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Importance of tropical tuna for seabird foraging over a marine productivity gradient

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ABSTRACT: Foraging with tuna is a well-documented seabird strategy, referred to as facilitated foraging. However, despite this behaviour being considered almost obligatory in nutrient-poor tropical waters, little data exist on its relative importance to individual colonies. Therefore, to examine facilitated foraging under different patterns of nutrient availability, we tracked wedge-tailed shearwaters *Ardenna pacifica* from 2 colonies, one tropical and one subtropical, situated in waters of contrasting productivity. Shearwater foraging behaviour was assessed relative to oceanographic covariates and predicted distributions for multiple tropical tuna species and age-classes, simulated by an existing ecosystem model (SEAPODYM). Shearwaters from both colonies undertook long trips to deep, pelagic waters close to seamounts and foraged most often at fronts and eddies. Micronektonic and adult tuna age classes were highly correlated in space. Predation between these tuna age classes represents a likely source of facilitated foraging opportunities for shearwaters. At broad spatial scales, shearwaters consistently foraged in areas with higher predicted adult skipjack and micronektonic tuna densities and avoided adult bigeye tuna. At finer spatial scales, dynamic ocean features aggregated tuna of all sizes. Enhanced tuna density at these locations increased the likelihood of shearwater foraging activity. Long trips in the tropics targeted oligotrophic waters with higher tuna densities. Long trips in the subtropics targeted enhanced productivity, but in some years shifted to target the same oligotrophic, tuna-dense waters used by tropical conspecifics. We conclude that facilitated foraging with tuna is consistently important to the tropical breeding population and becomes increasingly important to the subtropical population in years of low marine productivity.

KEY WORDS: Facilitated foraging · Micronekton · Productivity · SEAPODYM · Tuna · Wedge-tailed shearwater

INTRODUCTION

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

However, the difficulty associated with monitoring seabird and sub-surface predator activity concurrently means that facilitated foraging is often inferred. Inference comes from overlap in seabird and sub-surface predator prey items (Ashmole & Ashmole 1967, Ménard et al. 2013) and trophic niches (Kojadinovic et al. 2008, Young et al. 2010a), although often the results of such studies are inconclusive. Facilitated foraging has also been inferred, but not quantified, from overlap between seabird foraging tracks and areas of high sub-surface predator activity in commercial fisheries (Catry et al. 2009, Weimerskirch et al. 2010, McDuie & Congdon 2016). Finally, oceanographic data have shown that the densities of tropical, diurnal, piscivorous seabirds are driven by a well-stratified, deep thermocline, which is associated with higher sub-surface predator densities (Ballance et al. 1997, Spear et al. 2001).

The bulk of our knowledge on facilitated foraging comes from at-sea observations (Au & Pitman 1986, Spear et al. 2007). At-sea observations enable quantification of instances of seabirds using facilitated foraging, but have their limitations. The cost of vessel hire has led some studies to make observations from fishing vessels. However, as these vessels target sub-surface predators, results are biased towards overestimation of facilitated foraging events (Jaquemet et al. 2004, Hebshi et al. 2008). At-sea observations using transects are unbiased and have contributed significantly to our understanding of facilitated foraging, primarily in the eastern and central tropical Pacific (Au & Pitman 1986, Spear et al. 2007) and tropical Indian Oceans (Thiebot & Weimerskirch 2013). However, all at-sea survey methods are limited by the prohibitive cost of undertaking simultaneous surveys in different regions and an inability to determine the provenance of birds being observed. As such, no previously available method has been able to quantify the individual- or population-level decisions of seabirds on whether to preferentially target sub-surface predators. Consequently, there has been no way to determine the relative importance of facilitated foraging opportunities for specific seabird colonies. Our present study provides a framework to do so.

Limited availability of suitable nesting habitat can lead to seabird colonies being located where local marine resources are sub-optimal (Navarro & González-Solís 2009). Under these constraints, many pelagic foraging seabirds use a bimodal foraging strategy, where ‘short trips’ (1–3 d in shearwaters; Baduini & Hyrenbach 2003) in resource-poor local waters are used almost exclusively to provision chicks at the expense of adult condition. Following a series of short trips, adults undertake a ‘long trip’ (5–17 d) to more distant foraging sites, where they can quickly regain condition (Weimerskirch 1998, Weimerskirch & Cherel 1998). To achieve this, long trips are said to access ‘productive distant waters’ (Weimerskirch 1998). As most bimodal foraging studies come from temperate and polar regions, ‘productive’ has become synonymous for high primary productivity or chlorophyll a (chl a) concentration, aggregated by shelf or frontal features (Waugh et al. 1999, Catard et al. 2000, Klomp & Schultz 2000, Stahl & Sagar 2000, reviewed in Baduini & Hyrenbach 2003). Seabirds breeding in the subtropics may have the opportunity to access similar large-scale areas of high primary productivity using bimodal foraging (Paiva et al. 2010). However, since such features are rare in tropical systems, we hypothesise that tropical-breeding seabirds target increased sub-surface predator densities as an alternative, because of the greater facilitated foraging opportunities this provides.

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

This study aims to estimate the relative importance of facilitated foraging with tropical tuna for 2 wedge-tailed shearwater populations in waters with contrasting productivity. Relative importance is quantified from spatial association between shearwater tracking data, oceanographic covariates and modelled tropical tuna distributions. We tested 2 facilitated foraging hypotheses at opposing spatio-temporal scales, thus expecting that: (1) tropical tuna distributions influence the selection of wedge-tailed shearwater core-area locations (defined by the 50% utilization distribution [UD] from kernel analysis) at broad spatial scales; and (2) tropical tuna distributions influence the likelihood of wedge-tailed shearwater foraging activity at fine spatial scales. We additionally test 2 facilitated foraging hypotheses at opposing ends of a productivity gradient, expecting that: (3) wedge-tailed shearwater in tropical waters do not adhere to the temperate model of ‘productive’ long-trip destinations and instead target tuna; and (4) wedge-tailed shearwater breeding in sub-tropical waters adhere to the temperate model of ‘productive’ long-trip destinations and do not target tuna.

MATERIALS AND METHODS

Study area and logger deployment

This study was carried out at Heron Island (23°26'S, 151°51'E) in the Capricorn Bunker Island Group, Great Barrier Reef, and Lord Howe Island (31°33'S, 159°05'E) in the northern Tasman Sea, Australia. Both islands support large breeding colonies of wedge-tailed shearwaters (Marchant & Higgins 1990). We deployed GPS loggers on wedge-tailed shearwaters at Lord Howe Island in 2014, 2015 and 2016 and concurrently at Heron Island in 2015, and deployed platform terminal transmitter (PTT) loggers at Heron Island in 2011 and 2013 (McDuie et al. 2015). All loggers were deployed during the chick-rearing period (February–April). I-gotU GT-120 GPS loggers (Mobile Action Technology) were modified to use smaller 100 mAh batteries, sealed in heat-shrink tubing and programmed to obtain fixes every 10 min (Freeman et al. 2013). Solar-powered ARGOS PTTs (PTT-100; Microwave Telemetry) relay data via satellite and were programmed to obtain fixes continuously. We deployed both GPS and PTT loggers to 3 central tail feathers using Tesa® 4651 Tape, total deployment weight of both logger types was ~10.5–12 g, within the 3–5% body weight limit for the species (McDuie et al. 2015).

Tracking data preparation and analyses

All data handling and statistical analyses were performed in the statistical software environment program R, version 3.2.4 (R Core Team 2016). Tracking data were pre-processed prior to analyses using a speed filter, removing points exceeding a maximum velocity of 50 km h^{-1} (McDuie et al. 2015); additionally, GPS tracks were gap filled using interpolation to 10 min intervals (Weimerskirch et al. 2006). As loggers were active for several days, multiple foraging trips were observed for most individuals. To split long trips from short trips within multi-day GPS tracks we used the R ‘tripsplit’ function from the ‘marine IBA’ package (Lascelles et al. 2016) and isolated long trips (>4 d duration; Congdon et al. 2005) for further analysis. We could not determine individual foraging trips within multi-day PTT tracks (due to near colony positional error) so we removed all fixes from tracks within the ‘short-trip zone’ of 300 km around Heron Island (McDuie et al. 2015).

To identify core areas used by each colony for each year of long-trip tracking data, we employed kernel analysis using the package ‘adehabitatHR’ (Calenge 2006). All locations within each colony–year combination were used with a grid size of 0.5 km and, for consistency, the same smoothing parameter (h) of 20 km for GPS and PTT data following McDuie et al. (2015). The 50% UD was selected from resultant kernels to represent the core area used by wedge-tailed shearwaters in each year (Hamer et al. 2007). To identify behavioural states and thereby identify foraging locations, we applied hidden Markov models (HMM) to the GPS data. We constructed a single HMM using the full GPS tracking dataset, including an identifier for each trip, using the package ‘moveHMM’ (Michelot et al. 2016). For each consecutive GPS point, the step length and turning angle were calculated, producing 3 distributions consistent with foraging, resting and transiting behaviours observed in HMM studies of boobies (Oppel et al. 2015) and shearwaters (Dean et al. 2013). The fitted HMM was then used to classify each GPS point as foraging, resting or transiting.

Oceanographic data

We created a static covariate for depth (BTY) from the 30 arc-second General Bathymetric Chart of the World (GEBCO) and calculated a static covariate for distance to seamount using the Global Seamount Database (Kim & Wessel 2011) and package ‘raster’ (Hijmans 2016). Gridded oceanographic data were accessed from NOAA ERDDAP servers using the ‘rerddap’ package (Chamberlain 2016) (Table 1). We accessed oceanographic climatologies in the form of long-term, monthly averages: primary productivity (PRO), 1997–2016; and sea surface temperature (SST), 1985–2016. We used the March data product as our covariate as it is central to the wedge-tailed shearwater chick-rearing period. We accessed very fine temporal scale Ekman upwelling (EKM, 1 d) and sea surface height anomaly (SSHA, 1 d) data as these products were cloud free. We also accessed coarser scaled data on chl a concentration (CHL, 8 d), SST (1–8 d) and sea surface temperature anomaly (SSTA, 1–8 d), to counter daily missing values due to cloud cover. In a further step to fill data gaps due to clouds, we blended 2 CHL, SST and SSTA products from different data sources to create single covariates (Table 1).

Tropical tuna data

Tuna covariates were generated using the Spatial Ecosystem and Population Dynamics Model (SEAPODYM). SEAPODYM is an age-structured population model describing spatial and temporal dynamics of top predator species in a direct link with prey biomass and environmental variability (Lehodey et al. 2008). SEAPODYM uses a sub-model to predict the distribution of prey, which provides a habitat-quality index for tuna that varies by age class and species (Lehodey et al. 2010). This habitat is based on the distribution of simulated micronekton, which we here define as mobile and free-swimming macro-zooplankton, fish and squid species between ~10 and ~250 mm. Micronekton are classified into functional groups by their vertical habitat and diel migration pattern, with the spatio-temporal transfer of energy between them described using allometric scaling equations and ocean currents. The top predator model describes the age-structured spatial population of tunas across 4 distinct life stages (termed larval, juvenile, immature young and mature adult) and includes anthropogenic forcing in the form of effort and catch from multiple fisheries. Driving both models are ocean biophysical variables (temperature, currents, oxygen and primary production) that characterise the marine environment of predator dynamics (Lehodey & Senina 2009) and age-dependent accessibility functions describing the sub-model micronekton biomass available to top predators. SEAPODYM solves these internal models using advection-diffusion-reaction equations over a network of regularly spaced grid points and a discrete time step (e.g. 1° square × 1 mo), outputting predictions on the spatial dynamics of large pelagic predators (Lehodey et al. 2008, Senina et al. 2008). SEAPODYM can be optimised and parameterised for different marine predator species and regions (Abecassis et al. 2013, Dragon et al. 2014) or different exercises, such as climate change prediction (Senina et al. 2016).

For our region, SEAPODYM predictions were available on the distribution of biomass (g m^{-3}) for 3 tuna species: yellowfin tuna Thunnus albacares (YFT), bigeye tuna T. obesus (BET) and skipjack tuna Katsuwonus pelamis (SKJ). For each species we selected distributions of adult (ADU) and micronektonic (MIC) age classes, which vary spatially due to their differing access to prey, behaviour and density-dependent mortality representing cannibalism (Lehodey et al. 2008). Adult tuna are not shearwater prey. Therefore, we assume associations between wedge-tailed shearwaters and adult tuna represent facilitated foraging. Micronektonic tuna are between 1 and 3 mo old with fork lengths from ~30 mm up to ~100 mm (SKJ) and ~250 mm (YFT and BET) (Davies et al. 2014, Harley et al. 2014, Langley et al. 2014); wedge-tailed shearwater association with micronektonic tuna could represent direct predation of smaller individuals or facilitated foraging with larger individuals. We also selected SEAPODYM predictions under fished conditions to represent real-life tuna distributions, such as heavier long-lining effort closer to the Australian east coast (Trebilco et al. 2010).

To test our hypotheses we compiled 2 datasets at opposing spatio-temporal scales, the first was built with broad-scale, decadal-averaged data (hereafter termed the 'climatology' dataset/model), the second built with fine-scale, weekly averaged data (defined as high resolution and hereafter abbreviated as the ‘hi-res’ dataset/model; Fig. S1 in the Supplement at **www-int-res.com/articles/suppl/m123p456_supp.pdf**). The climatology dataset included BTY, distance to seamount (SMT), PRO, SST and tuna covariates from INTERIM parameterised SEAPODYM predictions (1° × 1 mo) for the month of March (SKJ: 1979–2010 average; BET and YFT: 1986–2010 average) (Table 1). The hi-res dataset included BTY, SMT, CHL, SST, SSTA, SSHA, EKM and tuna covariates from INDESO V2 parameterised SEAPODYM predictions (0.25° × 1 wk). Tuna data were not available for 2016, so hi-res models were constructed for 2014 and 2015 only.

Covariate extraction

To standardise climatology model covariate extraction we used a 0.1° grid, taking all pixels within the 50% UD core areas as presence and generating pseudo-absence pixels, defined as locations where absence is probable but uncertain, for logistical regression. Pseudo-absence pixels were randomly generated, at a rate of random 3:1 presence pixels, within a hypothetical maximum foraging range for each colony. The range was set at 1400 km from each colony (maximum distance observed in our data; Heron Island 2013), refined by removing land and areas beyond the species range, e.g. south of the sub-tropical front (del Hoyo et al. 1992). For hi-res models, we reclassified behaviour-classed tracking data for logistic regression, assigning foraging and resting locations as presences, as tropical seabirds can ‘drift forage’ (using a surface ‘sit-and-wait’ strategy; Conners et al. 2015), and transiting locations as absences. We extracted values from covariates for climatology and hi-res model locations using the package ‘raster’ (Hijmans 2016).

Multicollinearity and spatial autocorrelation

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

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

Statistical modelling

To test the influence of different broad-scale oceanographic and tuna covariates on selection of wedge-tailed shearwater core-area location, we used generalized linear models (GLM). GLMs had a binary response, treating core-area locations as 1 and total foraging range pseudo-absences as 0, and were constructed separately for Lord Howe and Heron Island. To test the effect of different high-resolution oceanographic and tuna covariates on the likelihood of wedge-tailed shearwater foraging, we used generalized linear mixed models (GLMM), fitted in package 'lme4' (Bates et al. 2015), with bird identity as the random intercept (Hamer et al. 2007, Grecian et al. 2016). GLMMs had a binary response, treating foraging or resting locations as 1 and transiting locations as 0, and were constructed separately for each year and colony (Lord Howe Island 2014, 2015 and Heron Island 2015). To effectively accommodate non-linearity, but not over-fit relationships, we permitted covariates in hi-res models to take either a linear or second-degree polynomial form. Model residuals and diagnostics were plotted and checked as per Zuur et al. (2009), and model terms were selected using both forwards and backwards selection based on likelihood ratio tests (χ^2) and confidence intervals (Bolker et al. 2009). Model explanatory power was evaluated by constructing receiver operating characteristic (ROC) curves (Hanley & McNeil 1982) and calculating the associated area under the ROC curve (AUC) in the package 'verification' (NCAR 2015). Goodness of fit was assessed for GLM using McFadden's pseudo R^2 (Azen & Traxel 2009) in the package 'pscl' (Jackman 2015) and assessed for GLMM split into marginal (variance explained by fixed effects) and conditional (variance explained by fixed + random effects) pseudo R^2 components (Nakagawa & Schielzeth 2013) in the package 'MuMIn' (Bartoń 2016).

RESULTS

Tracking data

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

PCA and collinearity

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

PCA of 13 covariates within the Heron Island 2015 hi-res dataset revealed that the first 2 principal components account for 56.3% of the variance in the data (PC1 = 33.9%, PC2 = 22.4%); PCA of the same covariates within the Lord Howe Island 2015 hi-res dataset revealed that the first 2 principal components account for 67.5% of the variance in the data (PC1 = 55.9%, PC2 = 11.6%); and PCA of the same covariates within the Lord Howe Island 2014 hi-res dataset revealed that the first 2 principal components account for 64.4% of the variance in the data (PC1 = 48.8%, PC2 = 15.6%) (Fig. 3). The hi-res ordinations again show consistent clustering of tuna covariates: the Lord Howe Island 2014 and 2015 PCAs show all tuna covariates correlated with PC1 (2014 Pearson's R^2 = 0.68 – 0.98, 2015 Pearson's R^2 = 0.7 – 0.94), and the Heron Island 2015 PCA shows lower correlation of all tuna with PC1 (Pearson's R^2 = 0.52 – 0.79) as PC2 appears to split tuna covariates into 2 clusters (Fig. 3).

Climatology models

At broad scales, wedge-tailed shearwaters from both colonies selected core areas, within their foraging range, that were closer to seamounts (Heron Island: $\chi^2_1 = 54.49$, $p < 0.001$, Lord Howe Island: $\chi^2_1 = 53.71$, $p < 0.001$; Table 3) and in deeper waters (Heron Island: $\chi^2_1 = 17.08$, $p < 0.001$, Lord Howe Island: $\chi^2_1 = 24.29$, $p < 0.001$). Primary productivity was negatively associated with the selection of core-area location for wedge-tailed shearwaters breeding on Heron Island: the model predicted that for every 100 mg C m^{-2} d^{-1} increase in primary productivity, an area is 12.16 times less likely to be selected as a core area by Heron Island shearwaters ($\chi^2_1 = 263.6$, $p < 0.001$; Fig. 4B). Primary productivity was not significant to selection of core-area location for wedge-tailed shearwaters breeding on Lord Howe Island ($\chi^2_1= 2.46$, $p = 0.117$). Each climatology model included 2 tuna covariates, one as a proxy for the major-tuna cluster (selected to have minimal correlation with non-tuna covariates) and the other which was uncorrelated with the major-tuna cluster. Micronektonic yellowfin (YFT_MIC) was the proxy and micronektonic bigeye (BET_MIC) the uncorrelated covariate in the Heron Island model, while micronektonic bigeye was the proxy and adult yellowfin (YFT_ADU) the uncorrelated covariate in the Lord Howe Island model (Fig. 2). The Heron Island climatology model predicted that for each additional 100 g m^{-2} of tuna biomass an area contains, it is 1.04 times more likely to be selected as a core area by wedge-tailed shearwaters if the tuna are micronektonic yellowfin ($\chi^2_1 = 14.81$, $p = 0.001$), and 2.06 times more likely to be selected if the tuna are micronektonic bigeye ($\chi^2_1 = 235.24$, $p < 0.001$). The Lord Howe Island climatology model predicted that for each additional 100 g m^{-2} of tuna biomass an area contains, it is 1.42 times more likely to be selected as a core area by wedge-tailed shearwaters if the tuna are micronektonic bigeye ($\chi^2_1 = 70.35$, $p = 0.001$; Fig. 4A), but 1.71 times less likely to be selected if the tuna are adult yellowfin ($\chi^2_1 = 15.39$, $p < 0.001$). Validation of Heron Island climatology model confirmed the final model fitted the data well (AUC = 0.97) and explained a good proportion of the variance (McFadden's $R^2 = 0.71$). Validation of Lord Howe Island climatology model confirmed the final model also fitted the data well (AUC = 0.98) and explained a similar proportion of the variance (McFadden's $R^2 = 0.75$).

Hi-res models

The likelihood of wedge-tailed shearwater foraging was not significantly influenced by bathymetry, and only shearwaters from Heron Island in 2015 were more likely to forage closer to seamounts (Table 4, Fig. 5E). Shearwaters from Lord Howe Island in 2014 were more likely to forage at higher chl a concentrations (Fig. 5L) while sea surface height anomalies influenced the likelihood of foraging in shearwaters from Heron Island in 2015 only (Fig. 5D). Ekman upwelling and sea surface temperature anomalies influenced likelihood of shearwater foraging in every instance (Table 4, Fig. 5). The proxy selected to represent the major-tuna cluster was micronektonic bigeye (BET_MIC) in the Heron Island 2015 model, adult skipjack tuna (SKJ_ADU) in the Lord Howe Island 2015 model and micronektonic yellowfin tuna (YFT_MIC) in the Lord Howe Island 2014 model (Fig. 3). Models predicted that for each additional 100 g m^{-2} of tuna biomass an area contains, shearwaters from Heron Island in 2015 were 1.3 times more likely to forage there (Table 4, Fig. 5C), shearwaters from Lord Howe Island in 2015 were 2.23 times more likely to forage there (Fig. 5H) and shearwaters Lord Howe Island in 2014 were 1.13 times more likely to forage there (Fig. 5K). Validation of the Heron Island 2015 model confirmed the final model fitted the data adequately (AUC = 0.79) and explained a good proportion of the variance (marginal $R^2 = 0.31$, conditional $R^2 = 0.47$). Validation of the Lord Howe 2015 model confirmed the final model also fitted the data adequately (AUC = 0.73) and explained a similar proportion of the variance (marginal $R^2 = 0.29$, conditional $R^2 = 0.51$). Validation of the Lord Howe 2014 model confirmed the final model fitted the data identically (AUC = 0.73) but explained a smaller proportion of the variance (marginal R^2 = 0.17, conditional R^2 = 0.30).

DISCUSSION

Wedge-tailed shearwater distributions and oceanography

Our results show that the long-trip destinations of wedge-tailed shearwaters breeding on Heron Island lie predominantly to the northeast of the colony in the Coral Sea, adding support for consistent use of this area over multiple years (McDuie et al. 2015). Our results also show, for the first time, that during chick-rearing, wedge-tailed shearwaters from Lord Howe Island undertake long trips to predominantly different regions in different years. In 2014 and 2016, wedge-tailed shearwater long-trip destinations were distributed west of Lord Howe Island in the Tasman Sea over the Tasmantid Seamounts that run parallel to the east Australian shelf, while in 2015, long-trip destinations were predominately far to the north of Lord Howe Island in the Coral Sea, almost overlapping with conspecifics foraging from Heron Island. Whether long trips at Lord Howe Island are undertaken as part of a coordinated dual-foraging strategy similar to that observed at Heron Island (Congdon et al. 2005), or more opportunistically, is currently unknown. However, these results demonstrate that the unimodal foraging strategy observed by Peck & Congdon (2005) at Lord Howe Island during early chick-rearing appears to alter in the later stages of chick-rearing (Jakubas et al. 2014) and/or between breeding seasons (Granadeiro et al. 1998).

Our results show that both wedge-tailed shearwater populations selected core areas in deep pelagic waters that were close to seamounts; these findings mirror those of other studies into the species' bathymetric preferences (Catry et al. 2009, McDuie et al. 2015, McDuie & Congdon 2016). At fine spatial scales, wedge-tailed shearwaters from Heron Island in 2015 were more likely to forage close to seamounts, but bathymetry and seamounts did not influence conspecifics foraging from Lord Howe Island. These results indicate that marine topography may be used by wedge-tailed shearwaters to locate profitable foraging areas at broad but not fine spatial scales. Fine-scale foraging behaviour is likely to be triggered by sea surface temperature anomalies and Ekman upwelling, which influenced the likelihood of foraging in all models. Collectively, these 2 dynamic covariates identify frontal areas of water mixing and associated upwelling and downwelling. Our results are consistent with those of other studies that indicate that these dynamic phenomena are major mechanisms of prey aggregation for seabirds in lower latitude waters (Spear et al. 2001, Hyrenbach et al. 2006, Weimerskirch et al. 2010, McDuie & Congdon 2016).

Tuna relationships

We found tuna distributions to influence wedge-tailed shearwater core-area location and likelihood of foraging in every instance, supporting both our broad-scale and fine-scale hypotheses. This means that wedge-tailed shearwaters sought out areas of increased tuna biomass, which at the regional scale are relatively stable between years, and that they home in on aggregations of tuna for foraging at fine scales. Our results describe the importance of facilitated foraging opportunities in 2 seabird populations and are expressed in an ecologically meaningful way, i.e. using tuna density increases of 100 g m^{-2}, interpretable as the weight of one micronektonic tuna (165 mm long; Harley et al. 2014), or a large meal for a wedge-tailed shearwater. For example, we predict that in 2015, for every additional micronektonic tuna encountered per square metre of ocean, it was 2.23 times more likely that wedge-tailed shearwaters from Lord Howe Island would forage there and 1.3 times more likely that conspecifics from Heron Island would forage there. Such predictions demonstrate the potential of our approach to quantify facilitated foraging opportunities. However, they also come with the caveat that they are only as accurate as the underlying modelled tuna distributions.

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

Only in the Heron Island climatology model did shearwaters associate with a micronektonic tuna (bigeye) outside of the major-tuna cluster. Even small micronektonic tuna are proficient swimmers (Graham et al. 2007) and it is unlikely that wedge-tailed shearwaters from these colonies possess the diving ability (maximum recorded dive depth of 12 m; Peck & Congdon 2006) to capture them without subsurface predator assistance during the day. This suggests that subsurface predators not considered in our models, such as cetaceans (Au & Pitman 1986), billfish (Family: Istiophoridae) or dolphinfish Coryphaena hippurus (Young et al. 2010b), also facilitate wedge-tailed shearwater foraging in this region.

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

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

Effect of productivity gradient on long-trip destinations

We found that the tropical wedge-tailed shearwater population did not adhere to the ‘temperate long-trip model’ by seeking out areas of high primary productivity, but instead targeted regions of high tuna biomass. The subtropical population at times adhered to the ‘temperate long-trip model’ but also targeted tuna. The Heron Island results are consistent with wedge-tailed shearwater non-breeding preferences, where birds exploit warm, oligotrophic waters in the Indian (Catry, et al. 2009) and Pacific Oceans (McDuie & Congdon 2016) when freed from the need to central-place forage. Our results also support the suggestion of a temporal and spatial decoupling between satellite surface-measured primary productivity and micronekton/tuna aggregation in tropical oceans (Lehodey et al. 1998, McDuie & Congdon 2016).

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

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

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Table 1. Summary of oceanographic and tuna covariates used in the broad- and fine-scale models. BET: bigeye tuna Thunnus obesus; YFT: yellowfish tuna T. albacares; SKJ: skipjack tuna Katsuwonus pelamis; ADU: adult; MIC = micronektonic

Covariate (units)	Abbreviation	Temporal resolution	Spatial resolution	Data source (provider)
High resolution dynamic covariates				
Chlorophyll a concentration (mg m^{-3})	CHL	8 d	4 km	MODIS & VIIRS (NASA)
Sea surface temperature (°C)	SST	8 & 1 d	0.1° & 0.25°	POES & AVHRR (NOAA)
Sea surface temperature anomaly (°C)	SSTA	8 & 1 d	0.1° & 0.25°	POES AVHRR (NOAA)
Sea surface height anomaly (m)	SSHA	1 d	0.083°	HYCOM & NCODA (NRL)
Ekman upwelling (m d^{-1})	EKM	1 d	0.25°	Metop ASCAT
Climatology and static covariates				
Primary productivity (mg C m^{-2} d^{-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 d	0.25°	INDESO V2 Fished (SEAPODYM) (unavailable in 2016)
Tuna monthly biomass distribution (g m^{-2})	BET_ADU, BET_MIC,	Monthly (30 yr mean)	1°	INTERIM Fished (SEAPODYM)

YFT_ADU, YFT_MIC, SKJ_ADU, SKJ_MIC

Table 2. Summary of wedge-tailed shearwater GPS and platform terminal transmitter (PTT; *) tracked long trips collected during the study. The core area is the 50% utilization distribution from kernel analysis of each tracking dataset.

Island Colony	Year	No. of 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

Table 3. Climatology logistical regression models of wedge-tailed shearwater presence–absence against broad-scale oceanographic and tuna covariates. The following coefficients (β) and SE are expressed in terms of a 100 unit change: tuna covariates (100 g m^{-2}), seamount distance (100 km) and bathymetry (100 m). All covariates have significance $p < 0.001$. Core-area and foraging range covariate values are expressed as means ± SD

Colony	Covariate	β ± SE	Core area	Foraging range
Heron Island				
	Intercept	1.195 ± 1.304		
	Productivity (mg C m^{-2} d^{-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 (km)	–1.169 ± 0.176	84.56 ± 45.07	168.10 ± 144.98
	Bathymetry (m)	0.048 ± 0.010	3429 ± 1069	2772 ± 1359
	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		

Table 4. Hi-res logistical regression models of wedge-tailed shearwater probability of foraging against fine-scale oceanographic and tuna covariates. The strength (χ^2) and effect direction of each covariate are given for each of the 3 colony–year models. Covariates with significance $p < 0.01$ are shown in bold and the corresponding effect given; NA indicates that the covariate was not included in a model due to multicollinearity. Positive and negative effect directions are denoted by ↑ and ↓ respectively, and in the case of a polynomial relationship the value at which foraging is most or

least (denoted by *) likely is given. For coefficient (β) and SE values, see Table S1 in the Supplement at www-int-res.com/articles/suppl/m123p456_supp.pdf

	Heron Island 2015		Lord Howe Island 2015		Lord Howe Island 2014	
Covariate	Effect	Strength (χ^2)	Effect	Strength (χ^2)	Effect	Strength (χ^2)
Bathymetry (m)		0.40		3.80		NA
Seamount distance (km)	↓	**38.77**		0.80		0.04
Chlorophyll a concentration (mg m^{-3})		NA		NA	↑	**9.67**
Ekman upwelling (m d^{-1})	**0.22**	**16.83**	**–0.43***	**65.61**	**0.67***	**48.91**
Sea surface temperature anomaly (°C)	↑	**29.46**	**–0.17**	**101.77**	↓	**6.57**
Sea surface height anomaly (m)	**0.62**	**33.27**		NA		3.27
Tuna biomass (g m^{-2})	↑	**26.07**	↑	**230.21**	↑	**66.14**

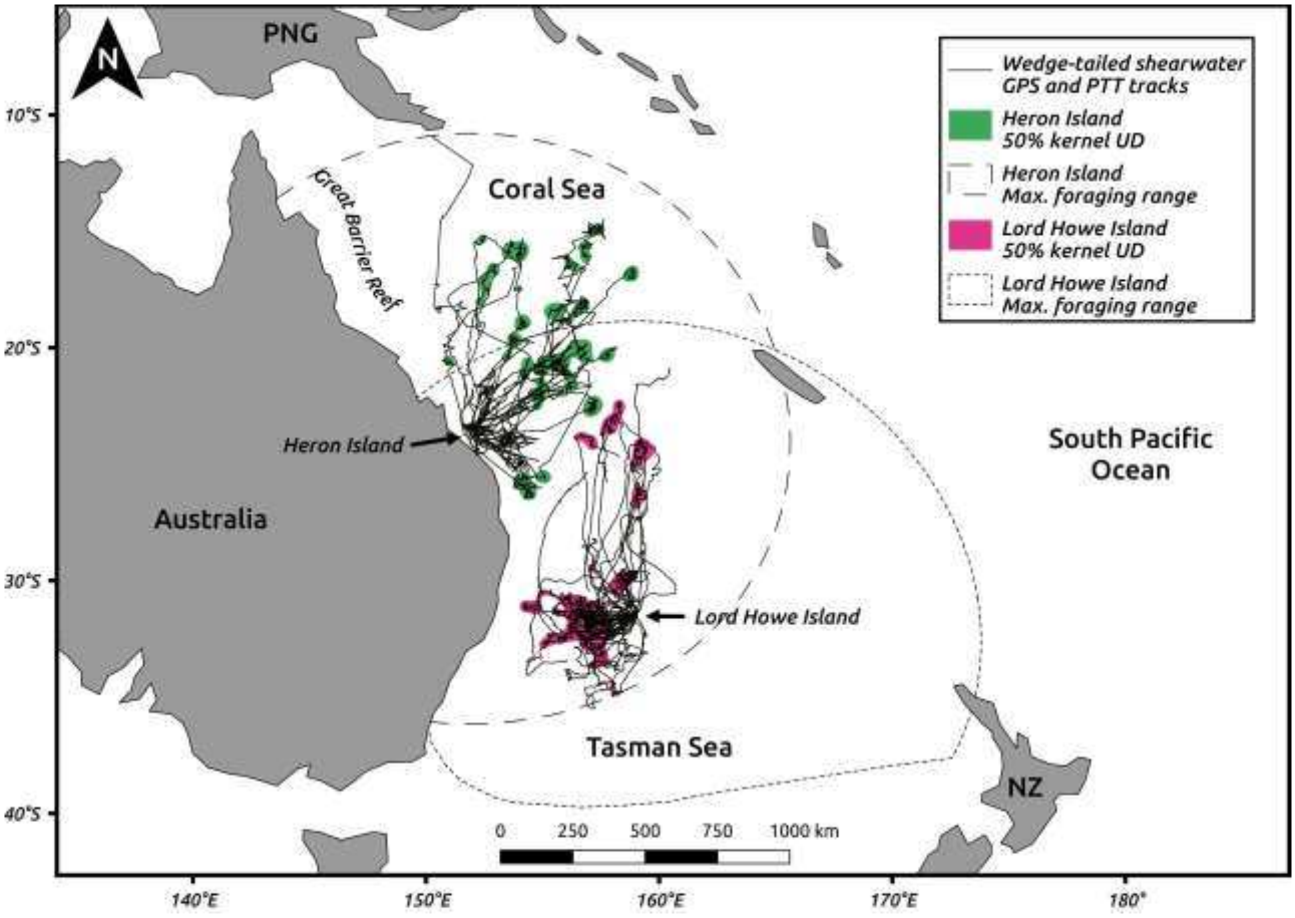

Fig. 1. Wedge-tailed shearwater long-trip tracking data collected from birds rearing chicks on Heron Island and Lord Howe Island between 2011 and 2016, overlaid with 50% kernel utilisation distribution (UD) core-use areas for each colony

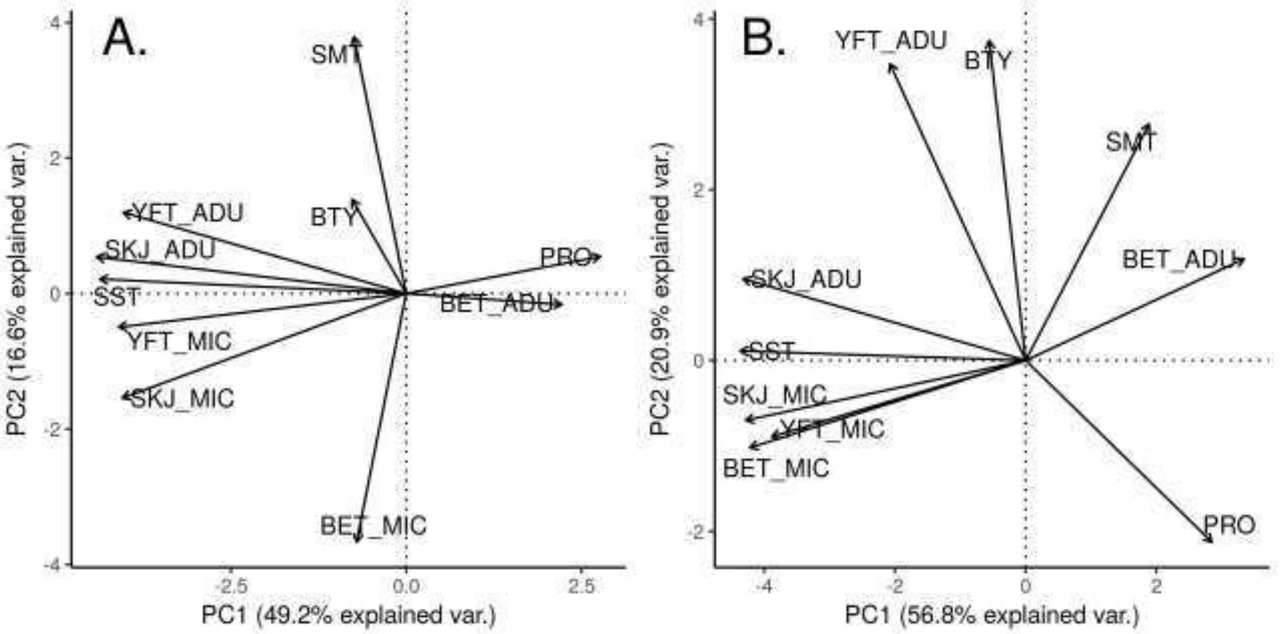

Fig. 2. Ordination from principal components analysis of broad-scale oceanographic and tuna covariates used in climatology models of wedge-tailed shearwaters breeding from (A) Heron Island, and (B) Lord Howe Island. YFT: yellowfin tuna Thunnus albacares; BET: bigeye tuna T. obesus; SKJ: skipjack tuna Katsuwonus pelamis; ADU: adult; MIC: micronekton; BTY: bathymetry; PRO: primary productivity; SMT: distance to seamount; SST: sea surface temperature

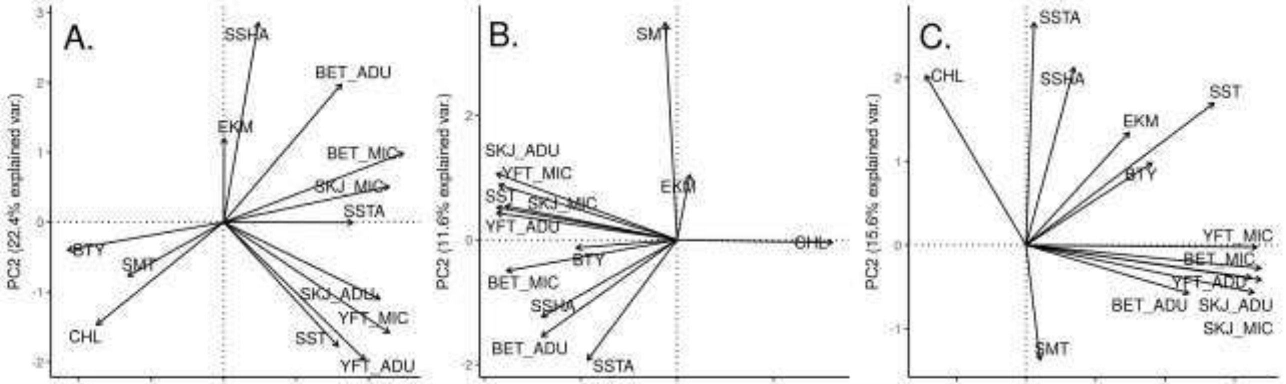

Fig. 3. Ordination from principal components analysis of fine-scale oceanographic and tuna covariates used in hi-res models of wedge-tailed shearwaters tracked with GPS from (A) Heron Island in 2015, (B) Lord Howe Island in 2015 and (C) Lord Howe Island in 2014. YFT: yellowfin tuna Thunnus albacares; BET: bigeye tuna T. obesus; SKJ: skipjack tuna Katsuwonus pelamis; ADU: adult; MIC: micronekton; BTY: bathymetry; CHL: chl a concentration; EKM: Ekman upwelling; PRO: primary productivity; SMT: distance to seamount; SSHA: sea surface height anomaly; SST: sea surface temperature; SSTA: sea surface temperature anomaly

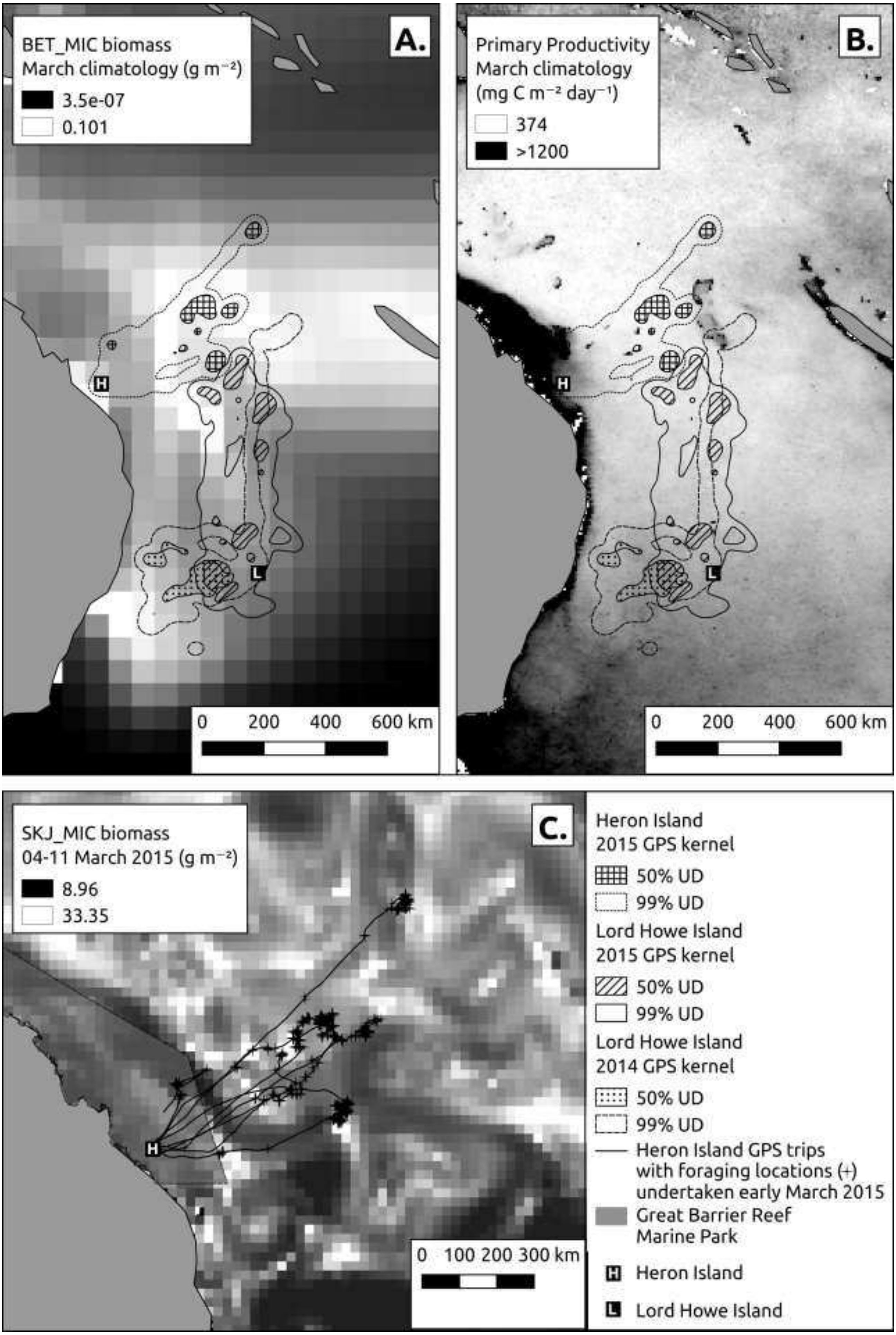
A.
BET_MIC biomass
March climatology (g m⁻²)
3.5e-07
0.101
H
L
0 200 400 600 km
B.
Primary Productivity
March climatology
(mg C m⁻² day⁻¹)
374
>1200
H
L
0 200 400 600 km
C.
SKJ_MIC biomass
04-11 March 2015 (g m⁻²)
8.96
33.35
H
0 100 200 300 km
Heron Island
2015 GPS kernel
50% UD
99% UD
Lord Howe Island
2015 GPS kernel
50% UD
99% UD
Lord Howe Island
2014 GPS kernel
50% UD
99% UD
Heron Island GPS trips
with foraging locations (+)
undertaken early March 2015
Great Barrier Reef
Marine Park
Heron Island
Lord Howe Island

Fig. 4. GPS tracking data of breeding wedge-tailed shearwaters shown as (A) kernel utilisation distributions (UDs) overlaying SEAPODYM-predicted long-term mean micronektonic bigeye tuna biomass for March, (B) kernel UDs overlaying long-term mean primary productivity for March, and (C) individual foraging trips from Heron Island overlaying SEAPODYM-predicted weekly micronektonic skipjack tuna biomass

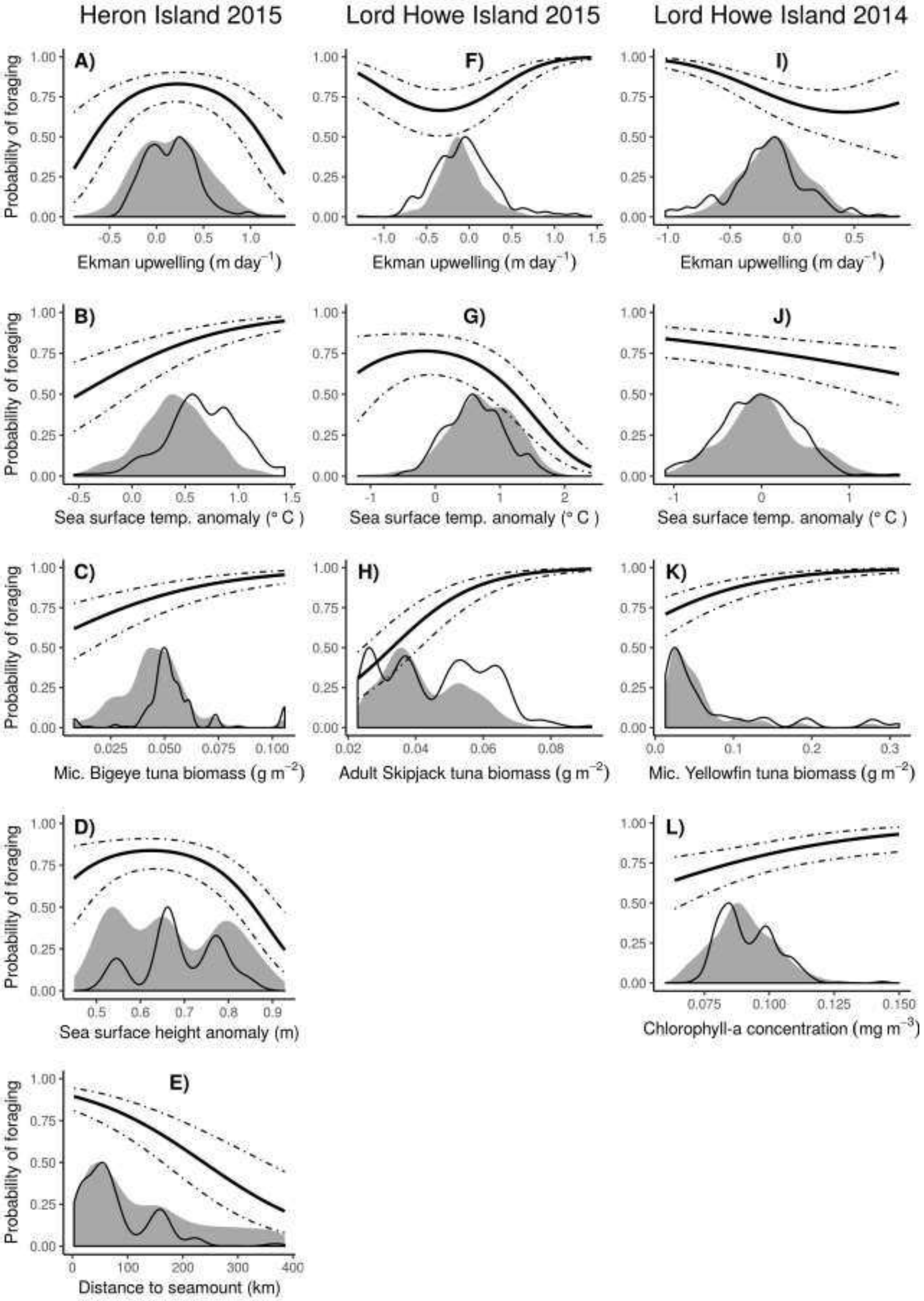
Heron Island 2015
Lord Howe Island 2015
Lord Howe Island 2014
Probability of foraging
0.00
0.25
0.50
0.75
1.00
A)
Ekman upwelling (m day^{-1})
-0.5
0.0
0.5
1.0
F)
Ekman upwelling (m day^{-1})
-1.0
-0.5
0.0
0.5
1.0
1.5
I)
Ekman upwelling (m day^{-1})
-1.0
-0.5
0.0
0.5
B)
Sea surface temp. anomaly (° C)
-0.5
0.0
0.5
1.0
1.5
G)
Sea surface temp. anomaly (° C)
-1
0
1
2
J)
Sea surface temp. anomaly (° C)
-1
0
1
C)
Mic. Bigeye tuna biomass (g m^{-2})
0.025
0.050
0.075
0.100
H)
Adult Skipjack tuna biomass (g m^{-2})
0.02
0.04
0.06
0.08
K)
Mic. Yellowfin tuna biomass (g m^{-2})
0.0
0.1
0.2
0.3
D)
Sea surface height anomaly (m)
0.5
0.6
0.7
0.8
0.9
L)
Chlorophyll-a concentration (mg m^{-3})
0.075
0.100
0.125
0.150
E)
Distance to seamount (km)
0
100
200
300
400

Fig. 5. Mean (solid line) and 95% confidence interval (dot-dashed line) predictions of wedge-tailed shearwater foraging probability in relation to fine-scale tuna and oceanographic covariates. Density plots are overlaid showing the distributions of foraging (black line) and non-foraging (grey shading) samples for each covariate. Mic.: micronektonic tuna age classes