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.

32 **INTRODUCTION**

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

34 crustaceans (Ridoux 1994, Brooke 2004). The foraging niche of seabirds is influenced by a range

35 of factors, including environmental conditions (Waugh & Weimerskirch 2003, Amélineau et al.

36 2016, Jakubas et al. 2017), prey availability (Baird 1991, Camprasse et al. 2017), morphological

37 characteristics and their influence on flight performance (Phillips et al. 2004, 2005, Navarro et al.

38 2013), and interspecific competition (González-Solís et al. 2008, Phillips et al. 2008, Kokubun et

39 al. 2016). Competition is thought to promote foraging niche divergence since species occupying

40 the same ecological niche cannot theoretically coexist through time (Schoener 1974). Seabirds

41 may separate their resources on several dimensions, with studies showing divergence in foraging

42 zone (González-Solís et al. 2008, Barger et al. 2016), diving depth (Mori & Boyd 2004), the

43 timing of breeding (Granroth-Wilding & Phillips 2019), and seasonal patterns of activity

44 (Phillips et al. 2008). In particular, divergence in diet has been proposed as an important

45 mechanism in reducing niche overlap (Ridoux 1994, Surman & Wooller 2003, Pratte et al.

46 2017).

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

48 is a key region for Australian seabirds, supporting a large proportion of breeding populations of

49 at least 11 major species (Table 1; Ross et al. 2001). This area is considered a region of low

50 primary productivity (Gibbs et al. 1986, Gibbs et al. 1991) that occurs at the confluence of three

51 main ocean currents. The warm, oligotrophic waters of the East Australian Current (EAC) flow

52 southward along the eastern edge of Bass Strait (Ridgeway & Godfrey 1997, Sandery & Kämpf

53 2007) while the South Australian Current (SAC) advects warm water from the west onto the

54 shelf which then flows eastward through Bass Strait (Sandery & Kämpf 2007). The latter is the

55   major source of Bass Strait water and is strongest in winter (Ridgeway & Condie 2004, Sandery

56   & Kämpf 2007). In summer, a weakening or reversal of this eastward-flowing trend occurs

57   (Gibbs et al. 1986, Sandery & Kämpf 2007). Finally, in winter, cold, nutrient-rich sub-Antarctic

58   surface water (SASW) enters Bass Strait from the south (Gibbs 1992) where it mixes with the

59   EAC and SAC along the sub-Tropical Convergence (STC, Prince 2001).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

78   ubiquitous seabirds in Bass Strait, breeding sympatrically on numerous offshore islands

79   (Schumann et al. 2014). They are known to feed on a variety of fish, cephalopod and/or

80   crustacean prey (Harper 1976, Montague et al. 1986, Schumann et al. 2008, Chiaradia et al.

81   2010). Previous foraging ecology studies indicate that the little penguin is an inshore forager

82   relying mainly on small pelagic schooling fish (Cullen et al. 1992, Chiaradia et al. 2010), while

83   the pelagic short-tailed shearwater, with a foraging range extending to the Antarctic waters

84   (Woehler et al. 2006, Cleeland et al. 2014), and the smaller and more neritic fairy prion and

85   common diving petrel, feed on a wide range of small prey, concentrating predominantly on

86   coastal krill (*Nyctiphanes australis*) and myctophid fish (Harper 1976, Weimerskirch & Cherel

87   1998, Schumann et al. 2008). However, in Bass Strait, information on spatial and temporal

88   variation in the ecology of these species is limited to the at-sea foraging behaviour of little

89   penguins and short-tailed shearwaters (e.g. Collins et al. 1999, Chiaradia et al. 2010, Berlincourt

90   & Arnould 2015a, b) and there is almost no information on the small procellariforms

91   (Underwood 2012).

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

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

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

95   species within Bass Strait.

96

97   **MATERIAL & METHODS**

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

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

100   1). In summer, the study species were sampled in mid, early and late chick-rearing, respectively

101   for the little penguin (Reilly & Cullen 1981), the short-tailed shearwater (Vertigan 2010) and the

102   fairy prion (Harper 1976) (Fig. 2). In winter, sampling occurred during the inter-breeding period

103   for the little penguin (Reilly & Cullen 1981) and fairy prion (Harper 1976) and incubation for the

104   common diving petrel (Schumann et al. 2008) (Fig. 2). The trophic niches of little penguins,

105   short-tailed shearwaters, fairy prions and common diving petrels were determined using two

106   complementary techniques. Trophic information was derived from stable isotope values in whole

107   blood of each species in western, central and eastern Bass Strait, and stomach samples were

108   collected from the seabirds in central Bass Strait to assess the relative importance of prey and

109   inform interpretation of the stable isotope results. Procellariiform study species were banded and

110   little penguins were micro-chipped to avoid sampling the same individual more than once. All

111   research was conducted under permit from Deakin University (animal ethic permit: AWC A9-

112   2008) and the Department of Sustainability and Environment (Permit No. 10004530), and access

113   to the islands was provided by Parks Victoria.

114

115   ***Dietary analysis***

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

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

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

119   Strait (Fig. 1). Adult little penguins were sampled in both winter and summer (n = 20 and 22,

120   respectively), short-tailed shearwater and fairy prion diet samples were collected in summer only

121   (n = 51 and 20, respectively) and common diving petrels were sampled in winter only (n = 6)

122   (Fig. 2). Due to logistical constraints and few individuals onshore in some years, it was not

123   possible to sample all species in all years.

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

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

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

127   1987) and, in most cases, the majority of prey remains were ejected on the second (final) flush,

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

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

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

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

132   unsalted) immediately before release.

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

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

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

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

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

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

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

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

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

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

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

144   nearest number. Similarly, the highest number of upper or lower squid beaks in a sample was

145   used to estimate the abundance of cephalopods and only unbroken beaks were measured to

146   estimate size (Tollit et al. 1997). Hard prey remains that could not be quantified, such as fish

147   scales, were assigned a numerical abundance of one. The frequency of occurrence of prey

148   remains was calculated as the proportion of samples containing identifiable remains in which a

149   particular prey type occurred while the numerical abundance was expressed as the mean number

150   of each prey taxon encountered in samples.

151

152   ***Stable isotope analyses***

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

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

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

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

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

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

159   (Bearhop et al. 2002).

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

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

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

163   149°55'E). A total of 278 (167 in summer, 111 in winter), 177 (summer only), 88 (66 in

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

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

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

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

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

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

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

171   inter-digital vein in the foot.

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

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

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

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

176   comparisons of $\delta^{13}C$ values among groups (Bond & Jones 2009). Isotope ratios in whole blood

177   were measured using a continuous-flow isotope ratio mass spectrometer, with analyses

178   conducted by the Isotope Ratio Mass Spectrometry service in the Research School of Biology,

179   Australian National University (Canberra, Australia). The values of stable isotope abundances

180   were expressed in δ-notation as the deviation from standards in parts per thousand according to

181   the equation:

182

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

184

185   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.

186   1994a). $R_{standard}$ values were based on Vienna Pee Dee Belemnite for ^{13}C, and atmospheric

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

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

189

190   ***Statistical analyses***

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

192   2018). To investigate the effect of geographic, inter-annual and seasonal variations in stable

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

194   2014). Terms were added sequentially, model selection was based on Akaike's information

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

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

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

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

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

200   season. The Standard Ellipse Area corrected (SEA_C; 40% probability of containing a

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

202   Bayesian estimate of the standard ellipse and its area (SEA_B) were used to measure the overlap

203   of the isotopic niches between groups (Jackson et al. 2011). The niche overlap was estimated as

204   the isotopic area of overlap from the maximum likelihood fitted ellipses of two given groups.

205

206   **RESULTS**

207   ***Diet***

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

209   2011 in order to inform interpretation of the stable isotope results. Samples were collected from

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

211   2009 and 2010, from fairy prions in summer 2011 and from common diving petrels in winter

212   2008 and 2009. Overall, 79, 84, 95 and 40 % of little penguin, short-tailed shearwater, fairy prion

213   and common diving-petrel samples, respectively, contained identifiable fresh prey remains.

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

215   crustaceans (Table 2). Not all taxa could be identified to species level. Little penguins ingested

216   crustaceans, comprising isopods, amphipods and/or copepods, but consumed mainly jack

217   mackerel in winter and Australian anchovy *Engraulis australis* in summer, though high numbers

218   of post-larval fish were also ingested in summer (Table S1 in the Supplement). The diets of all

219   three procellariform species were dominated by euphausiids, particularly coastal krill

220   (*Nyctiphanes australis*), representing 78 – 96 % of the mean number of prey items consumed by

221   these species (Table S2 and Table S3 in the Supplement). Other important prey taxa included

222   *Euphausia* sp. and the hyperiid amphipod *Themisto australis* for short-tailed shearwaters, the

223   megalopa stage of a swimming crab species *Ovalipes* sp. for fairy prions and hyperiid amphipods

224   for common diving-petrels. For short-tailed shearwaters, the abundance of crustaceans was

225   significantly higher in 2010 than in 2009 (Wilcoxon-test, w = 126.5, p-value < 0.01), mainly

226   driven by the variation in number per samples of coastal krill (n = 118.9 ± 52.6 and n = 969.6 ±

227   194.2 in 2009 and 2010, respectively).

228

229   ***Stable isotopes analysis***

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

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

232   18.1 ‰ for little penguins, between -23.7 and -20.4 ‰ for short-tailed shearwaters, between -

233   21.0 and -18.3 ‰ for fairy prions and between -21.4 and -19.4 ‰ for common diving petrels.

234   Whole blood δ^{15}N values ranged between 10.8 and 16.0 ‰ for little penguins, between 7.8 and

235   11.4 ‰ for short-tailed shearwaters, between 8.8 and 14.8 ‰ for fairy prions and between 10.9

236   and 14.5 ‰ for common diving petrels (Fig. S1 in the Supplement).

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

238   regions and years (Fig. 3 and 4). Inter-annual variations of δ^{13}C values were significant in all

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

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

241   δ^{13}C differences between regions for the short-tailed shearwater, for the three other species

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

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

244   explained, respectively, 43, 37 and 58 % of the variance for the δ^{13}C model, butonly 2 % for the

245   short-tailed shearwater. For δ^{15}N, the best models retained, with interactions, the δ^{13}C, the region

246   and the year (and season for the little penguin and fairy prion) as significant variables explaining

247   60 % to 93 % of the deviance (Table S4 in the Supplement). For δ^{15}N, while "season" explained

248   27.1% of the model (winter data available only for WBS in 2009), this variable was not

249   significant for the little penguin (0.2%). No significant inter-seasonal variations of δ^{13}C in blood

250   of little penguin and fairy prion were found (except in CBS, paired t-test or Wilcoxon-test: $P <$

251   0.01). Significant inter-annual differences were recorded in all regions (Paired t-test or

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

253   metrics (Tables 3, 4 and Table S5 in the Supplement). Similarly, for each year, the δ^{15}N values

254   varied significantly between region for the little penguin, fairy prion and common diving petrel

255   (Paired t-test or Wilcoxon-test: $P < 0.01$). For the short-tailed shearwater, a spatial difference in

256   δ^{15}N values was detected between WBS and EBS in 2010 (Paired t-test t_{37} = -2.19, $P < 0.05$), but

257   no other significant differences were found. The models for δ^{13}C retained the region and year as

258   significant variables for all the study species, explaining 55 % to 70 % of the variance (Table S4

259   in the Supplement).

260   The four study species occupied different isotopic niches in all years and each region (Fig. S1 in

261   the Supplement). Values of δ^{13}C and δ^{15}N in whole blood of short-tailed shearwaters were

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

263   in all three years (paired t-test or Wilcoxon-test: p < 0.01, Table 3 and Table S5 in the

264   Supplement). In contrast, mean δ^{15}N values in blood of little penguins typically showed the

265   greatest enrichment in both winter and summer, though this varied spatially and inter-annually

266   (Table 3 and 4). Isotopic δ^{13}C values of little penguins and fairy prions were relatively similar,

267   but tended to be higher than those of common diving-petrels in winter, particularly in CBS.

268   While the isotopic niche of the fairy prion overlapped sparsely with the common diving petrel

269   (SEA$_B$ overlap < 8.1%), and with little penguin in 2009 and 2011 (SEA$_B$ overlap < 4.9%), niche

270   overlap with the little penguin was important in 2010 (maximum SEA$_B$ overlap = 21.8% in

271   winter 2010 in WBS, Table S5 in the Supplement).

272

273   **DISCUSSION**

274   Foraging niches of sympatric seabird species diverge in a variety of spatial and temporal ways

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

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

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

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

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

280

281   *Diet*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

301 & Cherel 1998, Woehler et al. 2006, Raymond et al. 2010, Einoder et al. 2011, Berlincourt &

302 Arnould 2015b) where they feed mainly on coastal krill, and myctophid fish and Antarctic krill,

303 respectively (Montague 1986, Weimerskirch & Cherel 1998). In the 2010 samples, a limited

304 number of birds (n = 4) had stomach contents dominated by stomach oil and digested *Euphausia*

305 sp, suggesting they had returned from long trips to Antarctic waters (Weimerskirch & Cherel

306 1998).

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

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

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

310 1988, Gill et al. 2011, Woehler et al. 2014). Despite limited data on the diet of fairy prions and

311 common diving petrels in Bass Strait, their stomach contents confirmed the importance of coastal

312 krill to these species in the Australasian region (Harper 1976, Schumann et al. 2008). These

313 results, together with estimates of trip duration in previous studies (1-3 d trips at sea, Harper

314 1976, Bocher et al. 2000a, b, Navarro et al. 2013, Zhang et al. 2018), suggest that both breeding

315 fairy prions and common diving petrels most likely forage within Bass Strait or in the vicinity of

316 the continental shelf. This analysis emphasises the value of a multi-tools approach when

317 considering niche segregation, as here, while stomach analysis can suggest substantial dietary

318 overlap among the procellariiforms, isotopic and tracking analysis may be able to tease the

319 species apart into separate foraging niches.

320

321 ***Spatial variability in isotopic niche***

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

323 2002), it might be expected that isotopic values for short-tailed shearwaters would reflect a

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

340   specific niche segregation but also density-dependent competition (Ainley et al. 2004, Wakefield

341   et al. 2013), with the smallest colonies having a more flexible foraging area. Indeed, the CBS

342   population is considerably bigger than the WBS and EBS populations, with 755,400, 30,000 and

343   6,000 breeding pairs, respectively (Bowker 1980, Pescott 1976, Fullagar & Heyligers 1996,

344   Schumann et al. 2014). This is in accordance with previous tracking studies (Berlincourt &

345   Arnould 2015b) that observed inter-annual longitudinal and latitudinal variation in the long trip

346   foraging areas of short-tailed shearwater from the small populations in WBS and EBS. Despite

347 the geographic and temporal differences in δ^{13}C observed, there were no major differences in the

348 δ^{15}N values between regions in the present study, highlighting the consistency of the diet of

349 short-tailed shearwaters in the Southern Ocean.

350 For little penguins, fairy prions and common diving petrels, seasonal and geographic differences

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

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

353 Bass Strait. For example, the SAC may transport cold waters from the west into Bass Strait

354 (Mickelson et al. 1992, Sandery & Kämpf 2007), weakening towards the east (Sandery & Kämpf

355 2007) where the EAC increases in prevalence, bringing warmer nutrient-poor water into north-

356 eastern Bass Strait (Gibbs 1992). This was reflected in δ^{13}C values in the whole blood of little

357 penguins and fairy prions, where values were systematically lower in CBS than in WBS and

358 EBS. Similar observations have been reported for Australian fur seals where δ^{13}C values in blood

359 plasma of individuals from CBS were consistently lower than those from EBS (Arnould et al.

360 2011). In winter, however, spatial differences in isotopic values declined. This may reflect the

361 homogenization of Bass Strait waters in winter due to a greater influence of the SAC and SASW

362 during this period (Prince 2001, Sandery & Kämpf 2007).

363

364 ***Inter-annual trophic variability***

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

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

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

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

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

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

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

372   of the species. However, inter-annual variation in δ^{15}N values could also reflect a variation in

373   main prey species consumed, with little penguins known to have important inter-annual

374   variability in their diet (Gales & Pemberton 1990, Cullen et al. 1992, Chiaradia et al. 2010). In

375   the present study, individuals from CBS in summer 2009 consumed predominantly Australian

376   anchovy, a species exploiting higher trophic levels than other prey targeted by little penguins

377   (Espinoza et al. 2009, van der Lingen et al. 2009). As previously highlighted by Chiaradia et al.

378   (2010), δ^{15}N values are higher during years with an important proportion of anchovy in little

379   penguin diet. Therefore, it is likely that the low δ^{15}N values in summer 2010 in the present study

380   was due to a depletion of Australian anchovy in the diet, potentially due to a reduced availability

381   in the region. This is consistent with previous reports indicating inter-annual flexibility in little

382   penguin at-sea foraging behaviour in relation to environmental conditions that directly influence

383   prey abundance (Berlincourt & Arnould 2015a, Camprasse et al. 2017). Indeed, in WBS and

384   CBS, the niche space occupied by little penguins in 2010 was much larger than in 2009 and

385   2011, indicating a larger trophic diversity (Layman et al. 2007), possibly due to the absence of

386   the usual main prey. Similarly, for both fairy prions and common diving petrels, δ^{15}N values in

387   the whole blood of both species in the region varied substantially between years, suggesting a

388   potential variation in the importance of their main prey (coastal krill) in their respective diet.

389   Significant inter-annual differences in the density and biomass of coastal krill in southern Bass

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

391

392   ***Trophic and isotopic niche segregations***

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

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

395   short-tailed shearwaters always occupied the lowest. Little penguin δ^{15}N values were

396   nevertheless lower than those of the top predators shy albatross and Australian fur seal (Arnould

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

398   (Angel et al. 2016), that predominantly consumes pilchards and anchovy (Bunce 2001) (Fig. 5).

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

400   remarkably lower than those of the much smaller white-faced storm petrels (Underwood 2012)

401   (Fig. 5), which consume a significant proportion of fish in addition to coastal krill (Underwood

402   2012). These results, combined with the stomach content analysis, confirm that coastal krill was

403   a key prey taxon in all three procellariforms in central Bass Strait. During breeding, both fairy

404   prions and common diving petrels return to the nest every night (Harper 1976, Payne & Prince

405   1979), suggesting that they forage mainly on the shelf near their colonies. Elsewhere, fairy

406   prions take prey from the surface waters (Harper 1987, Prince & Morgan 1987) whereas

407   common diving petrels exploit depths averaging 2-4m (Navarro et al. 2013, Navarro et al. 2014,

408   Dunphy et al. 2015). Likewise, despite isotopic signatures showing self-maintenance feeding in

409   the Southern Ocean, short-tailed shearwaters forage on coastal krill over the shelf near colonies

410   during short trips (Einoder et al. 2011, Berlincourt & Arnould 2015b), resulting in the potential

411   for interspecific overlap in the foraging zones of the three procellariforms. However, short-tailed

412   shearwaters forage at deeper depths (average 13 m) during local trips (Weimerskirch & Cherel

413   1998). While the foraging zones and dive depths of little penguins may overlap with those of

414   short-tailed shearwaters (Berlincourt & Arnould 2015a, 2015b), the limited distance travelled per

415   trip and fish-based diet of little penguins would reduce competition with procellariforms.

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

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

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

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

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

421   1992) may overlap with the other species. Interspecific competition may, therefore, intensify in

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

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

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

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

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

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

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

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

430   region (Mills et al. 2008, Chambers et al. 2011). Similarly, significant mortality events, poor

431   chick growth and population declines in short-tailed shearwaters in Tasmania have been

432   previously attributed to local prey shortages (Vertigan 2010). Declines in coastal krill availability

433   may also indirectly impact little penguins since this species is an important dietary component of

434   several of their prey taxa (Harris et al. 1979, O'Brien 1988). The predicted increase in the

435   strength of the EAC with climate change (Cai et al. 2005) could, therefore, have severe negative

436   consequences for the Bass Strait seabird community (Chambers et al. 2011).

437

438   **CONCLUSIONS**

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

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

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

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

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

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

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

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

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

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

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

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

451 et al. 2004, 2009, Cleeland et al. 2014, Berlincourt & Arnould 2015a, b). Such information may

452 help elucidate the likelihood of interspecific competition in this assemblage of seabirds.

453

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461

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

Some of the population estimates were not updated for at least three decades (*e.g.* Brothers et al. 2001) and may represent a source of error.

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) δ^{13}C and δ^{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.

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)	-

Winter mean (± SD) δ^{13}C and δ^{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.

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)	-	-

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.
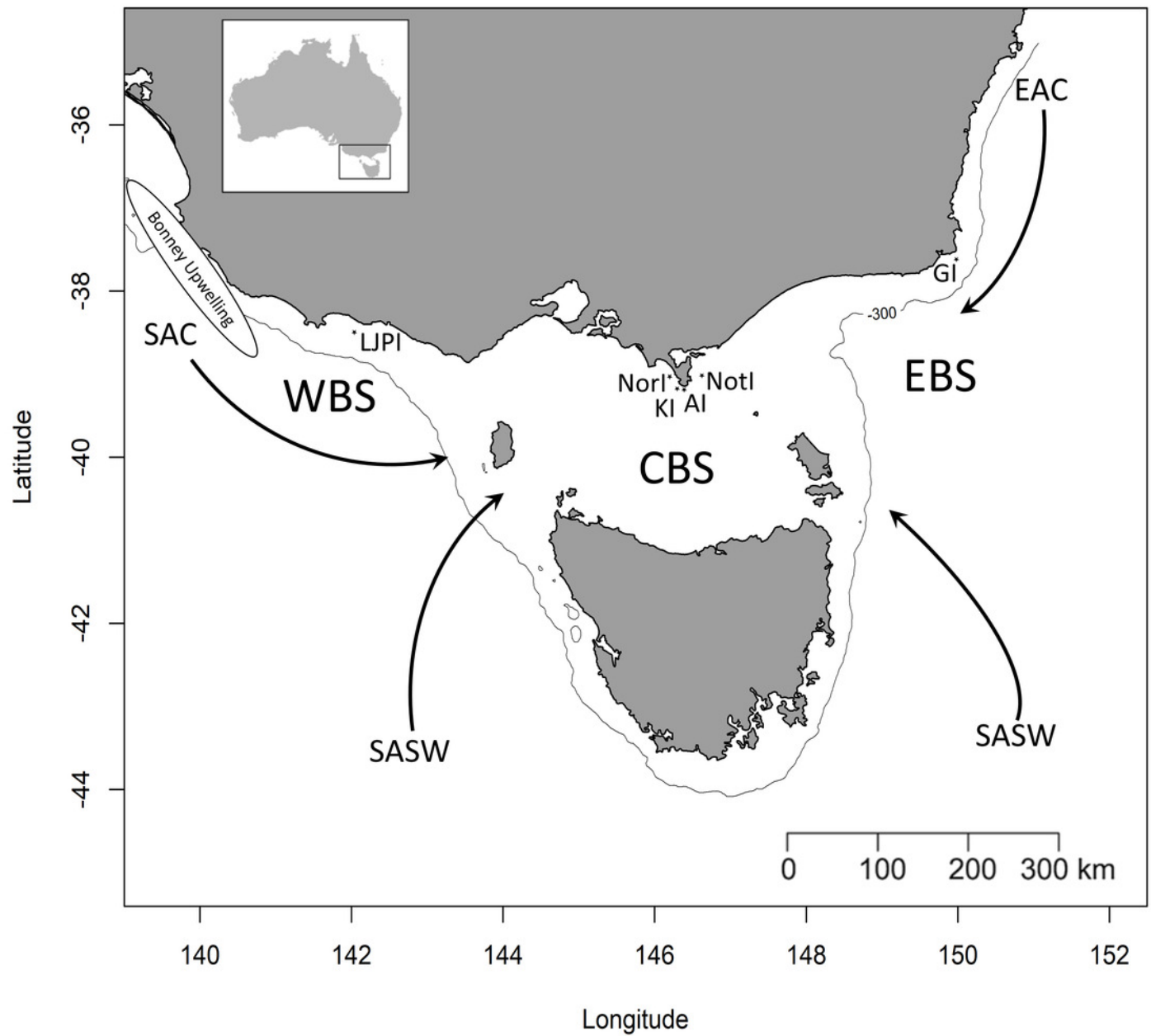
Figure 2

Phenology and sampling period of little penguin (LP), short-tailed shearwater (STSW), fairy prion (FP) and common diving petrel (CDP) in Bass Strait.

Blocks with vertical and horizontal lines correspond to incubation and chick-rearing period, respectively. Grey shaded blocks correspond to the winter and summer sampling periods.
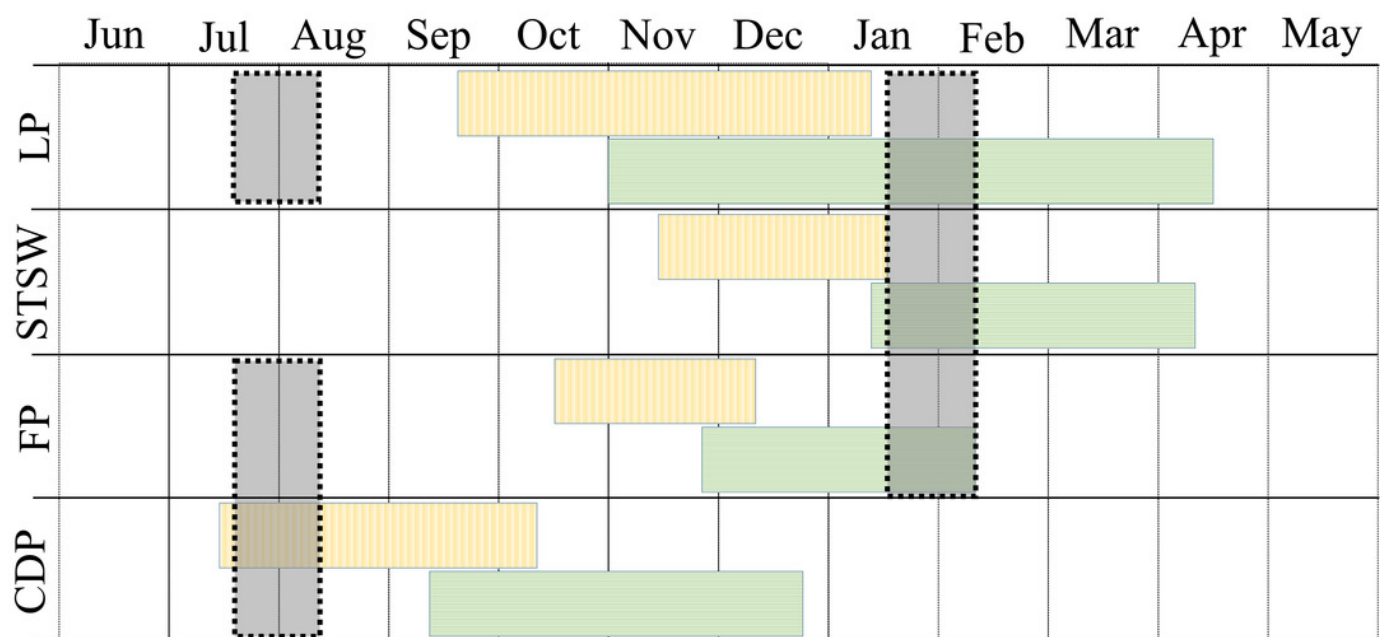
Figure 3

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

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: Whole blood δ¹³C (‰) vs whole blood δ¹⁵N (‰) scatter plots for Little penguin (A–C), Short-tailed shearwater (D–F), and Fairy prion (G–H) across WBS, CBS, and EBS regions for years 2009, 2010, and 2011.
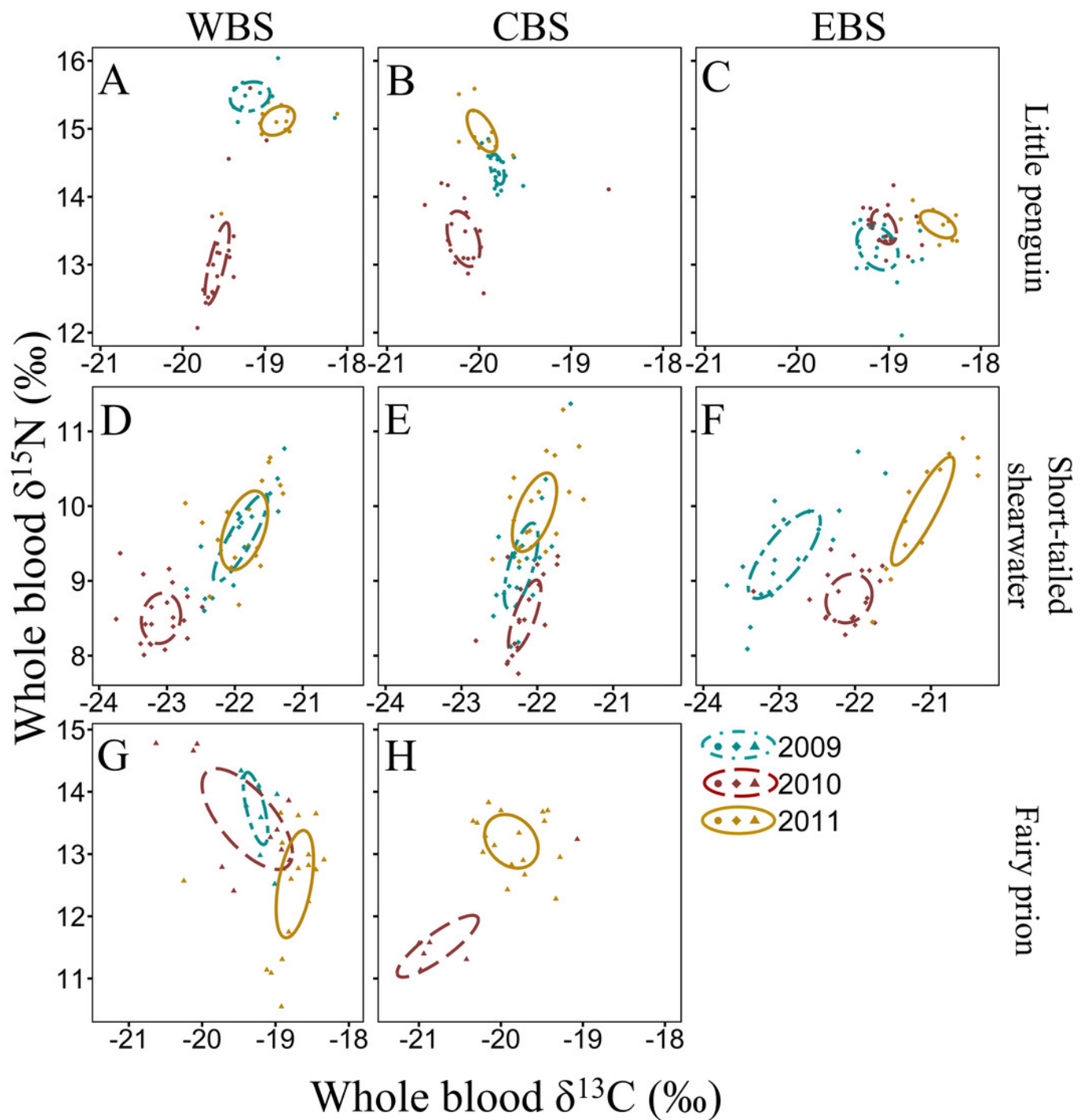
Figure 4

Winter inter-annual variation of δ^{13}C and δ^{15}N values (‰) in whole blood of little penguins (A,B,C) and common diving petrels (D,E): 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.
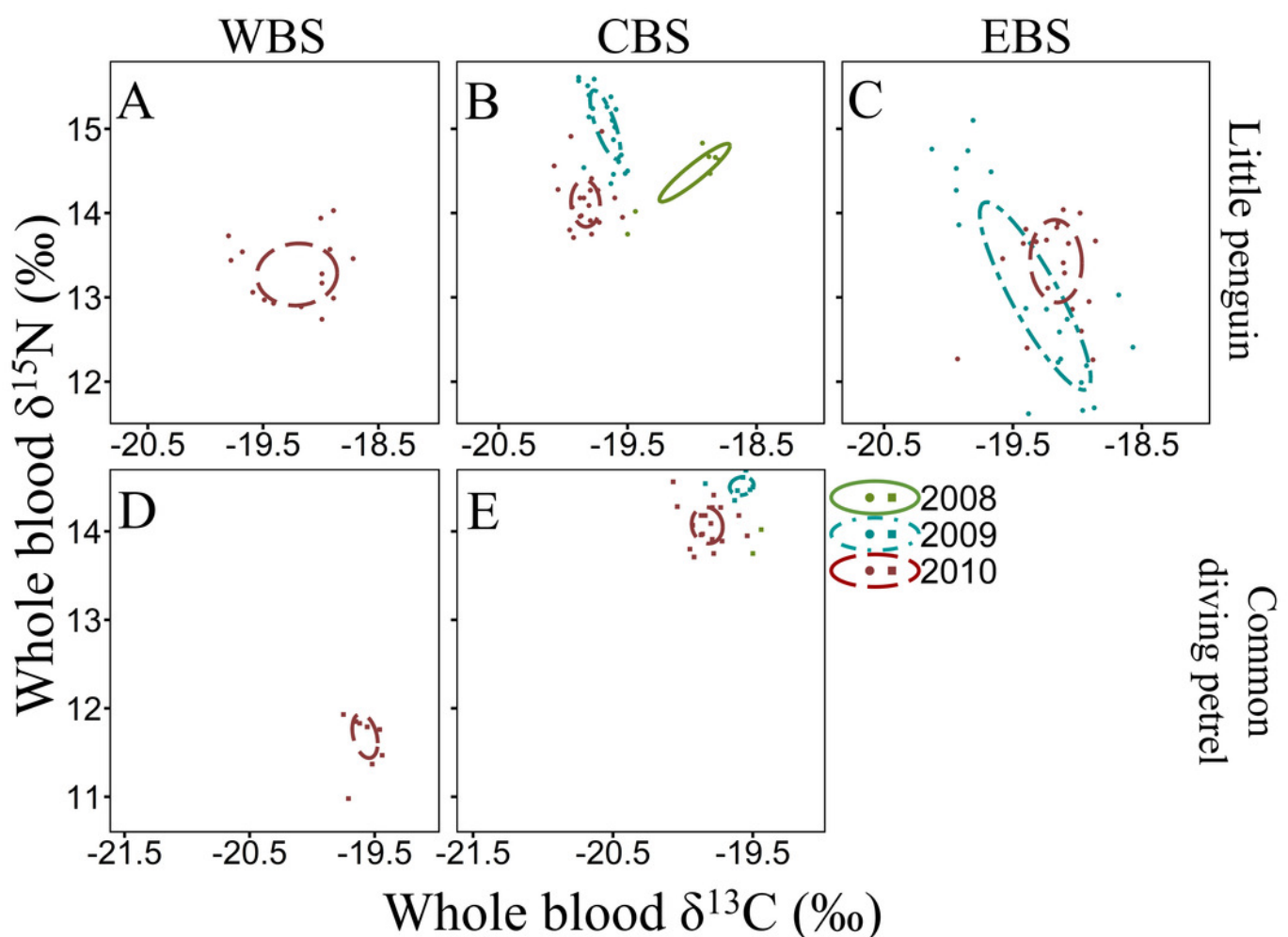
Figure 5

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

Little penguin (LP, n = 278; present study; summer and winter combined), short-tailed shearwater (STSW, n = 177; present study; summer and winter combined), fairy prion (FP, n = 88; present study; summer and winter combined), common diving petrel (CDP, n = 38; present study; summer and winter combined), Australasian gannet (GA, n = 27; Angel et al. 2016; summer), white-faced storm petrel (WFST, n = 17; Underwood 2012; summer), shy albatross (SA, n = 8; Cherel et al. 2013; summer) and Australian fur seal (AFS, n = 242; Arnould et al. 2011; winter). 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.