The diet of greater crested terns off southeast Australia varies with breeding stage and sea surface temperature

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Abstract

Monitoring seabird diet can provide insights into marine ecosystems that are logistically difficult or costly to observe with traditional fisheries survey methods. Using digital photography, we described the diet of greater crested terns (*Thalasseus bergii*) breeding on Montague Island (36°15' S, 150°13' E), a colony located in an oceanographically dynamic region of southeast Australia. We investigated how the type and size of prey brought back to the colony changed in relation to both breeding stage and variation in local environmental conditions. 2469 prey items were identified to species or family level over 35 consecutive days of photo-sampling in 2018. Australian anchovy (*Engraulis australis*), a surface-schooling clupeid fish, was the most abundant prey returned to the colony during all breeding stages (84.5%). The proportion of anchovy increased from 77.0% when birds were provisioning their adult partners during incubation, to 92.4% when they were provisioning chicks, suggesting selective foraging behaviour on this energy-rich species to facilitate rapid chick growth. Anchovy size was significantly larger during incubation (91.1 ± 14.9 mm), smaller during early chick provisioning (71.8 ± 11.0 mm), and increased slightly during mid provisioning (79.6 ± 11.9 mm), indicating adaptive prey selection that is matched to the physical requirements of different breeding stages. The proportion of anchovy prey was also influenced by sea surface temperature (SST), with anchovy becoming more dominant with increasing local SSTs, up to ~17.5 °C. This study gives new insight into the types of prey that are seasonally available to predators in this region. The strong specialisation by greater crested terns for one energy-rich species of schooling fish (anchovy) suggests that variation in the size and composition of their prey may serve as an indicator of change in the pelagic ecosystem off southeast Australia.

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Introduction

Upper trophic-level predators such as seabirds can act as sentinels of changes in marine ecosystems, with their demography, behaviour and physiology reflecting variability in oceanographic and ecological conditions (Hazen et al. 2019). For example, temporal changes in the occurrence, abundance and size of prey that seabirds consume can be used as indicators of food availability and ecosystem structure (Suryan et al. 2002; Parsons et al. 2008), and can provide an early warning of anthropogenic impacts on food webs (Green et al. 2015). Monitoring seabird diets can therefore be an important tool to inform conservation biology and ecosystem-based fisheries management (e.g. Lorentsen et al. 2018; Thayne et al. 2019; Hazen et al. 2019).

During the breeding season, the foraging range of seabirds is constrained by central-place foraging, which requires individuals to return to the colony between foraging trips to incubate eggs or provision their young (Cairns 1988). Optimal foraging theory for central-place foraging

predicts that single-prey loaders (species including guillemots and terns that carry a single whole prey item per foraging trip back to the colony) should maximise the energy load per unit foraging by providing large, or energetically rich prey items to their chick (Orians and Pearson 1979; Pichegru et al. 2007). This behaviour is assumed to be adjusted to energetic requirements and ingestion capabilities of developing juveniles, with parents selecting increasingly larger fish as the chick grows, to optimise the energy gained by offspring during each feeding event (Batchelor and Ross 1984). This means that birds must forage efficiently within a relatively short distance of the colony, to select high-quality prey items.

While intrinsic constraints imposed by provisioning requirements may influence prey selection during breeding, the availability of prey also varies with extrinsic environmental conditions. Temporal variation in oceanographic conditions can have a strong effect on the foraging success of seabirds, which can impact their body condition, growth and ultimately reproductive performance (Harwood et al. 2015). This is particularly true during the breeding season when birds are restricted to finding prey within a limited distance from the colony and cannot move to more favourable foraging areas. Local prey distribution and abundance can be strongly affected by variables at seasonal timescales, including phenological changes in sea surface temperature (SST). Seasonal changes in SSTs affect the spatial distribution and abundance of small pelagic fishes, which are an important food source for many seabird species (Hansen et al. 2001; Peck et al. 2021). In Norway, for example, sea temperature controls plankton production, which in turn influences the abundance of the Atlantic puffin's (*Fratercula arctica*) main prey, first-year herring, mediating fledgling success in this population (Durant et al. 2003).

Seabird prey availability also varies at short (i.e. daily) time scales (White 2008) in response to, for example, weather events. Prey capture by seabirds under adverse weather conditions can be exacerbated by poor flight performance, or by reductions in prey detectability or catchability (Elliott et al. 2014; Kogure et al. 2016). High wind speeds and wave heights affect the visual capabilities of seabirds due to changes in water turbidity, requiring more above-water searching for key prey species (Elliott et al. 2009). For example, there is evidence that high wind speeds influence foraging success in seabirds, as indicated by a decrease in the dominant prey captured, as well as a reduction in prey energetic value and size (Stienen et al. 2000; Elliott et al. 2014; Howells et al. 2017). Examining both intrinsic (i.e. physical requirements of chicks vs. adults) and extrinsic (i.e. environmental variability) processes affecting prey capture are crucial for understanding spatiotemporal differences in diet composition.

Here, we used digital photo sampling (Gaglio et al. 2017) as a non-invasive method to study food provisioning of greater crested terns (*Thalasseus bergii*) at Montague Island, an ecologically important breeding site for seabirds and fur seals in southeast Australia. Montague Island is situated in the path of the strengthening East Australian Current (EAC), in an ocean warming hotspot where SSTs are rising faster than the global average (Wu et al. 2012; Hobday & Pecl 2014), and faster than elsewhere on the Australian coast (Malan et al. 2021). Understanding the foraging ecology of marine predators breeding in this region and how this is related to local environmental variability will give new insight into the prey species that are seasonally available in this region, and provide a baseline for future studies seeking to understand the effects of climate change on this coastal pelagic ecosystem (Carroll et al. 2016).

We assessed the type and size of single prey items brought back to the colony by terns throughout the breeding season in 2018. We also quantified differences in prey composition between incubation, when terns bring prey back for their partner at shift-change, and chick provisioning at different stages of chick development. We focussed our analyses on the proportion and size of anchovy brought back to the nest, as anchovy was found to be the dominant prey species brought back to this colony, and is an important energy-rich species in the diet of marine top predators in southeast Australia (Hoedt and Dimmlich 1994; Hobday 1992) and crested terns elsewhere (McLeay et al. 2009; Chiaradia et al. 2002; Gaglio et al. 2018). Given that anchovy is a locally abundant, lipid-rich prey item, we tested our predictions that (1) the proportion of anchovy in the diet would increase during chick provisioning stages, to facilitate the rapid growth of small chicks (Batchelor and Ross 1984); (2) that anchovy standard length (SL) would decrease between incubation and the early chick provisioning period when offspring are small, then increase during mid provisioning as parents adjust prey size in accord with the ingestion capabilities of growing chicks. We also examined diet composition of greater crested terns in response to short-term variation in environmental variables. We predicted that (3) the proportion of anchovy returned to the colony would decrease under adverse environmental conditions (e.g. strong winds, high waves and anomalously warm SSTs) that influence the availability and/or catchability of surface-schooling prey.

Methods

Study site and species

This study was undertaken at Montague Island (36°15' S, 150°13' E), an 81 ha nature reserve located approximately 9 km off the coast of southeast New South Wales, Australia.

Greater crested terns nest in the open on the island at high densities. The tern colony on Montague Island comprises multiple sub-colonies; this study was conducted on the largest and most accessible one, consisting of ca. 1000 breeding pairs in 2018 (Fig. 1a; counted from a wide-angle photograph of the colony taken on 20 October 2018). The study was conducted over 35 consecutive days from 2 October to 5 November during the 2018 greater crested tern breeding season. Similar to other greater crested tern colonies (e.g. Gaglio et al. 2018), chicks hatch synchronously on Montague Island. Therefore, the first chick sighting was selected as the day of hatching and the start of provisioning (23 October 2018—study day 22). Breeding stages were classified as incubation, early provisioning and mid provisioning, and the study covered the full period from incubation to mid provisioning. During incubation, partners alternatively incubate the nest and bring single prey items to their mate when they change shifts. Early provisioning comprised the week following hatching during which both parents provision the chick in the nest scrape (Watson 2012), and mid provisioning the subsequent week when chicks start to leave the nest (Gaglio et al. 2018).

Photographic sampling

Greater crested tern diet was investigated using digital photography to assess differences between adults and chicks in the size and type of prey consumed over the course of the study period following Gaglio et al (2017). Adult terns carrying prey in their bill were photographed as they returned to the colony (Fig. 1a) using a Canon (Tokyo, Japan) 50D camera fitted with a Canon EF 70–300 mm f/4.0–5.6 IS USM tele zoom lens set to: (1) shutter speed priority 1/2500–1/4000 s depending on light conditions, (2) automatic ISO, (3) high-speed continuous shooting, (4) autofocus on AI servo (autofocus system for continuous tracking of moving subjects), and (5) large Jpeg file format. The tele zoom lens was set to autofocus with the image stabiliser on.

Every day, photos of birds arriving with prey at the colony were taken continuously during three two-hour sessions (morning session from 0700 to 0900 h, midday session from 1100 to 1300 h and afternoon session from 1500 to 1700 h AEST; after daylight savings from 0800 to 1000 h, 1200 to 1400 h and 1600 to 1800 h AEDT), in sum a sampling effort of 210 h. Photos were taken from a different vantage point during each session to account for sun position. Photos were taken as a photo-set consisting of three images, with the sharpest selected for prey identification and measurements. The distance between the vantage points and the closest bird was approximately 5 m. The birds did not show any sign of stress or disturbance due to the presence of the photographer and sessions were limited to two hours to avoid observer fatigue.

Identification of prey species

All blurred and unclear images (due to e.g. distance, position of prey in the bill, light conditions and other restrictions) were excluded from the analyses. From the remaining photographs, prey was identified to the highest possible taxonomic resolution (usually to species or family level), based on morphological characteristics (Fig. 1b–k). Fish identification was undertaken by comparing photographs with published images and fish identification guides from the Australian Museum (<https://australian.museum/learn/animals/fishes>), and subsequently verified by multiple species experts from the NSW Department of Primary Industries and the University of New South Wales, Australia.

Estimation of anchovy size

Australian anchovy was chosen as a standard by which to compare the size of prey brought back to the colony during different breeding stages using the method detailed by Gaglio et al. (2017). Importantly, Gaglio et al (2017) used the European anchovy (*E. encrasicolus*) to create length regressions for anchovy eye diameter, head and operculum width. These equations were applied to measurements of Australian anchovy in this study. The morphometric characteristics of both species are very similar, although the European anchovy is slightly larger than the Australian anchovy (average length 13.5 vs. 12 cm; Whitehead et al. 1988). Since this study aimed to compare relative fish length within the sample rather than illustrating variability in absolute fish length, regression equations calculated for European anchovy were used with the caveat that these measurements may consistently bias the true length of Australian anchovy photographed in this study.

Environmental factors

Key environmental variables that are likely to influence either the distribution or abundance of prey species in the greater crested terns' foraging range, and/or the terns' ability to catch them were selected for analysis. These included wind speed, sea surface temperature (SST) and wave height. Wind speed (km/h) was recorded by the Australian Bureau of Meteorology weather station (IDN60801) located at the lighthouse on Montague Island (www.bom.gov.au). Wind measurements were made using an automatic anemometer with an accuracy of $\pm 5\%$ of the wind speed for wind speeds ≥ 10 m/s. Wind data were recorded as the average of 10 min bursts at 30 min intervals.

Gap-free daily records of satellite-derived SST at a $0.05^\circ \times 0.05^\circ$ spatial resolution were measured by the UK Met Office's Operational Sea Surface Temperature and Ice

Fig. 1 **a** Photo of the greater crested tern colony taken from a light-house at Montague Island, New South Wales, showing the photographer at vantage point 1 capturing photo-sets of adult terns carrying single-prey items to the colony at a distance that does not cause disturbance to nesting birds. **b** The resulting close-up image of the prey used for identification and measurements. Examples of tern prey items: **b** Australian anchovy, *Engraulis australis*; **c** Trevally spp. (juvenile), Centrolophidae spp.; **d** Barracouta, *Thyrstites atun*; **e** Southern calamari squid, *Sepioteuthis australis*; **f** Eastern sea garfish, *Hyporhamphus australis*; **g** Redbait, *Emmelichthys nitidus*; **h** King gar, *Scomberesox saurus*; **i** Goatfish spp. (juvenile), Mullidae spp.; **j** Silver sweep, *Scorpius lineolata*; **k** Bluebottle fish, *Nomeus gronovii*

Analysis (OSTIA) system (downloaded from marine.copernicus.eu). Based on previous observations of the terns' foraging range from Montague Island (O'Hara 2016), SST values were averaged across an area spanning 35° to 37° north to south, from the coast out to the edge of the continental shelf (i.e. 200 m depth isobath). Because SST was available at a daily temporal resolution, daily values were assigned to multiple photography sessions within a day.

Wave height (m) was recorded by the NSW Department of Planning, Industry and Environment's (DPIE) Batemans Bay offshore Waverider buoy (35°44'25", 150°19'03"; <https://mhl.nsw.gov.au/Station-BATBOW>; approximately 53 km north of Montague Island). Data were recorded in bursts (lasting approximately 34 min long starting on the hour) at 0.5-s intervals. Wave height for each of these periods is defined as the mean height of the largest 33% of waves.

Previous GPS tracking work on Montague Island showed that in most years, tern foraging trips last on average 2.2–3.1 h (O'Hara 2016). Hence any photo taken at the colony during a two-hour sampling period could reflect foraging conditions up to two or more hours earlier than the actual sampling time. Therefore, wind and wave data were assigned to a photo session by taking an average of each variable across a four-hour period starting two hours prior to each session.

Data analysis and statistics

The number of each prey species as a proportion of the total number of prey photographed throughout the study period was calculated to quantify the diet composition of greater crested terns during the 2018 breeding season on Montague Island. Key prey species, i.e. species making up > 1% of the diet, were identified to simplify graphical illustrations and statistical analyses. The proportion of each prey type was calculated for each two-hour photo session, and compared between breeding stages.

A chi-squared goodness-of-fit test was conducted to assess differences in diet composition between incubation and chick provisioning. A generalised linear mixed model (GLMM) with beta error structure and logit function was used to investigate the effect of breeding stage on the proportion of anchovy returned to

the breeding colony by adult terns. Prior to analysis, the response variable (anchovy proportion) was compressed to avoid absolute values of zero or one by taking $y = (y \times (n - 1) + 0.5) / n$, where n is the sample size (Smithson and Verkuilen 2006). The model was fitted in R using the package 'glmmTMB' (version 1.0.1; Brooks et al. 2017). Similarly, a linear mixed model (LMM; R package 'lme4'; Bates et al. 2014) was used to investigate the effect of breeding stage on the dependent variable anchovy SL. Each of the models included breeding stage as fixed term and study day ($N=35$ days) as crossed random effect to account for the repeated three-session per day design. Finally, a post hoc test was performed using the package 'emmeans' (version 1.4.6; Lenth 2020) to investigate the effect within each breeding stage category. Results were Tukey-adjusted for multiple testing. For all analyses, model assumptions were checked following Zuur et al (2009).

To visualise differences in prey composition in relation to breeding stage, a non-metric multidimensional scaling plot (NMDS) was generated using the R package 'vegan' (Oksanen 2011). NMDS is an ordination technique to represent the position of data points in multidimensional space using distance measures and a reduced number of dimensions (typically 2). The Hellinger transformation was applied to remove any tendency for the main prey to be excessively dominant (Borcard et al. 2018). The Bray–Curtis dissimilarity index was used to create a distance matrix that reflects the multidimensional distance between data points with objects grouped closer together being more similar. Ellipses were plotted to depict the centroid and inertia of each breeding stage.

Generalised additive mixed models (GAMMs) using a beta regression and logit function were used to assess the influence of environmental variables (SST, wave height, wind speed) on the proportion of prey species in the diet. GAMMs, as an extension to GLMMs, allow an estimation of potential non-linear relationships between continuous explanatory variables and the response. The models were fitted using the R package 'mgcv' (version 1.8-31; Wood 2006). Smoother terms were applied to explanatory environmental variables and were generated using regression splines. Explanatory variables also included breeding stage as a fixed effect and study day as crossed random effect to account for intraclass correlations among day-specific sampling events. An alpha level of 0.05 was used to determine statistical significance. All statistical analyses were carried out in R (v3.5.3; R Core Team 2017).

Results

Diet composition

Over the 35 consecutive days of photo sampling, 3280 photo-sets were taken, yielding images of 2469 prey items

(76%) identifiable to species or family level. 1265 prey items were identified during incubation and 1204 items during provisioning (early provisioning: $n=482$, mid provisioning: $n=722$ prey items). Single prey items brought back to the

colony were almost exclusively fish, with only one cephalopod species identified during the 2018 breeding season (Table 1).

Table 1 Numbers and proportions of prey species photographed in the bills of greater crested terns returning to the colony at Montague Island in 2018 according to the breeding stage of the terns. A total of

2469 prey items were identifiable to species or family level of which 1265 prey were identified during incubation (adult diet) and 1204 during provisioning stages (chick diet)

Common name	Scientific name	Family	Adult		Chick		Total	
			<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
Australian anchovy	<i>Engraulis australis</i>	Engraulidae	974	77.0	1112	92.4	2086	84.5
Barracouta	<i>Thyrsites atun</i>	Gempylidae	114	9.0	6	0.5	120	4.9
Trevally spp.	Indet. spp.	Centralophidae	76	6.0	10	0.8	86	3.5
Goatfish spp.	Indet. spp.	Mullidae	7	0.6	40	3.3	47	1.9
Bluebottle fish	<i>Nomeus gronovii</i>	Nomeidae	12	0.9	22	1.8	34	1.4
Eastern sea garfish	<i>Hyporhamphus australis</i>	Hemiramphidae	20	1.6	7	0.6	27	1.1
Southern calamari squid	<i>Sepioteuthis australis</i>	Loliginidae	27	2.1	1	0.1	28	1.1
Redbait	<i>Emmelichthys nitidus</i>	Emmelichthyidae	22	1.7	0	0.0	22	0.9
King gar	<i>Scomberesox saurus</i>	Scomberesocidae	7	0.6	1	0.1	8	0.3
Silver sweep	<i>Scorpius lineolata</i>	Scorpididae	5	0.4	2	0.2	8	0.3
Pilotfish	<i>Naucrates ductor</i>	Carangidae	1	0.1	1	0.1	2	0.1
Flying fish spp.	Indet. spp.	Exocoetidae	0	0.0	1	0.1	1	0.04

Fig. 2 Daily variation in greater crested tern diet across study period ($n=35$ days) and breeding stages: incubation (study day 1–21), early provisioning (study day 22–28), mid provisioning (study day 29–35). Depicted are the seven main prey species (Australian anchovy, bar-

racouta, bluebottle fish, eastern sea garfish, goatfish spp., southern calamari squid, trevally spp.) and other fish (prey items making up a total abundance of <1% over the breeding season) returned to the breeding colony

Fig. 3 Non-metric multidimensional scaling plot (NMDS) showing differences in prey composition across three breeding stages (incubation, early provisioning, mid provisioning) by greater crested terns at Montague Island. Sample points represent the daily mean contributions of each of the seven main prey species (Australian anchovy, barracouta, bluebottle fish, eastern sea garfish, goatfish spp., southern calamari squid, trevally spp.) and other fish (OF, prey items making up a total abundance of < 1% over the breeding season) returned to the breeding colony. The three colours represent each different breeding stage, while ellipses highlight the centre of gravity and inertia of each breeding stage

Seven main prey types were identified of which Australian anchovy was the dominant species during all breeding stages (84.5%, Table 1). The diet was more diverse during incubation compared to early provisioning (Figs. 2, 3). During incubation, in addition to anchovy, other prey such as barracouta, trevallies and southern calamari squid were frequently brought back to the colony but their abundance decreased once chicks hatched. In contrast, species such as bluebottle fish and goatfish occurred more frequently in the diet of crested terns provisioning chicks, compared to incubation (Table 1; Figs. 2, 3).

There was a significant difference in the proportion of anchovy returned to the colony between the incubation (adult diet) and chick provisioning periods (χ^2 test, $X = 13.72$, $p < 0.01$), with terns selecting less anchovy when bringing prey back to the adult partner. Specifically, the mean proportion of anchovy in the diet increased significantly from 77.0% (incubation) to 92.9% once chicks hatched (early provisioning). During mid provisioning, the proportion of anchovy was 91.9%. This was significantly higher than during incubation, but not significantly different from early provisioning (Fig. 4a). Statistical results for differences in anchovy proportions between breeding stages are summarised in Table 2.

Anchovy size

423 images (~20%) out of 2086 prey items identified as anchovy were used to measure anchovy size. The standard length (SL) of anchovies brought back to the colony

ranged from 19.7 to 143.4 mm. Anchovies were largest during incubation when birds were bringing fish back for their partner (mean $\pm$ SD = 91.1 ± 14.9 mm, $n = 193$). There was a significant decrease in anchovy SL to a mean size of 71.8 ± 11.0 mm, $n = 84$ during early provisioning (Fig. 4b). Anchovy SL increased slightly to 79.6 ± 11.9 mm, $n = 146$ during mid provisioning which was significantly smaller than incubation, but not significantly different from the early provisioning stage (Table 3).

Diet composition in relation to environmental factors

The GAMM revealed that the proportion of anchovy in the diet of greater crested terns increased with warmer SSTs, with the rate of increase slowing slightly at SSTs above 17.5 °C (Fig. 5). Neither wind speed nor wave height had a significant influence on the proportion of anchovy returned to the breeding colony (Table 4).

Discussion

This study quantified the type and size of prey exploited by a marine predator, the greater crested tern, during the 2018 breeding season at Montague Island, Australia. Using photographic sampling of prey items brought back to the colony, diet data were related to breeding stage and variation in local environmental conditions.

Fig. 4 **a** The proportion of anchovy and **b** anchovy standard length (mm) in the diet of greater crested terns across three breeding stages (incubation, early provisioning, mid provisioning) at Montague Island in the 2018 breeding season. Box plots show the median and first and third quartile; whiskers extend to the 1.5 times the interquartile range. Black dots represent outliers. Significance levels are depicted as * $p \leq 0.05$ and ** $p < 0.01$

Table 2 Relationship between breeding stage (incubation, early provisioning, mid provisioning) on the proportion of anchovy in the diet of greater crested terns in 2018. Mean (%) anchovy proportion and Tukey test adjusted p values from comparisons across breeding stages are presented

Dependent variable	Breeding stage	Mean (%)	Estimate	Std. error	z ratio	p value	
						Early prov	Mid prov
Anchovy proportion	Incubation	77.0	− 0.957	0.277	− 3.459	< 0.01	0.046
	Early prov	92.9	− 0.648	0.268	− 2.414	–	0.62
	Mid prov	91.9	0.309	0.332	0.931	–	–

Bold values represent significant results

Table 3 Relationship between breeding stage on anchovy standard length (mm) estimated from photo-samples ($n=423$) of greater crested terns in 2018. Mean (SD) and Tukey test adjusted p values

Dependent variable	Breeding stage	Mean (SD) mm	Estimate	Std. error	z ratio	p value	
						Early prov	Mid prov
Anchovy SL	Incubation	91.1 (14.9)	18.24	5.18	3.52	< 0.01	0.05
	Early prov	71.8 (11.0)	12.07	4.93	2.45	–	0.58
	Mid prov	79.6 (11.9)	– 6.17	6.15	– 1.00	–	–

Bold values represent significant results

Fig. 5 Partial effect of the environmental covariate SST on the proportion of anchovy returned to the greater crested tern breeding colony at Montague Island, Australia, in 2018. $s(x,y)$ is the smoothing term, with x the explanatory variable and y the estimated degrees of freedom of the smoothing term. Pointwise 95% confidence intervals are shown for each model fit **Table 4** Relationship between environmental variables (SST, wave height, wind speed) on the proportion of anchovy in the diet of greater crested terns using generalised additive mixed models (GAMMs). GAMM results include breeding stage as fixed effect.

Dependent variable	Environmental variable (smooth term)	Estimated degrees of freedom	χ^2	p value	Deviance explained
Anchovy proportion	SST	1.54	10.57	0.02	33%
	Wave height	1.75	1.68	0.41	36.2%
	Wind speed	2.22	3.67	0.22	44.7%

Bold values represent significant results

Prey composition and size

Small surface-schooling clupeids, dominated by the Australian anchovy (*Engraulis australis*), were the most abundant prey type returned to the colony during the breeding season, consistent with findings on diet composition of crested terns in other geographic locations and oceanographic systems: in South Africa, anchovy (*E. spp.*) were found to be the most abundant prey items of crested terns at multiple colonies (Walter et al. 1987; Gaglio et al. 2018). Elsewhere in Australia, the diet composition of juvenile crested terns in Victoria was dominated by two prey species, Australian anchovy and Jack mackerel (*Trachurus declivis*) (Chiaradia et al. 2002). Crested terns in South Australia were more

from comparisons across three breeding stages, incubation ($n=193$), early provisioning ($n=84$), and mid provisioning ($n=146$) are presented

Shown are the estimated degrees of freedom (edf), χ^2 and p values for each environmental parameter, as well as the percent deviance explained as measure of model performance

generalist predators feeding predominantly on Australian anchovy, sardine (*Sardinops sagax*) and blue sprat (*Sprattellus robustus*) (McLeay et al. 2009), highlighting that variation in the distribution of prey species and environmental factors that affect foraging are likely to influence diet composition at different sites. Barracouta was the second most abundant prey in the diet in our study and is also an important prey species of crested terns in both Victoria and South Australia (Chiaradia et al. 2002; McLeay et al. 2009). Barracouta in southern New South Wales spawn in late winter (July–August; Bray and Schultz 2020), which may explain the occurrence of smaller (juvenile) barracouta in the diet of adult crested terns at the onset of the spring breeding season. Their absence later in the season may be because they grow

too large for chicks to swallow. Some demersal fish species were also found in the diet, including bluebottle fish. While demersal as adults, bluebottle fish are pelagic as juveniles and occur near the sea surface where they were presumably captured by terns (Bray 2020). Southern calamari squid occurred in small numbers and are also demersal, in shallow (< 10 m) inshore waters, but are occasionally also found near the surface (Norman and Reid, 2000).

The proportion and size of anchovy returned to the breeding colony varied between incubation and chick provisioning, with chicks consuming a significantly higher proportion of anchovy than adults during early and mid provisioning. Anchovies returned to the breeding colony were smallest during early chick rearing. Hatchlings are limited in the size of prey they can swallow and this means parents need to select smaller prey at sea. As chicks grow, parents may need to adjust for their increasing energetic requirements to maximise growth rates. The observed increase in anchovy size with chick age supports previous findings that there is size-selective predation by adult terns through the breeding season in response to changing energetic demands of nestlings (Hulsman et al. 1989; Shealer 1998; McLeay et al. 2009; Gaglio et al. 2018). However, while these findings suggest active prey selection by adult terns in response to breeding stage, the influence of spatiotemporal availability of prey on diet composition should not be discounted.

Environmental factors

Environmental factors, such as temperature, drive the distribution and abundance of schooling fish, and thus the availability of prey to upper trophic levels in the ocean (Bertrand et al. 2008). The East Australian Current (EAC) transports warm and nutrient-depleted water southward along the New South Wales coastline (Suthers et al. 2011). This highly variable and dynamic system has intensified over recent decades (Phillips et al. 2020), with local SSTs off southeast Australia rising at a rate that is 3–4 times greater than the global average (Wu et al. 2012), and the area around Montague Island being a particular hotspot of warming within this region (Malan et al. 2021). The flow-on effects of these EAC dynamics include shifts in the distribution of pelagic fishes (Hobday et al. 2011; Champion et al. 2021), phytoplankton (Thompson et al. 2009), and larval recruitment (Cetina-Heredia et al. 2015).

In this study, SST was positively correlated with the proportion of anchovy returned to the breeding colony. The relationship between the spatial distribution of small pelagic fish stocks and environmental factors (e.g. temperature) have been reported in marine ecosystems globally (Peck et al. 2021), such as in the Patagonian stock of Argentinian anchovy, *E. anchoita* (Hansen et al. 2001). In accordance with our findings, greater crested terns

in South Australia, which mainly prey on clupeid fishes during chick provisioning stages, typically foraged over warmer waters (18–21 °C) that are shallow and are associated with high levels of chlorophyll *a* (McLeay et al. 2010). An earlier study in South Australia found that anchovy spawning was triggered by higher SSTs in spring (Kent et al. 2013) and larvae were more abundant in shelf waters with SSTs < 20 °C near upwelling zones (Dimmlich et al. 2004). Ultimately, the impact of EAC dynamics and ocean warming on the foraging behaviour and breeding phenology of marine top predators, like greater crested terns, in southeast Australia may accelerate under future climate change (Phillips et al. 2020), making this seabird population an interesting study system and a potential future indicator of ecosystem change in response to ocean warming.

In additional previous research undertaken at Montague Island, Carroll et al (2016) concluded that reduced prey capture of forage fish by little penguins (*Eudyptula minor*) associated with anomalously cool SSTs might reflect a period early in the breeding season when water temperature had not been warm enough to facilitate phytoplankton growth, resulting in a lower local abundance of planktivorous fish. Likewise, SST > 21 °C impaired prey capture success at the end of the penguin's breeding season, related to a stronger influence of the warm EAC at this time (Phillips et al. 2020). Montague Island penguins have been shown to match the distribution of schooling forage fish like anchovy around the island when foraging, indicating that their prey capture success reflects local changes in prey availability that might be important for other sympatric predators such as greater crested terns (Carroll et al. 2017). Range-restricted species, such as breeding seabirds, may thus be particularly sensitive to the local availability of key prey species at crucial times in their breeding cycle (Crawford et al. 2006).

Breeding phenology in birds is likely timed to coincide with periods of peak resource availability. The prevalence of anchovy in the diet increased with SST in this study, and SST was seasonally elevated during chick provisioning stages (see online resources Fig. 1). It is possible that the timing of breeding is linked to elevated levels of production, indicated by greater proportions of energy-rich prey (e.g. anchovy) in the diet during chick provisioning. In support of the latter, anchovy abundance and availability to Peruvian seabirds increased during the period of chick provisioning with a peak around the time of fledging, suggesting breeding timing is adjusted to optimal environmental conditions facilitating chick or fledgling survival (Passuni et al. 2016). Importantly, the extent to which a dietary shift in this study can truly be linked to prey availability and its influence by environmental covariates such as SST would require additional research on estimates of fish stock composition and abundance around Montague Island by, for example, local

fishery assessments or acoustic surveys (e.g. Green et al. 2015; Carroll et al. 2017; Thayne et al. 2019). Undertaking this research would allow greater insight into the mechanisms underpinning variability in diet composition in marine predators in southeast Australia, and give further insight into whether the diet of breeding crested terns can provide a useful indicator of changing conditions in the coastal pelagic ecosystem in southeast Australia.

Conclusion

This study found that the diet of greater crested terns off southeast Australia was dominated by a single, energy-rich small pelagic fish (Australian anchovy). The proportion and size of this key prey species within the diet of greater crested terns was found to vary with sea surface temperature and breeding stage, respectively. This reflects a combination of selective foraging behaviour of the terns to meet the changing energetic demands of partners and chicks, and spatio-temporal changes in the availability of their prey. Further studies should preferably examine seabird diet composition and fitness parameters (e.g. chick body condition and survival) simultaneously, as well as the spatial and temporal availability of prey in the terns' foraging areas to disentangle these effects and to make inferences for management and predictions of anthropogenic impacts on this species. By showing a strong selectivity for only one energy-rich species of schooling fish, we suggest that greater crested terns may be an informative bioindicator of changes in the pelagic ecosystem, as has been suggested for other specialised seabird species (Courtens et al. 2017; Hazen et al. 2019).

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Author contributions RH, GC, KQ conceived the ideas and designed the study; KQ collected the data; KQ and CC processed photographs and collated data; KQ and GC analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they do not have conflicts of interest or competing interests.

Ethics approval This project was conducted under NSW NPWS Scientific Licence SL170064 and Macquarie University Animal Research Authority 2014-057. All applicable international, national, and institutional guidelines for the care and use of animals were followed.

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