecutive austral summer breeding seasons (2005/06 and 2006/07). Approximately 30,000-70,000 Black noddies nest on Heron Island each season (Dyer et al., 2005). Black noddies lay a single-egg clutch and typically only one clutch per season (Higgins and Davies, 1996). Sexes are morphologically indistinguishable in the field (Gauger, 1999) and pair-bonding is strong; only the members of a mated pair attend any particular nest (Ashmole, 1962). Both parents take turns brooding, with the chick constantly brooded for a few days after hatching, then left unattended most of the day (Gauger, 1999). Parents feed their chick by regurgitation, with food offered in several small batches immediately upon their return from foraging; unclaimed food is retained by the parent (Higgins and Davies, 1996).

5.1.2. Experimental design

Four treatment groups of chicks were exposed to differences in prey availability over the two years; one treatment group was strictly observational and three were experimental and involved supplemental feeding. During the 2005/06 breeding season (December 2005 and January 2006) chick rearing coincided with an anomalous warm-water event (Fig. 13) and low prey availability (this study). Eighteen breeding pairs from this year were monitored and are referred to here as the low food treatment. The 2006/07 breeding season (December 2006 and January 2007) coincided with periods of slightly below-average sea-surface temperatures (SSTs) (Fig. 13). A group of 8 breeding pairs from this year was monitored in an unmanipulated ‘normal’ food treatment. Two levels of supplementary feeding of chicks were imposed on two separate groups of 7 and 6 breeding pairs in 2006/07. These feeding treatments mimicked conditions of ‘medium-high’ and ‘high’ prey availability respectively (see ‘Supplementary feeding’ below). In all cases, each breeding pair was included in only a single treatment. The four treatments investigated here could not be replicated in both years, but estimates of other environmental variables including ambient temperature, precipitation, and wind did not differ consistently or substantially in magnitude between years (Devney, unpublished data). Here I am less interested in statistical significance among treatment than exploring the range of possible responses of these birds to realistic levels of environmental variation. Hence, the treatments examined here illustrate the scope of the responses by this species to the range of environments imposed upon them by natural environmental variation (2005/06) and my experimental manipulations (2006/07).

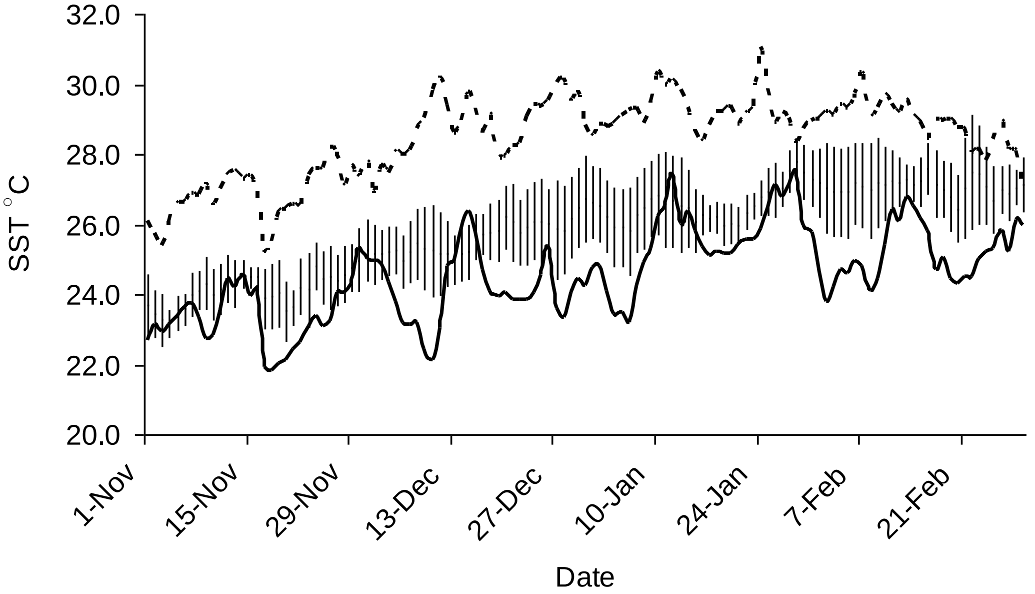


Figure 13. Sea-surface temperature for the November – March austral summers of 2005/06 (dashed line, mean: 28.27 ± 0.15 °C) and 2006/07 (solid line, mean: 24.14 ± 0.19 °C) averaged by 24-hour period from data collected hourly by temperature loggers submerged at 0 – 3 m depth at seven locations in the Heron Island lagoon. Vertical lines show a confidence interval (95% CI) envelope around the mean lagoonal sea-surface temperature during austral summers between 1995 and 2007 (26.09 ± 0.09 °C). 2005/06 and 2006/07 SSTs were outside the 95% CI envelope on nearly all days investigated.

At least one adult from each study nest was captured by hand and colour-banded for individual identification. Hatching dates of chicks were determined either by checking the status of each nest daily, or estimated from linear regressions of culmen length against chick age (Congdon, 1991). All chicks studied hatched within 5 days of the peak hatching date in the study area. Chicks were weighed to the nearest 0.1g using an electronic scale at 06:00 and 18:00 hrs each day from 28 November – 23 December 2005 (range of ages = 5 – 27 days; mean = 11.92 ± 0.23 (SE) days) and from 28 November 2006 – 5 January 2007 (range of ages = 5 – 39 days; mean = 16.17 ± 0.71 (SE) days). Chick culmen, tarsus and wing chord lengths were estimated (± 0.1 mm) every second day using digital calipers.

In 2005, adult provisioning rates at nests were also assessed during 12-hr nest watches between ~06:30 – 18:30 hrs on 20 out of the 26 days on which chicks were weighed and measured. In 2006/07, and based on observations from 2005 that feeding was negligible during the middle of the day, adult provisioning rates were assessed during twice-daily 4 – 5 hour nest watches during the morning and afternoon (~06:30 – 11:00 hrs & 14:30 – 19:00 hrs) on 26 out of 39 days on which chicks were weighed and measured. Observers were positioned so that all nests (n = 18 in 2005/06 and n = 21 in 2006/07) were monitored simultaneously each day. Frequencies of feeding by individual parents were recorded and chicks were weighed before and after feeding events. Meal sizes were then calculated from changes in chick body mass that were corrected for mass lost through digestion, respiration and excretion between weighings, using equations based on natural rates of mass loss for this species (as per Hamer and Hill, 1993, Devney unpublished data). Meal sizes and feeding frequency were determined for each adult at individual nests. Black noddies at this location are accustomed to high levels of human disturbance, often nesting within meters of high-intensity human activity (i.e., housing, footpaths, and dining halls). The level of disturbance associated with this study is unlikely to have influenced my results given this acclimation to human activity and similar disturbance levels across years and treatments.

5.1.3. Supplementary feeding

Chicks in the medium-high and high food treatments in 2006/07 were hand-fed supplemental food consisting of freshly thawed White pilchards (*Sardinops neopilchardus*), a member of the family Clupeidae and prey of Black noddies (Cooper, 1948, Harrison et al., 1983). Pilchards were stored frozen until required and warmed to ambient temperature (about 28 °C) before being mashed slightly and delivered to chicks. The amount and frequency of food supplementation varied between the two groups of supplemented chicks. Chicks in the medium-high supplementation treatment received ~one-third of the total food provisioned by both its parents per day (mean = 9.36 ± 0.36 g, or 0.137 ± 0.003 grams per gram of chick, n = 182) daily by a single meal at 06:00 hrs over a total of 24 days, ranging between the average ages of 5.3 ± 0.3 and 36.3 ± 0.3 days (from 2 – 8 December, 11 – 22 December and 28 December 2006 – 2 January 2007). Chicks in the high food supplementation treatment were fed the equivalent of ~two-thirds of the total food provisioned by both its parents per day (mean = 16.21 ± 0.52 g, or 0.261 ± 0.005 grams per gram of chick, n = 156) via two supplementary meals provided daily, one at 06:00 hrs and another at 14:00 hrs. The amount of food provisioned by adults increased as chick mass increased. Therefore, in order to supplement food at these predetermined levels, the mass of food to be supplemented was determined from previous measurements of provisioning for that chick. Chicks in the control (normal food treatment) group in 2006/07 were subjected to the same degree of handling, but received no supplementary food.

Black noddies roost in colonies at night and depart to forage at dawn. When foraging, each parent returns to feed their chick 1 – 3 meals per day, exclusively during daylight hours (Gauger, 1999). Therefore, supplements given at 06:00 and 14:00 hrs ensured that chicks in the supplemented groups received food just prior to their parents returning to feed them. Despite these chicks having received supplemental food they were still capable of accepting meals from their parents. The average quantity of food delivered per meal by a foraging adult is about 12 g, but chicks as young as 5 days of age can consume >20 g of food in a single meal (Devney, unpublished data).

5.1.4. Chick condition and vocal behaviour

To examine whether provisioning by adult Black noddies was related to chick condition, provisioning by adults was explored as a function of chick body condition (Weimerskirch et al., 2001). The body condition of individual chicks relative to their body size was estimated prior to feeding (at 06:00 hrs) on every second day of the study. Condition was estimated by regressing chick body mass against tarsus size for all chicks every two days and then dividing the chick-specific residuals from each analysis by the predicted values from the regression equation obtained for the same day (as per (as per Hamer and Hill, 1993)). When assessing chick condition, a subset of the data for which all meals were actually measured in a day (rather than from using the corrections from mass loss due to digestion, respiration, and excretion) was used.

In some seabird species, begging by chicks indicates their condition (Hamer et al., 2006). Therefore, throughout the experiment, I examined whether or not chicks begged for food when adults returned to nests during daily nest watches. Chicks beg by uttering chirping calls and assuming a begging posture only in the presence of a parent (Higgins and Davies, 1996). Sometimes, both Black noddy parents return to the nest to feed their chick within a few minutes of each other. When this occurs, the possibility of a second meal rapidly following the first may not initiate a begging response from the chick. Thus, in order to use vocal behaviour as an estimate of chick satiation between nests and days, I only monitored begging, whether or not at least one begging chirp was vocalized by a chick, prior to the first meal delivered by an adult to a particular nest each day.

It was not possible to weigh adults each time they arrived at their nests to provision young. Therefore, to determine whether adults with supplemented chicks adjusted the amount of food they collected at-sea based on chick condition, or alternatively, whether they returned with food that was not subsequently fed to chicks, I did two things. First, hand-feeding of chicks was stopped twice during the study, once on 9 – 10 December 2006 and again on 3 – 4 January 2007, but nest observations continued as usual. This was done to see if meal sizes delivered to chicks would increase. Second, the presence/absence of chick begging when an adult returned from the first foraging trip of the day was recorded and assessed between food treatment groups to see whether chick satiation levels were influencing meal sizes.

5.1.5. SST data

Sea-surface temperature (SST) data were obtained from seven Seabird Temperature Recorders (SBE39) deployed by the Australian Institute of Marine Science (AIMS) within a 7 km radius of the Heron Island lagoon. For each monitoring station, daily average SSTs were computed from the SST measurements recorded every hour at depths from 0.3 – 1.6 m. Temperature data from each monitoring site were compared with data collected during the same period at each of the other monitoring sites. All temperatures from *in-situ* loggers were highly correlated with each other, with r values for each day ranging between 0.768 and 0.986 ($P < 0.001$).

In general, Black noddies forage between 15 and 80 km from nesting or roosting islands (Higgins and Davies, 1996, Ashmole and Ashmole, 1967). However, in this study, flocks of foraging birds were frequently observed from Heron Island, foraging just beyond the nearby reef edge (Devney, pers. obs.). Thus, to determine the comparability between daily SSTs collected locally using *in situ* loggers and more distant SSTs remotely sensed by satellite, local temperature data obtained from loggers were compared with daily average SST data derived from between one or two daily ‘snapshot’ images from an Advanced Very High Resolution Radiometer (Ver. 3) flown onboard a NOAA 18 series satellite (Skirving et al., 2002) between 12:30 and 15:10 hrs Australian Eastern Standard Time. The mean temperatures from the seven *in situ* loggers were significantly correlated with satellite-derived values averaged for the 50x50 km grid square centred on Heron Island ($F_{1,18} = 7.49$, $r = 0.542$, $P = 0.014$). I used the local *in situ* SST data in preference to the remotely sensed

SSTs in my assessments because *in situ* data were available for more days of the study as logger data are unaffected by cloud cover.

5.1.6. Statistical analyses

All data were tested for normality and homogeneity of variance; data that did not conform to these assumptions were $\log_{10}$ transformed. Student’s t-test, ANOVA and linear regression were used for further analysis where these assumptions were met. Group differences were assessed using Tukey’s tests.

I used residuals from least squares regressions of mass, and wing and tarsus lengths versus age to test whether growth between 5 and 21 days was linear. Linear growth was assumed where the residuals of such regressions were approximately normally distributed around zero. Similar periods of linear chick growth have been documented in a number of other seabird species (Massias and Becker, 1990, Nisbet et al., 1995) and are useful for intra-specific comparisons by providing an estimate of chick growth throughout a specific chick-rearing period. The slopes of these linear models for mass, tarsus length and wing length from each chick were then compared among feeding treatments using one-way ANOVA.

Two-way repeated-measures ANOVA was used to test for changes in meal sizes and begging frequency between periods with and without supplementation (2006/07 only). These comparisons were made between treatment groups and supplementation periods. To measure plasticity of adult foraging behaviour in daily meal mass provided to chicks and feeding frequency, a single average value for each of these variables was derived for each nest. In this way, independence of the samples was maintained and the effect of flexibility of the pair of adults was sampled. These values were then compared for group differences using one-way ANOVA.

In order to assess the response of a parent to an individual chick's condition over time, estimates of a chick's condition at any point should be statistically independent of its condition on other days in the comparison (i.e., there should be no temporal autocorrelation). Time series analysis of estimates of chick condition revealed significant autocorrelation between condition estimates taken at two-, but not four-day intervals in both sampling years. Thus, estimates of chick condition were compared to meal sizes provided by parents at four-day intervals.

Results below are presented as averages ± 1 standard error (S.E.), unless otherwise stated. All statistical analyses were performed using SPSS for Windows Version 17.0.

5.2. RESULTS

5.2.1. SST & foraging success

For a significant portion of the 2005/06 Black noddy breeding season (November –March), daily SSTs on the southern GBR exceeded long-term averages by 1 – 1.5 $^{\circ}$C (GBRMPA, 2006)(Fig. 13). Foraging success decreased with increasing SST in 2005/06, with SST negatively related to both $\log_{10}$ daily feeding frequency ($F_{1,18} = 70.80$, $r^2 = 0.797$ $P < 0.001$; Fig. 14a) and total daily meal mass ($F_{1,18} = 24.07$, $r^2 = 0.572$ $P = 0.001$; Fig. 14b) (per gram of chick) provided by adults. Similar relationships were not evident in 2006/07 ($\log_{10}$ daily feeding frequency: $F_{1,24} = 0.78$, $r^2 = 0.032$ $P = 0.385$; meal size: $F_{1,26} = 1.53$, $r^2 = 0.055$ $P = 0.228$; Figs. 14a and b).

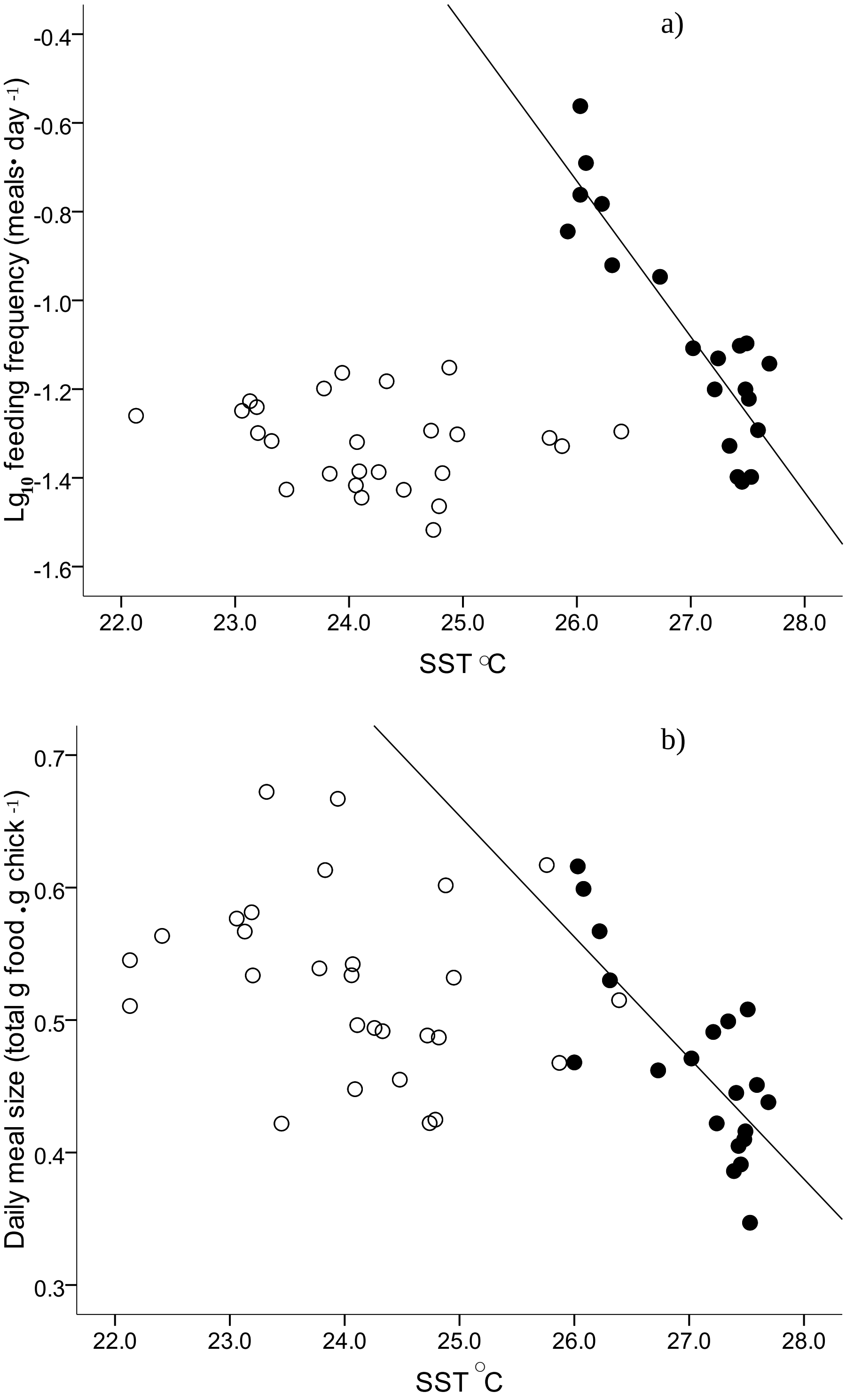


Figure 14. Relationships between provisioning variables of a) $\log_{10}$ transformed daily feeding frequency and b) total daily meal mass that were normalised for chick size (by dividing by grams of chick mass) and compared to day-to-day sea-surface temperature. Unsupplemented nests in 2005/06 (●, low food treatment) and unsupplemented nests in 2006/07 (○, normal food treatment).

5.2.2. Plasticity of parental care

Daily total meal sizes brought to chicks by adults during periods of differing prey availability differed significantly (Fig. 15a) with adults from the low natural food treatment and the high supplementation food treatment bringing the smallest meals and adults from the normal food treatment bringing the largest (one-way ANOVA, $F_{3,35} = 116.32$, $P < 0.001$). The mean number of meals fed to chicks each day over the study period was not the same among the four treatment groups (one-way ANOVA, $F_{3,35} = 4.36$, $P = 0.012$; Fig. 15b), with different feeding frequencies between the low food treatment and the medium-high supplementation treatment. However, between unsupplemented nests in both years (i.e., low and normal food) and all nests monitored in 2006/07 (normal food, medium-high and high supplementation), feeding frequencies were similar.

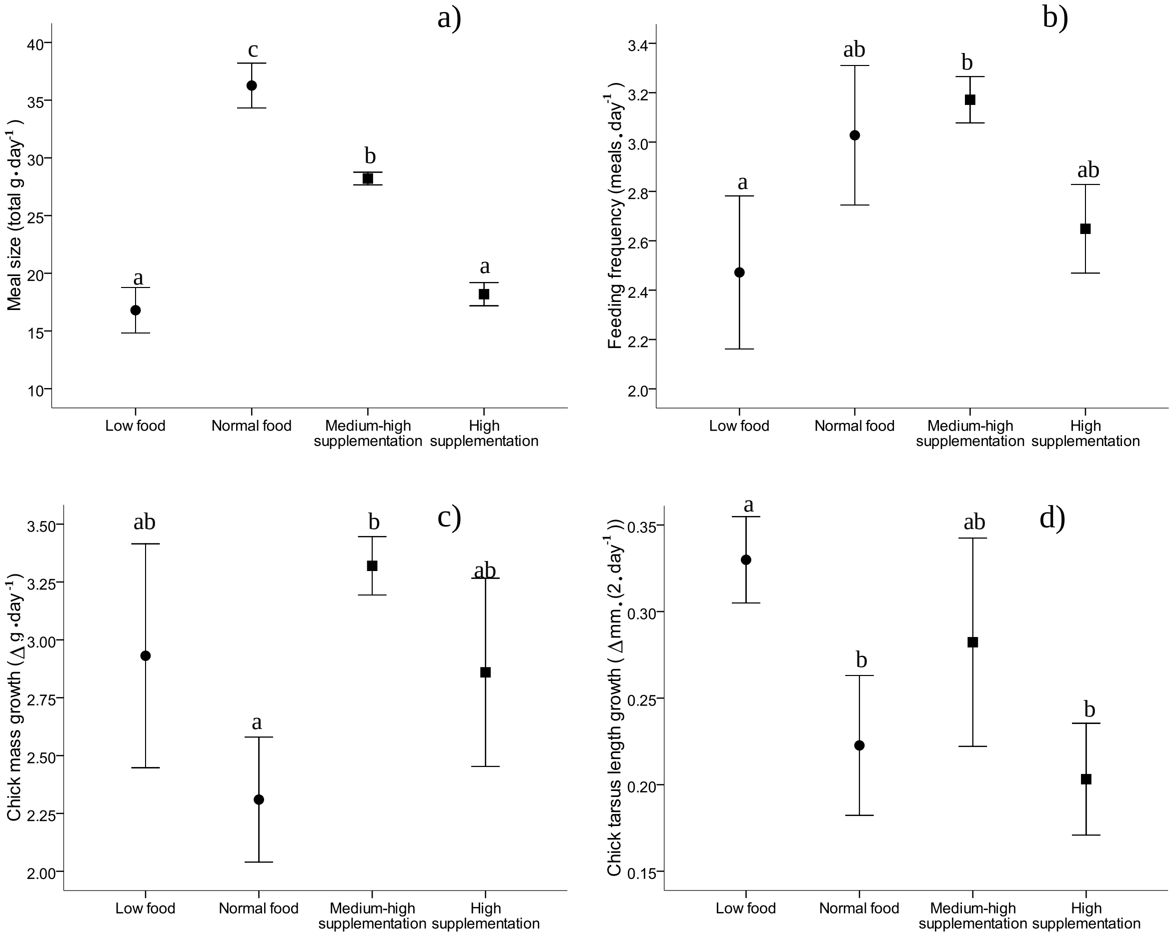


Figure 15. Mean ± 2 S.E. of total daily a) meal sizes (g) and b) number of meals provided by adult Black noddies that were exposed to four different prey availabilities, two of which were natural (low and normal food) and two of which included diet supplementation (medium-high and high supplementation). Mean c) chick mass accumulation (as 24-hr chick growth (g)) and d) skeletal growth (as 48-hr tarsus length (mm)) are also shown. Different letters above the error bars indicate significant differences at *P* = 0.05 level in a Tukey HSD test.

The results described above for the 2006/07 breeding season refer exclusively to the ‘chicks supplemented’ stage of the study: 2 – 8 December and 11 – 23 December, 28 December 2006 – 2 January 2007, and suggest that the total amount of food fed to chicks each day by their parents in the medium-high and high supplementation food treatment groups was significantly lower than for the normal food treatment chicks. Further supporting this result, repeated-measures ANOVA comparing meal sizes fed to chicks during supplementation and during two independent cessations of supplemental feeding (9 – 10 December and 3 – 4

January) in 2006/07 demonstrated that immediately upon cessation of supplementation, chicks from the supplemented treatment groups were fed daily meal sizes equal in size to that of unsupplemented chicks (interaction effect $F_{2,18} = 44.71$, partial $\eta^2 = 0.743$, $P < 0.001$; Fig. 16a). The significant interaction between supplementation stage and group resulted from an increase in the amount of food fed by adult Black noddies to their chicks in the experimental treatments (medium-high and high food treatments) between periods of supplementation and no supplementation, while total daily meal sizes fed by parents to the control chicks (normal food treatment) did not change.

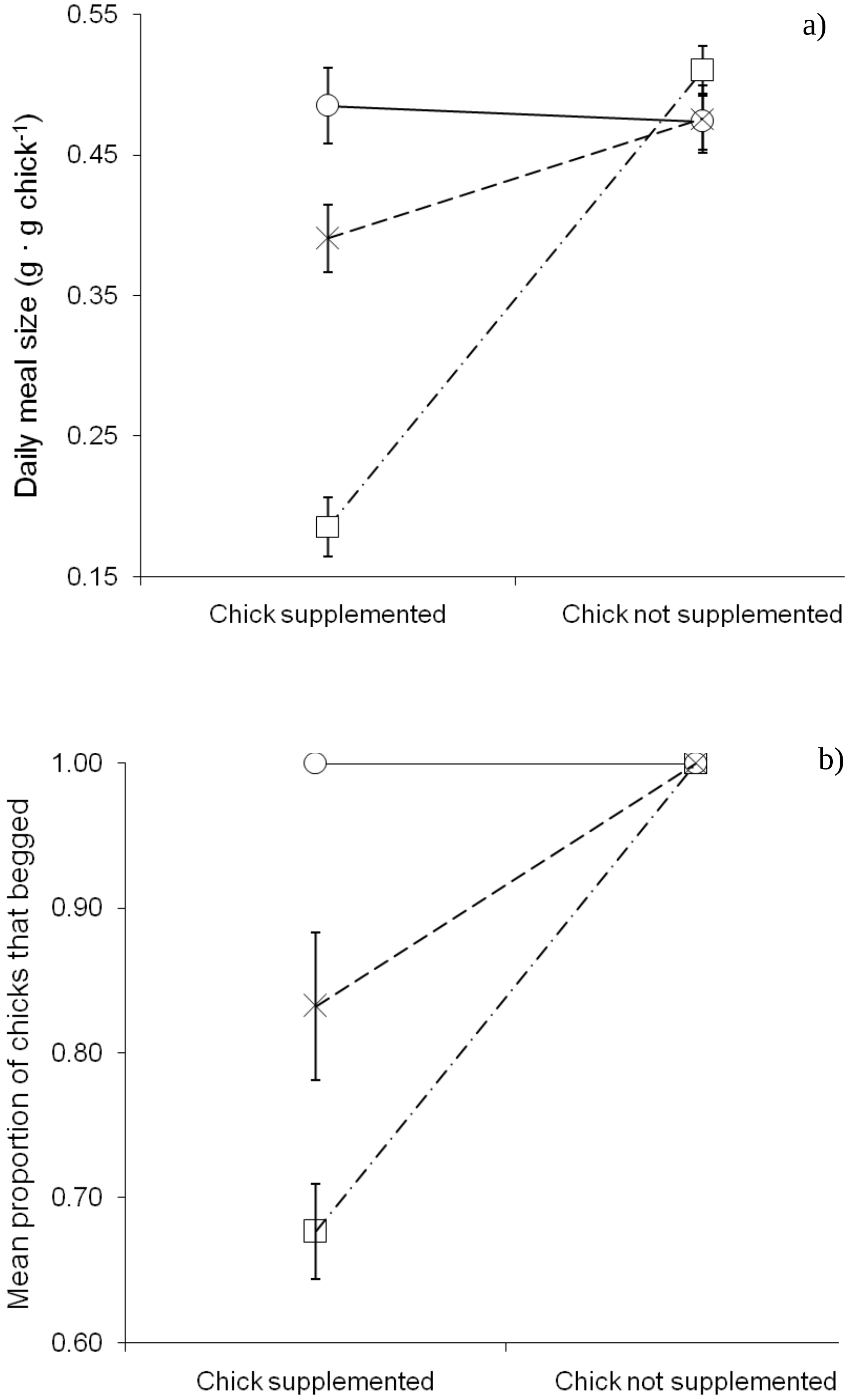


Figure 16. Differences in a) provisioning rates and b) the proportion of chicks that begged each day for their first meal of the day between the two stages of the study. During the 'chicks supplemented' stage, chicks from the medium-high (x) and high (□) food treatments were hand-fed supplementary food (2 – 8 December, 11 – 23 December and 28 December 2006 – 2 January 2007; *n* = 27 days), while chicks from the normal (○) food treatment were not fed additional food. In the second stage supplementation ceased and all chicks were fed by their parents only (9 – 10 December 2006 and 3 – 4 January 2007; *n* = 4 days).

5.2.3. Chick growth and condition

The rate at which chicks increased in mass differed among treatments (one-way ANOVA, $F_{3,35} = 4.62$, $P = 0.010$), with medium-high food supplementation resulting in the fastest mass accumulation (Fig. 15c). Chick morphological responses to differences in food availability also differed among treatments, with chick structural growth (tarsus length) increasing fastest in the low food treatment and slowest in the normal and high supplementation food treatments (one-way ANOVA $F_{3,35} = 11.11$, $P < 0.001$; Fig. 15d). The rate of chick wing growth was similar amongst all treatments (one-way ANOVA $F_{3,35} = 1.69$, $P = 0.188$).

When the condition of unsupplemented chicks (i.e., low food treatment (2005/06), normal food treatment (2006/07)) was compared against the total amount of food brought to these chicks each day, there were no statistical differences in the slopes of the lines between years ($F_{1,33}= 0.06$, $P = 0.807$). The total amount of food brought to chicks each day by their parents was positively related to chick condition (ANCOVA: $F_{1,33}= 4.96$, $r^2 = 0.326$, $P = 0.033$; Fig. 17). There was a significant difference in the intercepts of the regression lines ($F_{1,33}= 12.08$, $P = 0.001$) with chicks in the normal food treatment being in significantly better condition compared to low food treatment chicks at any given meal size.

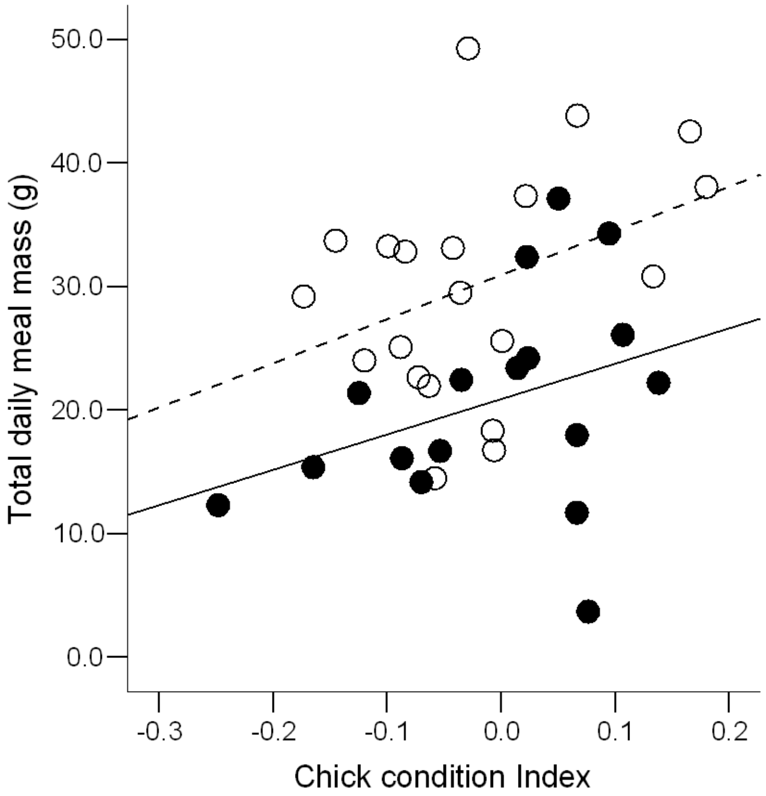


Figure 17. Effect of chick condition on total daily meal sizes provided to unsupplemented Black noddy chicks by their parents in 2005/06 (●, low food treatment) and in 2006/07 (○, normal food treatment).

5.2.4. Vocal behaviour of chicks

During periods of food supplementation the proportion of supplemented chicks that begged for the first meal delivered by one of their parents each day was less than unsupplemented chicks (repeated-measures ANOVA, interaction between treatment group and supplementation stage, $F_{2,18} = 22.61$, partial $\eta^2 = 0.715$, $P < 0.001$; Fig. 16b). The significant interaction effect occurred because the high food supplementation chicks increased begging more than medium-high food supplementation chicks upon cessation of artificial feeding. All chicks, regardless of treatment group, begged for their first meals on the same and subsequent days after cessation of supplementary feeding (Fig. 16b).

5.3. DISCUSSION

5.3.1. Adult provisioning

This study further supports within-season variation in SST as a robust descriptor of foraging success across a range of tropical seabird taxa (Peck et al., 2004, Chapter 4). During the austral summer of 2005/06, hotter than average SSTs significantly and negatively impacted provisioning rates of adult Black noddies. As SSTs increased, total daily meal sizes (Fig. 14b) and feeding frequency (Fig. 14a) declined. These results are similar to those found for Sooty terns (*Onychoprion fuscata*) breeding on the northern GBR (Chapter 4) and Wedge-tailed shearwaters (*Ardenna pacifica*) breeding on the southern GBR (Peck et al., 2004). Thus significant negative impacts of day-to-day variation in SST have now been observed across multiple taxa and at widely spaced locations on the GBR. Similar processes appear to operate in other geographic regions (Hedd et al., 2002, Quillfeldt et al., 2007a) suggesting that predicted increases in SST linked to global warming may have significant negative impacts on foraging and reproductive success in many seabird species worldwide.

During 2005/06 total food delivered to chicks per unit time was lower than in 2006/07 (Fig. 15a). Breeding adults in 2005/06 were only able to achieve short-term increases in chick feeding rates suggesting that Black noddy adults did not compensate for low food availability through increased feeding rates, or by delivering larger meals. Similarly, although total meal sizes fed to chicks by adults each day were reduced when the chicks' meals were artificially supplemented (Fig. 15a), adults did not vary their meal delivery rates (Fig. 15b). Cessation of chick supplementation twice during the study also resulted in immediate increases in meal sizes fed to chicks (Fig. 16a). Combined with changes in chick begging behaviour (Fig. 16b), my results suggest that when background levels of food availability are high, chick intake is predominantly controlled by chick satiation levels communicated through begging intensity.

These results suggest that adult provisioning patterns are largely fixed and may have been selected for by limitations in the food processing capacity of chicks (Takahashi et al., 1999).

The reduction in total meal sizes brought to chicks each day in the medium-high and high food treatments closely matched the rate at which chicks in the experimental group were artificially supplemented (Fig. 15a), supporting the idea that chicks were limited by their capacity to process food. Similarly, a parent at its departure from the nest cannot anticipate the needs of the chick at its return, especially where both parents provision (Ashmole, 1971). Instead, chick needs appear to be perceived by a parent upon its return to the nest through the begging behaviour of its chick. Thus, it is more likely that provisioning by parents in this long-lived species is regulated by an investment pattern typical of other long-lived species where parents limit their current reproductive investment in order not to jeopardize their future reproductive success (Croxall, 1982, Navarro and González-Solís, 2007).

However, my results also suggest that feeding rates by parents of this species are not absolutely fixed. During 2005/06, adults fed at higher rates during an interval of slightly higher than normal sea-surface temperature (i.e., ~1 ^{o}C) (Fig. 14a). This increased feeding frequency was not accompanied by a concurrent increase in total food supplied to chicks (Fig. 14b) and was not maintained at higher temperatures. In contrast, pelagic foraging Wedge-tailed shearwaters and Sooty terns breeding on the GBR have not demonstrated a similar capacity to increase provisioning rates during periods of poor food availability, either within- or between-seasons (Peck et al., 2004, Chapter 4). A number of factors may explain the noddies' limited ability to increase provisioning rates beyond normal background rates, including differences in foraging ecology between offshore foraging Black noddies and these more pelagic species (Hulsman, 1988) or access to variety in prey types (Surman and Wooller, 2003, Diamond, 1983).

In both years of this study, body condition and daily meal sizes were positively correlated in naturally fed chicks (i.e., low and normal food treatments) (Fig. 17). Adults of some species of seabirds are capable of responding to chick condition by altering provisioning rates (Hamer et al., 1999, Weimerskirch et al., 2000, Congdon et al., 2005). However, the ability of adults to provision based on chick needs is influenced by a number of factors, including the distance the species travels to its feeding grounds (Duriez et al., 2000), prevailing environmental conditions (Weimerskirch et al., 2001), and adult body condition (Tveraa et al., 1998). Seabirds appear to gauge chick condition through begging behaviour (Hamer et al., 2006, Quillfeldt et al., 2007b). My measure of whether chicks begged or not, however, cannot be used to determine whether Black noddy adults responded to variation in chick begging frequency and/or intensity; further assessments would be needed to resolve this.

5.3.2. Chick development

In 2006/07, chicks in the medium-high food supplementation treatment accumulated mass at a faster rate than controls (Fig. 15c). Despite this, supplemented chicks in both treatments were unable to take advantage of extra provisions by increasing the growth rate of other structural traits (Fig. 15d). Therefore, during periods of high prey availability, offspring growth and development in this species appears to be largely inflexible. Such inflexibility may have evolved as a result of the relative costs and benefits of rapid growth in these chicks and trade-offs among the allocation of resources to growth and maintenance (Mangel and Stamps, 2001, Gebhardt-Henrich and Richner, 1998). Rapid growth can impose increased energy requirements (Ricklefs et al., 1998), which becomes particularly costly when food becomes limited (Van Heezik and Davis, 1990).

When food availability was low during 2005/06, the rate of structural growth increased despite the poorer condition of chicks (Fig. 15d). The reasons for this increase in structural development at the expense of body condition are currently unknown and undocumented elsewhere. This phenomenon could result from either chick skeletal growth being maladaptive under stressful conditions of low food availability, or reflect an adaptive shift in energy allocation. Such a maladaptive growth response may have resulted from nutrient shortages for bone development (Tilgar et al., 2002, Mangel and Stamps, 2001) in 2005/06. However, diet compositions between years were not significantly different (Devney, unpublished data), suggesting that this was not the case. During 2006/07 when food was more abundant, energy required for maintenance may also have been greater, or energy may have been allocated to the growth and development of traits not measured here, in preference to tarsal growth. It is not clear why differential allocation may have occurred, though it could have been related to between-year variation in other environmental conditions not measured here which may influence metabolic rates and water loss (Ricklefs and White, 1981). It could also be that during the better food year in 2006/07, poorer quality or less experienced birds may have been able to breed than in 2005/06, when low food availability precluded all but the best individuals from breeding.

The chick growth responses to low, normal, medium-high and high prey availability observed here suggest that growth rate reaction norms in Black noddy chicks may have resulted from selection imposed by consistently low or highly variable food availability typical of tropical oceans (Messié and Radenac, 2006). Also, if adult foraging behaviour and chick developmental patterns in Black noddies are facultative (plastic) responses to chick condition then both should vary according to changes in these parameters. My results suggest that this was not the case. Both adult foraging and chick development in this species are relatively inflexible and show limited ability to adjust to large-scale variation in food availability over the short-term. The future frequency of intense anomalous warm water events (Walther et al., 2002) may favour greater plasticity (e.g., Réale et al., 2003) if associated with greater total environmental variation. However, my findings suggest that the Black noddy, and probably similar offshore and pelagic foraging tern species, may be unable to respond rapidly to future changes in sea-surface temperatures and other climate-associated environmental variation through plasticity of developmental or behavioural traits.

CHAPTER 6

Publication arisen:
Devney, C.A., Short, M. and Congdon, B.C. 2009. Cyclonic and anthropogenic influences on terns of the Great Barrier Reef, Australia. *Wildlife Research* 36, 368-378.

6.0. INTRODUCTION

Population dynamics of organisms can be strongly affected by a combination of natural and anthropogenic stressors (Sæther, 1997, Hughes and Connell, 1999), including weather, food resources, habitat quality, human activity, disease and parasites, interspecific competition, predation, and population density. Hence, the importance of examining a broad range of potential drivers when assessing regulators of populations cannot be underestimated (Halpern et al., 2007). A comprehensive approach is particularly important in marine ecosystems where a mixture of threats already affect these systems (Lewison et al., 2004, Glover and Smith, 2003, Clarke and Harris, 2003).

The Great Barrier Reef (GBR), Australia is a complex marine ecosystem that is home to a diverse array of fauna, many of which are of conservation concern both within the GBR and elsewhere (Hoyt, 2001, Schreiber et al., 2002, Berkelmans et al., 2004, Johnson and Marshall, 2007). In particular, concern regarding the status of seabirds on the GBR has recently intensified because of clear evidence of substantial population declines for multiple species at a reef-wide scale (Congdon et al., 2007). Tropical seabird population declines are not unique to the GBR (Benoit and Bretagnolle, 2002, Schreiber et al., 2002, Brooke, 2004, Feare et al., 2003) and may be climate-related (Ramos et al., 2002, Peck et al., 2004, Smithers et al., 2003, Chapter 3), or may be related to direct or indirect human pressure, through industries such as tourism (Benoit and Bretagnolle, 2002) and fisheries (Blaber et al., 1998).

Michaelmas Cay on the northern GBR is an important tropical seabird nesting site in the GBR World Heritage Marine Park. The three seabird species breeding in largest numbers at the cay, the pelagic foraging Sooty tern (*Onychoprion fuscata*) and Common noddy (*Anous stolidus*), and the inshore foraging Crested tern (*Thalasseus bergii*) are among the most abundant species in tropical regions (Sibley and Monroe, 1990) and in Australia (Serventy et al., 1971, Blakers et al., 1984). Since 1984 Queensland Parks and Wildlife Service (QPWS) has been conducting approximately monthly counts of all breeding and non-breeding seabirds present on Michaelmas Cay. Recent assessments of population trends at this location suggest that El Niño Southern Oscillation-associated changes to subsurface and surface water characteristics negatively impact provisioning rates and breeding participation in the two pelagic species, but not the inshore forager (Chapters 3 & 4).

In addition to the already identified impacts, global warming is predicted to intensify threats from tropical cyclones (Bister and Emanuel, 2002, Goldenberg et al., 2001, Emanuel, 2005) to seabirds (King et al., 1992, Benoit and Bretagnolle, 2002, Surman and Wooller, 1995) and to other coastal tropical and subtropical species (Hughes and Connell, 1999, McKinnon et al., 2003, Langtimm and Beck, 2003, Chang et al., 1996). Cyclonic impacts on seabirds include the immediate effects from gale force winds tracking over breeding sites, as well as indirect impacts of wave inundation and erosion under the influence of enhanced waves, tides and currents (King, 1985).

The negative effects of extreme localised climatic events such as cyclones may intensify if seabird populations are also subject to anthropogenic threats (Hulsman et al., 1996, Votier et al., 2005). Such threats are increasing both globally and within the GBR system. For example, tourism on the GBR is a rapid growth industry, with visitation rates increasing by over 100% between 1983 – 1997 to an estimated 1.6 – 2.1 million visitor-days per annum (Valentine et al., 1997, Williams, 1996, Harriot, 2002). Similarly, global fisheries are increasingly coming into conflict with a large number of marine mammal and bird species (DeMaster et al., 2001, Blaber et al., 1998, Frederiksen et al., 2004b). Where seabirds are concerned, these conflicts can involve the indiscriminate removal of large amounts of fish biomass, key upper trophic level predators (Myers and Worm, 2003, Lewison et al., 2004), and/or changes to ecosystem dynamics, via such processes such as bycatch discarding (Blaber et al., 1995). Determining the impacts of these human-induced stresses on seabirds is complicated, as the effects may be realised as direct mortality (Tuck et al., 2001) and/or decreased production and survival (Frederiksen et al., 2004b). However, from a management perspective determining the potential for human activity to influence the reproductive biology of these species is critical to their long-term conservation.

I used 18 years of demographic data collected on the three principal seabird species breeding at Michaelmas Cay to investigate the potential influence of two threatening processes on long-term population trends; cyclone activity and anthropogenic disturbance. For cyclones, the direct effects of gale force winds tracking nearby, or directly over, the breeding colony were examined, as well as the indirect effects of changes in island size and nesting area. Two possible anthropogenic effects were also examined. First was the influence of tourist visitation on breeding population dynamics and second was the level of interaction between breeding seabirds and the northern longline and trawl fisheries.

6.1. METHODS

Michaelmas Cay is a small vegetated sand cay located on Michaelmas Reef (16º 36’ S, 145º 59’ E) in the northern GBR. Approximately monthly counts of all breeding and non-breeding seabirds on the cay were undertaken from May 1984 – November 2001. Details of specific data collection protocols are available in King et al. (1992). Briefly, counts were made as close to the 26th day of each calendar month as logistical constraints allowed. Early censuses (1984 – ~1990) were conducted by counting all the birds present on the cay in individual 10x20 m blocks established by a ‘permanent’ grid over the vegetated portion of the cay. However, progressive movement of the cay due to prevailing south-westerly winds and storm disturbance, combined with concern about the disturbance to birds that would result from reinstalling the grid, resulted in later counts being conducted using random visual markers. As all of the birds present on the cay were counted by both methods, potential discrepancies in the reliability of the data were not introduced with the change. Using the count data I calculated mean values of the numbers of breeding pairs for each year of the study period for three species, the Sooty tern (*Onychoprion fuscata*), Common noddy (*Anous stolidus*), and Crested tern (*Thalasseus bergii*). Rather than using maximum values, annual mean numbers of breeding pairs of each species were derived because 1) at all times of the year, breeding birds are present at Michaelmas Cay (QPWS, unpublished data) and 2) for Sooty terns breeding at Michaelmas Cay, multiple breeding peaks in a single year can occur (see ‘Results’). Annual indices of the numbers of breeding pairs of the three tern species were then compared against a comprehensive range of datasets detailing potential human and cyclonic impacts (Fig. 18).

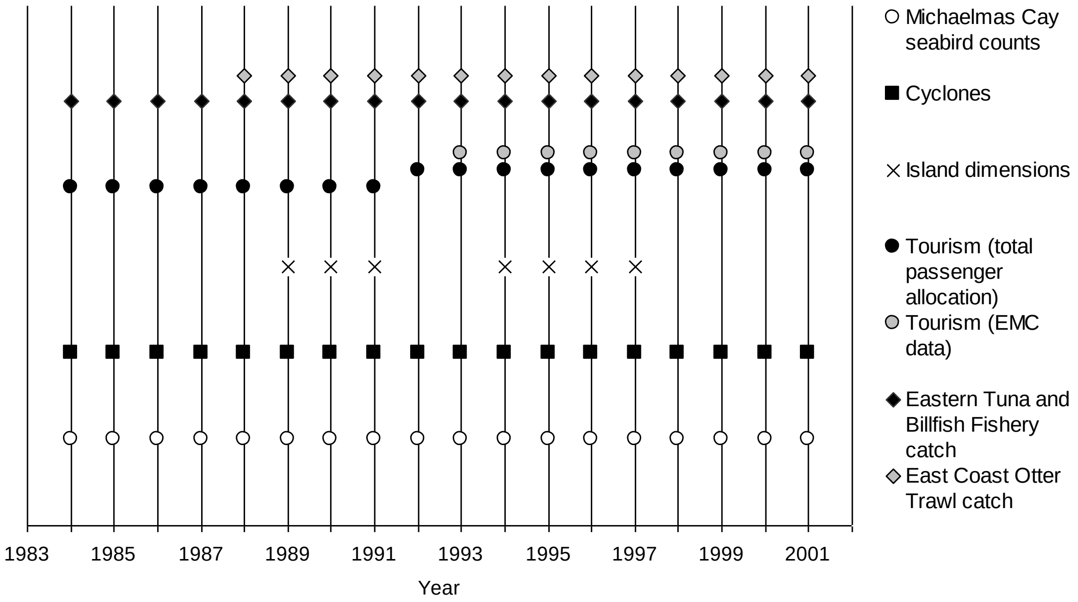


Figure 18. A timeline of data available for assessing potential impacts from cyclonic and human activity on seabird population dynamics at Michaelmas Cay. Numbers of breeding pairs of Sooty terns (*Onychoprion fuscata*), Common noddies (*Anous stolidus*), and Crested terns (*Thalasseus bergii*)(1984 – 2001) were assessed against: intensity data for tropical cyclones which passed within 200 km of the cay (1984 – 2001); changes to available nesting habitat (1989 – 1991 & 1994 – 1997); tourist visitation data from the Environmental Management Charge (EMC; 1993 onwards) and estimates of total passenger allocations through permits issued to commercial boat operators over two 'blocks' (1984 – 1991 & 1992 – 2001) between which permitted visitor numbers were changed; and fisheries data for the Eastern Tuna and Billfish Fishery (15 – 18 °S and 146 – 150 °E; 1984 – 2001) and the East Coast Otter Trawl (within ~100 km of Michaelmas Cay;1988 onwards).

6.1.1. Direct cyclone impacts

Wave damage for normal-sized cyclones in the GBR is restricted to a zone located within 100 – 200 km from a cyclone's path (Done, 1992, Connell et al., 1997), with risk of major disturbance likely at threshold distances of 25 – 100 km (Puotinen, 2004). Cyclonic intensity, commonly measured as central air pressure, largely determines the magnitude and extent of cyclone-generated winds and waves (Brown and Zeng, 1994), with the most damage occurring in the front left stormwise quadrant of the cyclone (Young and Hardy, 1993) in the southern hemisphere, or at an angle of approach of approximately 65° left or upwind of the forward motion vector (Kepert, 2001, Shapiro, 1983). Path and intensity data for all tropical cyclones (TC) occurring in the GBR region over the study period were downloaded from the Australian Bureau of Meteorology (BOM) (http://www.bom.gov.au/climate/how). Data were extracted on date/time latitude and longitude coordinates, central pressure, and radius to maximum winds (radius of the eye) for all major TCs (category 3 or greater during at least a portion of their lifespan) that passed within 200 km of Michaelmas Cay over the study period.

The angle of approach and the distance of the cyclone from Michaelmas Cay were calculated for each point. Cyclone intensity at Michaelmas Cay ($P_{M'mas}$) relative to the pressure of the cyclone at its measured location was determined using the following equation (Holland, 1980, McConochie et al., 1999): $P_{M'mas} = P_o + \Delta P * e^{-(R/r)B}$, where; $P_{M'mas}$ = pressure at Michaelmas Cay, P_o = central pressure, R = radius of maximum winds, r = distance from the centre of the eye to Michaelmas Cay, ΔP = ambient pressure – $P_{o,}$ $B = 7.3 – P_o /160$. For each year in which a cyclone occurred, the calculated $P_{M'mas}$ value for that cyclone was compared to mean number of breeding pairs of each species of seabird for the same year. To assess the impacts of a limited number of episodic events, a standard by which to measure cyclone-driven $P_{M'mas}$ was required. Thus for years in which there were no cyclones, $P_{M'mas}$ was calculated by averaging twice-daily recorded mean sea level pressure measurements collected from a BOM monitoring station at Low Isles Lighthouse (16°23'S, 145°33'E) located approximately 55 km north of Michaelmas Cay, for all days in the months January – May and November – December (cyclone season). Portions of years when cyclones occurred but were no longer present were ignored as incorporating these measurements would strongly dilute the determinability of impacts of these episodic and potentially catastrophic events.

Annual breeding Common noddies and Crested terns were nesting during every cyclone that impacted the cay. The impact of cyclones on Common noddy and Crested tern populations was investigated using simple linear regression with $P_{M'mas}$ as the predictor variable. The breeding status of the subannual breeding Sooty tern (see 'Results') varied during each cyclone occurrence. Thus, the relationship between adult Sooty tern population dynamics and cyclone intensity at the cay was examined using one-factor ANCOVA (Analysis of Covariance), with breeding status (breeding peak; non-breeding [note, however, nesting Sooty terns are present in low numbers throughout the year]) as factor and $P_{M'mas}$ as the covariate.

6.1.2. Indirect cyclone impacts

As geologically temporary features, coral cays respond to fluctuations in environmental conditions and are subject to considerable instability (Gourlay, 1983). However, vegetation is an important morphological stabilising factor on coral islands on the GBR (Heatwole et al., 1996). In Australia, vegetative cover is a prerequisite for breeding for both Sooty terns and Common noddies, while Crested tern nests may be located on bare sand, rock or sparse vegetation (Higgins and Davies, 1996).

Ten aerial photographs of Michaelmas Cay with suitable groundtruthing information were available for seven of the years between 1989 and 1997. Coral patterns on the reef flat and the location/size of stationary objects on the cay were used to scale and orientate the photographs. The photographs were digitalised and introduced into the Geographical Information System (GIS) ArcView (ESRI, 1999). The surface of the cay area that is above water level at high tide varies in altitude by less than ± 1m, and therefore slope was assumed to be zero. The total surface of the cay and the total area of vegetated terrain, considered to be appropriate habitat type, were calculated for each year for which aerial photographs were available.

Due to the small size of Michaelmas Cay and the period over which data on the size of the breeding populations of seabirds were collected, the use of satellite imagery for years outside of which aerial photographs were available (1984 – 1988 and 1998 – 2001) was deemed unfeasible. With a pixel size of 30 x 30 m, Landsat is not sufficiently accurate without appropriate groundtruthing information (no other images/GPS references could be found for this purpose) and other more accurate satellites such as IKONOS, SPOT and QuickBird were not launched until the final year of data collection on seabird population dynamics.

6.1.3. Direct anthropogenic impacts

Human disturbance in the seabird colony on Michaelmas Cay has been considered a long standing problem (King, 1993), with visitation in the early 1990s estimated to exceed 70,000 people per year. In 1986, in an attempt to reduce disturbance the maximum number of people allowed on the island at any one time was capped at 100 (GBRMPA and QPWS, 1986). But it was not until 1990 that visitors were excluded from entering the breeding colony by a fenced boundary that was erected along the vegetation line. The ‘countryside’ type fence can still be crossed by people illegally and so works mainly as a signal of a putative limit rather than as a complete barrier (Cassini et al., 2004). In 2000, the number of people allowed on the cay at any one time was further reduced to a maximum of 50 and the period of access was restricted to between 10:00 and 15:00 hrs (QPWS, 2000).

Prior to 1993, when tourist operators were first required to provide Environmental Management Charge (EMC) logbook returns documenting their use of the GBR Marine Park, data available on tourist use were limited and patchy (Valentine et al., 1997). Even after 1993, records of site-specific use, such as island visitation rates, were not collected until 2001. Thus quality data on the number of tourists visiting the northern GBR, formerly the ‘Cairns Section’, were only available monthly beginning in July 1993 (GBR Marine Park Authority; http://www.gbrmpa.gov.au/corp_site/key_issues/tourism/gbr_visitation/) and no visitation data were specifically available for Michaelmas Cay over the study interval.

King (1993) estimated the number of visitors accessing Michaelmas Cay prior to 1993 by using the total passenger allocations for all operators permitted on the cay for all days of the year (allowing for approximately 60% capacity) (King, 1993, QPWS unpub. data). I used this same technique to examine ‘relative’ visitor access to Michaelmas Cay in my study. Significant changes in 1992 to the number of permitted commercial boat operators at the cay provided broad estimates on numbers of tourists visiting the cay over two ‘blocks’ of the study period: 1984 – 1991 and 1992 – 2001.

6.1.4. Indirect anthropogenic impacts

In the Australian Exclusive Economic Zone, tropical seabirds are potentially influenced by three primary commercial fisheries: (i) pelagic longline fisheries targeting tuna (*Thunnus* spp.), (ii) demersal (bottom) longline fisheries targeting other species, and (iii) demersal trawl fisheries mainly targeting prawns (reviewed by DAAF, 2003). The Eastern Tuna and Billfish Fishery (ETBF - longline) operates in waters deeper than 200 m east of 142°13’E. The Coral Sea Fishery (CSF) encompasses shallow and deepwater line fishing and trawl fisheries, but operates seasonally and with limited fishing activity. The East Coast Otter Trawl (ECOT) fishery is the largest and most widespread fishery in tropical Australia (DEH, 2004). In the far northern section of the GBR Marine Park this fishery has a ratio of between 6:1 to 10:1 of bycatch to prawn catch (Poiner et al., 1999). This bycatch, mainly small fish, is discarded and available to scavenging birds (Blaber et al., 1995).

ETBF data on Japanese and domestic longline fishing effort (1984 – 2001) were obtained from the Australian Fisheries Management Authority (AFMA), with data available as the number of hooks set by month and the processed weight of catch for 1° latitude and longitude bands between 15 – 18 °S and 146 – 150 °E. CSF data were also obtained from AFMA but were patchy and only available beginning in 1998 and thus were not used in these assessments. Data on ECOT commercial prawn catch in tonnes and boat days over grid squares located in a subregion within ~100 km of Michaelmas Cay (H14, H15, H16, I14, I15, I16, I17, J15, J16, J17 on the Department of Primary Industries and Fisheries database; `http://chrisweb.dpi.qld.gov.au/CHRIS/)` were downloaded for the period between 1988 (beginning of logbook data) and 2001.

Statistics on fisheries catch per unit effort (CPUE) (kg 1000 hooks set^{-1} longline and kg boat-day^{-1} prawn trawl) were used as relative abundance indices (Montevecchi and Myers, 1997) to analyse the potential influence of two food resources on seabird breeding populations; small pelagic fish and associated underwater predators, and trawling discards, respectively. Tropical pelagic seabirds such as Sooty terns and Common noddies are largely dependent on underwater predators to force prey to the surface where it becomes available to aerial predators (Au and Pitman, 1986). On the other hand, Crested terns are nearshore foraging species which rely on plunge-diving to obtain prey from shallow nearshore waters (Higgins and Davies, 1996). Crested terns are also frequent trawl discard feeders whose diet may be comprised of up to 70% discards during open trawl seasons (Blaber et al., 1995). Common noddies may also feed on trawl discards. Trawlers also have been recorded to kill adult Crested terns (Minton, 1992).

6.1.5. Statistical analyses

All data were tested for normality and homogeneity of variances. Student's t-tests and linear regressions were conducted where these assumptions were met. Average values are given as ± 1 standard error (S.E.) and all significance was set to $P \leq 0.05$.

6.2. RESULTS

6.2.1. Population dynamics

Breeding populations of both the Sooty tern and Common noddy showed large fluctuations over the study period (Fig 19). Annual estimates of the numbers of breeding pairs of these two pelagic species were highly correlated with each other (ANOVA, $F_{1,16} = 29.923$, $r^2 = 0.652$, $P < 0.001$). Declines in the breeding populations of both Sooty terns (Fig. 19a) and

Common noddies (Fig. 19b) are apparent but not significant when data to 2001 are included (Sooty tern: $F_{1,16} = 0.617$, $r^2 = 0.037$, $P = 0.443$; Common noddy: $F_{1,16} = 0.082$, $r^2 = 0.005$, $P = 0.779$). This is, in part, because for one season in 2000, breeding numbers of both species were at levels not previously seen for over a decade (Fig. 19a, b). However, the mean annual number of breeding pairs of Sooty terns (±S.E.) counted on Michaelmas Cay decreased from 4917 ± 1440 in 1984 to 2707 ± 801 in 2001 at the rate of approximately 2.5% per year (equal to a 45% decline in 25 years and a 71% decline in 50 years)(Fig. 19a). Annual mean breeding pairs of Common noddies decreased from 1720 ± 430 in 1984 to 1263 ± 269 in 2001 at the rate of 1.5% per year (equal to a 30% decline in 25 years and a 52% decline in 50 years)(Fig. 19b). On the other hand, the number of Crested tern breeding pairs appears to have increased steadily between 1984 and 2001, although this trend is also not significant ($F_{1,16} = 1.005$, $r^2 = 0.059$, $P = 0.331$) from 95 ± 40 in 1984 to 432 ± 264 in 2001 at the rate of 4.3% per year (equal to a 175% increase in 25 years and a 687% increase in 50 years)(Fig. 19c).

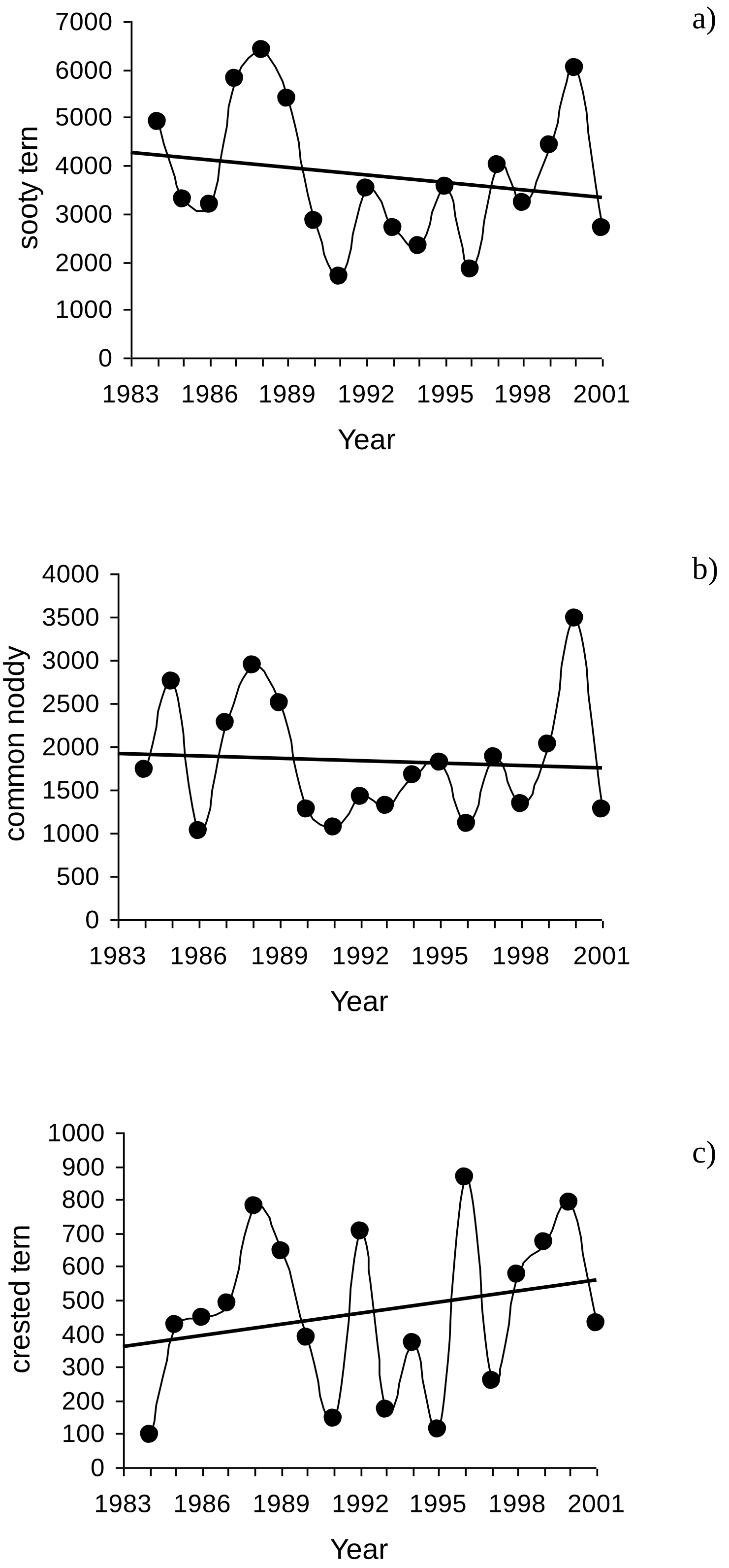


Figure 19. Population trends in annual mean number of breeding pairs of the three primary breeding seabirds at Michaelmas Cay, far north Queensland over an 18-year period between 1984 and 2001 including two pelagic species a) the Sooty tern (*Onychoprion fuscata*) and b) the Common noddy (*Anous stolidus*), and an inshore foraging species, c) the Crested tern (*Thalasseus bergii*).

6.2.2. Cyclones

Six category 3 or greater tropical cyclones passed within 200 km of Michaelmas Cay over the study period. These cyclones varied in intensity, strength of winds generated, distance from Michaelmas Cay, time spent within the vicinity of Michaelmas Cay, and angle of approach (Table 5), all of which affect the spatial distribution of high winds (Puotinen, 2004) and waves (Harmelin-Vivien, 1994) generated at individual reefs.

Table 5. Cyclone events recorded as greater than or equal to a category 3 cyclone (average wind speed 120-160 km/hr) which passed within 200 km of Michaelmas Cay (M'mas) between 1984 and 2001 (calculated from data provided by the Australian Bureau of Meteorology (BOM)). The pressure at Michaelmas Cay ($P_{M'mas}$) was calculated based on relationships between central pressure of the cyclone, radius of the eye and distance from the centre of the eye to the cay and angle of approach is the number of degrees off a direct approach (0°) of the cay.

Tropical Cyclone	Dates within 200 km M'mas Cay	Minimum distance from M'mas (km)	Minimum $P_{M'mas}$ (hPa)	Minimum angle of approach (°)
Winifred	31 Jan - 1 Feb 1986	111.9	975	40.1
Ivor	22 - 23 Mar 1990	34.6	999	16.8
Joy	22 - 25 Dec 1990	80.4	961	22.6
Justin	21 - 22 Mar 1997	11.3	990	8.0
Rona	11 - 12 Feb 1999	61.6	972	8.2
Steve	27 Feb 2000	27.8	980	2.5

Cyclones which struck during sensitive stages of breeding had immediate impacts on the numbers of birds breeding on the cay, most commonly through high mortality of eggs and/or chicks. For example, large numbers of Sooty tern and the Common noddy nests/offspring were destroyed by the onslaught of TC Winifred in January 1986. TC Ivor in March 1990 severely disrupted the breeding cycle of Sooty terns, which were at the time breeding in large numbers on the cay, and resulted in a subsequent series of small breeding peaks and a delayed breeding cycle of 18 months. The 18-month breeding cycle, which finished with a breeding peak in December 1990, was then disrupted by TC Joy in the same month. However, in some cases the disruption caused by major cyclones was minimal. TC Justin in March 1997 struck at the initiation of a Sooty tern breeding peak, when only 228 Sooty tern eggs were present on the cay, and caused only a slightly delayed breeding peak in May of the same year.

These immediate cyclonic impacts did not affect longer-term population trends for any of the three species. Interannually, the pressure at Michaelmas Cay ($P_{M'mas}$) was not related to the number of breeding pairs of Sooty terns present at the cay ($F_{1,14} = 0.145$, $r^2 = 0.050$, $P = 0.709$), with no differences between whether a sooty tern breeding peak was observed or not ($F_{1,14} = 0.043$, $P = 0.838$) and no interaction between the terms ($F_{1,14} = 0.048$, $P = 0.829$). The numbers of breeding pairs of Common noddies ($F_{1,16} = 0.056$, $r^2 = 0.003$, $P = 0.817$) and Crested terns ($F_{1,16} = 0.033$, $r^2 = 0.002$, $P = 0.858$) were also not related to $P_{M'mas}$.

From 1984 – 2001 Sooty terns breeding peaks exhibited a subannual periodicity (mean of 10.2 ± 0.8 months). This changed to 9.1 ± 0.6 months when cycles during which the breeding population was detrimentally impacted a cyclone were removed (TC Winifred in 1986, TCs Ivor and Joy in 1990). Common noddies displayed an annual breeding cycle (mean of 11.8 ± 0.7 months between peaks or 11.5 ± 0.7 months if these same potential cyclone-affected cycles are removed). Crested tern breeding frequency was only slightly affected by a single cyclone (TC Joy in 1990); with this data point removed, Crested terns bred annually (every 12.2 ± 0.4 months).

6.2.3. Island dimensions

No consistent increases or decreases were apparent in either the area of available nesting habitat (Pearson's r = -0.128, n = 7, P = 0.784 (two-tailed), mean 7635.60 ± 1426.86 m^2), or in total cay size (Pearson's r = -0.023, n = 7, P = 0.961, mean 19032.07 ± 4573.51 m^2) over the period for which aerial images were available (Fig. 20a, b). However, cyclones tracking nearby the island led to substantial short-term changes in the amount of available nesting substrate on the island (Fig. 20b, c), with 7800 m^2 of vegetated habitat available to breeding birds prior to the onset of TC Justin in 1997 and 2800 m^2 available two months later.

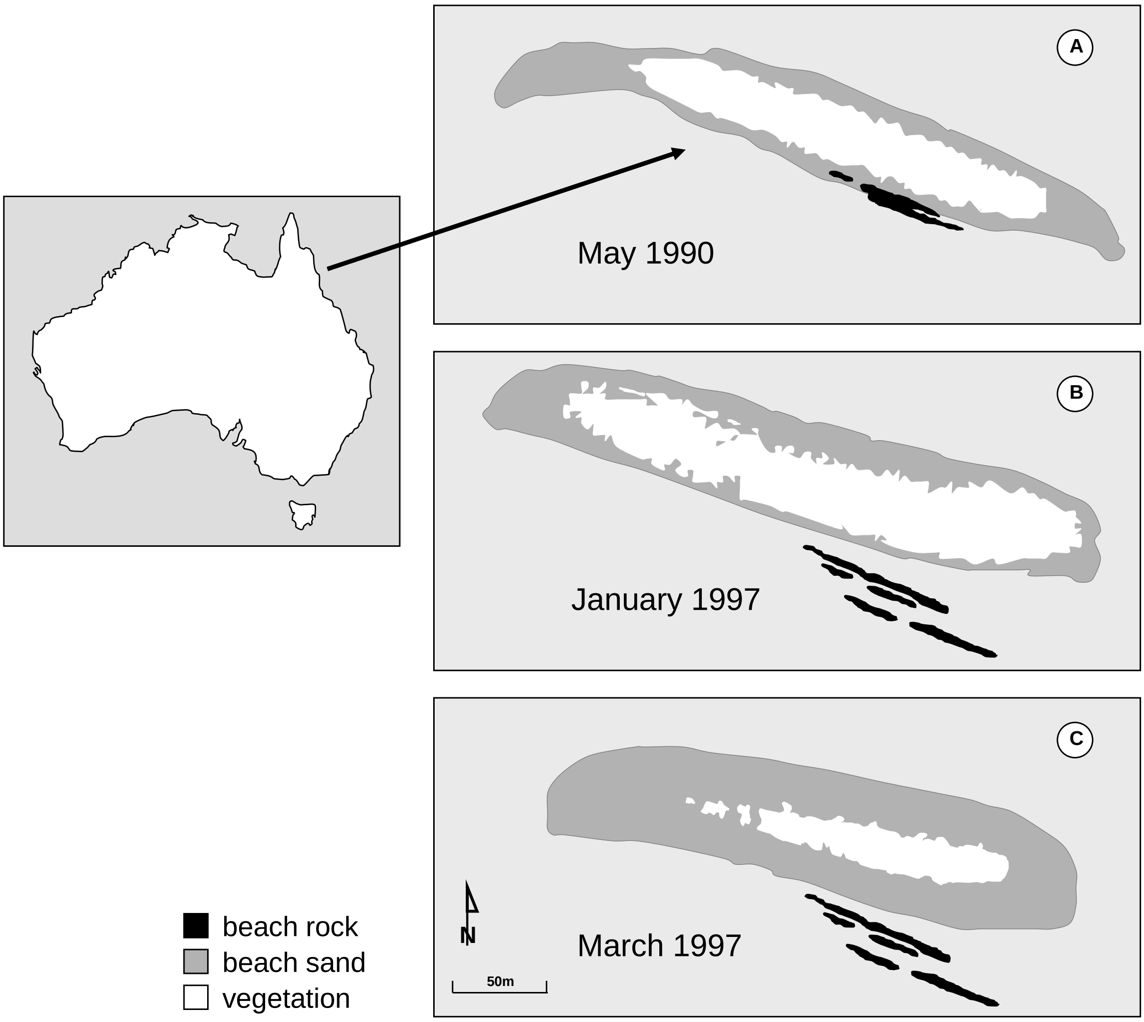


Figure 20. Michaelmas Cay, northern Great Barrier Reef. White areas represent vegetated surface suitable for nesting in 1990 a), in 1997 before Cyclone Justin b) and in 1997 after Cyclone Justin c). The inset shows the location of the cay on a map of Australia.

No significant relationships were detected between the mean amount of available vegetated nesting habitat each year and the mean number of breeding pairs of any species of seabird at Michaelmas Cay (Sooty tern: $F_{1,5} = 0.005$, $r^2 = 0.001$, $P = 0.945$; Common noddy: $F_{1,5} = 0.287$, $r^2 = 0.054$, $P = 0.615$; Crested tern: $F_{1,5} = 1.492$, $r^2 = 0.230$, $P = 0.276$). Nor were there trends between total cay size and breeding pairs (Sooty tern: $F_{1,5} = 2.180$, $r^2 = 0.304$, $P = 0.200$; Common noddy: $F_{1,5} = 5.140$, $r^2 = 0.507$, $P = 0.073$; Crested tern: $F_{1,5} = 0.001$, $r^2 = 0.001$, $P = 0.976$). However, these non-significant results should be interpreted with caution considering the small number of years for which aerial photographs were available.

6.2.4. Tourism

Logbook return data demonstrated that the number of tourists visiting the Cairns region of the GBR remained approximately stable over the period 1993 – 2001 (annual mean tourist visitation: 74505 ± 1741 people) with no significant interannual difference in visitation (Anova $F_{8,93} = 1.572$, $P = 0.114$). Annual mean human visitation and annual mean number of breeding pairs at the cay over this timeframe were not significantly related for any of the three seabird species (Sooty tern: $F_{1,7} = 0.085$, $r^2 = 0.087$, $P = 0.440$; Common noddy: $F_{1,7} = 0.590$, $r^2 = 0.005$, $P = 0.468$; Crested tern: $F_{1,7} = 0.806$, $r^2 = 0.103$, $P = 0.399$). Again, the limited number of years in which logbook return data were available means that the reliability of these tests is reduced and must be viewed circumspectly.

King (1993) used a gross estimation to determine that approximately 70,000 people were visiting Michaelmas Cay each year 1984 – 1991. During the second half of the study, I used the same technique to determine that approximately 126,000 people were visiting the cay each year 1992 – 2001 (based on total passenger allocations for all permitted operators at 60% capacity). While these estimates vary from the data provided through the EMC logbook returns (above), and may overestimate actual cay usage, their importance is that they provide a direct relative comparison between the two ‘blocks’ of time during which different permit allocation processes have been used. Visitation to Michaelmas Cay between these two permit ‘blocks’ did not appear to influence the mean annual number of breeding seabirds on the cay. Mean numbers of Sooty tern pairs present at the cay (±SE) between 1984 – 1991 (block 1) and 1992 – 2001 (block 2) did not vary (block 1: 4187 ± 589, block 2: 3436 ± 379; Student’s t-test, $t_{1,16}$ = 1.113, P = 0.282 (2-tailed)). Nor were there significant differences in mean annual numbers of Common noddies (block 1: 1945 ± 272, block 2: 1729 ± 216; $t_{1,16}$ = 0.630, P = 0.537), or the Crested terns (block 1: 426 ± 81, block 2: 495 ± 84; $t_{1,16}$ = -0.589, P = 0.564) between the two permit blocks.

6.2.5. Fisheries

Mean catch per year by the ETBF in the Michaelmas Cay region (947.15 ± 86.64 kg 1000 hooks set^{-1}) did not correlate with changes in the number of breeding pairs of any seabird species at the cay during the same year, or in the year following (Table 6). However, longline CPUE was correlated with average Sooty tern and Common noddy breeding numbers 2 years later (Fig. 21). A relationship between numbers of Crested terns breeding and longline CPUE was not present at any temporal scale (Table 6).

Table 6. Regression analyses results describing relationships between the annual average Eastern Tuna and Billfish Fishery (ETBF) catch per unit effort (CPUE, kg 1000 hooks set^{-1}) and the number of breeding pairs of Sooty tern, Common noddy and the Crested tern at Michaelmas Cay. Linear regression was used to explore annual associations between $\log_{10}$ CPUE and the number of breeding pairs of each species in the same year (*n*), one (*n* + 1) and two (*n* + 2) years later.

Year of seabird breeding participation relative to annual $\log_{10}$ CPUE yr *n*	Species	F	d.f.	r^2	*P*
year *n*	Sooty tern	0.215	1,16	0.013	0.649
	Common noddy	0.185	1,16	0.011	0.673
	Crested tern	0.072	1,16	0.004	0.792
year *n* + 1	Sooty tern	1.796	1,15	0.107	0.2
	Common noddy	0.02	1,15	0.001	0.889
	Crested tern	0.302	1,15	0.02	0.591
year *n* + 2	Sooty tern	**7.817**	**1,14**	**0.358**	**0.014**
	Common noddy	**12.11**	**1,14**	**0.464**	**0.004**
	Crested tern	3.842	1,14	0.215	0.07

Note: Significant relationships are in boldface.

Between 1988 and 2001, within ~100 km of Michaelmas Cay commercial prawn trawlers logged a CPUE (±SE) of 460.33 ± 15.17 kg boat-day^{-1}. There appeared to be a non-significant increase in CPUE over the interval (linear regression, $F_{1,12} = 3.470$, $r^2 = 0.224$, $P = 0.087$) that had no influence on seabird populations on the cay (linear regression, Sooty tern: $F_{1,12} = 0.448$, $r^2 = 0.036$, $P = 0.516$; Common noddy: $F_{1,12} = 0.675$, $r^2 = 0.053$, $P = 0.427$; Crested tern: $F_{1,12} = 0.030$, $r^2 = 0.002$, $P = 0.866$).

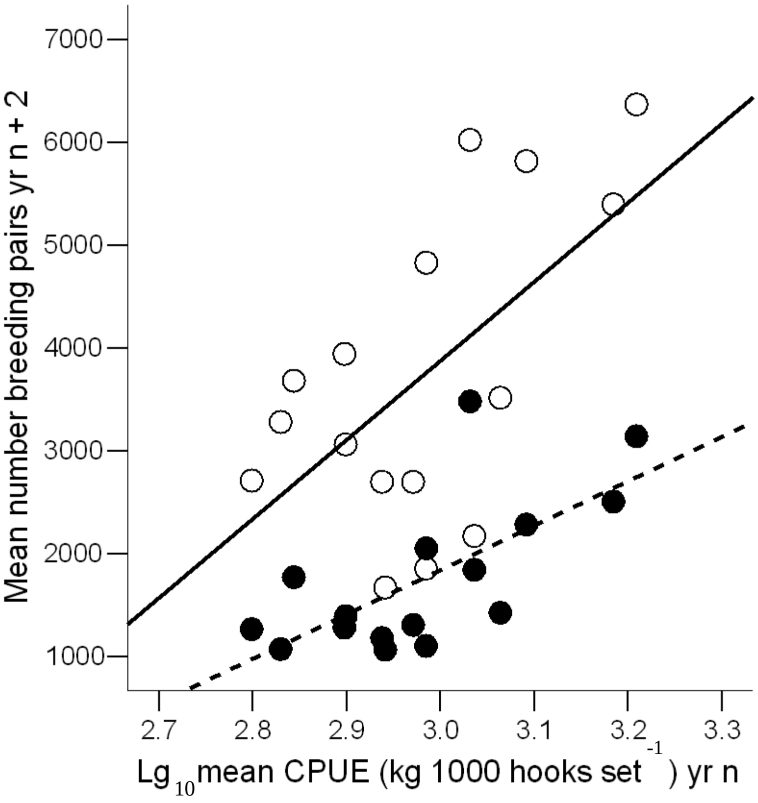


Figure 21. The average annual number of breeding pairs counted on Michaelmas Cay 1984 – 2001 for the Sooty tern (○) and Common noddy (●) two years following (*n* + 2) $\log_{10}$ mean annual Eastern Tuna and Billfish Fishery (ETBF) catch per unit effort (CPUE) in kg 1000 hooks set^{-1} between 15 – 18 °S and 146 – 150 °E each year (*n*).

6.3. DISCUSSION

Numbers of Sooty terns and Common noddies fluctuated substantially over the study interval, with populations of both species tending towards overall declines. Over the same period there was an increase in the size of the Crested tern population. Significant declines in populations of the pelagic species reported previously (De'ath, 1994, Hulsman et al., 1996, King et al., 1992) appear to have been arrested, in particular, by a year of extremely high breeding participation in 2000 (Fig. 19a, b). For both species, the breeding numbers observed in 2000 had not occurred in the preceding 10 years, a period well in excess of the pre-breeding phases (Higgins and Davies, 1996). It is unclear whether data collected in 2000 represent a recruitment pulse associated with productivity from Michaelmas Cay itself, or an unusual influx of breeding individuals from elsewhere. Without further data on recent population trends it is also not possible to tell whether the 2000 data represent a true recovery of these populations or not.

Of all the variables investigated in this study, tuna and billfish catch rates were shown to be the only significant predictor of seabird breeding population sizes at Michaelmas Cay. Longline catch per unit effort in the Michaelmas Cay region was positively correlated with the breeding numbers of both pelagic foragers two years later. One explanation for this finding is that decreases in the abundance of subsurface predators in the region result in a decline in prey availability to pelagic seabirds (Au and Pitman, 1986) and poor reproductive output, which is then followed by poor recruitment and/or reduced breeding participation two years later. Tuna abundance has already been shown to be a significant predictor of Sooty tern foraging success at this location (Chapter 5). However, the recruitment periods for Sooty terns and Common noddies are thought to be 4 – 5 and 3 – 4 years, respectively (Higgins and Davies, 1996). The relationships between forage fish abundance, prey availability, reproductive success and breeding participation in this system appear to be complex and require further investigation.

That Sooty terns at Michealmas Cay have multiple breeding peaks each year suggests that food availability, a key factor in the breeding success of Sooty terns (Le Corre, 2001), does not vary as significantly between seasons at this location as it does at more subtropical sites (Ashmole, 1963, Jaquemet et al., 2007, Schreiber et al., 2002). Instead, it appears that the development of oceanic features such as fronts that favour the aggregation of prey and the presence of subsurface predators may play a greater role in seabird breeding dynamics (Ballance et al., 2006, Chapter 3).

Breeding participation of Crested terns was not related to changes in the longline fishery’s CPUE at any temporal scale. Differences between this result and those obtained for the pelagic foraging species are likely due to differences in foraging ecology. Crested terns forage mainly over shallow reef flats and coastal shelf waters nearby their breeding islands (Surman and Wooller, 2003) and do not rely heavily on subsurface predator activity to be able to access prey (Higgins and Davies, 1996). Crested tern population dynamics at the cay were also not related to the trawl fishery’s CPUE despite previous suggestions that this species benefits heavily from trawl discards (Blaber et al., 1998). This could be because trawl discards were relatively constant between 1988 and 2001, thereby providing a stable food source.

Although individual cyclones had substantial impacts on the reproductive success of some Michaelmas Cay seabirds (De'ath, 1994, Hulsman et al., 1997, King et al., 1992), they had no noticeable impact on the longer-term trends in breeding numbers. This is supported by De'ath’s (2001) findings that early negative impacts on Common noddies from TCs Winifred and Joy were mitigated after impact periods of some one and three months subsequent to these cyclones, presumably because the affected birds re-layed (though this cannot be confirmed without individual identification). Management regimes in place, which include indefinite moratoriums on public access to the breeding colony following catastrophic events (Muir and Chester, 1992, QPWS unpub. data), presumably contribute to mitigating long-term impacts. However, increases in cyclone frequencies and/or intensities as a result of climate change and associated-ENSO variation have been predicted in the Australia region (Walsh and Ryan, 2000, Broadbridge and Hanstrum, 1998). Future changes in cyclone dynamics could result in increased mortality and reduced recovery periods for breeding seabirds on the

GBR. Increased cyclone-driven changes to cay size have the potential to impact nesting space for the pelagic foraging Sooty terns and Common noddies in particular, as they are more limited by their association with vegetation for nesting and have high levels of philopatry which limit inter-colony movements in these species (Higgins and Davies, 1996, Avise et al., 2000).

Tourist visitation to Michaelmas Cay does not appear to be having a substantial impact on long-term population trends for any of the three main breeding seabirds on the cay. This result should be viewed with some care considering the limited number of years for which EMC data were available and the broad estimates that were made using total passenger allocation numbers. However, in Chapter 7 I reported on two independent experiments that examined the impacts of tourism on breeding success in Sooty terns and Common noddies at Michaelmas Cay and determined that current management protocols appear to be appropriately facilitating shared usage between wildlife and the tourism industry at Michaelmas Cay. These combined results suggest that the strict visitor management protocols that have been implemented at the cay (GBRMPA and QPWS, 1986, QPWS, 2000), including construction of the fence in 1990, may be mitigating the potential negative influence of tourism to the seabird colony.

In summary, neither cyclones nor tourism had lasting negative impacts on the three most abundant seabird species breeding at Michaelmas Cay. However, the large fluctuations in the sizes of the breeding populations of these species, in particular the pelagic species, the inconclusive nature of the recent population trends, limited data availability on tourism trends and cay size, and potential for other negative stressors to impact these species suggest that a cautionary approach towards management of these populations is warranted and that strategies attempting to mitigate potential tourism and pelagic fisheries industries impacts should continue.

CHAPTER 7

Publication arisen:
Devney, C. A., and Congdon, B.C. 2009. Testing the efficacy of a boundary fence on an important tropical seabird breeding colony and key tourist destination. *Wildlife Research* 36, 353-360.

7.0. INTRODUCTION

Seabirds have a number of life-history characteristics that make them particularly sensitive to human disturbance (Carney and Sydeman 1999; Erwin 1980; Rodgers and Smith 1995). Seabirds are relatively accessible compared to most other marine organisms as they are found above water and are easy to view and in many cases easy to approach. In addition, seabirds frequently nest in large dense concentrations often on, or in, the ground making large numbers susceptible at any one time to intense and/or catastrophic events (Schreiber, 2002). Although this taxon appears to be capable of becoming tolerant to repeated human intrusion (Nisbet, 2000), disturbance from tourism at seabird rookeries has been suggested as a significant predictor of breeding success for some species (Anderson and Keith 1980; Giese 1996; Robertson 1997). With wide-spread growth in human visitation to these fragile ecosystems (Hall, 2001), there is an urgent need to find techniques for mitigating the potential negative impacts on seabird populations.

A number of methods have been employed to protect seabirds at breeding colonies. These include restricting the total number of visitors (Geist et al., 2005), or restricting visitor approach and movement through the use of physical barriers, such as fences (e.g. Burger et al., 1995, Larson, 1995). Fences provide a buffer zone between people and wildlife by fostering normal animal behaviour. Although few studies have been conducted on the efficacy of fences on bird taxa, at least one suggests that waterbirds exhibit increased tolerance towards visitors walking on the opposite side of a fence (Ikuta and Blumstein, 2003).

For tern colonies, it has been suggested that recommended safe set-back distances for human visits are between 50 and 200 m (Carney and Sydeman 1999; Erwin 1989; Rodgers and Smith 1995). These buffers are recommended because bird responses to human presence include stress, increased heart rate, decreased breeding success and flushing (Tarlow and Blumstein, 2007). However, the distance at which birds react to perceived threats vary based on the species (Erwin, 1989, Yorio et al., 2001, Burger, 1981), the nature and frequency of the disturbance (Fowler, 1999, Burger and Gochfeld, 1999); on visitor (Beale and Monaghan, 2004) and bird group sizes (Martínez-Abraín et al., 2008); on stage of breeding (de Villiers et al., 2005, Vos et al., 1985, Erwin, 1989); and on the starting distance of the perceived threat (Blumstein, 2003). An often effective alternative to buffer zones is to allow birds to habituate to regular benign human presence (Walker et al., 2006, Dunlop, 1996, Gyuris, 2004, Ikuta and Blumstein, 2003, Cooke, 1980).

On the Great Barrier Reef (GBR), Australia, increasing human presence since early this century has irrefutably contributed to changes in the size and composition of avifauna (Hulsman, 1984). For example, development of Heron Island, in the southern GBR led to the extirpation of Roseate terns (*Sterna dougallii*) (Hulsman, 1983, Hill and Rosier, 1989, Kikkawa, 1970). The possibility of similar negative impacts elsewhere is considerable given that tourism on the Great Barrier Reef is one of the fastest growing industries in the region (Valentine et al., 1997, Williams, 1996, Harriot, 2002).

Michaelmas Cay on the northern GBR is a critical seabird breeding colony and is also a prime tourist destination (GBRMPA and QPWS, 2001). Human disturbance in the seabird colony on Michaelmas Cay has been a problem in the past (Hulsman et al., 1996, Edwards, 1997, King, 1993), with visitation in the early 1990s exceeding 70,000 people per year (GBRMPA and QPWS, 2001). Concern about human impacts to seabird breeding success and the sustainability of vegetation on the cay (King et al., 1992) led Queensland Parks & Wildlife Service (QPWS) to erect a exclusionary boundary fence in 1990. This ‘countryside’ type fence can still be crossed by people and works mainly as a signal of a putative limit rather than as a complete barrier (Cassini et al., 2004). In the year 2000, tourism operators agreed to voluntarily cap the number of visitors allowed on the cay at any one time at 50 (GBRMPA and QPWS, 1986, QPWS, 2000); concurrently QPWS reduced the available human access area by a third of its original size and access was limited to between 10:00 and 15:00 hrs for all persons.

The aim of this study was to determine whether the non-restrictive fence at Michaelmas Cay was safeguarding breeding seabirds during peak breeding periods. To this end I conducted two separate investigations. First, using data already in existence, I explored the relationships between egg loss and proximity to the fence for the two most abundant breeding species on the cay, the Sooty tern (*Onychoprion fuscata*) and the Common noddy (*Anous stolidus*). Second, I monitored adult Sooty tern foraging success, meal composition, chick growth/survival and depredation of breeding attempts by gulls in the colony at two distances from the tourist fence. During both assessments minimum disturbance practices (Brown and Morris 1994; Brown and Morris 1995; Fetterolf 1981) were implemented by using video monitoring which maximised the ability to detect reproductive trends and visitor impacts, while minimising observer effects.

7.1. METHODS

7.1.1. Study site and design

Michaelmas Cay is a small vegetated sand cay located on Michaelmas Reef (16º 36' S, 145º 59' E) in the northern section of the GBR. The cay is ~1.8 ha in size with a vegetated area of approximately 300 m x 60 m (Fig. 22). On the leeward side of the cay a 75 m long x 1 m high boundary fence with trailing arms that run to the waters edge is located so that the back fence line sits on the 3 m tidal mark. Sooty terns (*Onychoprion fuscata*) and Common noddies (*Anous stolidus*) are long-lived pelagic foraging species which lay a single-egg clutch (Higgins and Davies, 1996). These species nest in dense aggregations on the ground and travel large distances to obtain food to provision offspring (Ballance and Pitman, 1999, Schreiber et al., 2002, Surman and Wooller, 2003).

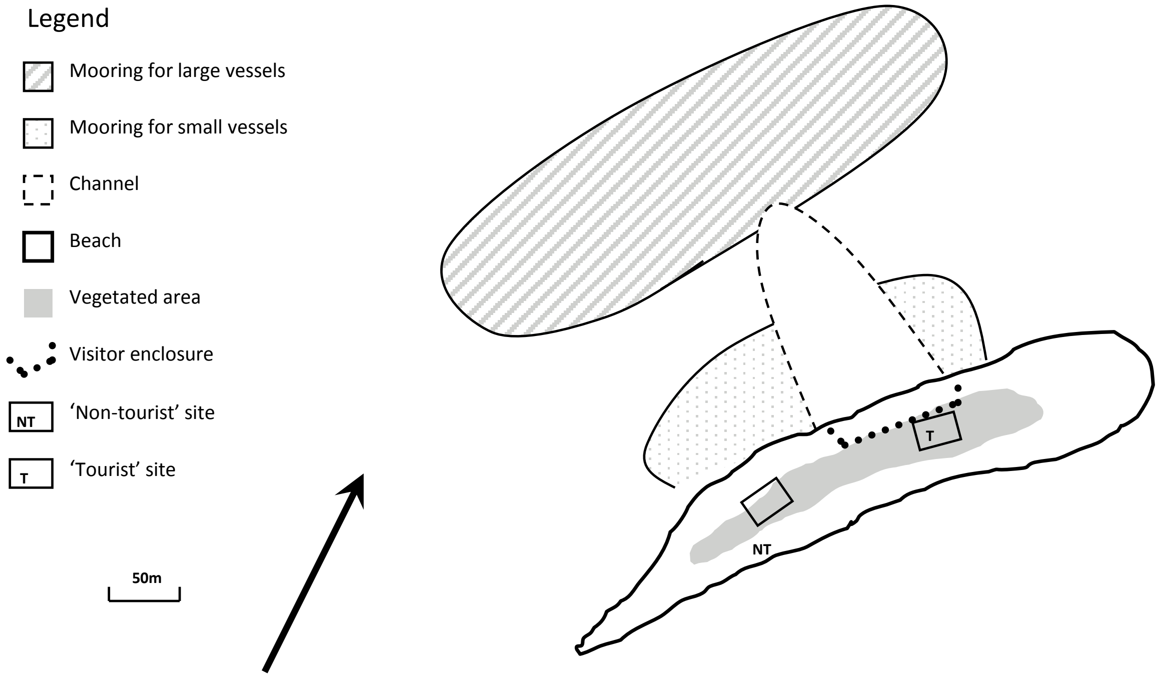


Figure 22. Map of Michaelmas Cay National Park showing the locations of the 'tourist' and 'non-tourist' study plots relative to the boundary fence that separates human visitors from fragile nesting habitat on the cay (adapted from GBRMPA and QPWS 1986). In Quasi-experiment 2, the tourist plot was located 5 m from the fence and breeding Sooty terns were exposed to regular human visitation while the non-tourist plot was ~50 m from the small area of the cay visited by humans.

7.1.2. Hatching success

In my first assessment I investigated egg losses for the two main species of breeding seabirds on the cay, the Sooty tern and the Common noddy, in relation to proximity to the fence during the 1999 – 2000 breeding season. For this assessment, I used data that were collected previously by another research. At weekly intervals between 30 Dec 1999 and 1 June 2000 hand held video footage was collected of all nests that were observable from a number of set locations behind the boundary fence. The footage was then compiled into photo mosaics of multiple regions of the island, with each mosaic including significant landmarks. These landmarks allowed individual nests to be identified and monitored on a weekly basis. Data were used to provide estimates of proportions of eggs lost per week for the two species combined, at four different distances from the boundary fence. Factors responsible for egg losses in this experiment were unknown but the potential for silver gull depredation to be important was examined in a later experiment (see below). Data from the two species were combined because of strong similarities in nesting behaviour and other life history characteristics (Higgins and Davies, 1996, Chapter 3).

Egg loss data for 30 – 40 nests per plot were obtained from a total of twelve 5 m x 5 m sampling plots; three replicate plots per distance from the fence (~3, 6, 18 and 36 m). Data on rates of egg loss among this number of nests were reliably collected from lens magnifications that framed a sampling plot of approximately 5 m x 5 m. Individual nests and eggs were clearly visible at these magnifications, and only nests where eggs were laid during the first two weeks of the study were used to track egg losses. Five sets of photo mosaics covering a seven-week period were created for each sampling plot. This was so that equivalent incubation periods could be assumed among plots and that any egg losses would not be due to chicks hatching and subsequently leaving the nest (before they were detected by the video equipment) to form crèches, which occurs after ~2 – 3 days of age for both species (Higgins and Davies, 1996).

7.1.3. Provisioning, growth, survival and predation

Sooty tern foraging success, meal composition, chick growth/survival, and depredation of breeding attempts by gulls were monitored at two sample plots on the cay during the April – June 2005 breeding season for this species. The plots used in this quasi-experiment did not spatially overlap with the ones in the previous quasi-experiment. One plot was within 5 m of the fenced-in tourist enclosure ‘tourist’ and a second plot was approximately 50 m from the enclosure ‘non-tourist’ (Fig. 22). Both plots were at equivalent stages of breeding;

additionally, plots were on the leeward side of the cay and were in locations with similar vegetation, topography and nesting densities of Sooty terns. In order to minimise disturbance in the interior of the colony and maximise similarity between plots, both were situated on the colony edge. Tourist plots were not replicated in this quasi-experiment as the large size of the tourist plot relative to the length of the fence line precluded effective replication. Similarly, the non-tourist plot was not replicated because of the potential adverse effects of accessing and banding chicks in multiple sections of the colony. This lack of replication reduces my ability to strongly infer that differences between the plots are directly attributable to proximity of the fence. However, a priority of this study was to minimise disturbance in the colony and strict permit conditions were applied in accordance. Nevertheless, the large plot sizes relative to both the size of the breeding colony and the area of interaction between tourists and birds, and the rigor used in insuring consistency in all other environmental factors between plots allows for the best possible examination of fence effects.

The same basic protocols were used at both plots in my second quasi-experiment. The tourist plot was monitored by an observer using binoculars within a few metres of the fence line; human visitors were already present within the fence enclosure and so any potential observer effect was integrated into the larger tourist effect. Conversely, the non-tourist plot was monitored either by an observer using a scope at a distance greater than 20 m from the plot, or by a digital camcorder at a distance of 3 – 5 m. These observation techniques were the best available for mitigating observer impacts (Keedwell and Sanders, 2002).

At both plots, a subset of 3 day old chicks was metal and colour-banded for individual recognition. Twenty chicks were banded in this way at the tourist plot and twenty-two at the non-tourist plot. All banding took place on 28 April 2005. Data were subsequently collected during 19 days from 6 May to 22 June 2005 (data were not collected every day during this period due to restrictions on access).

Adult feeding rates for a known number of similarly-aged banded (those mentioned above) and unbanded Sooty tern chicks were recorded continuously over periods of 2 – 3 hours. Both banded and unbanded chicks were monitored so as to increase sample sizes and to facilitate comparisons with data collected for Chapter 4. The use of unbanded chicks was also necessary as banded chicks were not always fed during the observation interval. Age estimates of unbanded chicks were derived from comparison with time-series photos taken of multiple known-age chicks. Detailed methods on how visual observations of provisioning rates were used to determine relative meal sizes provided by chicks are described in Chapter 4. Briefly, the observed size and width of prey items provided to chicks by their parents relative to the size of the adult's bill were recorded as a relative 'meal index'. For example, food items that were approximately the same length and width as the adult's bill were assigned a meal index value of 1; items that were one and a half times the length and the same width were given a value of 1.5, and so on. Total meal indices provided to groups of monitored chicks were combined each day and then divided by the number of chicks in the group to determine a relative meal index for each site during each day of the study. Feeding frequencies were comprised of the total number of deliveries per observation period divided by the number of chicks in the observation area and the number of minutes of observation. Prey items were also classified according to taxa as squid, fish or unknown during the observation intervals and mean daily proportions of each prey type were then calculated.

Colour-banded chicks were weighed and measured at banding and during three subsequent visits to the cay (12, 14 and 17 May 2005). Chick culmen, tarsus and wing chord lengths were measured using digital callipers (± 0.1 mm) and chicks were weighed to the nearest 0.1g using an electronic scale at 07:00 and 15:00 hrs. As a result of limited data points, morphometric data were insufficient to fit logistic growth curves but allowed for comparisons of relative mass and size changes between sites. Survival of all colour-banded chicks at the two sites was monitored throughout the study. Mortality was recorded if the chick was not seen for more than five consecutive observation days, and the chick was not seen again before the end of the study. Chicks that died before the final growth measurements were taken were excluded from all relative growth comparisons.

Silver gull predation on Sooty tern eggs and chicks was compared between the tourist and non-tourist breeding sites during this experiment in 2005. I defined a predation event as any depredation of a Sooty tern egg or chick (not necessarily the study chicks) within a 10 m radius of the plot being observed during the 2 – 3 hour observation interval. The strong similarities in between the non-tourist and tourist study plots (i.e. nesting densities, topography, vegetative composition) meant that predation ‘opportunities’ (number of eggs with nests and the number of chicks in the crèches) were approximately equal between the two study areas during observations. Data on predation were not included for days where a human observer was not present to monitor the non-tourist site, as on these days the camcorder was focused on the study chicks only and did not record a 10 m radius around the observation zone. The total number of predation events recorded during an observation interval was divided by the amount of observation time to generate rates of predation per hour.

7.1.4. Statistical analyses

Non-proportional data were tested for normality and homogeneity of variance and parametric ANOVA performed when these assumptions were met. Data from the large single treatment plot experiment were analysed using repeated-measures ANOVA. Measures of growth (mass, culmen, tarsus, and wing chord) from the same individuals provided the repeated-measures factor in analyses comparing differences between treatments and among days when measurements were taken. Sample day (28 April, 12, 14 and 17 May) was the within-subjects factor and treatment (tourist, non-tourist) was the between subjects factor. For significant relationships identified during these analyses I also performed Tukey's post-hoc comparisons followed by Bonferroni-corrections. Alternatively, nonrepeated-measures ANOVA was used in analyses of foraging success (meal index and feeding frequency) as daily mean values were analysed.

Silver gulls (*Larus novaehollandiae*) are observed at Michaelmas Cay throughout the year (King et al., 1992), and gulls frequently follow humans and use any disturbance to access and consume exposed eggs and/or small chicks (Anderson and Keith 1980; Bolduc and Guillemette 2003; King 1993; Kury and Gochfeld 1975). For analysis of both the proportion of egg loss at different distances from the fence and rate of silver gull predation the Levene's tests demonstrated that the assumption of normality was not strictly violated (mean proportion eggs lost each week: $F_{3,8} = 3.393$, $P = 0.074$; rate of predation events per hour: $F_{1,16} = 4.018$, $P = 0.062$). However, both distributions suggested an inaccurate estimation of the p-value was possible because of lack of homogeneity of variance and therefore these data were assessed using non-parametric Kruskal-Wallis and Mann-Whitney *U* tests, respectively. Repeated-measures ANOVA were not needed for these analysis as both species lay only a single egg clutch and therefore no nests could be measured a second time for the same egg loss or predation event. Proportional data on meal composition were assessed using chi-squared statistics. All statistical analyses were performed using SPSS for Windows Version 13.0 (SPSS, 2004) and significance was set at 0.05.

7.2. RESULTS

7.2.1. Hatching success

The median proportion of combined Sooty tern and Common noddy eggs lost per week did not differ significantly among the four distances (3, 6, 18 and 36 m) from the boundary fence ($\chi^2_3 = 1.77$, $P = 0.673$, n = 12), although variation in the proportion of eggs lost was substantially greater among plots at the two closest distances (3 & 6 m) to the fence (Fig 23). In these plots the proportion of eggs lost per week was either relatively low (≤ ~0.05) or high (≥ ~0.14) in any given sampling plot, while at plots further from the fence egg losses showed greater consistency at generally intermediate levels (~0.05 – 0.11, Fig 23).

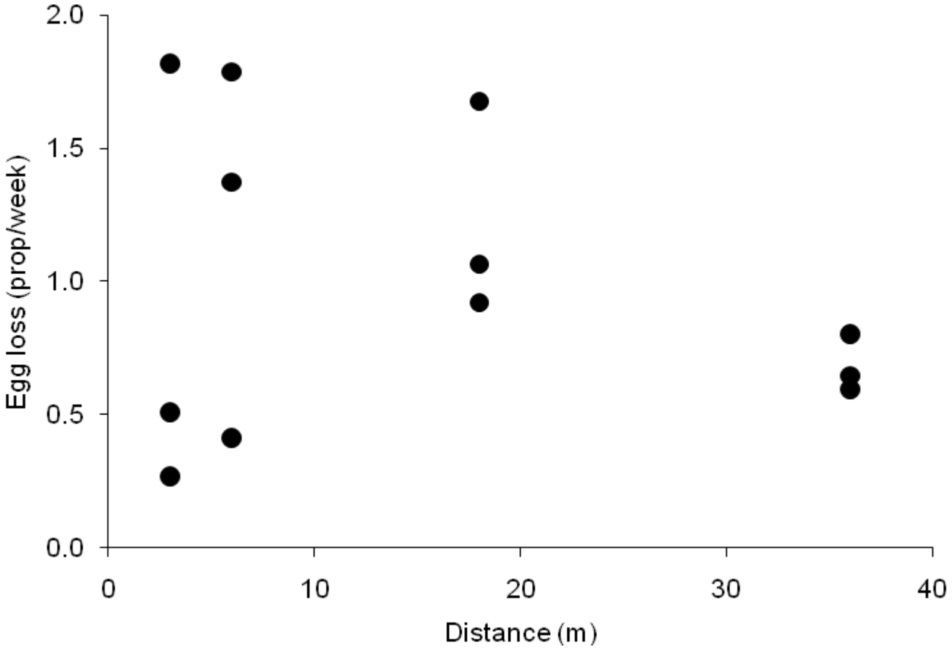


Figure 23. The mean proportion of Sooty tern and Common noddy eggs (combined) lost per week at four distances (three randomly chosen plots monitored at each of 3, 6, 18 and 36 m) from the tourist-in enclosure that protects nesting seabirds on Michaelmas Cay.

7.2.2. Foraging success, chick growth and survival

In my second quasi-experiment, there were no significant differences in either the amount of food provided to Sooty tern chicks ($F_{1,36} = 1.206$, $P = 0.279$) or the feeding frequency ($F_{1,36} = 0.617$, $P = 0.437$) between the tourist (meal index [mean ± S.E.]: 0.17 ± 0.03; feeding frequency 0.040 ± 0.010) and non-tourist (meal index: 0.24 ± 0.06; feeding frequency 0.055 ± 0.017) plots (Fig. 24). There were also no significant differences in meal composition (proportion of fish and squid provided) by Sooty tern parents between plots ($\chi^2_1 = 1.964$, $P > 0.10$, n = 31) (tourist plot [mean ± S.E.]: squid 0.60 ± 0.04, fish 0.24 ± 0.05, unknown 0.16 ± 0.03; non-tourist plot: squid 0.52 ± 0.10, fish 0.35 ± 0.08, unknown 0.14 ± 0.03) (Fig. 25).

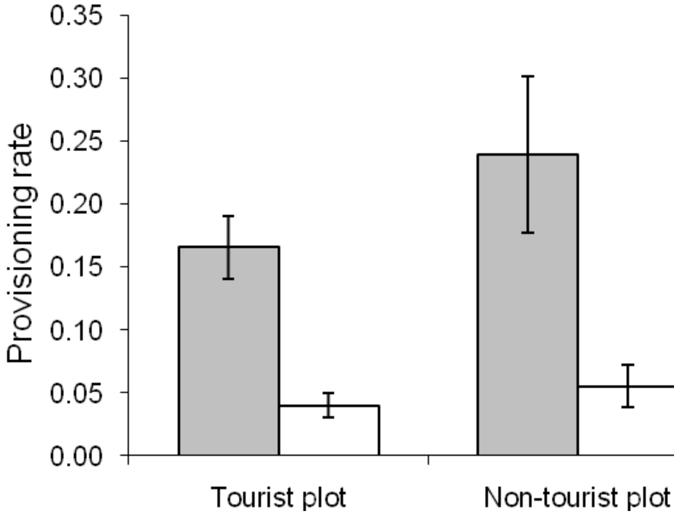


Figure 24. Comparison of mean provisioning rates of breeding adult Sooty terns nesting at sites located near the fenced enclosure (tourist plot) and ~50 m from the enclosure (non-tourist plot) (±S.E.). Meal indices (shaded bars) and feeding frequencies (white bars) are computed per day of chick age.

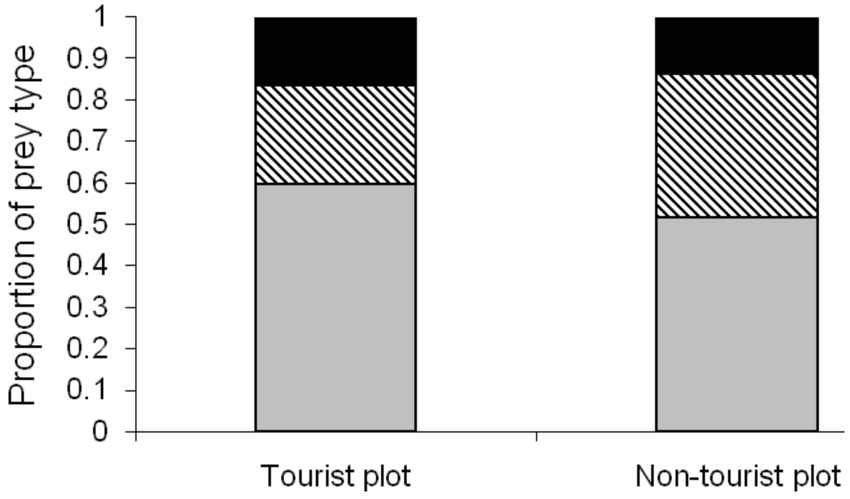


Figure 25. Meal compositions provided to Sooty tern chicks with prey categorised as either squid (shaded bar), fish (striped bar) or unknown (black bar) at the tourist and non-tourist plots. *n* represents the number of days for which data were available.

Sooty tern chick growth between ages 3 and 19 days was similar between plots (Fig. 26). Overall, the ANOVA showed that growth was not affected by treatment (mass, $F_{1,15} = 0.048$; $P = 0.829$; tarsus, $F_{1,15} = 0.881$; $P = 0.363$; culmen, $F_{1,15} = 0.323$; $P = 0.578$; wing chord, $F_{1,15} = 0.785$; $P = 0.390$). As expected for growing chicks the effect of measurement day (chicks were measured on 28 April, 12, 14 and 17 May 2005) was significant (mass, $F_{1,15} = 224.244$; $P < 0.001$; tarsus, $F_{1,15} = 351.275$; $P < 0.001$; culmen, $F_{1,15} = 558.745$; $P < 0.001$; wing, $F_{1,15} = 54.668$; $P < 0.001$). For all variables except skeletal growth (tarsus) there was no significant effect of the interaction between plot and day (mass, $F_{1,15} = 4.258$; $p = 0.057$; tarsus, $F_{1,15} = 7.676$; $P = 0.014$; culmen, $F_{1,15} = 0.001$; $P = 0.975$; wing, $F_{1,15} = 0.410$; $P = 0.532$). The post hoc tests showed that 3 day old Sooty tern chicks at the non-tourist plot had smaller tarsuses compared to chicks of the same age at the tourist plot (Fig. 26). This difference disappeared by the time the chicks were 14 days old and skeletal growth remained similar for chicks at the two treatment plots for the remaining measurements.

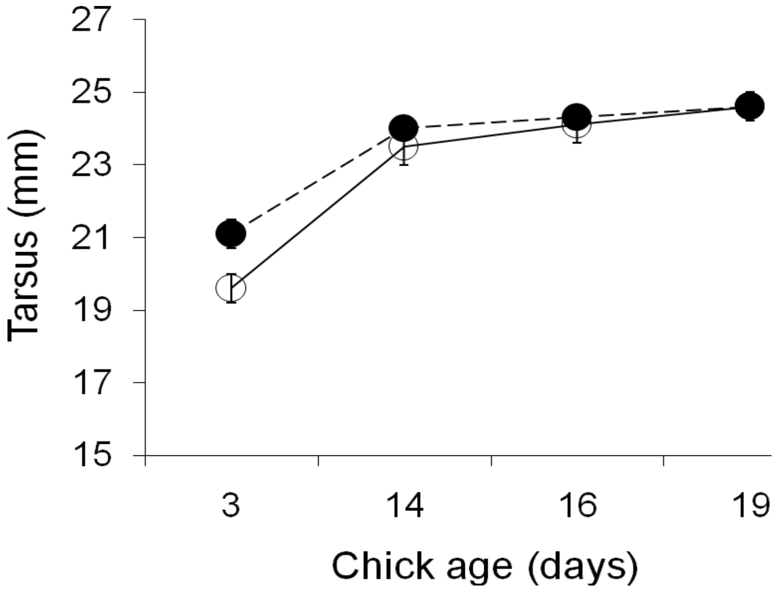


Figure 26. Tarsus measurements over time (means, ± S.E.) for Sooty tern chicks in relation to nesting site, at the tourist (●) and non-tourist plots (○).

Differences in early tarsal growth and silver gull predation did not translate into differential survival to fledging age (≥ 56 days) at the tourist plot compared to the non-tourist plot (χ^2_1 = 1.375, *P* = 0.241), where 80.0% (n = 20) and 63.7% (n = 22) banded chicks survived to fledge, respectively.

In 2005, the silver gull predation rate within a 10 m radius of the plots was greater at the tourist plot (tourist plot: 0.44 ± 0.11, non-tourist plot: 0.09 ± 0.05; Z = -2.356, *P* = 0.024, n = 18) (Fig. 27). In most cases, it was Sooty tern eggs (90%, n = 18), rather than chicks (10%, n = 2) that were depredated by Silver gulls.

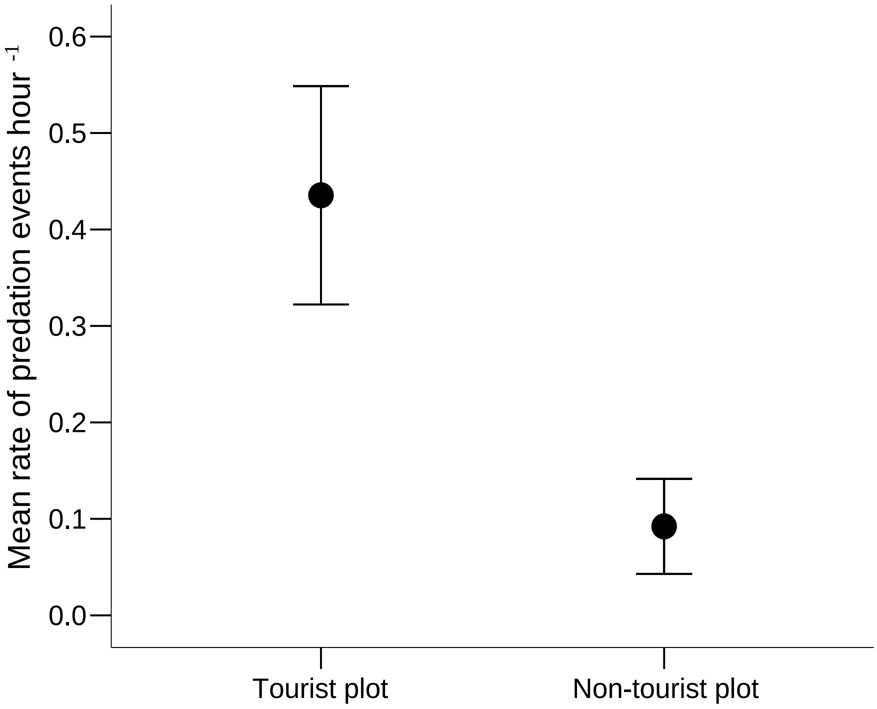


Figure 27. Recorded rates of predation by silver gulls (events h^{-1}) on Sooty tern eggs and chicks that were within a 10-m radius of the tourist and non-tourist plots. Error bars represent ±1 S.E.

7.3. DISCUSSION

There were no significant differences in median egg losses for Sooty terns and Common noddies combined, relative to distance from the tourist fence in 1999/2000. Similarly, in 2005 no significant differences were detected in Sooty tern feeding rates or diet composition between chicks from the non-replicated tourist and non-tourist plots. Overall growth and survival rates of Sooty tern chicks to fledging age also did not vary between the tourist and non-tourist plots in 2005. Combined, these findings suggest that in general the fenced enclosure which prohibits human access to all but a small area of Michaelmas Cay is effectively mitigating any large-scale measurable tourist impacts on pelagic seabird species nesting on the cay. This finding is also supported by other assessments (Chapter 6) that suggest long-term trends in breeding population sizes of these pelagic species are not correlated with changes in tourist visitation rates to the region.

There are a number of possible reasons why significant effects of human visitation were not detected in these experiments. Firstly, humans may represent 'pseudo' predators for wildlife, eliciting a flight or fight response comparable to those displayed when animals are subject to natural predators (Frid and Dill, 2002, Beale and Monaghan, 2004). During such times, nest contents can be spilled, exposed to predation, or perish from the exposure to the elements (Kury and Gochfeld, 1975, Anderson and Keith, 1980). However, seabirds exposed to frequent visitation may become habituated to human stimuli (Fowler, 1999, Yorio and Boersma, 1992). This habituation may occur as rapidly as within a single breeding season (Gyuris, 2004) and can occur in both adults and their offspring (Gyuris 2004; Walker *et al.* 2005; Walker *et al.* 2006). Similar habituation responses have been observed in other GBR breeding species, including the Black noddy (*Anous minutus*), the Wedge-tailed shearwater (*Ardenna pacifica*) (Hill and Barnes, 1989) and the Bridled tern (*Onychoprion anaethetus*) (Gyuris, 2004).

Alternatively, use of a non-complete barrier-type fence allows that people could have approached the ‘non-tourist’ plot and/or nesting locations at various distances from the fence on days or times when scientific observers were not present. Such intrusion would not have influenced the direct observations of chick provisioning behaviour or predation, but has the potential to influence chick growth and survival. However, access to the cay is restricted to five hours daily for all visitors and all large commercial tourism operators have guards who limit visitor movement while using the cay. Access by private or commercial persons outside of permitted hours has not been cited as a frequent occurrence (QPWS, pers. comm.). It is also possible that the seabirds at plots away from the fence were negatively influenced by the presence of either the video camera or observer using a scope, and deemed such observation method(s) equally as invasive as people using a nearby fenced area. However, the success of these remote systems elsewhere suggests this scenario is unlikely (Fetterolf, 1983, Keedwell and Sanders, 2002, Brown and Morris, 1994). While these last two alternatives require further investigation to be completely excluded, the evidence suggests that the most likely reason for the among- and between-plot similarities in the Sooty tern and Common noddy metrics reported here is habituation to human presence.

Despite the general lack of differences in growth and egg/chick survivorship attributable to tourist activity, seabirds breeding in the plot nearest to the fence experienced nearly five times greater depredation by gulls in 2005 and higher variation in rates of egg loss during incubation in 1999/2000. These effects may be related, particularly if tourism tends to drive egg losses (via disturbance that leads to predation) in some weeks but not in others. If so, this suggests that gull predation has the potential to significantly impact on hatching success and reproductive output at other times, depending on the intensity and duration of disturbance or other background environmental variation. Some predatory species such as gulls appear to associate the presence of humans with access to the nest contents of colonial breeding seabirds (Kury and Gochfeld, 1975), and several previous studies have demonstrated how visitor behaviour (e.g. approach type, walking speed, angle of approach) can influence whether seabirds leave nests abnormally exposed (Burger and Gochfield, 1981, Giese, 1998, Martín et al., 2004, Wilson et al., 1991).

While tourist impacts at Michaelmas Cay currently appear to be minimal, care should be taken in generalising the responses of seabirds here to other colonies or over longer time periods, particularly given the observed links between levels of gull predation and to the presence of tourists. The degree of sensitivity to human disturbance differs also among seabird species with different life history strategies (Yorio et al., 2001, Burger and Gochfeld, 1993, Holmes, 2007). For example, Common terns (*Sterna hirundo*) and Black skimmers (*Rhynchops niger*) appear to be more sensitive to human approaches compared to Royal and Least terns (*Sterna maxim* and *Sternula antillarum*) (Erwin, 1989). Here I have examined pelagic species of terns that have different nesting densities, do not flush as easily and are generally less sensitive to intrusion compared to inshore foraging species of this taxon (Higgins and Davies, 1996). Therefore, it is important to tailor management of visitation to breeding colonies to the particular circumstances (i.e., species composition, topography, colony size) of each location.

Similar care should be exercised when using this research to exclude tourism as a longer-term driver of seabird demographic change at Michaelmas Cay. Whether tourism is impacting the colony as a whole can only be determined by sampling at several colonies with control sites that are unimpacted by tourism. I was unable to find suitable controls in the region. In any case, differences in habituation among locations due to relative rates/historical periods of exposure to human visitors may bias results of inter-colony comparisons (Fowler 1999; Gandini and Frere 1996). Moreover, the relative risks of predation, the density of competitors at other sites, and changes in topography between colonies which modify the detectability of human visitors, could all affect animal responses at individual colonies (Gill et al., 2001).

In summary, my two independent experiments have demonstrated that the effects of human visitation on the reproductive output of pelagic terns breeding at Michaelmas Cay appear minimal. Measurable impacts are limited to increased short-term depredation of eggs by silver gulls. I have no evidence that this depredation translates into differential egg survivorship over a single breeding cycle, but care should be taken in assuming that this impact is not important under varying background environmental conditions or tourist visitation rates. Negative impacts on other demographic parameters appear to be largely mitigated by the fenced enclosure which concentrates visitors in a small part of the breeding colony. Presumably, this fence is allowing birds nearby the visitation area to habituate while leaving the remainder free of disturbance. As at Michaelmas Cay, the effectiveness of a non-complete barrier-type fence elsewhere would require self-restraint by tourists and/or monitors to enforce the boundary established by the fence.

My findings suggest that at Michaelmas Cay, and possibly other similar locations on the GBR, future disturbance to the seabird rookery may be effectively quantified by monitoring gull predation levels, and this factor warrants further examination. Combined with results from similar studies (Cobley and Shears 1999; Fowler 1999; Gyuris 2004; Nisbet 2000; Shealer and Haverland 2000), my findings suggest that accommodating the interests of both nature-based tourism and the long-term conservation of seabird breeding colonies is possible. Furthermore, use of a protective barrier such as a fence allows birds to behave as they would in an undisturbed environment by providing areas of refuge within highly visited habitats.

8.0. SYNTHESIS

Seabirds are imperilled by a number of threatening processes. First and foremost of these threats is climate change (Doney et al., 2012), primarily through predicted increases in SST (Ainley et al., 2010, Barbraud et al., 2011, Congdon et al., 2007) and changes to the major weather patterns which influence upwelling, such as the ENSO (reviewed by Grémillet and Boulinier, 2009). Seabirds are also potentially vulnerable to predicted changes in the frequency and intensity of storms and cyclones, ocean acidification, and sea level rise (reviewed by Chambers et al., 2011). These threats may be exacerbated by anthropogenic threats, including commercial fishing, disturbance by visitors to island breeding and roosting grounds, pollution, destruction of breeding habitat and the introduction of exotic plants and animals on breeding and foraging grounds (Schreiber and Burger, 2002).

The body of research presented in this thesis demonstrates that climate variation and the associated changes to the ENSO, thermocline depth, chlorophyll concentration, and short-term SSTs are having detrimental impacts on multiple species across the GBR ecosystem. The species affected include the Sooty tern and the Common noddy breeding at Michaelmas Cay, northern GBR, and the Black noddy breeding at Heron Island, southern GBR. These three species share a number of life-history characteristics. They are all pelagic or offshore foraging tern species. Sooty terns, Common noddies and Black noddies all have large breeding populations. The three pelagic/offshore foragers are also generally synchronous breeders, are generally natal site faithful and they feed regurgitated food to young at relatively long intervals, rather than provision young with whole fish more frequently (Higgins and Davies, 1996). Consequently, their chicks have longer pre-fledging periods and slower overall growth rates and parents are more likely to forego breeding rather than change breeding locations. Combined, these life-history characteristics that make the three tern species studied here, and probably other pelagic and offshore foraging tropical tern species, particularly sensitive to ENSO-associated fluctuations in food availability.

That the pelagic and offshore foraging species were detrimentally impacted similarly by increased SSTs and fluctuations in food availability related to climate variation is consistent with findings elsewhere. In Western Australian tropical seabird colonies, increased breeding deferral, delayed breeding and reduced breeding success in pelagic foraging Wedge-tailed shearwaters and three pelagic foraging terns (the Sooty tern, Common noddy, and Lesser noddy (*Anous tenuirostris*)) tends to occur during stronger ENSO events (Dunlop et al., 2002, Surman and Nicholson, 2009). In Western Australia, as with the research findings reported in this thesis, negative ENSO-effects have only been observed for pelagic and offshore-foraging species, with no similar influences detected in the inshore foraging Crested terns (Gaughan et al., 2002). In the Coral Sea, off the northeast Australian coastline, large-scale ENSO processes have also been associated with negative impacts on tropical seabird breeding success, with significant declines in populations of Great (*Fregata minor*) and Least frigatebirds (*Fregata ariel*) and possibly Black noddies related to population crashes at the time of the 1997 to 1998 El Niño event (Baker et al., 2004). Population data at Raine Island, far northern GBR, indicate a potential progressive decline in breeding populations of at least 10 of the 14 breeding species (Batianoff and Cornelius, 2005), including the Common noddy, the Sooty tern, the Bridled tern, the Red-footed booby (*Sula sula*), Least frigatebird, Brown booby (*Sula leucogaster*), Red-tailed tropicbird (*Phaethon rubricauda*), Masked booby (*Sula dactylatra*) and Wedge-tailed shearwater. A lack of other mechanisms for the apparent declines, and the fact that the species which commonly form foraging associations at-sea have similar declining trends, highlights depletion of marine food stocks linked to changing climate and oceanographic regimes and/or human influences such as trawling as the most likely possible driving factors (Congdon et al., 2007). Similarly, on the Swain Reefs, southern GBR, negative population trends for Brown boobies (Heatwole et al., 1996) are thought to be related to decreases in food availability associated with three significant El Niño events that occurred between 1984 and 1995.

Outside of Australia, in the Indian Ocean, tropical seabird reproductive biology has also been strongly tied to ENSO-driven processes. In the Seychelles, seasonal-scale variation in ENSO intensity and SST have been correlated with changes in both food availability and timing of breeding for Common noddies and Roseate terns (Ramos et al., 2002, Ramos et al., 2006). Also in the Seychelles, lower reproductive success in White-tailed tropicbirds (*Phaethon lepturus*) has been linked to lower ocean productivity during periods of El Niño-like conditions (Ramos et al., 2005). Red-tailed tropicbirds in the central Pacific Ocean have also demonstrated reduced provisioning and chick growth as the nutrient content of the water decreases and fish die or leave the area during El Niño events (Schreiber, 1994).

The only inshore foraging species, the Crested tern, in this study did not demonstrate a response to any of the climate variables measured. Crested tern populations were generally increasing over the study period (Chapter 6). This finding is consistent with other comparative results among species of different taxa, both in Australia (Gaughan et al., 2002, Surman et al., 2002) and abroad (Frederiksen et al., 2004a, Schreiber and Schreiber, 1984, Kitaysky and Goluvova, 2000). In the north Pacific, piscivorous and planktivorous feeding seabirds responded differently to changes in SST and associated variation in macro- and meso-zooplankton (Kitaysky and Goluvova, 2000), while in the North Sea, species responded differently to environmental cues based on their dispersal characteristics (Frederiksen et al., 2004a). For Crested terns in this study, there are a number of potential buffers to possible negative impacts from climate variability in the foraging ecology of this species and related taxa. Nearshore and inshore foraging species tend to have more flexible foraging behaviours (Blaber et al., 1998), are not reliant on subsurface predator activity to access prey (Higgins and Davies, 1996), and do not generally display natal site fidelity (Higgins and Davies, 1996). Inshore seabird species also have higher prey diversity (Diamond, 1983), which may serve as a safeguard against decreases in the availability of particular prey types.

Offshore foraging Black noddies in this study faced wide variation in SST and associated changes in prey availability, and adults were unable to modify their foraging behaviour while chicks did not demonstrate variable growth rates (Chapter 5). These limitations suggest that the ability of this species to buffer climate change impacts by altering behaviour or via developmental plasticity is restricted. Adult Little penguins (*Eudyptula minor*) in south-eastern Australia were also unable to adjust their foraging behaviour during periods of decreased food availability, but chicks reduced mass growth and delayed development when provisioning rates were reduced (Chiaradia and Nisbet, 2006). The more flexible developmental patterns in Little penguin chicks compared to Black noddy chicks may be because, as temperate species, Little penguins breed in more productive oceans compared to subtropical and tropical species (Behrenfeld et al., 2006) and thus are likely to face smaller variations in food supply. Therefore, chicks may be able to optimise growth through increased developmental plasticity without risking starvation during periods of extremely low provisioning (Schew and Ricklefs, 1998). However, based on the limited data available from this study and elsewhere in Australia on potential plasticity in life-history characteristics of seabirds to buffer against future climate change (Chambers et al., 2011), generalisations about adaptive capacity of seabirds are difficult and regional and species- or taxa-specific assessments are required.

Predicted future climate change will drive seabird species to 1) adjust feeding behaviour or other life-history characteristics to survive and reproduce within the same distribution zone, 2) modify their distribution zone, or 3) undergo extinction. Black noddies, and possibly similar pelagic or offshore foraging species, will have limited capacity to adjust feeding behaviour or chick growth characteristics over the short term in response to climate change. The potential for the species examined here to modify their distribution zones is unknown. There are effectively three known prey resource bases (Coral Sea mounts, the Southern GBR along the eastern edge of the continental shelf, and local foraging) available for seabirds breeding on the GBR. If one or more of these prey resource bases has islands with suitable vegetation located within the foraging radii of these species, then nesting is possible. Currently, the biomass of seabirds on the GBR is concentrated where the majority of coral cays occur, in the far northern and southern ends of the reef, on the outer parts of the continental shelf. Climate change-related loss of coral cays as breeding habitat or changes in food supply in the northern and southern GBR would likely alter the distribution of seabirds to the central GBR, where continental islands predominate above the inner and middle sections of the continental shelf.

8.1. Future Research

Based on the findings compiled in this thesis, predicted increases in both SST (Lough, 2009) and the intensity or frequency of ENSO events (Zhang et al., 2008) are likely to have serious detrimental impacts on some component of the breeding biology of the pelagic and offshore foraging tropical seabird species breeding throughout the GBR and in other tropical areas. However, information on additional species and on location-specific interactions between changing oceanography and seabird prey availability is required to close the knowledge gap regarding generalised seabird responses to climate variability and change. In some cases, species or populations are recovering from previous anthropogenic impacts, and resolution of climate change impacts from other anthropogenic threats is needed for these species. With the current level of available information, options for local or regional scale management of climate impacts on seabirds remain very limited. This is because most impacts are directly linked to large-scale global climate phenomena rather than more local threatening processes.

For most species, evidence of responses to environmental variability and the functional processes driving these affects is limited. Monitoring approaches for some species may need to be reassessed and modified in order to better detect the impacts of climate change, and for monitoring potential adaptation efforts. Diverse statistical approaches are required to extract climate signals and determine current drivers, and to predict future trends. The development of regional multi-species indices using standardised time series from individual colonies would aid in generating broader environmental monitoring and response tools.

Whether species can adapt to predicted future climate change relies in part on species being able to move to alternate habitats as habitats are altered by climate change. In order to address this question, it must be clarified whether species have fixed habitat choices with definable boundaries, what the range of places an individual species will breed/adapt to is, whether there are alternative nesting sites available elsewhere for species to recolonise and what amount of nesting and foraging habitat overlap is available for similar species (i.e. those using the same niche). Answering these questions will foster increased resilience of conservation-dependent seabirds impacted by climate variation and change by enlightening management decisions and conservation activities.

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