

Understanding common dolphin and Australasian gannet feeding associations from nutritional and ethological perspectives

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Prey detection and subsequent capture is considered a major hypothesis to explain feeding associations between common dolphins and Australasian gannets. However, a current lack of insight on nutritional strategies with respect to foraging behaviours of both species has until now, prevented any detailed understanding of this conspecific relationship. Here we combine stomach content analysis (SCA), nutritional composition of prey, a multidimensional nutritional niche framework (MNNF) and videography to provide a holistic dietary, nutritional, and behavioural assessment of the feeding association between dolphins and gannets in the Hauraki Gulf, New Zealand. Dolphins consumed ten prey species, including grey mullet (*Mugil cephalus*) as the most representative by wet mass (33.4%). Gannets preyed upon six species, with pilchards (*Sardinops pilchardus*) contributing most of the diet by wet mass (32.4%) to their diet. Both predators jointly preyed upon pilchard, jack mackerel (*Trachurus* spp.), arrow squid (genus *Nototodarus*), and anchovy (*Engraulis australis*). Accordingly, the MNNF revealed a moderate overlap in the prey composition niche (0.42) and realized nutritional niche (0.52) between dolphins and gannets. This suggests that both predators coexist in a similar nutritional space, while simultaneously reducing interspecific competition and maximizing the success of both encountering and exploiting patchily distributed prey. Behavioural analysis further indicated that dolphin and gannets feeding associations are likely to be mutually beneficial, with a carouselling foraging strategy and larger pod sizes of dolphins, influencing the diving altitude of gannets. Our approach provides a new, more holistic understanding of this iconic foraging relationship, which until now has been poorly understood.

Keywords: *Delphinus delphis*, *Morus serrator*, multidimensional nutritional niche framework, foraging, mutualism, marine predators, Hauraki Gulf, SDG14.

Introduction

Enhanced feeding capabilities (i.e. facilitation of prey detection and capturing of food items that may be available to individuals) has been highlighted as a major hypothesis to explain heterospecific feeding associations (Morse, 1977). These temporary relationships are regarded as a major adaptive advantage in marine environments, especially when prey is patchily distributed and/or difficult to detect (Fauchald *et al.*, 2000). From the tropics to temperate and polar regions worldwide, heterospecific associations in marine environments are widespread in various taxa, including fish–octopus, fish–fish, seabirds–seabirds, seabirds–pinnipeds, seabirds–fish–cetaceans, and seabirds–sharks–cetaceans–pinnipeds (reviewed in Gatti *et al.*, 2021). Considerable attention has been given to the interactions between cetaceans and seabirds globally (Evans, 1982; Camphuysen and Webb, 1999; Vaughn *et al.*, 2007, 2010, 2011; Sutton *et al.*, 2019; Towers and Gasco, 2020). However, quantifying the currencies of these relationships (e.g. behaviours involved, energetic budget, spatial and temporal investment) in free-ranging predators remains notoriously challenging.

To understand the nature of heterospecific feeding associations in wild, highly mobile predators, models will benefit from information on species' properties that both influ-

ence individual fitness and shape responses to their environment (i.e. functional traits) (Kearney *et al.*, 2010; Houlihan *et al.*, 2017). Feeding related traits (e.g. food consumption, prey composition, and ecological niche) and behavioural strategies (degree of sociability and cooperation in foraging strategies) could provide fundamental insights into heterospecific feeding aggregations if studied in unison. Given that animal behaviour and physiological characteristics relate to the acquisition of nutrients and energy (Raubenheimer *et al.*, 2009), an integrated standardize approach is required to understand the complexities of these interactions and provide transferable ecological fresh insights. By integrating behaviour, nutrition and physiology, a multidimensional nutritional niche framework (MNNF, Machovsky-Capuska *et al.*, 2016a) provides a nutrient lens to the prey and diets consumed by organisms within an ecological niche context (i.e. prey composition and realized nutritional niches). Thus, understanding the nutritional requirements and foraging strategies of marine vertebrate predators is important, in order to predict how a species interacts with different trophic levels and their environment (Machovsky-Capuska and Raubenheimer, 2020).

Several studies on seabirds (Machovsky-Capuska *et al.*, 2018; Machovsky-Capuska and Raubenheimer, 2020), preda-

Received: April 6, 2022. Revised: June 19, 2022. Accepted: June 25, 2022

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tory fish (Machovsky-Capuska and Raubenheimer, 2020), turtles (Machovsky-Capuska et al., 2020a; Santos et al., 2020), cetaceans (Denuncio et al., 2017; Machovsky-Capuska and Raubenheimer, 2020; Machovsky-Capuska et al., 2020b), pinnipeds (Machovsky-Capuska and Raubenheimer, 2020; Denuncio et al., 2021), and sharks (Machovsky-Capuska and Raubenheimer, 2020; Grainger et al., 2020), have increasingly applied the MNNF to (i) understand how marine predators adjust their foraging behaviour and nutritional goals to environmental fluctuations (Machovsky-Capuska et al., 2018); (ii) explore the nutritional consequences of consuming plastics and anthropogenic pollutants (Machovsky-Capuska et al., 2019, 2020a, b; Santos et al., 2020, 2021; Stockin et al., 2021a, b); and (iii) disentangle the dynamics that facilitates coexistence with other sympatric species (Denuncio et al., 2021), and examine how they are likely to interact with humans (Grainger et al., 2020).

The Hauraki Gulf/Tikapa Moana, North Island, New Zealand, provides a quintessential coastal environment characterized by heterospecific feeding associations involving dynamic bait-ball that often composed of pilchards (*Sardinops pilchardus*), anchovies (*Engraulis australis*) or Jack mackerel (*Trachurus* spp.) (Stockin et al., 2008a; Wiseman et al., 2011; Purvin, 2015; Gostischa et al., 2021). Among these multiple sympatric predator–prey interactions, common dolphins (*Delphinus delphis*; hereafter dolphins) and Australasian gannets (*Morus serrator*; hereafter gannets) represent one of the most frequently observed associations during feeding events (Burgess, 2006; Stockin et al., 2008a, b, 2009a; de la Brosse, 2010; Purvin, 2015) and can serve as a model to understand the behavioural, ecological, and evolutionary dimensions of such interactions. While the local diet of both predators is well characterized (Meynier et al., 2008a; Machovsky-Capuska et al., 2011a; Tait et al., 2014; Peters et al., 2020), a current lack of insight on their nutritional strategies with respect to foraging behaviours has prevented any detailed understanding of this conspecific relationship until now.

Here, we combine dietary analysis (i.e. stomach content analyses [SCA]), nutritional composition of prey, the MNNF with Bayesian multivariate ellipses and videography to provide a holistic dietary, nutritional, and ethological assessment of the feeding association between dolphins and gannets in the Hauraki Gulf, New Zealand. In particular, we aim to (i) compare the prey, diets, and niche breadths of dolphins and gannets through a nutritional lens, specifically by (ii) exploring whether dolphin foraging behaviours influence gannet diving strategies.

Material and methods

Study area

The Hauraki Gulf is a shallow coastal feature of the North Island of New Zealand, which encompasses an area of ~4 000 km² and a maximum water depth ~60 m. Surrounded by the Auckland region, the Hauraki Plains, the Coromandel Peninsula, and Great Barrier Island, this semi-enclosed body of water is riddled with islands and shallow reefs that extend into waters of the western Pacific Ocean. Water circulation in the gulf is primarily driven by tides and wind (Heath, 1985; Gaskin and Rayner, 2013) and, accordingly, has historically been an area of high primary productivity (Zeldis et al., 2004), subject to large environmental fluctuations (Srinivasan et al., 2015).

Sampling procedures and SCA

During 2009 and 2010, the diet of adult (physically mature, >1.8 m) dolphins ($n = 18$) and adult, non-breeding gannets ($n = 22$) were assessed using SCA of carcasses opportunistically collected as beachcast or dead floating in the waters of the Hauraki Gulf (36°51'S, 174°46'E), north of Auckland city. Only carcasses deemed to be of fresh or mild decomposition (Stockin et al., 2009b) were included in this study.

Post-mortem sampling of gannets followed standardized avian protocols (Work, 2000). In summary, carcasses were typically stored frozen until subsequent examination. Upon dissection, individual prey items were extracted from the upper gastrointestinal tract including the oral cavity, oesophagus, and stomach. All ingested prey items were individually weighed to 0.1 g, and stomach contents subsequently rinsed through a 0.25-mm-mesh sieve until clean to extract diagnostic prey remains, predominantly fish otoliths and cephalopod beaks (Wingham, 1985; Duffy and Jackson, 1986).

Dolphins were examined post-mortem using standardized protocols (Stockin et al., 2009b). The gastrointestinal tract was ligated and the extracted for subsequent analysis. Stomach contents of each dolphin were carefully rinsed through a 0.25-mm-mesh sieve. Diagnostic hard parts (predominately otoliths and cephalopod beaks with some jaw bones) were identified to the lowest possible taxonomic level using the reference collection (Massey University, following Meynier et al., 2008a) and published guides (Clarke, 1986; Smale et al., 1995). Prey size and mass for each species were further estimated at an accuracy of 0.5 mm, using regression equations from the literature (Smale et al., 1995; Fea et al., 1999; Lu and Ickeringill, 2002) based on otolith length (or width when the tip was broken), lower beak rostral length (LRL) for squid, or lower beak hood length (LHL) for octopods and sepiolids, as outlined by Meynier et al. (2008a). Prey size and mass were then subsequently used to estimate the percentage of total prey wet mass that the species contributed to the overall diet (M%, wet weight).

Proximate composition analysis

For prey species that contributed >1% wet mass to the diets of both dolphins and gannets, we collected 30 individual samples from 7 species for subsequent proximate composition analyses. We further extracted proximate compositional data from Tait et al., (2014) for the remaining three species (Table 1). Carbohydrates are known to constitute a negligible content on squid and marine fish species (Craig et al., 1978), thus we measured the proximate composition of protein (P), lipid (L), water (W), and ash (A). Following Bligh and Dyer (1959), we further measured total L (ether extract), whereas Kjeldahl analysis was used to measure total nitrogen (N) and then converted into P ($N \times 6.25$, AOAC 981.10, AOAC, 2005). A convection oven at 125°C was used to dry samples and estimate W from their moisture loss (AOAC 950.46; AOAC, 2002). Ash was measured by the ignition of samples in a furnace at 550°C (AOAC 920.153; AOAC, 2005).

Video footage collection and behavioural analysis

Behavioural analysis was performed on aerial video footage of dolphin and gannet feeding associations in the Hauraki Gulf involving 13 feeding events (totalling 40 min duration) collected during 2010. Video footage was collected using a Canon XH A1S high-definition video camera (25 frames s⁻¹)

Table 1. Dietary importance of prey items expressed as wet mass, proximate composition, and energy content of common dolphins (CD) and Australasian gannets (AG) in the Hauraki Gulf, New Zealand. Note: N = sample size.

| Common name | Scientific name | Mass % | | N | Proximate composition (wet mass %) | | | | Energy content (Kj g ⁻¹) | | | References |
|-------------------|-------------------------------|--------|-------|---|------------------------------------|-------|-------|-----------|--------------------------------------|------|------|---------------------------|
| | | CD | AG | | L | P | W | P:L ratio | P_E | L_E | T_E | |
| Grey mullet | <i>Mugil cephalus</i> | 33.40 | – | 3 | 6.50 | 16.80 | 74.20 | 2.58 | 2.41 | 2.86 | 5.26 | Present study |
| Pilchard | <i>Sardinops pilchardus</i> | 28.64 | 32.38 | 6 | 1.16 | 17.64 | 80.00 | 15.21 | 0.43 | 3.00 | 3.43 | Tait <i>et al.</i> (2014) |
| Jack mackerel | <i>Trachurus</i> spp. | 26.58 | 6.18 | 6 | 1.20 | 18.30 | 79.30 | 15.25 | 0.44 | 3.11 | 3.56 | Tait <i>et al.</i> (2014) |
| Arrow squid | <i>Nototodarus</i> spp. | 7.56 | 2.32 | 5 | 1.81 | 17.10 | 79.90 | 9.45 | 0.67 | 2.91 | 3.58 | Present study |
| Snapper | <i>Pagrus auratus</i> | 3.01 | – | 3 | 1.94 | 21.95 | 74.04 | 11.31 | 0.72 | 3.73 | 4.45 | Present study |
| Garfish | <i>Hyporhamphus ibi</i> | 0.33 | – | 5 | 8.04 | 20.83 | 69.32 | 2.60 | 2.97 | 3.54 | 6.52 | Present study |
| Anchovy | <i>Engraulis australis</i> | 0.20 | 14.14 | 5 | 3.22 | 16.30 | 79.30 | 5.09 | 1.19 | 2.77 | 3.96 | Present study |
| Bobtail squid | <i>Sepioidae</i> spp. | 0.15 | – | – | – | – | – | – | – | – | – | No data |
| Conger eel | <i>Congridae</i> spp. | 0.06 | – | – | – | – | – | – | – | – | – | No data |
| Broad squid | <i>Sepioteuthis australis</i> | 0.06 | – | 5 | 1.21 | 14.50 | 83.10 | 11.98 | 0.45 | 2.47 | 2.91 | Present study |
| Yellow eye mullet | <i>Aldrichetta forsteri</i> | – | 27.45 | 5 | 6.08 | 16.80 | 75.92 | 2.76 | 2.25 | 2.86 | 5.11 | Tait <i>et al.</i> (2014) |
| Kahawai | <i>Arripis trutta</i> | – | 17.52 | 3 | 4.89 | 19.15 | 74.03 | 4.06 | 1.81 | 3.26 | 5.06 | Present study |

Table 2. Behavioural characteristics of the different feeding events and workups encountered in the Hauraki Gulf, New Zealand.

| Feeding Events | Workups | Predators presence | Group size | | Behaviours |
|----------------|---------|--------------------|------------|---------|------------|
| | | | Dolphins | Gannets | |
| 1 | 1 | DG | <100 | <100 | C-SD-LA |
| 2 | 1 | DG | <100 | <100 | C-SD-LA |
| 3 | 1 | DG | <100 | <100 | C-SD-LA |
| 4 | 2 | G | – | <100 | – |
| 5 | 1 | G | – | <100 | – |
| 6 | 1 | G | – | <100 | – |
| 7 | 1 | G | – | <100 | – |
| 8 | 1 | G | – | <100 | – |
| 9 | 1 | G | – | <100 | – |
| 10 | 2 | DG | ≥100 | ≥100 | C-SD-LA |
| 11 | 2 | DG | ≥100 | ≥100 | C-SD-LA |
| 12 | 1 | DG | ≥100 | ≥100 | C-SD-LA |
| 13 | 1 | DG | ≥100 | ≥100 | C-SD-LA |

Abbreviations: D: dolphins; G: gannets; C: carouseling; SD: synchronous diving; LA: line-abreast.

with a 20 mm zoom lens, at a consistent height of 5 m above the water surface on board the *Dolphin Explorer*, a 20-m commercial dolphin-watching catamaran operated 4.5 h trips daily. Foraging events were also observed using 8 × 40 Pentax handheld binoculars and characterized as follows: (i) the species present (e.g. dolphins and gannets vs. gannets only), (ii) the number of foragers (gannets: <100 and ≥100, and dolphins: <100 and ≥100), (iii) the number of workups they formed, and (iv) their different foraging strategies (Table 2). The upper limit of both gannets and dolphins was considered when making group size estimates, taking into consideration fission/fusion events (Burgess, 2006; Stockin *et al.*, 2008a). All group size and behavioural observations were conducted by a single observer to avoid inter-observer bias.

Feeding events were defined as temporary groups of predators that assemble to exploit patches of prey. Workups were defined as highly intense gannet diving events within a confined spatiotemporal area in a feeding event (Purvin, 2015). Thus, it is possible that a feeding event comprised several workups. The beginning of each workup, either in the presence or absence of dolphins, was marked by the initiation

of the diving activity by aerial plummeting gannets, until the birds stopped diving in the same area (Burgess, 2006). Following Neumann and Orams (2003) and Burgess (2006), the dolphin foraging strategies were classified as (i) *carouseling*, when dolphins circulate the perimeter of the bait-ball keeping the fish stationary and densely concentrated at the water surface; (ii) *line-abreast*, where a foraging group of dolphins cooperatively drives prey ahead of them; and (iii) *synchronous diving*, in which many members of a foraging group dive simultaneously and resurface in synchrony under fish schools.

Gannets were tracked at a constant zoom with the horizon included as a frame of reference to allow determination of the position of each individual relative to the horizontal plane (Land, 1999). Following Machovsky-Capuska *et al.* (2011b), a mean body length of 89 cm for adult gannets was used as a size reference for individual plunge diving height estimations recorded as either <5 or ≥5 m above the water surface. Dives were classified as “synchronous” when multiple aerial gannets plunge into the water simultaneously and “solo” when only one individual gannet was involved (Machovsky-Capuska, 2012).

Data analysis

Proportions-based Nutritional Geometry (PNG, Raubenheimer, 2011) combined with Bayesian multivariate ellipses (Jackson *et al.*, 2011) and the MNNF (Machovsky-Capuska *et al.*, 2016a) were used to explore the three-dimensional relationships between the wet mass proportions of P, L, and W from prey species, diets, and niches of both dolphins and gannets. Following Machovsky-Capuska *et al.* (2016a), the variety of prey compositions eaten are known as prey composition niche, whereas the diets composed of consuming different prey are known as realized nutritional niches. To estimate the prey composition and realized nutritional niche breadths of dolphins and gannets from proportional data, we combined the MNNF with standard ellipse areas for small sample sizes (SEAc, Syväranta *et al.*, 2013), following Machovsky-Capuska *et al.* (2018).

Differences in SEAc between dolphins and gannets (prey composition niches and realized nutritional niches) were assessed by producing a range of possible posterior estimates (SEAb). These estimated resulted from 2×10^4 iterations with two chains, a burning of 1×10^3 and thinning of 10, using Markov chain Monte Carlo simulations combined with Bayesian inference (Grainger *et al.*, 2020). The *maxLikOverlap* function was subsequently applied to estimate the proportional overlap area between two ellipses (overlap ellipses were equal to 1, whereas distinctive ellipses were equal to 0) (SIBER package, Jackson *et al.*, 2011). We considered ≥ 0.60 as a significant overlap (Schoener, 1968 and Guzzo *et al.*, 2013), >0.31 – 0.59 as moderate overlap and low overlap as ≤ 0.30 .

Levene's test for homoscedasticity and Shapiro–Wilk's test for normality were initially applied to the data. We converted P and L wet masses to energy (E) values using $P = 17$ and $L = 37 \text{ kJ g}^{-1}$ (N.R.C., 1989). To explore whether the nutritional composition (logit transformed wet mass proportions of P, L, W, the protein-to-lipid ratio P:L and energy (E)) of prey and diets differ between predators, we fitted linear models (LMs) using the *lm* function (Bates *et al.*, 2015) with the nutritional composition from prey and diets as the response.

Video footage of *feeding events* and *workups* was analysed frame-by-frame using Avidemux v2.6. Possible correlations between characteristics of dolphin behaviours, group sizes, and gannet diving behaviours (height, degree of synchronization) were examined using General Estimating Equations (GEE) with binomial distribution (GEE's; *geepack* Package, Liang and Zeger, 1986; Højsgaard *et al.*, 2006). Following Pan (2001), we assessed model fit using the quasi likelihood under the independence model criterion (QIC), with the lowest value model signalling the best fit. GEE tests were nested using *feeding event* and *workup* categories to account for the inability to identify individual gannets between *workups* and the inherent correlation between gannet behaviours within the same group, by including an additional variance component for correlation structure within the data clusters. Data are reported as mean and standard error. All analyses were performed using the statistical software environment R4.1.2 (R Core Team, 2021).

Results

A total of 40 stomachs were examined including gannets ($n = 22$) and dolphins ($n = 18$). For all the individuals exam-

ined, the presence of undigested prey in the upper gastrointestinal track supports mortality of an acute as opposed to chronic nature (i.e. from a prolonged underlying health or disease mechanism; Stockin *et al.*, 2009b). Non-breeding adult male ($n = 17$) and female ($n = 5$) gannets were collected on the beach or dead floating on the water. While a mixture of sexually immature ($n = 11$) and mature ($n = 7$) dolphins were included in this study, all individuals were physically mature based on total body length. Sample size restricted our ability to consider the effect of sex and year on diet.

Diet composition and nutritional niche breadths of dolphins and gannets

Dolphins consumed 10 prey species, with only 5 species contributing $>1\%$ wet mass, including grey mullet (*Mugil cephalus*) as the most representative by wet mass (33.40%). Gannets preyed upon six species that all contributed $>1\%$ mass, with pilchards contributing most to their diet by wet mass (32.38%; Table 1). Across all the prey species consumed, both predators ingested pilchard, jack mackerel, arrow squid (genus *Nototodarus*) and anchovy.

Prey consumed by dolphins had an energy content that ranged from 2.91 to 6.52 kJ g^{-1} and a wet mass P:L = 2.58:1.0 to P:L = 15.25:1.0, whereas the prey consumed by gannets ranged from 3.43 to 5.11 kJ g^{-1} and wet mass P:L = 2.76:1.0 to 15.25:1.0 (Table 1, Figure 1). No differences were observed in the wet mass proportional composition of P (LM, $F_{1,66} = 0.30$, $p = 0.59$), L (LM, $F_{1,66} = 0.07$, $p = 0.79$), W (LM, $F_{1,66} = 0.38$, $p = 0.54$), and PL (LM, $F_{1,66} = 0.01$, $p = 0.91$) or the total energy content (LM, $F_{1,66} = 0.16$, $p = 0.69$) of the prey consumed by dolphins and gannets. A comparison of the prey composition niche breath (SEAc) between predators demonstrated that dolphins (16.4) had a significantly broader niche breadth compared to gannets (6.9) (Probability $\text{SEAb}_{\text{dolphin}} > \text{SEAb}_{\text{gannet}} = 0.99$, <0.05), with a 0.42 degree of overlap between niches (Figure 1).

The nutritional composition of diets of dolphins and gannets ranged from P:L = 2.8:1.0 to 15.3:1.0 (Figure 2). The estimated wet mass composition of the diet of dolphins was $17.79 \pm 0.35\%$ P, $2.91 \pm 0.41\%$ L, $77.80 \pm 0.69\%$ W, and P:L = 10.38 ± 0.15 , whereas for gannets, this was $17.55 \pm 0.20\%$ P, $2.77 \pm 0.35\%$ L, $78.39 \pm 0.42\%$ W, and a P:L = 10.22 ± 1.25 . A comparison of the diets between dolphins and gannets suggested no differences in the mass proportion of P (LM, $F_{1,38} = 0.11$, $p = 0.74$), L (LM, $F_{1,38} = 1.78$, $p = 0.19$), W (LM, $F_{1,38} = 0.49$, $p = 0.49$) and the P:L (LM, $F_{1,38} = 0.87$, $p = 0.36$). The realized nutritional niche breath (SEAc) of dolphins (3.0) was significantly narrower than the niche of gannets (5.7) (probability $\text{SEAb}_{\text{dolphin}} < \text{SEAb}_{\text{gannet}} = 0.97$, <0.05), showing a 0.52 degree of niche overlap between predator (Figure 2).

Foraging behaviours that shape dolphin and gannet interactions

Behavioural analysis of the 40 min of video footage revealed 13 feeding events that included 16 independent workups (Table 2), thus accounting for a field effort of 3 510 min (~ 58 h). From the total number of workups recorded, 50% ($n = 8$) involved the presence of dolphins and gannets, and 50% ($n = 8$) involved gannets foraging alone. Group sizes of dolphin and gannet associations varied from <100 individuals (33.3%, $n = 3$) to ≥ 100 individuals (66.7%, $n = 6$).

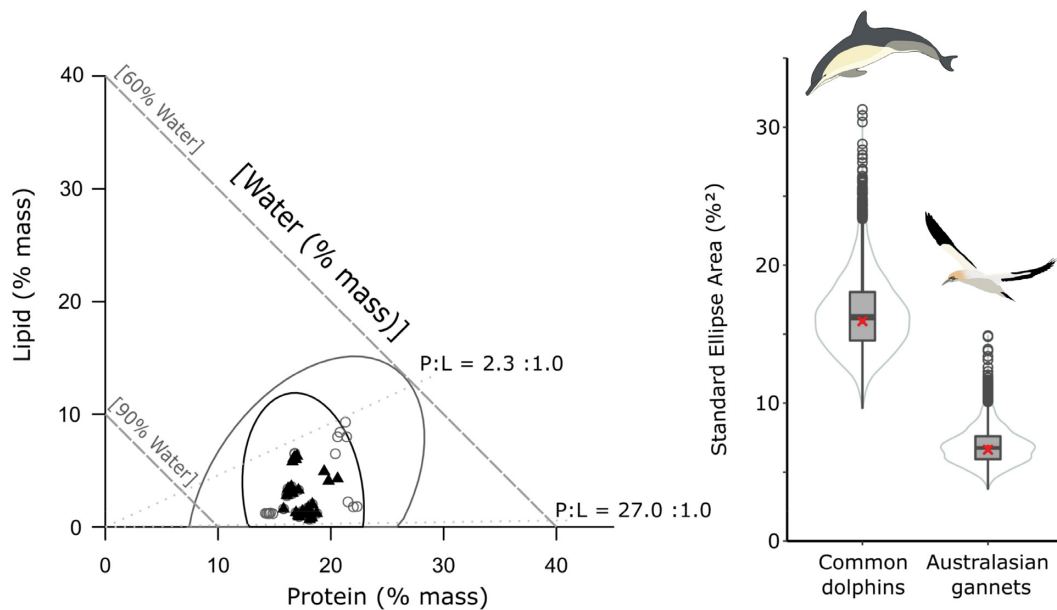


Figure 1. The prey composition niches (established by the range of prey consumed by a species, sensu Machovsky-Capuska et al., 2016a) for dolphins and gannets in the Hauraki Gulf, New Zealand. Left: Proportions Nutritional Geometry (PNG) showing the nutritional composition of prey consumed by common dolphins (grey hollow circles) and Australasian gannets (black triangles) and the differences in their niche breadths measured as the small sample corrected standard ellipse areas (SEAc) for dolphins (SEAc: 16.4, grey ellipse) and gannets (SEAc: 6.9, black ellipse). Right: Violin plots (box plots combined with mirrored kernel densities) comparing the Bayesian SEA estimates (SEAb) for the prey composition niches of each species. Maximum-likelihood estimated SEAc is indicated by red crosses, whereas SEAb is shown by red dots.

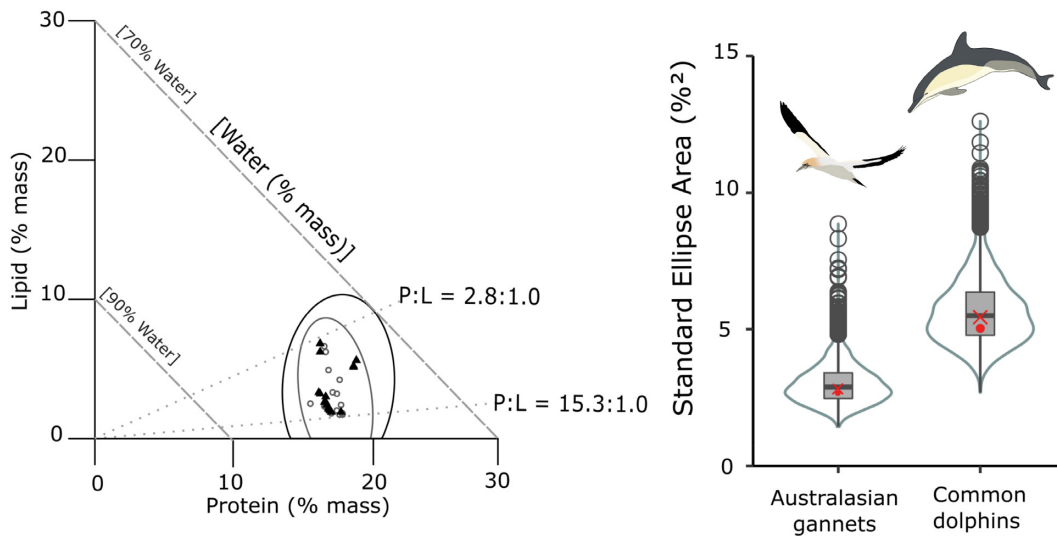


Figure 2. The realized nutritional niches (the range of diets composed by feeding on different prey, sensu Machovsky-Capuska et al., 2016a) for dolphins and gannets in the Hauraki Gulf, New Zealand. Left: Proportions Nutritional Geometry (PNG) showing the nutritional composition of individual diets consumed by dolphins (grey hollow circles) and gannets (black triangles) and their distinct niche breadths estimated as the small sample corrected standard ellipse areas (SEAc) for dolphins (SEAc: 3.0, grey ellipse) and gannets (SEAc: 5.7, black ellipse). Right: Violin plots (box plot combined with mirrored kernel densities) comparing the Bayesian SEA estimates (SEAb) for the realized nutritional niches of dolphins and gannets. Maximum-likelihood estimated SEAc is indicated by red crosses, whereas SEAb is shown by red dots.

During all workups, we recorded 1 652 gannet dives, from which 79% ($n = 1299$) were in the presence of dolphins and 21% ($n = 353$) with birds foraging alone. From the total number of dives registered, 75.1% ($n = 1241$) commenced at ≥ 5 m above sea level, with only 24.9% ($n = 412$) of dives occurring at < 5 m. The size of gannet diving groups was significantly influenced by the presence of dolphins (GEE: Wald $\chi^2 = 53\,337.2$, $p < 0.0001$). However, no differences were ob-

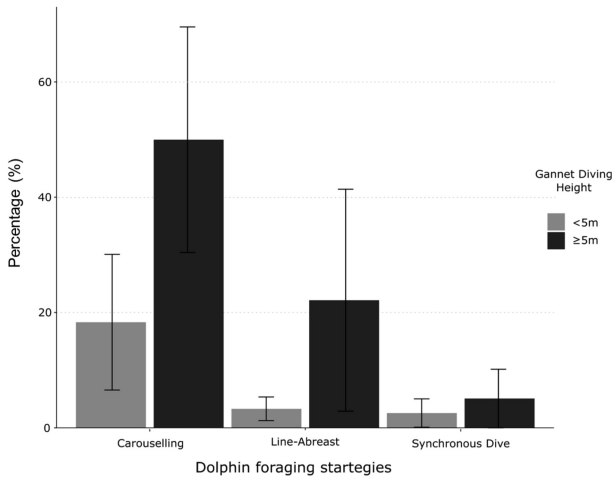
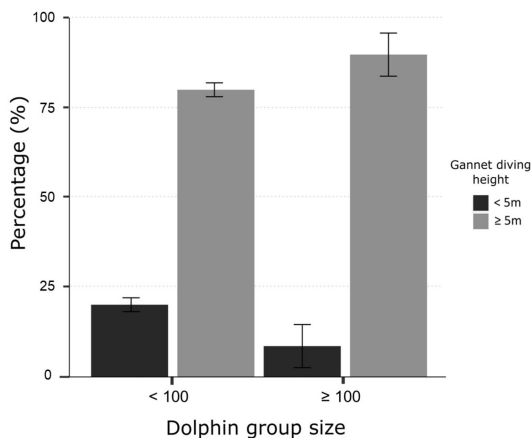
served in the heights and synchronization of gannet dives with and without dolphin engagement (respectively, GEE: Wald $\chi^2 = 3.3$, $p = 0.07$; Wald $\chi^2 = 0.0$, $P = 0.89$).

Our analysis revealed that the foraging strategies of dolphins do affect gannet diving behaviour. Specifically, the carousel foraging strategy used by dolphins significantly increased the proportion of gannet dives ≥ 5 m (GEE: Wald $\chi^2 = 35.05$, $p < 0.001$, Table 3, Figure 3). Although not sig-

Table 3. Relationships between dolphin foraging strategies and group size with the degree of gannet diving synchronization and dive heights.

| | | Effect size | SE | Wald | <i>p</i> |
|-----------------|------------------------|--------------|-------------|--------------|--------------------|
| Diving height | ~ Carouselling | -1.86 | 0.31 | 35.05 | < 0.0001 |
| | ~ Synchronous dive | -0.22 | 0.6 | 0.14 | 0.71 |
| | ~ Line-abreast | 1.73 | 0.93 | 3.47 | 0.06 |
| | ~ Dolphin group (>100) | 4.78 | 0.82 | 34.14 | < 0.0001 |
| Synchronization | ~ Carouselling | 0.19 | 0.24 | 0.64 | 0.42 |
| | ~ Synchronous dive | 0.08 | 0.79 | 0.01 | 0.92 |
| | ~ Line-abreast | 0.11 | 0.73 | 0.02 | 0.88 |
| | ~ Dolphin group (>100) | -0.12 | 0.74 | 0.03 | 0.87 |

Significant differences are represented in bold.

**Figure 3.** The relationship between dolphin foraging strategies and gannet diving heights (m). Bars represent standard error (± 2SE).**Figure 4.** Dolphin group size influences the percentage of plunge diving heights (m) performed by gannets. Bars represent standard error (± 2SE).

nificant (GEE: Wald $\chi^2 = 3.47$, $p = 0.06$, Table 3), a similar trend was also evident when dolphins adopted a line-abreast behaviour foraging strategy. No relationship was observed between synchronous diving in dolphins and gannet diving heights or between the different dolphin foraging strategies and the degree of synchronization of gannet dives (Table 3). Our findings also showed that dolphin group size influenced the percentage of plunge diving heights performed by gannets (GEE, Wald $\chi^2 = 34.1$, $p < 0.0001$, Table 3, Figure 4).

Discussion

Interactions between marine apex predators may have a significant role on the structuring and functioning of their communities (Ritchie and Johnson, 2009; Baum and Worm, 2009). Given that both dolphins and gannets play a key role in driving ecological interactions (Stockin *et al.*, 2008a; Machovsky-Capuska *et al.*, 2016b) and serve as bio-monitor species (Srinivasan *et al.*, 2015; Stockin *et al.*, 2021a, b), an understanding of the extent of these relations and their ecological role, is important to preserve healthy marine ecosystems. Our study provides nutritional and ethological perspectives, that reveal how foraging strategies of dolphins shape these multispecies interactions while feeding on patchily distributed marine prey.

A nutritional lens to dolphin and gannet feeding associations

Current understanding of the diet of marine predators has been achieved using different indirect techniques (e.g. SCA, faeces, regurgitations, stable isotopes, fatty acids, and DNA metabarcoding), that are known for their individual advantages and limitations (reviewed in Young *et al.*, 2015). However, linking such complementary approaches offers the most robust means of gaining both dietary and foraging insights (Majdi *et al.*, 2018). Our analysis showed that most of the nutritional dietary intake of dolphins (88.6%, wet mass) is achieved by combining the proximate compositions of grey mullet, pilchards, and jack mackerel. For gannets, majority of nutritional dietary intake (91.5%, wet mass), occurred via the consumption of pilchard, yellow eye mullet, kahawai, and anchovy. These results are consistent with previous findings that suggest both predators' prey upon surface schooling anchovy, pilchard, and jack mackerel within the Hauraki Gulf (Tait *et al.*, 2014; Peters *et al.*, 2020). While vital to many marine predators coexisting in the area (Gostischa *et al.*, 2021), the availability of prey across the Hauraki Gulf is subject to the East Auckland Current, shelf-upwelling patterns, and environmental oscillations that influence the nutrient production (Zeldis *et al.*, 2004). Thus, a lack of current information on stocks of jack mackerel, grey mullet, and pilchard prevents a comprehensive understanding of the sustainability of these marine predator populations within the region (Hauraki Gulf Forum, 2020).

Understanding the foraging strategies and nutritional requirements of marine predators is critical to predict how these species adjust to changes in prey composition and availability in heterogenous environments (Österblom *et al.*, 2008; Machovsky-Capuska *et al.*, 2016b). While our results showed no differences in the nutritional composition of diets, both predators relied on the consumption of species with high en-

ergy content, high % L and low P:L. For instance, dolphins relied on grey mullet (5.3 kJ g^{-1} , 6.5% L, and P:L = 2.6) and gannets on yellow eye mullet (5.1 kJ g^{-1} , 6.1% L, and P:L = 2.8), that were also mixed with low energy content, low %L, high P:L prey to achieve their respective intakes. The ability to combine nutritionally complementary prey (species with different P:L) to achieve similar diet intakes has previously been reported in gannets (Machovsky-Capuska *et al.*, 2016b), mink (*Mustela vison*, Mayntz *et al.*, 2009), and juvenile white sharks (*Carcharodon carcharias*, Grainger *et al.*, 2020). Such findings are furthermore, consistent with prior studies that suggest the likelihood that prey selection in aquatic predators is likely to be driven by macronutrient balance instead of energy acquisition (Mayntz *et al.*, 2009; Machovsky-Capuska *et al.*, 2016b, c; Machovsky-Capuska and Raubenheimer, 2020).

Characterising the prey composition and realized nutritional niche breaths, provides novel insights in the degree of generalism of a species (Machovsky-Capuska *et al.*, 2016a, 2018) and their ability to interact with multiple trophic levels (reviewed in Machovsky-Capuska and Raubenheimer, 2020; Denuncio *et al.*, 2021). At a prey composition level, dolphins showed a broader niche (16.4) comparatively to gannets (6.9), with several non-exclusive explanations available to explain this pattern. First, while both species are known to predominantly consume small prey items (<12.0 cm), dolphins also ingest larger fish (>20.0 cm) that are highly profitable in terms of nutrients and energy intake (Meynier *et al.*, 2008a, b; Machovsky-Capuska *et al.*, 2018). Second, distinct morphological and evolutionary differences between dolphin and gannet gastrointestinal systems (e.g. mouth and gut size) that lead to differences in prey processing, digestion efficiency, and retention time of nutrients (Stevens and Hume, 1998). Third, a differential physiological ability to convert protein and lipids into metabolized energy could potentially influence nutrient-specific foraging decisions as suggested in gannets (Machovsky-Capuska *et al.*, 2016b; reviewed in Machovsky-Capuska and Raubenheimer, 2020; Machovsky-Capuska *et al.*, 2020b) and considered for different life stages within dolphins (Meynier *et al.*, 2008b; Spitz *et al.*, 2010). Fourth, dolphins exhibit oceanic, neritic, and coastal foraging strategies (Meynier *et al.*, 2008a; Meissner *et al.*, 2015; Filby *et al.*, 2013; Peters and Stockin, 2022; Dwyer *et al.*, 2020), whereas gannets are coastal predators (Wingham, 1985). Thus, this distinct ability to exploit the Hauraki Gulf likely plays an important role in the extent of their prey composition niches. At a realized nutritional niche level, gannets (5.7) exhibit a broader niche breadth compared to dolphins (3.0). This is consistent with previous evidence which suggests gannets are nutritional generalists in both the prey and diets they consume (Machovsky-Capuska *et al.*, 2018). The greater degree of selectivity within dolphins may relate to the nutritional needs associated with reproduction and lactation (Young and Crockett, 1994).

Niche overlap has been suggested to discern the extent of species interactions, in which maximal tolerable intersection should be inverted to the intensity of competition (Pianka, 1974). A moderate overlap in the prey composition niche (0.42) and realized nutritional niche (0.52) between dolphins and gannets suggests that both predators coexist in a similar nutritional space, while reducing interspecific competition and maximizing the success of encountering and exploiting patchily distributed prey (Pruitt *et al.*, 2009; Anderwald *et al.*, 2011; Thiebault *et al.*, 2014, 2016; Tremblay *et al.*, 2014).

The behavioural ecology of feeding associations

Temporal feeding associations involving different species have a greater benefit compared to single species foraging events, if the species involved have a reduced resource overlap, decreasing the costs of competition (Pruitt *et al.*, 2009). Thus, the moderate niche observed here between dolphins and gannets likely enables behavioural interactions when foraging. While both species are constrained by their respective morphologies and distinctive feeding mechanisms, gannets are suggested to take advantage of dolphins which herd prey to the surface (Camphuysen and Webb, 1999; Neumann and Orams, 2003). Our analysis showed that when dolphins carousel feed, gannets significantly increased their dive heights to ≥ 5 m. Carouselling serves as a particular foraging strategy employed by dolphins for creating a visual and acoustic barrier (Neumann and Orams, 2003; Burgess, 2006). This strategy keeps fish stationary and densely packed in a bait-ball at the surface, with individual dolphins patrolling the edges of the school, while others dart through the centre of the bait-ball, increasing feeding success (Burgess, 2006). During this dolphin strategy, gannets are more likely to dive into these bait-ball aggregations (Neumann and Orams, 2003; Vaughn *et al.*, 2007, 2010) by reaching high altitudes to visually detect prey from an aerial perspective (Lee and Reddish, 1981; Machovsky-Capuska *et al.*, 2011a, 2012), using V-shaped dives to capture fish from within these dense stationary surface schools (Machovsky-Capuska *et al.*, 2011b, 2013a).

Larger dolphin groups are expected to herd prey close to the surface for longer periods of time, thus increasing their foraging efficiency (Acevedo-Gutiérrez, 2002; Neumann and Orams, 2003; Vaughn *et al.*, 2010). During the presence of larger groups of foraging dolphins (>100 individuals), workups further intensify gannet activity, as characterized by high-altitude U-shaped dives into dense schools, enabling high (95%) prey capture success rates (Machovsky-Capuska *et al.*, 2011a, 2013a). Animal-borne GPS loggers showed that during single foraging trips from their colonies, gannets have a high diving frequency of 4.8 dives h^{-1} that are confined within small spatiotemporal areas (Machovsky-Capuska *et al.*, 2013b). It is therefore likely, that these high-performance diving events could be associated with larger dolphin groups that enable gannets to undertake successive multiple dives in a workup while fish schools remain concentrated (Thiebault *et al.*, 2016). However, smaller dolphin group sizes involving fewer foragers, may lead to less condensed bait-balls, increasing herding efforts and energetic feeding costs per dolphin (Vaughn *et al.*, 2011). Under these circumstances, gannets likely use shallow V-shaped dives to assess prey density and subsequent deeper U-shaped dives to capture prey by underwater flapping, like gentoo penguins (*Pygoscelis papua*), strategies for maximizing the energetic cost of feeding (Wilson *et al.*, 1996; Machovsky-Capuska *et al.*, 2013a).

Dolphin and gannet feeding associations have typically been described as unidirectional in benefit to gannets, with dolphins spending energy to concentrate bait-balls near the surface and gannets diving within their aerobic capacity (Evans, 1982; Camphuysen and Webb, 1999). However, the evidence presented herein suggests that feeding associations between dolphins and gannet may be substantially more beneficial to both predators than previously considered (Burgess, 2006; Astarloa *et al.*, 2019; Gostischa *et al.*, 2021). For example, as large seabirds (89 cm, Machovsky-Capuska *et al.*,

2011b), gannets can use underwater wing flapping momentum to reach 23 m in 42 s during U-shaped dives (Green *et al.*, 2009). Such agility not only provides significant opportunity to capture up to five fish within a dive (Machovsky-Capuska *et al.*, 2011b) but notably prevents prey from successfully regrouping subsurface. Second, omnidirectional coordinated attacks on prey have been suggested to increase capture success for dolphins (Vaughn *et al.*, 2007, 2010). Lett *et al.* (2014) developed modelling techniques that quantified these predator-prey dynamics, confirming the field-based patterns observed here in the wild.

The question of sampling effort is particularly relevant to demonstrating the nutritional and behavioural interactions between dolphins and gannets. From a nutritional perspective, the definition of ecological niche encompasses all resources needed to maintain a population during their different life cycle phases (Pulliam, 2000). The sampling regime in our study provided a unique representation on how these predators overlap in their main prey items consumed, prey composition niche breadths, and realized niche breadths. The proposed results are consistent with previous studies that also estimated the nutritional niche ranges of common dolphins and gannets (Machovsky-Capuska *et al.*, 2018; Machovsky-Capuska and Raubenheimer, 2020; Machovsky-Capuska *et al.*, 2020b), although additional sampling might, of course, provide further resolution. Regarding the behavioural findings presented here, there are considerable challenges of collecting behavioural data on dynamic predators foraging in the wild (Machovsky-Capuska *et al.*, 2016c; Hughey *et al.*, 2018). The use of a commercial tourism catamaran as a platform of opportunity to collect such behavioural data further adds to the challenge. Nonetheless, historical studies from this same platform have a well-established value to address scientific questions on free-ranging marine predators related to their behavioural ecology (de la Brosse, 2010; Meissner *et al.*, 2015; Purvin, 2015; Gostischa *et al.*, 2021) and the influence of climate change in their habitat use (Srinivasan *et al.*, 2015), among others. While the use of an opportunistic platform can present several trade-offs (Hupman *et al.*, 2014) we are confident that our sampling regime had sufficient resolution to support the mutualistic nature of the foraging interactions between free ranging dolphin and gannets.

By combining indirect diet estimates with proximate composition analysis and Bayesian ellipses under the MNNE, our study not only overcame potential individual methodological limitations to estimate the prey composition and nutritional niche breadths of two marine predators but further provided fresh insight on the ability of these species to coexist in the wild while foraging in nutritionally complex marine environments. Our ethological assessment indicated that dolphin and gannets feeding associations are likely mutually beneficial, with dolphin behaviour and pod size influencing gannet diving heights and prey capture success. We conclude, that our approach offers significant advantages to understanding the iconic foraging relationships, here between dolphins and gannets. Such findings offer potential to not only explore wider cetacean-bird interactions (Vaughn *et al.*, 2007, 2010, 2011; Sutton *et al.*, 2019; Towers and Gasco, 2020) but also better understand cooperative feeding between different cetacean species (Clua and Grosvalet 2001; Wiseman *et al.*, 2011; Zaeschmar *et al.*, 2013).

Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

Author contributions

KAS and GEMC contributed to the conception, design of the study, and manuscript preparation. GEMC and CP collected the field data, KAS, LM and GEMC collected the postmortem data. CA with the assistance from GEMC and KS analysed the data and designed the figures and tables. LM contributed additional unpublished data and assisted with manuscript formatting. KAS and GEMC created the Supplementary material. All authors discussed the contents of the manuscript and contributed to manuscript editing and revision.

Funding

KAS is supported by the Royal Society Te Aparangi Rutherford Discovery Fellowship (2019–2024). Nutritional analyses were funded by a Massey University Strategic Research Excellence Fund (SREF RM23810) awarded to KAS.

Declaration of competing interest

All authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgement

Access to carcasses was kindly supported by Mana Whenua and facilitated under research permits AK-26359-FAU (gannets) and 39239-MAR (dolphins) issued to Massey University by the New Zealand Department of Conservation. Nutritional analyses were completed at the Nutritional Laboratory, Massey University, New Zealand. Ethological data were supported by Auckland Whale and Dolphin Safaris, who provided vessel access to video foraging activities analysed herein. We thank Katharina Peters and the wider Cetacean Ecology Research Group, Massey University, for use of gannet and dolphin graphics and their assistance with post mortem sampling, respectively.

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Handling Editor: C J Camphuysen