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1 **Understanding common dolphin and Australasian gannet feeding**
2 **associations from an ethological and nutritional perspective**

3
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32 **Abstract**

33 Prey detection and subsequent capture is considered a major hypothesis to explain feeding
34 associations between common dolphins and Australasian gannets. However, a current lack of
35 insight on nutritional strategies with respect to foraging behaviours of both species has until
36 now, prevented any detailed understanding of this conspecific relationship. Here we combine
37 stomach content analysis, nutritional composition of prey, a multidimensional nutritional
38 niche framework (MNNF) and videography to provide a holistic dietary, nutritional, and
39 behavioural assessment of the feeding association between dolphins and gannets in the
40 Hauraki Gulf, New Zealand. Dolphins consumed 10 prey species, including grey mullet
41 (*Mugil cephalus*) as the most representative by wet mass (33.4%). Gannets preyed upon six
42 species, with pilchards (*Sardinops pilchardus*) contributing most of the diet by wet mass
43 (32.4%) to their diet. Both predators jointly preyed upon pilchard, jack mackerel (*Trachurus*
44 spp.), arrow squid (genus *Nototodarus*) and anchovy (*Engraulis australis*). Accordingly, the
45 MNNF revealed a moderate overlap in the prey composition niche (0.42) and realized
46 nutritional niche (0.52) between dolphins and gannets. This suggests that both predators
47 coexist in a similar nutritional space, while simultaneously reducing interspecific competition
48 and maximizing the success of both encountering and exploiting patchily distributed prey.
49 Behavioural analysis further indicated that dolphin and gannets feeding associations are
50 likely to be mutually beneficial, with a carouselling foraging strategy and larger pod sizes of
51 dolphins, influencing the diving altitude of gannets. Our approach provides a new, more
52 holistic understanding of this iconic foraging relationship, which until now has been poorly
53 understood.

54

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

57

58 **1. Introduction**

59 Enhanced feeding capabilities (i.e., facilitation of prey detection and capturing of food items
60 that may be available to individuals) has been highlighted as a major hypothesis to explain
61 heterospecific feeding associations (Morse, 1977). These temporary relationships are
62 regarded as a major adaptive advantage in marine environments, especially when prey is
63 patchily distributed and/or difficult to detect (Fauchald et al., 2000). From the tropics to
64 temperate and polar regions worldwide, heterospecific associations in marine environments
65 are widespread in various taxa including fish-octopus, fish-fish, seabirds-seabirds, seabirds-
66 pinnipeds, seabirds-fish-cetaceans and seabirds-sharks-cetaceans-pinnipeds (reviewed in
67 Gatti et al., 2021). Considerable attention has been given to the interactions between
68 cetaceans and seabirds globally (Evans, 1982; Camphuysen and Webb, 1999; Vaughn et al.,
69 2007, 2010, 2011; Sutton et al., 2019; Towers and Gasco, 2020). However, quantifying the
70 currencies of these relationships (e.g., behaviours involved, energetic budget, spatial and
71 temporal investment) in free ranging predators remains notoriously challenging.

72 To understand the nature of heterospecific feeding associations in wild, highly mobile
73 predators, models will benefit from information on species' properties that both influence
74 individual fitness and shape responses to their environment (i.e., functional traits) (Kearny et
75 al., 2010; Houlahan et al., 2017). Feeding related traits (e.g., food consumption, prey
76 composition, and ecological niche) and behavioural strategies (degree of sociability and
77 cooperation in foraging strategies) could provide fundamental insights to heterospecific
78 feeding aggregations if studied in unison. Given that animal behaviour and physiological
79 characteristics relate to the acquisition of nutrients and energy (Raubenheimer et al., 2009),
80 an integrated standardize approach is required to understand the complexities of these
81 interactions and provide transferable ecological fresh insights. By integrating behaviour,

82 nutrition and physiology, a multidimensional nutritional niche framework (MNNF,
83 Machovsky-Capuska et al., 2016a) provides a nutrient lens to the prey and diets consumed by
84 organisms within an ecological niche context (i.e., prey composition and realized nutritional
85 niches). Thus, understanding the nutritional requirements and foraging strategies of marine
86 vertebrate predators is important, in order to predict how a species interacts with different
87 trophic levels and their environment (Machovsky-Capuska and Raubenheimer, 2020).

88 Several studies on seabirds (Machovsky-Capuska et al., 2018; Machovsky-Capuska
89 and Raubenheimer, 2020), predatory fish (Machovsky-Capuska and Raubenheimer, 2020),
90 turtles (Machovsky-Capuska et al., 2020a, Santos et al., 2020), cetaceans (Denuncio et al.,
91 2017; Machovsky-Capuska and Raubenheimer, 2020; Machovsky-Capuska et al., 2020b),
92 pinnipeds (Machovsky-Capuska and Raubenheimer, 2020; Denuncio et al., 2021) and sharks
93 (Machovsky-Capuska and Raubenheimer, 2020; Grainger et al., 2020), have increasingly
94 applied the MNNF to: (i) understand how marine predators adjust their foraging behaviour
95 and nutritional goals to environmental fluctuations (Machovsky-Capuska et al., 2018), (ii)
96 explore the nutritional consequences of consuming plastics and anthropogenic pollutants
97 (Machovsky-Capuska et al., 2019, 2020a,b; Santos et al., 2020, 2021; Stockin et al., 2021
98 a,b), and (iii) disentangle the dynamics that facilitates coexistence with other sympatric
99 species (Denuncio et al., 2021), and examine how they are likely to interact with humans
100 (Grainger et al., 2020).

101 The Hauraki Gulf, North Island New Zealand, provides a quintessential coastal
102 environment characterised by heterospecific feeding associations involving dynamic bait ball
103 that often composed of pilchards (*Sardinops pilchardus*), anchovies (*Engraulis australis*) or
104 Jack mackerel (*Trachurus* spp.) (Stockin et al., 2008a; Wiseman et al., 2011; Purvin, 2015;
105 Gostischa et al., 2021). Among these multiple sympatric predator-prey interactions, common
106 dolphins (*Delphinus delphis*; hereafter dolphins) and Australasian gannets (*Morus serrator*;

107 hereafter gannets) represent one of the most frequently observed associations during feeding
108 events (Burgess, 2006; Stockin et al., 2008a, b, 2009a; de la Brosse, 2010; Purvin, 2015) and
109 can serve as a model to understand the behavioural, ecological and evolutionary dimensions
110 of such interactions. While the local diet of both predators is well characterised (Meynier et
111 al., 2008a; Machovsky-Capuska et al., 2011a; Tait et al., 2014; Peters et al., 2020), a current
112 lack of insight on their nutritional strategies with respect to foraging behaviours has
113 prevented any detailed understanding of this conspecific relationship until now.

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

121

122 **2. Materials and Methods**

123 *2.1. Study Area*

124 The Hauraki Gulf / Tīkapa Moana is a shallow coastal feature of the North Island of New
125 Zealand, which encompasses an area of ca. 4000 sq km and a maximum water depth ~60 m.
126 Surrounded by the Auckland region, the Hauraki Plains, the Coromandel Peninsula, and
127 Great Barrier Island, this semi enclosed body of water is riddled with islands and shallow
128 reefs that extend into waters of the western Pacific Ocean. Water circulation in the gulf is
129 primarily driven by tides and wind (Heath, 1985; Gaskin and Rayner, 2013) and accordingly,
130 has historically been an area of high primary productivity (Zeldis et al., 2004), subject to
131 large environmental fluctuations (Srinivasan et al., 2015).

132

133 *2.2. Sampling procedures and stomach content analysis*

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

139 Post-mortem sampling of gannets followed standardised avian protocols (Work,
140 2000). In summary, carcasses were typically stored frozen until subsequent examination.
141 Upon dissection, individual prey items were extracted from the upper gastrointestinal tract
142 including the oral cavity, oesophagus, and stomach. All ingested prey items were individually
143 weighed to 0.1 g, and stomach contents subsequently rinsed through a 0.25-mm-mesh sieve
144 until clean to extract diagnostic prey remains, predominantly fish otoliths and cephalopod
145 beaks (Wingham, 1985; Duffy and Jackson, 1986).

146 Dolphins were examined post-mortem using standardised protocols (Stockin et al.,
147 2009b). The gastrointestinal tract was ligated and the extracted for subsequent analysis.
148 Stomach contents of each dolphin were carefully rinsed through a 0.25 mm mesh sieve.
149 Diagnostic hard parts (predominately otoliths and cephalopod beaks with some jaw bones)
150 were identified to the lowest possible taxonomic level using the reference collection (Massey
151 University, following Meynier et al., 2008a) and published guides (Clarke, 1986; Smale et
152 al., 1995). Prey size and mass for each species were further estimated at an accuracy of
153 0.5mm, using regression equations from the literature (Smale et al., 1995; Fea et al., 1999; Lu
154 and Ickeringill, 2002) based on otolith length (or width when the tip was broken), lower beak
155 rostral length (LRL) for squid, or lower beak hood length (LHL) for octopods and sepiolids,
156 as outlined by Meynier et al. (2008a). Prey size and mass were then subsequently used to

157 estimate the percentage of total prey wet mass that the species contributed to the overall diet
158 (M%, wet weight).

159

160 *2.3. Proximate composition analysis*

161 For prey species that contributed >1% wet mass to the diets of both dolphins and gannets, we
162 collected 30 individual samples from seven species for subsequent proximate composition
163 analyses. We further extracted proximate compositional data from Tait et al. (2004) for the
164 remaining three species (Table 1). Carbohydrates are known to constitute a negligible content
165 on squid and marine fish species (Craig et al., 1978), thus we measured the proximate
166 composition of protein (P), lipid (L), water (W) and ash (A). Following Bligh and Dyer
167 (1959), we further measured total L (ether extract), whereas Kjeldahl analysis was used to
168 measured total nitrogen (N) and then converted to P ($N \times 6.25$, AOAC 981.10, AOAC, 2005).
169 A convection oven at 125 °C was used to dry samples and estimate W from their moisture
170 loss (AOAC 950.46; AOAC, 2002). Ash was measured by the ignition of samples in a
171 furnace at 550 °C (AOAC 920.153; AOAC, 2005).

172

173 *2.4. Video footage collection and behavioural analysis*

174 Behavioural analysis was performed on aerial video footage of dolphin and gannet feeding
175 associations in the Hauraki Gulf involving 13 feeding events (totalling 40 minutes min
176 duration) collected during 2010. Video footage was collected using a Canon XH A1S high-
177 definition video camera (25 frames s⁻¹) with a 20 mm zoom lens, at a consistent height of 5 m
178 above the water surface on board the *Dolphin Explorer*, a 20 m commercial dolphin-watching
179 catamaran operated 4.5 h trips daily. Foraging events were also observed using 8 x 40 Pentax
180 handheld binoculars and characterised as follows: i) the species present (e.g., dolphins and
181 gannets vs gannets only), ii) the number of foragers (gannets: <100 and ≥ 100, and dolphins:

182 <100 and ≥ 100), iii) the number of workups they formed and iv) their different foraging
183 strategies (Table 2). The upper limit of both gannets and dolphins was considered when
184 making group size estimates, taking into consideration fission/fusion events (Burgess, 2006;
185 Stockin et al 2008a). All group size and behavioural observations were conducted by a single
186 observer to avoid inter observer bias.

187 Feeding events were defined as temporary groups of predators that assemble to
188 exploit patches of prey. Workups were defined as highly intense gannet diving events within
189 a confined spatiotemporal area in a feeding event (Purvin, 2015). Thus, it is possible that a
190 feeding event comprised several workups. The beginning of each workup, either in the
191 presence or absence of dolphins, was marked by the initiation of the diving activity by
192 plummeting gannets from the air, until the birds stopped diving in the same area (Burgess,
193 2006). Following Neumann and Orams (2003) and Burgess (2006), the dolphin foraging
194 strategies were classified as: i) *carouselling*, when dolphins circulate the perimeter of the
195 bait-ball keeping the fish stationary and densely concentrated at the water surface; ii) *line-*
196 *abreast*, where a foraging group of dolphins cooperatively drives prey ahead of them, and iii)
197 *synchronous diving*, in which many members of a foraging group dive simultaneously and
198 resurface in synchrony under fish schools.

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

206

207 2.5. Data analysis

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

218 Differences in SEAc between dolphins and gannets (prey composition niches and
219 realised nutritional niches) were assessed by producing a range of possible posterior estimates
220 (SEAb). These estimated resulted from 2×10^4 iterations with 2 chains, a burning of 1×10^3
221 and thinning of 10, using Markov chain Monte Carlo simulations combined with Bayesian
222 inference (Grainger et al., 2020). The *maxLikOverlap* function was subsequently applied to
223 estimate the proportional overlap area between two ellipses (overlap ellipses were equal to 1
224 whereas distinctive ellipses were equal to 0) (SIBER package, Jackson et al., 2011). We
225 considered ≥ 0.60 as a significant overlap (Schoener, 1968 and Guzzo et al., 2013), >0.31 to
226 0.59 as moderate overlap and low overlap as ≤ 0.30 .

227 Levene's test for homoscedasticity and Shapiro-Wilk's test for normality were initially
228 applied to the data. We converted P and L wet masses to energy (E) values using $P = 17$ kJ/g
229 and $L = 37$ kJ/g (N.R.C., 1989). To explore whether the nutritional composition (logit
230 transformed wet mass proportions of P, L, W, the protein to lipid ratio -P:L- and energy (E))
231 of prey and diets differ between predators, we fitted linear models (LMs) using the *lm*

232 function (Bates et al., 2015) with the nutritional composition from prey and diets as the
233 response.

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

246

247 **3. Results**

248 A total of 40 stomachs were examined including gannets (n=22) and dolphins (n=18). For all
249 the individuals examined, the presence of undigested prey in the upper gastrointestinal track
250 supports mortality of an acute as opposed to chronic nature (ie from a prolonged underlying
251 health or disease mechanism; Stockin et al. 2009b). Non-breeding adult male (n=17) and
252 female (n=5) gannets were collected on the beach or dead floating on the water. While a
253 mixture of sexually immature (n=11) and mature (n=7) dolphins were included in this study,
254 all individuals were physically mature based on total body length. Sample size restricted our
255 ability to consider the effect of sex and year on diet.

256

257 *3.1. Diet composition and nutritional niche breadths of dolphins and gannets*

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

263 Prey consumed by dolphins had an energy content that ranged from 2.99 Kj/g to 5.84
264 Kj/g and a wet mass P:L = 2.58:1.0 to P:L = 15.25:1.0, whereas the prey consumed by
265 gannets ranged from 3.42 Kj/g to 5.11 Kj/g and wet mass P:L = 2.76:1.0 to 15.25:1.0 (Table
266 1, Fig. 1A). No differences were observed in the wet mass proportional composition of P
267 (LM, $F_{1,66} = 0.30$, $p = 0.59$), L (LM, $F_{1,66} = 0.07$, $p = 0.79$), W (LM, $F_{1,66} = 0.38$, $p = 0.54$)
268 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
269 the prey consumed by dolphins and gannets. A comparison of the prey composition niche
270 breath (SEAc) between predators demonstrated that dolphins (16.4) had a significantly
271 broader niche breadth compared to gannets (6.9) (Probability $SEAb_{\text{dolphin}} > SEAb_{\text{gannet}} = 0.99$,
272 <0.05), with a 0.42 degree of overlap between niches (Fig. 1B).

273 The nutritional composition of diets of dolphins and gannets ranged from P:L =
274 2.8:1.0 to 15.3:1.0 (Fig. 2A). The estimated wet mass composition of the diet of dolphins was
275 $17.79 \pm 0.35\%$ P, $2.91 \pm 0.41\%$ L, $77.80 \pm 0.69\%$ W and P:L = 10.38 ± 0.15 , whereas for
276 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 = $10.22 \pm$
277 1.25 . A comparison of the diets between dolphins and gannets suggested no differences in
278 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,
279 $F_{1,38} = 0.49$, $p = 0.49$) and the P:L (LM, $F_{1,38} = 0.87$, $p = 0.36$). The realised nutritional niche
280 breath (SEAc) of dolphins (3.0) was significantly narrower than the niche of gannets (5.7)
281 (Probability $SEAb_{\text{dolphin}} < SEAb_{\text{gannet}} = 0.97$, <0.05), showing a 0.52 degree of niche overlap
282 between predator (Fig. 2B).

283

284 *3.2. Foraging behaviours that shape dolphin and gannet interactions.*

285 Behavioural analysis of the 40 min of video footage revealed 13 feeding events that included
286 16 independent work ups (Table 2), this accounting for a field effort of 3510 min (58 h).
287 From the total number of workups recorded, 50% (n = 8) involved the presence of dolphins
288 and gannets, and 50% (n = 8) involved gannets foraging alone. Group sizes of dolphin and
289 gannet associations varied from < 100 individuals (33.3%, n = 3) to \geq 100 individuals
290 (66.7%, n = 6).

291 During all workups, we recorded 1652 gannet dives, from which 79% (n = 1299)
292 were in the presence of dolphins and 21% (n = 353) with birds foraging alone. From the total
293 number of dives registered, 75,1% (n =1241) commenced at \geq 5 m above sea level, with only
294 24.9% (n = 412) of dives occurring at < 5m. The size of gannet diving groups was
295 significantly influenced by the presence of dolphins (GEE: Wald $\chi^2=$ 53337.2, $P < 0.0001$).
296 However, no differences were observed in the heights and synchronization of gannet dives
297 with and without dolphin engagement (respectively, GEE: Wald $\chi^2=$ 3.3, $P = 0.07$; Wald $\chi^2=$
298 0.0, $P = 0.89$).

299 Our analysis revealed that the foraging strategies of dolphins do affect gannet diving
300 behaviour. Specifically, the carouselling foraging strategy used by dolphins significantly
301 increased the proportion of gannet dives \geq 5m (GEE: Wald $\chi^2 =$ 35.05, $P < 0.001$, Table 3,
302 Fig. 3). Although not significant (GEE: Wald $\chi^2 =$ 3.47, $P = 0.06$, Table 3), a similar trend
303 was also evident when dolphins adopted a line-abreast behaviour foraging strategy. No
304 relationship was observed between synchronous diving in dolphins and gannet diving heights
305 or between the different dolphin foraging strategies and the degree of synchronization of
306 gannet dives (Table 3). Our findings also showed that dolphin group size influenced the

307 percentage of plunge diving heights performed by gannets (GEE, Wald $\chi^2 = 34.1$, $p < 0.0001$,
308 Table 3, Fig. 4).

309

310 **4. Discussion**

311

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

320

321 *4.1. A nutritional lens to dolphin and gannet feeding associations*

322 Current understanding of the diet of marine predators has been achieved using different
323 indirect techniques (e.g., stomach content analysis, faeces, regurgitations, stable isotopes,
324 fatty acids and DNA metabarcoding), that are known for their individual advantages and
325 limitations (reviewed in Young et al., 2015). However, linking such complementary
326 approaches offers the most robust means of gaining both dietary and foraging insights (Majdi
327 et al., 2018). Our analysis showed that most of the nutritional dietary intake of dolphins
328 (88.6%, wet mass) is achieved by combining the proximate compositions of grey mullet,
329 pilchards and jack mackerel, whereas for gannets (91.5%, wet mass), this occurred via the
330 consumption of pilchard, yellow eye mullet, kahawai and anchovy. These results are
331 consistent with previous findings that suggest both predators' prey upon surface schooling
332 anchovy, pilchard and jack mackerel within the Hauraki Gulf (Tait et al., 2014; Peters et al.,

333 2020). While vital to many marine predators coexisting in the area (Gostischa et al., 2021),
334 the availability of prey across the Hauraki Gulf is subject to the East Auckland Current, shelf
335 upwelling patterns and environmental oscillations that influence the nutrient production
336 (Zeldis et al., 2004). Thus, a lack of current information on stocks of jack mackerel, grey
337 mullet, and pilchard prevents a comprehensive understanding of the sustainability of these
338 marine predator populations within the region (Hauraki Gulf Forum, 2020).

339 Understanding the foraging strategies and nutritional requirements of marine
340 predators is critical to predict how these species adjust to changes in prey composition and
341 availability in heterogenous environments (Österblom et al., 2008; Machovsky-Capuska et
342 al., 2016b). While our results showed no differences in the nutritional composition of diets,
343 both predators relied on the consumption of species with high energy content, high %L and
344 low P:L. For instance, dolphins relied on grey mullet (4.8 Kj/g, 6.5%L and P:L= 2.6) and
345 gannets on yellow eye mullet (5.1 Kj/g, 6.1%L and P:L=2.8), that were also mixed with low
346 energy content, low %L, High P:L prey to achieve their respective intakes. The ability to
347 combine nutritionally complementary prey (species with different P:L) to achieve similar diet
348 intakes has previously been reported in gannets (Machovsky-Capuska et al., 2016b), mink
349 (*Mustela vision*, Mayntz et al., 2009), and juvenile white sharks (*Carcharodon carcharias*,
350 Grainger et al., 2020). Such findings are furthermore, consistent with prior studies that
351 suggest the likelihood that prey selection in aquatic predators is likely to be driven by
352 macronutrient balance instead of energy acquisition (Mayntz et al., 2009; Machovsky-
353 Capuska et al. 2016b,c; Machovsky-Capuska and Raubenheimer, 2020).

354 Characterising the prey composition and realized nutritional niche breaths, provides
355 novel insights in the degree of generalism of a species (Machovsky-Capuska et al., 2016a,
356 2018) and their ability to interact with multiple trophic levels (reviewed in Machovsky-
357 Capuska and Raubenheimer, 2020; Denuncio et al., 2021). At a prey composition level,

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

379 Niche overlap has been suggested to discern the extent of species interactions, in
380 which maximal tolerable intersection should be inversely related to the intensity of competition
381 (Pianka, 1974). A moderate overlap in the prey composition niche (0.42) and realized
382 nutritional niche (0.52) between dolphins and gannets suggests that both predators coexist in

383 a similar nutritional space, while reducing interspecific competition and maximizing the
384 success of encountering and exploiting patchily distributed prey (Pruitt et al., 2009;
385 Anderwald et al., 2011; Thiebault et al., 2014, 2016; Tremblay et al., 2014).

386

387 *4.2. The behavioural ecology of feeding associations*

388 Temporal feeding associations involving different species have greater benefit compared to
389 single species foraging events, if the species involved have a reduced resource overlap
390 decreasing the costs of competition (Pruitt et al., 2009).

391 Thus, the moderate niche observed here between dolphins and gannets likely enables
392 behavioural interactions when foraging. While both species are constrained by their
393 respective morphologies and distinctive feeding mechanisms, gannets are suggested to take
394 advantage of dolphins which herd prey to the surface (Camphuysen and Webb, 1999;
395 Neumann and Orams, 2003). Our analysis showed that when dolphins carousel feed, gannets
396 significantly increased their dive heights to ≥ 5 m. Carouselling serves as a particular foraging
397 strategy employed by dolphins for creating a visual and acoustic barrier (Neumann and
398 Orams, 2003; Burgess, 2006). This strategy keeps fish stationary and densely packed in a
399 bait-ball at the surface, with individual dolphins patrolling the edges of the school while
400 others dart through the centre of the bait ball, increasing feeding success (Burgess, 2006).
401 During this dolphin strategy, gannets are more likely to dive into these bait ball aggregations
402 (Neumann and Orams, 2003; Vaughn et al., 2007, 2010) by reaching high altitudes to visually
403 detect prey from an aerial perspective (Lee and Reddish, 1981; Machovsky-Capuska et al.,
404 2011a, 2012), using the initial momentum phase of V-shaped dives to capture fish from
405 within these dense stationary surface schools (Machovsky-Capuska et al., 2011b, 2013a).

406 Larger dolphin groups are expected to herd prey close to the surface for longer
407 periods of time, thus increasing their foraging efficiency (Acevedo-Gutiérrez, 2002;

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

423 Dolphin and gannet feeding associations have typically been described as
424 unidirectional in benefit to gannets, with dolphins spending energy to concentrate bait balls
425 near the surface and gannets diving within their aerobic capacity (Evans, 1982; Camphuysen
426 and Webb, 1999). However, the evidence presented herein suggests that feeding associations
427 between dolphins and gannet may be substantially more beneficial to both predators than
428 previously considered (Burgess, 2006; Astarloa et al., 2019; Gostischa et al., 2021). For
429 example, as large seabirds (89 cm, Machovsky-Capuska et al., 2011b), gannets can use
430 underwater wing flapping momentum to reach 23 mts in 42 s during U-shaped dives (Green
431 et al., 2009). Such agility not only provides significant opportunity to capture up to five fish
432 within a dive (Machovsky-Capuska et al., 2011b), but notably prevents prey from

433 successfully regrouping subsurface. Secondly, omnidirectional coordinated attacks on prey
434 have been suggested to increase capture success for dolphins (Vaughn et al., 2007, 2010).
435 Lett et al. (2014) developed modelling techniques that quantified these predator-prey
436 dynamics, confirming the field-based patterns observed here in the wild.

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

458 By combining indirect diet estimates with proximate composition analysis and
459 Bayesian ellipses under the MNNF, our study not only overcame potential individual
460 methodological limitations to estimate the prey composition and nutritional niches breadths
461 of two marine predators, but further provided fresh insight on the ability of these species to
462 coexist in the wild, while foraging in nutritionally complex marine environments. Our
463 ethological assessment indicated that dolphin and gannets feeding associations are likely
464 mutually beneficial, with dolphin behaviour and pod size influencing gannet diving heights
465 and prey capture success. We conclude, that our approach offers significant advantages to
466 understanding the iconic foraging relationships, here between dolphins and gannets. Such
467 findings offer potential to not only to explore wider cetacean-bird interactions (Vaughn et al.,
468 2007, 2010, 2011; Sutton et al., 2019; Towers and Gasco, 2020) but also better understand
469 cooperative feeding between different cetacean species (Clua and Grosvalet 2001; Wiseman
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471

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482

483 **Author statements**

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

490

491 **Declaration of Competing Interest**

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

494

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