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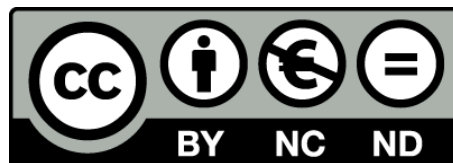
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Importance of tuna for tropical seabirds

1 The importance of tropical tuna for seabird foraging over a marine
2 productivity gradient

3

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10

11 **Abstract**

12 Foraging with tuna is a well-documented seabird strategy, referred to as facilitated foraging.
13 However, despite this behaviour being considered almost obligatory in nutrient-poor tropical
14 waters, little data exist on its relative importance to individual colonies. Therefore, to examine
15 facilitated foraging under different patterns of nutrient availability we tracked Wedge-tailed
16 Shearwaters *Ardenna pacifica* from two colonies, one tropical and one subtropical, situated in
17 waters of contrasting productivity. Shearwater foraging behaviour was assessed relative to
18 oceanographic covariates and predicted distributions for multiple tropical tuna species and age-
19 classes, simulated by an existing ecosystem model (SEAPODYM). Shearwaters from both colonies
20 undertook long-trips to deep, pelagic waters close to seamounts and foraged most often at fronts and
21 eddies. Micronektonic and adult tuna age-classes were highly correlated in space. Predation
22 between these tuna age-classes represents a likely source of facilitated foraging opportunities for
23 shearwaters. At broad-scales, shearwaters consistently foraged in areas with higher predicted adult

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24 skipjack and micronektonic tuna densities and avoided adult bigeye tuna. At finer-scales, dynamic
25 ocean features aggregated tuna of all sizes. Enhanced tuna density at these locations increased the
26 likelihood of shearwater foraging activity. Long-trips in the tropics targeted oligotrophic waters
27 with higher tuna densities. Long-trips in the subtropics targeted enhanced productivity, but in some
28 years shifted to target the same oligotrophic, tuna-dense waters used by tropical conspecifics. We
29 conclude that facilitated foraging with tuna is consistently important to the tropical breeding
30 population and becomes increasingly important to the subtropical population in years of low marine
31 productivity.

32

33 **Key words:** facilitated foraging, micronekton, productivity, SEAPODYM, tuna, Wedge-tailed
34 Shearwater

35 **Introduction**

36

37 Tropical waters are generally considered less productive than their temperate counterparts
38 (Longhurst & Pauly 1987). In temperate and polar waters, predictable physical oceanographic
39 processes e.g. fronts, upwellings, ice and shelf edges reliably aggregate seabird prey, whereas in
40 tropical waters seabird prey are scarcer and more patchily distributed (Ainley & Boekelheide 1983,
41 Ballance & Pitman 1999, Weimerskirch 2007). Despite such constraints, abundant communities of
42 seabirds exist in tropical waters (King 1974). For tropical seabirds the single most important
43 foraging strategy, believed to overcome poor prey predictability, is to feed in multi-species flocks in
44 association with sub-surface predators, primarily tunas (Au & Pitman 1986, Ballance & Pitman
45 1999, Spear et al. 2007). Sub-surface predators are believed to be crucial for driving prey upwards
46 and making them available to surface feeding seabirds (facilitated foraging) (Ashmole & Ashmole
47 1967, Clua & Grosvalet 2001). Although facilitated foraging occurs in polar (Thiebot &
48 Weimerskirch 2013), temperate (Goyert et al. 2014) and sub-tropical waters (Clua & Grosvalet
49 2001, Vaughn et al. 2008), the level of seabird community reliance on sub-surface predators is
50 unparalleled in the tropics (Ballance & Pitman 1999, Spear et al. 2007).

51

52 However, the difficulty associated with monitoring seabird and sub-surface predator activity
53 concurrently means that facilitated foraging is often inferred. Inference comes from overlap in
54 seabird and sub-surface predator prey items (Ashmole & Ashmole 1967, Ménard et al. 2013) and
55 trophic niches (Kojadinovic et al. 2008, Young et al. 2010a), although often the results of such
56 studies are inconclusive. Facilitated foraging has also been inferred, but not quantified, from
57 overlap between seabird foraging tracks and areas of high sub-surface predator activity in
58 commercial fisheries (Catry et al. 2009, Weimerskirch et al. 2010, McDuie & Congdon 2016).

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59 Finally, oceanographic data has shown that the densities of tropical, diurnal, piscivorous seabirds
60 are driven by a well-stratified, deep thermocline, which is associated with higher sub-surface
61 predator densities (Ballance et al. 1997, Spear et al. 2001).

62

63 The bulk of our knowledge on facilitated foraging comes from at-sea observations (Au & Pitman
64 1986, Spear et al. 2007). At-sea observations are able to quantify instances of seabirds using
65 facilitated foraging, but have their limitations. The cost of vessel hire has led some studies to make
66 observations from fishing vessels. However as these vessels target sub-surface predators, results are
67 biased towards overestimation of facilitated foraging events (Jaquemet et al. 2004, Hebshi et al.
68 2008). At-sea observations using transects are unbiased and have contributed significantly to our
69 understanding of facilitated foraging, primarily in the eastern and central tropical Pacific (Au &
70 Pitman 1986, Spear et al. 2007) and tropical Indian oceans (Thiebot & Weimerskirch 2013).
71 However, all at-sea survey methods are limited by the prohibitive cost of undertaking simultaneous
72 surveys in different regions and an inability to determine the provenance of birds being observed.
73 As such, no previously available method has been able to quantify the individual, or population-
74 level decisions of seabirds on whether to preferentially target sub-surface predators or not.
75 Consequently, there has been no way to determine the relative importance of facilitated foraging
76 opportunities for specific seabird colonies. Our current study provides a framework to do so.

77

78 Limited availability of suitable nesting habitat can lead to seabird colonies being located where
79 local marine resources are sub-optimal (Navarro & González-Solís 2009). Under these constraints
80 many pelagic foraging seabirds use a bimodal foraging strategy, where 'short-trips' (1-3 days in
81 shearwaters; Baduini & Hyrenbach 2003) in resource-poor local waters are used almost exclusively
82 to provision chicks at the expense of adult condition. Following a series of short-trips adults

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83 undertake a 'long-trip' (5-17 days) to more distant foraging sites where they can quickly regain
84 condition (Weimerskirch 1998, Weimerskirch & Cherel 1998). To achieve this, long-trips are said
85 to access 'productive distant waters' (Weimerskirch 1998). As most bimodal foraging studies come
86 from temperate and polar regions 'productive' has become synonymous for high primary
87 productivity or chlorophyll-*a* concentration, aggregated by shelf or frontal features (Waugh et al.
88 1999, Catard et al. 2000, Klomp & Schultz 2000, Stahl & Sagar 2000, reviewed in Baduini &
89 Hyrenbach 2003). Seabirds breeding in the subtropics may have the opportunity to access similar
90 large-scale areas of high primary productivity using bimodal foraging (Paiva et al. 2010). However,
91 since such features are rare in tropical systems, we hypothesise that tropical-breeding seabirds target
92 increased sub-surface predator densities as an alternative, because of the greater facilitated foraging
93 opportunities this provides.

94

95 The wedge-tailed shearwater is a tropical seabird known to associate heavily with tuna when
96 foraging in multiple regions (Au & Pitman 1986, Jaquemet et al. 2004, Hebshi et al. 2008), and has
97 been shown to capture most of its prey through facilitated foraging (Spear et al. 2007). The wedge-
98 tailed shearwater populations breeding off eastern Australia adopt a bimodal foraging strategy in
99 tropical waters of the Coral Sea (Congdon et al. 2005) and a more unimodal strategy in sub-tropical
100 waters of the Tasman Sea, although some long-trips are made (Peck & Congdon 2005). East
101 Australian wedge-tailed shearwater populations have access to a range of marine habitats (shelf,
102 seamount and frontal systems; Hobday et al. 2011) and sub-surface predator populations in the
103 region include numerous tuna species (Young et al. 2010b).

104

105 This study aims to estimate the relative importance of facilitated foraging with tropical tuna for two
106 wedge-tailed shearwater populations in waters with contrasting productivity. Relative importance is

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107 quantified from spatial association between shearwater tracking data, oceanographic covariates and
108 modelled tropical tuna distributions. We tested two facilitated foraging hypotheses at opposing
109 spatio-temporal scales, thus expecting that: 1) tropical tuna distributions influence the selection of
110 wedge-tailed shearwater core-area locations (defined by the 50% Utilization Distribution (UD) from
111 kernel analysis) at broad scales; and 2) tropical tuna distributions influence the likelihood of wedge-
112 tailed shearwater foraging activity at fine scales. We additionally test two facilitated foraging
113 hypotheses at opposing ends of a productivity gradient, expecting that: 3) wedge-tailed shearwater
114 in tropical waters do not adhere to the temperate model of 'productive' long-trip destinations and
115 instead target tuna; and 4) wedge-tailed shearwater breeding in sub-tropical waters adhere to the
116 temperate model of 'productive' long-trip destinations and do not target tuna.

117

118 **Methods**

119

120 **Study area and logger deployment**

121 This study was carried out at Heron Island (23°26' S, 151°51' E) in the Capricorn Bunker Island
122 Group, Great Barrier Reef and Lord Howe Island (31°33' S, 159°05' E) in the northern Tasman
123 Sea, Australia. Both islands support large breeding colonies of wedge-tailed shearwaters (Marchant
124 & Higgins 1990). We deployed GPS loggers on wedge-tailed shearwaters at Lord Howe Island in
125 2014, 2015 and 2016 and concurrently at Heron Island in 2015, and deployed Platform Terminal
126 Transmitter (PTT) loggers at Heron Island in 2011 and 2013 (McDuie et al. 2015). All loggers were
127 deployed during the chick-rearing period (Feb-April). I-gotU GT-120 GPS loggers (Mobile Action
128 Technology) were modified to use smaller 100mAh batteries, sealed in heat-shrink tubing and
129 programmed to obtain fixes every 10 minutes (Freeman et al. 2013). Solar-powered ARGOS PTTs
130 (PTT-100; Microwave Telemetry, USA) relay data via satellite and were programmed to obtain

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131 fixes continuously. We deployed both GPS and PTT loggers to 3 central tail feathers using Tesa®
132 4651 Tape, total deployment weight of both logger types was ~ 10.5-12 g, within the 3-5% body
133 weight limit for the species (McDuie et al. 2015).

134

135 **Tracking data preparation and analyses**

136 All data handling and statistical analyses were performed in the statistical software environment
137 program R, version 3.2.4 (R Core Team 2016). Tracking data were pre-processed prior to analyses
138 using a speed filter, removing points exceeding a maximum velocity of 50 km/h (McDuie et al.
139 2015), additionally GPS tracks were gap filled using interpolation to 10 minute interval
140 (Weimerskirch et al. 2006). As loggers were active for several days multiple foraging trips were
141 observed for most individuals. To split long-trips from short-trips within multi-day GPS tracks we
142 used the R 'tripsplit' function from the 'marine IBA' package (Lascelles et al. 2016) and isolated
143 long-trips (>4 days duration; Congdon et al. 2005) for further analysis. We could not determine
144 individual foraging trips within multi-day PTT tracks (due to near colony positional error) so
145 removed all fixes from tracks within the 'short-trip zone' of 300 km around Heron Island (McDuie
146 et al. 2015).

147 To identify core-areas used by each colony for each year of long-trip tracking data, we employed
148 kernel analysis using the package 'adehabitatHR' (Calenge 2006). All locations within each colony-
149 year combination were used with a grid size of 0.5 km and, for consistency, the same smoothing
150 parameter (h) of 20 km for GPS and PTT data following McDuie et al. (2015). The 50% UD was
151 selected from resultant kernels to represent the core-area used by wedge-tailed shearwaters in each
152 year (Hamer et al. 2007). To identify behavioural states and thereby identify foraging locations, we
153 applied Hidden Markov Models (HMM) to the GPS data. We constructed a single HMM using the
154 full GPS tracking dataset, including an identifier for each trip, using the package 'moveHMM'

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155 (Michelot et al. 2016). For each consecutive GPS point the step length and turning angle were
156 calculated, producing three distributions consistent with foraging, resting and transiting behaviours
157 observed in HMM studies of boobies (Oppel et al. 2015) and shearwaters (Dean et al. 2012). The
158 fitted HMM was then used to classify each GPS point as either foraging, resting or transiting.

159

160 **Oceanographic data**

161 We created a static covariate for depth (BTY) from the 30 arc-second General Bathymetric Chart of
162 the World (GEBCO) and calculated a static covariate for distance to seamount using the Global
163 Seamount Database (Kim & Wessel 2011) and package 'raster' (Hijmans 2016). Gridded
164 oceanographic data were accessed from NOAA ERDDAP servers using the 'rerddap' package
165 (Chamberlain 2016) (Table 1). We accessed oceanographic climatologies in the form of long term,
166 monthly averages: primary productivity (PRO), 1997-2016; sea surface temperature (SST), 1985-
167 2016. We used the March data product as our covariate as it is central to the wedge-tailed
168 shearwater chick-rearing period. We accessed very fine temporal scale Ekman upwelling (EKM,
169 1d) and sea surface height anomaly (SSHA, 1d) data as these products were cloud free. We also
170 accessed coarser scaled data on Chlorophyll-*a* concentration (CHL, 8d), sea surface temperature
171 (SST, 1-8d) and sea surface temperature anomaly (SSTA, 1-8d), to counter daily missing values due
172 to cloud cover. In a further step to fill data gaps due to clouds, we blended two CHL, SST and
173 SSTA products from different data sources to create single covariates (Table 1).

174

175 **Tropical tuna data**

176 Tuna covariates were generated using the Spatial Ecosystem and Population Dynamics Model
177 (SEAPODYM). SEAPODYM is an age-structured population model describing spatial and
178 temporal dynamics of top predator species in a direct link with prey biomass and environmental

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179 variability (Lehodey et al. 2008). SEAPODYM uses a sub-model to predict the distribution of prey,
180 which provides a habitat-quality index for tuna that varies by age-class and species (Lehodey et al.
181 2010). This habitat is based on the distribution of simulated micronekton, which we here define as
182 mobile and free-swimming macro-zooplankton, fish and squid species between ~10 mm and ~250
183 mm. Micronekton are classified into functional groups by their vertical habitat and diel migration
184 pattern, with the spatio-temporal transfer of energy between them described using allometric scaling
185 equations and ocean currents. The top predator model describes the age-structured spatial
186 population of tunas across four distinct life stages (termed larval, juvenile, immature young, and
187 mature adult) and includes anthropogenic forcing in the form of effort and catch from multiple
188 fisheries. Driving both models are ocean biophysical variables (temperature, currents, oxygen, and
189 primary production) that characterise the marine environment of predator dynamics (Lehodey &
190 Senina 2009) and age-dependent accessibility functions describing the sub-model micronekton
191 biomass available to top predators. SEAPODYM solves these internal models using advection-
192 diffusion-reaction equations over a network of regularly spaced grid points and a discrete time step
193 (e.g. 1° square x 1 month), outputting predictions on the spatial dynamics of large pelagic predators
194 (Lehodey et al. 2008, Senina et al. 2008). SEAPODYM can be optimised and parameterised for
195 different marine predator species and regions (Abecassis et al. 2013, Dragon et al. 2014) or different
196 exercises, such as climate change prediction (Senina et al. 2016).

197

198 For our region SEAPODYM predictions were available on the distribution of biomass (g m^{-3}) for
199 three tuna species: yellowfin tuna *Thunnus albacares* (YFT), bigeye tuna *T. obesus* (BET) and,
200 skipjack tuna *Katsuwonus pelamis* (SKJ). For each species we selected distributions of adult (ADU)
201 and micronektonic (MIC) age-classes which vary spatially due to their differing access to prey,
202 behaviour and density-dependent mortality representing cannibalism (Lehodey et al. 2008). Adult

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203 tuna are not shearwater prey. Therefore, we assume associations between wedge-tailed shearwaters
204 and adult tuna represent facilitated foraging. Micronektonic tuna are between 1-3 months old with
205 fork lengths from ~30 mm up to ~100 mm (SKJ) and ~250 mm (YFT and BET) (Davies et al. 2014,
206 Harley et al. 2014, Langley et al. 2014), wedge-tailed shearwater association with micronektonic
207 tuna could represent direct predation of smaller individuals or facilitated foraging with larger
208 individuals. We also selected SEAPODYM predictions under fished conditions to represent real-life
209 tuna distributions, such as heavier long-lining effort closer to the Australian east coast (Trebilco et
210 al. 2010).

211
212 To test our hypotheses we compiled two datasets at opposing spatio-temporal scales, the first was
213 built with broad scale, decadal-averaged data (hereafter termed the climatology dataset/model), the
214 second built with fine scale, weekly-averaged data (defined as high resolution and hereafter
215 abbreviated as the 'hi-res' dataset/model; Appendix 1). The climatology dataset included BTY,
216 SMT, PRO, SST and tuna covariates from INTERIM parameterised SEAPODYM predictions (1° x
217 1 month), for the month of March (SKJ: 1979-2010 average, BET and YFT: 1986-2010 average)
218 (Table 1). The hi-res dataset included BTY, SMT, CHL, SST, SSTA, SSHA, EKM and tuna
219 covariates from INDES0 V2 parameterised SEAPODYM predictions (0.25° x 1 week). Tuna data
220 were not available for 2016, so hi-res models were constructed for 2014 and 2015 only.

221

222 **Covariate extraction**

223 To standardise climatology model covariate extraction we used a 0.1 degree grid, taking all pixels
224 within the 50% UD core-areas as presence and generating pseudo-absence pixels, defined as
225 locations where absence is probable but uncertain, for logistical regression. Pseudo-absence pixels
226 were randomly generated, at a rate of random 3:1 presence pixels, within a hypothetical maximum

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227 foraging range for each colony. The range was set at 1400 km from each colony (maximum
228 distance observed in our data; Heron Island 2013), refined by removing land and areas beyond the
229 species range e.g. south of the sub-tropical front (del Hoyo et al. 1992). For hi-res models we
230 reclassified behaviour-classed tracking data for logistic regression, assigning foraging and resting
231 locations as presences, as tropical seabirds can 'drift forage' (using a surface 'sit-and-wait' strategy;
232 Connors et al. 2015), and transiting locations as absences. We extracted values from covariates for
233 climatology and hi-res model locations using the package 'raster' (Hijmans 2016).

234

235 **Multicollinearity and spatial autocorrelation**

236 Collinearity between covariates is an ever present issue in regression-type analyses of ecological
237 data (Dormann et al. 2013), and continually persistent in marine habitat modelling exercises
238 (Goyert et al. 2014, Lavers et al. 2014, McDuie & Congdon 2016). We explored the climatology
239 and hi-res covariate datasets for collinearity using pairwise Pearson's correlations with scatterplots
240 of covariates (Zuur et al. 2010). We identified significant collinearity between covariates (Pearson's
241 $r^2 > 0.9$), particularly around SST and tuna covariates. To understand the sources of collinearity,
242 identify correlated clusters and select proxy covariates to use in models, we standardised our
243 covariates and carried out Principal Components Analyses (PCA) in the package 'vegan' (Oksanen
244 et al. 2016). To help interpret PCA ordination plots, Pearson's R^2 values were calculated between
245 the covariates and the principal components (Quinn & Keough 2001). For each dataset we aimed to
246 retain covariates for modelling that had a pairwise Pearson's $R^2 < 0.5$ with others and selected a
247 single tuna covariate that minimised correlation with non-tuna covariates, to act as a proxy for all
248 covariates correlated within tuna clusters (Dormann et al. 2013).

249

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250 Spatial autocorrelation (SAC) is another issue inherent in species distributional data, and failure to
251 account for it can result in non-independence of model residuals causing bias in parameter estimates
252 and increasing type I errors (Dormann et al. 2007). We checked Pearson's residuals from
253 climatology and hi-res models for SAC using the package 'ncf' (Bjornstad 2016), calculating
254 Moran's I values over distances: 1-2500 km (climatology models) and 1-1000 km (hi-res models).
255 Climatology models showed high levels of SAC (Moran's I > 0.9), to accommodate the spatial
256 structure we calculated an autocovariate term over the 50 nearest neighbours following Bardos et al.
257 (2015), inclusion of this term reduced model SAC to acceptable levels (Moran's I < 0.22) (McDuie
258 & Congdon 2016). hi-res models showed lower, but still present, levels of SAC (Moran's I < 0.4),
259 we reduced SAC in this tracking dataset by subsampling locations to every third point, resulting in
260 models with Moran's I < 1.5 (Perotto-Baldivieso et al. 2012).

261

262 **Statistical modelling**

263 To test the influence of different broad scale oceanographic and tuna covariates on selection of
264 wedge-tailed shearwater core-area location, we used generalized linear models (GLM). GLMs had a
265 binary response, treating core-area locations as 1 and total foraging range pseudo-absences as 0, and
266 were constructed separately for Lord Howe and Heron Island. To test the effect of different high-
267 resolution oceanographic and tuna covariates on likelihood of wedge-tailed shearwater foraging, we
268 used generalized linear mixed models (GLMM), fitted in package 'lme4' (Bates et al. 2015), with
269 bird identity as the random intercept (Hamer et al. 2007, Grecian et al. 2016). GLMMs had a binary
270 response, treating foraging or resting locations as 1 and transiting locations as 0, and were
271 constructed separately for each year and colony (Lord Howe Island 2014, 2015 and Heron Island
272 2015). To effectively accommodate non-linearity, but not over-fit relationships, we permitted
273 covariates in hi-res models to take either a linear or second-degree polynomial form. Model

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274 residuals and diagnostics were plotted and checked as per Zuur et al. (2009) and models' terms were
275 selected using both forwards and backwards selection based on likelihood ratio tests (χ^2) and
276 confidence intervals (Bolker et al. 2009). Model explanatory power was evaluated by constructing
277 receiver operating characteristic (ROC) curves (Hanley & McNeil 1982) and calculating the
278 associated area under the ROC curve (AUC) in package 'verification' (NCAR 2015). Goodness of
279 fit was assessed for GLM using McFadden's pseudo R^2 (Azen & Traxel 2009) in package 'pscl'
280 (Jackman 2015) and assessed for GLMM split into marginal (var. explained by fixed effects) and
281 conditional (var. explained by fixed + random effects) pseudo R^2 components (Nakagawa &
282 Schielzeth 2013) in package 'MuMIn' (Bartoń 2016).

283

284 **Results**

285

286 **Tracking data**

287 In total, 62 long-trips were recorded during the study. GPS battery life allowed individual
288 shearwaters to be tracked with GPS for an average of 5.1 ± 1.1 days when making long-trips lasting
289 on average 9 ± 1.4 days; representing 57% of their time at-sea (Table 2). Wedge-tailed shearwaters
290 were tracked with PTTs for an average of 8.9 ± 0.9 days. On average, wedge-tailed shearwaters on
291 long-trips from Lord Howe Island travelled up to 495 ± 166 km from their colony whereas
292 conspecifics from Heron Island travelled up to 672 ± 62 km on long-trips from their colony (Fig. 1).
293 The core-areas of wedge-tailed shearwaters on long-trips from Heron Island were located in the
294 same general region each year (centroid: $19^\circ 48'$ S, $155^\circ 36'$ E), whereas core-areas of conspecifics
295 from Lord Howe Island were located in the same general region in 2014 and 2016 (centroid: $31^\circ 48'$
296 S, $156^\circ 42'$ E), but not in 2015 (Table 2).

297

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298 **PCA and collinearity**

299 PCAs of oceanographic and tuna covariates within the climatology and hi-res datasets showed high
300 levels of correlation between covariates and consistent clustering of the same covariates in both
301 datasets. PCA of 10 covariates within the Heron Island climatology dataset revealed that the first 2
302 principal components account for 65.7% of the variance in the data (PC1 = 49.2%, PC2 = 16.5%),
303 and for PCA of the same covariates within the Lord Howe Island climatology dataset, the first 2
304 principal components account for 77.7% of the variance in the data (PC1 = 56.8%, PC2 = 20.9%;
305 Fig. 2). In both ordinations PC1 represents a positive relationship with latitude: higher SST and
306 tropical tuna biomass in the Coral Sea is associated with negative PC1 values where-as higher PRO
307 and BET_ADU biomass in the Tasman Sea is associated with positive PC1 values. In the Heron
308 Island ordination PC2 represents an inverse relationship with proximity to a central seamount
309 region and in the Lord Howe Island ordination PC2 represents a positive relationship with
310 longitude. In both ordinations adult skipjack tuna (joined by adult yellowfin tuna in the Heron
311 Island PCA) was clustered with micronektonic skipjack and yellowfin tunas (joined by
312 micronektonic bigeye tuna in the Lord Howe Island PCA), hereafter termed the 'major-tuna cluster'.
313 In each PCA the major-tuna cluster was highly correlated with PC1 (Heron Island Pearson's $R^2 =$
314 $0.88 - 0.96$, Lord Howe Island Pearson's $R^2 = 0.85 - 0.95$) and SST (Fig. 2).

315

316 PCA of 13 covariates within the Heron Island 2015 hi-res dataset revealed that the first 2 principal
317 components account for 56.3% of the variance in the data (PC1 = 33.9%, PC2 = 22.4%), PCA of
318 the same covariates within the Lord Howe Island 2015 hi-res dataset revealed that the first 2
319 principal components account for 67.5% of the variance in the data (PC1 = 55.9%, PC2 = 11.6%)
320 and PCA of the same covariates within the Lord Howe Island 2014 hi-res dataset revealed that the
321 first 2 principal components account for 64.4% of the variance in the data (PC1 = 48.8%, PC2 =

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322 15.6%; Fig. 3). The hi-res ordinations again show consistent clustering of tuna covariates, the Lord
323 Howe Island 2014 and Lord Howe Island 2015 PCAs show all tuna covariates correlated with PC1
324 (2014 Pearson's $R^2 = 0.68 - 0.98$, 2015 Pearson's $R^2 = 0.7 - 0.94$), the Heron Island 2015 PCA
325 shows lower correlation of all tuna with PC1 (Pearson's $R^2 = 0.52 - 0.79$) as PC2 appears to split
326 tuna covariates into two clusters (Fig. 3).

327

328 **Climatology models**

329 At broad scales, wedge-tailed shearwaters from both colonies selected core-areas, within their
330 foraging range, that were closer to seamounts (Heron Island: $\chi^2_1 = 54.49$, $p = <0.001$, Lord Howe
331 Island: $\chi^2_1 = 53.71$, $p = <0.001$; Table 3) and in deeper waters (Heron Island: $\chi^2_1 = 17.08$, $p =$
332 <0.001 , Lord Howe Island: $\chi^2_1 = 24.29$, $p = <0.001$). Primary productivity was negatively associated
333 with the selection of core-area location for wedge-tailed shearwaters breeding on Heron Island, the
334 model predicted that for every $100 \text{ mg C m}^{-2} \text{ day}^{-1}$ increase in primary productivity, an area is 12.16
335 times less likely to be selected as a core-area by Heron Island shearwaters ($\chi^2_1 = 263.6$, $p = <0.001$;
336 Fig. 4B). Primary productivity was not significant to selection of core-area location for wedge-
337 tailed shearwaters breeding on Lord Howe Island ($\chi^2_1 = 2.46$, $p = 0.117$). Each climatology model
338 included two tuna covariates, one as a proxy for the major-tuna cluster (selected to have minimal
339 correlation with non-tuna covariates) and the other which was uncorrelated with the major-tuna
340 cluster. Micronektonic yellowfin (YFT_MIC) was the proxy and micronektonic bigeye (BET_MIC)
341 the uncorrelated covariate in the Heron Island model, while micronektonic bigeye was the proxy
342 and adult yellowfin (YFT_ADU) the uncorrelated covariate in the Lord Howe Island model (Fig. 2).
343 The Heron Island climatology model predicted that for each additional 100 g m^{-2} of tuna biomass an
344 area contains, it is 1.04 times more likely to be selected as a core-area by wedge-tailed shearwaters
345 if the tuna are micronektonic yellowfin ($\chi^2_1 = 14.81$, $p = 0.001$), and 2.06 times more likely to be

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346 selected if the tuna are micronektonic bigeye ($\chi^2_{1} = 235.24, p = <0.001$). The Lord Howe Island
347 climatology model predicted that for each additional 100 g m⁻² of tuna biomass an area contains, it
348 is 1.42 times more likely to be selected as a core-area by wedge-tailed shearwaters if the tuna are
349 micronektonic bigeye ($\chi^2_{1} = 70.35, p = 0.001$; Fig. 4A), but 1.71 times less likely to be selected if
350 the tuna are adult yellowfin ($\chi^2_{1} = 15.39, p = <0.001$). Validation of Heron Island climatology model
351 confirmed the final model fitted the data well (AUC = 0.97) and explained a good proportion of the
352 variance (McFadden's R² = 0.71). Validation of Lord Howe Island climatology model confirmed the
353 final model also fitted the data well (AUC = 0.98) and explained a similar proportion of the
354 variance (McFadden's R² = 0.75).

355

356 **Hi-res models**

357 The likelihood of wedge-tailed shearwater foraging was not significantly influenced by bathymetry,
358 and only shearwaters from Heron Island in 2015 were more likely to forage closer to seamounts
359 (Table 4; Fig. 5E). Shearwaters from Lord Howe Island in 2014 were more likely to forage at
360 higher Chlorophyll-*a* concentrations (Fig 5L) while sea surface height anomalies influenced
361 likelihood of foraging in shearwaters from Heron Island in 2015 only (Fig. 5D). Ekman upwelling
362 and sea surface temperature anomalies influenced likelihood of shearwater foraging in every
363 instance (Table 4; Fig. 5). The proxy selected to represent the major-tuna cluster was micronektonic
364 bigeye (BET_MIC) in the Heron Island 2015 model, adult skipjack tuna (SKJ_ADU) in the Lord
365 Howe Island 2015 model and micronektonic yellowfin tuna (YFT_MIC) in the Lord Howe Island
366 2014 model (Fig. 3). Models predicted that for each additional 100 g m⁻² of tuna biomass an area
367 contains, shearwaters from Heron Island in 2015 were 1.3 times more likely to forage there (Table
368 4; Fig. 5C), shearwaters from Lord Howe Island in 2015 were 2.23 times more likely to forage there
369 (Fig. 5H) and shearwaters Lord Howe Island in 2014 were 1.13 times more likely to forage there

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370 (Fig. 5K). Validation of the Heron Island 2015 model confirmed the final model fitted the data
371 adequately (AUC = 0.79) and explained a good proportion of the variance (marginal $R^2 = 0.31$,
372 conditional $R^2 = 0.47$). Validation of the Lord Howe 2015 model confirmed the final model also
373 fitted the data adequately (AUC = 0.73) and explained a similar proportion of the variance
374 (marginal $R^2 = 0.29$, conditional $R^2 = 0.51$). Validation of the Lord Howe 2014 model confirmed
375 the final model fitted the data identically (AUC = 0.73) but explained a smaller proportion of the
376 variance (marginal $R^2 = 0.17$, conditional $R^2 = 0.30$).

377

378 **Discussion**

379

380 **Wedge-tailed Shearwater distributions and oceanography**

381 Our results show that the long-trip destinations of Wedge-tailed shearwaters breeding on Heron
382 Island lie predominantly to the north-east of the colony in the Coral Sea, adding support for
383 consistent use of this area over multiple years (McDuie et al. 2015). Our results also show, for the
384 first time, that during chick-rearing wedge-tailed shearwaters from Lord Howe Island undertake
385 long-trips to predominantly different regions in different years. In 2014 and 2016 wedge-tailed
386 shearwater long-trip destinations were distributed west of Lord Howe Island in the Tasman Sea over
387 the Tasmantid Seamounts that run parallel to the east Australian shelf, while in 2015 long-trip
388 destinations were predominately far to the north of Lord Howe Island in the Coral Sea, almost
389 overlapping with conspecifics foraging from Heron Island. Whether long-trips at Lord Howe Island
390 are undertaken as part of a coordinated dual-foraging strategy similar to that observed at Heron
391 Island (Congdon et al. 2005), or more opportunistically is currently unknown. However, these
392 results demonstrate that the unimodal foraging strategy observed by Peck & Congdon (2005) at
393 Lord Howe Island during early chick rearing appears to alter in the later stages of chick-rearing

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394 (Jakubas et al. 2014), and/or between breeding seasons (Granadeiro et al. 1998).

395

396 Our results show that both Wedge-tailed Shearwater populations selected core-areas in deep pelagic
397 waters that were close to seamounts, these findings mirror those of other studies into the species'
398 bathymetric preferences (Catry et al. 2009, McDuie et al. 2015, McDuie & Congdon 2016). At fine
399 scales, wedge-tailed shearwaters from Heron Island in 2015 were more likely to forage close to
400 seamounts but bathymetry and seamounts did not influence conspecifics foraging from Lord Howe
401 Island. These results indicate that marine topography may be used by wedge-tailed shearwaters to
402 locate profitable foraging areas at broad but not fine scales. Fine scale foraging behaviour is likely
403 to be triggered by sea surface temperature anomalies and Ekeman upwelling which influenced
404 likelihood of foraging in all models. Collectively, these two dynamic covariates identify frontal
405 areas of water mixing and associated up and down-welling. Our results are consistent with other
406 studies that indicate that these dynamic phenomena are major mechanisms of prey aggregation for
407 seabirds in lower latitude waters (Spear et al. 2001, Hyrenbach et al. 2006, Weimerskirch et al.
408 2010, McDuie & Congdon 2016).

409

410 **Tuna relationships**

411 We found tuna distributions to influence Wedge-tailed Shearwater core-area location and likelihood
412 of foraging in every instance, supporting both our broad scale and fine scale hypotheses. This
413 means that wedge-tailed shearwaters sought out areas of increased tuna biomass, which at the
414 regional scale are relatively stable between years, and that they home in on aggregations of tuna for
415 foraging at fine scale. Our results describe the importance of facilitated foraging opportunities in
416 two seabird populations and are expressed in an ecologically meaningful way: using tuna density
417 increases of 100g m^{-2} , interpretable as the weight of one micronektonic tuna (165 mm long; Harley

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418 et al. 2014), or a large meal for a wedge-tailed shearwater. For example we predict that in 2015, for
419 every additional micronektonic tuna encountered per m² of ocean, it was 2.23 times more likely that
420 wedge-tailed shearwaters from Lord Howe Island would forage there and 1.3 times more likely that
421 conspecifics from Heron Island would forage there. Such predictions demonstrate the potential of
422 our approach to quantify facilitated foraging opportunities. However, they also come with the
423 caveat that they are only as accurate as the underlying modelled tuna distributions.

424

425 The major-tuna cluster identified in each PCA, and represented in each model by a single covariate,
426 showed that densities of most tunas were positively associated with: each other, wedge-tailed
427 shearwater selection of core-areas, and shearwater likelihood of foraging. The major-tuna cluster
428 represents significant spatial overlap in the distribution of adult and micronektonic tunas. In
429 locations where this cluster of tunas co-occurs we envisage a scenario where micronektonic tuna
430 and similar sized micronekton (30-250 mm) prey upon each other and attract adult tunas through
431 cannibalism and inter-species predation (Allain et al. 2007, Allain 2010). Predation within the
432 cluster takes place in epipelagic waters because micronektonic tuna have a non-developed swim
433 bladder that confines them to surface waters (Magnuson 1973). As such, where the major-tuna
434 cluster occurs, micronekton of appropriate size to be wedge-tailed shearwater prey (up to 145 mm;
435 Harrison et al. 1983) are preyed upon by tuna in surface waters, presenting clear facilitated foraging
436 opportunities.

437

438 Only in the Heron Island climatology model did shearwaters associate with a micronektonic tuna
439 (bigeye) outside of the major-tuna cluster. Even small micronektonic tuna are proficient swimmers
440 (Graham et al. 2007) and it is unlikely that wedge-tailed shearwaters from these colonies possess
441 the diving ability (maximum recorded dive depth of 12m; Peck & Congdon 2006) to capture them

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442 without subsurface predator assistance during the day. This suggests that subsurface predators not
443 considered in our models, such as cetaceans (Au & Pitman 1986), billfish (family: Istiophoridae) or
444 dolphinfish *Coryphaena hippurus* (Young et al. 2010b), also facilitate wedge-tailed shearwater
445 foraging in this region.

446

447 At broad scales, our results suggest wedge-tailed shearwaters are consistent facilitated foraging
448 commensals of adult skipjack tuna, intermittent facilitated foraging commensals of adult yellowfin
449 tuna, and that adult bigeye tuna do not facilitate wedge-tailed shearwater foraging. Many tropical
450 seabirds are known to associate foraging with skipjack tuna (Au & Pitman 1986, Jaquemet et al.
451 2004, Hebshi et al. 2008). Frequent seabird association with skipjack could be due to their greater
452 biomass, relative to other tunas in tropical seas, fostering greater facilitated foraging opportunities.
453 Additionally, the smaller size of skipjack, relative to other tunas, means that they also target suitable
454 sized prey (mean prey length 42 mm; Roger 1994) for wedge-tailed shearwaters (mean prey length
455 57 mm; Harrison et al. 1983). However, larger yellowfin and bigeye also feed on very small prey
456 relative to their own size (Ménard et al. 2006) and could conceivably target shearwater-sized prey.
457 Tuna occupy different vertical niches based on their size (which limits thermal tolerance) and
458 biology (i.e. development of the swim bladder in yellowfin and bigeye); larger tunas can spend
459 more time foraging for prey in deep water within and below the thermocline. During the day, adult
460 bigeye are typically found deepest, followed by yellowfin and then skipjack (Schaefer et al. 2009,
461 Schaefer & Fuller 2013, Scutt Phillips et al. 2015). Consequently, the predominantly surface-
462 dwelling skipjack tuna (and micronektonic tuna age-classes) are more often encountered by diurnal
463 seabirds and thus more likely to serve as facilitated foraging hosts than larger adult yellowfin or
464 bigeye.

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465 Tuna biomass in the Coral and Tasman Seas changes throughout the year following spawning and
466 seasonal changes in water temperature and habitat. Regional tuna spawning times are poorly
467 known, however skipjack and yellowfin are thought to spawn year-round depending on water
468 temperature (Schaefer 1996, Schaefer 2001) and bigeye are thought to spawn from October to
469 December (Evans et al. 2008). Regional tuna movement broadly follows thermal boundaries (Evans
470 et al. 2011), this is especially true for less thermally tolerant skipjack and micronektonic tunas,
471 which SEAPODYM models to follow the southward advance of warm water in the austral summer
472 and subsequent retreat north in the winter. This regional spawning and movement pattern causes
473 annual densities of tunas in the major-tuna cluster to peak in the southern Coral Sea in the austral
474 summer. In fact, adult bigeye spawning in December would produce ~250mm micronektonic
475 offspring in March (Nicol et al. 2011). This means that skipjack and micronektonic tuna biomass
476 peaks within the foraging range of wedge-tailed shearwaters at a time when they have the highest
477 energy demands of chick-rearing. If facilitated foraging with tuna is as important for wedge-tailed
478 shearwater populations as we suggest, then tuna seasonality could have an important role in shaping
479 wedge-tailed shearwater breeding phenology, as proposed for productivity in Indian Ocean
480 conspecifics (Catry et al. 2009).

481

482 **Effect of productivity gradient on long-trip destinations**

483 We found that the tropical wedge-tailed shearwater population did not adhere to the ‘temperate
484 long-trip model’ by seeking out areas of high primary productivity, but instead targeted regions of
485 high tuna biomass. The subtropical population at times adhered to the ‘temperate long-trip model’
486 but also targeted tuna. The Heron Island results are consistent with wedge-tailed shearwater non-
487 breeding preferences, where birds exploit warm, oligotrophic waters in the Indian (Catry, et al.
488 2009) and Pacific oceans (McDuie & Congdon 2016) when freed from the need to central-place

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489 forage. Our results also support the suggestion of a temporal and spatial decoupling between
490 satellite surface-measured primary productivity and micronekton/tuna aggregation in tropical
491 oceans (Lehodey et al. 1998, McDuie & Congdon 2016).

492

493 At broad scales the selection of core-areas by wedge-tailed shearwaters from sub-tropical Lord
494 Howe Island appeared uninfluenced by primary production. However, this was due to variation in
495 long-trip destinations between years. In 2014 wedge-tailed shearwater foraging was positively
496 associated with increased chlorophyll-*a* concentration and the population exploited sub-tropical
497 waters west of Lord Howe Island. In 2015 shearwater foraging was negatively related to
498 chlorophyll-*a* concentration and the population exploited tropical waters north of Lord Howe
499 Island. In 2014 the Lord Howe Island result conforms to our prediction for a sub-tropical shearwater
500 colony, where long-trip foraging destinations target enhanced productivity driven by oceanic fronts
501 (Baduini & Hyrenbach 2003, Paiva et al. 2010), but in 2015 the result does not. In 2015 wedge-
502 tailed shearwater likelihood of foraging was more strongly associated with tropical tuna densities.
503 Individuals clearly transited over waters of the Tasman Sea, which are usually high in productivity,
504 to reach oligotrophic waters with high tuna biomass in the Coral Sea. A potential explanation is that
505 in years like 2015, productivity in the Lord Howe region becomes reduced, through a distancing or
506 reduction in strength of the Tasman Front (Mulhearn 1987, Przeslawski et al. 2011). Wedge-tailed
507 shearwaters remained in sub-tropical waters to the west of Lord Howe Island in 2014 and 2016,
508 indicating that the 2015 northward movement could mark a departure from normal conditions,
509 however additional years of data are needed to confirm this.

510

511 Although it is unclear what triggers wedge-tailed shearwaters from Lord Howe Island to switch
512 long-trip destinations, it is unequivocal that both shearwater populations preferentially target tuna in

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513 some years. At the same time of year in 2015, individuals from both populations undertook long,
514 purpose-directed flights towards almost the exact same region of the southern Coral Sea, indicating
515 an *a priori* expectation of high resource availability at these sites. This is not the indirect, looping
516 flight that tropical seabirds use to exploit unpredictable resources (Weimerskirch 2007,
517 Weimerskirch et al. 2010). Rather, it suggests that the tropical tuna biomass targeted by these flights
518 was not patchily distributed or ephemeral at broad spatio-temporal scales. The apparent reliability
519 of this resource suggests that in tropical systems, facilitated foraging with tuna can act as a
520 consistently available 'productive' long-trip destination, analogous to chlorophyll-*a* concentration in
521 temperate systems. In terms of population-level reliance on tuna we suggest that facilitated foraging
522 with tuna is consistently important to sustain breeding in the Heron Island wedge-tailed shearwater
523 population. Primary productivity *per se* appears more important to the Lord Howe Island wedge-
524 tailed shearwater population in most years, although facilitated foraging with tuna becomes an
525 important strategy under certain conditions. As such, the relative importance of facilitated foraging
526 for wedge-tailed shearwater populations appears to be dependent upon their access to reliable areas
527 of high primary productivity.

528

529

530

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532

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546

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800

801 **Tables**802 **Table 1.** Summary of oceanographic and tuna covariates used in broad and fine scale models

Covariate (units)	Abbreviation	Temporal resolution	Spatial resolution	Data source (provider)
High resolution dynamic covariates				
Chlorophyll- <i>a</i> concentration (mg m ⁻³)	CHL	8 day	4 km	MODIS & VIIRS (NASA)
Sea surface temperature (°C)	SST	8 & 1 day	0.1° & 0.25°	POES & AVHRR (NOAA)
Sea surface temperature anomaly (°C)	SSTA	8 & 1 day	0.1° & 0.25°	POES AVHRR (NOAA)
Sea surface height anomaly (m)	SSHA	1 day	0.083°	HYCOM & NCODA (NRL)
Ekman upwelling (m day ⁻¹)	EKM	1 day	0.25°	Metop ASCAT
Climatology and static covariates				
Primary productivity (mg C m ⁻² day ⁻¹)	PRO	Monthly (20 yr mean)	4.4 km	SeaWiFS & AVHRR (NASA & NOAA)
Sea surface temperature (°C)	SST	Monthly (30 yr mean)	4.4 km	AVHRR (NOAA)
Bathymetry (m)	BTY	Static	0.083°	GEBCO
Distance to seamount (km)	SMT	Static	0.083°	Global seamount database
Tuna distribution covariates				
Tuna weekly biomass distribution (g m ⁻²)	BET_ADU, BET_MIC, YFT_ADU, YFT_MIC, SKJ_ADU, SKJ_MIC	7 day	0.25°	INDESO V2 Fished (SEAPODYM) (unavailable in 2016)
Tuna monthly biomass distribution (g m ⁻²)	BET_ADU, BET_MIC, YFT_ADU, YFT_MIC, SKJ_ADU, SKJ_MIC	Monthly (30 yr mean)	1°	INTERIM Fished (SEAPODYM)

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804 **Table 2.** Summary of Wedge-tailed Shearwater GPS and PTT* tracked long-trips collected during
 805 the study. The core-area is the 50% utilization distribution from kernel analysis of each tracking
 806 dataset.

Island Colony	Year	n trips	Max colony distance (km)	Trip length (km)	Tracked days	Trip length (d)	Core-area centroid (Lat, Long)
Lord Howe	2016	19	328 ± 114	1165 ± 381	4.4 ± 1.3	6.9 ± 2.3	-31.8, 157.2
Lord Howe	2015	14	661 ± 291	1986 ± 590	5.9 ± 2.3	9.9 ± 3.3	-27.7, 158.1
Lord Howe	2014	8	498 ± 292	1588 ± 561	6 ± 1.7	9.6 ± 4	-31.8, 156.2
Heron	2015	8	625 ± 223	1532 ± 510	3.9 ± 1.5	9.5 ± 2	-20.4, 156.9
Heron *	2013	9	744 ± 312		8.3 ± 3.2		-19.8, 154.2
Heron *	2011	3	649 ± 375		9.7 ± 2.3		-19.2, 155.7

807

808

809 **Table 3.** Climatology logistical regression models of wedge-tailed shearwater presence-absence
 810 against broad scale oceanographic and tuna covariates. The following coefficients (β) and std. errors
 811 (SE) are expressed in terms of a 100 unit change: tuna covariates (100 g m⁻²), seamount distance
 812 (100 km) and bathymetry (100 m). All covariates have significance $p < 0.001$. Core-area and
 813 foraging range covariate values are expressed as mean ± standard deviation

Colony	Covariate	$\beta \pm SE$	Core-area	Foraging range
Heron Island	Intercept	1.195 ± 1.304		
	Productivity (mg C m ⁻² day ⁻¹)	-0.025 ± 0.002	425.53 ± 42.62	534.80 ± 154.28
	Seamount distance (km)	-0.698 ± 0.099	96.38 ± 83.85	167.52 ± 125.95
	Bathymetry (m)	0.034 ± 0.008	2756 ± 940	2709 ± 1389
	Micronektonic bigeye tuna biomass (g m ⁻²)	0.721 ± 0.056	0.084 ± 0.017	0.066 ± 0.021
	Micronektonic yellowfin tuna biomass (g m ⁻²)	0.040 ± 0.010	0.334 ± 0.060	0.268 ± 0.150
	Autocovariate	0.129 ± 0.005		
Lord Howe Island	Intercept	-4.681 ± 0.706		
	Seamount distance	-1.169 ± 0.176	84.56 ± 45.07	168.10 ± 144.98

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(km)				
Bathymetry	0.048 ± 0.010	3429 ± 1069	2772 ± 1359	
(m)				
Micronektonic bigeye tuna biomass (g m ⁻²)	0.350 ± 0.048	0.067 ± 0.010	0.045 ± 0.030	
Adult yellowfin tuna biomass (g m ⁻²)	-0.534 ± 0.137	0.027 ± 0.008	0.029 ± 0.007	
Autocovariate	0.112 ± 0.004			

814

815

816 **Table 4.** Hi-res logistical regression models of wedge-tailed shearwater probability of foraging

817 against fine scale oceanographic and tuna covariates. The strength (χ^2) and effect direction of each

818 covariate is given for each of the three colony-year models. Covariates with significance $p < 0.01$

819 are shown in bold and the corresponding effect given, NA indicates that the covariate was not

820 included in a model due to multicollinearity. Positive and negative effect directions are denoted by

821 \uparrow and \downarrow respectively, and in the case of a polynomial relationship the value at which foraging is

822 most or least (denoted by *) likely is given. For coefficient (β) and std. error values see Appendix 2

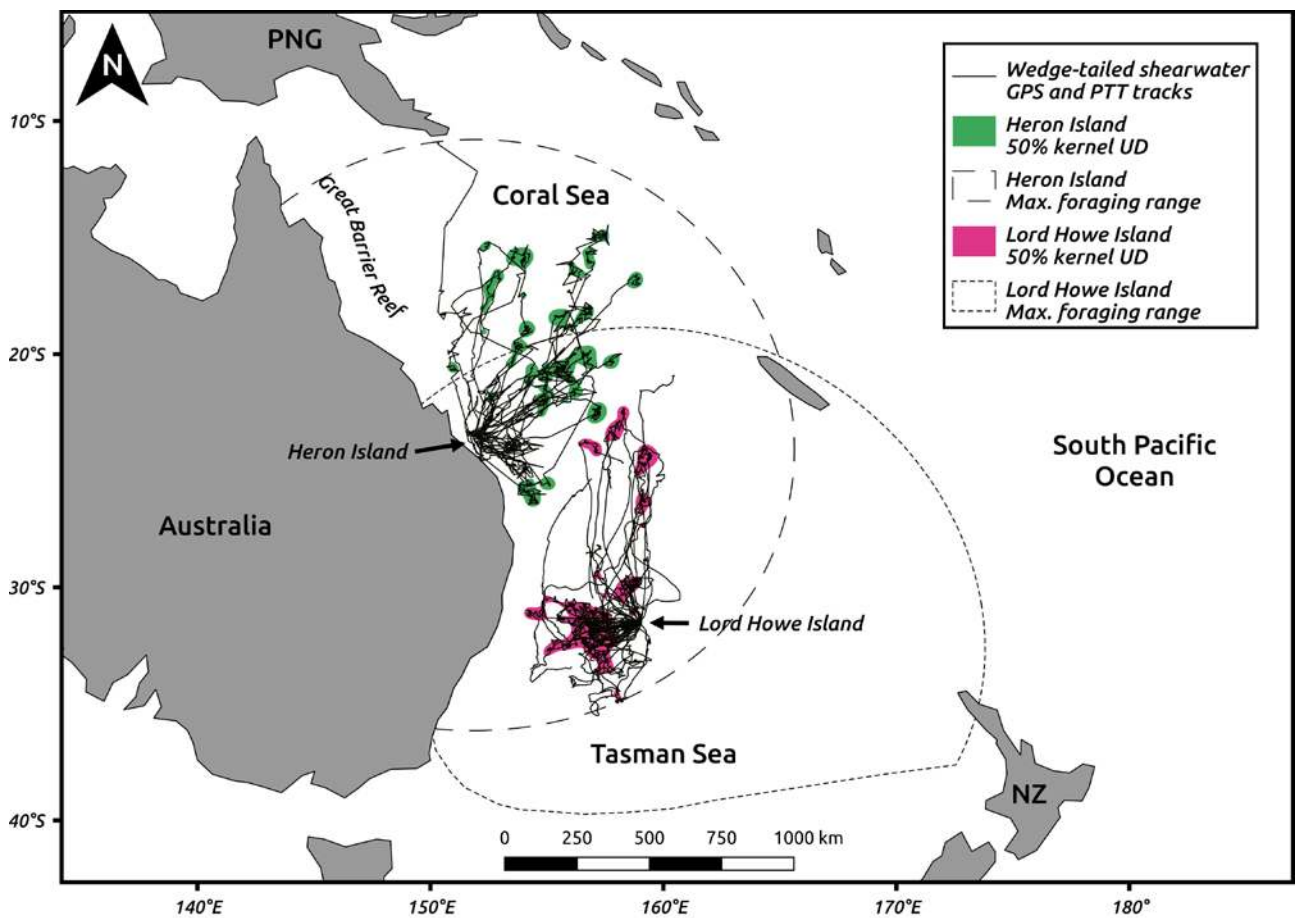
823

Covariate	Heron Island 2015		Lord Howe Island 2015		Lord Howe Island 2014	
	Effect	Strength (χ^2)	Effect	Strength (χ^2)	Effect	Strength (χ^2)
Bathymetry (m)		0.40		3.80		NA
Seamount distance (km)	\downarrow	38.77		0.80		0.04
chlorophyll- <i>a</i> concentration (mg m ⁻³)		NA		NA	\uparrow	9.67
Ekman upwelling (m day ⁻¹)	0.22	16.83	-0.43*	65.61	0.67*	48.91
Sea surface temperature anomaly (°C)	\uparrow	29.46	-0.17	101.77	\downarrow	6.57
Sea surface height anomaly (m)	0.62	33.27		NA		3.27
Tuna biomass (g m ⁻²)	\uparrow	26.07	\uparrow	230.21	\uparrow	66.14

824

825 **Figures**

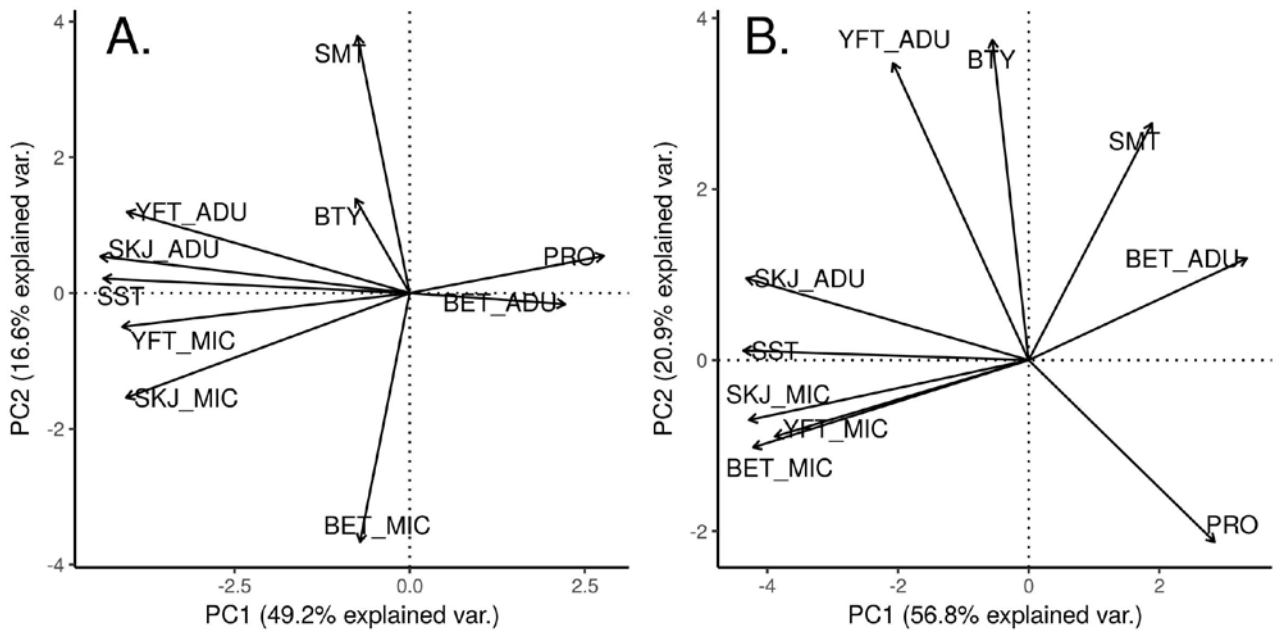
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828 **Fig. 1.** Wedge-tailed Shearwater long-trip tracking data collected from birds rearing chicks on
829 Heron Island and Lord Howe Island between 2011 and 2016, overlaid with 50% kernel utilisation
830 distribution (UD) core-use areas for each colony

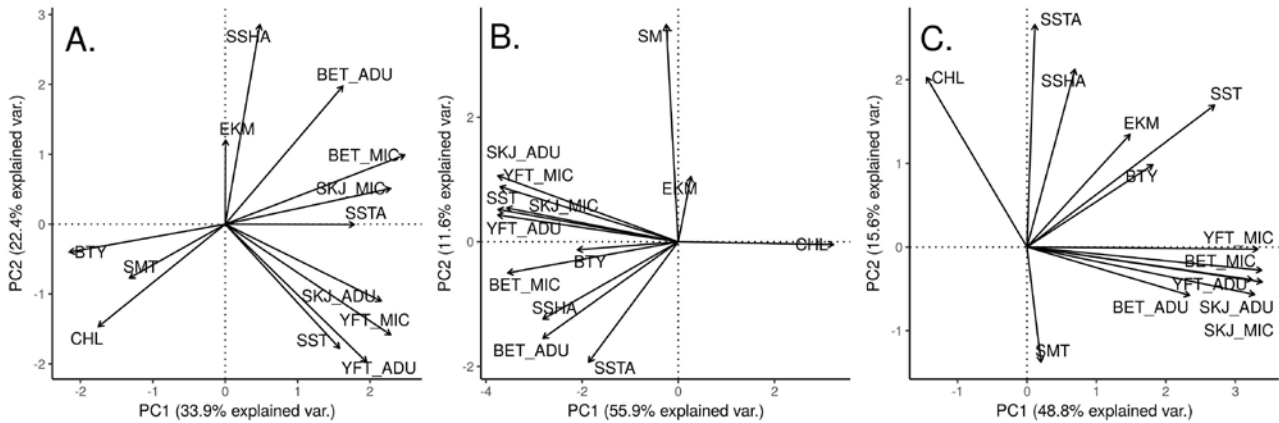
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831

832 **Fig. 2.** Ordination from principal components analysis of broad scale oceanographic and tuna
 833 covariates used in climatology models of Wedge-tailed Shearwaters breeding from (A) Heron
 834 Island, and (B) Lord Howe Island

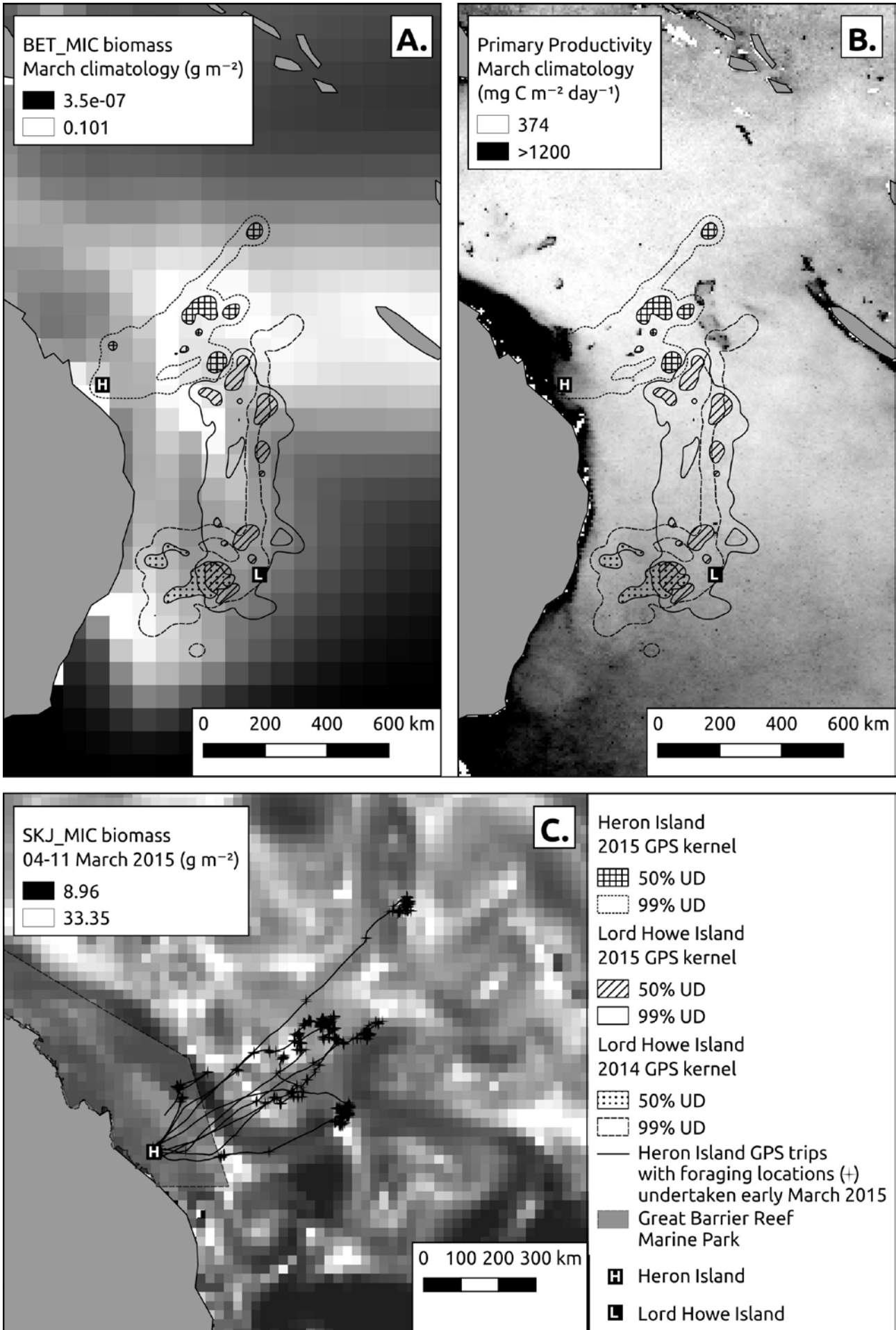
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837 **Fig. 3.** Ordination from principal components analysis of fine scale oceanographic and tuna
 838 covariates used in hi-res models of Wedge-tailed Shearwaters tracked with GPS from (A) Heron
 839 Island in 2015, (B) Lord Howe Island in 2015, and (C) Lord Howe Island in 2014

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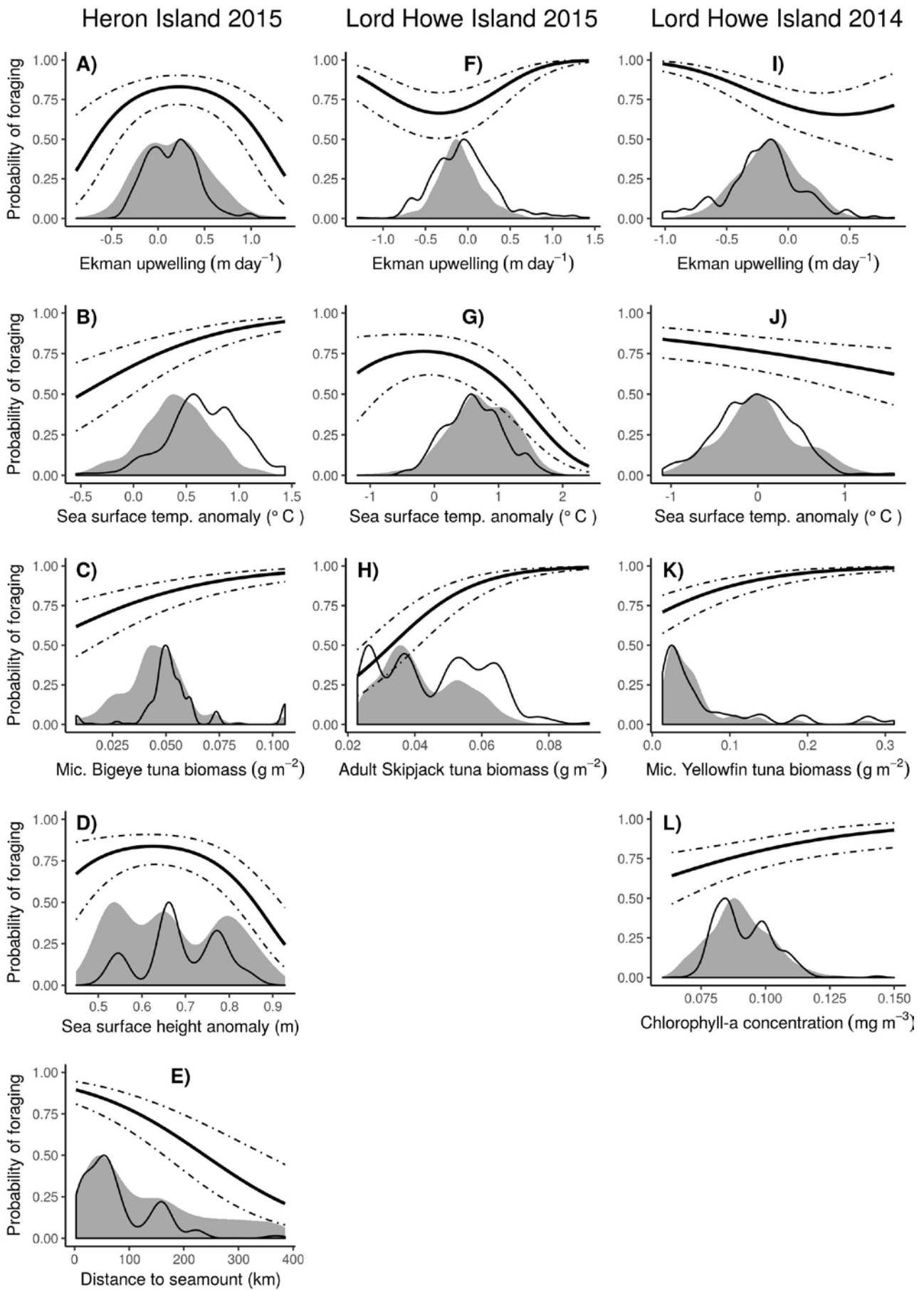


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841 **Fig. 4.** GPS tracking data of breeding Wedge-tailed Shearwaters shown as (A) kernel utilisation
842 distributions (UDs) overlaying SEAPODYM-predicted long-term mean micronektonic bigeye tuna
843 biomass for march, (B) kernel UD overlaying long-term mean primary productivity for march, and
844 (C) individual foraging trips from Heron Island overlaying SEAPODYM-predicted weekly
845 micronektonic skipjack tuna biomass.

846

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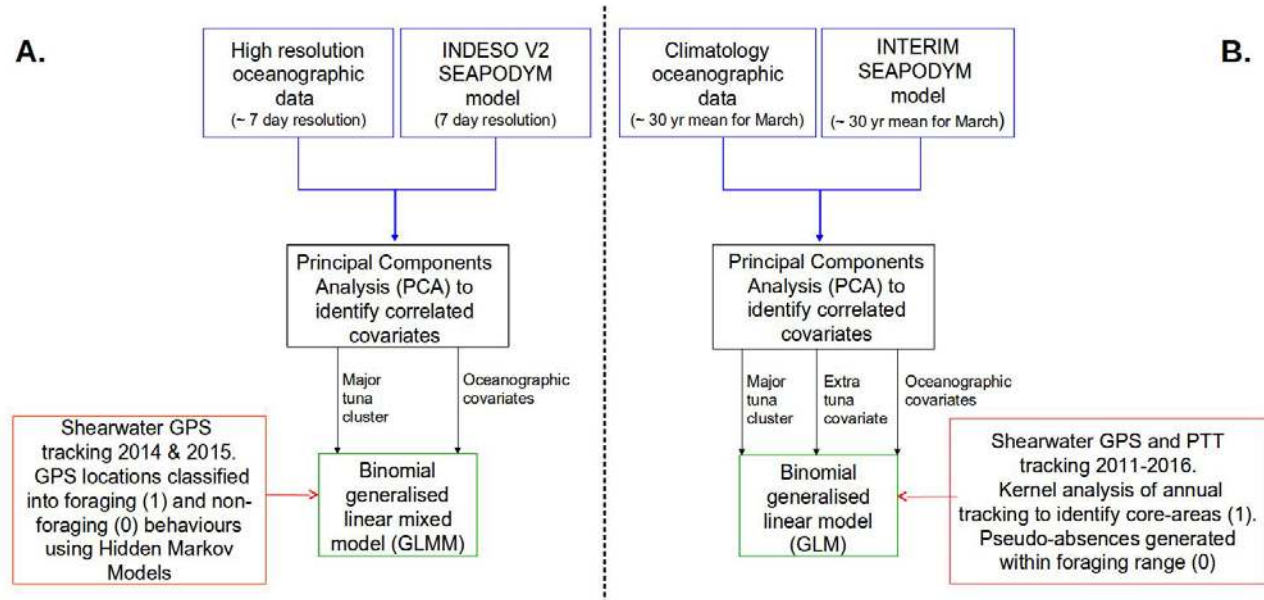


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848 **Fig. 5.** Mean (solid line) and 95% confidence interval (dotted line) predictions of Wedge-tailed
849 Shearwater foraging probability in relation to fine scale tuna and oceanographic covariates. Density
850 plots are overlaid showing the distributions of foraging (black line) and non-foraging (grey shade)
851 samples for each covariate. 'Mic.' refers to micronektonic tuna age-classes

852 **Appendix**

853 **Appendix 1.** Flow chart showing input data and analyses steps taken for: A. hi-res models; and B.
 854 climatology models (separated by dotted line).



855

856

857

858 **Appendix 2.** Logistical regression coefficients for hi-res models of wedge-tailed shearwater
 859 probability of foraging against fine scale oceanographic and tuna covariates. The following
 860 coefficients (β) and std. errors (SE) are expressed in terms of a 100 unit change: tuna covariates
 861 (100 g m⁻²), seamount distance (SMT) (100 km)

862

Colony – Year	Covariate	$\beta \pm SE$
Heron Island 2015		
	Intercept	-11.829 ± 3.764
	poly(EKM)1	0.900 ± 0.392
	poly(EKM)2	-2.000 ± 0.515
	SSTA	1.499 ± 0.275
	poly(SSHA)1	3.773 ± 1.086
	poly(SSHA)2	-3.019 ± 0.775
	SMT	-0.907 ± 0.157

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BET_MIC 0.265 ± 0.052

Lord Howe Island 2015

Intercept -2.583 ± 0.416
poly(EKM)1 1.064 ± 0.163
poly(EKM)2 1.592 ± 0.310
poly(SSTA)1 -0.201 ± 0.230
poly(SSTA)2 -0.604 ± 0.143
SKJ_ADU 0.804 ± 0.055

Lord Howe Island 2014

Intercept -2.182 ± 0.859
poly(EKM)1 -1.240 ± 0.350
poly(EKM)2 1.454 ± 0.621
SSTA -0.430 ± 0.167
SSHA 0.860 ± 0.477
YFT_MIC 0.119 ± 0.016
Chlorophyll-*a* 0.232 ± 0.080
