

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

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Received: 21 December 2008 / Accepted: 28 April 2009 / Published online: 18 May 2009
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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 clupeids (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 clupeids 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 (Nettle-ship 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 Piatt 1990; Montevecchi 1993). For instance, adults that are provisioning chicks face different energetic constraints to adults that are only

Communicated by S. Garthe.

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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 effort provisioning 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; Vermeer et al. 1987; Mahon et al. 1992; Leopold et al. 1996; Davoren and Burger 1999; Barrett et al. 2007).

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, 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; 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 sand eel 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 (Fig. 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.

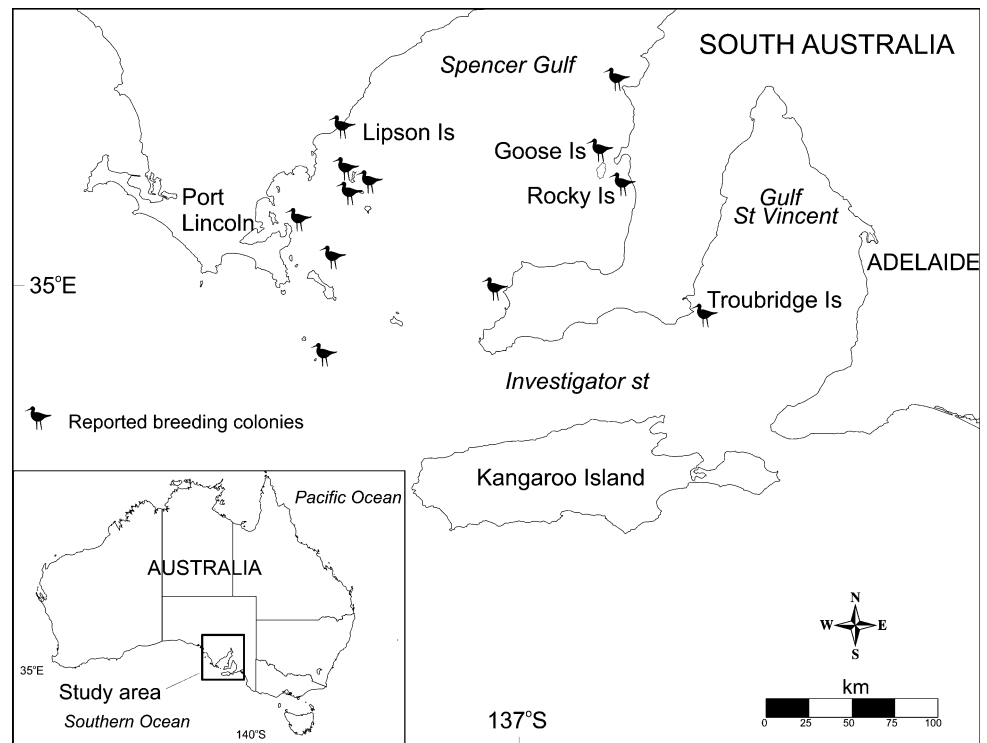
We investigated the diet of crested terns at four colonies in gulf waters of South Australia during their breeding seasons between 2003 and 2008. We hypothesise that the diet of crested terns will exhibit ontogenetic differences as a function of a trade-off between the physical ingestion capabilities 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 2003/2004 to 2007/2008. We refer to seasons as belonging to the year that sampling or breeding began, respectively (e.g. 2005/2006 = 2005) (Fig. 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 3,000 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 (3–35 ha) in southern Spencer Gulf (Fig. 1). The colonies at these islands are generally smaller, numbering approximately 900 breeding pairs at Goose Island, 2,000 at Lipson Island and 1,300 at Rocky Island, respectively (McLeay, unpublished data).

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



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.

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.

Table 1 Regression formulae used to estimate prey biomass contribution of major prey taxa found in crested tern diets

Prey type	Mass/length	Source	Mass/CFR	Source	OL v Length	Source	Other equations used	Source
Family Engraulidae <i>Engraulis australis</i>	$M = 6E-05 \times FL^{2.56}$	1	$M = 1E-04 \times CFR^{2.75}$	1	$SL = 45.64 \times OL^{0.74}$	2	$M = 1.71 \times 10^{-6} SL^{3.38}$	2
Class Cephalopoda <i>Nototodarus gouldi</i>	$M = 2.2E-03 \times ML^{2.00}$	1						
Family Gempylidae <i>Thyrsites atun</i>	$M = 2E-06 \times FL^{3.13}$	1	$M = 1.9E-03 \times CFR^{2.58}$	1	$FL = 22.6 \times OL^{1.42}$	5		
Family Clupeidae <i>Spratelloides robustus</i>	$M = 2E-05 \times FL^{2.79}$	1	$M = 5E-04 \times CFR^{2.26}$	1	$TL = 54.33 \times OL^{1.02}$	2	$M = 3.54 \times 10^{-7} TL^{3.67}$	2
Family Monacanthidae <i>Acanthaluteres</i> sp.	$M = 1E-05 \times TL^{2.97}$	1	$M = 3E-07 \times CFR^{3.36}$	1				
Class Cephalopoda <i>Sepioteuthis australis</i>	$M = 6E-04 \times ML^{2.5}$	4						
Family Monacanthidae <i>Thamnaconus degeni</i>	$M = 5E-05 \times TL^{2.69}$	1	$M = 6E-07 \times CFR^{3.30}$	1				
Family Hemiramphidae <i>Hyporhamphus melanochir</i>	$M = 2E-07 \times TL^{3.56}$	1	$M = 1E-06 \times CFR^{3.73}$	1	$SL = 68.7 \times OL^{0.82}$	2	$M = 3.27E-08 \times SL^{3.79}$	2
Family Atherinidae- unidentified	$M = 4.45 \times 10^{-6} SL^{3.14}$	2 # <i>A. hepsetoides</i>	$M = 3E-04 \times CFR^{2.25}$	1	$SL = 21.12 \times OL^{1.21}$	2	$M = 4.45E-06 \times SL^{3.14}$	2
Family Odacidae- unidentified	$M = 5E-07 \times TL^{3.55}$	1	$M = 7E-11 \times CFR^{5.11}$	1				
Family Carangidae <i>Pseudocaranx</i> sp.	$M = 3E-05 \times FL^{2.85}$	1	$M = 4.33E-02 \times CFR^{1.58}$	1				
Family Mullidae <i>Upeneichthys vlamingii</i>	$M = 9.7E-03 \times FL^{3.14}$	cm						
Family Sillaginidae <i>Sillago bassensis</i>	$M = 6E-03 \times FL^{3.12}$	3 # <i>Upeneichthys</i> sp.						
Family Sphyraenidae <i>Sphyraena novaehollandiae</i>	$M = 2.4E-02 \times FL^{2.53}$	3.						
Family Clupeidae <i>Sardinops sagax</i>	$M = 5E-06 \times FL^{3.16}$	1	$M = 8E-07 \times CFR^{4.09}$	1	$SL = 32.07 \times OL^{1.35}$	2	$M = 6.43E-06 \times SL^{3.11}$	2
Family Pempheridae <i>Parapriacanthus elongatus</i>	$M = 3E-05 \times FL^{2.81}$	1	$M = 2E-04 \times CFR^{2.39}$	1	$FL = 27.3 \times OL^{0.95}$	6		
Family Aripididae <i>Arripis georgianus</i>	$M = 5E-06 \times FL^{3.25}$	1	$M = 4E-06 \times CFR^{3.65}$	1	$FL = 25.606 \times OL^{0.98}$	7		
Family Carangidae <i>Trachurus</i> sp.	$M = 2E-06 \times FL^{3.43}$	1	$M = 6.3E-03 \times CFR^{1.84}$	1	$FL = 16.796 \times OL^{1.33}$	8		
Family Clupeidae <i>S. sagax</i> and <i>E. australis</i> pooled	$M = 7E-06 \times FL^{3.06}$	1	$M = 2E-06 \times CFR^{3.78}$	1				
Family Monacanthidae- unidentified and <i>Acanthaluteres</i> sp. pooled	$M = 3E-05 \times TL^{2.75}$	1	$M = 2E-05 \times CFR^{2.55}$	1				
Family Apogonidae <i>Vincentia</i> sp.	$M = 1E-04 \times TL^{2.57}$	1						

Mass measured in g. Length measurements in mm except where listed

Sources for data referenced are: 1 L. J. McLeay, unpublished data; 2 TMAG in Furlani et al. 2007; 3 <http://www.fishbase.org/>; 4 M. Steer (SARDI Aquatic Sciences), unpublished data; 5 CMAR in Furlani et al. 2007; 6 A. Weibkin (SARDI Aquatic Sciences), unpublished data; 7 W. Dimmlich (Falkland Island Government Fisheries Dept.), unpublished data; 8 R. Kirkwood in Furlani et al. 2007; *M* mass, *FL* length to caudal fork, *ML* mantle length, *CFR* caudal fin-ray length, *SL* standard length, *OL* otolith length

Regressions based on different species to those found in this study

The relative importance of the prey composition of chick and adult diets was assessed by estimating the percentage biomass contribution of each prey taxon. 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:

$$\text{ACPMR} = \frac{\text{Mean mass of individual prey taxa in adult diets}}{\text{Mean mass of individual prey taxa in chick diets}}$$

For ACPMR = 1, the mean mass of individual prey taxa in chick and adult diets are the same. If ACPMR >1, the mass of individual prey consumed by adults was larger than consumed by chicks. For ACPMR <1, the mass of individual prey in chick diets is smaller than in adult diets. To assess differences between the early, middle and late stages of the chick-provisioning period, we used the ACPMR 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 ($1,000 \text{ g} \pm 5 \text{ g}$) 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 \pm SD.

Results

Prey composition

Between 2003 and 2007, a total of 2,146 and 3,921 prey were identified from 1,400 and 1,561 regurgitates collected from chicks and adults, respectively. Samples represented a reconstructed biomass of 67.3 kg. In total, 47 fish, 5 cephalopod and three crustacean taxa were identified (Tables 2, 3, 4, 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, 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 *Parapriscanthus elongatus* comprised >66% of the total prey biomass consumed by chicks or adults at all locations (Tables 2, 3, 4, 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, 3, 4, 5, 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 clupeids (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

Prey type	2003			2004			2005			2006			2007			(2064) Total												
	(101) Chick	(30) Inc	(76) E Adult	(136) E Adult	(139) Inc Adult	(109) E Adult	(71) E Adult	(41) M Chick	(16) M Adult	(136) L Chick	(4) L Adult	(27) Inc Adult	(75) E Adult	(134) E Adult	(39) M Chick		(22) M Adult	(67) L Chick	(13) L Adult	(235) Inc Adult	(81) E Chick	(99) E Adult	(105) M Chick	(95) M Adult	(44) L Chick	(169) L Adult		
<i>Fish</i>																												
Family Monacanthidae	0.5	7.9	5.6	5.6	60.4	0.8	38.5	12.4	5.6	9.0	2.3	16.0	4.7	20.2	11.0	18.4	59.3	1.2	46.4	21.6	43.5	16.4	12.0	28.0				
<i>T. degeni</i>																												
Family Clupeidae <i>S. sagax</i>	4.5	42.5	6.9	47.2	15.5	16.2	13.2	5.8	9.8	21.2	27.6	17.8	1.3	38.6	6.0	9.6	23.8	18.3	26.0	15.4	13.7	27.4	31.5	21.2				
Family Gempylidae <i>T. atun</i>	31.9	22.8	27.9	24.1	0.5	3.7	63.5	42.1	19.4	7.0	50.3	27.2	48.8	24.9	25.3	27.3	0.4	7.8	2.7	4.2	0.7	1.6	5.2	16.0				
Family Engraulidae <i>E. australis</i>	42.2	11.6	18.7	6.6	3.7	30.0	11.3	21.3	20.3	27.5	13.1	16.1	6.7	28.0	2.3	20.5	33.3	3.1	21.9	4.5	24.4	8.5	35.1	23.4	12.9			
Family Hemiramphidae <i>H. melanochir</i>	6.2	9.2	3.7	7.0	6.8	28.5	2.9	10.0	59.1	11.8	11.8	1.3	1.8	12.3	7.9	3.8	1.1	6.1	2.7	3.8	5.3	3.3	6.1					
Family Clupeidae <i>S. robustus</i>	4.5	0.6	33.6	4.9	7.2	1.0	0.4	0.4	0.4	0.4	8.1	0.4	1.0	0.7	0.7	1.1	35.3	1.3	16.2	0.4	6.3	0.5	3.5					
Family Penphoridae <i>P. elongatus</i>	0.7		0.5		0.4	4.9	0.4	0.6	0.6	0.6	1.9	4.1	2.3	0.4	0.4	3.4	4.2	3.5	7.0	17.1	1.9	8.2	2.8					
Class Actinopterygii- unidentified	1.5	2.3			4.0	16.3	1.8	5.1	1.5	1.5	4.2	3.6		1.7	2.7	0.8	3.5	0.9	0.6	0.5	1.0	2.1						
Family Arripidae <i>A. georgianus</i>	1.1		0.9		2.8	15.6	1.2	1.7	1.7	1.7	4.8	0.5	1.7	0.9	0.9	0.2	4.7	0.3	1.9	0.8	1.7	1.4						
Family Monacanthidae- unidentified	2.6		0.6		1.5	0.1	1.9	0.1	1.4	13.1	1.3	0.4		0.7	11.4	0.6	0.3	1.3	0.2	1.7	0.1	2.4	1.0					
Family Odacidae- unidentified	1.6		3.0		0.2	1.4	0.2	4.6	4.6	4.6	0.9	0.1		2.5	2.5	0.3	0.4	2.0	3.2	0.4	1.3	8.1	1.0					
Family Gonorynchidae <i>G. greyi</i>			0.2		0.2	0.1	0.2	0.1	0.1	0.1	0.4	0.1		0.2	0.2	0.3	0.4	2.0	0.4	0.4	0.4	0.9	0.3					
Family Emmelichthyidae <i>E. nitidus nitidus</i>			1.3		1.3	1.3	4.6	2.4	2.4	2.4													0.3					
Family Scorpaenidae- unidentified	0.9		0.9				0.4	0.4	0.4	0.4				0.9	0.9	0.3	0.3	0.4	0.8	0.8	0.2	2.3	0.2					
Family Scombridae <i>S. australasicus</i>																1.3	0.3	0.6	0.2	0.2	2.3	0.2						
Family Monacanthidae <i>Acanthaluteres</i> sp.			0.2		0.4	0.3	0.6	0.4	0.4	0.4													0.2					
Family Clupeidae <i>E. teres</i>	0.3															1.2							0.2					
Family Sillaginidae <i>S. bassensis</i>					0.8														2.6				0.2					
Family Callorhynchidae <i>C. milii</i>													0.4						0.5	1.3	0.1							
Family Atherinidae-unidentified																			1.5	0.1	0.1							
Family Diodontidae <i>D. nichthemeris</i>			2.4		0.3	0.5	20.8	20.8	20.8	20.8														0.1				
Family Carangidae- <i>Pseudocaranx</i> sp			2.0				2.7	2.7	2.7	2.7														0.1				
Family Carangidae- <i>P. wrighti</i>	1.4				0.4	1.1	1.9	1.9	1.9	1.9									0.6					0.1				
Family Monacanthidae <i>S. granulatus</i>							0.4	0.4	0.4	0.4														0.1				
Family Gerreidae <i>P. melbournensis</i>			0.8				0.2	0.2	0.2	0.2				0.7	0.7	0.1			1.2					0.1				
Family Carangidae <i>Trachurus</i> sp.							0.4	0.4	0.4	0.4														0.1				
Family Terapontidae <i>P. octolineatus</i>							0.6	0.6	0.6	0.6				1.1	1.1				0.9					0.1				

Table 2 continued

Prey type	2003			2004			2005			2006			2007			(2064) Total														
	Chick	Inc	Adult	(30) Chick	(76) E Adult	(136) E Adult	(139) Inc Adult	(109) E Chick	(71) E Adult	(41) M Chick	(16) M Adult	(136) L Chick	(4) L Adult	(27) Inc Adult	(75) E Chick		(134) E Adult	(39) M Chick	(22) M Adult	(67) L Chick	(13) L Adult	(235) Inc Adult	(81) E Chick	(99) E Adult	(105) M Chick	(95) M Adult	(169) L Chick	(44) L Adult		
Family Apogonidae <i>Vincentia</i> sp.			0.6			0.1																								0.1
Family Odacidae- <i>H. semifasciata</i>																														<0.1
Family Gobiessocidae <i>Alabes</i> sp.																														<0.1
Family Apogonidae- unidentified																														<0.1
Family Syngnathidae <i>H. rostratus</i>										0.2																				<0.1
Family Mugilidae <i>A. forsteri</i>																														<0.1
Family Labridae <i>N. balteatus</i>																														<0.1
Family Odacidae- unidentified																														<0.1
Family Clinidae- <i>Ophichinus</i> sp.																														<0.1
Family Mullidae <i>U. vlamingii</i>																														<0.1
Family Syngnathidae <i>Hippocampus</i> sp.																														<0.1
Family Apogonidae <i>S. cephalotes</i>																														<0.1
Family Notocheiridae <i>I. rhothophilus</i>																														<0.1
Family Monacanthidae <i>B. jacksonianus</i>																														<0.1
Family Syngnathidae- unidentified																														<0.1
Family Tetraodontidae- unidentified																														<0.1
Family Tetraodontidae <i>C. richiei</i>																														<0.1
<i>Cephalopods</i>																														<0.1
Class Cephalopoda <i>N. gouldi</i>																														0.5
Class Cephalopoda <i>S. australis</i>																														0.3
Class Cephalopoda- unidentified																														0.2
Family Sepiidae <i>E. tasmanica</i>																														<0.1
Family Sepiidae <i>S. apama</i>																														<0.1
<i>Crustaceans</i>																														<0.1
Order Decapoda <i>M. latissulcatus</i>																														0.1
Order Isopoda- unidentified																														<0.1
Family Decapoda- unidentified																														<0.1
<i>Insects</i>																														<0.1
Class Insecta- unidentified																														0.2
Total	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	

Taxa with biomass totals over 15% are in bold. The number of regurgitates examined is in brackets
Inc: incubation period, *E*: early provisioning period, *M*: mid provisioning period, *L*: late provisioning period

Table 3 Percent biomass contribution found in regurgitates from crested tern chicks and adults at Goose Island in 2005

Prey type	2005				
	(22) Inc Adult	(4) E Chick	(32) M Chick	(13) M Adult	(71) Total
<i>Fish</i>					
Family Clupeidae <i>S. sagax</i>	42.3	76.5	33.9	54.6	40.7
Family Engraulidae <i>E. australis</i>	14.9	23.5	33.9	18.2	24.6
Family Hemiramphidae <i>H. melanochir</i>	31.2				14.1
Family Gempylidae <i>T. atun</i>			15.2	24.5	10.0
Family Odacidae- unidentified			15.2		4.2
Family Pempheridae <i>P. elongatus</i>	5.0			1.5	2.6
Family Sphyracidae <i>S. novaehollandiae</i>	4.5				2.1
Class Actinopterygii- unidentified	2.0				0.9
Family Clupeidae <i>S. robustus</i>			1.3		0.4
Family Monacanthidae- unidentified			0.5		0.1
Family Syngnathidae- unidentified	0.1				<0.1
<i>Cephalopods</i>					
Class Cephalopoda <i>S. australis</i>				1.2	0.3
Total	100	100	100	100	100

Taxa with biomass totals over 15% are in bold. The number of regurgitates examined is in brackets

Inc incubation period, *E* early provisioning period, *M* mid provisioning period, *L* late provisioning period

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 $P \leq 0.05$). 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, 3, 4, 5). High proportions of Degens leatherjacket in adult diets at Troubridge Island also contributed to spatial differences (Tables 2, 3, 4, 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, 3, 4, 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, $P \leq 0.05$). In adults the main prey contributing to interannual differences were sardine, Degens leatherjacket and barracouta (ANOSIM, $P \leq 0.05$) (Tables 2, 3, 4, 5).

Intra-annual variation in prey composition

The prey composition of chick diets varied significantly within the breeding season (ANOSIM, $P \leq 0.05$) typically

due to the large variation in the consumption of clupeids (sardine, Australian anchovy and blue sprat) between early and subsequent provisioning stages (mid/late) (Tables 2, 3, 4, 5). There were no clear intra-annual trends in prey composition at any location (Tables 2, 3, 4, 5), but the abundance of blue sprat and Australian herring in chick diets typically decreased as the breeding season progressed (Tables 2, 4, 5). In contrast, there was typically little intra-annual variation in the prey composition of adult diets (ANOSIM $P \geq 0.05$) (Tables 2, 3, 4, 5).

Prey size

The average mass of all prey taxa consumed by chicks ranged between 7.4 ± 4.5 g in early provisioning to 10.7 ± 9.3 g in late provisioning. Prey consumed by adults averaged between 10.4 ± 8.1 g in late provisioning to 11.6 ± 10.4 g 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 $P \leq 0.05$) (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 4 Percent biomass contribution found in regurgitates from crested tern chicks and adults at Lipson Island in 2005 and 2006

Prey type	2005		2006							(413) Total
	(30) M Chick	(9) M Adult	(97) Inc Adult	(10) E Chick	(19) E Adult	(47) M Chick	(23) M Adult	(129) L Chick	(51) L Adult	
<i>Fish</i>										
Family Monacanthidae <i>T. degeni</i>	15.5	23.6	48.0		24.7	22.8	67.3	24.1	41.0	35.3
Family Clupeidae <i>S. sagax</i>	7.5		13.4	28.6	16.5	28.9	9.2	24.6	11.1	17.0
Family Hemiramphidae <i>H. melanochir</i>	34.2		11.1		20.2	1.6	12.9	3.9	3.9	9.2
Family Gempylidae <i>T. atun</i>	0.0		2.0		2.7	5.0		20.9	11.2	8.5
Family Engraulidae <i>E. australis</i>	25.9	69.0	1.8	11.2	10.6	9.3	8.8	7.2	2.8	7.3
Family Arripidae <i>A. georgianus</i>	6.8		4.9	25.6	15.8	12.1		5.2	5.2	6.2
Class Actinopterygii- unidentified	4.5		4.7	11.9	2.3	8.3		2.7	14.0	5.3
Family Clupeidae <i>E. teres</i>			4.8	0.0	2.6			3.6	2.9	3.0
Family Clupeidae <i>S. robustus</i>			4.7	22.6		3.1		0.2		2.0
Family Pempheridae <i>P. elongatus</i>			0.2			1.8		3.0	0.5	1.1
Family Odacidae- unidentified			1.2					0.6	3.3	1.0
Family Monacanthidae- unidentified	1.3	7.4	0.7	0.1	1.8	0.2	1.8	0.3	1.4	0.9
Family Carangidae <i>Trachurus sp.</i>			1.2					0.7		0.6
Family Callorhynchidae <i>C. milii</i>						4.7				0.4
Family Mullidae <i>U. vlamingii</i>	4.3					0.0				0.3
Family Atherinidae- unidentified			0.2							0.1
Family Apogonidae <i>Vincentia sp.</i>						1.0				0.1
Family Odacidae- <i>H. semifasciata</i>						1.2				0.1
Family Monacanthidae <i>B. jacksonianus</i>								0.1		<0.1
<i>Cephalopods</i>										
Class Cephalopoda- unidentified								1.0	2.1	0.5
Class Cephalopoda <i>N. gouldi</i>								0.9		0.2
Class Cephalopoda <i>S. australis</i>					0.7			0.2	0.6	0.2
<i>Crustaceans</i>										
Order Decapoda <i>M. latisulcatus</i>			1.1		2.1			0.8		0.7
Total	100	100	100	100	100	100	100	100	100	100

Taxa with biomass totals over 15% are in bold. The number of regurgitates examined is in brackets

Inc incubation period, *E* early provisioning period, *M* mid provisioning period, *L* late provisioning period

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; Fig. 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 (Fig. 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 (Fig. 2). Sardine in the diet of chicks (8.4 g ± 0.9) were significantly smaller than sardine found in the diets of adults on the same day (28.7 g ± 3.6) (ACPMR = 2.21 – 4.89; $Z = 3.68$, $P \leq 0.05$; Fig. 2). High ACPMR values (>1) for barracouta, Degens leather-jacket 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

Table 5 Percent biomass contribution found in regurgitates from crested tern chicks and adults at Rocky Island in 2007

Prey type	2007							(413) Total
	(164) Inc Adult	(15) E Chick	(30) E Adult	(53) M Chick	(53) M Adult	(79) L Chick	(19) L Adult	
<i>Fish</i>								
Family Clupeidae <i>S. sagax</i>	45.6	16.4	50.5	50.4	53.7	45.6	36.4	46.1
Family Engraulidae <i>E. australis</i>	5.2	5.8	12.9	17.5	6.7	37.8	38.9	13.1
Family Hemiramphidae <i>H. melanochir</i>	10.6		14.9	1.6	10.1	4.2	7.8	9.1
Family Odacidae- unidentified	9.9	25.4	1.5		1.4	7.4		7.0
Family Pempheridae <i>P. elongatus</i>	8.5	2.5	4.9	1.4	3.1	1.3	9.4	6.0
Class Actinopterygii- unidentified	5.6	3.9	3.9	1.2	2.6	0.6	2.1	3.9
Family Clupeidae <i>E. teres</i>	4.0		1.9		6.1			3.0
Family Clupeidae <i>S. robustus</i>	2.3	9.6	1.4	4.9	1.0	1.1	5.1	2.4
Family Gempylidae <i>T. atun</i>	3.2	10.3	0.7	1.2	0.9			2.2
Family Arripidae <i>A. georgianus</i>	0.5	22.7	3.5	2.2	0.7	0.8		1.3
Family Monocanthidae <i>T. degeni</i>	1.7	2.2			1.6			1.2
Family Odacidae- <i>H. semifasciata</i>	0.2			11.4				0.8
Family Atherinidae- unidentified	0.6	1.2	2.1		1.0		0.3	0.6
Family Syngnathidae- unidentified			1.3		4.3			0.6
Family Sillaginidae <i>S. bassensis</i>					4.5			0.6
Family Scombridae <i>S. australasicus</i>	0.6				1.2			0.5
Family Monocanthidae- unidentified	0.3		0.5		0.2	0.3		0.3
Family Carangidae <i>Trachurus sp.</i>	0.5							0.3
Family Terapontidae <i>P. octolineatus</i>				3.5		0.9		0.3
Family Carangidae- <i>P. wrighti</i>	0.3							0.2
Family Apogonidae- unidentified				1.2				0.1
Family Gobiesocidae- unidentified	0.2							0.1
Family Gobiidae <i>G. semivestitus</i>					0.9			0.1
Family Diodontidae <i>D. nichthemerus</i>				1.2				0.1
Family Gerreidae <i>P. melbournensis</i>	0.1			1.1				0.1
Family Monocanthidae <i>Acanthaluteres sp.</i>				0.6				
<i>Cephalopods</i>								
Class Cephalopoda <i>S. australis</i>				0.6				
<i>Insects</i>								
Class Insecta- unidentified	0.1							
	100	100	100	100	100	100	100	100

Taxa with biomass totals over 15% are in bold. The number of regurgitates examined is in brackets

Inc incubation period, *E* early provisioning period, *M* mid provisioning period, *L* late provisioning period

selecting these prey at a similar size for themselves and their chicks ($P \geq 0.05$; Fig. 2).

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 ± 3.2 g) and 2007

(8.2 ± 2.2 g), compared to Goose Island (6.7 ± 2.0 g) and Rocky Island (5.4 ± 1.4 g), 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 ± 34.9 vs. 12.7 ± 5.1 g, $Z = 2.244$, $P = 0.025$). Similarly, chicks at Troubridge Island consumed larger Degens leatherjacket (16.1 ± 5.6 g) than at Lipson Island in the late provisioning period of 2006 (11.3 ± 5.0 g) ($Z = 2.160$, $P = 0.031$).

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

Site	Year	Chick-provisioning stage								
		Early			Middle			Late		
		<i>R</i>	<i>P</i>	Spp	<i>R</i>	<i>P</i>	spp	<i>R</i>	<i>P</i>	spp
Troubridge Is	2004	0.164	0.001	bs (25.5*), sard (23.1**), bar (20.2**)						
Troubridge Is	2005	0.195	0.001	deg (26.3**), anch (20.0*), sard (11.4*)	0.131	0.018	anch (27.3*), bar (23.7*), deg (13.4**)	0.258	0.008	anch (19.9*), bar (17.4*), gar (14.5**)
Troubridge Is	2006	0.129	0.001	bar (25.8**), sard (21.8*), anch (14.0*)	0.085	0.014	anch (22.2*), bar (21.4*), deg (13.4**)	0.008	0.428	
Troubridge Is	2007	0.254	0.001	deg (24.3**), bs (20.3*), sard (15.0**)	0.092	0.001	deg (26.1**), anch (16.7*), sard (12.3*)	0.079	0.016	anch (24.8*), sard (20.1**), deg (14.3*)
Goose Is	2005				-0.061	0.871				
Lipson Is	2005				0.039	0.267				
Lipson Is	2006	0.121	0.016	ah (22.1*), deg (15.7**), sard (15.7**)	0.067	0.017	deg (35.5**), sard (15.1*), gar (11.9**)	0.005	0.351	
Rocky	2007	0.229	0.002	sard (25.0**), ah (22.6*), bs (10.9*)	0.031	0.010	sard (33.1*), anch (19.0*), gar (7.7**)	0.077	0.089	

Significant *P* values are given in bold

Species key: *anch* Australian anchovy *E. australis*, *sard* Australian sardine *S. sagax*, *bar* barracoutta *Thyrsites 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

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

	Chicks		Adults	
	Avg (±SD) Mass (g)	Length (mm) Avg (±SD)	Mass (g) Avg (±SD)	Length (mm) Avg (±SD)
Australian herring	6.5 (3.8)	77 (12)	11.7 (16.7)	85 (30)
Barracoutta	19.1 (19.2)	163 (43)	12.3 (7.4)	146 (21)
Blue sprat	5.3 (1.1)	84 (7)	5.2 (1.2)	83 (6)
Degens leatherjacket	11.7 (4.9)	96 (16)	17.7 (7.0)	112 (17)
Australian anchovy	7.8 (2.8)	107 (14)	6.8 (2.3)	102 (15)
Southern sea garfish	15.4 (17.1)	154 (34)	31.4 (22.7)	189 (42)
Sardine	11.9 (6.5)	106 (18)	17.1 (13.8)	115 (26)

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 ± 7.4 vs. 15.3 ± 6.6 g) ($t = 2.491$, $P = 0.015$). 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 $P \geq 0.05$).

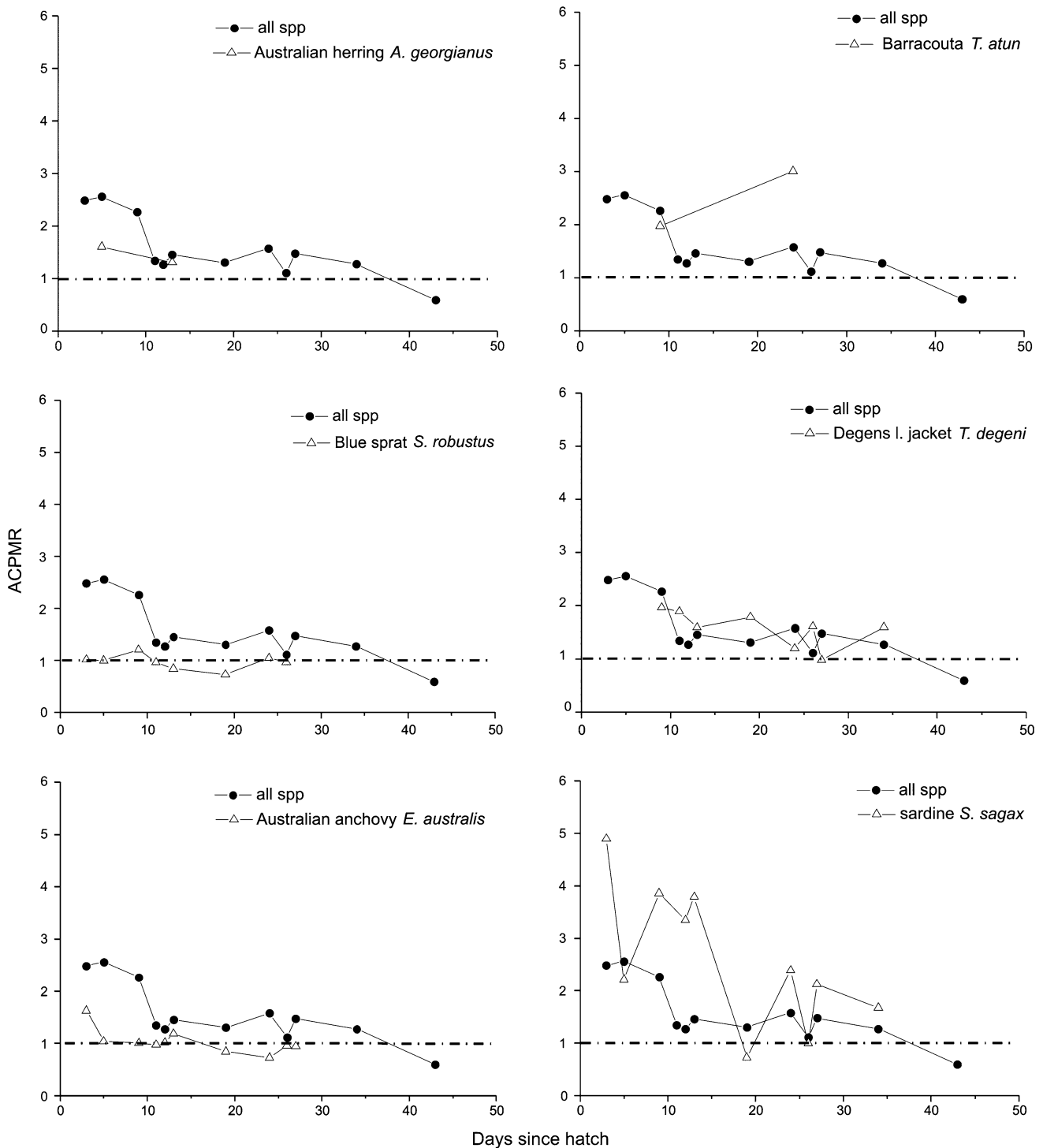


Fig. 2 Within season differences in mass of individual prey found in chick and adult diets for key prey species and all species pooled from Troubridge Island in 2007 (ACPMR adult to chick prey mass ratio)

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 (Fig. 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 ± 3.1 vs. late 11.5 ± 4.2 g, $Z = 2.520$, $P = 0.012$; Australian anchovy: early 6.7 ± 2.8 vs. late 8.0 ± 2.1 g,

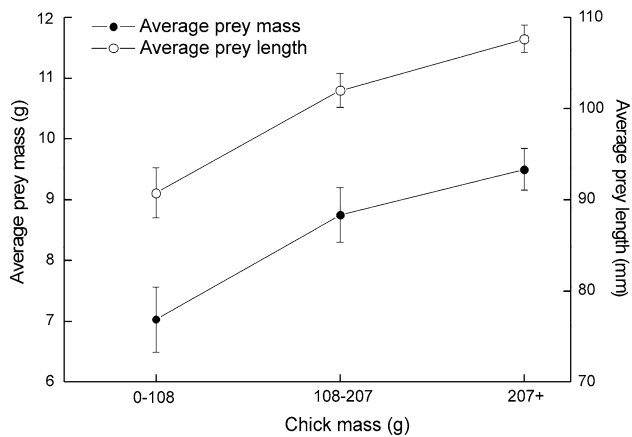


Fig. 3 The relationship between chick mass and average individual prey mass/length (spp/locations pooled) (\pm SE)

$Z = 2.461$, $P = 0.014$) (Rocky 2007, sardine: mid 9.6 ± 3.9 g vs. late 13.3 ± 6.8 g, $Z = 2.636$ $P = 0.008$; Australian anchovy: mid 5.4 ± 1.4 vs. late 8.0 ± 2.7 g, $t = 4.243$, $P \leq 0.001$).

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 ± 1.4 vs. late 8.7 ± 1.4 g, $t = 1.951$, $P = 0.061$; Rocky 2007: Australian anchovy mid 5.6 ± 1.5 vs. late 7.3 ± 1.6 g, $t = 2.872$, $P = 0.008$).

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 clupeids (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 40 g 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 clupeids (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 clupeids were of higher calorific value and had 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 Hobsum 2000; Jaquemet et al. 2008). Clupeids 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 the 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 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 SASFs 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 (Fig. 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).

Acknowledgments This study was principally supported through the Australian Government's Fisheries Research and Development Corporation (FRDC) Grants Scheme (PN 2005/031), co-funded by the South Australian Sardine Fishery. We also thank the South Australian Department for Environment and Heritage for financial assistance through the Wildlife Conservation Fund. All diet sampling and bird handling procedures were carried out under South Australian scientific research permit A24684. We thank volunteers A. Baylis, G. French, A. Ivey, T. Kemper, J. McKenzie, R. Mayo, G. McLeay, H. McLeay, L. K. McLeay, M. McLeay, A. Newman, J. Nichols, C. Platt, P. Rogers, and A. Wiebkin for their assistance during field operations, and C. and J. Johnson for providing logistical support and accommodation on Troubridge Island. We are grateful to A. Wiebkin, M. Steer and W. Dimmlich for providing data relating to prey regressions and P. Rogers and anonymous referees for useful comments that greatly improved the manuscript.

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