Trophic niches of a seabird assemblage in Bass Strait, south-eastern Australia

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The foraging niches of seabirds are driven by a variety of factors, including competition for prey that promotes divergence in foraging niches. Bass Strait, south-eastern Australia, is a key region for seabirds, with little penguins *Eudyptula minor*, short-tailed shearwaters *Ardenna tenuirostris*, fairy prions *Pachyptila turtur* and common diving-petrels *Pelecanoides urinatrix* being particularly abundant in the region. The trophic niches of these species were investigated using isotopic values in whole blood and by identifying prey remains in stomach contents. The four species occupied different isotopic niches that varied between 3 years and 3 regions. Little penguins consumed mainly fish whereas the three procellariforms primarily consumed coastal krill *Nyctiphanes australis*. The dietary similarities between the procellariforms suggest that food resources are segregated in other ways, with interspecific differences in isotope niches possibly reflecting differential consumption of key prey, divergent foraging locations and depth, and differences in breeding phenology. Because oceanographic changes predicted to occur due to climate change may result in reduced coastal krill availability, adversely affecting these seabird predators, further information on foraging zones and feeding behaviour of small procellariform species is needed to elucidate more fully the segregation of foraging niches, the capacity of seabirds to adapt to climate change and the potential for interspecific competition in the region.

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15   **ABSTRACT**

16   The foraging niches of seabirds are driven by a variety of factors, including competition for prey

17   that promotes divergence in foraging niches. Bass Strait, south-eastern Australia, is a key region

18   for seabirds, with little penguins *Eudyptula minor*, short-tailed shearwaters *Ardenna tenuirostris*,

19   fairy prions *Pachyptila turtur* and common diving-petrels *Pelecanoides urinatrix* being

20   particularly abundant in the region. The trophic niches of these species were investigated using

21   isotopic values in whole blood and by identifying prey remains in stomach contents. The four

22   species occupied different isotopic niches that varied between 3 years and 3 regions. Little

23   penguins consumed mainly fish whereas the three procellariforms primarily consumed coastal

24   krill *Nyctiphanes australis*. The dietary similarities between the procellariforms suggest that food

25   resources are segregated in other ways, with interspecific differences in isotope niches possibly

26   reflecting differential consumption of key prey, divergent foraging locations and depth, and

27   differences in breeding phenology. Because oceanographic changes predicted to occur due to

28   climate change may result in reduced coastal krill availability, adversely affecting these seabird

29   predators, further information on foraging zones and feeding behaviour of small procellariform

30   species is needed to elucidate more fully the segregation of foraging niches, the capacity of

31   seabirds to adapt to climate change and the potential for interspecific competition in the region.

33   Key words: seabirds, stable isotopes, isotopic niche, trophic niche, diet, segregation, Southern

34   Ocean.

36   **INTRODUCTION**

37   Seabirds are major consumers of marine biomass, feeding on a variety of fish, cephalopods and

38   crustaceans (Ridoux 1994). The foraging niche of seabirds is influenced by a range of factors,

39   including environmental conditions (Waugh & Weimerskirch 2003), prey availability (Baird

40   1991), morphological characteristics and their influence on flight performance (Phillips et al.

41   2004, 2005), and interspecific competition (González-Solís et al. 2008, Phillips et al. 2008).

42   Competition is thought to promote foraging niche divergence since species occupying the same

43   ecological niche cannot theoretically coexist through time (Schoener 1974). Seabirds may

44   separate their resources on several dimensions, with studies showing divergence in foraging zone

45   (González-Solís et al. 2008, Barger et al. 2016), diving depth (Mori & Boyd 2004), the timing of

46   breeding, and seasonal patterns of activity (Phillips et al. 2008). In particular, divergence in diet

47   has been proposed as an important mechanism in reducing niche overlap (Ridoux 1994, Surman

48   & Wooler 2003).

49   Bass Strait, the shallow continental shelf area between mainland Australia and Tasmania (Fig. 1),

50   is a key region for Australian seabirds, supporting large breeding populations of at least 11 major

51   species comprising more than 15 million breeding pairs (Table 1; Ross et al. 2001). This area is

52   considered a region of low primary productivity (Gibbs et al. 1986, Gibbs et al. 1991) which

53   occurs at the confluence of three main ocean currents. The warm, oligotrophic waters of the East

54   Australian Current (EAC) flow southward along the eastern edge of Bass Strait (Ridgeway &

55   Godfrey 1997, Sandery & Kämpf 2007) while the South Australian Current (SAC) advects warm

56   water from the west onto the shelf which then flows eastward through Bass Strait (Sandery &

57   Kämpf 2007). The latter is the major source of Bass Strait water and is strongest in winter

58   (Ridgeway & Condie 2004, Sandery & Kämpf 2007). In summer, a weakening or reversal of this

59   eastward-flowing trend occurs (Gibbs et al. 1986, Sandery & Kämpf 2007). Finally, cold,

60   nutrient-rich sub-Antarctic surface water (SASW) enters Bass Strait from the south (Gibbs 1992)

61   where it mixes with the EAC and SAC (Prince 2001). Upwelling of SASW occurs along the

62   shelf edges of Bass Strait (Gibbs et al. 1986), particularly to the west in summer (McClatchie et

63   al. 2006), though upwelling in the east, where enrichment is possible throughout the year (Prince

64   2001), is also important (Gibbs et al. 1986).

65   The relative influence of the currents and upwelling systems affecting Bass Strait varies

66   spatially, seasonally and inter-annually (Prince 2001, Sandery & Kämpf 2005). This affects the

67   reproductive success of seabirds in Bass Strait, presumably due to shifts in prey availability

68   (Mickelson et al. 1992). Additionally, climate change is predicted to weaken the SAC (Feng et

69   al. 2012) and increase the strength of the EAC, resulting in warming along the path of its

70   strengthening (Cai et al. 2005). This is likely to have a considerable impact on the marine

71   ecosystem of Bass Strait. Seabird assemblages in other parts of the world have shown differential

72   responses to shifts in ocean regimes in parameters such as breeding success, population size and

73   survivorship due, at least in part, to changes in prey availability (Croxall et al. 2002). Knowledge

74   of the trophic relationships and diets of Bass Strait seabirds is crucial for predicting their

75   population responses to environmental change. This information is important for the

76   conservation of these marine predators and for the refinement of sustainable fisheries

77   management practices. At present, the trophic structure of Bass Strait seabird community is

78   poorly understood, with trophic niches of most pelagic species not yet described or based on a

79   few localised studies that did not address spatial or temporal variation. Accordingly, it is not

80   known whether, or how, they diverge in foraging niche.

81 The little penguin *Eudyptula minor*, short-tailed shearwater *Ardenna tenuirostris*, fairy prion

82 *Pachyptila turtur* and common diving petrel *Pelecanoides urinatrix* are the most abundant and

83 ubiquitous seabirds in Bass Strait, breeding sympatrically on numerous offshore islands (Ross et

84 al. 2001). They are known to feed on a variety of fish, cephalopod and/or crustacean prey

85 (Harper 1976, Montague et al. 1986, Schumann et al. 2008, Chiaradia et al. 2010). Previous

86 foraging ecology studies indicate that the little penguin is an inshore forager relying mainly on

87 small pelagic schooling fish (Cullen et al. 1992, Chiaradia et al. 2010), while the pelagic short-

88 tailed shearwater, and the smaller, more neritic fairy prion and common diving petrel, feed on a

89 wide range of small prey, concentrating predominantly on coastal krill (*Nyctiphanes australis*)

90 and myctophid fish (Harper 1976, Weimerskirch & Cherel 1998, Schumann et al. 2008).

91 However, in Bass Strait, information on spatial and temporal variation in the ecology of these

92 species is limited to the at-sea foraging behaviour of little penguins and short-tailed shearwaters

93 (e.g. Collins et al. 1999, Chiaradia et al. 2010, Berlincourt & Arnould 2015a, b) and there is

94 almost no information on the small procellariforms.

95 The aims of the present study, therefore, were to: 1) determine the trophic niche using both

96 stomach contents and stable isotope analysis; 2) assess the degree of niche overlap; and overall

97 3) investigate inter-annual and geographic variation in the isotopic niche of these four abundant

98 species within Bass Strait.

99

100 **MATERIAL & METHODS**

101 The study was conducted during the winters (July – August) of 2008 – 2010 and summers

102 (January – February) of 2009 – 2011 in three regions of Bass Strait, south-eastern Australia (Fig.

103   1). The trophic niches of little penguins, short-tailed shearwaters, fairy prions and common

104   diving-petrels were determined using two complementary techniques. Trophic information was

105   derived from stable isotope values in whole blood of each species in western, central and eastern

106   Bass Strait, and stomach samples were collected from the seabirds in central Bass Strait to assess

107   the relative importance of prey and inform interpretation of the stable isotope results. All

108   research was conducted under permit from Deakin University (AWC A9-2008) and the

109   Department of Sustainability and Environment (Permit No. 10004530).

110

111   ***Dietary analysis***

112   Stomach contents analysis provides information on the composition and abundance of prey

113   consumed (Duffy & Jackson 1986). Stomach samples were collected from the four seabird

114   species on Notch (38°56'S, 146°37'E) and Kanowna (39°10'S, 148°16'E) Islands in central Bass

115   Strait (Fig. 1). Adult common diving petrels were sampled in winter (n = 6), little penguins were

116   sampled in both winter and summer (n = 20 and 22, respectively), and fairy prion and short-

117   tailed shearwater diet samples were collected in summer only (n = 20 and 51, respectively). Due

118   to logistical constraints and few individuals onshore in some years, it was not possible to sample

119   all species in all years.

120   Adult birds were captured as they came ashore at night after foraging at sea. Diet samples were

121   collected using the water-offloading technique. While it is possible that not all stomach contents

122   were retrieved, stomach flushing is an effective technique for diet estimation in seabirds (Gales

123   1987) and, in most cases, the majority of prey remains were ejected on the second (final) flush,

124   as evidenced by clear water being ejected. After flushing, birds were given an electrolyte

125   solution of Vytrate or Lectade (Jurox Pty Ltd, NSW), and placed into boxes for recovery

126   (Chiaradia et al. 2003). Little penguins and short-tailed shearwaters were also provided with a

127   meal, delivered via a stomach tube, of homogenised pilchard (purchased snap-frozen and

128   unsalted) immediately before release.

129   Diet samples were frozen (-20ºC) or stored in 70% ethanol after collection. Crustacean remains

130   were initially identified to lower taxonomic levels with reference to Ritz et al. (2003). Sagittal

131   otoliths, scales, fish mouth parts and cephalopod beaks were identified by comparison to

132   reference atlases (Neira et al. 1998, Lu & Ickeringill 2002, Furlani et al. 2007) and collections

133   (held by Phillip Island Nature Parks and Deakin University).

134   Fresh prey items were washed with water and separated from accumulated ones. To estimate the

135   numerical abundance of crustacean prey, the heads of amphipods and whole bodies of copepods,

136   isopods and crab megalopa were counted directly while individual eyes of krill and stomatopods

137   were counted and divided by two. Left and right otoliths were counted and the side comprising

138   the greater number considered representative of the minimum number of each fish taxon per

139   sample. Where otoliths were unidentifiable, their abundance was halved and rounded to the

140   nearest number. Similarly, the highest number of upper or lower beaks in a sample was used to

141   estimate the abundance of cephalopods and only unbroken beaks were measured to estimate size

142   (Tollit et al. 1997). Hard prey remains that could not be quantified, such as fish scales, were

143   assigned a numerical abundance of one. The frequency of occurrence of prey remains was

144   calculated as the proportion of samples containing identifiable remains in which a particular prey

145   type occurred while the numerical abundance was expressed as the mean number of each prey

146   taxon encountered in samples.

147

148   ***Stable isotope analyses***

149   Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) values in tissues have been used to infer the diet of a

150   range of marine species (Hobson & Welch 1992, Hobson 1993, Cherel et al. 2007). Stable

151   isotope values of δ^{13}C values allow discrimination between benthic and pelagic prey (e.g., Cherel

152   et al. 2007) and inshore and offshore feeding (Hobson et al. 1994b), while δ^{15}N in tissues show

153   enrichment with increasing trophic levels (Hobson et al. 1994a). Information derived from whole

154   blood, as used in the present study, reflects dietary integration of approximately four weeks

155   (Bearhop et al. 2002).

156   Blood samples (< 0.2 ml) were collected from seabirds resident in western (WBS - Lady Julia

157   Percy Island: 38°25'S, 142°00'E), central (CBS - Notch, Kanowna, Norman: 39°02'S, 146°12'E

158   and Anser Islands: 39°09'S, 146°18'E) and eastern Bass Strait (EBS - Gabo Island: 37°34'S,

159   149°55'E). A total of 278 (167 in summer, 111 in winter), 177 (summer only), 88 (66 in

160   summer, 22 in winter) and 38 (winter only) stable isotope profiles were obtained from little

161   penguins, short-tailed shearwaters, fairy prions and common diving petrels, respectively. Adult

162   individuals (not sampled for diet determination) were captured as they returned to their nesting

163   burrows at night or taken from their burrows during the day. Little penguins and short-tailed

164   shearwaters were captured by hand, common diving-petrels were captured in mist nets, and fairy

165   prions were captured by hand or using hand nets as they approached their burrows. Upon

166   capture, blood was collected into a heparinised syringe via venipuncture of the tarsal vein or an

167   inter-digital vein in the foot.

168   Blood samples were stored frozen (-20ºC) and, prior to analysis, oven dried (60ºC) and

169   homogenised using a mortar and pestle. The low lipid content of whole blood does not typically

170   necessitate lipid extraction (Cherel et al. 2005a). Indeed, all mean values of C:N mass ratio

171 encompassed a narrow range (3.1-3.7) indicating low lipid content and, thus, allowing accurate

172 comparisons of $\delta^{13}C$ values among groups. Isotope ratios in whole blood were measured using a

173 continuous-flow isotope ratio mass spectrometer, with analyses conducted by the Isotope Ratio

174 Mass Spectrometry service in the Research School of Biology, Australian National University

175 (Canberra, Australia). The values of stable isotope abundances were expressed in δ-notation as

176 the deviation from standards in parts per thousand according to the equation:

177

178 $\delta X = [(R_{sample}/R_{standard}) - 1]$

179

180 where X is ^{15}N or ^{13}C and R represents the corresponding $^{15}N/^{14}N$ or $^{13}C/^{12}C$ ratios (Hobson et al.

181 1994a). $R_{standard}$ values were based on Vienna Pee Dee Belemnite for ^{13}C, and atmospheric

182 nitrogen (N^2) for ^{15}N. Based on variation between repeats of a standard material, measurement

183 error was estimated to be ± 0.20 and ± 0.15 ‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively.

184

185 ***Statistical analyses***

186 All statistical analyses were conducted in the R statistical environment 3.5.1 (R Core Team

187 2018). To investigate the effect of geographic, inter-annual and seasonal variations in stable

188 isotope values, generalised linear models (GLM) were fitted using the *lme4* package (Bates et al.

189 2014). Terms were added sequentially, model selection was based on Akaike's information

190 criterion (AIC), and the global models were checked to ensure normality and homoscedasticity

191 of the residuals. Post-hoc tests were conducted using analyses of variance (ANOVA) and *t*-tests,

192   or Kruskal-Wallis and Wilcoxon rank sum tests where transformations did not improve data

193   distributions. The stable isotope Bayesian ellipses in R (*SIBER* package; Jackson et al. 2011)

194   were used to determine the isotopic niche width of each species in each region, for each year and

195   season. The Standard Ellipse Area corrected (SEA$_C$; 40% probability of containing a

196   subsequently sampled datum regardless of sample size) was used to quantify niche width. The

197   Bayesian estimate of the standard ellipse and its area (SEA$_B$) were used to measure the overlap

198   of the isotopic niches between groups (Jackson et al. 2011).

199

200   **RESULTS**

201   ***Diet***

202   Stomach content samples were obtained from individuals between August 2008 and January

203   2011 in CBS order to inform interpretation of the stable isotope results. Samples were collected

204   from little penguins in both winter and summer (2008-2009), from short-tailed shearwaters in

205   summer 2009 and 2010, from fairy prions in summer 2011 and from common diving petrels in

206   winter 2008 and 2009. Overall, 79, 84, 95 and 40 % of little penguin, short-tailed shearwater,

207   fairy prion and common diving-petrel samples, respectively, contained identifiable fresh prey

208   remains.

209   Stomach samples of studied seabird species contained remains of fish, cephalopods and

210   crustaceans (Table 2). Not all taxa could be identified to species level. Crustacean remains,

211   comprising isopods, amphipods and/or copepods were ingested by little penguins, but consumed

212   mainly jack mackerel in winter and Australian anchovy *Engraulis australis* in summer, though

213   high numbers of post-larval fish were also ingested in summer (Table S1 in the Supplement).

214   The diets of all three procellariform species were dominated by euphausiids, particularly coastal

215   krill, which represented 78 – 96 % of the mean number of prey items consumed by these species

216   (Table S2 and Table S3 in the Supplement). Other important prey taxa included *Euphausia* sp.

217   and the hyperiid amphipod *Themisto australis* for short-tailed shearwaters, the megalopa stage of

218   a swimming crab species *Ovalipes* sp. for fairy prions and hyperiid amphipods for common

219   diving-petrels. For short-tailed shearwaters, the abundance of crustaceans was significantly

220   higher in 2010 than in 2009 (Wilcoxon-test, w = 126.5, p-value < 0.01), mainly driven by the

221   variation in number per samples of coastal krill (n = 118.9 ± 52.6 and n = 969.6 ± 194.2 in 2009

222   and 2010, respectively).

223

224   ***Stable isotopes analysis***

225   Blood samples were collected from all four species in WBS and CBS, and from little penguins

226   and short-tailed shearwaters in EBS (Table 3 and 4). Values of $\delta^{13}C$ range between -20.6 and -

227   18.1 ‰ for little penguins, between -23.7 and -20.4 ‰ for short-tailed shearwaters, between -

228   21.0 and -18.3 ‰ for fairy prions and between -21.4 and -19.4 ‰ for common diving petrels.

229   Whole blood $\delta^{15}N$ values range between 10.8 and 16.0 ‰ for little penguins, between 7.8 and

230   11.4 ‰ for short-tailed shearwaters, between 8.8 and 14.8 ‰ for fairy prions and between 10.9

231   and 14.5 ‰ for common diving petrels (Figure in the Supplement).

232   For all four species, stable isotope values in whole blood showed intraspecific variation between

233   regions and years (Fig. 2 and 3). Inter-annual variations of $\delta^{13}C$ values were significant in all

234   species in most regions (Paired *t*-test or Wilcoxon-test: *P* < 0.01) except for short-tailed

235   shearwater and common diving petrel in CBS (*t*-test: *P* > 0.07). While there was no pattern in

236 $\delta^{13}C$ differences between regions for the short-tailed shearwater, for the three other species

237 values in CBS were generally lower than those from WBS (0.56 ‰ to 1.40 ‰ lower) (Tables 3

238 and 4). Indeed, for the little penguin, fairy prion and common diving petrel, the variable "region"

239 explained, respectively, 63, 42 and 58 % of the variance for the $\delta^{13}C$ model, and only 2 % for the

240 short-tailed shearwater. For $\delta^{15}N$, the best models retained, with interactions, the $\delta^{13}C$, the region

241 and the year as significant variables explaining 57 % to 93 % of the deviance (Table S4 in the

242 Supplement). Significant inter-annual differences were recorded in all regions (Paired t-test or

243 Wilcoxon-test: $P < 0.01$), but no clear pattern was detected in the values or the isotopic niche

244 metrics (Tables 3 and 4). Similarly, for each year, the $\delta^{15}N$ values varied significantly between

245 region for the little penguin, fairy prion and common diving petrel (Paired t-test or Wilcoxon-

246 test: $P < 0.01$). For the short-tailed shearwater, a spatial difference in $\delta^{15}N$ values was detected

247 between WBS and EBS in 2010 (Paired t-test $t_{37} = -2.19$, $P < 0.05$), but no other significant

248 differences were found. The models for $\delta^{13}C$ retained the region and year as significant variables

249 for all the study species, explaining 58.6 % to 79.3 % of the variance (Table S4 in the

250 Supplement).

251 The four study species occupied different isotopic niches in all years and each region (Figure in

252 the Supplement). Values of $\delta^{13}C$ and $\delta^{15}N$ in whole blood of short-tailed shearwaters were

253 significantly lower (with no isotopic niche overlap) than those of the other species in each region

254 all three years (paired t-test or Wilcoxon-test: $p < 0.01$, Table 3). In contrast, mean $\delta^{15}N$ values in

255 blood of little penguins typically showed the greatest enrichment in both winter and summer,

256 though this varied spatially and inter-annually (Table 3 and 4). Isotopic $\delta^{13}C$ values of little

257 penguins and fairy prions were relatively similar, but tended to be higher than those of common

258 diving-petrels in winter, particularly in CBS. While the isotopic niche of the fairy prion

259   overlapped sparsely with the common diving petrel (SEA$_B$ overlap < 8.1%), and with little

260   penguin in 2009 and 2011 (SEA$_B$ overlap < 4.9%), niche overlap with the little penguin was

261   important in 2010 (maximum SEA$_B$ overlap = 21.8% in winter 2010 in WBS, Table 3 and 4).

262

263   **DISCUSSION**

264   Sympatric seabird species diverge in their foraging niche in a variety of spatial and temporal

265   ways (Waugh & Weimerskirch 2003, González-Solís et al. 2008, Davies et al. 2009). Bass Strait

266   is occupied by an abundant marine avifauna (Ross et al. 2001), with little previously known of

267   the trophic niches of most species. Combining stomach contents and stable isotope analyses, the

268   present study has shown that the four most abundant and ubiquitous species generally occupy

269   different trophic niches that vary among regions, years and season.

270

271   ***Diet***

272   The little penguin is considered an inshore generalist forager relying mostly on small pelagic

273   prey such as Clupeiformes (Cullen et al. 1992, Chiaradia et al. 2010, Sutton et al. 2015). In the

274   present study, stomach contents of little penguins in summer were similar to that previously

275   reported, with Australian anchovy and post-larval fish contributing the majority of samples. In

276   contrast, winter stomach contents were dominated by jack mackerel, highlighting a seasonal

277   switch in the availability of the main prey of little penguins. Such differences have also been

278   shown in little penguins from Albatross Island in southern Bass Strait (Gales & Pemberton 1990)

279   and Phillip Island in northern Bass Strait (Cavallo et al. 2018). While recent studies have

280   observed that jellyfish can contribute a substantial proportion of the little penguin diet (Sutton et

281 al. 2015, Cavallo et al. 2018), no evidence of such prey were found in the present study. This

282 could potentially be due to rapid digestion of gelatinous prey in comparison to fish or

283 crustaceans (Cavallo et al. 2018), emphasising the limitation of traditional stomach content

284 analyses, or reflect inter-annual differences in available prey types.

285 Stomach contents of short-tailed shearwaters in the present study were similar to those of

286 individuals from Tasmania (Weimerskirch & Cherel 1998, Cherel et al. 2005b). The main

287 identified prey was the coastal krill, indicating that sampled birds were mostly returning from

288 short foraging trips over the continental shelf (Blackburn 1980, Weimerskirch & Cherel 1998).

289 Indeed, during the breeding season, short-tailed shearwaters alternate between short (1-2 d) local

290 trips within 35-70 km of the colony and long trips (10-20 d) to Antarctic waters (Weimerskirch

291 & Cherel 1998, Einoder et al. 2011, Berlincourt & Arnould 2015b) where they feed mainly on

292 coastal krill, and myctophid fish and sub-Antarctic krill, respectively (Montague 1986,

293 Weimerskirch & Cherel 1998). In the 2010 samples, a limited number of birds (n = 4) had

294 stomach contents dominated by stomach oil and digested *Euphausia* sp, suggesting they had

295 returned from long trips to Antarctic waters (Weimerskirch & Cherel 1998).

296 Coastal krill occurs in neritic waters of eastern Australia, where other krill species are rare or

297 absent (Blackburn 1980). Due to its abundance, it plays a key role in the coastal ecosystem,

298 reflected by its dominance in the diets of various cetacean, seabirds and fish species (O'Brien

299 1988, Gill et al. 2011). Despite limited data on the diet of fairy prions and common diving petrels

300 in Bass Strait, their stomach contents confirmed the importance of coastal krill to these species in

301 the Australasian region (Harper 1976, Schumann et al. 2008). These results, together with

302 estimates of trip duration in previous studies (1-3 d trips at sea, Harper 1976, Bocher et al.

303   2000a, b, Navarro et al. 2013, Zhang et al. 2018), suggest that both fairy prions and common

304   diving petrels most likely forage within Bass Strait or in the vicinity of the continental shelf.

305

306   ***Spatial variability in isotopic niche***

307   Since whole blood integrates dietary information over approximately four weeks (Bearhop et al.

308   2002), it might be expected that isotopic values for short-tailed shearwaters would reflect a

309   combination of both their local and Antarctic foraging areas (Berlincourt & Arnould 2015b),

310   thereby masking any differences in blood isotope values between foraging zones. However,

311   Cherel et al. (2005b) showed that while most of the food consumed by short-tailed shearwaters

312   during short local trips is allocated to their chick, adults feed for themselves when foraging

313   further south and, therefore, have a truly Antarctic blood isotopic signature. In the present study,

314   values of $\delta^{13}C$ in whole blood of short-tailed shearwaters were comparable to those of other

315   procellariforms foraging in subantarctic waters (Cherel et al. 2002a, Cherel et al. 2002b,

316   Quillfeldt et al. 2005) but were slightly higher than those in plasma of short-tailed shearwaters

317   from south Tasmania (Cherel et al. 2005b).

318   Interestingly, the $\delta^{13}C$ values of short-tailed shearwaters varied significantly between the three

319   study regions in Bass Strait, indicating possible foraging spatial segregation within the Southern

320   Ocean by individuals from the different regions. As $\delta^{13}C$ values are higher in subtropical than in

321   Antarctic waters (Cherel & Hobson 2007, Cherel et al. 2007, 2010, Jaeger et al. 2010), this

322   suggests a latitudinal segregation in the foraging areas between the three sampled populations.

323   However, this variation was not consistent across years, with strong inter-annual variability in

324   $\delta^{13}C$ values for birds from WBS and EBS compared to CBS. This could suggest not only colony-

325   specific niche segregation but also density-dependent competition (Wakefield et al. 2013), with

326   the smallest colonies having a more flexible foraging area. Indeed, the CBS population is

327   considerably bigger than the WBS and EBS populations, with 755,400, 30,000 and 6,000

328   breeding pairs, respectively (Bowker 1980, Pescott 1976, Fullagar & Heyligers 1996, Schumann

329   et al. 2014). This is in accordance with previous tracking studies (Berlincourt & Arnould 2015b)

330   that observed inter-annual longitudinal and latitudinal variation in the long trip foraging areas of

331   short-tailed shearwater from the small populations in WBS and EBS. Despite the geographic and

332   temporal differences in δ^{13}C observed, there were no major differences in the δ^{15}N values

333   between regions in the present study, highlighting the consistency of the diet of short-tailed

334   shearwaters in the Southern Ocean.

335   For little penguins, fairy prions and common diving petrels, temporal and geographic differences

336   in isotopic signatures are likely to reflect differences in prey availability associated with the

337   strength of the prevailing of ocean currents and upwelling systems in the different regions of

338   Bass Strait. For example, in summer, the SAC may transport prey and nutrient-enriched waters

339   from the west into Bass Strait (Mickelson et al. 1992, Sandery & Kämpf 2007), weakening

340   towards the east (Sandery & Kämpf 2007) where the EAC increases in prevalence, bringing

341   warmer nutrient-poor water into north-eastern Bass Strait (Gibbs 1992). This was reflected in

342   δ^{13}C values in the whole blood of little penguins and fairy prions, where values were

343   systematically lower in CBS than in WBS and EBS. Similar observations have been reported for

344   Australian fur seals where δ^{13}C values in blood plasma of individuals from CBS were

345   consistently lower than those from EBS (Arnould et al. 2011), highlighting the influence of

346   SASW (depleted in δ^{13}C) on CBS waters (Gibbs 1992). In winter, however, spatial differences in

347   isotopic values declined. This may reflect the greater influence of the SAC in Bass Strait during

348   the winter period (Sandery & Kämpf 2007).

349

350   *Inter-annual trophic variability*

351   The isotope values in the whole blood of little penguins from WBS and CBS in summer are

352   within the range previously reported from Phillip Island in CBS (Chiaradia et al. 2010, Chiaradia

353   et al. 2012), with the exception of 2010 when δ^{15}N values were significantly lower in both

354   regions. This could reflect fluctuations in isotopic baseline signatures due to different water

355   masses and variable strength of the currents influencing the regions where individuals foraged.

356   Indeed, as reported by Polito et al. (2019), variations in oceanic factors such as chlorophyll-*a*

357   concentration can substantially alter mean isotope values independently of any change in the diet

358   of the species. However, this could also reflect a variation in main prey species consumed, with

359   little penguins known to have important inter-annual variability in their diet (Gales & Pemberton

360   1990, Cullen et al. 1992, Chiaradia et al. 2010). In the present study, individuals from CBS in

361   summer 2009 consumed predominantly Australian anchovy, a species exploiting higher trophic

362   levels than other prey targeted by little penguins (Espinoza et al. 2009, van der Lingen et al.

363   2009). As previously highlighted by Chiaradia et al. (2010), δ^{15}N values are higher during years

364   with an important proportion of anchovy in little penguin diet. Therefore, it is likely that the low

365   δ^{15}N values in summer 2010 in the present study was due to a depletion of Australian anchovy in

366   the diet, potentially due to a reduced availability in the region. This is consistent with previous

367   reports indicating inter-annual flexibility in little penguin at-sea foraging behaviour in relation to

368   environmental conditions that directly influence prey abundance (Berlincourt & Arnould 2015a,

369   Camprasse et al. 2017). Indeed, in WBS and CBS, the niche space occupied by little penguins in

370   2010 was much larger than in 2009 and 2011, indicating a larger trophic diversity (Layman et al.

371   2007), possibly due to the absence of the usual main prey. Similarly, for both fairy prions and

372 common diving petrels, δ^{15}N values in the whole blood of both species in the region varied

373 substantially between years, suggesting variation in the consumption of their main prey, coastal

374 krill. Significant inter-annual differences in the density and biomass of coastal krill in southern

375 Bass Strait have previously been observed (Young et al. 1993).

376

377 ***Trophic and isotopic niche segregations***

378 In the present study, interspecific comparisons of stomach contents and δ^{15}N values revealed that

379 little penguins typically occupied the highest trophic positions of the four seabird species while

380 short-tailed shearwaters always occupied the lowest. High little penguin δ^{15}N values were

381 nevertheless lower to those of the top predators shy albatross and Australian fur seal (Arnould et

382 al. 2011; Cherel et al. 2013), but were close to the values of the large Australasian gannet (Angel

383 et al. 2016), which predominantly consumes pilchards and anchovy (Bunce 2001) (Figure 4). In

384 contrast, δ^{15}N values of short-tailed shearwaters, fairy prions and common diving petrels were

385 remarkably lower than those of the much smaller white-faced storm petrels (Figure 4), which

386 consume a significant proportion of fish in addition to coastal krill (Underwood 2012). These

387 results indicated that coastal krill was a key prey taxon in all three procellariforms in central Bass

388 Strait. During breeding, both fairy prions and common diving petrels return to the nest every

389 night (Harper 1976, Payne & Prince 1979), suggesting that they forage mainly on the shelf near

390 their colonies. Elsewhere, fairy prions take prey from the surface waters (Harper 1987, Prince &

391 Morgan 1987) whereas common diving petrels exploit depths averaging 2-4 m (Navarro et al.

392 2013, Navarro et al. 2014, Dunphy et al. 2015). Likewise, despite isotopic signatures showing

393 self-maintenance feeding in the Southern Ocean, short-tailed shearwaters forage on coastal krill

394 over the shelf near colonies during short trips (Einoder et al. 2011, Berlincourt & Arnould

395   2015b), resulting in the potential for interspecific overlap in the foraging zones of the three

396   procellariforms. However, short-tailed shearwaters forage at deeper depths (average 13 m)

397   during local trips (Weimerskirch & Cherel 1998). While the foraging zones and dive depths of

398   little penguins may overlap with those of short-tailed shearwaters (Berlincourt & Arnould 2015a,

399   2015b), the limited distance travelled per trip and fish-based diet of little penguins would reduce

400   competition with procellariforms.

401   In addition to segregation of diet and foraging behaviour, the four species differ in their breeding

402   phenologies. Common diving petrels, fairy prions and short-tailed shearwaters lay their eggs in

403   late July, late October and late November, respectively (Harris 1979, Marchant & Higgins 1990).

404   Thus, there is limited overlap in the breeding periods of the three procellariforms. However, the

405   protracted and variable breeding season of little penguins (Reilly & Cullen 1981, Cullen et al.

406   1992) may overlap with the other species. Interspecific competition may, therefore, intensify in

407   years of low fish prey availability. Indeed, previous studies have documented the presence of

408   coastal krill in the diet of little penguin during years of low prey availability (Cullen et al. 1992).

409   The dependence of these seabird species on relatively few prey types (such as coastal krill,

410   pilchard or anchovy) may increase the impacts of reductions in prey abundance. Climate models

411   have described an intensification of the EAC due to large-scale changes in ocean circulation in

412   the Southern Hemisphere (Cai 2006), produced in association with an increasing trend in the

413   Southern Annular Mode (Cai et al. 2005). During years of intensified EAC, Young et al. (1993)

414   reported a dramatic drop in coastal krill biomass. This is likely to adversely affect seabirds in the

415   region. Similarly, significant mortality events, poor chick growth and population declines in

416   short-tailed shearwaters in Bass Strait have been previously attributed to local prey shortages

417   (Vertigan 2010). Declines in coastal krill availability may also indirectly impact little penguins

418   since this species is an important dietary component of several of their prey taxa (Harris et al.

419   1979, O'Brien 1988). The predicted increase in the strength of the EAC with climate change (Cai

420   et al. 2005) could, therefore, have severe negative consequences for the Bass Strait seabird

421   community.

422

423   **CONCLUSIONS**

424   In summary, the present study has shown that the isotopic niches of seabirds in Bass Strait vary

425   significantly between regions, years and seasons. These differences are likely to result from

426   changes in prey availability driven by variations in ocean currents and local productivity. Despite

427   interspecific similarities in diet, divergence in the relative foraging niche is likely to reduce

428   interspecific competition for prey, though this may become more important in years of low prey

429   availability. The low diversity of prey taxa ingested by these seabirds suggests that they are

430   vulnerable to changes in the availability of key prey. In order to better understand the foraging

431   niches of the Bass Strait community of seabirds, as well as their capacity to adapt to changing

432   environmental conditions, more detailed information on their foraging zones and feeding

433   behaviour is required. This is particularly important for the small procellariforms in light of the

434   paucity of information in south-eastern Australia, in contrast to the numerous studies that have

435   been conducted on little penguins and short-tailed shearwaters in the region (*e.g.* Ropert-Coudert

436   et al. 2004, 2009, Berlincourt & Arnould 2015a, b). Such information may help elucidate the

437   likelihood of interspecific competition in this assemblage of seabirds.

438

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446

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Main species of seabirds breeding in Bass Strait, indicating the estimated number of breeding pairs, the proportion of total Australian populations (based on Ross et al. 2001), and the major group of prey consumed.

Species	Abundance (number of breeding pairs)	% of the Australian population	Groups of main prey	Reference
Shy albatross	5 200	35 %	Fish/cephalopods	Alderman et al. 2011, Hedd & Gales 2001
Short-tailed shearwater*	14 600 000	75 %	Crustaceans/Fish	Weimerskirch & Cherel 1998, Brothers et al. 2001, Schumann et al. 2014
Common diving petrel*	98 500	63 %	Crustaceans	Brothers et al. 2001, Schumann et al. 2008, Schumann et al. 2014
Fairy prion*	97 000	7 %	Crustaceans	Brothers et al. 2001, Schumann et al. 2014
White-faced storm petrel	94 500	25 %	Crustaceans	Brothers et al. 2001, Underwood 2012
Little penguin*	353 000	82 %	Fish	Cullen et al. 1992, Brothers et al. 2001, Dann & Norman 2006, Schumman et al. 2014
Australasian gannet	16 800	85 %	Fish	Bunce et al. 2002, Bunce 2001
Black faced cormorant	4 400	55 %	Fish	Brothers et al. 2001, Taylor et al. 2013
Pacific gull	1 500	82 %	Scavenge - polyvorous	Brothers et al. 2001, Leitch et al. 2014
Silver gull	50 000	35 %	Scavenge - polyvorous	Brothers et al. 2001, Leitch et al. 2014
Crested tern	10 400	13 %	Fish	Brothers et al. 2001, Chiaradia et al. 2012

*study species

Percentage of numerical abundance of the main groups of prey recovered from stomach contents of little penguins, short-tailed shearwaters, fairy prions and common diving petrels in Central Bass Strait.

	Little penguin (n = 42)	Short-tailed shearwater (n = 51)	Fairy prion (n = 20)	Common diving petrel (n = 6)
Fish (%)	74.1	1.8	>0.1	-
Cephalopods (%)	4.8	0.2	-	-
Crustaceans (%)	21.1	98.0	99.9	100

Summer mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values (‰) in whole blood and isotopic niche metrics of little penguins, short-tailed shearwaters and fairy prions from western, central and eastern Bass Strait.

Standard ellipse area corrected (SEA_C); Bayesian standard ellipse area (SEA_B); Total convex hull area (TA). Ecological explanations for Layman metrics are provided in the Supplement. The samples were collected in summer (January-February) 2009, 2010 and 2011.

		Western Bass Strait			Central Bass Strait			Eastern Bass Strait		
		Little penguin	Short-tailed shearwater	Fairy prion	Little penguin	Short-tailed shearwater	Fairy prion	Little penguin	Short-tailed shearwater	Fairy prion
$\delta^{13}C$ (‰)	2009	-19.1 ± 0.4 (n = 10)	-21.9 ± 0.4 (n = 16)	-19.2 ± 0.2 (n = 8)	-19.8 ± 0.1 (n = 18)	-22.2 ± 0.3 (n = 20)	-	-19.0 ± 0.3 (n = 18)	-22.9 ± 0.5 (n = 20)	-
	2010	-19.5 ± 0.2 (n = 20)	-23.1 ± 0.3 (n = 20)	-19.5 ± 0.6 (n = 10)	-20.1 ± 0.4 (n = 19)	-22.2 ± 0.3 (n = 20)	-20.5 ± 0.7 (n = 6)	-19.0 ± 0.2 (n = 20)	-22.1 ± 0.4 (n = 20)	-
	2011	-18.9 ± 0.3 (n = 20)	-21.9 ± 0.4 (n = 20)	-18.8 ± 0.4 (n = 18)	-19.9 ± 0.2 (n = 10)	-22.0 ± 0.3 (n = 20)	-19.8 ± 0.3 (n = 17)	-18.5 ± 0.2 (n = 10)	-21.1 ± 0.5 (n = 13)	-
$\delta^{15}N$ (‰)	2009	15.5 ± 0.3 (n = 10)	9.5 ± 0.6 (n = 16)	13.7 ± 0.6 (n = 8)	14.4 ± 0.2 (n = 18)	9.3 ± 0.7 (n = 20)	-	12.9 ± 0.9 (n = 18)	9.4 ± 0.6 (n = 20)	-
	2010	13.2 ± 0.9 (n = 20)	8.5 ± 0.4 (n = 20)	13.6 ± 0.9 (n = 10)	13.4 ± 0.5 (n = 19)	8.6 ± 0.5 (n = 20)	11.7 ± 0.8 (n = 6)	13.6 ± 0.3 (n = 20)	8.8 ± 0.3 (n = 20)	-
	2011	15.0 ± 0.4 n = (20)	9.7 ± 0.6 (n = 20)	12.5 ± 0.9 (n = 18)	14.9 ± 0.3 (n = 10)	9.9 ± 0.6 (n = 20)	13.2 ± 0.5 (n = 17)	13.6 ± 0.2 (n = 10)	9.9 ± 0.7 (n = 13)	-
$\delta^{13}C$ range (‰)	2009	1.2	1.4	0.5	0.4	1.0	-	0.7	2.1	-
	2010	0.8	1.3	1.8	2.0	1.1	1.9	0.6	1.7	-
	2011	1.4	1.4	1.9	0.6	1.2	1.1	0.6	1.4	-
$\delta^{15}N$ range (‰)	2009	0.9	2.2	1.8	0.8	3.2	-	2.8	2.6	-
	2010	3.5	1.4	2.4	1.6	1.6	2.1	1.1	1.1	-
	2011	1.6	2.0	3.1	1.0	2.0	1.5	0.7	2.5	-
SEA_C	2009	0.32	0.47	0.35	0.07	0.45	-	0.64	0.75	-
	2010	0.32	0.42	1.55	0.62	0.36	0.87	0.15	0.44	-
	2011	0.34	0.68	1.26	0.18	0.51	0.53	0.14	0.58	-
SEA_B	2009	0.32	0.55	0.37	0.08	0.47	-	0.65	0.80	-
	2010	0.34	0.42	1.64	0.62	0.37	1.39	0.15	0.44	-
	2011	0.35	0.68	1.26	0.19	0.52	0.53	0.14	0.70	-
% SEA_B Overlap[*]	2009	-	0	4.9	-	0	-	-	0	-
	2010	-	0	15.8	-	0	11.5	-	0	-
	2011	-	0	0	-	0	1.7	-	0	-
TA	2009	0.69	1.16	0.46	0.20	1.38	-	1.29	2.08	-
	2010	1.11	1.15	2.27	1.73	1.03	0.86	0.44	1.15	-
	2011	0.75	1.71	3.15	0.31	1.36	1.17	0.24	1.04	-

*compared to little penguin (for each region and year)

Winter mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values (‰) in whole blood and isotopic niche metrics of little penguins, fairy prions and common diving petrels from western, central and eastern Bass Strait.

Standard ellipse area corrected (SEA$_C$); Bayesian standard ellipse area (SEA$_B$); Total convex hull area (TA). Ecological explanations for Layman metrics are provided in the Supplement. The samples were collected in winter (July-August) 2008, 2009 and 2010.

		Western Bass Strait			Central Bass Strait			Eastern Bass Strait		
		Little penguin	Fairy prion	Common diving petrel	Little penguin	Fairy prion	Common diving petrel	Little penguin	Fairy prion	Common diving petrel
$\delta^{13}C$ (‰)	2008	-19.2 ± 0.4 (n = 3)	-	-	-19.0 ± 0.3 (n = 7)	-	-20.8 ± 0.8 (n = 10)	-	-	-
	2009	-20.0 ± 0.4 (n = 2)	-	-	-19.7 ± 0.1 (n = 20)	-	-20.8 ± 0.2 (n = 4)	-19.3 ± 0.5 (n = 20)	-	-
	2010	-19.3 ± 0.6 (n = 16)	-19.2 ± 0.4 (n = 18)	-19.6 ± 0.1 (n = 8)	-19.8 ± 0.1 (n = 20)	-19.5 ± 0.3 (n = 3)	-20.9 ± 0.3 (n = 15)	-19.2 ± 0.3 (n = 20)	-	-
$\delta^{15}N$ (‰)	2008	13.0 ± 0.1 (n = 3)	-	-	14.4 ± 0.4 (n = 7)	-	12.0 ± 1.1 (n = 10)	-	-	-
	2009	13.3 ± 0.4 (n = 2)	-	-	15.0 ± 0.4 (n = 20)	-	14.3 ± 0.2 (n = 4)	13.1 ± 1.2 (n = 20)	-	-
	2010	13.2 ± 0.6 (n = 16)	11.4 ± 1.4 (n = 18)	11.6 ± 0.3 (n = 8)	14.2 ± 0.3 (n = 20)	12.2 ± 0.3 (n = 3)	12.2 ± 0.2 (n = 15)	13.3 ± 0.6 (n = 20)	-	-
$\delta^{13}C$ range (‰)	2008	na	-	-	0.7	-	2.7	-	-	-
	2009	na	-	-	0.4	-	0.3	1.6	-	-
	2010	1.1	1.6	0.3	0.5	na	1.0	1.1	-	-
$\delta^{15}N$ range (‰)	2008	na	-	-	1.1	-	3.6	-	-	-
	2009	na	-	-	1.3	-	0.4	3.5	-	-
	2010	1.3	4.8	0.9	1.3	na	0.7	1.8	-	-
SEA_C	2008	na	-	-	0.17	-	0.90	-	-	-
	2009	na	-	-	0.13	-	0.17	1.03	-	-
	2010	0.49	1.65	0.13	0.15	na	0.21	0.50	-	-
SEA_B	2008	na	-	-	0.27	-	1.52	-	-	-
	2009	na	-	-	0.14	-	0.15	1.13	-	-
	2010	0.49	1.68	0.13	0.15	na	0.21	0.50	-	-
% SEA_B Overlap*	2008	-	-	-	-	-	0	-	-	-
	2009	-	-	-	-	-	0	-	-	-
	2010	-	21.8	0.5	-	-	0	-	-	-
TA	2008	na	-	-	0.20	-	1.63	-	-	-
	2009	na	-	-	0.32	-	0.11	2.63	-	-
	2010	0.92	5.18	0.18	0.46	na	0.49	1.34	-	-

*compared to little penguin (for each region and year)

Figure 1

Simplified representation of the three study areas and the major water masses influencing the region.

Western Bass Strait (WBS); Central Bass Strait (CBS); Eastern Bass Strait (EBS); Lady Julia Percy Island (LJPI); Norman Island (NorI); Kanowna Island (KI); Answer Island (AI); Notch Island (NotI); Gabo Island (GI); South Australian Current (SAC); Sub-Antarctic Surface Water (SASW); East Australian Current (EAC) from Sandery & Kämpf 2005. The solid line indicates the location of the 300 m isobath.
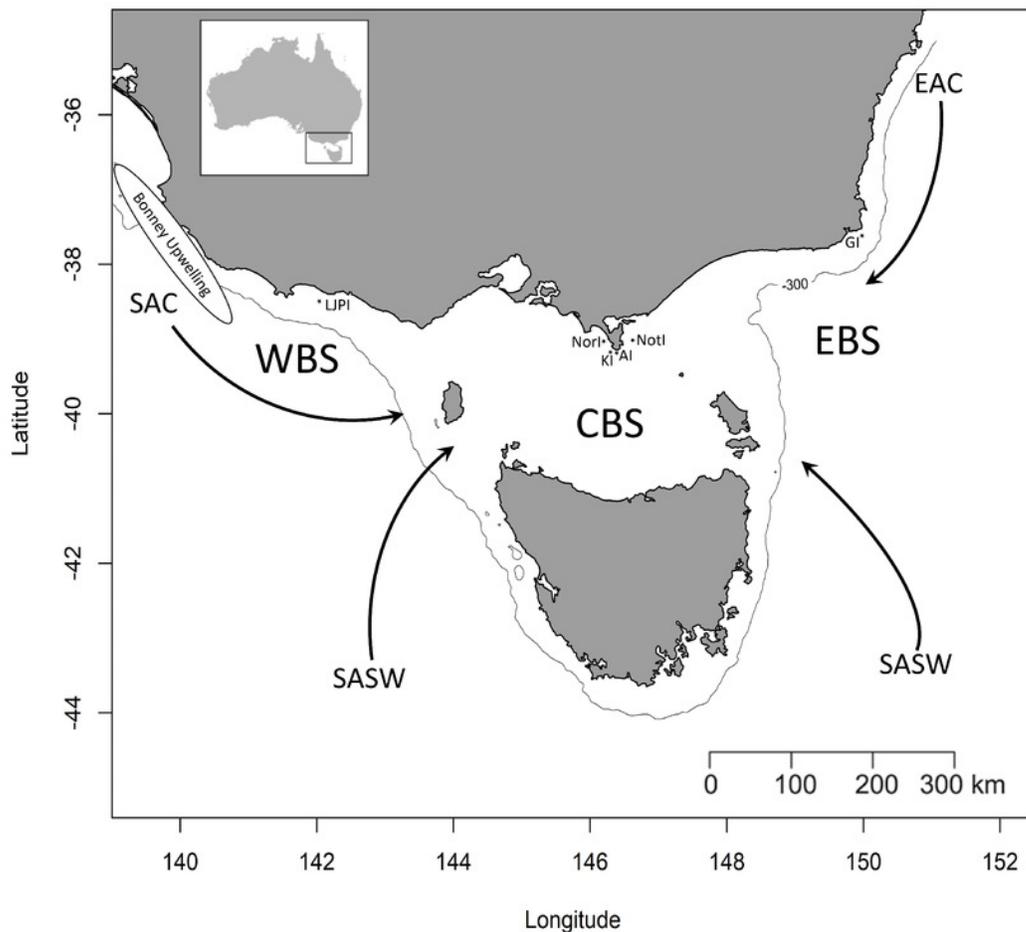
Figure 2

Summer inter-annual variation of δ^{13}C and δ^{15}N values (‰) in whole blood of little penguins, short-tailed shearwaters and fairy prions: western Bass Strait (WBS), central Bass Strait (CBS) and eastern Bass Strait (EBS).

Solid lines represent the standard ellipses corrected for sample size (SEAc) based on δ^{13}C and δ^{15}N values in summer 2009, 2010 and 2011. Note that the ranges for x and y axes are different for each species.
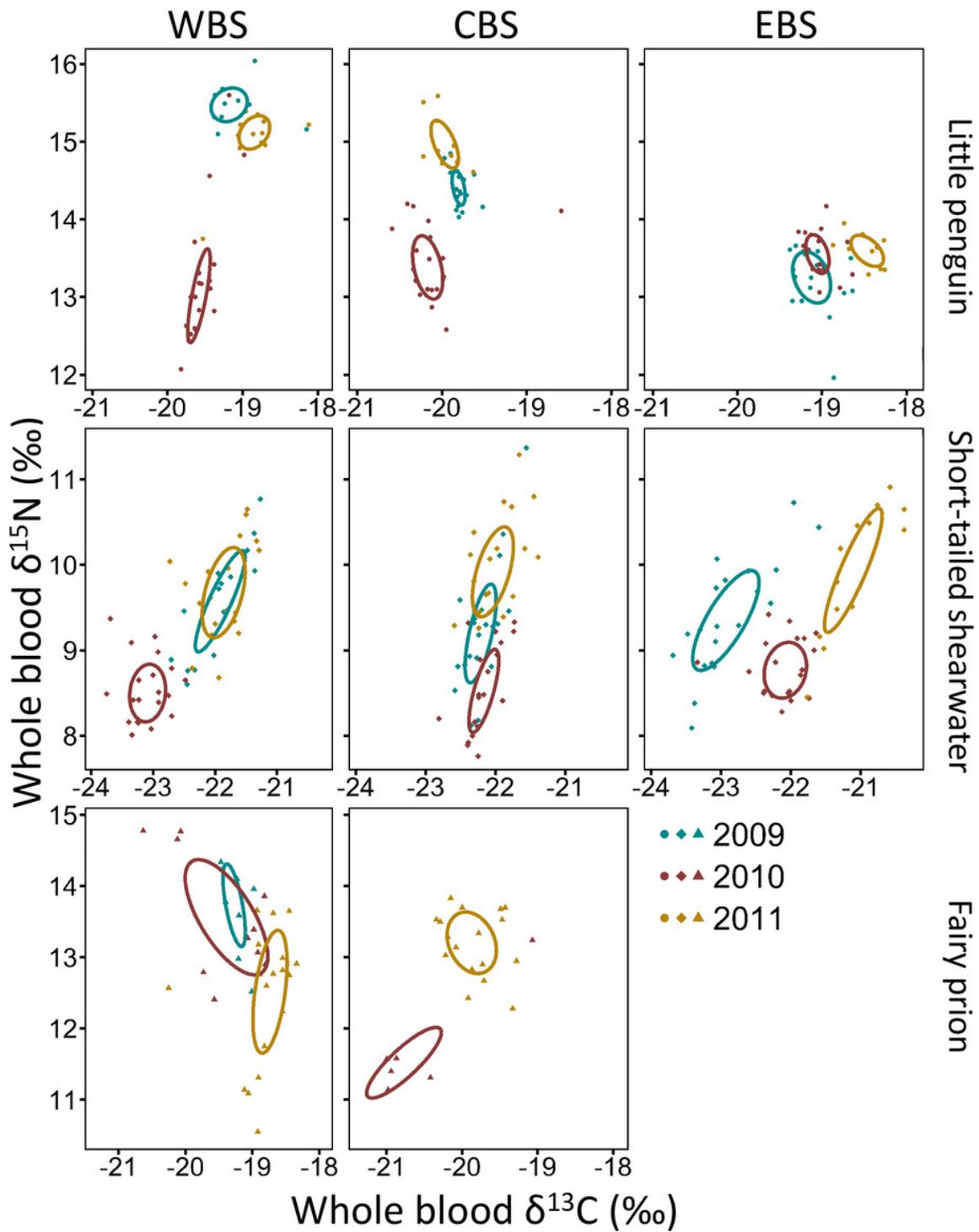
Figure 3

Winter inter-annual variation of δ^{13}C and δ^{15}N values (‰) in whole blood of little penguins and common diving petrels: western Bass Strait (WBS), central Bass Strait (CBS) and eastern Bass Strait (EBS).

Solid lines represent the standard ellipses corrected for sample size (SEAc) based on δ^{13}C and

δ^{15}N values in winter 2008, 2009 and 2010. Note that the range for x and y axes are different

for each species.
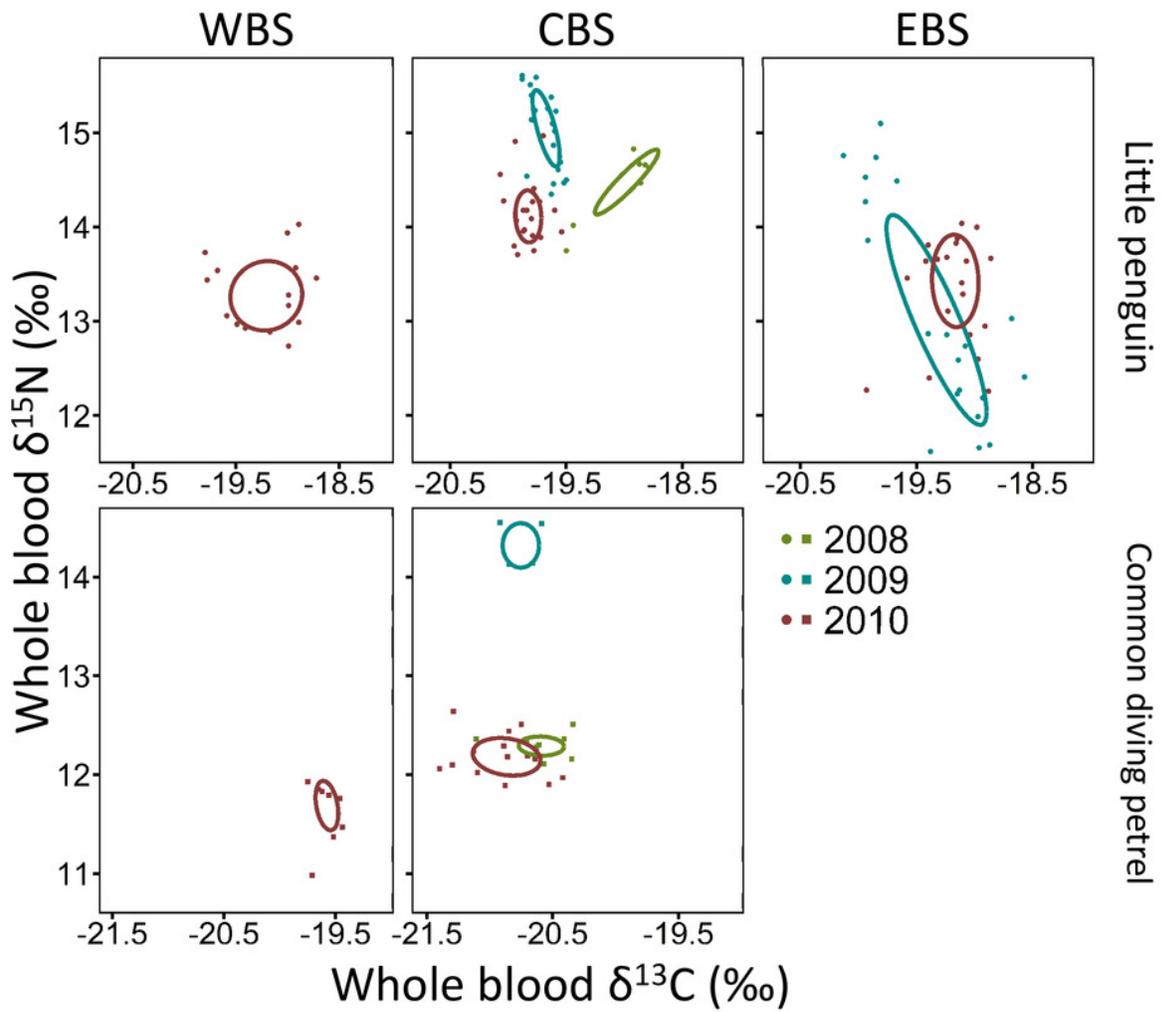
Figure 4

Summary of δ^{13}C and δ^{15}N values (‰) in whole blood of the main marine predators in Bass Strait region.

Little penguin (LP, n = 278; present study), short-tailed shearwater (STSW, n = 177; present study), fairy prion (FP, n = 88; present study), common diving petrel (CDP, n = 38; present study), Australasian gannet (GA, n = 27; Angel et al. 2016), white-faced storm petrel (WFST, n = 17; Underwood 2012), shy albatross (SA, n = 8; Cherel et al. 2013) and Australian fur seal (AFS, n = 242; Arnould et al. 2011). The isotopic values of WFST and SA were calculated from data on chick feathers (Underwood 2012) and adult feathers (Cherel et al. 2013), respectively, and corrected using mean correction factors in Cherel et al. 2014.