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Waggitt, James; Cazenave, Pierre W.; Evans, Peter; Howarth, Leigh; Van der Kooij, Jeroen; Hiddink, Jan

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Combined measurements of prey availability explain habitat-selection in foraging seabirds

James J Waggitt [1]; Pierre W Cazenave [2]; Leigh M Howarth [1]; Peter G H Evans [1,4]; Jeroen van der Kooij [5]; Jan G Hiddink [1]

[1] School of Ocean Sciences, Bangor University, Menai Bridge LL59 5AB, UK
[2] Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, UK
[4] Sea Watch Foundation, Ewyn Y Don, Bull Bay, Amlwch LL68 9SD, UK
[5] Centre for Environment, Fisheries and Aquaculture Science, Lowestoft NR33 0HT, UK

Abstract

Understanding links between habitat characteristics and foraging efficiency help to predict how environmental change could influence populations of top-predators. This study examines whether measurements of prey (clupeids) availability varied over stratification gradients, and determined if any of those measurements coincided with aggregations of foraging seabirds (common guillemot *Uria aalge*, Manx shearwater *Puffinus puffinus*) in the Celtic Sea, UK. The probability of encountering foraging seabirds was highest around fronts between mixed and stratified water. Prey were denser and shallower in mixed water, and encounters with prey most frequent in stratified water. Therefore, no single measurement of increased prey availability coincided with the location of fronts. However, when considered in combination, overall prey availability was highest in these areas. These results show that top-predators may select foraging habitats by trading-off several elements of prey availability. By showing that top-predators select areas where prey are switching between behaviours, these results also identify a mechanism that could explain the wider importance of edge habitats for these taxa. As offshore developments (e.g. marine renewable energy installations) change patterns of stratification, their construction may have consequences on the foraging efficiency of seabirds.

Key Words. Foraging efficiency; stratification; fronts; edge habitats; marine renewable energy installations

1. Introduction

It is important to understand how environmental changes could influence populations through changes in reproductive and survival rates. For many animals, foraging efficiency is a major component in their ability to raise offspring and prolong their lifespan [1]. To maximise foraging efficiency, animals should increase their consumption of resources, whilst reducing the energy spent locating and capturing these resources [1]. For diving seabirds exploiting shoaling fish, their consumption of resources is related to prey density [2], whereas the energy spent locating and capturing these resources can be divided into two components: the horizontal distance flown to locate prey, and the vertical distance dived to access prey [3]. Therefore, favourable habitats would contain dense, shallow and prevalent prey. As the behaviour of shoaling fish is strongly influenced by their surrounding environment [4,5], identifying which prey behaviour(s) are selected by seabirds is important for assessing impacts of environmental change on their foraging efficiency.

Interactions between currents and bathymetry are influential processes in shallow seas [6]. Turbulent energy originating from interactions between strong currents and shallow seabeds generally results in vertical mixing, with relatively similar chemical and physical properties persisting across depths. By contrast, combinations of slower currents and deeper seabeds often result in vertical stratification, with chemical and physical properties differing greatly between lower and upper depths. The latter is most evident during the heating of surface waters in springtime, resulting in vertical temperature gradients. The abundance of foraging seabirds is often related to measures of stratification [7,8], in particular fronts at the interface of mixed and stratified water [9]. However, without multiple-measurements of prey availability (shoal density, depth and encounter rates) across stratification gradients, it is difficult to explain its importance in habitat-selection. Quantifying prey availability across stratification gradients, and then understanding which measurement(s) of prey availability are selected by seabirds, would also to help to assess whether changes in stratification patterns could influence their foraging efficiency.

The Celtic Sea in the UK is characterised with strong gradients in stratification, owing to considerable variations in tidal currents and depths. Within the Celtic Sea, shoaling fish in the clupeid family (sprat *Sprattus sprattus*, herring *Clupea harengus* and sardine *Sardina pilchardus*) are important components of common guillemot *Uria aalge* and Manx Shearwater *Puffinus puffinus* diet, which breed in large numbers on the neighbouring

Pembrokeshire coastline [10,11]. This study uses concurrent measurements on foraging common guillemots, foraging Manx shearwaters and clupeids to test: (1) whether measurements of prey availability varied across stratification gradients, and (2) which measurement(s) of prey availability coincided with aggregations of foraging seabirds?

2. Material and Methods

The research vessel Prince Madog surveyed seven transects across the northern Celtic Sea (Fig. 1) at approximately 10 kt over 8 days between April 5th and 20th 2016. The study period coincided with the spring bloom, and enhanced levels of primary productivity in the region [12]. A stratification index (Hunter-Simpson parameter, $SI = log_{10}(h/u^3)$, where h is the water depth and u is the maximum depth-averaged current speed) was calculated across the study area. Current speeds (ms^{-1}) represented maximum values between April 1st and 31st 2016, and were sourced from an existing hydrodynamic model [13]; seabed depth (m) was sourced from EMODnet (http://www.emodnet-hydrography.eu/). Before calculations of *SI*, current speed and depth were transposed onto a 1 km orthogonal grid using kriging interpolation. Kriging was performed in the 'automap' package [14] in R (version 3.2.5, R Development Core Team, 2016) . The position of the front was identified by *SI* values of approximately 1.9 log_{10} m^{-2} s^3 (Fig. 1) [6].

The presence/absence of foraging seabirds and measurements of prey availability were quantified at 1-minute intervals during transects. Seabirds were recorded using human observations and a strip-transect survey. A single observer counted all foraging seabirds up to 300m on one-side of the vessel, which was alternated to avoid looking into strong winds or sunlight [15]. As seabirds rest between feeding bouts [16], foraging seabirds included those actively diving/searching and also those sitting on the sea surface. Non-foraging seabirds were those transiting through the area or following the research vessel. Common guillemots and Manx shearwaters were the most frequently encountered species (50 and 15% of sightings, respectively). Prey were recorded using a calibrated Simrad EK60 split-beam echosounder operating at 38 and 120 kHz. A series of existing algorithms were applied to identify the backscatter associated with clupeids [17]. The resulting echograms were integrated over 5 m depth bins. Three measurements of prey availability were calculated: (1) prey density, represented by the mean value of Nautical Area Scattering Coefficient (NASC) among depth bins; (2) the minimum depth of prey, which was expressed as a negative number; (3) the presence or absence of prey. Higher values of shoal size, shoal depth and frequency of shoal encounters were deemed to represent greater availability to foraging seabirds (dense, shallow and prevalent prey).

Relationships between seabirds, prey availability and *SI* were quantified using a series of generalized linear (GLM) and generalized linear mixed effect models (GLMM). For models focussing on seabirds, sea state (Beaufort scale) and distance to breeding colony (Km) were included as explanatory variables due to higher detections of seabirds in calmer weather and near nests, respectively. With the exception of models focussing on prey depth, distance covered (km) per minute was included as a statistical offset due the increased likelihood of encountering seabirds/prey when travelling faster. Detailed information on model setup and performance are provided in the supplementary material.

Predicted variations in foraging seabirds and prey availability across *SI* gradients were calculated from model parameters. An effect size (ES) was provided for each of these calculations by dividing the maximum by the minimum predicted value; therefore, quantifying the relative change across *SI* gradients. Predictions focussed on *SI* values between 1 and 2.5, where the vast majority of surveys were performed (98% of the time). A combined measurement of prey availability across *SI* gradients was then calculated from these predictions. To do so, predictions of prey density, prey depth and the probability of encountering prey were first mean-centered to make them directly comparable. The combined measurement of prey availability for a given *SI* value was then represented by the minimum of these three predictions. By using the minimum rather than the mean, this approach identified habitats where prey was relatively dense, shallow and prevalent. Analyses were performed using the 'mgcv' package [18] in R (version 3.2.5, R Development Core Team, 2016).

3. Results

As expected, the probability of encountering foraging common guillemots ($\chi^2 = 17.02$, $p < 0.01$) and Manx shearwaters ($\chi^2 = 10.32$, $p < 0.01$) was highest around the front (Fig. 2). Effect sizes revealed a considerably stronger association for Manx shearwaters (*ES* = 135.05) than common guillemots (*ES* = 5.58). Measurements of prey availability also showed significant relationships with *SI*. However, relationships differed among prey behaviours (Fig. 2). The probability of encountering prey was significantly higher in stratified water (χ^2 =

7.83, p = 0.02), whereas prey density (χ^2 = 9.44, p < 0.01) and prey depth (χ^2 = 13.89, p<0.01) was significantly larger and shallower in slightly mixed water, respectively. Effect sizes were similar for prey density (*ES* = 2.41), prey depth (*ES* = 1.86) and encounters with prey (*ES* = 2.51). In isolation, measurements of prey availability were considered moderate at the front. However, the combined measurement of prey availability was highest in this area i.e. coinciding with aggregations of foraging seabirds (Fig. 2). Additional statistical outputs (distance to colony, sea state) are provided in the supplementary material.

4. Discussion

Prey availability is an important factor governing the habitat-selection of top-predators [1]. However, few studies establish connections between habitat characteristics, measurements of prey availability, and the presence of marine top-predators [5,19,20]. Consequently, it is difficult to explain associations between marine top-predators and habitat characteristics. By showing differences in prey availability across stratification gradients, this study provides insights into associations between foraging seabirds and stratification [7,8]. In the northern Celtic Sea, it seems that foraging seabirds did not favour any single aspect of prey behaviour, but traded-off several aspects when selecting optimal habitats within their range. However, the scarcity of foraging seabirds in areas with particularly low prey prevalence suggests that prey encounters are a limiting factor in habitat selection. In combination, these results show that prey availability needs treating as a multi-dimensional measurement when assessing the habitat-selection of top-predators [19].

Edges at the interface of contrasting habitats are often important for top-predators [21]. This generally holds true for marine top-predators; fronts between mixed and stratified water usually support dense aggregations of foraging seabirds, believed to result from enhanced primary production and the subsequent attraction of shoaling fish [9]. This study found no evidence for denser prey at fronts. However, it did find prey behaviour differing on either side of the front. Prey aggregated at shallower depths in mixed water, whereas prey dispersed at deeper depths in stratified water. This result suggests that the importance of edges for top-predators is also explained by the transitional behaviour of prey moving between habitats. For instance, a lack of cohesion in clupeid shoals changing in size and depth may increase their vulnerability to predation [2].

It is possible that seabirds target previously productive habitats, which no longer contains favourable foraging opportunities on their return [22]. In which case, arguments for trade-offs between prey availability and transitional behaviours cannot hold true. However, top-predators repeatedly exploit fronts, suggesting that they provide favourable and persistent foraging opportunities [9]. Moreover, the location and physical properties of fronts are also consistent in time and space [6]. Therefore, it seems likely that variations in prey availability and seabird presence recorded across *SI* during surveys are representative of longer periods.

The increasing numbers of marine renewable energy installations (MREI) are expected to change stratification patterns across expansive areas, either directly through the exploitation of currents [23] or by creating turbulent energy [13] For instance, an array of ~2800 tidal stream turbines in the Pentland Firth, UK may reduce current speeds by upto 15% in the surrounding region [23]. Studies investigating the potential impacts of environmental change on seabirds generally focus on prey abundance [24]. Following the findings of this study, it is recommended that changes in prey availability also need consideration.

Ethics

There were no ethical issues with this work.

Data Accessibility

Data are archived in the Dryad digital repository at https://datadryad.org/review?doi=doi:10.5061/dryad.7gj5781.[25].

Authors Contributions

J.J.W. conceived the study, performed seabird observations, conducted statistical analysis and wrote the manuscript; L.M.H. and J.G.H. organised research cruises; P.W.C. provided hydrodynamic model outputs; J.V.K. processed the echosounder data; P.W.C, L.M.H, P.G.H.E, J.V.K and J.G.H. edited the manuscript. All authors approved the final version of the manuscript, and agree to be held accountable for the content therein.

Competing Interests

The authors declare no competing interests.

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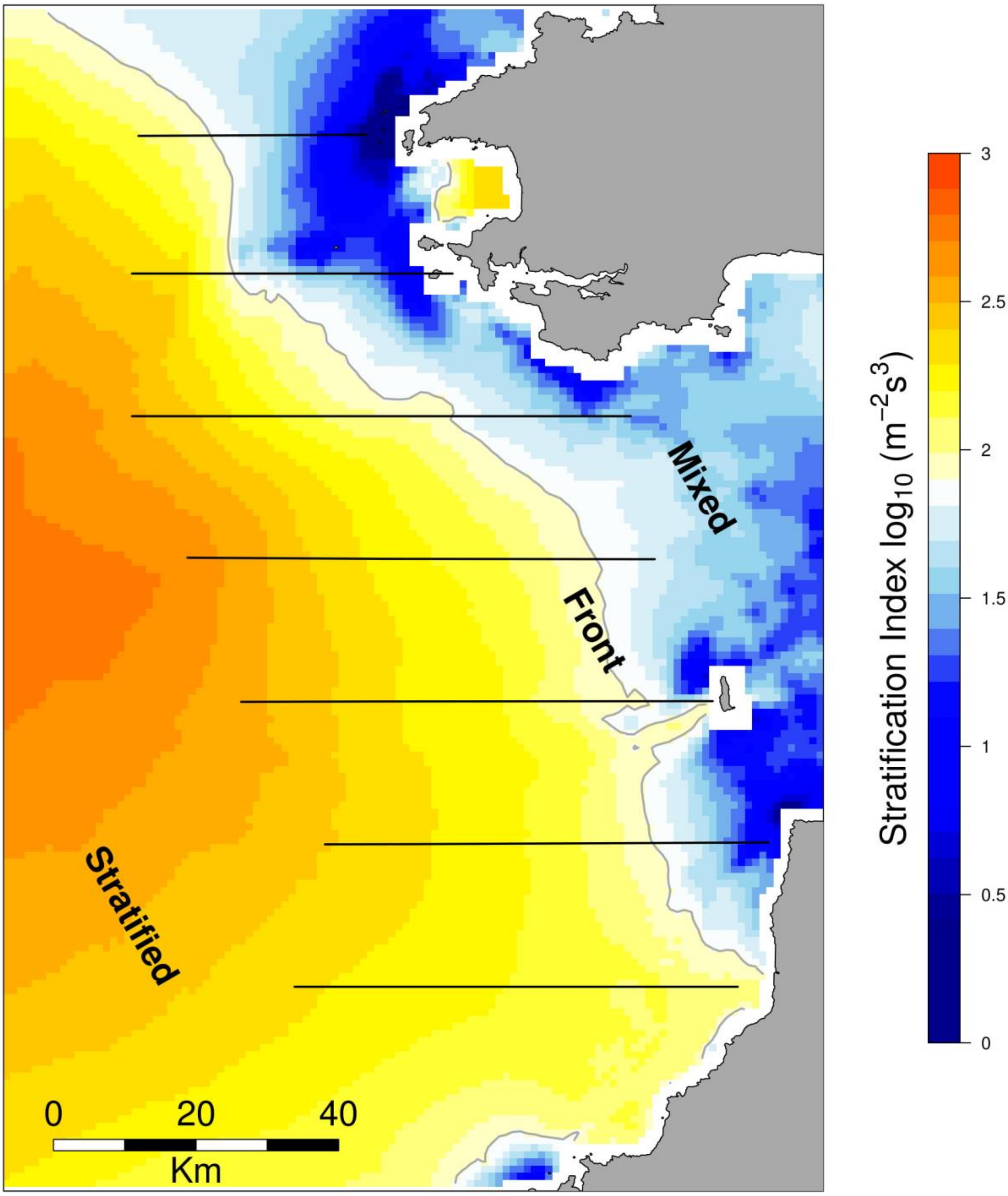

Figure 1. The study area and spatial variation in values of the stratification index in the northern Celtic Sea, UK. Areas of mixed and stratified areas are indicated, and the position of the tidal front is shown with a grey line. The transect lines are shown with a black line.

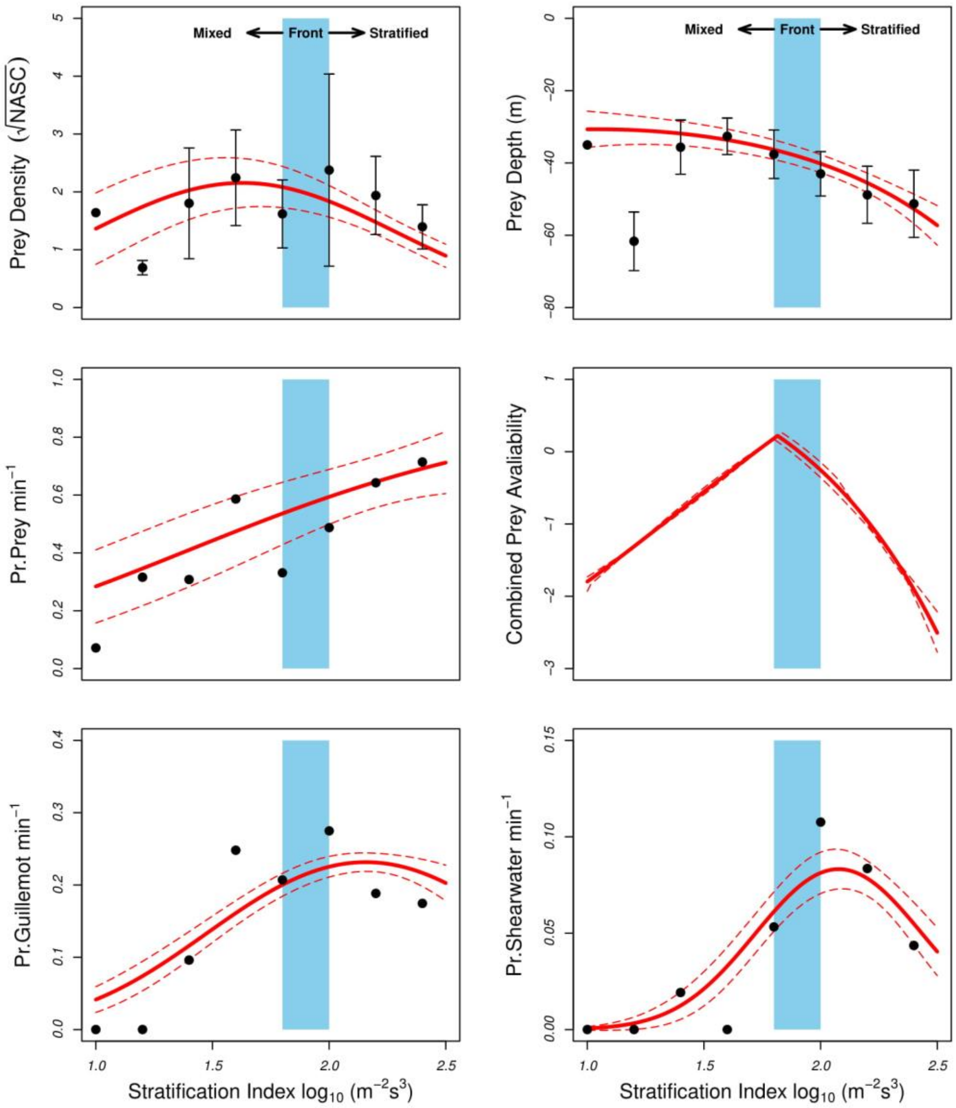

Figure 2. Variations in predicted values of prey density, probability of encountering prey minimum depth of prey, combined measurements of prey availability, the probability of encountering a foraging common guillemot *Uria aalge*, and the probability of encountering a foraging Manx shearwater *Puffinus puffinus* across stratification gradients. Recorded values are presented as summaries of values per 0.2 increments in stratification gradients. Solid red lines represent predicted values; dashed red lines represent standard errors in predicted values; black points represent recorded values; black error-bars represent standard deviation of recorded values. Predicted values were calculated using parameter estimation from a series of generalized linear (GLM) and generalized linear mixed effect models (GLMM)

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