THE LIFE HISTORY CHARACTERS, REPRODUCTIVE CONSTRAINTS AND FORAGING STRATEGIES OF A NERITIC SEABIRD, THE CRESTED TERN

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A thesis submitted in complete fulfilment of the requirements for the Doctor of Philosophy

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Thesis declaration

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“Science, like all creative activity, is exploration, gambling and adventure. It does not lend itself very well to neat blueprints, detailed road maps, and central planning. Perhaps that's why it's fun” (Simon, 1964).

*and ........in the words of George Box “All models are wrong, some are useful”*

Adult crested tern from Troubridge Island (Photo provided courtesy of Mr Todd Kemper)
Abstract
This thesis examines the functional relationships between the diet, foraging behaviour and life history traits of crested tern populations in South Australia between 2004 and 2008. Diet analyses indicated that crested terns are a generalist predator on surface-schooling fishes. Clupeiform fish (Australian anchovy *Engraulis australis*, sardine *Sardinops sagax*) comprised a large component of the diet of crested terns. Ontogenetic differences in prey size indicated that adults selected small prey for their chicks during early provisioning but increased the size and rate of prey delivered throughout the breeding season as chicks grew. Adults also selected higher quality prey for their chicks compared to what they consumed themselves. Chick and adult diets may have reflected spatial differences in the species composition of prey assemblages near colonies and a North-South gradient in prey size. I also investigated the provisioning patterns of crested terns and how reproductive timing and adult body condition affect the growth and survival of crested tern chicks. Provisioning rates were related to the daily mass change of chicks, and chick growth was correlated with asymptotic mass, suggesting that prey availability and adult foraging proficiency influences fledgling size. Parental ‘quality’ affected reproductive performance. Adults with good body condition hatched chicks earlier and early breeding was positively related to hatchling mass, fledgling condition and chick survival. Adults aged <7 years had significantly poorer body condition and hatched their chicks later compared to adults ≥7 years. However, adult body condition also varied within cohorts, indicating that reproductive performance is affected by phenotypic differences in parental quality. Consequently, the growth of crested tern populations may be most sensitive to the foraging behaviour and reproductive output of high quality adults ≥7 years old. Disease-related mortality events in 1995 and 1998, which killed ~ 70% of adult sardine *Sardinops sagax* biomass, provided an opportunity to assess whether crested tern populations were affected by decreases in prey abundance. Age-specific information collected from adults indicated that chicks reared during poor prey conditions caused by the first sardine mortality event in 1995 exhibited lower rates of recruitment to the breeding colony. Females from cohorts reared <1 year after the end of each sardine mortality event also had smaller morphology compared to other age classes indicating that chick growth was reduced during periods of low sardine abundance. Analyses of foraging behaviour using GPS indicated that adults generally commuted to foraging grounds <40 km from the colony where they accessed prey from warm, shallow, near-surface waters that were relatively high in Chl-a (> 0.5 mg.m⁻³). Intra-specific variations in foraging behaviour reflected either prior knowledge of where prey aggregations exist, distinctions in individual niche use driven by the types or sizes
of prey available, and/or alternate behavioural states (self feeding and provisioning). The restricted foraging range of crested terns while breeding may make them sensitive to competition with fisheries that operate within their foraging range. Diet and demographic information collected from crested tern populations may provide ecological performance indicators to enhance conservation strategies for crested tern populations and augment current fisheries management approaches.
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It seems appropriate to submit a thesis relating to animal life history strategies and population ecology during the 200th anniversary of Charles Darwin’s birth. As all who are involved with wildlife research would know, scientific collaboration is much more than the sum of its parts. A countless number of people assisted in bringing this work to fruition. Simon Goldsworthy, Tim Ward and David Paton showed tremendous enthusiasm as supervisors of my research. Thanks to you all for our numerous chats, giving me the free reign to take the research where I wanted and pulling me back to reality when it was required.

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Chapter 1. General Introduction

Life history strategies

The study of animal ecology aims to describe the relationships between individuals, populations and species, and the ultimate and proximate pressures of selection acting within their environment. At an individual level, an animal's behavioural responses to its environment are shaped by phenotypic characters or its developmental stage (de Kroon et al. 2000). At the population level, these responses are integrated and expressed in broad characters such as age-specific survival and reproduction (Begon et al. 1986). A species can be classified according to its life-history traits that reflect natural selection on the key maturational, survivorship and reproductive schedules of its life (Stearns 1977, Musick 1999). These traits include growth, size, age at maturity, fecundity and longevity, and are representative of the way individuals allocate time and energy. The partitioning of resources to one activity must be to the detriment of another, and natural selection will favour the allocation of resources to traits that maximise an individual's fitness (Roff 1992, Stearns 1992, Saether and Bakke 2000). Life history theory provides a framework for describing how these 'trade-offs' or 'bet hedging strategies' affect individual fitness. Understanding the factors that constrain resource allocation behaviour may assist in identifying the mechanisms that shape life history strategies and influence population growth.

The foraging behaviour of an animal determines how much energy it can allocate to survival and reproduction. Optimal foraging theory aims to describe selection on foraging behaviour under a set of conditions, via the assumption that higher fitness is attained by maximising the net rate of energy acquired (Begon et al. 1986). The constraints placed on energy acquisition and allocation are different while animals are breeding, because parents must adjust their foraging behaviour according to their own energetic requirements and those of their offspring. Many animals provision their offspring at fixed breeding sites such as nests or colonies. Models of central place foraging attempt to describe how animals maximise energy acquisition and delivery rates from patches of surrounding prey that vary in density, load-size and distance from the central place (Orians and Pearson 1979). Classic models predict that the energy delivered to offspring should increase with the distance travelled from the central place because as travel time increases, the net rate of energy gained by offspring declines (Orians and Pearson 1979, Olssan et al. 2008). This trade-off in energy requires that parents make decisions on how to best allocate the available resources to maximise fitness.
Seabirds provide tractable subjects for studying how resource partitioning strategies affect fitness while breeding at a central place. They are readily studied while breeding on land and forage within marine environments characterised by spatial and temporal variations in biophysical processes and prey abundance. As apex predators they are long lived, and have high adult survival rates, long maturation periods, and low reproductive output. These characters are thought to reflect adaptations that buffer their populations against variations in prey availability (Lack 1954, Boyd et al. 2006). Decreases in prey availability within their foraging range may act to increase investment in behaviour that maintains survival at the expense of reproduction (Drent and Dann 1980, Monaghan et al. 1989). For example, Arctic terns Sterna paradisaea reduce the amount of food delivered to the second chick in their brood, or abandon nesting attempts during poor prey conditions (Monaghan et al. 1989, Monaghan et al. 1992). This strategy may confer a selective advantage by increasing the residual reproductive value (reproductive potential) of an individual over its lifetime (Hamer et al. 2002). Understanding the relationships between seabirds and their prey requires information on the types of prey harvested (dietary width), the type of foraging mode employed, and how their foraging and life history responses vary in response to different prey conditions.

**Diets: generalists versus specialists**

Prey species vary in their profitability to predators due to differences in energy density or nutrient value. In terms of optimal foraging, predators that are generalist in the types of prey they target may sacrifice profitability for time and energy by acquiring lower quality prey that are more commonly available. Conversely, specialists may spend more time and energy searching for high quality prey that are less available. The success of either strategy depends on the net rate of energy acquired. Few seabird species specialise on a particular prey. For those that do, measures of foraging behaviour and reproductive performance have been shown to be sensitive to changes in prey abundance in near colony waters. For instance, brown pelicans Pelecanus occidentalis prey almost exclusively on anchovy Engraulis mordax and their breeding success is highly dependent on anchovy abundance (Anderson and Gress 1982). A generalist strategy is more common in seabirds, and most likely evolved due to the variable conditions of prey availability typical of marine ecosystems (Begon et al. 1986). Generalist seabirds may switch to alternate prey if the availability of one prey decreases, but prey-switching may be less optimal in terms of maximising energy acquisition rates and fitness,
because prey species vary in their calorific value, and the energetic costs associated with foraging for alternate species may increase (Suryan et al. 2000).

Seabird diet studies provide a tool for assessing the type, size, mass, and quality of prey available to seabirds within their foraging range while breeding. Dietary shifts may correlate with oceanographic conditions (Montevecchi 1993, Hedd et al. 2002). In Canada, the diet and reproductive performance of Cassin’s auklet Ptychoramphus aleuticus was positively correlated with copepod abundance and late, cold, spring oceanographic patterns (Hedd et al. 2002). Diet information may also be used to calculate prey consumption rates, and to develop bioenergetics and ecosystem models (Weins and Scott 1975, Bunce 2001, Goldsworthy et al. 2003). These types of models highlight the flow of energy through food webs and can be used to evaluate how the abundance of predators relates to changes in the abundance of their prey, thereby assisting in the development of resource management strategies (Scandol et al. 2005).

Seabirds often prey on species taken in commercial fisheries. Modelling by Furness (1984) indicated that seabirds consume up to 30% of annual pelagic fish production in many marine systems. Diet data may provide fishery independent recruitment indices or indicators of stock abundance (Berutti and Colclough 1987, Cairns 1992, Montevecchi 1993, Velarde et al. 2004). In the Gulf of California a strong positive correlation was found between the proportion of sardine Sardinops sagax in the diet of elegant terns Sterna elegans and the amount of sardine taken by commercial fishing operations (Velarde et al. 2004). In South Africa, the percentage of sardine in the diet of Cape gannets Sula capensis was significantly related to commercial catch over annual intervals (Berutti and Colclough 1987). Studies have also linked seabird demographic responses to the abundance of commercially fished species (Anderson and Gress 1982, Barrett 1991, Cairns 1992, Velarde et al. 2004, Crawford et al. 2006, Pichegru et al. 2007). For example, the biomass of northern anchovy Engraulis mordax in the southern Californian Bight is positively correlated with the diet and breeding success of brown pelicans Pelecanus occidentalis californicus (Anderson and Gress 1982). Similarly, kittiwake Rissa tridactyla breeding success is highly dependent on the abundance of sandeels in the North Sea, and sandeel fishing ceases if kittiwake breeding success drops below 0.5 chicks per nest for three consecutive years (ICES 2002).

Research suggests that seabird diets vary among species at multiple spatial and temporal scales due to separation in the habitats accessed by different individuals, sexes, life history stages or...
populations (Montevecchi and Myers 1995, 1996, Thayer and Sydeman 2007, and reviewed in Barrett et al. 2007). For example, many seabirds provide higher quality prey to their chicks than what they eat themselves, thereby maximising the amount of energy delivered per trip (Hodum and Hobson 2000, Jaquemet et al. 2008). Diets may vary within the breeding season as parents respond to the increased energetic demands of growing chicks by selecting larger or more energy rich prey (Dunn 1980, Shealer 1998). Spatial and annual variations in diet are also common due to variations in oceanographic conditions and associated changes in the abundance of different prey species near colonies (Montevecchi and Myers 1995, Reid et al. 1997, Thayer and Sydeman 2007). The spatial and temporal variations in prey-species composition and size necessitate that many samples are collected from different life-history stages and colonies over long periods so that the functional relationships between diet, biophysical conditions, and behavioural, physiological or demographic responses can be elucidated.

Foraging behaviour

The foraging behaviour of adult seabirds may be sensitive to decreases in prey abundance near the colony and several studies have correlated reductions in prey availability to increases in foraging effort (Burger and Piatt 1990, Davoren 2000, Hedd et al. 2002). Measures of foraging behaviour have the greatest potential for signalling changes in prey abundance because they are directly linked to prey conditions near the colony (Cairns 1987). Seabirds may increase foraging effort to maintain provisioning rates and maximise reproduction. For example, adult great skuas *Catharacta skua* increase foraging effort during poor prey conditions to maintain consistent rates of prey delivery to their chicks (Hamer et al. 1991). In terms of life history theory, adult provisioning effort may be expected to reach a maximum threshold at which point any further increase will only increase the likelihood of adult mortality.

The extent to which an individual can increase its foraging effort while breeding depends on the flexibility of its foraging mode. Surface foraging species, such as terns, which obtain prey by plunge diving, may be more sensitive to decreases in prey availability than species that obtain prey via subsurface diving, because they are more restricted in the types of prey they can access (Monaghan et al. 1989, Monaghan et al. 1996, Stienen et al. 2000). Studies of sympatrically breeding species support this notion. For instance, arctic terns, which forage at the surface, abandon breeding attempts when sandeel availability is low; whereas common
guillemots *Uria aalge* breed successfully under the same prey conditions because they are able to access prey from a variety of depths (Furness and Tasker 2000).

Species that regurgitate multiple prey in a macerated form to their offspring also have different constraints to ‘single prey loaders’, which provision their chicks with single prey (Ramos et al. 1998, Shealer 1998, Stienen et al. 2000). Central place foraging models predict that adults should maximise their provisioning effort per unit time of foraging, by selecting and returning meals that are as large or energetically-rich as possible (Orians and Pearson 1979, Davoren and Burger 1999). For single prey loaders, the size of prey acquired is regulated by what adults can physically carry in their bill and the size of prey that their chicks can ingest (Hulsman et al. 1989, Ramos et al. 1998, Shealer 1998). For seabirds that provide macerated prey to offspring, the amount of prey acquired and delivered is limited by what they can carry in their stomach. As a result, species that deliver multiple macerated prey to their offspring are not as restricted in their foraging range. The evolution of multiple prey loading is taken to its extreme among procellariiform species that provision their chicks with macerated prey that is concentrated as energetically dense stomach oil (Weimerskirch and Cherel 1998). This strategy allows them to undertake trips lasting up to two weeks to forage from highly productive areas at great distances from the colony (Drent and Dann 1980, Weimerskirch 1998). As a consequence, they provision their chicks less frequently over protracted chick rearing periods. In contrast, species that single prey load such as terns, deliver several small prey throughout a single day. This strategy restricts the distance they can travel from the colony and may make them relatively more sensitive to decreases in prey availability in near-colony waters.

Intra-specific differences in foraging behaviour and niche use may occur due to age-related foraging proficiency or due to an individual’s knowledge of where prey are located (foraging area fidelity) (Irons 1998, Lewis et al. 2006, Weimerskirch 2007). The ability to learn where prey resources are aggregated may confer individuals a fitness advantage as it would help to maximise the net rate of energy transfer between parents and offspring (Irons 1998, Bradshaw et al. 2004). Intra-specific differences in foraging behaviour may also reflect adult foraging decisions mediated by adult body condition and chick energetic requirements (Schew and Ricklefs 1998, Weimerskirch 1998). Procellariiform species perform a dual foraging strategy when rearing chicks, which involves alternating long duration trips (6-29 days) with short duration trips (1-5 days) (Baduini and Hyrenbach 2003). Short trips maintain the rate of energy flow to chicks, whereas longer trips to oceanic waters where prey are higher in
abundance, enable adults to maintain their body condition (Chaurand and Weimerskirch 1994).

For colonial animals, foraging near the central place may deplete prey resources, thereby increasing the cost of provisioning offspring and affecting parental fitness (Ashmole 1963, Birt et al. 1987). This constraint on fitness has been proposed as a selective force driving sympatric speciation and may result in differences in habitat use between sexes or conspecifics (den Boer 1986, McDonald 2002, Gremillet et al. 2004, Svanback and Bolnick 2007). Studies of individual specialisation in the foraging behaviour of seabirds are rare. Woo et al. (2008) found that diet and foraging behaviour varied significantly between individual Brünnich’s guillemots *Uria lomvia*. Niche differences occurred between individuals as a result of differences in flight time, dive depth and dive shape. These differences were not attributed to individual variations in body mass or physiology. Specialisation was ascribed to the memory of predictable foraging sites and the adoption of optimal foraging behaviours.

Recent technological advances in telemetry and remote sensing have enhanced the understanding of the relationships between seabirds and their environment, and shown their foraging behaviour is inherently linked to biophysical factors that influence the distribution of their prey (Charrassin and Bost 2001, Davoren et al. 2003, Weimerskirch et al. 2008). Physical processes may aggregate nutrients and increase levels of primary, secondary and tertiary production at particular depths, boundary fronts, or bathymetric features (e.g. seamounts) (Shealer 2002). However, large temporal and spatial variation in biophysical processes cause shifts in habitat quality and seabirds must adjust their foraging behaviour in order to maximise rates of energy acquisition (Guinet et al. 1997, Suryan et al. 2006, Pinaud and Weimerskirch 2007). Measures of ecosystem conditions via standard survey methods (e.g. ship transects) are often time consuming and costly to implement. Bio-logging data relating to the behavioural responses of foraging seabirds at prey ‘hotspots’ may provide a cost-effective alternative for interpreting ecosystem conditions. It also provides a means of interpreting the relationships between foraging behaviour, life history variation and population growth.

**Chick growth**

In the same way that variation in prey availability affects foraging behaviour, it also indirectly influences growth responses of chicks, and numerous studies have linked measures of chick growth to indices of prey abundance near seabird colonies (Ricklefs et al. 1984, and see Cairns
Natural selection should favour adaptations of chick physiology, behaviour and morphology that best minimise the impact of variations in prey availability on their survival (Schew and Ricklefs 1998). The growth adaptations of seabird chicks reflect the prey conditions and environments in which they live. Pelagic species are often reliant on prey aggregations at long distances from the colony and their chicks may have to fast for long periods. King penguin *Aptenodytes patagonicus* chicks buffer the long intervals between meals by converting large meal masses to lipid stores which they use while parents are away (Hamer et al. 2002). In contrast, chicks of smaller neritic species such as terns, have a limited gut capacity, consume small meals and are provisioned several times a day (Hamer et al. 2002). These interspecific differences in provisioning strategies have consequences for chick growth rates and development. Species that provision their chicks frequently may have shorter pre-fledging periods than chicks that receive prey at infrequent intervals. This minimises the time they are constrained by prey conditions near to the colony, and once fledged they are able to move closer to where prey are aggregated.

Cairns (1987) proposed that chick growth rates vary most when prey abundance is low, and are constrained to a physiological maximum when prey abundance is high. Maximum chick size measures (e.g. fledging mass) may provide better indicators of prey conditions than growth rates because the energy requirements of older chicks may stretch their parent’s provisioning capacity. In the longer term, growth retardation may result in smaller adult body size (Schew and Ricklefs 1998), lower rates of juvenile or adult survival (Harris et al. 1992, Cam et al. 2003), or delayed recruitment (Coulson and Porter 1985, Becker et al. 2001). For instance, common tern *Sterna hirundo* chicks with relatively high growth rates and asymptotic mass, recruited earlier and had higher rates of breeding success as relatively large adults (Wendeln and Becker 1999, Becker et al. 2001). These impacts highlight how the prey conditions experienced by offspring are expressed in future demographic parameters and population dynamics.

**Demographic studies**

A central goal of wildlife conservation and management is to measure how populations respond to variations in survival and reproduction caused by changes in ecosystem conditions. Life history theory predicts a trade-off between current and future reproductive success. An extension of this relationship predicts that natural selection should reduce variation in the life history traits that most influence population growth (i.e. traits with the highest ‘elasticities’).
(Stearns 1977, Caswell 2000, Saether and Bakke 2000). For long lived species, population growth is highly sensitive to decreases in adult survival, and adult survival should exhibit less variation than reproductive success (Stearns 1977, Saether and Bakke 2000). Results from seabird studies support these predictions. The reproductive success of many seabird species varies inter-annually in response to ecosystem and prey conditions (Anderson and Gress 1982, Monaghan et al. 1989, Harris and Wanless 1990, Furness and Tasker 2000, Wanless et al. 2005). Nonetheless, the sensitivity of reproductive success to prey conditions varies between species as a function of their dietary width (previously discussed, above) and breeding phenology. Species with multiple egg clutches are able to vary clutch sizes over a range of prey conditions (Monaghan et al. 1992), whereas species with single egg clutches may abandon nesting when prey conditions are particularly poor (Montevecchi 1993, PRBO 2005).

The survival rates of adult seabirds also generally remain stable (Oro et al. 2004, Harris et al. 2005, Jenouvrier et al. 2005a). However, because seabirds are long lived, their population growth is sensitive to even small decreases in adult survival. This fact is exemplified by severe declines of many albatross populations due to incidental mortality of adult birds in commercial long-line fisheries (Croxall et al. 1990, Arnold 2005). Although decreases in the survival of adult seabirds are largely attributed to large-scale impacts such as pollution, fishing related mortality, predation, or severe climatic shifts such as ENSO (Phillips et al. 1999, Jones et al. 2002), some studies indicate that adult survival may also be sensitive to the costs of breeding under poor prey conditions (Nur and Sydeman 1999, Oro and Furness 2002). Adult survival is difficult to measure accurately, and requires mark-recapture studies that are costly to conduct over long periods. Survival rate estimates may be confounded by the dispersal of individuals, and the time lag associated with collecting data means that the functional relationships between ecosystem processes and survival are retrospective, and therefore inadequate for use as a predictive tool in assessing ecosystem conditions (Greenwood et al. 1993, PRBO 2005). Nonetheless, because seabird populations are highly sensitive to changes in adult survival, survival analyses are crucial in assessing longer term environmental and anthropogenic factors that affect the status of seabird populations. Estimates of survival provide important inputs for population models and allow the level of co-variation between demographic traits to be discerned, thereby providing greater insight into the mechanisms that influence population growth.
To understand the links between ecosystem conditions, demographic rates and population change, it is necessary to identify how temporal changes in ecosystem conditions act on different phenotypes or stages of life history (Coulson et al. 2001). An individual that possesses morphological, behavioural, or physiological characters that are favourable to high rates of adult survival or reproduction will have more descendents in future generations than an animal that does not (Wendeln and Becker 1999, Williams et al. 2002). Phenotypic variations in reproductive success and survival may result from individual specialisation in foraging behaviour (Werner and Sherry 1987, Woo et al. 2008) or inherited morphological or physiological traits resulting from the conditions experienced during offspring development (Gaillard et al. 1998, Moreno et al. 1999, Barbosa et al. 2000, Cam et al. 2003, Blums et al. 2005). For instance, dominant chicks from two-chick kittiwake broods were shown to have relatively higher adult survival and reproductive success compared to their siblings (Cam et al. 2003). Fitness variations relating to age may be explained by older individuals possessing more foraging skill or reproductive experience (Sydeman et al. 1991, Weimerskirch 1992, Pyle et al. 2001, Lewis et al. 2006). Alternatively, age-related fitness variations are explained by increased reproductive effort with age (Pugesek 1981, Weimerskirch 1992). If experience increases fitness, then both survival and reproductive rates should increase with age until senescence. Conversely, if there is a trade-off between reproductive effort and survival, then survival rates should decrease with age as more resources are allocated to reproduction (Weimerskirch 1992). Seabird research supports both hypotheses and it is likely that individual quality affects both reproductive performance and any associated tradeoff with adult survival (Weimerskirch 1992).

The effects of phenotypic and age variation on fitness are hard to separate, and are poorly understood for seabird populations due to the difficulty in obtaining long term individual survival and breeding histories. Nonetheless, age-specific and phenotypic variations in reproduction and adult survival have been correlated with body condition and/or reproductive timing (Monaghan et al. 1989, Weimerskirch 1992, Wendeln and Becker 1999, Lewis et al. 2006). These relationships provide a means to assess the factors that influence demographic rates under different ecosystem conditions, and allow examination of the factors underlying the selection and evolution of life history traits. Importantly, modelling the specific components that contribute to fitness variation between individuals of different quality or age allows the underlying variance in demographic rates to be calculated.
Ecosystem based fisheries management and seabird conservation

Worldwide fisheries landings average over 100 million tonnes annually and over a half of all fisheries are considered fully exploited (Botsford et al. 1997). Small pelagic fish from the Order Clupeiformes are a key link in food webs and are dominant targets of commercial fisheries worldwide, comprising seven of the top 10 species (Botsford et al. 1997). The increased focus of commercial fishing on lower trophic level species, such as sardines, anchovies and krill in the last 60 years has occurred due to the ‘fishing down’ of higher trophic level fish stocks, improvements in fishing techniques and the demand for fodder by the aquaculture sector (Pauly et al. 1998). Small pelagic fish populations undergo large fluctuations in abundance due to variations in biophysical processes that influence primary and secondary production, and are therefore susceptible to overfishing (Radovich 1981, Pauly et al. 1998, Schwartzlose et al. 1999, Alheit and Hagen 2001). Moreover, these fish not only form the target of major commercial fisheries, but also comprise the diet of many high-order marine predators.

In recognition of the role of fisheries in ecosystem degradation and their impacts on target and non-target species, international and domestic environmental laws now formally recognise the need to manage fisheries according to principles of ecologically sustainable development. As a result, detailed and ongoing scientific impact assessments are required for all species potentially influenced by fishing operations (Fletcher et al. 2002). This includes the assessment of trophic impacts. To determine the effects of fishing on target and non-target species, a detailed understanding of the interactions and processes that sustain ecosystem composition, structure and function is required. In an attempt to manage marine ecosystems as a whole, managers have been looking to incorporate ecological performance indicators from apex predators into fisheries management (Croxall 1989). The strength of data from marine predators is twofold. Firstly, it may enhance knowledge of stock biomass conditions thereby augmenting information collected more traditionally from single species stock assessments, natural history studies and risk assessments (Hall and Mainprize 2004, Scandol et al. 2005). Secondly, it may be used to monitor the conservation status of predator populations, thereby addressing the principles of ecologically sustainable development. Demographic data collected from predator populations can be used to develop population models (e.g. Leslie matrix models, life table models, population projection matrices). Population models are invaluable as a management tool in assessing the health of predator populations under different ecosystem conditions and regimes of resource use (Chastel et al. 1993, Weimerskirch et al. 1997, Caswell
2000, Clarke et al. 2003, Doherty et al. 2004, Oro et al. 2004, Jenouvrier et al. 2005b). They also provide a means to link observed population trends to perturbations that affect vital rates (retrospective analyses), and assess the sensitivity of population growth to variations in different life history traits (prospective analyses) (Caswell 2000). In this way, they are able to highlight the stage of life history that requires management action, and help to establish targets (reference points) for demographic rates of protected, threatened or endangered species that will maximise the potential of population recovery (Williams et al. 2002).

Search for the ‘ultimate’ sentinel’ of ecosystem health

The functional relationships between seabird foraging behaviour, physiology, demography and ecosystem conditions have been the focus of seabird research for over 30 years, and have enhanced the knowledge of ecosystem processes, environmental perturbations, health of marine systems and the state of fisheries (Nettleship et al. 1984, Cairns 1987, Croxall 1989, Monaghan et al. 1989, Montevecchi 1993, ICES 2000, Schreiber and Burger 2002, Crawford 2004, Boyd et al. 2006). If seabird data are to be useful as indicators of ecosystem conditions, they should be easily obtained, sensitive to the conditions measured and have low variability in response (Dale and Beyeler 2001, Frederiksen et al. 2007). A prior understanding of the factors that constrain individual behavioural and population responses is required so that the functional relationships of the past are good predictors of ecosystem or prey conditions of the future (Piatt et al. 2007). This can only be achieved through basic knowledge of the ecology of the species concerned. Seabird responses to environmental perturbations and variations in prey availability vary in their sensitivity over different spatial and temporal scales (Table 1). Responses also vary due to individual, colony and species-specific differences in foraging behaviour, physiology and vital rates (Wilson 1992, Schreiber 2002). The widespread information available from seabird foraging and demographic studies suggests that the ideal indicator species would be one that 1) is inflexible and energetically expensive in its foraging methods, 2) is restricted in its dietary width, foraging range and niche use, 3) has large clutch sizes and variable reproductive success and 4) has high, stable rates of adult survival (Furness and Tasker 2000). The idea of an ‘ultimate sentinel’ of ecosystem conditions existing may be a paradox. Such a species may be prone to extinction as it would be unlikely able to buffer the stochastic variations in prey availability typical of marine ecosystems. The wide-ranging species and parameter-specific responses to ecosystem perturbations suggest that monitoring programs should incorporate information from as wide a range of parameters, populations and species as practical. This approach has been adopted by the Convention on the
Conservation of Antarctic Marine Living Resources (CCAMLR) where key foraging and demographic parameters are monitored from ‘dependent’ predator species within Antarctic waters. This information is then assessed against data relating to biophysical processes and fisheries catches to infer ecosystem health (www.ccamlr.org/ 18th Sept 2009). Table 1 summarises some of the seabird parameters used in assessing changes in ecosystem conditions and prey availability, their sensitivity, and the temporal scale at which each metric indicates change (adapted from Cairns 1987). The data recorded from crested tern populations and provided in this thesis are also listed.
Table 1. Seabird monitoring parameters, measures, and methodologies used to examine variations in prey availability. The sensitivity and temporal scale at which each metric indicates prey availability is listed. The parameters monitored in this study are also listed (adapted from Cairns 1987). Symbols used D days, W weeks, Y years, Dec decades.

<table>
<thead>
<tr>
<th>Monitoring parameter</th>
<th>Measure</th>
<th>Methodology (Field, laboratory, analytical)</th>
<th>Prey conditions over which metric is sensitive</th>
<th>Integration period</th>
<th>Monitored in this study</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Diet</strong></td>
<td>Prey composition (size, mass, nutritional value)</td>
<td>Nest monitoring at breeding colonies, regurgitate analysis- BOM calorimetry</td>
<td>All</td>
<td>All</td>
<td>Yes</td>
</tr>
</tbody>
</table>
| **Forage based-activity measures** | Nest attendance  
Trip duration or habitat use  
Chick provisioning rates  
Energetic requirements, energetic expenditure | Nest monitoring  
Telemetry, spatial analyses  
Nest monitoring at breeding colonies  
Tritium (Doubly labelled water) experiments | Moderate to good  
Moderate to good  
Moderate to good  
Moderate to good | D, W  
D, W,  
D, W  
D, W | Yes  
Yes  
Yes  
No |
| **Breeding**         | Egg size  
Clutch size  
Mean lay or hatch date | Nest monitoring at breeding colonies  
Nest monitoring at breeding colonies  
Nest monitoring at breeding colonies | Poor to moderate  
Poor to moderate  
Poor to moderate | W  
W  
W | No  
No  
Yes |
| **Physiological**    | Chick growth rate  
Fledgling mass and age  
Body condition (body mass indices)  
Body condition (blood assays) | Nest monitoring, Morphology measurements  
Nest monitoring, Morphology measurements, Banding  
Nest monitoring, Morphology measurements  
Blood collection | Poor to moderate  
Poor to moderate  
Poor  
Poor | D, W  
D, W  
D, W  
W | Yes  
Yes  
Yes  
No |
| **Demographic**      | Population number (breeding pairs)  
Population census (number of breeding colonies)  
Survival (Adult, immature)  
Breeding success  
Age structure of population  
Immigration, Emigration rate | Field census, photographic or ground counts, Banding, recaptures, population modelling, Mark-recapture analysis  
Field census  
Banding, Mark-recapture analysis  
Banding, Mark-recapture analysis  
Banding, Mark-recapture analysis  
Banding, Mark-recapture analysis | Very poor  
Poor to moderate  
Very poor  
Poor to moderate  
Poor to moderate | W, Y, Dec  
W, Y Dec  
Y, Dec  
Y, Dec  
Y, Dec | Yes  
No  
No  
Yes  
Yes |
Background to the study

Sardine are the target of Australia’s largest volume fishery, the South Australian Sardine Fishery (SASF), which uses purse-seining methods to provide sardine *Sardinops sagax* to the Southern bluefin tuna *Thunnus maccoyii* mariculture industry in South Australia. This fishery has grown rapidly since its inception in 1991, reaching a total annual catch in 2005 of 39,000 tonnes (Ward et al. 2008). The negative effects of overfishing small pelagic fish on apex predators are well documented (Duffy 1983, Burger and Cooper 1984, Crawford and Dyer 1995). However, the ecological processes and interactions influencing the habitats used by fisheries in South Australia are poorly understood. In response to the growth of the SASF, lack of knowledge about local ecosystem function, and concerns about the fishery’s potential impacts on higher order predators, Australian scientists and fisheries managers developed a project to identify performance indicators from a suite of predators that inhabit waters targeted by the SASF (Shanks 2004) (FRDC PN 2005/031). Crested terns are an apex predator common to South Australian marine ecosystems and are known to prey on surface schooling clupeiform species such as sardine (Hulsman et al. 1989, Smith 1993, Chiaradia et al. 2002). Some of the data presented in this thesis will be assessed for its suitability in providing performance indicators for sardine stock management and used to develop trophic models for the pelagic marine ecosystem of South Australia (FRDC PN 2005/031).

Objectives of the study

The primary aim of this thesis is to describe the functional relationships between the diet, foraging behaviour and life history traits of crested terns. I examine these relationships in the context of phenotypic and age-specific constraints, and ontogeny. Specifically the aims of the study were to:

1. Assess the diet of crested tern chicks and adults, and whether there were any temporal, spatial and ontogenetic differences in prey composition and size.
2. Measure the demographic and morphological responses of a tern population to two mass mortalities of one of their major prey, sardine *Sardinops sagax*.
3. Measure the growth and survival responses of crested tern chicks to differences in adult provisioning rates, and in response to phenotypic and age-specific differences in parental quality reflected in adult body condition and reproductive timing.
4. Describe the fine-scale foraging patterns and habitat use of adult crested terns while provisioning chicks

Structure of the thesis

The thesis is arranged as six chapters, comprising the general introduction, four data chapters and a general discussion. The data chapters are presented as a series of papers that are published or awaiting publication, and are entirely self-contained. As a consequence, some material is duplicated. The first data chapter (Chapter 2) uses the effects of two mass sardine *Sardinops sagax* mortality events as a ‘natural’ experiment to assess the impacts of prey depletion on recruitment and morphology of crested terns reared during years of low sardine biomass. Chapter 3 describes the diets of crested terns. It investigates the ontogenetic, temporal and spatial patterns in the composition and size of prey in the diet of crested terns, and the underlying sources of variation contributing to the patterns observed. Chapter 4 assesses how rates of chick growth and survival vary in response to provisioning patterns, and to phenotypic and age specific variations in reproductive timing and adult body condition. Chapter 5 uses data collected from GPS units deployed on adult crested terns to describe their fine-scale foraging behaviour and habitat use while provisioning their chicks. Chapters 2 and 3 were published in 2009 by the *ICES Journal of Marine Science* and *Marine Biology*, respectively, and are reproduced here with their permission. Chapters 4 and 5 are currently in review at *Behavioral Ecology* and *Marine Ecology Progress Series*, respectively. In chapter 6 the key findings of all chapters are integrated and discussed. I also detail how future research could augment the findings of this study, and consider how data collected from crested tern populations could be used to enhance fisheries management strategies and conservation outcomes for crested tern populations.
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CHAPTER 1    General Introduction


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Chapter 2. Demographic and morphological responses to prey depletion in a crested tern *Sterna bergii* population: Can fish mortality events highlight performance indicators for fisheries management?


Statement of authorship: Appendix A
Abstract
Disease-related mortality events in 1995 and 1998, which killed ~ 70% of adult sardine Sardinops sagax biomass, provided an opportunity to assess whether crested tern populations were affected by decreased prey abundance. We investigated the diet, age structure and morphology of a crested tern population to determine whether survival and growth were reduced for cohorts reared in years immediately following sardine mortality events. The diet of chicks and adults differed significantly. Australian anchovy Engraulis australis and sardine were the dominant prey in the diets of chicks, comprising an average of 36.3 and 14.6% of individuals, respectively. Degens leatherjacket Thamnoconus degeni dominated prey in adult diets, comprising an average of 51.9% of individuals. Age-specific information collected from banded adults indicated that the cohort reared after the first sardine mortality event in 1995 exhibited significantly lower rates of recruitment to the breeding colony compared to that predicted by life-table analyses, suggesting survival was reduced in response to absence of sardine. Females from cohorts reared < 1 year after the end of each sardine mortality event (in 1995 and 1999), had smaller morphology compared to other age classes suggesting chick growth was reduced during periods of low sardine abundance. Future data relating to diet, and the survival and growth of crested tern chicks could provide performance indicators for management of sardine populations and aid in the development of conservation strategies for crested tern populations.

Key words: crested tern, demography, ecosystem based management, indicator, morphology, prey availability, sardine, seabird, Sterna bergii, survival.
CHAPTER 2   Demographic and morphological responses

Introduction

Top predators are downstream in terms of energy flow through marine ecosystems and may be indicative of ecosystem status and performance (Boyd et al. 2006). Ecosystem Based Fisheries Management (EBFM) is looking towards predator-based performance measures to inform management decisions relating to prey (stock) biomass, and to ensure that the conservation status of predator populations is maintained (Crawford 2004, Hall and Mainprize 2004, Boyd et al. 2006). Numerous seabird studies have shown links between changes in prey availability and measures of demography, foraging, reproduction, and fisheries (Anderson et al. 1980, Uttley et al. 1989, Montevecchi 1993, Montevecchi and Myers 1995, Furness and Tasker 2000, ICES 2001, Hall and Mainprize 2004, Boyd et al. 2006, Scott et al. 2006), and seabird data are now used to inform management decisions in several fisheries (ICES 2001, 2002, Lewis et al. 2001). Nevertheless, the suitability of a predator in providing performance measures for use in EBFM depends on knowledge of how they respond to changes in prey availability.

Fish from the Order Clupeiformes (Sardine, anchovy and sprats) are a key link in food webs and the target of commercial fisheries worldwide. In shelf waters of South Australia sardine *Sardinops sagax* and Australian anchovy *Engraulis australis* form a dominant component of the small pelagic fish assemblage (Ward et al. 2001a, Crawford 2004, Dimmlich et al. 2004). Recently the South Australian Sardine Fishery (SASF), which uses purse-seining methods to provide sardine *Sardinops sagax* to the Southern bluefin tuna *Thunnus maccoyii* mariculture industry in South Australia, has expanded in terms of catch, effort and investment. It is now Australia’s largest fishery (by weight), with an annual catch in 2006 of approximately 25 000 t (Figure 1). The effects of ‘forage fish’ overfishing on apex predators such as seabirds are well documented. Purse-seine fishing in Namibia and South Africa between 1956 and 1980 induced stock collapse of sardine and anchovy, causing populations of African penguin (*Spheniscus demersus*) and cape gannets (*Morus capensis*) to fall to almost one half (Burger and Cooper 1984, Crawford and Dyer 1995, Crawford 1998). In response to the rapid growth of the SASF, and concerns about its potential ecological impacts, Australian fisheries managers are looking to incorporate reference points for sardine predators into management plans (Shanks 2004).

In March 1995 and October 1998 > 70% of the sardine stock biomass in southern Australia was killed over a period of 3-4 months (Gaughan et al. 2000, Ward et al. 2001b). An exotic
herpesvirus originating in South Australia and spreading 2500 km east and west, was considered to be the cause (Jones et al. 1997, Murray et al. 2003). Sardine spawning biomass estimates provided via application of the daily egg production method in the years immediately following (1996 and 1999), reflected the effect of mortality events (Figure 1) (Ward et al. 2001a). In Victoria, negative impacts on apex predators were documented for little penguins *Eudyptula minor*, little terns *Sterna albifrons* in 1995/96 (Dann et al. 2000, Taylor and Roe 2004) and Australasian gannets *Morus serrator* in 1998/99 (Bunce and Norman 2000, Bunce et al. 2005). These studies were a precedent for our research.
CHAPTER 2     Demographic and morphological responses

Figure 1. Commercial sardine *Sardinops sagax* landings and annual estimates of spawning biomass obtained via application of the Daily Egg Production Method between 1995 and 2006.

Crested terns are a small surface-feeding seabird that preys on small pelagic fishes such as sardine and Australian anchovy or squid (Hulsman et al. 1989, Chiaradia et al. 2002, present study). During the breeding season adults lay one egg, which they incubate for approximately 28 days (Langham and Hulsman 1986). After hatching, chicks are provisioned by both parents at the breeding colony for up to two months. Many seabird species have evolved strategies to maximise foraging effort and rates of prey delivery to chicks during the breeding season. For instance, penguins are able to carry large volumes of prey that they then regurgitate to their chicks. In contrast, crested terns are generally single prey loaders (i.e. they deliver one prey item to their chicks at a time). This strategy requires that they forage for themselves before returning prey of suitable size to their chick. The requirement to locate prey regularly from surface waters near the colony may make them sensitive to changes in prey availability if they are unable to switch to alternative prey.

In this study we tested the hypothesis that the mass sardine mortalities in March 1995 and October 1998 negatively affected the survival and growth of cohorts reared in the summer immediately following (i.e. December to January of 1995/1996 and 1999/2000), when sardine biomass was most reduced. This hypothesis was tested based on the rationale that crested terns are known to feed on fishes such as sardine that dominate the small pelagic fish
assemblage of South Australia. Also, life history theory predicts that natural selection will act to preserve the stage of life history at which survival and reproduction are least variable (Saether and Bakke 2000). Hence in long-lived seabirds, annual survival may be favoured at the expense of reproductive investment during periods of low prey availability (Furness and Tasker 2000, ICES 2001). The number of adult crested terns breeding in all years of chick banding at Troubridge Island has remained relatively constant (Waterman unpublished data).

Hence, we predict that survival of crested tern chicks was lower during periods of low sardine biomass, and that this is reflected in lower recruitment of the 1995 and 1999 cohorts to the breeding colony. Similarly, the growth of chicks reared during periods of low sardine biomass is likely reflected in the age-specific morphology of adults because chicks attain over 70% of body mass and 60% culmen length (CL) in < 2 months after hatching (Langham and Hulsman 1986, Schew and Ricklefs 1998).

Our study involved (1) measuring the prey composition of crested terns to assess whether sardine formed a major component of the diet in a year when sardine biomass was large, and whether there were differences between the diet of chicks and adults, (2) determining the age-structure of the breeding colony to test for age-specific differences in recruitment and (3) examining the age-specific morphology of adult crested terns to test whether crested terns reared in periods of low sardine availability had smaller morphology compared to other cohorts.

Based on our findings we discuss whether survival and growth of crested tern chicks is influenced by sardine availability, and whether ecological data collected from crested tern colonies can be applied as performance indicators for crested tern populations and in management of the SASF.
Methods

Study site
This study was conducted at Troubridge Island in Gulf St Vincent, South Australia during the breeding seasons of crested terns between November and February in 2004/05, 2005/06 and 2006/07 (Figure 2). We refer to seasons or cohorts as belonging to the year that sampling or breeding began respectively (e.g. 1999/00 = 1999). The Troubridge Island colony is one of the largest in gulf waters of South Australia, with ~3500 pairs in 2005 (McLeay unpublished data), and lies at the eastern extent of the region where the majority of the commercial catch is taken by the SASF (Figure 2).

Diet sampling
Regurgitates were collected between 23 November 2005 and 25 January 2006 from crested tern chicks (n = 258) aged 0-5 weeks. Regurgitates were collected from adults (n = 214) that were incubating eggs and provisioning chicks < 1 week old between 28 October and 21
December 2005. Chicks and adults were caught by hand and hand-held nets respectively. To minimise disturbance to the colony during each visit, birds were caught by moving systematically from one end of the colony to the other. This also ensured no bird was caught more than once per visit. Samples, which were mainly undigested, were placed in a plastic bag and frozen before being sorted in the laboratory, where individual prey were separated and identified to the lowest taxonomic group possible. Species level identification of individuals from the families Clupeidae and Engraulidae (sardine and Australian anchovy) was sometimes not possible. I.e. individuals may have been either one of these species. Hence, to determine the most important prey, we allocated unidentified individuals from these families proportionally to the groups identified specifically as sardine or Australian anchovy. The dietary composition of chicks and adults was analysed by two methods:

1. Percentage numerical abundance (the proportion of the total number of individual prey items made up by each prey taxon). To standardise for individuals that consumed more individual prey items, the average percent of each taxon was calculated over all regurgitates.

2. Relative occurrence (RO), calculated as the frequency of occurrence (FOO) of a taxon in samples (i.e. the percentage of the total number of samples in which each taxon was present) divided by the sum of FOOSs of all taxa. Unlike FOO, RO contributions total 100% (Montague and Cullen, 1987).

Diet data (percentage numerical abundance) did not conform to assumptions of normality and homoscedasticity, so to assess whether chick and adult diets differed significantly in composition and whether absence of sardine could have influenced chicks and adults differently, nonparametric analysis of similarity (ANOSIM), on a Bray-Curtis similarity matrix (PRIMER version 5.1.2, PRIMER-E Ltd., Plymouth, UK) was used (alpha set at ≤ 0.05). ANOSIM is a hypothesis-testing procedure that generates a probability value and a test statistic (R), which lies between 1 and –1. High positive R-values indicate greater variation among groups than within groups, and negative values indicate high levels of within group variation compared to between groups. Values of R equal to zero represent the null hypothesis of no significant difference between groups. The differences in the contributions of prey species to diet were determined using Similarity Percentages (SIMPER, Plymouth Routines in
Multivariate Ecological Research), which indicated the proportion of the difference between the diets of chicks and adults for which each prey taxon was responsible (Catalan et al. 2006).

**Age structure**
Banding of crested tern chicks at Troubridge Island commenced in December 1966 (Waterman et al. 2003). Since 1975, an average of 1348 chicks (SE = ± 111.6; range 640 - 2350) have been banded annually, but no banding occurred between 1976 and 1985. The age distribution of the breeding adults from 2004 to 2006 was determined by capturing adults on their nests with a hand-held net, recording band numbers, and referencing these against band records. The number of chicks banded each year was not the same so inter-annual differences in age structure were standardised by calculating the percentage of birds per cohort that were resighted. This was done by dividing the total number of individuals recaptured from each cohort by the total number of chicks that were banded in the same cohort. Age frequency distributions were then constructed for the colony from the relative proportions of each cohort present.

**Survival**
A static life table was created from age data obtained for all adults recaptured between 2004 and 2006 (Caughley, 1977, Evans and Hindell, 2004). Static life tables assume a stable age structure and that population size is stationary. The crested tern population at Troubridge Island is believed to have stationary growth and a stable age structure. Data from banded adults indicates a high degree of philopatry and there is no evidence for the occurrence of transients in this population (Waterman et al. 2003, this study). Population size during the banding period (1975-2006) has also remained stable (Waterman unpublished data, McLeay unpublished data). Nonetheless, age class data did not meet the assumptions of a static life table (i.e. that the frequency of each age class $x$ is $\geq x + 1$: Caughley 1977) so cohort frequency data were smoothed using OriginPro® with a log-polynomial regression:

$$ \log f_x = a + bx + cx^2 + dx^3 + \ldots . etc $$

where $f_x$ is the sampled frequency of age $x$ and $a$, $b$, $c$ and $d$ are constants. To reduce the sum of squares, fitting was carried out in stages, assuming mortality was constant with age, until the addition of further terms did not result in further significant reductions in the sum of squares. Survival was modelled from the time that breeding was first recorded (4 y) up to the
maximum age of breeding recorded (29 y, this study). The parameters of the static life table calculated, based on those developed by Caughley (1977) were:

\[ l_x : \text{survivorship, the probability at age } x \text{ of surviving to age } x \]
\[ d_x : \text{mortality, the probability of dying in each age interval } x \text{ to } x + 1. \]
\[ q_x : \text{mortality rate} \]
\[ p_x : \text{survival rate} \]

To assess age-specific patterns of survival we used Chi square tests to determine whether observed age frequencies deviated from those derived from the log-polynomial regression (expected).

**Morphology**

Adult birds with bands that were captured from their nests had the following morphological characters measured with vernier callipers (± 0.01mm): Culmen length (\( CL \)): from base of forehead feathers to tip of bill; bill depth (\( BD \)): vertical thickness of the bill at the anterior edge of the nostrils; head length (\( HL \)): distance from occiput to the tip of the bill. Birds were also weighed (± 5 g) before release and after any regurgitates were collected.

**Sex dimorphism**

Crested terns are known to be sexually dimorphic (Woehler et al. 1991). To separate age-specific differences in size and survival from sex-related differences, we constructed a discriminant function model for a subset (reference group) of birds captured in 2005. During the peak laying period in early November 2005, newly incubating birds, which had laid within 24 hours, were caught and assigned a score of 0-3 using cloacal sexing criteria (Boersma and Davies 1987). After morphological measurements were recorded, each individual was colour banded and released. When the mate returned, it was caught, assigned a cloacal score and measured. One way ANOVA or Komolgorov-Smirnov tests were used to assess differences in morphology between males and females of the reference group (\( n = 67 \)) \( p \leq 0.05 \). All analyses were undertaken using SPSS® and data were tested for assumptions of normality and homoscedasticity using Shapiro-Wilks’ test and Box’s M-test, respectively.

We then constructed discriminant functions (Jack-knifed and cross-validated) using SPSS® (version 15 for Windows) from the variables that described head and bill morphology and
mass for the reference group of adults with differences in cloacal sexing criteria >1 (n = 67 individuals comprising 34 pairs). The discriminant function that best classified sex from discriminant scores calculated from adult morphology was used to assign sex to each known-age individual that was captured and measured between 2004-06 (n = 1227). Individuals were assigned a sex based on whether their scores assigned from the discriminant function were greater or less than the ‘cutoff’ score, which was calculated from the weighted mean of the two group centroids of the reference group. Age related trends in morphology were then plotted for each morphological variable and sex.

**Age- and sex-specific differences in morphology**

To test the hypothesis that smaller age-specific morphology ($CL$, $BD$, $HL$) was caused by a reduction in the abundance of sardines, we allocated individuals (pooled for three seasons 2004-2006) of each sex to a treatment group.

Group 1: chicks hatched < 1 year after the end of each sardine mass-mortality event (i.e. the cohorts that were banded in December 1995 and 1999).

Group 2: chicks hatched in other years.

Treatment groups were assigned on the rationale that the timing of each sardine mortality event was different (March 1995 vs October 1998) and took 4 months to complete. Hence, the effects of decreased sardine abundance on crested terns were assumed to be most severe following the completion of a sardine mortality event and not while fish were still dying. Morphological data did not conform to assumptions of normality and homoscedasticity so non-parametric analysis of similarity (ANOSIM) (for which R values are reported), on a Bray-Curtis similarity matrix (PRIMER version 5.1.2, PRIMER-E Ltd., Plymouth, UK) was used to test for significant differences in morphology between each treatment group for males (n = 652) and females (n = 575) ($p \leq 0.05$). ANOSIM tests the null hypothesis that within-group similarities do not exceed between group similarities. Similarity Percentages (SIMPER, Plymouth Routines in Multivariate Ecological Research) were used to determine which measure of morphology ($CL$, $BD$, $HL$) most contributed to the observed differences between treatment groups. Data from individuals caught and measured after the first recapture were excluded.
Results

Diet

In total, 36 prey taxa were identified from 839 individual prey items in 472 regurgitates (Table 1). Twenty-six species were identified from chick and adult diet samples collected over 19 and 17 days, respectively over the course of the breeding season (November–January). Fish comprised over 93% of all prey taxa identified. Australian anchovy *Engraulis australis* and sardine *Sardinops sagax* were the main prey consumed by chicks, comprising 36.3 and 14.6% of all individual prey items found, respectively (Table 1). Degens leatherjacket *Thamnoconus degeni* were the most common prey item in the diet of adults, comprising an average of 51.9% of individual prey items, and present in nearly 40% of samples (RO) (Table 1). The difference between chick and adult diets was significant (ANOSIM, $R = 0.209$, $p \leq 0.001$) due to the variation in the abundance of these species in chick and adult diets (SIMPER Australian anchovy 21.3%; sardine 10.8%; Degens leatherjacket 28.6%). Differences suggest adult foraging effort may be partitioned according to the dietary requirements of adults and/or that of their chicks.
Table 1. Diet of *Sterna bergii* chicks and adults on Troubridge Island between 23 November 2005 and 25 January 2006. RO = relative occurrence

<table>
<thead>
<tr>
<th>Species/Taxa</th>
<th>Chicks Average abundance (%)</th>
<th>Adults Average abundance (%)</th>
<th>RO</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family Engraulidae <em>Engraulis australis</em></td>
<td>36.3</td>
<td>32.4</td>
<td>12.2</td>
</tr>
<tr>
<td>Family Clupeidae <em>Sardinops sagax</em></td>
<td>14.6</td>
<td>20.3</td>
<td>8.1</td>
</tr>
<tr>
<td>Family Gempylidae <em>Thryraites atun</em></td>
<td>11.6</td>
<td>10.2</td>
<td>1.4</td>
</tr>
<tr>
<td>Family Arrildiidae <em>Arrilpis geomurians</em></td>
<td>7.5</td>
<td>6.8</td>
<td>0.8</td>
</tr>
<tr>
<td>Class Actinopterygii- unidentified</td>
<td>5.8</td>
<td>6.5</td>
<td>3.5</td>
</tr>
<tr>
<td>Family Clupeidae <em>Spratelloides robustus</em></td>
<td>4.7</td>
<td>4.5</td>
<td>0</td>
</tr>
<tr>
<td>Family Monacanthidae <em>Thamnacronus degani</em></td>
<td>4.1</td>
<td>3.7</td>
<td>51.9</td>
</tr>
<tr>
<td>Family Monacanthidae- unidentified</td>
<td>3</td>
<td>3.1</td>
<td>3.2</td>
</tr>
<tr>
<td>Family Pempheridae <em>Parapromanchus elongatus</em></td>
<td>1.9</td>
<td>2.4</td>
<td>1.4</td>
</tr>
<tr>
<td>Family Hemiramphidae <em>Hyporhamphus melanocha</em></td>
<td>1.8</td>
<td>1.8</td>
<td>5.8</td>
</tr>
<tr>
<td>Family Odacidae- unidentified</td>
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<td>1.3</td>
<td>0.8</td>
</tr>
<tr>
<td>Family Monacanthidae <em>Acanthalepterus sp.</em></td>
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<td>0.8</td>
<td>0.9</td>
</tr>
<tr>
<td>Family Carangidae <em>Pseudoscaris wrighti</em></td>
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<td>0.5</td>
<td>0.2</td>
</tr>
<tr>
<td>Family Emmelichthyidae <em>Emmelichthys nitidus nitidus</em></td>
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<td>0.5</td>
<td>0.7</td>
</tr>
<tr>
<td>Family Labridae <em>Haletta sp</em></td>
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<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td>Class Cephalopoda- unidentified</td>
<td>0.5</td>
<td>0.5</td>
<td>0.1</td>
</tr>
<tr>
<td>Class Cephalopoda <em>Sepiolthys australis</em></td>
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<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Class Cephalopoda <em>Notodoras Gouldi</em></td>
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<td>0.3</td>
<td>0</td>
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<tr>
<td>Class Notacanthidae- unidentified</td>
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<td>0.3</td>
<td>4.6</td>
</tr>
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<td>Family Mugilidae <em>Aldrichetta forsteri</em></td>
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<td>0.3</td>
<td>0</td>
</tr>
<tr>
<td>Family Diodontidae <em>Diodon nithmerus</em></td>
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<td>0.3</td>
<td>0.5</td>
</tr>
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<td>0.3</td>
<td>0</td>
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<td>Family Notacanthidae <em>Sto rhophilus</em></td>
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<td>0.3</td>
<td>0</td>
</tr>
<tr>
<td>Family Labridae <em>Neodax balteatus</em></td>
<td>0.3</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td>Family Gonorynchidae <em>Gonorynchus greyi</em></td>
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<td>0.5</td>
<td>0.1</td>
</tr>
<tr>
<td>Order Decapoda- unidentified</td>
<td>0.2</td>
<td>0.3</td>
<td>0</td>
</tr>
<tr>
<td>Family Syngnathidae <em>Hypselogonathus rostratus</em></td>
<td>0.2</td>
<td>0.3</td>
<td>0</td>
</tr>
<tr>
<td>Family Terapontidae <em>Pelates octolineatus</em></td>
<td>0.2</td>
<td>0.3</td>
<td>0.1</td>
</tr>
<tr>
<td>Order Isopoda- unidentified</td>
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<td>0</td>
<td>0.2</td>
</tr>
<tr>
<td>Family Clinidae- unidentified</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
</tr>
<tr>
<td>Family Carangidae- unidentified</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
</tr>
<tr>
<td>Family Monacanthidae <em>Scobinichthys granulatus</em></td>
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<td>0</td>
<td>0.5</td>
</tr>
<tr>
<td>Family Syngnathidae <em>Hippocampus sp</em></td>
<td>0</td>
<td>0</td>
<td>0.7</td>
</tr>
<tr>
<td>Family Sillaginidae <em>Silago bassensis</em></td>
<td>0</td>
<td>0</td>
<td>0.2</td>
</tr>
<tr>
<td>Family Apogonidae <em>Vincentia sp</em></td>
<td>0</td>
<td>0</td>
<td>0.5</td>
</tr>
<tr>
<td>Order Decapoda <em>Melicertus latissulcatus</em></td>
<td>0</td>
<td>0</td>
<td>0.4</td>
</tr>
</tbody>
</table>

**Total n prey items** | **414** | **425** |

Age structure

Age structures constructed from adult resight information indicated that crested terns live for up to 29 y (Figure 3). The minimum age of first breeding at Troubridge Island was 4 y in 2006 (Figure 3). There was substantial variation in the percent of resights recorded between cohorts.
in each year. Chicks reared in 1985, 1995 and 1999-2002 each comprised < 5% of the
breeding population in each season sampled (Figure 3). The reason for the scarcity of the 1985
cohort is unclear. No sardine biomass data are available for this period. The relatively low
percentage of individuals from the 1995 cohort coincides with sardine mass-mortality events,
which occurred < 1 year before. Not all individuals from cohorts reared between 1999 and
2002 had reached sexual maturity and had only partly recruited to the breeding colony at the
time of sampling.
Figure 3. Age structure of *Sternula bergii* breeding at Troubridge Island over three seasons of recaptures. Shaded bars represent cohorts reared <1 y after the completion of each *Sardinops sagax* mortality event.
**Patterns of survival**

Age-specific values of survivorship ($l_x$), mortality ($d_x$) and their associated rates were calculated from the static life table (Table 2). These values are based on a stationary age distribution, which was calculated from smoothed frequency values for each cohort. The probability of dying between age intervals peaked between 9 and 15 y. The frequency of resights for 7 of 17 cohorts differed significantly from those predicted by the model ($\chi^2$ test, $p \leq 0.05$, Table 2). The number of individuals in the 1995 cohort, which were reared 8 months after the mass mortality in March 1995, was significantly less than that predicted by the model ($\chi^2 = 62.08, p \leq 0.001$, Table 2). The observed frequency of adults resighted in the colony from the cohorts of 1985 (19 y), 1999 (5 y) and 2000 (4 y) was also significantly lower than expected (1985 $\chi^2 = 6.34, p \leq 0.05$; 1999 $\chi^2 = 54.83$, and 2000 $\chi^2 = 111.99, p \leq 0.001$, Table 2). In contrast, significantly more individuals from 1987, 1992 and 1997 were present in the colony than predicted by the model (1987 $\chi^2 = 25.46, p \leq 0.001$; 1992 $\chi^2 = 8.29, p \leq 0.05$; 1997 $\chi^2 = 160.14, p \leq 0.001$, Table 2).
Table 2. The number of chicks banded and the observed and predicted frequencies of adults crested terns *Sterna bergii* in each cohort at Troubridge Island, South Australia. Percent resight of cohorts, static life table parameters and $\chi^2$ test results for variation between observed and predicted frequencies of adults are listed. Significant tests ($p \leq 0.001, p \leq 0.05$) are in bold. Data from all seasons are pooled and ages are calculated as of December 2004.

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Number of chicks banded per cohort</th>
<th>Age (yrs)</th>
<th>Observed frequency</th>
<th>Predicted frequency</th>
<th>Percent resight</th>
<th>$l_x$ (survivorship)</th>
<th>$d_x$ (mortality)</th>
<th>$q_x$ (mortality rate)</th>
<th>$p_x$ (survival rate)</th>
<th>$\chi^2$</th>
<th>$p$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>1 000</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>0.2</td>
<td>1.000</td>
<td>0.005</td>
<td>0.005</td>
<td>0.995</td>
<td>112.0</td>
<td>$\leq 0.001$</td>
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<tr>
<td>2000</td>
<td>1 700</td>
<td>4</td>
<td>10</td>
<td>131.2</td>
<td>0.7</td>
<td>0.995</td>
<td>0.020</td>
<td>0.020</td>
<td>0.980</td>
<td>54.8</td>
<td>$\leq 0.001$</td>
</tr>
<tr>
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<td>2 100</td>
<td>5</td>
<td>46</td>
<td>130.6</td>
<td>2.7</td>
<td>0.975</td>
<td>0.035</td>
<td>0.036</td>
<td>0.964</td>
<td>0.9</td>
<td>0.33</td>
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<tr>
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<td>1 600</td>
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<td>117</td>
<td>128.0</td>
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<td>0.940</td>
<td>0.048</td>
<td>0.051</td>
<td>0.949</td>
<td>160.1</td>
<td>$\leq 0.001$</td>
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<td>7</td>
<td>264</td>
<td>123.4</td>
<td>13.9</td>
<td>0.893</td>
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<td>8</td>
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<td>990</td>
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<td>0.273</td>
<td>0.052</td>
<td>0.190</td>
<td>0.810</td>
<td>25.5</td>
<td>$\leq 0.001$</td>
</tr>
<tr>
<td>1987</td>
<td>940</td>
<td>17</td>
<td>66</td>
<td>35.8</td>
<td>8.6</td>
<td>0.221</td>
<td>0.045</td>
<td>0.203</td>
<td>0.797</td>
<td>1.2</td>
<td>0.26</td>
</tr>
<tr>
<td>1986</td>
<td>800</td>
<td>18</td>
<td>35</td>
<td>29.0</td>
<td>5.4</td>
<td>0.176</td>
<td>0.038</td>
<td>0.216</td>
<td>0.784</td>
<td>6.3</td>
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</tr>
<tr>
<td>1985</td>
<td>1 598</td>
<td>19</td>
<td>11</td>
<td>23.1</td>
<td>0.8</td>
<td>0.138</td>
<td>0.031</td>
<td>0.228</td>
<td>0.772</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No banding</td>
<td>20  *</td>
<td>18.1</td>
<td>0</td>
<td>0.138</td>
<td>0.031</td>
<td>0.228</td>
<td>0.772</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No banding</td>
<td>21  *</td>
<td>14.0</td>
<td>0</td>
<td>0.107</td>
<td>0.026</td>
<td>0.240</td>
<td>0.760</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No banding</td>
<td>22  *</td>
<td>10.6</td>
<td>0</td>
<td>0.081</td>
<td>0.020</td>
<td>0.252</td>
<td>0.748</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No banding</td>
<td>23  *</td>
<td>7.9</td>
<td>0</td>
<td>0.061</td>
<td>0.016</td>
<td>0.264</td>
<td>0.736</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No banding</td>
<td>24  *</td>
<td>5.9</td>
<td>0</td>
<td>0.045</td>
<td>0.012</td>
<td>0.276</td>
<td>0.724</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No banding</td>
<td>25  *</td>
<td>4.2</td>
<td>0</td>
<td>0.032</td>
<td>0.009</td>
<td>0.287</td>
<td>0.713</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No banding</td>
<td>26  *</td>
<td>3.0</td>
<td>0</td>
<td>0.023</td>
<td>0.007</td>
<td>0.298</td>
<td>0.702</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No banding</td>
<td>27  *</td>
<td>2.1</td>
<td>0</td>
<td>0.016</td>
<td>0.005</td>
<td>0.309</td>
<td>0.691</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No banding</td>
<td>28  *</td>
<td>1.5</td>
<td>0</td>
<td>0.011</td>
<td>0.004</td>
<td>0.320</td>
<td>0.680</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1975</td>
<td>900</td>
<td>29</td>
<td>1</td>
<td>1.0</td>
<td>0.1</td>
<td>0.008</td>
<td>0.0</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Total: 26,248, 1,246, and 100.
Discriminating sex
Males of the reference group were significantly larger than females for bill depth, culmen length and head length ($p \leq 0.05$), but body mass did not differ significantly between sexes (Table 3). The sex of individuals was most accurately assigned by a discriminant function that combined measurements of head and bill morphology and body mass:

$$D = (1.178*BD) + (0.378*CL) + (0.584*HL) + (-0.023*\text{Mass}) - 50.432 \quad \text{Equation (1)}$$

Where $D$ is the discriminant score, and $BD$, $CL$ and $HL$ are bill depth (mm), culmen length (mm) and head length (mm) respectively.

Equation (1) classified 88.1% of all grouped cases and cross-validated grouped cases correctly. Based on the reference group, the discriminant function classified 84.8 and 91.2% of males and females correctly. Standardised discriminant function analyses indicated that $HL$ was the most useful measurement in discriminating sex.

Table 3. Bill morphology and mass measurements of male and female crested terns sexed from cloacal examination (Reference group). Significant differences ($p \leq 0.001$) between male and female bill size or mass are shown in bold. Symbols: SD standard deviation.

<table>
<thead>
<tr>
<th>Character</th>
<th>Sex</th>
<th>Mean</th>
<th>SD</th>
<th>Range</th>
<th>$p$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bill depth (mm)</td>
<td>Male</td>
<td>12.3</td>
<td>0.42</td>
<td>11.6 - 13.4</td>
<td>$\leq 0.001$</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>11.8</td>
<td>0.41</td>
<td>11.3 - 13.3</td>
<td></td>
</tr>
<tr>
<td>Culmen length (mm)</td>
<td>Male</td>
<td>61.4</td>
<td>2.07</td>
<td>57.4 - 65.2</td>
<td>$\leq 0.001$</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>58.6</td>
<td>2.23</td>
<td>54.5 - 63.8</td>
<td></td>
</tr>
<tr>
<td>Head length (mm)</td>
<td>Male</td>
<td>116.5</td>
<td>2.56</td>
<td>111.3 - 122.6</td>
<td>$\leq 0.001$</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>112.1</td>
<td>2.65</td>
<td>107.5 - 118.0</td>
<td></td>
</tr>
<tr>
<td>Body mass (g)</td>
<td>Male</td>
<td>340.8</td>
<td>20.88</td>
<td>285 - 390</td>
<td>0.508</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>337.4</td>
<td>20.97</td>
<td>300 - 385</td>
<td></td>
</tr>
</tbody>
</table>

Age- and sex-specific patterns of morphology
Equation 1 was used to assign sex to 652 males and 575 females from 18 cohorts (Figure 4). Females in cohorts reared < 1 year after the end of a sardine mortality event (i.e. Group 1) were significantly smaller in morphology ($CL$, $BD$, $HL$) compared to females from other cohorts (Group 2) ($ANOSIM R = 0.063, p = 0.045$). The size of females differed between the two groups mainly due to differences in $HL$ (SIMPER 49.1%) and $CL$ (SIMPER 42.8%). The bill morphology of males did not differ significantly in size between treatment groups.
(ANOSIM $R = 0.02, p = 0.338$) however non-significant trends in bill morphology ($CL$ and $HL$) were apparent for males reared in 1995 (aged 9 y) but not males reared in 1999 (aged 5 y) (Figure 4).
Figure 4. Trends in age structure (years) and age specific morphology (± SE) for breeding male and female Sterna bergii at Troubridge Island between 2004 and 2006 (data pooled and ages corrected for individuals alive as of December 2004). Shaded bars represent cohorts reared < 1 year after the completion of each Sardinops sagax mortality event.
Discussion

One of the main concerns in modern fisheries management and marine conservation is the threat of stock collapse to apex predators. Age structure information indicated that crested terns reared after the first sardine mortality event in 1995 exhibited significantly lower rates of recruitment to the breeding colony compared to other age classes. Also, females from cohorts reared in 1995 and 1999, < 1 year following both sardine mortality events, had smaller morphology compared to other age classes. The importance of sardine in the diet of crested tern chicks in 2005 supports the inference that prey absence caused by mass mortality of sardine was responsible for these negative effects and suggests crested terns are sensitive to large scale decreases in sardine abundance. Age-specific information is often lacking in seabird studies because of the logistical constraints associated with banding many individuals over long periods of time. Moreover, inferences about foraging or breeding responses are made difficult by a lack of information about prey abundance. Our study was fortuitous in being able to correlate a long time series of demographic data for a banded seabird population with data from annual fisheries assessments that indicated two periods of prey depletion (Gaughan et al. 2000, Ward et al. 2001a, Figure 1).

We found that crested terns display the life history characters of delayed sexual maturity (4 y) and longevity common to many seabird species, and consistent with a K-selected life history strategy (Monaghan et al. 1989, Schreiber and Burger 2002, Jenouvrier et al. 2003). They also have high annual adult survival, small clutch sizes, variable reproductive output and exhibit extended parental care (Dunlop 1985, Crawford et al. 2002, McLeay unpublished data). The observed variation in recruitment between age classes may reflect variation in the survival of pre-breeding individuals. Moreover, the low recruitment documented for the 1995 cohort was likely related to high chick mortality observed in December 1995 (C. Johnson pers. comm.) and not juvenile mortality. Chick mortality has been related to food supply for many seabird species (Anderson et al. 1980, Monaghan et al. 1989, Uttley et al. 1989, Monaghan 1992, Dann et al. 2000, ICES 2001, Lewis et al. 2001, Taylor and Roe 2004). Adults are constrained within their foraging range near to the colony while provisioning chicks. Hence chick phases are likely to be more sensitive to decreases in prey abundance because, unlike juveniles, they cannot move to where prey may be more abundant.

The strength of 1996 and 1997 cohorts suggests that prey conditions recovered quickly to allow increased chick production. The high sardine biomass estimate of 1998 suggests strong
recruitment of sardine occurred after the 1995 mortality event (Rogers and Ward 2006, Figure 1.). Hence, survival of crested tern chicks in later years may have been aided by an increase in the availability of juvenile sardine. Similarly, expansion in the distribution of Australian anchovy into waters previously dominated by adult sardine could have improved chick production and lead to the higher rates of recruitment observed for the 1996 and 1997 cohorts (Ward et al. 2001a).

Compared to adults, the diet of crested tern chicks contained significantly higher proportions of sardine and Australian anchovy and lower proportions of Degens leatherjacket. Differences in diet may be related to limitations in the size range or shape of prey items that chicks can ingest (Hulsman et al. 1989, Ramos et al. 1998, McLeay unpublished data). Abundance of juvenile sardine (0-1 y fish) may have been reduced in the months following the March 1995 and October 1998 events due to depressed levels of sardine egg production associated with the mortality of adult sardine (Ward et al. 2001a). In 1998 the herpesvirus also killed large numbers of juvenile sardine (Gaughan et al. 2000, Ward et al., 2001a). Juvenile sardine comprise a large proportion of the sardine component in the diet of crested terns (McLeay unpublished data). Hence, decreases in the abundance of juvenile sardine (0+) may have been responsible for lower rates of chick survival in 1995 and reduced growth of chicks reared in 1995 and 1999.

Responses of seabirds to changes in the abundance and distribution of their prey depend on the flexibility of the foraging strategy employed and may vary at different spatial and temporal scales (Cairns 1987, Montevecchi 1993). Species with flexible behaviour might be less affected by conditions of low prey availability than species that forage at maximum capacity (Burger and Piatt 1990, Cairns 1992, Montevecchi 1993). Smaller surface-feeding species such as crested terns are likely to be more constrained by variations in prey abundance, because they feed only in upper water layers and need first to provision themselves before locating and returning prey of a suitable size to their chick (Davoren and Montevecchi 2003). A reduction in sardine abundance near the colony during sardine mortality events may have acted to increase the time allocated by adults to finding alternative suitable prey, thereby reducing the total amount of prey delivered to chicks and causing decreases in chick growth and survival (Cairns 1987, Montevecchi 1993).
Prey quality can also affect chick growth and survival. Sardine have a high calorific value compared to other fish species and may contain key nutritional elements required for the physiological processes that regulate chick growth and survival (Pichegrou et al. 2007). Nutritional deficiencies have been blamed for breeding failure in other seabird populations. For instance lower energy ‘junk food’ was thought to be the cause of breeding failure in common guillemots *Uria aalge* in the North Sea despite normal feeding rates being maintained (Wanless et al. 2005). The nutritional value of different prey items taken by crested terns in South Australian waters is unknown. Future calorimetric and nutritional analyses of prey items may highlight the relationships between dietary composition, breeding success and growth.

Cairns (1987) postulated that chick growth rates vary most when prey abundance is low, and are intrinsically restrained when prey abundance is high. Numerous seabird studies have explored this hypothesis and many have linked chick growth and fledgling size to indices of prey abundance (Ricklefs et al. 1984, Cairns 1987, Safina et al. 1988, Barrett and Rikardsen 1992, Montevecchi 1993). Reduced growth rates can also increase chick or post-fledging mortality (Gebhardt-Henrich and Richner 1998). Female crested terns from cohorts reared < 1 year following both sardine mortality events had significantly smaller morphology than females from other cohorts suggesting crested tern chicks at Troubridge Island experienced nutritional deficiency following depletion of a major prey. The fact that males from cohorts reared in seasons following sardine mortality events (Group 1) did not exhibit significantly smaller morphology was unexpected. Inaccuracies in the discriminant function used to assign a sex to recaptured adult individuals may have caused this result. If males that were reared immediately after mortality events were relatively small, these males may have been incorrectly classified as large females thereby reducing our ability to detect small males. Similarly, large females may have been incorrectly classified as small males.

Seabird diet and performance measures such as breeding success have been correlated with prey abundance in northern hemisphere fisheries for over 20 years, and are now used in models to inform management decisions (Monaghan et al. 1989, Lewis et al. 2001, ICES 2002, Velarde et al. 2004). For instance, CPUE of Pacific sardine *Sardinops caeruleus* was accurately predicted (73%) by a model based on the proportion of sardine in the diet of elegant terns *Sterna elegans*, reproductive success of Heerman’s Gulls *Larus heermanni* and springtime sea-surface temperature in the Gulf of California (Velarde et al. 2004). In the North Sea, breeding success of black-legged kittiwakes *Rissa tridactyla* are now used as reference points to trigger
decision rules for the commercial sandeel fishery (ICES 2002). Sandeel fishing ceases if the breeding success of kittiwakes drops below 0.5 chicks per nest for three consecutive years (ICES 2002). Availability of juvenile (0+) sandeels is crucial in influencing kittiwake chick survival (Monaghan 1992), and measures of breeding success act as a pre-recruit index to protect kittiwake populations and preserve fish stocks.

The significant component of sardine in the diet of crested tern chicks suggests that future diet measures may provide additional information about sardine stock status. Also, the demographic and morphometric analyses in this study suggest that the survival and growth of crested tern chicks is influenced by the abundance of sardine. Juvenile sardine comprise a large proportion of the sardine found in the diet of crested tern chicks (McLeay unpublished data). Hence, the strength of future data relating to diet, or chick growth and survival, may lie in the ability to predict sardine recruitment. Quantitative fishery-independent assessment of recruitment is rare for small pelagic fishes (cf. van der Lingen and Merkle 1999). The abundance of juvenile fish is rarely known and is expensive to collect. Dietary information and measurements of chick growth and survival are easy and cost-effective to collect, and these data can provide real-time indicators of juvenile sardine abundance. Moreover, such data could provide information about fishery-induced localised depletion. Between 2001 and 2006 the majority of the annual sardine catch was taken from Spencer Gulf and Investigator Strait (Figure 2). At least 10 crested tern colonies lie in close proximity to these areas. Annual monitoring of these colonies coupled with spatial analyses of SASF catch data and sardine biomass estimates provided via the daily egg production method, could indicate whether sardine fishing operations are influencing crested tern diet, or chick growth and survival. Combined with demographic analyses, this information could be used for developing risk assessments for crested tern populations. Comparison with sites outside areas used by the SASF would be necessary to determine whether measured responses to changes in sardine stock abundance are fishery-related and/or environmentally driven. Such approaches could augment current assessments of sardine biomass in South Australia, aid fisheries management strategies adopted for this fishery, and ensure that fishing does not exacerbate any environmentally driven decreases in stock abundance.
References


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Wanless S, Harris MP, Redman P and Speakman JR (2005) Low energy values of fish as a probable cause of breeding failure in the North Sea. Marine Ecology Progress Series 294:1-8


Chapter 3. Size matters: variation in the diet of chick and adult crested terns

Authors: L.J. McLeay, B. Page, S.D. Goldsworthy, T.M. Ward and D.C. Paton

Statement of authorship: Appendix B
Abstract

We investigated ontogenetic, temporal and spatial patterns in the composition and size of prey in the diet of crested terns Sterna bergii. Diet analyses indicated that crested terns are a generalist predator on surface-schooling clupeiform fishes (Australian anchovy Engraulis australis, sardine Sardinops sagax and blue sprat Spratelloides robustus), Degens leatherjacket Thamnaconus degeni, southern sea garfish Hyporhamphus melanochir, Australian herring Arripis georgianus, slender bullseye Parapriacanthus elongatus and barracouta Thyrsites atun. Ontogenetic differences in prey size indicated that adults are constrained in their foraging behaviour during the early chick provisioning period by the need to self feed and select smaller prey that can be ingested by their chicks. Chicks consumed significantly higher proportions of clupeiform fishes than adults, which consumed mainly Degens leatherjackets and barracouta, suggesting that adults may select higher quality prey for their chicks compared to what they consume themselves. Spatial differences in prey composition were driven by differing proportions of sardine, Australian anchovy and Degens leatherjacket and could reflect local differences in the abundances of these prey. The size of prey taxa consumed by adults also reflected a North-South gradient in prey size. The large component of juvenile sardine in the diet of crested terns suggests future dietary measures may inform fisheries managers about changes in local juvenile sardine abundance. These data could assist in highlighting any fishery-related decreases in sardine recruitment and help ensure commercial fishing practices address principals of Ecologically Sustainable Development developed for Australian fisheries.
Introduction

Research on marine predators has the potential to underpin ecosystem based management because being at the top of marine food webs, they reflect changes in marine system processes through measures of their diet, demography, behaviour or physiology. Particular focus has been placed on using seabirds as indicators because they are easily accessed, and several studies have linked seabird data to ecosystem health and changes in prey abundance (Nettleship et al. 1982, Cairns 1987, Montevecchi 1993, ICES 2000, Schreiber and Burger 2002). However, seabird responses to changes in ecosystem processes and prey availability are varied, and if species are to be useful as indicators of change a prior understanding is required of the factors that constrain seabird behaviour and influence diet and seabird responses (Crawford 2004, Hall and Mainprize 2004, Boyd et al. 2006).

Seabird foraging behaviour and reproduction are constrained during breeding by the availability of prey within their foraging range, their reproductive state, and innate characters of reproductive phenology and physiology (Cairns 1987, Burger and Platt 1990, Montevecchi 1993). For instance, adults that are provisioning chicks face different energetic constraints to adults that are only self-feeding. During provisioning adults must balance their own energetic requirements with that of their chicks by adjusting foraging behaviour. This dichotomy represents a trade-off between somatic and reproductive investment (Swihart and Johnson 1986). Prey favoured while self-feeding may be available at distances and travel times that exceed the fasting abilities of chicks during the breeding season (Weimerskirch 1998, Barrett et al. 2007). Also, single prey loaders such as terns or guillemots, which must first provision themselves before locating and returning single prey items of a suitable size to their chicks, have different foraging constraints to species such as penguins that regurgitate macerated prey to their chicks (Furness and Tasker 2000, Stienen et al. 2000). For single prey loaders, central-place foraging theory predicts that adults should maximise their provisioning effort per unit time of foraging by providing as large or energetically rich prey as possible (Orians and Pearson 1979, Davoren and Burger 1999). However, adult foraging behaviour during chick provisioning is also regulated by what chicks can physically ingest and chick energetic requirements as they grow. Consequently, chick and adult diets may differ as a function of prey selection by adults at different stages of breeding (Hulsman et al. 1989, Ramos et al. 1998, Shealer 1998). Despite the different intrinsic constraints imposed on seabirds by species specific foraging behaviour and reproduction over the course of the breeding season, only a few studies have simultaneously examined the diets of chicks and adults (Cairns 1984,

Seabird dietary studies provide a profile of prey composition, size, mass, quality and availability, thereby highlighting the key trophic linkages within a species’ foraging range and differences between places and periods (Cairns 1987, Montevecchi 1993, Montevecchi and Myers 1995, Montevecchi and Myers 1996, Jaquemet et al. 2008). Diet data also provide a means of assessing links between seabird behavioural responses and the environment. Several studies have linked seabird diet information to oceanographic indices and estimates of prey abundance, and these data have sometimes been used to inform management decisions (Hislop and Harris 1985, Montevecchi et al. 1987, Croxall 1989, Monaghan et al. 1989, Montevecchi 1993, Montevecchi and Myers 1995, Lewis et al. 2001, ICES 2002, Frederiksen et al. 2004, Velarde et al. 2004). For instance, in the North Sea, the diet and breeding success of black-legged kittiwakes *Rissa tridactyla* is highly correlated with the abundance of sandeels *Ammodytes marinus*. If kittiwake production falls below 0.5 for 3 consecutive years commercial sandeel fishing is ceased (ICES 2002).

Crested terns *Sterna bergii*, are a small piscivorous plunge-diving seabird distributed throughout the Indo-Pacific and on all coasts of Australia. The total number of breeding colonies in South Australia is unknown but at least 12 colonies have been recorded in Gulf St Vincent and Spencer Gulf (Figure 1). A previous study of the diet, demographic and morphological characteristics of a crested tern *Sterna bergii* population in South Australia indicated that this species may be sensitive to changes in sardine abundance (McLeay et al. 2009). Other studies have described the diets of crested tern chicks (Walter et al. 1987, Hulsman et al. 1989, Smith 1993, Chiaradia et al. 2002) or adults (Walter 1984, Blaber and Wassenberg 1989, Surman and Wooler 2003) but not the ontogenetic, temporal or spatial patterns in diet. These data are required to understand how species-specific intrinsic constraints influence the types and sizes of prey consumed, and mediate demographic, behavioural or physiological responses.
Figure 1. Map of Gulf St Vincent and Spencer Gulf, South Australia showing the location of crested tern colonies (bird symbol).

We investigated the diet of crested terns at four colonies in gulf waters of South Australia during their breeding seasons between 2003 and 2008. We hypothesise that the diet of crested terns will exhibit ontogenetic differences as a function of a trade-off between the physical ingestion capabilities of chicks, and adult foraging behaviour that has evolved to maximise the amount of energy provided to chicks per foraging trip. We specifically ask 1) What are the key prey in the diets of chick and adult crested terns? 2) Are there ontogenetic differences in prey composition and size? and 3) Are there seasonal and spatial patterns in prey composition and size? We address these questions by quantifying the level of ontogenetic, spatial, temporal and variation in the prey composition and size of crested tern diets, and discuss how future information collected from crested terns may inform marine resource management.
Methods

Study sites

This study was carried out at four locations in South Australia during the breeding seasons (between November and February) in the years 2003/04 to 2007/08. We refer to seasons as belonging to the year that sampling or breeding began, respectively (e.g. 2005/06 = 2005) (Figure 1). Troubridge Island is a sand island approximately 260 ha in southern Gulf St Vincent (35°4’S, 137°49’33”E). The crested tern colony at Troubridge Island is the largest in South Australia, having approximately 3500 breeding pairs (McLeay unpublished data). Goose Island (34° 27’S, 137° 22’E), Lipson Island (34° 15’S, 136°15’E) and Rocky Island (34° 29’S, 37° 25’E) are smaller islands (3 to 35 ha) in southern Spencer Gulf (Figure 1). The colonies at these islands are generally smaller, numbering approximately 900 breeding pairs at Goose Island, 2000 at Lipson Island and 1300 at Rocky Island, respectively (McLeay unpublished data).

Diet sampling

When adults and chicks were caught they regurgitated spontaneously. We collected regurgitates from crested tern chicks aged 0-5 weeks and adults that were incubating eggs or provisioning chicks. To minimise disturbance to the colony, adults and chicks were caught by moving from one end of the colony to the other which ensured no bird was caught more than once per visit. Samples were placed in a plastic bag and frozen before being transported to a laboratory and sorted, where individual prey were separated and identified to the lowest taxonomic group possible. Individual prey that were whole were weighed (wet) to ± 0.01 g using a digital balance and length was measured to the nearest ± 1.0 mm. Individual prey were sometimes too digested to enable accurate measurements of mass and size. Prey mass and size were estimated using regression equations obtained from published information and from regressions constructed in this study for the relationships between, caudal fin-ray, otolith or body/mantle length measurements, and fish/cephalopod mass. Data for regressions constructed in this study were obtained by measuring whole individual prey in diet samples and from fish collected during fishery research surveys (Table 1). Fish prey identified in regurgitates often only consisted of the posterior body and caudal fin. Consequently, species level identification was not possible for some individuals from the families Clupeidae and Engraulidae and so they were grouped into a distinct group. To determine the most important prey, we allocated prey from this group, which could have been either sardine *Sardinops sagax* or Australian anchovy *Engraulis australis*, proportionally to the groups identified specifically as
sardine or Australian anchovy. For individual prey items that could be identified but not measured, the mean mass of individual cephalopod/fish species consumed by chicks/adults in the same location/year was used in biomass reconstructions. The unidentified prey biomass proportion was based on the minimum number of unidentified individuals, multiplied by the average mass of prey consumed by either chicks or adults in the same year at the same location.
Table 1. Regression formulae used to estimate prey biomass contribution of major prey taxa found in crested tern diets. Sources for data are referenced: 1. L.J. McLeod unpublished data; 2. TMAG in Furlani et al. 2007; 3. www.fishbase.org/; 4. M. Steer (SARDI Aquatic Sciences) unpublished data. 5. CMAR in Furlani et al. 2007. 6. A. Wiebkin (SARDI Aquatic Sciences) unpublished data. 7. W. Dimmlich (Falkland Island Government Fisheries Dept.) unpublished data. 8. R. Kirkwood in Furlani et al. 2007. # Regressions based on different species to those found in this study. M=mass, FL=length to caudal fork, ML=mantle length, CFR=caudal fin-ray length, SL=standard length, OL=otolith length. Mass measured in g. Length measurements in mm except where listed.

<table>
<thead>
<tr>
<th>Prey type</th>
<th>Mass/Length</th>
<th>Source</th>
<th>Mass/CFR</th>
<th>Source</th>
<th>OL v Length</th>
<th>Source</th>
<th>Other eqns. used</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family Engraulidae <em>Engraulis australis</em></td>
<td>(M = 6 \times 10^{-5} \times FL^{0.95})</td>
<td>1</td>
<td>(M = 1 \times 10^{-4} \times CFR^{2.555})</td>
<td>1</td>
<td>SL = 45.64 * OL^{0.34}</td>
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<td>(M = 2 \times 10^{-6} \times FL^{3.1327})</td>
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<td>(M = 1.9 \times 10^{-3} \times CFR^{2.7511})</td>
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<td>FL = 22.6 * OL^{1.42}</td>
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<td>(M = 2 \times 10^{-5} \times FL^{0.74})</td>
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<td>(M = 5 \times 10^{-4} \times CFR^{2.661})</td>
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<td>TL = 54.33 * OL^{1.02}</td>
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<td>M = 3.54 * 10^{-7} * TL^{3.67}</td>
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<td>(M = 3 \times 10^{-7} \times CFR^{3.3629})</td>
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<td>(M = 6 \times 10^{-7} \times CFR^{3.3032})</td>
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<td>(M = 6 \times 10^{-6} \times CFR^{3.721})</td>
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<td>Family Odocidae- unidentified</td>
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<td>Upeneichthys sp</td>
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<td>FL = 16.796 * OL^{1.3292}</td>
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<td>Clupeiformes <em>S. sagax</em> and <em>E. australis</em> pooled</td>
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<td>(M = 2 \times 10^{-6} \times CFR^{1.7776})</td>
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Data analysis
We apportioned our diet data from each colony to one of four groups based on the time of
the breeding season in which regurgitates were collected:

1) Incubation: samples collected from adults during incubation.
2) Early provisioning: samples collected from chicks and adults 1-10 days after hatching.
Chicks weighed 30-108 g during this time (McLeay unpublished data).
3) Mid provisioning: samples collected 11 and 25 days post-hatching when chicks weighed
108-207 g.
4) Late provisioning: samples collected >25 days post hatching when chicks weighed > 207 g.

The relative importance of the prey composition of chick and adult diets was assessed by
estimating the percentage biomass contribution of each prey taxon. Diet data did not conform
to assumptions of normality and homoscedasticity so ontogenetic, seasonal and spatial
differences in the species composition of chick and adult diets were assessed using
nonparametric analysis of similarity (ANOSIM), on a Bray-Curtis similarity matrix (PRIMER
version 5.1.2, PRIMER-E Ltd., Plymouth, UK) ($p \leq 0.05$). ANOSIM is a hypothesis-testing
procedure that generates a probability value and a test statistic ($R$), which lies between 1 and –1. High positive $R$-values indicate greater variation between groups than within groups, and negative values indicate high levels of within group variation compared to between groups. Values of $R$ equal to zero represent the null hypothesis of no significant difference between groups. Similarity Percentages (SIMPER, Plymouth Routines in Multivariate Ecological Research) were used to identify which prey taxa were responsible for the inter-group differences (Catalan et al. 2006).

To assess differences in the size of prey in chick and adult diets we calculated a ratio for the
mass of individual prey collected from chicks and adults on the same day and at the same site
(adult to chick prey mass ratio; ACPMR). We calculated the ACPMR for each prey species and
for all prey, where:

$$ACPMR = \frac{\text{Mean mass of individual prey taxa in adult diets}}{\text{Mean mass of individual prey taxa in chick diets}}.$$
For $\text{ACP} = 1$, the mean mass of individual prey taxa in chick and adult diets are the same. If $\text{ACP} > 1$ the mass of individual prey consumed by adults was larger than consumed by chicks. For $\text{ACP} < 1$ the mass of individual prey in chick diets is smaller than in adult diets. Data calculated by the ACP did not conform to assumptions of normality and homoscedasticity so to assess differences between the early, middle and late stages of the chick provisioning period we used the ACP in ANOSIM on a Bray-Curtis similarity matrix (PRIMER version 5.1.2, PRIMER-E Ltd., Plymouth, UK) ($p \leq 0.05$). Analyses were carried out between season stages that had > 2 samples collected from chicks and adults on the same day.

To assess the relationship between prey mass/length and chick mass we collected regurgitates from a sample of chicks that were weighed with a spring balance (1000g ± 5 g) after regurgitating. We assigned diet data to one of three groups, based on the mass of chicks, their approximate age (McLeay unpublished data) and the different stages of the chick provisioning period (see above) at the time of sampling.

To assess ontogenetic, seasonal and spatial differences in the mass of the main prey species we used T-tests, Mann Whitney tests or ANOVA, for which respective $t$, $Z$ and $F$ values are reported ($p \leq 0.05$ was used as the threshold of significance). All analyses were undertaken using SPSS® and data were tested for assumptions of normality and homoscedasticity using Shapiro-Wilks’ test and Box’s M test, respectively. The average sizes of prey are reported ± SD.
Results

Prey composition

Between 2003 and 2007, a total of 2146 and 3921 prey were identified from 1400 and 1561 regurgitates collected from chicks and adults, respectively. Samples represented a reconstructed biomass of 67.3 kg. In total, 47 fish, five cephalopod and three crustacean taxa were identified (Tables 2 - 5). Insects were found in samples from Troubridge Island and Rocky Island but contributed a low proportion of the total biomass (< 0.5) (Tables 2 and 5).

Australian anchovy *Engraulis australis*, sardine *Sardinops sagax*, blue sprat *Spratelloides robustus*, barracouta *Thyrsites atun*, Degens leatherjacket *Thamnaconus degeni*, southern sea garfish *Hyporhamphus melanochir*, Australian herring *Arripis georgianus* and slender bullseye *Parapriacanthus elongatus* comprised > 66% of the total prey biomass consumed by chicks or adults at all locations (Tables 2 - 5).

Ontogenetic variation in prey composition

Chick and adult diets differed significantly during the early and middle stages of the chick provisioning period (ANOSIM, \( p \leq 0.05 \)) (Tables 2 - 6). This pattern was consistent among all locations and years except at Goose Island and Lipson Island in 2005 where low numbers of adult samples were collected (N = 13, N = 9, samples respectively, Table 6). Ontogenetic differences were also apparent in late provisioning at Troubridge Island in 2005 and 2007 (Table 6). In the early provisioning period SIMPER results indicated that differences were attributed to higher relative proportions of clupeiform fishes (blue sprat, Australian anchovy and sardine) and Australian herring in chick diets, and sardine, barracouta and Degens leatherjacket in adult diets (Table 6). In the mid provisioning period diet differences were attributed to higher relative proportions of Australian anchovy, barracouta or sardine in chick diets, and Degens leatherjacket and/or garfish in adult diets (Table 6).
Table 2. Percent biomass contribution of prey taxa found in regurgitates from crested tern chicks and adults at Troubridge Island between 2003 and 2007. Taxa with biomass totals over 15% are in bold. Inc = Incubation period, E = early provisioning period, M = mid provisioning period, L = late provisioning period. The number of regurgitates examined is in brackets.

<table>
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<tr>
<th>Prey type</th>
<th>2003 (101)</th>
<th>2004 (103)</th>
<th>2005 (136)</th>
<th>2006 (136)</th>
<th>2007 (144)</th>
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<td></td>
<td>E Inc</td>
<td>E adult</td>
<td>E Inc</td>
<td>E adult</td>
<td>E Inc</td>
</tr>
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<td>0.4</td>
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Table 3. Percent biomass contribution found in regurgitates from crested tern chicks and adults at Goose Island in 2005. Taxa with biomass totals over 15% are in bold. Inc = Incubation period, E = early provisioning period, M = mid provisioning period, L = late provisioning period. The number of regurgitates examined is in brackets.

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Table 4. Percent biomass contribution found in regurgitates from crested tern chicks and adults at Lipson Island in 2005 and 2006. Taxa with biomass totals over 15% are in bold. Inc = Incubation period, E = early provisioning period, M = mid provisioning period, L = late provisioning period. The number of regurgitates examined is in brackets.

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Table 5. Percent biomass contribution found in regurgitates from crested tern chicks and adults at Rocky Island in 2007. Taxa with biomass totals over 15% are in bold. Inc = Incubation period, E = early provisioning period, M = mid provisioning period, L = late provisioning period. The number of regurgitates examined is in brackets.

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100 100 100 100 100 100 100 100 100
Table 6. Results of ANOSIM/ SIMPER (Primer 5©) analyses showing differences in prey composition between chick and adult crested tern diets throughout provisioning between 2004 and 2007. Significant p values are given in bold. Species key: anch Australian anchovy *E. australis*; sard Australian sardine *S. sagax*; bar barracouta *Thysites atun*; deg Degens leatherjacket *T. degeni*; bs blue sprat *S. robustus*; gar southern sea garfish *H. melanochir*; ah Australian herring *A. georgianus*. * Higher biomass contribution in chick diets. ** Higher biomass contribution in adult diets.

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<th>Site</th>
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<th>Early spp</th>
<th>Middle spp</th>
<th>Late spp</th>
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<td>bs (25.8*), sard (23.1**), bar (20.2**), anch (20.0*), sard (11.4*), anch (14.0*), sard (21.8*)</td>
<td>3.131 0.018</td>
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<td>deg (26.3**), anch (20.0*), sard (11.4*)</td>
<td>0.131 0.018</td>
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Spatial and interannual patterns in prey composition

There were significant differences in the prey composition of chick and adult diets between colonies in Gulf St Vincent (Troubridge Island) and Spencer Gulf (Goose Island, Lipson Island and Rocky Island) (ANOSIM, *p* ≤ 0.05). SIMPER analyses indicated that differences were a consequence of relatively high proportions of sardine in chick and adult diets from colonies in Spencer Gulf, and Australian anchovy at Troubridge Island (Tables 2 - 5). High proportions of Degens leatherjacket in adult diets at Troubridge Island also contributed to spatial differences (Tables 2 - 5).

There were no distinct interannual patterns in the prey composition of chick and adult diets at Troubridge Island between 2004 and 2007 (Tables 2-5). Differences among years were typically driven by large variation in the relative abundance of a few main prey. In chicks the main prey that varied from year to year were Australian anchovy, blue sprat and sardine (ANOSIM, *p* ≤ 0.05). In adults the main prey contributing to interannual differences were sardine, Degens leatherjacket and barracouta (ANOSIM, *p* ≤ 0.05) (Tables 2 - 5).

Intra-annual variation in prey composition

The prey composition of chick diets varied significantly within the breeding season (ANOSIM, *p* ≤ 0.05) typically due to the large variation in the consumption of clupeiform species (sardine, Australian anchovy and blue sprat) between early and subsequent provisioning stages (mid/late) (Tables 2 - 5). There were no clear intra-annual trends in prey composition at any location (Tables 2 - 5), but the abundance of blue sprat and Australian herring in chick diets typically decreased as the breeding season progressed (Tables 2, 4 and 5). In contrast there was typically little intra-annual variation in the prey composition of adult diets (ANOSIM, *p* ≥ 0.05) (Tables 2 - 5).

Prey size

The average mass of all prey taxa consumed by chicks ranged between 7.4 ± 4.5g in early provisioning to 10.7 ± 9.3g in late provisioning. Prey consumed by adults averaged between 10.4 ± 8.1g in late provisioning to 11.6 ± 10.4g in early provisioning. The average mass and length (all sites/years pooled) of Degens leatherjacket, southern sea garfish and sardine was significantly larger in adult diets compared to chick diets (all *p* ≤ 0.05) (Table 7). Conversely, the average mass and length of Australian anchovy, blue sprat and barracouta was significantly
larger in the diets of chicks compared to adult diets (all $p \leq 0.05$). Australian herring and slender bullseye were of similar size in chick and adult diets (all $p \geq 0.05$) (Table 7).

Table 7. Average mass and length of key prey species consumed by chicks and adults at all sites sampled

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<th>Adults</th>
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<td>Length (mm) Avg (± SD)</td>
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<td>6.5 (3.8)</td>
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<td>19.1 (19.2)</td>
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<td>5.3 (1.1)</td>
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<td>11.7 (4.9)</td>
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<td>154 (34)</td>
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<tr>
<td>Sardine</td>
<td>11.9 (6.5)</td>
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Ontogenetic variation in prey size

The adult to chick prey mass ratios (ACPMRs) indicated that adults generally fed their chicks smaller prey than they ate themselves for the entire nestling period at Troubridge Island in 2007 (ACPMR >1, Figure 2). During the early provisioning period in 2007 at Troubridge Island the mean mass of individual prey (all species pooled) in the diet of adults was more than double (Mean ACPMR = 2.43 ± 0.15) that of prey delivered to chicks (Figure 2). This trend in high ACPMR values for the early chick provisioning period was also evident at Troubridge Island between 2004 and 2006, Lipson Island in 2006 and Rocky Island in 2007. After 10 days the ACPMR decreased (Mean ACPMR = 1.26 ± 0.29), indicating that adults were providing chicks with prey more similar in size to what they ate themselves.

The high ACPMR in the early provisioning period could be attributed to the relatively smaller mass of common prey consumed by chicks (Figure 2). Sardine in the diet of chicks (8.4g ± 0.9) were significantly smaller than sardine found in the diets of adults on the same day (28.7g ± 3.6) (ACPMR = 2.21 – 4.89; Z = 3.68, $p \leq 0.05$, Figure 2). High ACPMR values (>1) for barracouta, Degens leatherjacket and Australian herring indicated these taxa were of smaller mass in the diet of chicks compared to adults. In contrast, the ACPMR of Australian anchovy and blue sprat did not differ significantly between chick and adult diets in any chick provisioning period indicating that adults were selecting these prey at a similar size for themselves and their chicks ($p \geq 0.05$, Figure 2).
Figure 2. Within season differences in mass of individual prey found in chick and adult diets for key prey species and all species pooled from Troubridge Island in 2007 (ACPMR = adult to chick prey mass ratio).
**Spatial differences in prey size**

Chicks typically consumed larger prey at Troubridge Island than in Spencer Gulf colonies. Australian anchovy consumed by chicks were significantly larger in the mid provisioning period at Troubridge Island in 2005 (9.7 ± 3.2g) and 2007 (8.2 ± 2.2g), compared to Goose Island (6.7 ± 2.0g) and Rocky Island (5.4 ± 1.4g), respectively (all \( p \leq 0.001 \)). Barracouta consumed in the mid chick provisioning period in 2005 were also larger at Troubridge Island compared to other sites (Troubridge vs Goose 2005: 45.6 ± 34.9g vs 12.7 ± 5.1g, \( Z = 2.244, p = 0.025 \)). Similarly, chicks at Troubridge Island consumed larger Degens leatherjacket (16.1 ± 5.6g) than at Lipson Island in the late provisioning period of 2006 (11.3 ± 5.0g)(\( Z = 2.160, p = 0.031 \)).

Prey taxa consumed by adults were also typically larger at Troubridge Island than Spencer Gulf colonies. Degens leatherjacket consumed by adults at Troubridge Island were significantly larger than sampled from Lipson Island during the early provisioning period in 2006 (Troubridge Is. vs Lipson Is.: 19.1 ± 7.4g vs 15.3 ± 6.6g) (\( t = 2.491, p = 0.015 \)). Australian anchovy and sardine were also significantly larger at Troubridge Island between 2005 and 2007 compared to other sites (\( p \leq 0.001 \)).

**Interannual differences in prey size**

There were no distinct interannual patterns in the size of prey in chick or adult diets at Troubridge Island between 2004 and 2007. Australian anchovy and sardine consumed by chicks were significantly larger throughout the entire chick provisioning period in 2005 compared to other years (\( p \leq 0.05 \)), but the size of most other key prey taxa found in chick diets did not typically vary between years (all \( p \geq 0.05 \)).

**Intra-annual differences in prey size**

In 2007 the average mass and length of prey (all taxa pooled) consumed by chicks at Troubridge Island and Rocky Island (locations pooled) increased throughout the provisioning period (Figure 3). The larger sardine and Australian anchovy provisioned during the mid and late provisioning periods contributed to this result (Troubridge 2007, sardine: early 8.4 ± 3.1g vs late 11.5 ± 4.2g, \( Z = 2.520, p = 0.012 \); Australian anchovy: early 6.7 ± 2.8g vs late 8.0 ± 2.1g, \( Z = 2.461, p = 0.014 \)) (Rocky 2007, sardine: mid 9.6 ± 3.9g vs late 13.3 ± 6.8g, \( Z = 2.636, p = 0.008 \); Australian anchovy: mid 5.4 ± 1.4g vs late 8.0 ± 2.7g, \( t = 4.243, p \leq 0.001 \)).
The size of the key prey taxa consumed by adults did not typically vary throughout the breeding season ($p \geq 0.05$). Nonetheless, Australian anchovy consumed by adults in the late provisioning period at Troubridge Island and Rocky Island in 2007 were significantly larger than Australian anchovy in adult diets earlier in the season (Troubridge 2007: Australian anchovy early 7.6 ± 1.4g vs late 8.7 ± 1.4g, $t = 1.951$, $p = 0.061$; Rocky 2007: Australian anchovy mid 5.6 ± 1.5g vs late 7.3 ± 1.6g, $t = 2.872$, $p = 0.008$).

Figure 3. The relationship between chick mass and average individual prey mass/length (spp/locations pooled) ($\pm$ SE).
Discussion

This study profiles the diet of crested tern chicks and adults, and highlights some of their key prey in South Australia. Our research confirms findings of previous studies, which indicated that crested terns are generalist predators that feed predominantly on surface-schooling clupeiform fishes (Australian anchovy, sardine and blue sprat) (Walter et al. 1987, Hulsman et al. 1989, Smith 1993, Chiaradia et al. 2002). Degens leatherjacket, barracouta, southern sea garfish, Australian herring and slender bullseye were also commonly utilised. The importance of different prey varied spatially, temporally, between chicks and adults, and between chicks of different ages.

The observed decreases in the adult to chick prey mass ratio (ACPMR) over the course of the chick provisioning period indicate that adults are constrained in their foraging behaviour by the need to select prey according to the physical ingestion capabilities of chicks during the early provisioning period (0-10 days). Crested tern chicks are small in comparison to many seabird species, weighing between 30 and 40g when hatched (approximately 10% of adult body mass), and are limited immediately post-hatch in the size of prey they can ingest (McLeay unpublished data). As chicks grow, energetic demands increase and adults may either increase the rate of fish delivered and/or deliver larger prey. Our research supports previous studies on other tern species, and indicates that adult crested terns adjust the size of prey provided to chicks as chicks grow throughout the nestling period (Hulsman et al. 1989, Ramos et al. 1998, Shealer 1998).

Seabirds provisioning chicks at a central place must adjust their foraging behaviour according to the distance of prey patches from their colony, their own prey requirements and the changing dietary requirements of their chicks. For single prey loaders such as crested terns, central-place foraging models predict that adults should increase the amount of energy delivered to chicks in line with the amount of time they spend away from the colony (Orians and Pearson 1979, Leopold et al. 1996). As a result, a crested tern that had conducted a long foraging trip would be expected to provision its chick with relatively large prey. Adults consumed larger prey than chicks throughout the provisioning period but differences in individual prey mass between chick and adult diets were greatest during early provisioning. These results indicate that small prey may not have been available in high enough densities near the colony to support self feeding.
Chicks also consumed higher proportions of clupeiform species (Australian anchovy, sardine and blue sprat) than adults, which consumed mainly Degens leatherjackets and barracouta. Previous research on little penguin *Eudyptula minor* diets at Troubridge Island showed these clupeiform fish are of higher calorific value and have higher amounts of lipid and protein than leatherjackets, southern-sea garfish or slender bullseye (A. Wiebkin unpublished data). This suggests that adult crested terns may select and provide higher quality prey to their chicks compared to what they consume themselves. Such a strategy has been demonstrated for other seabirds (Vermeer et al. 1987, Hodum and Hobson 2000, Jaquemet et al. 2008). Clupeiform fishes have a high calorific value and may contain key nutritional elements required for the physiological processes that regulate chick growth and survival (Pichegru et al. 2007). Poorer quality ‘junk food’ was the likely cause of breeding failure of common guillemots in the North Sea (Wanless et al. 2005). Future research should examine the relationship between breeding success, chick growth and diet quality for crested tern populations.

All diet studies have inherent biases which are associated with differences in prey-specific digestion rates and differential regurgitation of prey remains (Duffy and Jackson 1986, Gonzales-Solis et al. 1997, Barrett et al. 2007). The proportion of ingested prey in regurgitations varies according to when prey were captured and the type of prey ingested. Small prey or otoliths from fish remains may be digested more quickly than larger items and therefore underestimated in diet analyses. Our study was not completely free of these biases. However, crested terns provisioned their chicks with an average of 3.1 ± 1.9 SD single prey per day (McLeay unpublished data) indicating that they forage in waters near to the colony. Also, prey remains collected were generally always in good condition and could be easily identified. This is supported by our identification of >97% of the prey collected in this study. Also, fish otoliths used in prey weight regressions were obtained via fish dissections and were consequently not degraded. These factors reduced the potential bias associated with differences in prey or size-specific digestion rates.

The ontogenetic and seasonal variation in prey composition and size indicated by this study highlights the potential biases associated with disproportionate, non-systematic sampling of seabird diets throughout the breeding season. Detection of fine-scale temporal patterns in seabird diets are often inhibited by the cost and effort of collecting samples. Nonetheless, if the factors constraining foraging behaviour and driving patterns of diet variation are to be
elucidated, preliminary studies should attempt to stratify diet sampling from a range of life history stages throughout incubation and while adults are provisioning their chicks.

The diets of crested terns at Troubridge Island, Gulf St Vincent contained larger prey (Australian anchovy, sardine, Degens leatherjacket and barracouta) than colonies in Spencer Gulf and support the hypothesis proposed for other finfish species (Australian anchovy and King George whiting Sillaginodes punctata) of the occurrence of a spatial gradient in prey size from north of Spencer Gulf and Gulf St Vincent to the south (i.e smaller in north vs larger in south) (Fowler et al. 2000, Dimmlich and Ward 2006). The diets of crested terns at Spencer Gulf colonies had typically more sardine compared to diets sampled from Troubridge Island, Gulf St Vincent and may reflect differences in the abundance of sardine between the two gulfs. This finding is consistent with the lower estimates of sardine egg production calculated via annual fisheries assessment for Gulf St Vincent (Ward et al. 2008). A longer time series of diet data and continued sardine fishery assessment are required to assess whether the proportion of sardine in crested terns diets is related to sardine stock recruitment or adult sardine abundance.

Use of data in fisheries management

Small pelagic fish ('forage fish') are increasingly the target of commercial fisheries and form a key link between apex predators and lower trophic levels in many marine ecosystems. However their distribution and abundance is highly variable. The South Australian Sardine Fishery (SASF), which targets sardine and other small pelagic fishes, has grown in recent years and fisheries managers have raised concerns about the potential ecological impacts on apex predators such as crested terns (Shanks 2004). Previous research indicated that crested terns may be sensitive to large scale variations in sardine abundance (McLeay et al. 2009). However, before data from crested terns are applied in management it is first necessary to understand the intrinsic factors that underpin diet variation and mediate demographic, behavioural or physiological responses.

The large component of sardine, which were predominantly juveniles, in the diet of crested terns from Spencer Gulf colonies suggests that future dietary measures may provide additional information about changes in juvenile sardine abundance. Most of the SASF’s annual Total Allowable Catch (TAC) of sardine is taken in close proximity to at least 11 islands in Spencer Gulf where breeding of crested terns has been recorded (Figure 1) (McLeay et al. 2009). The
fishery does not currently target juvenile sardine, however localised depletion of adult sardine could reduce subsequent rates of sardine egg production and juvenile recruitment. Measures of crested tern diet, coupled with estimates of breeding success, foraging behaviour (provisioning), or physiology (chick growth) and fishery data (catch information: location, sardine length) may assist in highlighting whether fishing is indirectly impacting on the abundance of juvenile sardine. These data could help to ensure commercial fishing practices address principals of Ecologically Sustainable Development developed for Australian fisheries (Fletcher et al. 2002).
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CHAPTER 3

Diet variation


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Chapter 4. Keeping it in the family: provisioning strategies and the consequences of adult condition on reproductive timing and fitness in crested terns


Statement of authorship: Appendix C
Abstract

Seabirds vary in reproductive performance due to differences in foraging or reproductive proficiency that may be reflected in body condition or reproductive timing. We measured provisioning patterns, reproductive timing, adult body condition, and chick growth and survival for a single prey loader, the crested tern. Parents increased the rate and size of prey delivered to meet the increased energetic demands of their chicks. Provisioning rates were related to daily chick mass change, and chick growth was correlated with asymptotic mass, suggesting that prey availability and adult foraging proficiency influences fledgling size. Adults with good body condition hatched chicks earlier and early breeding was positively related to hatchling mass, fledgling condition and chick survival. Adults aged <7 years had significantly poorer body condition and hatched their chicks later compared to adults ≥7 years. However, adult body condition also varied significantly within cohorts, indicating that reproductive performance also reflects individual quality. Parental differences in reproductive performance, presented as variations in adult body condition during reproduction, may have long-term consequences for the fitness of offspring. These ‘family’ effects have important implications from a life history perspective and in regulating population growth. The growth of crested tern populations may be most sensitive to the foraging behaviour and reproductive output of high quality individuals ≥7 years old.

Key-words: demography, fitness, foraging ecology, life history theory, reproductive strategies.
Introduction

Animal life history strategies, foraging behaviour and physiology vary as a function of the selective pressures that are shaped by the environment in which they live. Seabird foraging and reproductive adaptations reflect the stochastic nature of prey availability that is typical of marine environments. As central place foragers seabirds are constrained during breeding by the need to adjust their foraging behaviour according to their own energetic requirements and those of their chicks. This trade-off between somatic and reproductive investment, which is a central element of life-history theory, occurs over long chick-provisioning periods (usually months) and incurs a large energetic cost to parents (Swihart and Johnson 1986, Monaghan et al. 1992, Stearns 1992). Seabirds are generally long lived, and reductions in prey availability near to colonies may act to alter foraging behaviour to favour adult survivorship and future reproductive potential at the expense of reproductive investment. Several studies have correlated decreases in prey availability to changes in foraging effort and reproductive performance (Ricklefs et al. 1984, Montevecchi 1993, Hedd et al. 2002, Pinaud et al. 2005, Harding et al. 2007).

Seabird responses to changes in prey availability vary between species, colonies and individuals, and many of these responses are mediated by the type of foraging behaviour employed. Species of penguin or auk that forage via subsurface diving have a wider access to available prey than surface foraging species such as terns (Stienen et al. 2000). Moreover, species that deliver more than one prey to their offspring per trip (multiple prey loaders) have different constraints from “single prey loaders”, which provision their chicks with single prey items (Ramos et al. 1998, Shealer 1998, Stienen et al. 2000). For single prey loaders, such as terns or guillemots, central-place foraging theory predicts that adults should maximise their provisioning effort per unit time of foraging, by selecting and returning as large or energetically-rich prey as possible (Orians and Pearson 1979, Davoren and Burger 1999). However, foraging decisions also depend upon the size of prey available and there exists a critical time above which the optimal foraging behaviour is to be unselective, i.e. the fitness gained by offspring and parent in searching further is outweighed by the fitness costs (Lessels and Stephens 1983). Also, the size of prey delivered by single prey loaders is regulated by what adults can physically carry and the physical ingestion capabilities of their chicks that may change as chicks grow (Hulsman et al. 1989, McLeay et al. 2009a).
Inter-colony variations in seabird provisioning and reproductive rates may indicate spatial differences in prey conditions (Montevecchi and Myers 1995, Gremillet et al. 2004, Thayer and Sydeman 2007). Provisioning behaviour and reproductive performance may also reflect temporal shifts in prey availability caused by seasonal changes in environmental conditions. In addition, the sensitivity of provisioning and reproductive parameters to changes in prey conditions varies at different temporal scales (Cairns 1987). Measures of provisioning integrate prey availability over the time taken to complete a foraging trip (hours to weeks), whereas chick growth rates or breeding success reflect prey conditions over the course of the breeding season (months). The type of response measured also determines its sensitivity to variations in prey availability. Adult foraging activities may be at a maximum during poor to moderate levels of prey abundance, and vary most when prey abundance is high when less time is devoted to locating prey (Cairns 1987). Conversely, chick growth rates and breeding success may vary most when prey abundance is low to moderate, and be less variable when prey abundance is high (Cairns 1987). Ideally a range of seabird parameters from different colonies should be monitored to gain an understanding of how foraging and reproductive performance are influenced by prey conditions at different spatial and temporal scales.

Poor prey conditions may be correlated with late breeding and subsequent reductions in chick growth rates and/or survival (Perrins 1970, Arnold et al. 2004, Drent 2006). In temperate marine systems the summer breeding seasons of seabirds are often associated with elevated production that declines as winter approaches (Hamer et al. 2002, Schreiber 2002). The reproductive performance of individuals that reproduce later may be poorer because they are not able to take advantage of the peak in prey availability. Alternatively, reproductive performance declines seasonally as a product of parental quality i.e. lower quality individuals reproduce later because they have less foraging or breeding experience (age effects) (Lewis et al. 2006, Field et al. 2007, Woo et al. 2008), or are in poorer condition due to differences in phenotypic traits (Drent and Dann 1980, Monaghan et al. 1989, Wendeln and Becker 1999, Blums et al. 2005). The “timing” and “parental quality” hypotheses are not independent (Arnold et al. 2004). Where seasonal changes in prey availability occur, all parents face a compromise between using the peak in prey resources to enhance their own body condition and provisioning prey to their chicks (Drent 2006). Seasonal changes in prey abundance may act differentially on adults depending on age or body condition and high quality individuals may be more proficient in acquiring and allocating resources towards reproduction. Offspring development during the provisioning period is determined by the interaction between adult
quality and environmental conditions, and may have long-term fitness consequences. Several studies have linked adult reproductive performance to the morphological or fitness traits inherited during early life history stages (Richner 1989a, Gaillard et al. 1998, Gebhardt-Henrich and Richner 1998, Cooch 2002, Cam et al. 2003, McLeay et al. 2009b). A key to understanding the processes that affect these dynamics lies in identifying such “family effects”.

Crested terns *Sterna bergii* are a small, plunge-diving seabird common in the Indo-Pacific and along all coasts of Australia. During the breeding season adults lay one egg that they incubate for approximately 28 days (Langham and Hulsman 1986). After hatching, chicks are provisioned with single prey items by both parents at the breeding colony. Adults are long-lived and in South Australia they have a well defined breeding season and are highly philopatric (McLeay et al. 2009b). A previous study of a crested tern population indicated that adults reared in years when their major prey, sardine *Sardinops sagax*, were absent, exhibited smaller morphology and lower rates of recruitment to the breeding population than expected (McLeay et al. 2009b). These characteristics provided an opportunity to examine some of the factors that may affect offspring growth and survival responses in a crested tern population.

We examined provisioning behaviour, and the effects of reproductive timing and adult body condition on the growth and survival of their chicks. In this study we specifically ask:

1) How do adult crested terns, as single prey loaders, adjust their provisioning behaviour over the course of the provisioning period in response to the increased energetic demands of chicks?

2) Do chick provisioning rates, chick growth rates and breeding success differ between colonies?

3) Does chick growth and survival vary due to differences in parental quality reflected in adult reproductive timing? We use age and body condition as proxies for adult quality.
Methods

Study site

This study was carried out between November and February in the years 2006/07 and 2007/08 at Troubridge Island (35°4’S, 137°49’E), Lipson Island (34° 15’S, 136°15’E) and Rocky Island (34° 29’S, 137° 25’E), South Australia (Figure 1). We further refer to seasons as belonging to the year that breeding began (e.g. 2006/07 = 2006). The crested tern colony at Troubridge Island is the largest in South Australia, consisting of approximately 3000 pairs (McLeay et al. 2009b). Colonies at Lipson and Rocky Island have approximately 2000 and 1300 breeding pairs, respectively (McLeay unpublished data).

![Figure 1. Map of Gulf St Vincent and Spencer Gulf, South Australia, showing the location of the study colonies (bird symbol).](image-url)
Reproduction, provisioning and chick growth

The timing of hatching and hatching success was monitored by marking between 140 and 200 nests at each colony during the incubation period. To avoid biases towards early nesting individuals we marked nests in different sections of the colony after the majority of adults had laid eggs. On each colony visit, nests were checked daily for signs of hatching and hatch dates were recorded. Eggs that did not hatch after 35 days were considered dead (Langham and Hulsman 1986). Hatching success was calculated as the proportion of eggs that hatched from eggs laid. Hatch date was measured relative to when the first egg among marked nests hatched.

To monitor chick provisioning, growth, and fledging success, we constructed a 30–45 cm high fence using 5mm wire mesh, around 40 to 100 nests at each colony. A 15 cm band of green shade-cloth was attached to the bottom of each fence to prevent injury to chicks and the fences incorporated enough vegetation to afford chicks shade and cover from predators. Nests within the fences were individually marked and monitored daily until all chicks hatched, at which point they were banded (within 2 days). To ensure birthdates/ages were assigned correctly only chicks that were observed to have hatched each day were included in analyses. Chicks were weighed (± 2g) at least once during weekly visits to the colony. Only chicks with ≥ 3 mass measurements taken over the course of the breeding season were included in analyses. Chick survival was monitored within each fence from hatch until death, or until chicks left the fenced areas, at which time they were considered to have fledged. Chick provisioning patterns were also monitored within a fence at each colony between 06:00 and 18:00 on three occasions during the breeding season. Observations were made from a portable hide at a distance of 10–15m with Leica (10 x magnification) binoculars. To aid individual recognition up to 25 chicks were dye marked with Nyanzol D and/or colour banded at least one day prior to provisioning data being recorded. When adults arrived with prey for their chicks, the time of delivery was recorded and we allocated the prey item to one of five size categories with reference to mean adult bill length (BL) (BL = 60.02 mm ± 2.9 SD; n = 2265): Category 1: 0.25-0.75*BL, Category 2: 0.75-1.25*BL, Category 3: 1.25-1.75*BL, Category 4: 1.75-2.25*BL, Category 5: 2.25-2.75*BL.

The mass of individual prey delivered to chicks was estimated using species-specific regression equations obtained from published information and from regressions constructed in a previous study (McLeay et al. 2009a). Provisioning rates were calculated as the total number
and mass (g) of prey delivered to chicks per 12 hour period. To validate prey delivery observations we recorded the type and size of prey delivered to 15 chicks located outside the enclosures. We caught these chicks and collected any prey that was voluntarily regurgitated. Prey from these regurgitates was then identified and their mass was calculated according to the methods outlined in McLeay et al. (2009a).

Age-related variation in reproductive timing and adult body condition

Banding of crested tern chicks at Troubridge Island commenced in December 1966 (Waterman et al. 2003). Since 1975, an average of 1348 chicks (SE = ± 111.6; range 640 - 2350) have been banded annually, but no banding occurred between 1976 and 1985. At Troubridge Island in 2007 we captured adults with bands from their nests with a hand-held net, recorded their band number, and measured their culmen length (± 0.01mm) and mass (± 5 g) before they were released back on their nests. We also recorded whether an egg or chick was present at each nest. Adult ages were calculated by referencing band numbers against band records.

Data analyses

As their chicks grow many birds adjust the amount of prey they provide to their young by increasing the rate or size of prey delivered (Swihart and Johnson 1986, Hulsman et al. 1989, Smith 1993, Ramos et al. 1998, Shealer 1998). Consequently, to compare within-season and between-site variation in chick provisioning rates (number and total mass of prey delivered to chicks per 12 hour period), we apportioned data to one of three groups based on the age of the chick at the time of provisioning:

1) Early provisioning: chicks aged 0 to 10 days post-hatch.
2) Mid provisioning: chicks aged 11 to 25 days.
3) Late provisioning: chicks aged >25 days.

To compare parameters of chick growth at each colony we fitted logistic curves using Curve Expert to mass measurements from chicks with ≥ 3 measurements taken over the course of the breeding season:

\[
W = \frac{A}{1 + e^{-K(t-t_l)}}
\]
where \( W \) represents mass at time \( t \) (days), \( A \) is the asymptote, \( I \) is the inflection point (time) at which 50% of growth is achieved, and \( K \) is a constant proportional to the overall growth rate (Ricklefs 1968). We also estimated hatch mass (\( M_0 \)), early growth rate (0-10 days) and linear growth rate (11-25 days) using the logistic growth equation derived for individual chicks.

We tested for within-season and between-colony differences in provisioning rates and growth parameters using ANOVA, Mann Whitney or t-tests (where appropriate). To evaluate the effect of changes in provisioning (grams of prey delivered per 12h) on daily changes in chick mass we used linear regression. Regression analysis was undertaken for provisioning and mass data collected for consecutive daily mass measurements of 47 chicks aged between 11–25 days, during their ‘linear’ phase of growth. Data from this period were used because growth rates are highest during this period and are most likely to be impacted by changes in the rate of provisioning (Ricklefs et al. 1998). Sample sizes for consecutive daily mass measurements were too small for meaningful statistical analysis at Lipson Island and Troubridge Island in 2006, so daily mass and provisioning data from these colonies were pooled.

Breeding success was measured from marked nests outside the enclosures and banded chicks within enclosures according to the methods described previously and was calculated as the product of hatching success and fledging success, respectively (i.e. Breeding success = hatching success*fledging success).

To assess the significance of variables (site, hatch date, hatch mass and linear growth rate) in explaining various parameters of growth (hatch mass, linear growth rate, \( K \), \( A \) and fledging age) we fitted generalised linear models (GLM) with a normal distribution and identity link function (SPSS© v15). To predict chick survival logistic regression analyses with a binomial distribution and a logit link function within GLM (SPSS© v15) were used to examine the significance of the above variables and interactions. To examine the effect of each individual variable in predicting growth and survival responses we removed each variable from the ‘full’ logistic model that included all terms of interest. We then tested for the significance of the variable by comparing the log-likelihood of the full and reduced models using \( G^2 \) statistics (Quinn and Keough 2002). Year and site were initially included as categorical variables in GLM models but GLM parameter estimates for year and site indicated that variation in the model was mostly explained by site. Year was subsequently removed from further analyses.
To assess age-related variations in the timing of breeding we calculated the proportion of nests from known-age adults that contained chicks between the start and peak time of hatching (16\textsuperscript{th}–28\textsuperscript{th} November) at Troubridge Island in 2007. Individual and age-related variations in adult body condition were assessed by constructing a body condition index (BCI) for adults captured at Troubridge Island in 2007 according to the methods of Le Corre et al. (2003):

\begin{equation}
(2) \quad \text{BCI} = 1 - \left( \frac{(\text{TM} - \text{OM})}{\text{TM}} \right)
\end{equation}

where TM is the theoretical body mass (g) calculated from the regression between mass and culmen length (CL) (\( \text{TM} = 3.15 \times \text{CL} + 146.9, \text{F} = 108.3, p = \leq 0.001 \)) and OM is the observed body mass (g). For BCI < 1 the adult body mass is lighter than expected. Conversely, for a BCI > 1 adult body mass is heavier than expected.

Data relating to the variation in the body condition index (BCI) among and between cohorts did not conform to assumptions of normality and homoscedasticity so was compared using nonparametric analysis of similarity (ANOSIM), on a Bray-Curtis similarity matrix (PRIMER version 5.1.2, PRIMER-E Ltd., Plymouth, UK) \((p \leq 0.05)\). ANOSIM is a hypothesis-testing procedure that generates a probability value and a test statistic \((R)\), which lies between 1 and –1. High positive \(R\)-values indicate greater variation between groups than within groups, and negative values indicate high levels of within-group variation compared to that between groups. Values of \(R\) equal to zero represent the null hypothesis of no significant difference between groups. We also tested for differences in BCI between young (3–6 years) and older adults (7+years) using Mann-Whitney U-tests. Age groups were selected based on the rationale that adults are not fully recruited to the breeding colony until they are 7 years old (McLeay unpublished data). Consequently, adults aged < 7 years may be of lower quality (i.e. have less breeding experience and lower BCI). All data were tested for assumptions of normality and homoscedasticity using Komolgorov-Smirnov/Shapiro-Wilks’ tests and Levene’s test.
CHAPTER 4  Chick growth, survival and provisioning

Results

Provisioning

Regurgitate analysis indicated that observations of prey delivery to chicks identified up to 93.3% of prey correctly to Family and 86.7% of individual prey to species. Estimated prey mass derived with reference to adult bill length did not differ significantly from that measured from the same prey identified in regurgitates ($t = 0.886, p = 0.390, df = 14$). The total mass of prey delivered to chicks ($g/12 \text{ h}$) typically increased between early and mid/late chick provisioning periods at all colonies ($\forall p \leq 0.05$, Figure 2A). However, this trend was not apparent at Lipson Island in 2006 where chicks received between $10.8 \pm 7.4$ and $14.2 \pm 12.0$ g/12 h ± SD (Figure 2A). The increase in the total prey mass delivered to chicks at Troubridge Island in 2006 and 2007, and Rocky Island in 2007 was typically associated with an increase in the individual mass and number of prey delivered between early chick provisioning and mid/late chick provisioning periods ($\forall p \leq 0.05$, Figure 2A–C).

The total mass ($g/12 \text{ h}$) and number of prey delivered to chicks did not differ significantly among colonies during early provisioning ($\forall p \geq 0.05$, Figure 2A, C). During the mid provisioning period the total mass of prey delivered to chicks at Troubridge Island in 2006 and Rocky Island in 2007 was similar ($>20g/12 \text{ h}$, $t = 1.44, p \geq 0.05$, Figure 2A). Chicks at these colonies received a significantly greater total mass of prey than at Lipson Island in 2006 and Troubridge Island in 2007 ($p \leq 0.05$, Figure 2A). At Troubridge Island in 2006 the increase in the mass of prey delivered to chicks was accompanied by a significant increase in the number of prey delivered relative to all other colonies ($\forall p \leq 0.05$, Figure 2C). At Rocky Island in 2007 the increase in the total mass of prey delivered was associated with larger individual prey being delivered compared to other colonies ($\forall p \leq 0.05$, Figure 2B). During the late chick provisioning period the number of prey delivered did not differ significantly between colonies ($p \geq 0.05$, Figure 2B, C). However, the total mass of prey delivered to chicks ($g/12 \text{ h}$) was significantly lower at Lipson Island in 2006 compared to all other colonies ($\forall p \leq 0.05$, Figure 2A) and associated with the delivery of relatively smaller prey (Figure 2B).
Figure 2. Variation between colonies in A. Number of prey delivered per 12 hr, B. Mean mass of individual prey delivered and C. total mass (g) of all prey delivered per 12 hr for different provisioning stages/ chick age categories. (Chicks observed: Troubridge Island 2006, n = 75; Lipson Island 2006, n = 63; Troubridge Island 2007, n = 57; and Rocky Island 2007, n = 74). (Error bars are ± SE). Early = chicks aged 0–10 days; Mid = chicks aged 11–25 days; Late = chicks aged > 25 days.
Colony variation in chick hatching and growth parameters

Chick hatching occurred between 15 November and 18 December at all colonies. Mean hatch mass ($M_0$) showed little variation between colonies, ranging from 37.6g to 41.3g, but hatchlings were significantly larger at Troubridge Island in 2006 compared to Troubridge and Rocky Island in 2007 (both $p \leq 0.05$, Table 1).

Table 1. Parameters of hatching and growth estimated for crested tern chicks (alive v dead) between 2006 and 2007. (symbols: $M_0$, chick mass at hatching; $K$, logistic growth equation constant proportional to the overall growth rate; $I$, time to reach 50% of asymptotic mass; $A$, asymptotic mass)(all values ± SE).

<table>
<thead>
<tr>
<th>Location</th>
<th>n</th>
<th>Hatching period</th>
<th>$M_0$ (g)</th>
<th>Early growth rate (g.day$^{-1}$)</th>
<th>Linear growth rate (g.day$^{-1}$)</th>
<th>$K$</th>
<th>$I$ (days)</th>
<th>$A$ (g)</th>
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<tbody>
<tr>
<td><strong>Alive</strong></td>
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<tr>
<td>Lipson Is 2006</td>
<td>46</td>
<td>18th Nov to 16th Dec</td>
<td>40.8 ± 1.56</td>
<td>7.3 ± 0.2</td>
<td>0.12 ± 0.00</td>
<td>15.3 ± 1.6</td>
<td>285.5 ± 4.1</td>
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<tr>
<td>Troubridge Is 2006</td>
<td>82</td>
<td>21st Nov to 17th Dec</td>
<td>41.3 ± 0.76</td>
<td>6.8 ± 0.2</td>
<td>0.13 ± 0.00</td>
<td>13.5 ± 0.5</td>
<td>259.2 ± 3.9</td>
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<tr>
<td>Rocky Is 2007</td>
<td>56</td>
<td>26th Nov to 9th Dec</td>
<td>37.7 ± 0.87</td>
<td>7.3 ± 0.1</td>
<td>0.12 ± 0.00</td>
<td>14.5 ± 0.5</td>
<td>277.7 ± 3.4</td>
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<tr>
<td>Troubridge Is 2007</td>
<td>47</td>
<td>15th Nov to 18th Dec</td>
<td>37.8 ± 1.17</td>
<td>8.1 ± 0.2</td>
<td>0.13 ± 0.00</td>
<td>14.7 ± 0.7</td>
<td>295.8 ± 3.6</td>
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<tr>
<td><strong>Dead</strong></td>
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<tr>
<td>Lipson Is 2006</td>
<td>12</td>
<td></td>
<td>33.0 ± 2.2</td>
<td>6.0 ± 1.3</td>
<td>0.18 ± 0.02</td>
<td>207.8 ± 24.1</td>
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<tr>
<td>Troubridge Is 2006</td>
<td>5</td>
<td></td>
<td>45.7 ± 3.1</td>
<td>3.5 ± 2.2</td>
<td>0.21 ± 0.05</td>
<td>139.2 ± 13.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rocky Is 2007</td>
<td>3</td>
<td></td>
<td>38.4 ± 1.7</td>
<td>4.8 ± 0.7</td>
<td>0.15 ± 0.00</td>
<td>205.7 ± 2.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Troubridge Is 2007</td>
<td>3</td>
<td></td>
<td>36.7 ± 2.4</td>
<td>5.0 ± 1.2</td>
<td>0.11 ± 0.02</td>
<td>210.4 ± 30.7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Early growth rate ($0 – 10$) and overall chick growth rate ($K$) did not vary significantly between colonies ($p \geq 0.05$, Table 1). Chicks reached 50% of asymptotic mass ($I$) between 13.5 and 15.3 days (Table 1). Chicks at Troubridge Island in 2007 exhibited significantly higher rates of linear growth (11 – 25 days post hatch) (8.1g ± 0.02g per day) compared to other colonies ($p \leq 0.05$, Table 1). Conversely, chicks at Troubridge Island in 2006 attained lower linear growth rates compared to chicks at other colonies (all $p \leq 0.05$, Table 1). Colony differences in linear growth were also reflected in measures of asymptotic mass ($A$) (all $p \leq 0.05$, Table 1). Linear growth rate and $A$ were significantly positively correlated at all colonies (all $p \leq 0.05$) except Lipson Island ($r^2 = 0.064, p =0.114$), indicating that chick growth between 11 and 25 days post hatch may have a significant influence on fledgling size ($A$).

The low mortality of chicks at Troubridge Island and Rocky Island between 2006 and 2007 precluded most within-colony comparisons of hatching and growth parameters between alive and dead chicks (Table 1). At Lipson Island chicks that died had significantly lower hatching
mass \( (M_0) \) and asymptotic mass \( (A) \) compared to chicks that fledged \( (M_0; Z = 2.762, p = 0.006; A: Z = 3.202, p = 0.001) \) (Table 1). The linear growth rate of dead chicks at Lipson Island was also lower than chicks that survived, however differences were not statistically significant (Table 1). Conversely, rates of early growth did not differ between chicks that died and those that survived (Table 1).

**Relationship between provisioning and growth**

Consecutive daily measurements of chick mass during the mid provisioning period, which coincided with the linear growth phase, indicated that chick mass varied ±20g over 24 hours. Daily mass change during this period was significantly correlated with the total mass of prey delivered in the previous day \( (g/12\ h) \) \( (r^2 = 0.090, p = 0.038, df = 47) \).

**Breeding success**

Hatching success was high at all colonies and ranged between 0.95 and 0.98 eggs hatched/ laid (Table 2). Fledging success was more variable between colonies but also high, ranging from 0.77 at Lipson Island in 2006 to 0.95 at Rocky Island in 2007 (Table 2). Consequently, breeding success was high at all colonies sampled in 2006 and 2007 ranging from 0.73 at Lipson Island in 2006 to 0.93 at Troubridge Island in 2006 (Table 2). Chick mortality was highest in the mid and late provisioning periods (Figure 3). During early growth (0–10 days) at Lipson Island chick mortality increased from 0.02 to ~0.11 chicks per day for both the mid and late growth phases (Figure 3).

Table 2. Estimates of hatching, fledging and breeding success (Breeding success = hatching success* fledging success) at crested tern colonies in South Australia between 2006 and 2007. Number of individuals used for each calculation is given in parentheses.

<table>
<thead>
<tr>
<th>Location</th>
<th>Hatching success</th>
<th>Fledging success</th>
<th>Breeding success</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lipson Is 2006</td>
<td>0.946 (112)</td>
<td>0.767 (60)</td>
<td>0.726</td>
</tr>
<tr>
<td>Troubridge Is 2006</td>
<td>0.983 (118)</td>
<td>0.943 (87)</td>
<td>0.927</td>
</tr>
<tr>
<td>Rocky Is 2007</td>
<td>0.964 (83)</td>
<td>0.949 (59)</td>
<td>0.915</td>
</tr>
<tr>
<td>Troubridge Is 2007</td>
<td>0.967 (92)</td>
<td>0.940 (50)</td>
<td>0.909</td>
</tr>
</tbody>
</table>
Factors affecting growth and survival of crested tern chicks.

The results of our GLM for the effects of site, hatch date, chick mass at hatching ($M_0$) and linear growth rate on chick hatching, growth and survival responses are presented in Tables 3 and 4. Hatch mass ($M_0$) and all growth variables except $K$, which remained constant, varied significantly between colonies ($p \leq 0.05, n = 231$, Table 3). Hatch mass ($M_0$) was negatively correlated with hatch date ($p < 0.001, n = 231$, Table 3). Chicks that hatched later in the breeding season also attained smaller asymptotic mass ($A$) and fledged at a significantly younger age than chicks that hatched early (both $p \leq 0.05, n = 231$, Table 3). However, hatch date was not a significant predictor of either growth rate measure (i.e. linear growth rate or $K$) ($p \geq 0.05, n = 231$, Table 3). The age at which chicks fledged was also negatively correlated with linear growth rate and hatch mass, indicating that chicks with larger mass at hatching or higher growth rates fledged younger (both $p \leq 0.05, n = 231$, Table 3).
Table 3. Results of generalised linear modelling for the effects of site, hatch date, hatch mass (M₀) and linear growth rate on chick growth responses (M₀, hatching mass; Linear growth rate; K, constant proportional to the overall growth rate; A, asymptotic mass and Fledging age, n = 231). Partial regression coefficients for site (entered as a factor) are shown. Ref. is reference level for factor = site (Troubridge Is 2007). The p values are based on individual terms being excluded from the full effects model. Variables contributing significantly to the variation in each response are highlighted in bold.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>M₀</th>
<th>Linear growth rate</th>
<th>K</th>
<th>A</th>
<th>Fledging Age</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>β</td>
<td>SE</td>
<td>G²</td>
<td>p</td>
<td>β</td>
</tr>
<tr>
<td>Site</td>
<td>32.2</td>
<td>&lt;0.001</td>
<td>38.5</td>
<td>&lt;0.001</td>
<td>2.5</td>
</tr>
<tr>
<td>Lipson Is. 2006</td>
<td>7.05</td>
<td>1.79</td>
<td>-0.80</td>
<td>0.24</td>
<td>-0.006</td>
</tr>
<tr>
<td>Troubridge Is. 2006</td>
<td>2.49</td>
<td>1.68</td>
<td>-1.45</td>
<td>0.22</td>
<td>-0.002</td>
</tr>
<tr>
<td>Rocky Is. 2007</td>
<td>-3.84</td>
<td>1.99</td>
<td>-1.06</td>
<td>0.27</td>
<td>-0.008</td>
</tr>
<tr>
<td>Hatch date</td>
<td>-0.34</td>
<td>0.08</td>
<td>17.6</td>
<td>&lt;0.001</td>
<td>-0.02</td>
</tr>
<tr>
<td>Hatch mass M₀</td>
<td>-0.34</td>
<td>0.08</td>
<td>17.6</td>
<td>&lt;0.001</td>
<td>-0.02</td>
</tr>
<tr>
<td>Linear growth rate</td>
<td>43.05</td>
<td>1.86</td>
<td>8.42</td>
<td>0.25</td>
<td>0.131</td>
</tr>
<tr>
<td>Intercept</td>
<td>43.05</td>
<td>1.86</td>
<td>8.42</td>
<td>0.25</td>
<td>0.131</td>
</tr>
</tbody>
</table>
Site was a significant predictor of chick survival ($p \leq 0.001$, Table 4) and was explained by the lower survival of fledglings at Lipson Island in 2006 (Table 2, Figure 3). Chicks that hatched later in the season had a lower probability of survival than chicks that hatched early ($p = 0.003$, Table 4). In addition, the probability of survival increased significantly for chicks that had high linear growth rates or greater hatch mass ($M_0$) (both $p \leq 0.001$, Table 4). The logistic regression also indicated a significant interaction between site and linear growth rate, likely due to the significant difference in linear growth rates between chicks at different colonies ($p \leq 0.001$, Tables 3 and 4). There was also a significant positive correlation between the interaction term Hatch date* Linear growth rate and survival, possibly resulting from the influence of hatch date on chick growth ($p = 0.103$, Table 3) and the strong positive correlation between linear growth rate and survival ($p < 0.001$, Table 4).
Table 4. Results of generalised linear modelling for the effects of site, hatch date, hatch mass ($M_0$), linear growth rate and relevant interactions on chick survival. Partial regression coefficients for site (entered as a factor) are shown. Ref. is reference level for factor = site (Troubridge Island 2007). The $p$ values are based on individual terms being excluded from the full effects model. Variables contributing significantly to the full model are highlighted in bold.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\beta$</th>
<th>SE</th>
<th>$G^2$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Survival</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lipson Is. 2006</td>
<td>6.529</td>
<td>7.80</td>
<td></td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Troubridge Is. 2006</td>
<td>13.920</td>
<td>7.89</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rocky Is. 2007</td>
<td>-16.908</td>
<td>17.37</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Troubridge Is. 2007</td>
<td>Ref.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hatch date</td>
<td>-0.539</td>
<td>0.36</td>
<td>8.79</td>
<td>0.003</td>
</tr>
<tr>
<td>Hatch mass $M_0$</td>
<td>0.100</td>
<td>0.28</td>
<td>12.78</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Linear growth rate</td>
<td>0.514</td>
<td>1.17</td>
<td>53.84</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Site*$M_0$</td>
<td>3.73</td>
<td>0.053</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lipson Is 2006</td>
<td>0.015</td>
<td>0.17</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Troubridge Is 2006</td>
<td>-0.165</td>
<td>0.18</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rocky Is 2007* M0</td>
<td>0.110</td>
<td>0.26</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Troubridge Is 2007</td>
<td>Ref.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site * Linear growth rate</td>
<td>12.51</td>
<td></td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Lipson Is 2006</td>
<td>-1.327</td>
<td>0.75</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Troubridge Is 2006</td>
<td>-0.872</td>
<td>0.73</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rocky Is 2007</td>
<td>2.284</td>
<td>1.80</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Troubridge Is 2007</td>
<td>Ref.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hatch date * $M_0$</td>
<td>0.002</td>
<td>0.01</td>
<td>0.12</td>
<td>0.729</td>
</tr>
<tr>
<td>Hatch date * Linear growth rate</td>
<td>0.088</td>
<td>0.04</td>
<td>7.71</td>
<td>0.006</td>
</tr>
<tr>
<td>$M_0$ * Linear growth rate</td>
<td>0.001</td>
<td>0.03</td>
<td>0.002</td>
<td>0.964</td>
</tr>
<tr>
<td>Intercept</td>
<td>-5.926</td>
<td>10.34</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Adult condition and reproductive timing**

Chicks reared by older adults hatched earlier in the breeding season than chicks reared by younger adults. This was indicated by a significant positive correlation between adult age and the proportion of nests from known-age adults that contained chicks during the peak period of hatching ($r^2 = 0.65, p = 0.001$) (Figure 4). Body condition (BCI) varied within and between cohorts (Figure 5). Analysis of between-cohort variation in BCI indicated that individuals $<7$ years of age had significantly lower BCI than individuals $\geq 7$ years of age ($Z = 2.573$, $p = 0.010$). Chicks reared in 1995 (aged 12 years) during a mass mortality of sardine had BCI comparable to individuals $<7$ years of age (Figure 5). However, within cohort variation in BCI was as great as between-cohort variation (ANOSIM, $R = 0.003, p = 0.353$) indicating that body condition was not only influenced by age (Figure 5). In addition, there was a significant positive correlation between BCI and the proportion of nests that had chicks present during the peak period of hatching ($r^2 = 0.216, p = 0.039$). These results indicate that adult body
condition varies as a function of both individual quality and age, and has a significant influence on the timing of adult breeding.
CHAPTER 4   Chick growth, survival and provisioning

Figure 4. The relationship between the proportion of nests that contained chicks during the peak period of hatching (arcsine transformed) and adult age at Troubridge Island in 2007. Bands represent 95% confidence intervals. ($p = 0.001$).

Figure 5. Box and whisker plot showing variation of adult body condition (BCI) with age (years) in 2007 at Troubridge Island. Line indicates a BCI of 1 where an adult has its expected mass according to its culmen length. Confidence Limits: box limits = 25th and 75th percentiles, whisker limits = 5th and 95th percentiles. (Total adults n=737; range: 3y (n=2) – 10y (n=137).
Discussion

Provisioning

Our study highlights several factors that influence the foraging behaviour of adult crested terns and the growth and survival of their chicks. Comparison of chick growth rates confirm that the energy demands of chicks increase substantially during linear growth. Adult seabirds commonly increase their provisioning effort to meet this increased energy demand prior to their chicks fledging (Dunn 1980, Ricklefs and White 1981, Shealer 1998, Hedd et al. 2002). Models of central-place foraging for single prey loaders such as crested terns predict that they should adjust their foraging behaviour to meet the increased energetic demands of their chicks by increasing either: 1) the ‘quality’ (energetic content per mass) of prey delivered; 2) the size of prey delivered; or 3) the rate of individual prey delivered (Orians and Pearson 1979, Davoren and Burger 1999). Previous research on crested tern chick diets indicated that there were no seasonal patterns in the type of prey species delivered (McLeay et al. 2009a). Field experiments by Shealer (1998) identified size-selective foraging behaviour for roseate terns, and other studies have shown that terns adjust their provisioning behaviour over the breeding season by increasing the size of prey delivered rather than the rate of prey delivery (Hulsman et al. 1989, Smith 1993, Shealer 1998, Stienen et al. 2000). Crested terns also provide their offspring with larger prey as the breeding season progresses. However, we found that they exhibit a more flexible foraging strategy by also increasing the rate of prey delivered to their chicks as their chicks grow.

Parental provisioning behaviour is influenced by the size and density of prey available, the distance of prey aggregations from the colony, the physiological condition of adults, and the time since offspring were last fed (Swihart and Johnson 1986). Where foraging behaviour incurs a cost to the parent, in terms of influencing its future fitness or survival, there may be a critical time or level of prey abundance below which an optimal foraging strategy favours time spent toward acquiring the energy needed for self maintenance over time spent provisioning offspring (McLaughlin and Montgomerie 1990, Waite and Ydenburg 1996, Welham and Beauchamp 1997). We have no information about prey abundance or the type/size of individual prey available to adults within their foraging range, but this hypothesis potentially explains the observed inter-colony differences in the total mass of prey delivered to chicks during the mid and late provisioning periods. For example, at Lipson Island the lower mass of individual prey and total mass of prey delivered to chicks during mid and late provisioning, suggests that adult foraging behaviour may have favoured time spent on self-feeding over time
spent provisioning. In contrast the comparatively high number and total mass of prey delivered to chicks during mid provisioning at Troubridge Island in 2006 may represent foraging behaviour that devoted less time to self feeding, and more time to size-selective predation and offspring provisioning. In summary, parents will be able to better afford size-selective provisioning behaviour and maximise provisioning rates if they have the time available.

Growth

Analyses of provisioning rates and chick mass change over consecutive days indicated that the total mass of prey delivered to chicks was related to daily growth. Growth during the linear phase of chick development was significantly correlated with asymptotic mass. Consequently, prey availability and foraging proficiency during the linear phase of chick growth may be important determinants of fledgling size. This finding is supported by the higher rate of linear growth and larger asymptotic mass attained by chicks at Troubridge Island in 2007 compared to other sites. The fitness consequences of prey-related reductions on chick growth and final fledgling or adult size are better studied for passerines (Cooch, 2002, Gebhardt-Henrich and Richner, 1998 for a review) than seabirds (but see Cam et al. 2003). Retardation during early somatic growth may have long-term fitness consequences for an individual through its impact on final adult body size (Gebhardt-Henrich and Richner 1998, Schew and Ricklefs 1998, Cooch 2002). For instance, carrion crow *Corvus corone* chicks attain significantly smaller body size when reared under poor food conditions compared to chicks reared with an unlimited food supply (Richner et al. 1989). Adult carrion crows reared in habitats where food was abundant are larger, acquire breeding territories more easily and have comparatively higher rates of reproductive success compared to smaller adults (Richner 1989b). Good chick-growth conditions may also result in enhanced rates of recruitment into the breeding population (Gebhardt-Henrich and Richner 1998, Cam et al. 2003). In kitiwakes *Rissa tridactyla* high chick-growth rates and hatch order are positively correlated with recruitment (Coulson and Porter 1985, Cam et al. 2003). Similarly, crested tern chicks reared in 1995 during mass mortality of sardine, which are a major prey of crested terns, had smaller adult morphology and exhibited lower rates of recruitment than chicks reared in years when sardine abundance was high (Gaughan et al. 2000, Ward et al. 2001, McLeay et al. 2009b). These results indicate that the conditions experienced by parents have lifetime fitness consequences for their offspring.
Our study indicates that crested tern chicks exhibited marked variation in fledgling condition. Chicks at Troubridge Island in 2006 fledged over 12% lighter than chicks reared at Troubridge Island in 2007. Despite this difference the high reproductive success exhibited during these years suggest conditions of prey availability were generally good. Data relating to chick condition could be applied as a covariate in future mark-recapture analyses to model recruitment probability and the consequences of pre-fledging condition on individual or age-specific vital rates. This information is rare for seabird populations because they are long lived and exhibit deferred maturity. Future study of this population would facilitate a better understanding of the phenotypic and demographic components that influence lifetime breeding success.

**Body condition and reproductive timing**

Life history theory predicts that during times of low prey availability, foraging behaviour should favour self maintenance over provisioning (Swihart and Johnson 1986). One of the key mechanisms regulating whether parents devote time to self feeding or provisioning is adult body condition (see Drent and Dann 1980, Witter and Cuthill 1993, Wendeln and Becker 1999 for reviews). Our results indicate that adults in good condition hatched chicks earlier and early breeding was positively related to hatch mass, fledgling condition and chick survival. We found that body condition was mediated by age in young breeders. Adults aged <7 years had significantly poorer body condition and hatched their chicks later compared to adults ≥7 years, indicating that age-related breeding and foraging experience may influence adult body condition and reproductive performance. Age is an important factor that determines body condition, reproductive timing and reproductive success in seabirds (Greig et al. 1983, Saether 1990, Sydeman et al. 1991, Forslund and Part 1995, Shealer and Burger 1995, Bunce et al. 2005, Lewis et al. 2006). Alternative explanations attribute age-related increases in body condition to the disappearance of low quality phenotypes from the population over time (the selection hypothesis) (Weimerskirch 1992, Forslund and Part 1995) or to increased reproductive effort with age (see Wendeln and Becker 1999 for a review). Adult body condition also varied significantly within cohorts, indicating that early breeding and its positive relationship with hatch mass, fledgling condition and chick survival is not only related to age but also reflects inter-individual variation. In this regard our results support the findings of Wendeln and Becker (1999) who found high inter- and low intra-individual variation in the body condition of adult common terns (*S. hirundo*), and a positive relationship between adult
body condition and chick growth and survival. However, unlike our study, they found that age did not have a pronounced influence on adult body condition and reproductive performance.

The influence of adult foraging conditions on offspring and adult body condition during the breeding season may have long-term fitness consequences. This was demonstrated by the poor body condition of adults aged 12 years, which were reared during 1995, when one of their primary prey were not available. Similarly, the future survival prospects of parents may also be influenced by the interaction of prey availability on adult body condition during reproduction (Stearns 1992, Golet et al. 1998, Blums et al. 2005). These inherited “family” effects have important implications from a perspective of life history evolution and in regulating population growth (Cam et al. 2003). Our study indicates that the growth of crested tern populations is likely to be most significantly affected by environmental and prey conditions that reduce the foraging efficiency and reproductive output of high-quality individuals ≥7 years old.
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Chapter 5. Fine-scale foraging behaviour and habitat use of a short-ranging seabird, the crested tern


Statement of authorship: Appendix D
CHAPTER 5    Foraging and habitat use

Abstract

We report the first use of satellite tracking technology on a seabird weighing < 400g. Global Positioning System (GPS) units weighing < 22g and dive loggers were deployed on adult crested terns Sterna bergii brooding young chicks. Individuals typically commuted to foraging grounds < 40 km from the colony where their travel speeds slowed to ≤ 10 km.h⁻¹, presumably as prey encounter rates increased. The total distance travelled by individuals ranged between 4.5 and 118 km. Trip durations ranged between ~6 min to ~4h 17 min, and were positively correlated with the maximum distance and total distance travelled from the colony. Foraging behaviour, examined in relation to habitat characteristics (benthic habitat type, depth, SST, Chl-a), was typically associated with warm (19-21°C), shallow (< 20 m), near-surface (< 2 m) waters that were relatively high in Chl-a (> 0.5 mg.m⁻³). The most well supported model (GLMM) of foraging behaviour indicated a positive relationship between time spent at sea, distance travelled and Chl-a, suggesting individuals spent relatively more time foraging at greater distances from the colony in zones of higher primary production. The timing and location of crested tern breeding may be linked to the twofold increase in primary production near to Troubridge Island over the austral summer. Individual differences in the length (distances and duration) of foraging trips conducted reflect either prior knowledge of where prey aggregations exist, distinctions in individual niche use driven by the types or sizes of prey available, and/or alternate behavioural states (self feeding and provisioning). The restricted foraging range of crested terns while breeding may make them sensitive to competition with fisheries that operate within their foraging range.

Key words: Bio-logging, Foraging ecology, Seabird, GPS, Habitat partitioning
**Introduction**

As central-place foragers during the breeding season, marine predators such as seabirds and otariid seals must balance their energetic requirements with those of their offspring (Orians and Pearson 1979). As a result, characters of their foraging behaviour reflect the fasting abilities of their offspring and conditions of prey availability near breeding sites (Swihart and Johnson 1986, Cairns 1987, Burger and Piatt 1990). For seabirds, which are further constrained by the need to provision their young with whole or macerated prey, parents would be expected to forage as near to the colony as prey conditions and energetic requirements allow. However, the availability of prey near colonies may be influenced by density dependent effects caused by the cooperative foraging behaviour of conspecifics (Davoren et al. 2003), and large colonies of breeding seabirds may deplete prey resources around a colony (Ashmole 1963, Birt et al. 1987). Prey availability is also influenced by the habitat characteristics near to colonies and several studies have related the foraging behaviour of seabirds to biological and physical features (e.g. bathmetry, SST, Chl-a) (Guinet et al. 1997, Becker and Beissinger 2003, Suryan et al. 2006, Peltonen et al. 2007, Weimerskirch et al. 2008).

The link between habitat use and the foraging behaviour of large seabirds (> 400g) has received particular attention in recent years due to the development of animal-borne telemetry devices and remote sensing techniques (Guinet et al. 1997, Gremillet et al. 2004, Suryan et al. 2006, Pinaud and Weimerskirch 2007). These studies have found that seabird foraging responses vary between species and populations due to local biophysical conditions that enhance productivity. Foraging behaviour also differs between individuals as a product of foraging-site fidelity and breeding phenology. Although cooperative foraging may enhance the rate at which prey are acquired at prey ‘hotspots’, there exists a critical level of prey density at which the optimal foraging behaviour for an individual is to relocate effort to an area that is more energetically profitable. Individuals that best modify their foraging behaviour in response to existing prey conditions and density dependent processes that act on prey availability, may be conferred a selective advantage through increased breeding success (Lea et al. 2002). Consequently, a range of foraging behaviours may exist within one general ‘mode’ of behaviour. Characterising the different foraging tactics exhibited by conspecifics may provide insights into the factors that shape the evolution of foraging behaviour and life history strategies, and is important in identifying the significance of prey hotspots (Lea et al. 2002).
The size of bio-logging devices has precluded research of the fine scale patterns of foraging behaviour of smaller seabirds (< 400g), and the foraging behaviour of terns remains one of the most poorly resolved aspects of their biology. Previous research is limited to radiotelemetry studies, diet analyses or vessel-based surveys (Becker et al. 1993, Surman and Wooler 2003, Rock et al. 2007). These studies suggest that terns are generally more restricted in their foraging range while breeding compared to larger seabirds. The differences in distances travelled by small and large seabird species may relate to the type of foraging mode employed. The energetic costs of foraging are higher for terns, which locate prey by hovering over the sea surface, compared to larger species that glide or dive. Also, the provisioning strategy employed by terns requires that they return single prey to their chicks at regular intervals, thereby restricting their foraging range compared to species that provision their chicks with regurgitates. The recent development of GPS loggers < 25g allows the constraints on foraging behaviour to be more closely assessed than previous approaches such as shipboard surveys that are more limited in the spatial and temporal resolution of data they can provide. The collection of fine-scale data also allow foraging behaviour to be modelled in relation to habitat variables that can be incorporated in models as covariates.

During the breeding season adult crested terns *Sterna bergii* lay a single egg that they incubate for approximately 28 days (Langham and Hulsman 1986). After hatching, chicks are provisioned by both parents for approximately five weeks at the breeding colony. Crested terns are long-lived and in South Australia, have a well defined breeding season and are highly philopatric (McLeay et al. 2009b). Previous research identified that crested terns may be sensitive to large scale decreases in prey (McLeay et al. 2009b). Chicks reared in years when sardine *Sardinops sagax* abundance was low, exhibited smaller adult morphology and recruited at lower rates (McLeay et al. 2009b). The recent move towards an ecosystem-based approach to the management of marine resources requires information about the distribution and abundance of apex predators and their prey that is spatially explicit. Sardine *Sardinops sagax* form a major component of the diet of crested terns and are the target of Australia’s largest volume purse-seine fishery, the South Australian Sardine Fishery (Ward et al. 2001, Dimmlich et al. 2004, McLeay et al. 2009a). Consequently, data on the foraging ecology of crested terns may help identify regions where resource competition is most likely to occur.

In this study we report the first use of GPS tracking technology on a seabird weighing < 400g. We used newly developed satellite tracking technology, dive loggers and remote observations
to investigate the foraging behaviour of crested terns while provisioning young chicks in South Australia. We examine the fine-scale movement patterns of crested terns, identify groups of foraging behaviours via an objective multivariate clustering technique and analyse the physical and biological habitats most used by individuals while undertaking foraging trips during the breeding season. We predict that:

1) the distribution and behaviour of adult terns will reflect the density dependent processes and constraints associated with breeding at a central place;
2) foraging behaviour will correlate with the physical and/or biological conditions characteristic of near-colony waters;
3) individuals will display differences in foraging behaviour within a general mode of behaviour as a result of site fidelity and/or reproductive constraints, or to reduce intra-specific competition for resources.
Materials and Methods

Study site

The study was undertaken at Troubridge Island, southern Gulf St Vincent, South Australia (35°4’S, 137°49’E) in the austral summers of 2006 and 2007 (November/December) (Figure 1). Troubridge Island is a Conservation Park of approximately 260 ha comprised of sand. The surrounding waters of Gulf St Vincent are relatively protected and shallow (5 to 40 m), and characterised by benthic habitats comprised of bare sand, seagrass and rocky reefs (Tanner 2005). The crested tern colony at Troubridge Island is the largest in South Australia with 3000–3500 breeding pairs (McLeay unpublished data).

Figure 1. Sterna bergii. Location of study area, with 200m depth contour and known crested tern breeding colonies in South Australia.
Animal capture and logger deployment

Crested terns that were attending chicks < 5 days old were captured at their nests at sunrise (~0530) each day using hand-held nets. Crested terns do not forage at night and consequently adults present on their nest at sunrise were likely to undertake a foraging trip in the following 12 hours (McLeay unpublished data). To prevent chicks from leaving their nests while GPS units were being attached to their parents, we constructed a 20cm high fence made of 5mm wire mesh around each chick. A 15cm band of shade-cloth was attached to the bottom of each fence to prevent injury to chicks and the fence incorporated enough vegetation to afford chicks shade and cover from predators. GPS units were attached with Loctite 401 glue (Intek adhesives Ltd, England) to the feathers on the back of 21 adults, and each individual was dye marked with Nyanzol D and colour banded to aid individual recognition. Only adults weighing > 350 g were used in this study to minimise the GPS unit mass to body mass ratio. Attachment of GPS units required < 5 minutes from capture to release. Nests were monitored remotely at a distance of 30–40m with Leica (10 x 42X) binoculars until the adult returned to the nest, at which point it was recaptured and had the unit removed by cutting it away from the feathers with scissors. The attachment of GPS units to seabirds may potentially affect normal brooding and/or foraging behaviour. Only adults weighing > 350 g (mean 365 ± 15.1 g SD) were used in this study to minimise the GPS unit mass to body mass ratio. Nonetheless, GPS loggers represented between 5.2 and 6 % of adult body mass for the individuals used in the study, which is at the upper limit of what is generally recommended for tracking wild birds (Caccamise & Hedin 1985; Cochrane 1980). For this reason we attempted to minimise deployment times by catching individuals once they had returned from their first trip of the day. Adults showed no signs of handicap or distress following capture/recapture (i.e. they did not exhibit intensive preening behaviour) and returned to their chicks within 5 minutes of being released (Wilson et al. 1990). To further assess any effect of GPS unit attachment on behaviour we recorded the nest departure and arrival times (assumed foraging trip duration) of individuals with and without GPS units attached (Davoren & Montevercchi 2003).

Data collection

GPS units

We used micro-GPS units (µGPS, Sirtrack® Ltd, North Havelock, New Zealand) with an integrated antenna and housed within a urethane waterproof case. The overall weight of the unit when package was 21g (outer dimensions: ~37mm long x 22mm wide x 19mm high).
Units were programmed on a continuous loop duty cycle to record positions at 1 minute intervals to ensure data were recorded for 12-24 hours.

**Habitat variables**

Sea surface temperature (SST°C) and fluorescence data (chlorophyll-a, hereafter termed Chl-a, mg.m⁻³) were obtained from the Ocean Biology Processing Group (OBPG) at NASA Goddard Space Flight Center (GSFC) (http://oceancolor.gsfc.nasa.gov, 26th May 2009). We used data collected daily by the Moderate Resolution Imaging Spectroradiometer at 500 x 500m resolution (MODIS-Aqua sensors, Level 0). Data were processed to Level 3 by applying the OC3M/MSI12 Version 5.2.3 empirical algorithm using SeaDAS software (Baith et al. 2001, Franz 2006). This algorithm identifies and minimises the atmospheric effects on remotely sensed data using information collected on the different MODIS-Aqua spectral bands. Since cloud cover on many days during field work prevented daily measurement of SST and Chl-a, we used the weekly average of data (centred on the day of sampling). Where seven day averages were not available for the specified period, we used MODIS-derived data from the previous week.

Data relating to the type of benthic habitat surrounding Troubridge Island were obtained from Tanner (2005). Tanner (2005) assessed the benthic community structure using remote video surveys every 2 nm along east-west transects in Gulf St Vincent. Habitat types were assigned based on the predominant type of taxa recorded at each site. This resulted in the classification of eight benthic habitat types: Ascidian, Ascidian/Bryozoan, Bryozoan, Pinna (a bivalve mollusk), Sand, Scallops, Seagrass/Pinna, Seagrass. Bathymetric data were obtained from GeoScience Australia 1 x 1 km grid. The bathymetric depth values for each location were interpolated as functions of their distance from the nearest nodes and assigned to each 5 seconds (time) along a foraging path.

**Trip/wind direction**

To assess the direction of the foraging areas most visited by adult terns, in 2007/08 we recorded the number and bearing of adults returning from a foraging trip. Observations were made using a 360° search pattern with Leica (10 x 42X) binoculars for 10 minute periods between 0900–1100 hrs from a vantage point of ~4 m above the colony. The numbers of individuals, which were carrying fish in their bills, returning from distances > 500m was recorded within 45° sectors. Data relating to the prevailing wind direction during the study
Dive loggers

Dive gauges were plastic capillary tubes that were ~7cm long (2mm diameter), lined with indicator powder (icing sugar) and sealed at one end. As individuals dive, water is forced into the tube and dissolves the indicator powder at a predicted distance. In 2006 we attached dive gauges with Loctite 401 glue to the feathers on the back of 12 adult crested terns that were attending chicks. When adults returned from a single foraging trip the gauge was removed. We then measured the amount of indicator powder that was left in the tubing. The maximum dive depth attained during a foraging trip was then calculated using the equation of Burger and Wilson (1988):

\[
  d = 10.08 \left( \frac{L_s}{L_d} - 1 \right)
\]

Where \(d\) = maximum depth, 10.08 is the constant, \(L_s\) is the initial length of the indicator powder and \(L_d\) is the final length of the indicator powder after a foraging trip is completed. The error of depths recorded using this technique is usually < 10% (Burger and Wilson 1988).

Data analysis

GPS data were downloaded and filtered using the package ‘timeTrack’ (now named package ‘Trip’) (version 1.1–5, M. Sumner, University of Tasmania, Hobart) within R statistical software (version 2.3.0, R Development Core Team, R Foundation for Statistical Computing, Vienna) according to the methods of McConnell et al. (1992) and based on a maximum horizontal flight speed of 60km.h\(^{-1}\). We then assessed the proportion of time spent in an area (TSA) by each individual. To determine the TSA we assumed a constant horizontal flight speed between filtered locations and interpolated a new position for every five seconds (of time) along the individual’s track using the R statistical software and timeTrack package. The number of interpolated positions within a 250 x 250 m cell (62500m\(^2\)) of a predetermined grid were then summed and assigned to a central node. To ensure the duration of individual trips did not bias analyses, TSA data were converted to a proportion of the total time spent in each cell for each individual. Several other parameters were calculated from the GPS data to summarise the foraging behaviour of each individual: (1) Trip duration; defined as the time an
individual left the colony to the time it returned. (2) The total distance travelled (km); calculated as the sum of the distance (km) between all interpolated GPS positions along each individual’s track. (3) Maximum distance from the colony; calculated from the nest to the distal point reached on each foraging trip. (4) Elongation coefficient, which is the ‘straightness’ of the track and is measured as the ratio of the maximum straight line distance from the colony relative to the actual path (Guinet et al. 1997). Elongation ratios have a maximum of 0.5, which indicates little change in overall flight direction over the course of the track, whereas lower ratios indicate more turning. (5) Median bearing; the median compass bearing from the nest to each interpolated position (calculated using Oriana, version 2.02, Kovach Computing Services, Pentraeth, Wales). (6) Mean flight speed (km.h⁻¹); the distance between consecutive interpolated GPS locations divided by the duration (5 seconds). (7) Concentrated foraging behaviour; defined as the proportion of time spent in flight at speeds ≤10 km.h⁻¹. Low transit speeds are commonly used to identify foraging behaviour for marine predators (Nel et al. 2001, Gremillet et al. 2004, Awkerman et al. 2005, Weimerskirch et al. 2005, Simmons et al. 2007). To determine this value we examined a frequency distribution of the speeds of individuals between each interpolated position. A distinct peak in the frequencies was noted at speeds of ~5 km.h⁻¹. Unlike many seabirds, crested terns do not spend more than a few seconds sitting on the sea surface. Consequently, speeds ≤10 km.h⁻¹ are likely to indicate birds that have located, or are in the process of acquiring prey.

To identify whether the foraging behaviour of individual crested terns could be categorised into ecological groups based on behavioural parameters (see results Table 1), we used cluster analyses in PRIMER (Version 6). The Bray and Curtis association measure was used for the analyses, because it is an effective method for analysing multivariate ecological data (Beals 1984). Similarity profile permutation tests (SIMPROF) were used to identify significantly different groups based on the behavioural parameters and similarity percentages (SIMPER) were used to identify the foraging parameters that delineated different groups.

Two approaches were used to describe the physical and biological habitats used by adult crested terns while foraging. First, to compare general habitat use as a function of habitat availability, we overlaid a circle centred on Troubridge Island, with a radius centred on the maximum distance travelled from Troubridge Island by any tracked individual. We then calculated the TSA for all individuals over each habitat (depth, benthic habitat type, SST, Chl-a) and compared it to the proportion of each habitat available within the circle (modified from
Awkerman et al. 2005). Second, we extracted data relating to depth, benthic habitat type, SST and Chl-\textit{a} from each 250 x 250 m cell visited. Mapinfo (Version 8; Mapinfo Corporation, New York) was used to link physical and biological data to TSA data. We then used generalised linear mixed models (GLMM) in R to fit a series of models to the foraging (TSA) data. To account for variation in foraging behaviour of individuals we included ‘individual’ as the random effect. The proportion of TSA by each individual in each 250 x 250m cell was used as the response variable and we applied Akaike information criteria (AIC) to select the best model from a set of candidate models developed \textit{a priori}. Gaussian, Gamma and Binomial response models were considered with appropriate identity, inverse, logit and complimentary log-log link functions. AIC is useful as a comparative measure for models that are developed with different link and distributional assumptions (Bradshaw et al. 2004). Smaller AIC model values are preferred. For individuals that conducted multiple trips only the second track was used to avoid the potential analytical problems associated with temporal autocorrelation of foraging behaviour. The second track was typically longer, and as such, provided more data to assess habitat use. Spatial autocorrelation of foraging behaviour may result from individuals passing through near-colony areas, so GPS locations and their associated environmental data were removed for locations < 2km to the colony (Awkerman et al. 2005). Absence of strong co-linearity between predictor variables is also an important assumption of generalised linear modelling procedures so we investigated correlation between all variables using principal components analysis in SPSS (Version 15). Bathymetry was highly correlated with distance from colony and Chl-\textit{a} (Bathymetry Eigenvalue 0.089). Consequently, we separated these factors in all GLMM models fitted to foraging (TSA) data.

To test for differences in nest attendance patterns we performed a \textit{t}-test in SPSS (Version 15). SPSS was also used to check all data for assumptions of normality and homoscedasticity using Komolgorov-Smirnov/Shapiro-Wilks’ tests and Levene’s test. The average values of foraging parameters are presented $\pm$ SD.
Results

Summary

Table 1 summarises the GPS data collected from 25 foraging trips made by 21 adult crested terns. In total, 2201 unfiltered GPS locations were recorded. The pilot study undertaken in 2006 returned two foraging tracks and dive-depth data from 12 different individuals. In 2007, 23 tracks were recorded from 19 individuals (four individuals returned two tracks). Individuals foraged in near-surface neritic waters < 40 km from the colony. The maximum dive depth attained by individuals was 1.68 m (average 1.14 ± 0.27 m). Individuals travelled between 2.3 and 38.9 km (average 15.3 ± 10.3 km) from the colony and the total distance travelled by individuals ranged between 4.5 and 118 km (average 39.6 ± 29.0 km) (Table 1, Figure 2). The average flight speed of individuals ranged between 12.6 and 42.0 km.h\(^{-1}\) and foraging trip duration ranged from ~6 minutes to ~4 hours 17 minutes (average 1h 33 min ± 1h 17 min), and was positively correlated with the maximum distance from the colony (\(r^2 = 0.730\), df = 23, \(p < 0.001\)) and the total distance travelled (\(r^2 = 0.896\), df = 23, \(p < 0.001\)) (Table 1). The duration of foraging trips for GPS-equipped individuals was lower compared to individuals without GPS units attached (2h 38m ± 1h 48m v 3h 20m ± 1h 33m) but the difference was not significant (\(t = 1.514\), df = 52, \(p = 0.14\)).
Table 1. *Sterna bergii*. Summary data for individual tracks collected from adult crested terns via GPS in 2006 (n=2) and 2007 (n=23).

<table>
<thead>
<tr>
<th>Track</th>
<th>Date</th>
<th>n GPS locations</th>
<th>Trip duration (h: mm)</th>
<th>Total distance travelled (km)</th>
<th>Max. distance from colony (km)</th>
<th>Mean flight speed (km.h⁻¹)</th>
<th>Median bearing (overall)</th>
<th>Elongation coefficient</th>
<th>Concentrated foraging effort (prop. time ≤ 10km.h⁻¹)</th>
<th>Foraging group</th>
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Figure 2. Foraging trips of individuals (n tracks = 25) recorded via GPS in this study. Open circles indicate areas of concentrated foraging. Dashed and dotted lines indicate tracks recorded in 2006 (n = 2) and 2007 (n = 23, respectively.)
Foraging paths and areas of concentrated foraging

Individuals moved away from the colony on a specific bearing before reaching their distal point, where flight speed decreased $\leq 10 \text{ km.h}^{-1}$ as a product of concentrated foraging behaviour (Figures 2 and 3). Once concentrated foraging behaviour was initiated, individuals increased their turning rate and often circled back to locations previously visited (e.g. Figure 3, insert, Track 4.1). The outward and inward parts for most foraging trips were generally straight and parallel as indicated by the relatively large (68%) proportion of trips with high (> 0.35) elongation coefficients (Table 1, Figure 2). One individual conducted a more ‘looping’ flight path, returning to the colony from a different bearing to its outward phase (Figure 3, Track 9).

Figure 3. Sterna bergii. Short (16 min) and long (3 h 8 min) commuting trips (Tracks 4 and 4.1 respectively) and looping trip (4 h 16 min) (Track 9) of adult crested terns from Troubridge Island. Insert shows close up of Track 4.1 with numbers indicating the direction of travel. Circles represent areas where flight speed was <10km/h, i.e. concentrated foraging. Arrows show direction of travel. Shaded star represents Troubridge Island. Bathymetry contours (±10m) indicated by dotted line. All tracks derived from micro-GPS data recorded at 1 minute intervals and with positions interpolated every 5 seconds using timeTrack. See Table 1 for track summary data.
Most individuals (> 80%) spent < 20% of their time at speeds ≤ 10 km.h⁻¹ (Table 1). Four individuals conducted short trips < 10km in length and spent < 1% of their time conducting concentrated foraging (Tracks 4, 6, 14, 18, Table 1). The foraging paths of these individuals were also characterised by maximum attainable values in the coefficient of elongation (0.5), indicating little change in overall flight direction over the course of their track (Table 1). For all individuals, the proportion of time spent at speeds ≤ 10 km.h⁻¹ was significantly and positively correlated with trip duration ($r^2 = 0.225$, $p = 0.019$) and total distance travelled from the colony ($r^2 = 0.188$, $p = 0.030$). Of the four individuals that recorded two foraging trips, one returned to the same foraging area (Table 1, Tracks 12, 12.1). The other three individuals moved away from the colony at a different bearing from their preceding trip and travelled up to 5.4 times the distance (Table 1, Tracks 4, 4.1; 6, 6.1 and 12, 12.1).

**Trip direction versus wind direction**

Remote binocular observations of individuals returning to Troubridge Island indicated that over 90% of adult crested terns returned from bearings between 45° and 270° (NE to W) (Median 135°). Similarly, 72% of adult crested terns fitted with GPS devices returned from foraging trips at bearings between 45° and 270° (NE to W) (Median 130°). During the study period in 2007 the wind direction was mainly from the SSE (median 157°) indicating that individuals generally foraged into the prevailing wind and returned downwind from foraging grounds.

**Foraging groups**

The dendrogram in Figure 4 displays five significantly different foraging groups (SIMPROF permutation tests $p < 0.05$). Dissimilarities between foraging groups were evident in the SIMPER results, which indicated that the total distance travelled contributed to at least 55% of the variation observed for all between group comparisons, except groups 3 (Tracks 4, 18) and 4 (Tracks 6, 14) (Table 1), which were separated primarily due to significant differences in mean flight speed (Mean flight speed group 4 > group 3; Table 1, Figure 4). The maximum distance travelled by individuals from the colony was also an important factor that distinguished foraging groups, because it contributed 13.8–30.2% (SIMPER) of variation between groups (Figure 4).
CHAPTER 5     Foraging and habitat use

Figure 4. Dendrogram from standard hierarchical clustering of crested tern foraging trips. Dark lines represent groups of individual tracks separated at p<0.05 by SIMPROF. SIMPROF analysis based on the foraging parameters (except median trip bearing) listed in Table 1.

Physical and biological habitats

Depth

Approximately 60% of the waters used by crested terns within a 38.9 km radius of Troubridge Island (maximum foraging distance, Table 1) are 30–40 m deep (Figure 5). Adult crested terns foraged predominantly (> 60% TSA) over waters < 20 m in depth, which was significantly shallower than waters available within their entire foraging range (χ² = 544.0, df = 3, p <0.001) (Figure 5).

Benthic habitat

Approximately 72% of foraging occurred over sand habitat which comprised the majority of available benthic habitat in waters NE to SW (bearing 45° to 270°) of Troubridge Island (Figure 5). Individuals also spent ~20% of their time foraging over ascidian, bryozoan, scallop and seagrass habitats located in waters within 20 km, and W to N (bearing 270° to 360°) of the colony, but no time foraging over Pinna or Seagrass/Pinna (Figure 5). Although foraging was typically random over benthic habitats, individuals spent more time foraging over ascidian and ascidian/bryozoan benthos, and less time foraging over pinna and pinna/seagrass than expected (χ² = 100.1, df = 7, p <0.001) (Figure 5).
Figure 5. Percentage of time spent (TSA) at different physical and biological habitat types for individuals tracked by GPS between 2006 and 2007.
Sea Surface Temperature (SST)

Figure 6A depicts the typical pattern of sea surface temperature around Troubridge Island during the brooding period in 2007. Sea surface temperatures (SST) ranged between 17.1 and 20.4°C but were generally 1–2°C warmer in inshore coastal waters compared to waters of central Gulf St Vincent (Figures 6A). Adults showed preference towards foraging over waters ranging between 19 and 21°C. These areas were significantly warmer than the areas available within their entire foraging range (Figure 5) ($\chi^2 = 36.0$, df = 3, p < 0.001) (Figure 5).

Figure 6. Maps showing typical SST (A) and Chl-a (mg/m³) concentration (B) around Troubridge Island in 2007 (from MODIS satellite data, 7 day average for period 19/11/07 to 25/11/07).
Data derived from MODIS satellite imagery for the brooding period in 2007 indicated that Chl-\(\text{a}\) within the foraging range of adult crested terns ranged between 0.18 and 1.94 mg.m\(^{-3}\) (average 0.60 \(\pm\) 0.47 mg.m\(^{-3}\)) but was typically low (< 0.5 mg.m\(^{-3}\)). Primary production was higher (> 0.5 mg.m\(^{-3}\)) in shallow inshore coastal waters and coincident with the thermal front located in waters between the SW and NE (bearing of 270° to 45°) of Troubridge Island (Figures 6A and 6B). Adults spent a high proportion of time (~55%) foraging over waters with Chl-\(\text{a}\) levels > 0.5 mg.m\(^{-3}\). These areas had significantly higher primary production compared to other habitats available within their entire foraging range (\(\chi^2 = 293.7, \text{df} = 3, p < 0.001\)) (Figure 5).

**Generalised linear model selection**

Residual plots and AIC values indicated that the most suitable GLMM incorporated a Gaussian error structure and identity link function to model the proportion of time spent in area (TSA) as a function of the habitat variables (Table 2). A complimentary log-log transformation was used to capture the strong right skew of TSA. The best (top 7) models from the full candidate set of models, and ‘full’ and null models are presented in Table 2. The most well supported model included distance from colony and Chl-\(\text{a}\) (Table 3). This model explained 6.1% of the deviance from the null model (100\[1801.14 – 1691.06\]/1801.14) (Table 2), and there was strong support for the effects of distance from shore and Chl-\(\text{a}\) on TSA (Chl-\(\text{a}\), \(G^2 = 7.6, 1 \text{ df}, p = 0.006\); Distance from shore, \(G^2 = 76.6, 1 \text{ df}, p < 0.001\)). In addition, models that included distance from shore outperformed models that included bathymetry independently. These results indicate that the TSA increased mainly as a function of distance from the colony and in response to increased levels of primary production (Chl-\(\text{a}\)). There was little support for the effects of SST or benthic habitat type on TSA. When these variables were removed from the full model, AIC values improved by ~7.5 and 19.7 points, respectively (Table 2).
Table 2. Results of the top 7 generalised linear mixed-effects models (GLMM) showing the effects of marine habitat variables on time spent in area (TSA) for crested terns foraging from Troubridge Island. Analyses were undertaken for time spent by crested terns within 250 x 250m grid cells (n cells visited = 2495). ‘Individual’ was included in all models as a random effect. Environmental variables, chlorophyll $a$ (Chl-$a$) and sea surface temperature (SST) were included as fixed effects. Benthic habitat type (benth) was included as a categorical fixed effect. Notation: $k =$ number of parameters; Dev = deviance; LL = log-likelihood; AIC = Akaike’s information criterion; $\Delta$AIC is the change in Akaike’s information criterion between the best and candidate model. The null (intercept only) and full (all factors of interest) models are also listed.

<table>
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<th>Model</th>
<th>$k$</th>
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<th>LL</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
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</table>
CHAPTER 5     Foraging and habitat use

Discussion
How organisms use their surrounding habitats while breeding is key to understanding the factors that constrain their reproduction and population growth. This study is the first to use GPS to record the fine-scale temporal and spatial foraging patterns and habitat use for a seabird < 400g. The advent of lightweight GPS tracking technology has revolutionised the ability to record the fine-scale foraging behaviour and habitat use of small seabirds. Our results support those obtained via vessel surveys and radio-tracking studies for other tern species while breeding, and showed crested terns conducted short foraging trips close (< 38.9 km) to the colony (Becker et al. 1993, Surman and Wooler 2003, Rock et al. 2007). The fasting ability of offspring is the main factor determining how far parents can travel while foraging. Chicks of smaller species such as terns are provisioned several times a day with small, single prey (Hamer et al. 2002). This behaviour reflects the limited gut capacity of chicks, and contrasts with the provisioning strategies of other seabird species that forage over long distances and deliver macerated prey at intervals of up to two weeks (e.g. short tailed shearwaters, Puffinus tenuirostris, Weimerskirch and Cherel 1998).

The size/mass of loggers (21 g) represented between 5.2 and 6 % of the body mass of individuals used in our study, and are at the upper limit of what is generally recommended for birds (3-5% of body mass) (Caccamise & Hedin, Cochran 1980). It is possible that the behaviour of some individuals may have initially been altered due to logger attachment. The duration of foraging trips was shorter for individuals equipped with GPS compared to that of non-equipped birds. Short-term behavioural adjustments may have been apparent in the short trips undertaken when individuals were initially released. For this reason we omitted short trips (< 5 km) from habitat analyses. Nonetheless, ~85% of the GPS tracks collected indicated no signs of altered foraging behaviour and our study is the first to provided high resolution patterns of movement of a tern species in relation to the biophysical characteristics of their habitat.

Foraging behaviour and distance
The finding that foraging trip duration was positively related to the total and maximum distance travelled from the colony is common in studies of marine central place foragers (Boyd 1999, Harcourt et al. 2002, Page et al. 2006). The total and maximum distance travelled were also the main factors contributing to differences in foraging behaviour between the groups of individuals identified in cluster analyses. Individual differences in foraging trip
length (distances or duration) may result from variations in prey availability and/or prior knowledge of where prey aggregations exist. Although we did not measure prey abundance, adults typically exhibited a ‘commuting’ type of foraging strategy while provisioning young chicks (Weimerskirch 2007). This strategy was reflected in the concentrated foraging behaviour displayed by individuals at distances > 5km from the colony, and by the significant effect of distance from colony identified in the GLMM. Commuting strategies are common among seabirds while breeding, and may result from behaviour that bypasses the zone of prey depletion that exists around large seabird colonies (‘Ashmole’s halo’) to access denser and more energetically profitable prey aggregations at greater distances (Ashmole 1963, Birt et al. 1987, Weimerskirch et al. 2005, Gaston et al. 2007, Elliot et al. 2009). Commuting behaviour may also indicate that individuals have prior knowledge about where to find prey aggregations.

Fidelity towards a foraging area is common among marine predators and implies a highly developed navigation ability, spatial memory and learning (Le Boeuf et al. 2000). Many consecutive tracks from the same individual are required to assess the extent to which foraging behaviour is fixed by prior knowledge, however, site fidelity was evident in one individual that returned successive tracks from the same area (Tracks 12, 12.1, see Table 1).

Differences in trip length may have been caused by alternate behavioral states of foraging such as provisioning and self feeding. Not all individuals exhibited extended bouts of concentrated foraging behaviour (< 10 km.h⁻¹) at the most distal parts of their track. Some undertook short trips within 10km of the colony and returned immediately. Central-place foraging models predict that parents should increase the amount of energy delivered to chicks in line with the amount of time they spend foraging away from the colony (Orians and Pearson 1979).

However, the foraging decisions of single prey loaders must also be balanced by what their chicks can physically ingest. The chicks of adults tracked in this study were all < 5 days old and consequently limited to ingesting prey < 100mm in size (McLeay et al. 2009a). If small prey were encountered close to the colony, adults may maximise the net rate of energy acquired and delivered by returning the prey immediately to offspring before undertaking a longer trip for self feeding. Consequently, the short trips exhibited by several adult crested terns in this study may reflect ‘size-selective’ foraging behaviour mediated by the dietary requirements of offspring during early provisioning.

Variations in trip length may also reflect intra-specific differences in niche use caused by differences in foraging experience, or behavioural tactics that minimise competition through
the targeting of different habitats. Adults typically foraged over sand habitats at greater distances from the colony, but a few individuals foraged over ascidian and ascidian/bryozoan habitats in inshore waters (< 20 km) SW to NE of the colony. Our GLMM did not identify benthic habitat type as a significant factor influencing TSA, possibly due to the low resolution of habitat data used, but the differences in trip length and foraging areas visited by adults may be indicative of the types of prey targeted. The small pelagic fish assemblage of offshore waters NE to SW of the colony in southern Gulf St Vincent is characterised by the presence of surface-schooling clupeiform species such as sardine and anchovy (Rogers et al. 2008). These species are commonly found in the diet of chick and adult crested terns from Troubridge Island and may have been targeted by adults foraging in these areas (McLeay et al. 2009a). Conversely, the large quantities of leatherjackets, garfish and blue sprat, which are also commonly found in crested tern diets, may reflect foraging behaviour over shallower, inshore habitats SW to NE of the colony (Gomon et al. 1994, McLeay et al. 2009a).

The amount of energy delivered to offspring has important consequences for their growth, survival and fitness, and is a product of the number, size and type of prey delivered. Because the size of prey delivered to young chicks is limited by what they can ingest, prey quality may be a factor that limits the total amount of energy delivered to chicks during early provisioning. Clupeiform fishes have higher amounts of lipid and protein than leatherjackets or southern-sea garfish, and may contain key nutritional elements required for the physiological processes that regulate chick growth and survival (Pichegru et al. 2007)(A. Wiebkin unpublished data). Crested terns that were provisioning chicks from areas where large clupeiform fishes are abundant may have better reproductive success than terns foraging in areas characterised by lower quality prey. These relationships were unclear in our study but are important in identifying the processes that underlie fitness variation and the growth of crested tern populations under different prey conditions.

**Foraging behaviour and habitat use**

Our results indicate that crested terns at Troubridge Island may use tail winds to return from their foraging grounds. This finding agrees with the hypothesis of Pennycuick (1989) that seabirds should forage upwind and return downwind to facilitate more efficient flight while carrying heavy prey loads. Habitat analyses indicated that adult crested terns typically foraged over warm (19–21°C), shallow (< 20 m), near-surface (< 2 m) waters that were high in Chl-a (> 0.5 mg.m⁻³). These biophysical characteristics are likely to reflect the distribution and
abundance of their prey. Crested terns foraging from Troubridge Island are generalist predators on small pelagic fishes such as Degens leatherjackets *Thamnaconus degeni*, and surface-s schooling clupeiform species such as sardine and Australian anchovy *Engraulis australis* (McLeay et al. 2009a). Crested tern chicks may be particularly dependent on small clupeiform fishes (McLeay et al. 2009a). These fish form a key link in pelagic marine food webs and their distribution and abundance has been correlated with sea surface temperature (SST) and enhanced levels of primary production (Chl-α) in ecosystems worldwide (Paloma et al. 2008, Tsagarakis et al. 2008). By accessing fish aggregations in shallow reliable habitats where production is enhanced, adult crested terns minimise foraging trip durations, and maximise foraging success and rates of provisioning while breeding (Page et al. 2006).

The results of our GLMM support our more general habitat analysis, and the hypothesis that the foraging behaviour of crested terns is more concentrated in areas of higher primary production. Of the habitat variables included in our candidate model set, Chl-α best explained the increases in time spent foraging within an area (TSA). Central place foragers commonly use areas where patches of prey are aggregated by physical factors (Guinet et al. 1997, Awkerman et al. 2005, Simmons et al. 2007) and/or elevated levels of primary productivity (e.g. Chl-α) (Hyrenbach et al. 2002, Weimerskirch et al. 2004, Page et al. 2006, Suryan et al. 2006). Previous analyses of chlorophyll data collected from SeaWifs sensors in southern Gulf St Vincent indicated that levels of primary production (Chl-α) increase twofold over the austral summer (October ~0.4 versus February ~0.8 mg.m⁻³) (Petrusevics 2008). The timing and location of breeding of crested terns may be strongly linked to the elevated levels of production in the region during this period.

There is a limited understanding of how physical and biotic processes influence the distribution and abundance of plankton in Gulf St Vincent. Our GLMM did not take into account the possible dilution (‘downstream’) effects of SST or Chl-α that affect secondary production and the subsequent distribution of prey (Guinet et al. 2001, Bradshaw et al. 2004). Also, we did not include the effects of tidal periodicity on foraging behaviour. Although other research has shown tidal cycles influence the foraging behaviour of terns in extremely shallow estuarine or inshore coastal habitats (Becker et al. 1993, Paiva et al. 2008), the influence of tide was not included in our model due to the low number of individuals tracked during each phase of tide. Tidal cycles may influence the distribution of prey in shallow habitats and future studies should attempt to explore the relationship between habitat use and tidal periodicity by
tracking more individuals. Also, the influences of site fidelity on foraging behaviour may dilute the fluid effects of physical or biotic processes that aggregate prey in regions near to foraging grounds. While our GLMM could not take these processes into account, predator foraging behaviour eventually depletes prey patches, and predators must relocate foraging effort to areas that are more energetically profitable (Bradshaw et al. 2004). Hence, the results of our GLMM captured this broad scale pattern of habitat use.

Management
Our study indicates that the foraging range of crested terns is constrained during breeding by the need to provision chicks from waters near to the colony. Consequently, crested tern populations may be vulnerable to changes in prey availability in near-colony waters while breeding. Southern Spencer Gulf lies to the west of Troubridge Island and is home to one of the largest aggregations of crested tern breeding colonies in the world (Figure 1)(McLeay unpublished data). This region is also targeted by the South Australian Sardine Fishery (SASF), which uses purse-seining methods to catch sardine *Sardinops sagax* for use as feed in the Southern bluefin tuna *Thunnus maccoyii* mariculture industry near Port Lincoln. In recent years the sardine fishery has expanded in terms of catch, effort and investment, but the trophic effects of fishing on sardine predators are unknown (McLeay et al. 2009b). The consequences of overfishing small pelagic fish, which are used by other predators such as seabirds, are well recognised. Commercial fisheries in southern Africa between 1956 and 1980 induced stock collapse of sardine and anchovy, causing populations of African penguin *Spheniscus demersus* and cape gannets *Sula capensis* to fall to almost one half (Burger and Cooper 1984, Crawford and Dyer 1995, Crawford 1998). Juvenile sardine comprise a major component of the diet of crested tern chicks near fishing operations (McLeay et al. 2009a). Although the SASF generally targets adult sardine, the effects of fishing on the recruitment of juvenile sardine near crested tern colonies in Spencer Gulf are poorly understood. The restricted foraging range exhibited by crested terns while breeding indicates that they may be sensitive to localised depletion of juvenile sardine near their colonies.

Future data relating to the foraging behaviour, diet, and breeding success at different colonies within this area should be collected concurrently from crested tern populations located inside and outside areas targeted by fishing operations. These data may provide information on the extent of foraging overlap between colonies and may resolve the relationships between foraging behaviour, habitat and density dependent factors that govern colony size. If this
information is combined with spatial analyses of sardine catches (fish size, effort) it may highlight whether fishing near breeding colonies is causing localised depletion of sardine and negatively affecting the breeding success and growth of crested tern populations.
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Chapter 6. General Discussion

Summary
This study examines functional relationships between the diet, foraging behaviour and life history traits of crested terns at three colonies in South Australia. Understanding these relationships requires knowledge of the underlying factors that influence the foraging behaviour of adult crested terns while breeding. While provisioning, parents must balance their own energetic requirements with those of their chick, and prey favoured for self-feeding may be available at distances and travel times that exceed their offspring's fasting abilities (Weimerskirch 1998, Barrett et al. 2007). The foraging behaviour of crested terns while breeding is also constrained by a single prey loading strategy. Models of central place foraging for single prey loaders predict that individuals should maximise their provisioning effort per unit time of foraging, by selecting and returning meals that are as large or energetically-rich as possible (Orians and Pearson 1979, Davoren and Burger 1999). This strategy requires that parents make decisions on whether to self-feed or deliver the prey to offspring based on their distance from the colony, and the size and type of prey available. How adult crested terns optimise their behaviour under these constraints determines how much energy they acquire for themselves and for their offspring, and has consequences for their reproductive performance and fitness.

These constraints provide a framework from which to discuss the key findings of this thesis. Specifically, I discuss how adults optimise their foraging effort in response to the changing dietary requirements of their chicks, and the relationship between crested terns, their prey and the habitats they use when foraging. The demographic responses of crested tern populations are discussed in terms of individual and age-specific contributions to reproduction, and in relation to the effects of large-scale declines in prey availability caused by two mass mortality events of sardine. Finally, I discuss how future research could augment the findings of this study, and consider how data collected from crested tern populations could be used to enhance management strategies for fisheries and conservation outcomes for crested tern populations.

Diet and foraging mode
Seabird dietary studies provide a profile of prey composition, size, mass, quality and availability, thereby highlighting the key trophic linkages within their foraging range (Cairns
1987, Montevecchi 1993, Barrett et al. 2007). Diet analyses also provide a way of linking seabird behavioural responses to changes in ecosystem conditions. The results presented in this study (Chapters 2 & 3) indicate that crested terns are generalist predators that typically target small-pelagic fish. Fish species from the Order Clupeiformes (Australian anchovy *Engraulis australis*, sardine *Sardinops sagax*) comprised a large component of the diet of crested terns. These species form a key link between apex predators and lower trophic levels in many marine ecosystems (Pauly and Tsukayama 1987). The different proportions of these prey found in the diet of crested terns at different colonies could reflect spatial variations in their abundance. For example, the relatively high proportion of sardine in diets sampled from crested tern colonies in southern Spencer Gulf may be indicative of the large biomass of sardine known to occur in this region (Ward et al. 2008). No information is available relating to how the foraging selectivity (‘electivity’) of crested terns varies according to their preference for particular prey species. Longer time series of diet data coupled with data from vessel-based assessments of prey biomass are required to relate prey abundance to crested tern diets.

Clupeiform fish species have a high calorific value and may contain key nutritional elements required for the physiological processes that regulate chick growth and survival (Pichegru et al. 2007). Chick and adult diets differed in prey composition. The higher proportion of clupeiform fishes in chick diets suggests that adults selected prey for their chicks that were of higher calorific value than the prey they consumed themselves. This seemingly altruistic strategy may increase breeding success by maximising the amount of energy delivered to chicks per trip. Furthermore, by enhancing foraging efficiency, adults may invest more time in other behaviours such as self-feeding or nest guarding. Changes in breeding success have been correlated with prey quality in other seabird populations. Breeding failure of common guillemots *Uria aalge* was linked to the provisioning of lower quality prey or ‘junk food’ in the North Sea (Wanless et al. 2005). Similarly, the breeding success of Arctic terns *Sterna paradisaea* and pigeon guillemots *Cepphus columba* was related to the energetic density of their major prey (Golet et al. 2000, Diamond and Devlin 2003). The provisioning of energetically-rich prey may also act to decrease chick fledging periods through its positive influence on chick growth. This strategy would allow fledglings and adults to move closer to areas where prey are aggregated more quickly, thereby releasing adults from the time and energetic costs of provisioning chicks at a central place.
The foraging decisions of adult crested terns are also constrained by the ingestion capabilities of their chick. Comparative analyses of the diets of chick and adult crested terns over the course of the breeding season indicated that prey size is an important factor mediating adult prey choice. During early provisioning adults are constrained by the need to locate prey small enough for their chicks to ingest. As chicks grow, this constraint is lifted but is replaced by the need to provide more energy to chicks. Adult crested terns responded to the increased energetic demand of their offspring over the course of the breeding season by increasing the rate of prey delivered and delivering larger prey. This result suggests that the energetic costs borne by adults while foraging are at a maximum when provisioning older chicks later in the breeding season. Older crested terns may have more experience in optimising the size and types of prey delivered to their chicks compared to younger adults. Age related increases in foraging proficiency have been positively correlated with breeding success in other seabird species (Greig et al. 1983, Wunderle 1991), and may explain the enhanced body condition of older individuals (≥7 years) that was associated with increased breeding performance (larger asymptotic mass ($\mathcal{A}$) of chicks and increased chick survival) reported in Chapter 4.

The fasting ability of offspring is a key factor limiting the foraging range of seabirds while provisioning. For tern species with a limited gut capacity a single prey loading strategy limits the distance that parents can travel from breeding sites because they must frequently deliver single prey to their offspring. Radio telemetry studies support the hypothesis that terns, as single prey loaders, should forage in near-colony waters while provisioning chicks (Becker et al. 1993, Rock et al. 2007). Information derived from the tracking data in Chapter 5 also indicated that the foraging range of crested terns was restricted to <40 km from the colony while rearing young chicks. It is possible there may be high levels of intra-specific competition among adult crested terns while provisioning chicks. Large numbers of seabirds breeding at a central place have the potential to deplete prey resources in waters near the colony (Ashmole 1963, Birt et al. 1987, Elliot et al. 2009). The accessibility of prey to crested terns is further restricted by their shallow diving ability. These factors may limit the availability of prey to crested terns and could have been important precursors to the evolution of a generalist predation strategy.

**Habitat use**

Variations in the size and composition of prey in chick and adult diets (Chapter 3) indicated that adults may use different habitats while alternating behaviour between provisioning and
The results of the tracking study (Chapter 5) also indicated that adults varied in their habitat use by undertaking short and long trips while provisioning young chicks. The variations in trip length recorded among and between individuals may reflect the distribution and abundance of different sized prey near the colony. Adults and chicks vary in their energetic needs, particularly when chicks are young. The density of small prey aggregations required by adults for self-feeding is likely to be higher than that needed for provisioning chicks. Although large numbers of colonial animals may deplete local prey resources, the density of small prey near the colony may be high enough to support chick provisioning, particularly when chicks are young and have lower energetic requirements. Therefore an adult encountering a prey item small enough for ingestion by its young chick may undertake a short trip to provision its chick rather than self-feed. I did not measure the size or abundance of prey aggregations near colonies, nor habitat use for adults provisioning chicks later in the brooding period. However, ontogenetic differences in prey composition and size were less apparent in late provisioning stages, indicating that adults may have used similar habitats for self-feeding and provisioning later in the breeding season when their chicks were more capable of ingesting larger prey.

How organisms distribute their foraging effort among different habitats while breeding is crucial to understanding the factors that determine individual fitness and constrain population growth. Individuals that choose less optimal habitats for foraging while breeding may be selected against (Krebs 1985). This thesis presents the first fine-scale tracking data for a seabird <400 g. GPS data are of high spatial resolution and enabled the different habitats used by crested terns to be discerned based on their depth, temperature, primary productivity and benthic characteristics. Although no benthic habitat associations were identified, adult foraging behaviour was typically associated with warm (19–21 °C), shallow (<20 m), neritic waters that were high in Chl-a (>0.5 mg m⁻³). These biophysical features are known to aggregate prey, such as clupeiform fishes, which formed a major component of crested tern diets. By accessing fish aggregations in shallow reliable habitats where production is enhanced, adult crested terns minimise foraging trip durations, and maximise foraging success and rates of provisioning while breeding.

The commuting style of foraging strategy employed by adult crested terns resembles that of many seabirds and may indicate that they have prior knowledge of where to locate prey (Weimerskirch 2007). The predictability of prey resources is a key factor influencing the
reproductive success of central place foragers as it enhances foraging efficiency and maximises the net rate of energy transfer between parents and offspring (Irons 1998, Bradshaw et al. 2004, Suryan et al. 2006). Mark-recapture records for crested terns at Troubridge Island indicate that they are highly philopatric at this site. Also, the timing of breeding at Troubridge Island is annual and synchronous, and breeding success, as indicated in Chapter 4 was high during the study period. Furthermore, adult foraging effort was closely associated with the relatively high levels of primary production that occur in this region during the austral summer (Petrusevics 2008). These factors indicate that the waters surrounding Troubridge Island provide suitable and reliable habitats for aggregating the large numbers of small pelagic prey required to support the successful breeding of one of the largest crested tern colonies in the southern hemisphere.

Population dynamics

Demographic data are essential for assessing how animal populations respond to variations in prey or ecosystem conditions. This study was fortuitous in being able to use demographic information from a long term banding program that was initiated in the 1960s (Waterman et al. 2003). It highlighted that crested terns are long-lived colonial animals that exhibit delayed maturity, stable rates of adult survival and variable rates of recruitment. These results provide insights into the processes that regulate crested tern populations. At Troubridge Island, crested terns recruited to breed at three years of age. This age resembled that recorded for crested terns in South Africa (Crawford et al. 2002). Unlike their study, which recorded a maximum age of breeding of 21 years, the maximum age of breeding recorded at Troubridge Island was 29 years. This finding suggests that crested terns are longer lived than previously inferred. The longevity of adults and their small clutch size indicate that crested tern populations may be sensitive to decreases in juvenile and adult survival (Saether and Bakke 2000).

Data relating to the survival of juveniles seabirds is notoriously difficult to obtain due to their dispersal away from the colony, and were not collected for crested terns in this study. Although, no empirical estimates of survival for adult crested terns were obtained, interannual trends in the age-structure of the colony at Troubridge Island were consistent during the study, indicating that adult survival rates were high and stable (Chapter 2). Breeding success was typically high at all sites, however the low recruitment rates of adults that were reared during sardine mass mortality events in 1995 indicate that the survival of early life history
stages may be variable. In accordance with life history predictions for long lived iteroparous
animals, adults should decrease their investment in reproduction during unfavourable
conditions (Monaghan et al. 1992). The low recruitment of the 1995 cohort at Troubridge
Island is most parsimoniously explained by the occurrence of reduced breeding success in
1995. It is likely that the reduced abundance of sardine near the colony in 1995 acted to
increase investment in adult survival at the expense of reproduction. Moreover, chick phases
are likely to be sensitive to decreases in prey abundance because, unlike juveniles, they cannot
move to where prey may be more abundant. These hypotheses are supported by the finding
that adults, which were reared under poor prey conditions in 1995 and 1999, had relatively
small morphology compared to other cohorts, indicating that they experienced nutritional
deficiencies as chicks when sardine abundance was low.

Animal populations may be most sensitive to the reproductive output of relatively few high
quality individuals in that they provide the next generation with the majority of recruits (Lewis
et al. 2006). Individuals within a population vary in reproductive performance due to age-
specific differences in foraging and reproductive experience (Sydeman et al. 1991,
Weimerskirch 1992, Pyle et al. 2001) and/or phenotypic differences (Wendeln and Becker
1999). Reproductive performance may also correlate with indirect measures of parental quality
such as timing of breeding, body size, body condition or foraging behaviour (Lewis et al.
2006). The results presented in Chapter 4 indicate that the reproductive performance of
crested terns varies in response to age-specific and phenotypic differences in parental quality.
Adults with good body condition hatched chicks earlier, and early breeding was positively
related to hatchling mass, fledgling condition and chick survival. Furthermore, crested tern
chicks reared in 1995 and 1999 during periods of low sardine abundance had relatively poor
body condition compared to other cohorts. Several studies have linked conditions experienced
during early life history to measures of animal fitness (Richner 1989, Gaillard et al. 1998,
Cooch 2002, Cam et al. 2003). For instance, the condition of chicks upon fledging has been
related to recruitment probability and measures of reproductive performance for several
species (Coulson and Porter 1985, Richner et al. 1989, Gebhardt-Henrich and Richner 1998,
Cam et al. 2003). Results presented in Chapter 4 support these studies and highlight how the
interaction between parental quality and ecosystem conditions can have long-term fitness
consequences for offspring. Such interactions have been described as being at the heart of the
relationship between evolutionary and ecological processes (Cam et al. 2003). For the
Troubridge Island population, measures of body condition indicated that age-related
reductions in reproductive performance were greatest for adults aged <7 years. For adults ≥7 years, phenotypic variations in body condition may be a greater determinant of reproductive performance. Consequently, the growth of crested tern populations at Troubridge Island may be most sensitive to the reproduction of high quality individuals ≥7 years old. Future studies conducted at Troubridge Island could obtain empirical measurements of breeding performance relating to the age-specific and phenotypic qualities of individuals. This type of research may facilitate a better understanding of how the early conditions experienced by chicks (e.g. sardine mass mortality events in 1995 and 1999) shape individual fitness and impact on the growth of crested tern populations.

Additional research
Recent studies have indicated that prey quality is an important factor influencing reproductive success. Future diet studies for crested terns should attempt to quantify the calorific value of their major prey so that chick growth and survival patterns can be related to the types of prey consumed. These data may highlight how changes in the relative abundance of different prey species would affect crested tern populations. Knowledge of the quantities, types and calorific value of the prey consumed by apex marine predators is also useful for developing bioenergetics models and models of ecosystem structure and function. Models such as Ecopath© allow the relative changes in biomass of key functional groups within ecosystems to be investigated under different scenarios of resource use (Goldsworthy et al. 2003, Scandol et al. 2005). The diet data presented in this thesis will be analysed further to estimate the annual consumption rates of crested terns in South Australia and used to develop ecotrophic models so that the trophic linkages in the South Australian pelagic ecosystem can be investigated (as part of FRDC PN 2005/031).

I was not able to determine whether individuals specialised in the types of prey they consumed. In addition, I could not discern if habitat use varied among or between individuals. Consecutive GPS tracks collected from the same individuals would have enabled me to resolve the level of variation within individual foraging behaviour and highlighted whether individuals specialised in their habitat use. Future studies could also deploy GPS units with foraging activity sensors to record when and where prey were being consumed along a foraging path. Studies should attempt to deploy loggers on adults throughout the breeding season to assess whether temporal changes in foraging behaviour occur due to the increased energetic requirements of offspring. Diet information (regurgitate analyses or remote
observations) could be collected from adults returning from foraging trips so that the size and type of prey consumed on a foraging trip can be related to habitat use.

An understanding of how foraging proficiency relates to age or body condition may also be gained by deploying GPS units and activity sensors on adults of known age and body condition. Inter-colony differences in foraging behaviour were not measured in this study. The large number of crested tern colonies in southern Spencer Gulf suggests that there may be high levels of intra-specific competition between colonies. Future tracking studies conducted concurrently on individuals at different colonies within this area may provide information on the extent of overlap between foraging zones, highlight any ‘cultural’ differences in foraging behaviour between colonies and whether foraging behaviour is related to colony size. Southern Spencer Gulf is characterised by the development of a frontal zone with high levels of secondary and tertiary production during summer and autumn (Bruce and Short 1993). It is also where a large proportion of the sardine catch is taken by the SASF. Tracking studies in this region may facilitate a better understanding of the degree of overlap with areas used by the SASF, and the connectivity between crested tern foraging behaviour and biophysical processes that enhance production.

Demographic data are crucial from a conservation perspective to identify the individuals, cohorts or life history stages that contribute most to population growth. Age specific information is rare for long-lived vertebrate populations due to the need to mark and recapture many individuals over long periods of time. However, it provides a vital tool to assess the factors that contribute to life history variation and regulate population size, thereby enabling conservation strategies to be better directed. The crested tern colony at Troubridge Island is unique in an international context in that over a quarter of the ~7000 adults are known age banded birds. This study did not quantify rates of adult survival via mark recapture analysis due to the low number of individuals recaptured. Long lived animals with low reproductive rates such as crested terns are highly sensitive to changes in adult survival (Musick 1999, Saether and Bakke 2000) and derivation of adult survival rates is a priority for future research. Future work recapturing banded adults at Troubridge Island will increase the number of recapture occasions of marked individuals and enable estimates of adult survival to be calculated using advanced statistical mark-recapture software such as Program MARK©. Similarly, data collected relating to chick and adult condition (e.g. chick growth parameters: asymptotic mass, growth rates, body condition), and ecosystem conditions (e.g. disease...
events), may be incorporated as covariates into multi-state mark-recapture models to
investigate the processes that influence adult survival. If coupled with estimates of age- or
state-based reproductive performance, the level of co-variation between demographic
parameters could be evaluated. These types of data would enable state or age based matrix
projection models for crested tern populations to be developed, and provide valuable insight
into the temporal processes regulating population growth. Such approaches may highlight the
key abiotic and biotic factors that are important in shaping individual fitness and help to
evaluate the long-term viability of crested tern populations.

**Conservation and management**

It has been proposed that seabird species that are restricted to foraging from surface waters
near their colony may be more sensitive to changes in prey abundance than species that access
prey below the surface layer and forage over large distances (Furness and Tasker 2000, Stienen
et al. 2000). Studies of the foraging behaviour and reproduction of surface-feeding seabirds in
northern hemisphere ecosystems support this notion (Monaghan et al. 1996, Suryan et al.
2000, Scott et al. 2006). However, unlike crested terns, which consume a wide variety of prey,
these species (arctic terns and black-legged kittiwakes) are more limited in their dietary width.
It is widely accepted that monophagous (specialist) seabirds are more sensitive to changes in
prey abundance because measures of their behaviour, physiology or demography reflect the
availability of the prey on which they specialise (Cairns 1992). Conversely, it is more difficult
to determine the prey conditions under which polyphagous (generalist) seabirds select
alternate prey (Cairns 1992, Montevecchi 1993).

The sensitivity of crested tern populations to decreases in sardine abundance from fishing
remains unquantified. Although crested terns may switch to alternate prey if fishing decreases
sardine abundance within their foraging range while breeding, the level of sardine biomass that
triggers such a response and the effects of prey switching are unknown. The information
presented in Chapter 2 indicates that recruitment rates and chick growth were reduced in
response to large-scale decreases in sardine biomass (~70 %) caused by an exotic herpesvirus
(Gaughan et al. 2000, Ward et al. 2001). The South Australian Sardine Fishery (SASF)
currently operates at exploitation rates of between 10 and 20 % of the adult sardine spawning
biomass (Ward et al. 2008). This harvest strategy equates to a biomass reduction that is at least
three times less than the biomass of sardine that was depleted by the disease events.
 Nonetheless, the majority of the sardine catch is taken from a relatively small area in southern
Spencer Gulf where there are at least ten colonies of crested terns, and the exploitation rate of sardine near crested tern colonies may far exceed 20%. Direct competition between the fishery and crested terns for sardine of the same size or year class is minimal. Fishing mainly targets adult sardine (>150 mm) and at least 90% of sardine consumed by crested terns in this study were juvenile. However, little is known about how concentrated fishing effort affects local-scale processes of sardine recruitment in areas used by crested terns while breeding. Large catches of adult sardine near crested tern colonies have the potential to cause localised depletion of sardine, and to reduce levels of sardine egg production and juvenile sardine recruitment.

Declines in prey populations are often associated with seabird breeding failures (Monaghan et al. 1989, Hamer et al. 2002, Crawford et al. 2006). Estimates of reproductive success from crested tern colonies near fishing operations in southern Spencer Gulf may be useful from a conservation perspective in providing ecological performance measures for assessing whether fishing operations are negatively impacting crested tern populations. Measures of reproductive success are straightforward and cost effective to obtain. Studies could be conducted at colonies located inside and outside areas targeted by the fishery, and coupled with research on diet, foraging behaviour and chick growth to highlight whether changes in reproductive success are related to prey conditions or other factors. Furthermore, fisheries managers should ensure that commercial fishing operations do not target juvenile sardine or other small pelagic fishes such as anchovy in areas near crested tern colonies in the future, because such operations would be in direct competition with crested tern populations.

The large proportion of juvenile sardine in the diets of crested terns may provide information about juvenile sardine abundance that could be used to augment current stock assessments of sardine. Traditionally, fisheries stock assessments have predicted stock size using the age or length of fish sampled from commercial landings as inputs in stage-based models or population viability analyses. However, fisheries often only target older fish and uncertainty in age or stage based population models is caused by a lack of information relating to the abundance of juvenile stages. Currently, management of the SASF is underpinned by biennial estimates of sardine biomass provided via a fishery-independent technique, the Daily Egg Production Method (DEPM). The DEPM provides estimates of sardine spawning biomass that are used to set quotas for the SASF in the following calendar year. Because stock assessments are biennial there is a two-year time lag between fishing activities and the next
estimate of stock abundance. Sardine recruit to the fishery aged 2-3 years (Ward et al. 2008).
Consequently, there may be considerable delay using biennial assessments in detecting years of poor sardine recruitment caused by overfishing or environmental perturbations. Moreover, the DEPM is considered imprecise (Cochrane et al. 1998). The establishment of sardine stock recruitment relationships using diet data collected from crested terns, coupled with age or length information collected from SASF landings could augment information provided via the DEPM, by providing a cost effective method of developing reliable population models for sardine. This approach could assist in the prediction of future sardine abundance and augment current biological information used to manage the fishery.
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FRDC PN 2005/031. (in production) Trophodynamics of the Great Australian Bight: assessing the need for an ecological allocation in the South Australian pilchard fishery,


Wanless S, Harris MP, Redman P and Speakman JR (2005) Low energy values of fish as a probable cause of breeding failure in the North Sea. Marine Ecology Progress Series 294:1-8


Appendices

Appendix A. Statement of authorship (Chapter 2)

Title: Demographic and morphological responses to prey depletion in a crested tern *Sterna bergii* population: Can fish mortality events highlight performance indicators for fisheries management?


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Appendix B. Statement of authorship (Chapter 3)

Title: Size matters: variation in the diet of chick and adult crested terns.


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Appendix C. Statement of authorship (Chapter 4)

Title: Keeping it in the family: provisioning strategies and the consequences of adult condition on reproductive timing and fitness in crested terns


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Appendix D. Statement of authorship (Chapter 5)

Title: Fine-scale foraging behaviour and habitat use of a short-ranging seabird, the crested tern

Marine Ecology Progress Series 2009, submitted.

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