

## RESEARCH ARTICLE

Functional Ecology



# Quantifying prey availability using the foraging plasticity of a marine predator, the little penguin

Catherine Cavallo<sup>1</sup> | André Chiaradia<sup>1,2</sup> | Bruce E. Deagle<sup>3,4</sup> | Graeme C. Hays<sup>5</sup> | Simon Jarman<sup>6</sup> | Julie C. McInnes<sup>3,7</sup> | Yan Ropert-Coudert<sup>8</sup> | Sonia Sánchez<sup>1</sup> | Richard D. Reina<sup>1</sup>

<sup>1</sup>School of Biological Sciences, Monash University, Clayton, VIC, Australia; <sup>2</sup>Conservation Department, Phillip Island Nature Parks, Cowes, VIC, Australia; <sup>3</sup>Australian Antarctic Division, Kingston, TAS, Australia; <sup>4</sup>CSIRO National Research Collections-Australian National Fish Collection, Hobart, TAS, Australia; <sup>5</sup>Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Geelong, VIC, Australia; <sup>6</sup>School of Biological Sciences, University of Western Australia, Perth, WA, Australia; <sup>7</sup>Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS, Australia and <sup>8</sup>Centre d'Etudes Biologiques de Chizé, UMR7372 CNRS, La Rochelle Université, Villiers-en-Bois, France

## Correspondence

Catherine Cavallo

Email: ccavallo.ecology@gmail.com

André Chiaradia

Email: achiaradia@penguins.org.au

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## Abstract

1. Detecting changes in marine food webs is challenging, but top predators can provide information on lower trophic levels. However, many commonly measured predator responses can be decoupled from prey availability by plasticity in predator foraging effort. This can be overcome by directly measuring foraging effort and success and integrating these into a measure of foraging efficiency analogous to the catch per unit effort (CPUE) index employed by fisheries.
2. We extended existing CPUE methods so that they would be applicable to the study of generalist foragers, which introduce another layer of complexity through dietary plasticity. Using this method, we inferred species-specific patterns in prey availability and estimated taxon-specific biomass consumption.
3. We recorded foraging trip duration and body mass change of breeding little penguins *Eudyptula minor* and combined these with diet composition identified via non-invasive faecal DNA metabarcoding to derive CPUE indices for individual prey taxa.
4. We captured weekly patterns of availability of key fish prey in the penguins' diet and identified a major prey shift from sardine *Sardinops sagax* to red cod *Pseudophycis bachus* between years. In each year, predation on a dominant fish species (~150 g/day) was replaced by greater diversity of fish in the diet as the breeding season progressed. We estimated that the colony extracted ~1,300 tonnes of biomass from their coastal ecosystem over two breeding seasons, including 219 tonnes of the commercially important sardine and 215 tonnes of red cod.
5. This enhanced pCPUE is applicable to most central-placed foragers and offers a valuable alternative to existing metrics. Informed prey-species biomass estimates extracted by apex and meso predators will be a useful input for mass-balance ecosystem models and for informing ecosystem-based management.

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## KEYWORDS

diet analysis, DNA barcoding, ecological indicators, eDNA, fish stock, foraging success, gelatinous plankton, phenotypic plasticity

## 1 | INTRODUCTION

As environmental changes propagate up food webs, high-order predators are particularly vulnerable, making them sensitive indicators of changing food web patterns (e.g. Boyd & Murray, 2001; Robinette, Howar, Sydeman, & Nur, 2007). Yet, many predator traits commonly used to measure predator–prey relationships can be obscured by behavioural plasticity of the predator. Individual predators may change their foraging approach to buffer themselves and their offspring against environmental variation (Grémillet et al., 2012). Conventional methods may not measure the imposed cost of changed foraging behaviour unless food is so scarce that predators reach the physiological limit of their plasticity, resulting in measurable demographic effects (Cairns, 1987). In particular, seabird population parameters have limited value as indicators of prey resources because they vary nonlinearly in relation to food availability (Piatt, Harding, et al., 2007). Demographic responses, such as changes in population-wide survivorship, reproductive success or recruitment, require a critical threshold to be reached (Harding et al., 2007; Piatt, Harding, et al., 2007), or are latent (Durant et al., 2009). This masks or delays crucial signals needed by managers to detect and act on declining resources and threatened populations (Piatt, Harding, et al., 2007). Adult seabirds may maintain their body condition and chick provisioning across varying prey availabilities through flexible time budgets (Litzow & Piatt, 2003), by increasing foraging effort (Chiaradia & Nisbet, 2006), provisioning frequency (Suryan, Irons, & Benson, 2000) or by switching prey (Abraham & Sydeman, 2006).

The confounding effect of foraging plasticity can be overcome by directly measuring parameters over which individuals exert control (e.g. effort). Simultaneous records of foraging effort and success can be integrated into a measure of foraging efficiency that assumes a proportional relationship between catch rate and abundance (Grémillet, 1997). This measure is analogous to the catch per unit effort (CPUE) index used by fisheries to account for fishing effort when estimating stock abundance (Maunder et al., 2006). Although direct proportionality is exceptional, an imperfect CPUE remains the industry standard used by fisheries in the absence of more reliable measures of fish population size, recruitment and distribution (Dunn, Harley, Doonan, & Bull, 2000; Hinton & Maunder, 2004; Maunder et al., 2006) and has been suggested for use with ecological indicators (Cairns, 1992).

Catch rates have been determined in ecological studies by recording foraging success via direct measures of total prey mass ingested over a trip (Grémillet, 1997) or through proxies such as prey capture attempts (Ropert-Coudert, Kato, Wilson, & Cannell, 2006; Zimmer et al., 2008), temperature drops in the stomach or oesophagus as an indication of a cold food item being swallowed by an endothermic

predator (Ropert-Coudert et al., 2001; Wilson, Culik, Bannasch, & Lage, 1994), beak angle and motion (Simeone & Wilson, 2003) or observation of food items caught by captive birds (Enstipp, Grémillet, & Jones, 2007), and dividing this measure by time spent foraging. These prey catch rates identify functional relationships between predator behaviour and overall resource availability, providing a more realistic view of predator responses for conservation managers (Enstipp et al., 2007). However, without taxon-specific diet data, inferences are limited to overall resource availability, except for those dietary specialists that feed on only a single prey species. Generalist predators add another level of complexity when they mitigate low-resource availability by switching prey species (Abraham & Sydeman, 2006), making inferences based on catch rates alone unreliable as estimates of patterns in lower trophic levels. However, when taxon-specific diet information is included, a CPUE-type index could be a robust measure of both predator efficiency and the availability of individual prey species. Generalist predators, whose diet composition reflects the availability of different prey types in the environment (Cullen, Montague, & Hull, 1991), could then be used to index the availability of a wide range of prey species.

Little penguins *Eudyptula minor* are high trophic level generalist predators that consume many ecologically and economically important fish (Cullen et al., 1991; Gales & Pemberton, 1990; Klomp & Wooller, 1988). These include primary prey items sardine *Sardinops sagax* and anchovy *Engraulis australis*, complemented by red cod *Pseudophycis bachus*, barracouta *Thyrstites atun* and jack mackerel *Trachurus declivis* and a wide array of marginal prey items (Cavallo et al., 2018; Chiaradia, Forero, Hobson, & Cullen, 2010; Cullen et al., 1991). Individual prey preference within a generalist population may confound CPUE studies, but there are no indications that individual specialization occurs in little penguins. Indeed, there is little variability between individuals within a sampling day (Chiaradia et al., 2010; Chiaradia, Ramírez, Forero, & Hobson, 2016). The proportion of prey species caught varies between colonies and with time but agrees with concurrent local commercial and research catches (Cullen et al., 1991; Klomp & Wooller, 1988), suggesting that little penguins consume prey relative to its availability in the foraging zone (Kowalczyk, Chiaradia, Preston, & Reina, 2015). They forage throughout their foraging trips, as expected of a generalist forager (Pelletier, Chiaradia, Kato, & Ropert-Coudert, 2014; Sánchez, 2019) and appear to reach a threshold stomach mass before returning to the colony, spending more days at sea rather than reducing meal sizes to chicks during lean times (Chiaradia & Nisbet, 2006; Saraux, Robinson-Laverick, Le Maho, Ropert-Coudert, & Chiaradia, 2011). At the breeding colony, the penguins' site fidelity and predictable use of walking paths facilitate the use of a transponder-based automated penguin monitoring system (APMS: Chiaradia & Kerry, 1999). This

system provides body mass, foraging trip duration and colony attendance to be monitored for individual birds in real time, avoiding the time lag and disturbance associated with many traditional seabird research methods (Kerry, Clarke, & Grant, 1993). Using an APMS, large datasets can be acquired over long time series with little disturbance to the colony.

In this study, we refine the CPUE index for ecological studies promoted by Cairns (1987) and introduced by Wilson (1992) and Grémillet (1997). We have integrated diet composition estimates measured using faecal DNA metabarcoding with foraging trip duration and body mass data from the APMS. We use this method to determine the availability of key prey fish species of little penguins over time and to estimate the biomass consumed by breeding little penguins.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site and system

We monitored little penguins at two sites within the Phillip Island colony in Victoria, south eastern Australia (38°31'S, 145°07'E) during the 2015–2016 and 2016–2017 breeding seasons (~August–March). The sites were <2 km apart and were 'Penguin Parade®', where penguins breed in artificial wooden nest-boxes, and 'Radio-tracking Bay', where penguins breed in natural burrows. We randomly selected 100 nests at each site for monitoring (details in Sánchez et al., 2018).

### 2.2 | Foraging success and trip duration

All penguins within the study site were equipped with passive identification transponders (PIT tags: Penguin Parade-Allflex, Australia and Radio Tracking Bay-Trovan, United Kingdom), which are injected subcutaneously between the scapulae (Chiaradia & Kerry, 1999). An APMS with weighbridge, located on the main path in and out of each breeding site, reads these PIT tags, recording individual identity, time and mass, thus allowing us to identify and calculate both the foraging trip duration and the body mass change of individuals during each foraging trip. We used the *R statistical language and environment* (R Core Team, 2013) to extract foraging trip information from the APMS dataset. We sorted the APMS data by PIT tag number and date, then compared each 'out' record with the previous 'in' record to identify distinct foraging trips made by individual birds. Two calculations could then be made from the mass and date data relating to these trips.

#### 2.2.1 | Foraging effort (trip duration)

*Foraging effort* was measured as foraging trip duration (days), because breeding little penguins typically leave on foraging trips just

before dawn and return to the colony at dusk (Daniel, Chiaradia, Logan, Quinn, & Reina, 2007), foraging throughout their time away from the colony (Ropert-Coudert et al., 2006; Sánchez, 2019). Trip duration was calculated as the return date minus the departure date (Saraux et al., 2011).

#### 2.2.2 | Foraging success (body mass change)

*Foraging success* was then measured as the change in body mass of individual birds over each foraging trip (*body mass change*; grams), calculated as the return mass minus the departure mass (Saraux, Chiaradia, Salton, Dann, & Viblanc, 2016; Saraux et al., 2011). No corrections were made for individual sex or mass because initial investigation with linear mixed-effects models indicated neither significantly affected foraging success (sex:  $t = -0.09$ ,  $df = 183$ ,  $p = 0.92$ ; body mass:  $t = -0.80$ ,  $df = 223$ ,  $p = 0.42$ ).

### 2.3 | Breeding stage

We checked 100+ nests to record the presence of adults, eggs or chicks—three times a week at Penguin Parade and once a week at Radio Tracking Bay due to differing accessibility (Sánchez et al., 2018). This frequency was required to detect discrete breeding stages of the little penguin breeding, which can be asynchronous among nests and significantly influence their foraging range and effort (Chiaradia & Kerry, 1999; Chiaradia & Nisbet, 2006; Kato, Ropert-Coudert, & Chiaradia, 2008). Breeding stages include a ~35.5 days (Chiaradia & Kerry, 1999) 'incubation', in which adults take turns incubating their eggs for 1–7 days while the partner forages at sea (Kato et al., 2008; Numata, Davis, & Renner, 2000); a variable (~14.5 days; Chiaradia & Kerry, 1999) 'guard', where small chicks are guarded by one parent while the other forages at sea, swapping roughly daily (Chiaradia & Kerry, 1999) and a 4- to 6-week 'post-guard', where both adults forage to provision their large chicks, which are left unattended in the burrow while parents are out at sea (Saraux et al., 2016). Foraging trips during the post-guard stage can range from 1 to 2 days when food is abundant and from 2 to 5 days when food is scarce (Chiaradia & Nisbet, 2006) with adults using longer trips to self-feed and recover condition (Saraux et al., 2011). Because of the need to frequently return to the colony to feed chicks and relieve partners, foraging range is most limited during the guard stage. For the distribution of breeding stages in this data, see Figure S1.

### 2.4 | Faecal DNA metabarcoding

Each week we sampled scats from approximately 50 nests of known individuals with eggs or chicks at each site. More than 800 scat samples were collected from 159 nests over the two sites. We used 384

samples from each year (randomized within month) for analysis and extracted DNA from approximately 30 mg of each homogenized scat sample, using a Promega Maxwell® 16 instrument and Maxwell® 16 Tissue DNA Purification Kits. PCR inhibitor concentrations in DNA extracts were reduced by mixing samples with 250 µl Roche Stool Transport and Recovery (S.T.A.R.) Buffer (Roche Diagnostics) prior to extraction.

We used a two-step PCR amplification process enabling amplification of each gene region, and subsequent attachment of unique 'index tag' sequences to each sample, allowing samples to be pooled for sequencing (Binladen et al., 2007). We used a universal primer (18S\_SSU; McInnes, Alderman, et al., 2017) to assess broad diet composition; and a group-specific primer (16S\_Fish; McInnes, Jarman, et al., 2017) to provide fish species identification. Detailed methodology can be found in Cavallo et al. (2018) and Table S1.

Following sequencing, the separate forward and reverse reads were merged using the *fastq\_mergepairs* function in USEARCH v8.0.1623 (Edgar, 2010, 2013). Amplicons that did not exactly match both the forward or reverse primers (either 18S\_SSU or 16S\_Fish primer pairs) and those with the number of expected errors >1 (maxee = 1.0) were excluded. The primer sequences were removed. Sequences from each marker for all samples were then clustered into molecular operational taxonomic units (mOTUs) using the *UPARSE* algorithm (Edgar, 2010, 2013) with a cut-off threshold of 97% similarity. The sequences from each sample were assigned to these mOTUs (-usearch\_global -id 0.97) and an OTU table was generated using a custom R script. To assign taxonomy to mOTUs, we used different approaches for each marker. For 18S\_SSU, we followed the procedure outlined in Cavallo et al. (2018), which provided class-level identification based on matches in the SILVA database (Quast et al., 2013). For 16S\_Fish, sequences were resolved to the lowest possible level based on matches to sequences of locally distributed species in GenBank using the NCBI Basic Local Alignment Search Tool (BLAST: Johnson et al., 2008) and then we manually curated the output (Table S1).

Following taxonomic identification of sequences, samples were filtered to retain only food sequences (i.e. penguin, parasite and contaminant sequences were excluded). Samples with fewer than 100 food sequences were discarded because these either contained insufficient DNA to analyse or were dominated by non-target DNA so that inferences about diet would be unreliable. Similarly, samples that were slow to amplify because of low template concentration (based on real-time PCR critical threshold values) were also discarded (see Table S1 for cut-off values for each marker).

We calculated the relative read abundance (RRA) of amplicons within each sample (Deagle et al., 2019). The RRA is the percentage of each prey taxon in each sample and is calculated by dividing the number of sequence reads of an individual taxon in a scat sample by the total number of food sequence reads in that sample and multiplying by 100. This was carried out for all food items in a sample (18S\_SSU data) and for individual fish

species in a sample. (16S\_Fish data). The mean RRA for each species was calculated for each month and each breeding season overall.

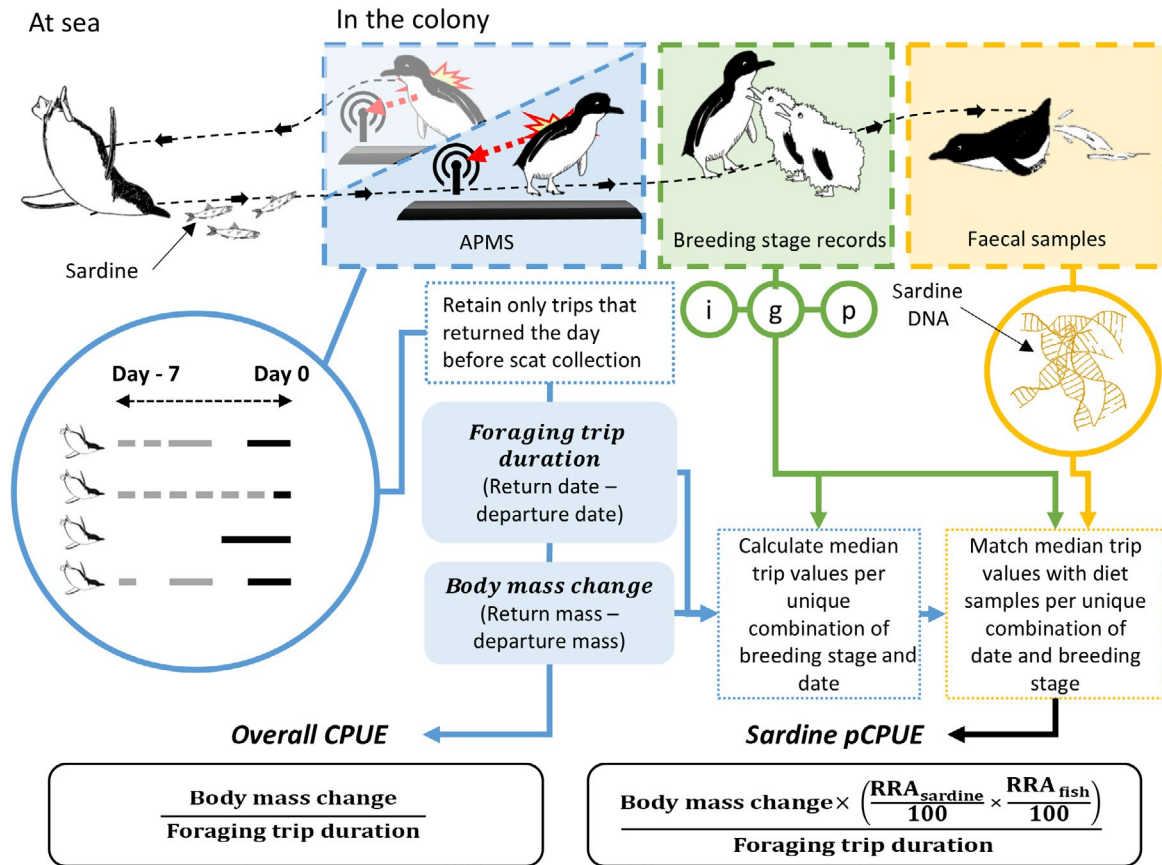
## 2.5 | Developing a prey-specific, predator-derived CPUE index (pCPUE)

We filtered APMS records so that only birds that returned on the day before each faecal sample collection were considered (Figure 1). We calculated foraging success (*body mass change* in grams) and effort (*foraging trip duration* in days) per trip. Weighbridge data can occasionally record multiple penguins crossing (recording erroneously high mass) or not detect a PIT tag (giving erroneously long foraging trips). To account for this, we retained only positive *body mass change* results <420 g (i.e. the maximum change in body mass for a foraging trip between 1 and 14 days long; Salton, Saraux, Dann, & Chiaradia, 2015) and filtered out *foraging trip durations* >7 days, which are rare for breeding little penguins as they can lead to nest desertion (Chiaradia & Kerry, 1999; Numata et al., 2000). DNA in little penguin scats presents dietary information from at least the four previous days (Deagle, Chiaradia, McInnes, & Jarman, 2010) and trip durations of breeding little penguins are usually <5 days (Chiaradia & Nisbet, 2006), especially during chick rearing (e.g. Saraux et al., 2016). We then calculated the prey-specific CPUE (g/day) of each fish species (hereafter pCPUE) and overall CPUE independent of diet (hereafter CPUE) as described by Figure 1. We used the medians for both *foraging trip duration* and *body mass change* because the data for each were skewed, and the median is less affected than the mean by extreme values in the tail. Since the differential demands of breeding stages may affect diet, all median calculations were made per breeding stage and date and then paired with diet data for birds at that breeding stage and date.

The 16s\_Fish primer only amplifies fish DNA and so only measures the fish portion of the diet. Therefore, we needed to multiply the RRA of the 16S\_Fish species sequences by the RRA of all 18S\_SSU fish sequences (Actinopterygii) in the samples to determine the proportion of each individual fish species within the total diet. The individual species RRA (e.g. sardine) values were scaled by the mean fish RRA for each breeding season (Actinopterygii: 18S\_SSU) rather than by monthly means, which could have been affected by secondary predation (Sheppard et al., 2005). See calculation example in Figure 1. The pCPUE was calculated only for fish species that accounted for more than 2% of the diet in one or more years. Code to replicate pCPUE and CPUE from weighbridge and diet data is included in the Supporting Information (Appendix S1).

## 2.6 | Estimating biomass consumption

We estimated biomass consumed by breeding little penguins in each season by multiplying the number of days spent foraging by an



**FIGURE 1** Details of the data generation and calculations of catch per unit effort (CPUE) and pCPUE (e.g. sardine). The method has three important data inputs: foraging success, which is recorded as mass change over a foraging trip, and foraging effort, which represents the duration of each foraging trip as obtained from the automated penguin monitoring system (APMS). The third input is diet composition, summarized as relative read abundance (RRA%). All inputs are averaged by breeding stage: incubation (i), guard (g) and post-guard (p)

individual breeding bird by the number of birds breeding in a season and then by the mean pCPUE of each prey species in the diet.

We estimated the number of foraging days ( $D_j$ ) undertaken by the average individual during a single nesting attempt per season  $j$  using.

$$D_j = \left( \frac{I_j + G_j}{2} \right) + P_j,$$

where  $I_j$ ,  $G_j$  and  $P_j$  are the mean number of days spent in incubation, guard and post-guard, respectively, by studied birds in season  $j$ . Note that in incubation and guard stages only one parent forages at a time, while in the post-guard stage both parents forage to provision chicks.

We then estimated the total number of birds in the population ( $N_j$ ) involved in one, two and three nesting attempts ( $i$ ) in season  $j$  as.

$$N_j = \sum_{i=1}^3 (A_{ij} \times 31,000),$$

where  $A_{ij}$  is the percentage of studied nests in season  $j$  that had at least one, two or three clutches, respectively, and 31,000 is the estimated size of the breeding population (Sutherland & Dann, 2014).

Finally, we calculated the consumption ( $C_{pj}$ ) of prey species  $p$  in season  $j$  using.

$$C_{pj} = \text{CPUE}_{pj} \times D_j \times N_j,$$

where  $\text{CPUE}_{pj}$  is the mean pCPUE of species  $p$  for season  $j$ .

The same approach was used to derive an estimate of the total prey consumption for each season.

## 2.7 | Statistical analysis

Prey availability varies both between and within years (Hobday, 1991) and central-placed foragers often display foraging differences between breeding stages, due to the varying demands placed upon them by growing offspring (Shaffer, Costa, & Weimerskirch, 2003). We used nonparametric conditional inference trees in R 3.4.4 (R Core Team, 2013) to investigate patterns in the pCPUE for individual fish species over years, months, stages and sites and to determine the relative importance of these variables. Species were gathered into a single response (*gather* function, *TIDYR* package; Wickham, 2017) and grouped by *Species*. August, February and March were dropped from analyses because they lacked observations for one or more combinations of



month and stage or month and season. Zero-inflation and overdispersion are common in environmental DNA metabarcoding data wherein many rare species are present in only a few samples and a few species dominate most samples (Xu, Paterson, Turpin, & Xu, 2015). Likelihood ratio tests (*lrtest* function, *LMTEST* package; Zeileis & Hothorn, 2002) indicated that our pCPUE data were both zero-inflated and overdispersed. Hence, we elected to investigate the complex relationships between terms using conditional inference trees (*ctree* function, *PARTY* package; Hothorn, Hornik, & Zeileis, 2006a, 2006b; Johnstone, Lill, & Reina, 2014).

We built a conditional inference tree that included *season*, *month*, *stage* and *site*. *Site* was included because birds at the two sites exhibit strong spatial foraging segregation, even though they are only 2 km apart (Sánchez et al., 2018). *Species* was included as a structural term to allow the tree to split pCPUE by prey species, rather than performing the analysis on the CPUE. We also included *burrow ID*, to determine whether repeated measures at this level had any effect on explaining variation in the data. We set the conditional inference tree to split only for  $p < 0.05$ , a conservative measure, since conditional inference trees are generally fit with a splitting structure of  $p < 0.1$ . Then, to explore the relative importance of variables, we built nonparametric random forests using *cforest* (package *PARTY*; Hothorn et al., 2006b) with controls ( $n = 100,000$  trees,  $mtry = 2$ ,  $replacement = FALSE$ ) set using the *cforest\_control* function. We retrieved the relative importance of variables from this random forest using the *varimp* function in *party* with arguments *conditional = TRUE*, *mincriterion = 0.95* and *threshold = 0.95* (Strobl, Boulesteix, Kneib, Augustin, & Zeileis, 2008).

### 3 | RESULTS

#### 3.1 | Penguin diet

The mean RRA of all fish (Actinopterygii) in the diet, identified by the 18S\_SSU primer set, was 62% in 2015–2016 and 64%

in 2016–2017 (Table 1), but individual samples varied widely. Crustacea, Mollusca, Cnidaria and Tunicata were also identified, the mean RRA of which varied over months and years. Fish had the highest RRA over both seasons, but in 2015–2016 there was moderately high RRA of salps, and in 2016–2017 moderately high RRA of calanoid copepods.

Using the 16S\_Fish primers, 82 individual fish mOTUs were isolated, with ~75 identified to genus or family levels and 50 identified to species level. Of these, 11 fish accounted for  $\geq 2\%$  of reads in the dataset in one or both years (Table 2). From September to December 2015, sardine accounted for 70%–86% of the data in each month. No single species accounted for  $>39.1\%$  of the data per month for the remainder of that breeding season. In September and October of 2016, red cod accounted for a mean RRA of 54.7% and 79.3% RRA, respectively, and in December 2016 and January 2017 barracouta accounted for 66.2% and 60.7%, mean RRA, respectively. The full 16S\_Fish diet composition is shown in Table S2.

#### 3.2 | Determining the pCPUE

Foraging success (*body mass change*) detected by the weighbridge was highly variable (Figure S2). In contrast, foraging effort was much less variable, with the median foraging effort (*trip duration*) consistently one day only (Figure S2). Consequently, CPUE (Figure 2a,b) followed foraging success closely in the years studied. The RRA of individual fish species in the penguin diet varied widely from month to month (Figure S2).

The colony maintained similar mean CPUE in both years studied ( $t = -0.47$ ,  $df = 425.14$ ,  $p = 0.64$ ). This was  $271.0 \pm SE 5.1$  g/day per individual in the 2015–2016 season and  $274.6 \pm 5.8$  g/day per individual in the 2016–2017 season. The monthly pattern appeared more variable in 2016–2017 than in 2015–2016 (Figure 2a,b).

The pCPUE of the key fish prey revealed dynamic diet and foraging behaviour over 2 years (Figure 2c,d). In October 2015,

**TABLE 1** Number of samples analysed by 18S\_SSU primer, with the relative read abundance (%) of classes that comprised  $\geq 2\%$  of the dataset in either year, split by season and month

	2015–2016							2016–2017						
	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Sep	Oct	Nov	Dec	Jan	Feb	Mar
<b>n Samples</b>	<b>8</b>	<b>57</b>	<b>53</b>	<b>49</b>	<b>54</b>	<b>5</b>	<b>28</b>	<b>24</b>	<b>81</b>	<b>67</b>	<b>17</b>	<b>20</b>	<b>9</b>	<b>6</b>
Actinopterygii	79.5	54.3	44.1	62.2	82.8	44.8 <sup>a</sup>	93.6	62	54.8	55.7	57	49.9	95.3	82
Calanoida	0.2	2.8	15.6	6.7	0.6	0	0.8	32.8	32.4	25.6	1.8	0	0.4	7.1
Copepoda (other)	0	0	0	0	0	0	0	0	0	0	34.3	18.3	0	0
Harpacticoida	2.1	7.1	1.5	1.4	0	0	0	0.1	0.3	0	0	0.2	0	0
Malacostraca	0	0	0.5	12.4	3.8	13.9	0.3	1.1	0.2	1.5	0.7	2.4	0.1	0.4
Oikopleuridae	0	0	3	7.6	7.7	11.5	2	0.8	6.2	2.9	2.5	28.8	2.8	6
Salpidae	11.9	33.1	24.4	3.3	0	0	0.9	0.2	0.5	2.5	0	0	0	0

<sup>a</sup>Low Actinopterygii RRA in January 2016 also coincided with high siphonophore RRA, of which sequences were abundant in that month but did not account for  $\geq 2\%$  of the dataset in that year.

TABLE 2 Number of samples analysed using the 16S\_Fish primer, with the relative read abundance (%) of species that comprised ≥2% of the dataset in each season, split by season and month

		2016–2017												2015–2016											
		2016						2017						2015						2016					
Common name	n Samples	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Jan	Feb	Mar	Jan	Feb	Mar	Jan	Feb	Mar	Jan
Australian sardine	5	54	86.8	70.3	75.8	24.6	3	7.6	25.5	10	5	12	1	23.1	26.6	1	23.1	26.6	1	23.1	26.6	1	23.1	26.6	
Jack mackerel	0	0	0	1.3	7.1	38.2	7.6	37.2	2.5	0	3.9	0	9.3	0.8	0.3	0	9.3	0.8	0	9.3	0.8	0	9.3	0.8	
Warehou sp.	1.5	0	0	15.2	5.4	10.1	8.7	0.6	10.1	5.9	24.8	4.2	0	0	0	0	0	0	0	0	0	0	0	0	
Barracouta	0	0	0	1.4	1.8	11	39.1	4.1	1.3	7.4	19	66.2	60.7	9.7	10.9	0	60.7	9.7	0	60.7	9.7	0	60.7	9.7	
Blue-finned leatherjacket	0	0	0	0.4	1.3	1.4	10.6	22.4	0	0	0	1.6	8.3	0	38.6	0	8.3	0	0	1.6	8.3	0	38.6	0	
Spiny gurnard	3	10	2.7	0	0.9	0	0	0	2.5	0.5	3.2	0.1	0	0	0.3	0	0	0	0	3.2	0.1	0	0	0.3	
Leatherjacket sp.	0	0	0	3.2	0.6	1.4	21.9	6.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Southern anchovy	0.4	0.9	0.3	4.2	1	2.6	6.9	0	0.2	0	0	0	1.7	14.4	2.2	0	1.7	14.4	0	0	0	1.7	14.4	2.2	
Weedfish sp.	0	0	0	1.8	0	5.2	0	1.7	0	0	0	0	9.2	0	0.4	0	9.2	0	0	0	0	0	0	0.4	
Velvet leatherjacket	0	0	0	0	0	0	0.1	0	0	0	8.4	14.5	2.9	0	0	0	2.9	0	0	0	0	0	0	0	
Red cod	7.7	0	2.3	0.6	3	2.3	0	0	54.7	73.9	29.8	0.3	0	0	0	0	0	0	0	0	0	0	0	0	
Bluespotted goatfish	—	—	—	—	—	—	—	—	0	0	0	0	2	49.2	6.6	0	2	49.2	0	0	0	2	49.2	6.6	

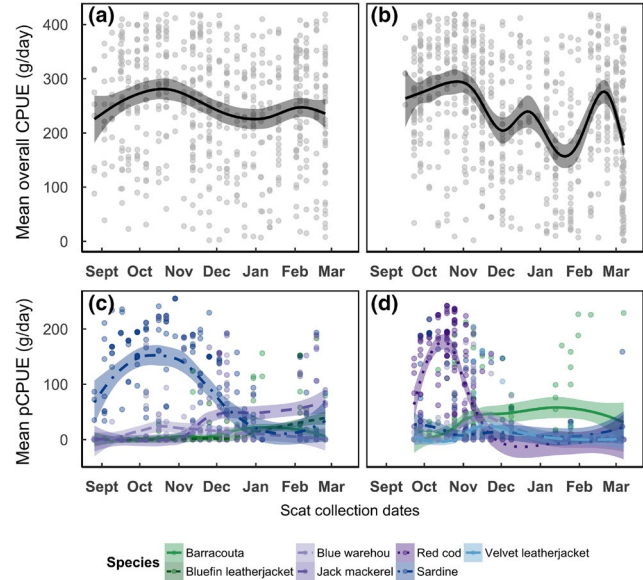
**FIGURE 2** Overall catch per unit effort (CPUE; a, b) and prey-specific catch per unit effort (pCPUE; c, d) for the 2015–2016 (a, c) and 2016–2017 (b, d) breeding seasons fitted as Loess smoothers (lines) with span = 0.75 over observed data (points). The shaded area represents the 95% confidence intervals. Note that pCPUE has a lower bound at zero and cannot assume negative values, but the smoother may extend below zero if there is a rapid transition from high to low values. Note that only the five species with the highest mean pCPUE in each season are displayed here for ease of visualization

little penguins ate a mean of  $148.4 \pm 14.0$  g/day sardine, but from December they ate a mean of  $<40$  g/day sardine and the fish component of the diet was spread across multiple species. For example, in February 2016, little penguins ate a mean of  $57.7 \pm 12.9$  g/day jack mackerel,  $41.3 \pm 11.2$  g/day bluefin leatherjacket,  $10.5 \pm 4.1$  g/day barracouta and  $21.5 \pm 9.2$  g/day sardine (Figure 2). The pCPUE of red cod showed a brief peak in October 2016 ( $165.4 \pm 7.8$  g/day) but the species was absent from December on. During February 2017, little penguins ate a mean of  $59.8 \pm 33.8$  g/day bluefin leatherjacket,  $38.4 \pm 38.1$  g/day barracouta,  $31.6 \pm 30.7$  g/day bluespotted goatfish and  $30.5 \pm 26.0$  g/day sardine.

Variable importance analysis within years showed that month was the most important explanatory variable for determining pCPUE and that other variables were not important (Figure 3a,b). The conditional inference tree in Figure 3c illustrates this further.

### 3.3 | Estimated breeding-season biomass consumption

The colony consumed an estimated  $618.0 \pm 11.7$  (M  $\pm$  SE) tonnes of fish during the 2015–2016 breeding season, and  $682.2 \pm 14.4$  tonnes in the 2016–2017 season. The sardine biomass extracted by little penguins in this colony during the 2015–2016 season was estimated



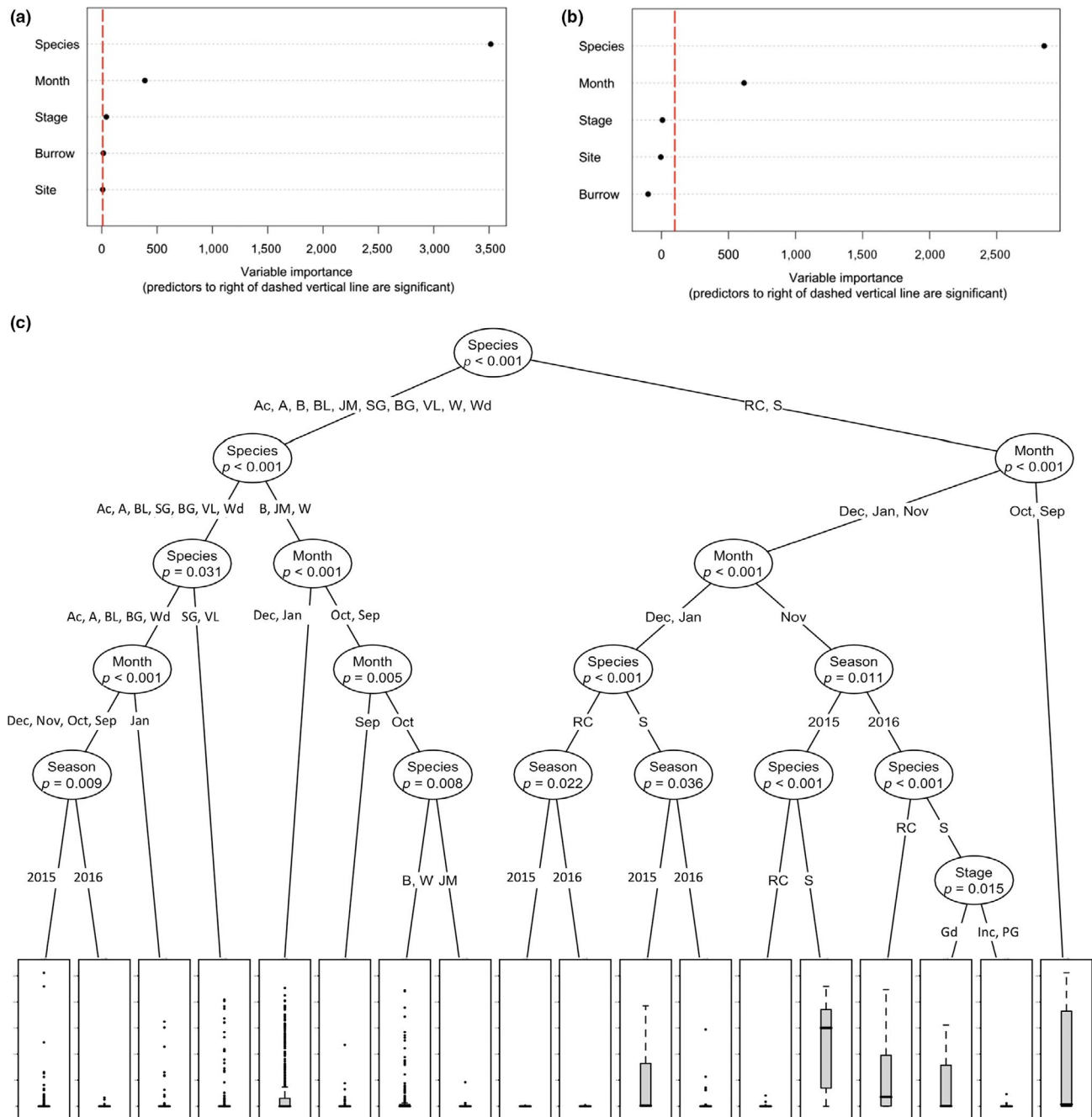
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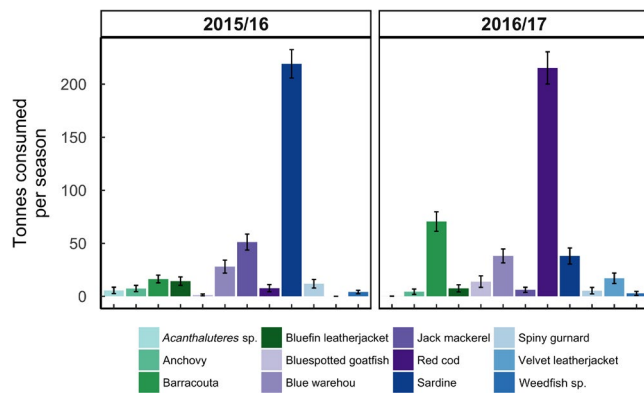


**FIGURE 3** Variable importance analysis (a, b) and conditional inference tree analysis (c) of factors explaining patterns in pCPUE. In the upper panels, conditional relative variable importance is shown for the five explanatory variables used to build the conditional inference tree for 2015/16 data (a) and 2016/17 data (b). Predictors to the right of the dashed vertical line are significant ( $p < 0.05$ ). Species was included as a structural term in both the conditional inference tree and variable importance analysis to separate pCPUE by species, to prevent the analysis being performed on the CPUE. Consequently, the influence of species on variable importance is structural only. In the lower panel, species are Ac, *Acanthaluteres* sp.; B, barracoota; BL, bluefin leatherjacket; BG, bluespotted goatfish; JM, jack mackerel; RC, red cod; S, sardine; SG, spiny gurnard; VL, velvet leatherjacket; W, warehou sp.; Wd, weedfish sp. Months are abbreviated to three letters and breeding stages are Inc, incubation; G, guard; PG, post-guard. The number of each node is shown in a small box inset in a larger oval bearing the relevant explanatory variable's name and associated p value. Categories for each split are shown immediately below the variable name box, for example, Node 1 is the first split and splits results into groups based on species, grouping sardine and red cod into one population, and all other species into another with a  $p < 0.001$ . Boxplots show pCPUE (g/day) medians, ranges and upper and lower quartiles

at  $219.1 \pm 13.4$  tonnes. Red cod biomass consumed by the colony in that year was estimated as  $7.7 \pm 3.4$  tonnes. Over the 2016–2017 season, we estimate that  $215.3 \pm 15.2$  tonnes of red cod and  $38 \pm 7.6$

tonnes of sardine were caught by Phillip Island penguins. Results for the 12 most common prey species and total catch across two breeding seasons are shown in Figure 4.





**FIGURE 4** Estimated consumption by penguins of fish species (tonnes per season  $\pm$  SE) that each constituted  $\geq 2\%$  of the total fish consumption in 2015–2016 (left) and 2016–2017 (right)

## 4 | DISCUSSION

We devised a prey-specific catch per unit effort (pCPUE) that we suggest will provide an index of prey availability for marine-predators across the spectrum of resource availability. The pCPUE allows for more direct inferences of breeding performance for marine animals such as seabirds that breed on land. It offers a more sensitive variable to detect short-term changes in the marine environment than conventional land-based variables on population demographics and reproductive success (Piatt, Harding, et al., 2007). Here, pCPUE indices varied significantly between breeding seasons, exposing a major prey shift from sardine in 2015–2016 to red cod in 2016–2017. Despite this, overall CPUE varied little between seasons, suggesting that penguins were able to maintain stable foraging effort and success despite marked changes in diet (Baudrot, Perasso, Fritsch, Giraudoux, & Raoul, 2016; Holling, 1959).

Over the study, foraging effort and success remained favourable compared with past studies (e.g. one-day vs multi-day trips; Chiaradia & Nisbet, 2006 and comparable 'meal sizes'; Saraux et al., 2011), so we interpret this pCPUE variation to index patterns of prey availability within the penguins' foraging range. Each year, a transition from a narrow to broad diversity fish diet coincided with a drop in CPUE, after which CPUE values increased to a lower peak. Higher pCPUE/CPUE values were attained during periods when a single species dominated the diet, perhaps indicating exploitation of a preferred food source that was abundantly available early in the season (Davies, 1977; Lacher Jr., Willig, & Mares, 1982). This food source may have then moved away from the penguins' feeding grounds (Birt, Birt, Goulet, Cairns, & Montevicchi, 1987), causing penguins to forage for a broader diet base (Chiaradia, Costalunga, & Kerry, 2003). It is also possible that these patterns reflect fish spawning and aggregation patterns because little penguins are gape-limited to catch mostly larval and juvenile fish ( $\sim 12$  cm: Cullen et al., 1991; Hobday, 1991) and there was concordance between pCPUE and the timing of spawning recorded by previous studies (Blackburn, 1950; Bruce, Neira, & Bradford, 2001; Sexton, Ward, & Huveneers, 2017). However, validation using simultaneous stock sampling would be necessary to investigate the source of these patterns.

Penguins typically undertook one-day foraging trips and so most variation in pCPUE was mediated through foraging success and diet composition. We expect this low foraging effort to be related to high resource availability. Concurrent measures of chick fledging rates indicated very high breeding success (chicks per pair: 2015/16 = 2.18, 2016/17 = 1.76; PINP, 2018) and, in fact, the two seasons studied were among the three most successful in the 50 years to 2017 (PINP, 2018). Above average breeding success is an accepted indicator of high resource availability onsite and elsewhere (Chiaradia & Nisbet, 2006; Kowalczyk, Chiaradia, Preston, & Reina, 2014). We anticipate foraging effort to exert greater influence over CPUE and pCPUE in lean years, when little penguins attempt to maintain foraging success by increasing trip duration during incubation (Kato et al., 2008) and post-guard reproductive stages (Chiaradia & Nisbet, 2006). High resource availability may also explain why we noted very little variation in the pCPUE between breeding stages, contrary to our expectations. Chiaradia and Nisbet (2006) found that meal-size delivered to chicks varied quadratically with chick age. Adults also start to lose mass and condition during the post-guard stage, undertaking short trips to provision young and longer trips for self-maintenance (Chiaradia & Nisbet, 2006; Saraux et al., 2016). These marked patterns are usually diminished or absent in years of high resource availability (Chiaradia & Nisbet, 2006) and we posit high resource availability as a potential cause of the lack of pCPUE variation between breeding stages.

The pCPUE enabled us to estimate the prey biomass extracted by a colony of little penguins containing >30,000 individuals. Biomass estimates like these provide insight on the effect of localized prey consumption on trophic interactions, and improve ecosystem-based management (Hansson et al., 2017). Little penguins in this region have high niche overlap with large populations of other marine predators (Bulman et al., 2012). Understanding the individual and combined impact of these major consumers will help us to plan for the sustainable future of the ecosystem and its components.

### 4.1 | A useful and adaptable index for ecosystem management

A single but robust index of prey availability, as proposed here, can assist in marine resource management (Jørgensen, 2009). We envision pCPUE time series enhancing ecological monitoring and improving inputs for ecosystem-based models for commercial stock management and threatened species conservation. For instance, pCPUE derived from predator colonies located within highly localized fisheries (Pichegru, Grémillet, Crawford, & Ryan, 2010) could provide information to ensure the sustainability of the fishery under true ecosystem-based management (e.g. Velarde, Ezcurra, & Anderson, 2013). A comprehensive picture of prey patterns over a larger region could be formed using several predator species with complementary ranges and water-column foraging depths. Adaptive management informed by pCPUE could ensure that prey resources

are maintained at a third or more of their maximum long-term biomass as has been proposed necessary to sustain seabird colonies and ecosystem resilience (Cury et al., 2011).

Fishery management is informed by estimates of stock spawning and recruitment, for which predator-derived information can fill an important gap (Scopel, Diamond, Kress, Hards, & Shannon, 2018; Velarde, Ezcurra, & Anderson, 2015). For example, red cod grow too large for little penguins to catch within a few month of spawning. They recruit to the fishery at 2 years of age and 50 cm long (Beentjes & Renwick, 2001). Therefore, a penguin-derived red cod pCPUE could be a useful predictor of cohort recruitment 2 years in advance, helping managers to set quotas accordingly (Beentjes & Renwick, 2001). We recommend that independent prey sampling be undertaken in conjunction with faecal DNA metabarcoding to validate the use of pCPUE in such a way.

Long-term pCPUE time series from generalist predators could provide information on changing prey distribution and phenology, including trends in invasive and threatened species, as well as the implications for predators, and the effectiveness of management (Boyer, Cruickshank, & Wratten, 2015). For example, we now know that >10% of seabird species consume diverse gelatinous prey (Thiebot & McInnes, 2019), some of which readily invade ecosystems and favour environments characterized by anthropogenic disturbance (Purcell, 2012; Richardson, Bakun, Hays, & Gibbons, 2009). These gelata have lower nutritional content than fish, crustaceans and squid (Cardona, Álvarez de Quevedo, Borrell, & Aguilar, 2012; Gales & Green, 1990). Rapid digestion of low energy-density gelatinous prey may allow high levels of energy assimilation to be achieved by foraging adults (reviewed in Hays, Doyle, & Houghton, 2018; Thiebot & McInnes, 2019). However, seabirds with low provisioning rates may incur reduced chick growth and fledging success if they deliver predominately nutrient-poor food to offspring (van Heezik & Davis, 1990). Linking pCPUE with levels of chick production and adult mass may be used to identify the impacts of consumption of low nutritional quality prey ('junk food', e.g. Alverson, 1992; Wanless, Harris, Redman, & Speakman, 2005).

## 4.2 | Caveats

This CPUE method relies heavily on measuring the most-appropriate parameters for the predator in question. For example, measuring foraging effort as trip duration in days is appropriate for little penguins because they are typically restricted to leaving and entering their colonies in the darkness, regardless of whether they forage for several hours, days or weeks (Daniel et al., 2007). Foraging trips of species that are not restricted in this way would be better recorded in hours (Clarke, Kerry, Irvine, & Phillips, 2002; Gaglio, Cook, McInnes, Sherley, & Ryan, 2018; Reid, Liddle, Prince, & Croxall, 1999).

The CPUE and pCPUE indices developed here are expected to be conservative. The gut passage time for a non-breeding little penguin is ~8 to 6 hr (Gales, 1988), though breeding individuals are expected to have slower passage times (Thouzeau, Peters, Le Bohec,

& Le Maho, 2004). Therefore, there will be minor information loss on trips longer than one day, resulting in a slight underestimation of foraging success (catch). Likewise, although little penguins forage throughout a trip (Ropert-Coudert et al., 2006; Sánchez, 2019), they are unlikely to be actively chasing prey for the entire time. Because we measured foraging effort as the total effort to bring a meal to their offspring (travel, search and capture), we potentially overestimate some effort. If our method is used in other systems, understanding the likely effect of such errors will require knowledge of the foraging behaviour and plasticity of the predator being employed.

Prey availability to predators may be considered a proxy for abundance (Velarde et al., 2013), but there are behavioural and environmental factors that can confound interpretation. Generalists may disproportionately feed on the most abundant prey (Jaworski, Bompard, Genies, Amiens-Desneux, & Desneux, 2013), and, when overall prey abundance is low, they may choose to target the most easily caught prey ('rank switching': Baudrot et al., 2016). If pCPUE analysis indicates that species A has declined, it may actually be that species B has become more available. For example, sardines are a primary prey for little penguins, whereas barracouta, red cod and jack mackerel are considered alternative prey (Chiaradia et al., 2016). Therefore, we could interpret the lack of sardine in the second year of the study to indicate a decline in sardine abundance or availability, but, we cannot discount a high abundance of red cod being the cause of the diet shift. The preference of individual seabirds and populations for certain prey species and sizes is another potential confounding issue for pCPUE. In this system, little penguins have diverse prey preferences, but are gape-limited to a prey-size up to ~12 cm (Cullen et al., 1991; Hobday, 1991). Therefore, we can draw inferences only on species that are present at or below this size within the colony's foraging area.

All measures of diet composition have their limitations (Bond & Jones, 2009; Deagle et al., 2019; Karnovsky, Hobson, & Iverson, 2012). In faecal DNA analysis, sources of error can include differences in digestion rates, gene copy number and amplification efficiencies, and false positives due to secondary predation (Deagle et al., 2019). Because we focus here on the fish component of the diet, error introduced by these factors is minimised. However, our estimates are affected by the proportion of fish in the diet. In some months, high RRA of crustacean or gelatinous sequences may indicate either direct or secondary predation (Sheppard et al., 2005; Thiebot & McInnes, 2019). In some cases, this likely represents targeted diet items (e.g. salps, Cavallo et al., 2018), while miniscule taxa are more likely to have been ingested within the gut of target prey (e.g. copepods and Oikopleurids, see Bowser, Diamond, & Addison, 2013). Therefore, the proportion of fish sequences in months dominated by taxa ingested through secondary predation is likely to be an underestimation. We lessened the uncertainty introduced in these months by scaling individual fish-species pCPUE by the mean proportion (RRA) of fish (Actinopterygii) in the diet in that season, rather than the monthly proportion. Consequently, we may have underestimated the pCPUE of individual fish species in some months as well as the seasonal consumption of some species. This does not affect

our estimates of total biomass extracted by the penguin population, only that of individual species and the resulting pCPUE and consumption estimates produced are conservative. Importantly, the DNA technique used here has a superior resolution to isotopic analysis or lavage (Chiaradia, Forero, McInnes, & Ramírez, 2014) despite its limitations.

Predator-derived indices of prey availability reduce our reliance on limited fisheries data. The pCPUE offers a quantitative index that allows us to make more robust inferences of foraging success for marine animals such as seabirds that breed on land. Unlike population demographics and reproductive success, the CPUE/pCPUE index is not affected by land-based changes in the nesting environment such as adverse weather, predation and human disturbance, making it more sensitive to detect changes in the marine environment.

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## AUTHORS' CONTRIBUTIONS

C.C., R.D.R., A.C., S.J., B.E.D., Y.R.-C. and G.C.H. conceived the project; C.C. and S.S.-G. performed the fieldwork; C.C. lead the laboratory analysis; B.E.D. and J.C.M. assisted with bioinformatics; C.C. conducted the statistical analysis and led the writing with contributions from all authors.

## ETHICS STATEMENT

This research was conducted under an Ethics Approval No. 2.2014 approved by Phillip Island Nature Parks Animal Ethics Committee number and Research Permit No. 10006148 from the Department of Environment, Land, Water and Planning of Victoria, Australia.

## DATA AVAILABILITY STATEMENT

Datasets and code to execute the pCPUE method are available in the FigShare repository at the following: 18s\_SSU sample library: <https://doi.org/10.26180/5ea7d9b786c4e>; 16s\_Fish sample library: <https://doi.org/10.26180/5ea7e0b0295b0>; APMS weighbridge data: <https://doi.org/10.26180/5ea7da58da29f>; Scat collection data: <https://doi.org/10.26180/5ea7dbaa1c190>; R Code: <https://doi.org/10.26180/5ea7dc0a4275b>.

## ORCID

Catherine Cavallo  <https://orcid.org/0000-0002-5451-8943>  
 André Chiaradia  <https://orcid.org/0000-0002-6178-4211>  
 Bruce E. Deagle  <https://orcid.org/0000-0001-7651-3687>  
 Graeme C. Hays  <https://orcid.org/0000-0002-3314-8189>

Simon Jarman  <https://orcid.org/0000-0002-0792-9686>

Julie C. McInnes  <https://orcid.org/0000-0001-8902-5199>

Yan Ropert-Coudert  <https://orcid.org/0000-0001-6494-5300>

Sonia Sánchez  <https://orcid.org/0000-0002-5850-694X>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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