

2018-11-15

# Oceanographic drivers of marine mammal and seabird habitat-use across shelf-seas: A guide to key features and recommendations for future research and conservation management

Cox, SL

<http://hdl.handle.net/10026.1/11734>

---

10.1016/j.ecss.2018.06.022

Estuarine, Coastal and Shelf Science

Elsevier

---

*All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.*

1 **Oceanographic drivers of marine mammal and seabird habitat-use across shelf-**  
2 **seas: A guide to key features and recommendations for future research and**  
3 **conservation management**

4 Cox, SL<sup>12+\*</sup>, Embling, CB<sup>1</sup>, Hosegood, PJ<sup>2</sup>, Votier, SC<sup>3</sup> and Ingram, SN<sup>1</sup>

5 <sup>1</sup>Marine Vertebrate Research Unit, University of Plymouth, Plymouth, PL4 8AA, UK

6 <sup>2</sup>Marine Physics Research Group, University of Plymouth, Plymouth, PL4 8AA, UK

7 <sup>3</sup>Environment and Sustainability Institute, University of Exeter, Penryn, TR10 9FE, UK

8 <sup>+</sup>Current address: UMR MARBEC SÈTE, Avenue Jean Monnet, CS 30171, 34203, Sète, FRANCE.

9 \*Corresponding author: slcox417@gmail.com (+33-04-99-57-32-48)

10 **ABSTRACT**

11 Mid-latitude (~30-60°) seasonally stratifying shelf-seas support a high abundance and diversity of  
12 marine predators such as marine mammals and seabirds. However, anthropogenic activities and  
13 climate change impacts are driving changes in the distributions and population dynamics of these  
14 animals, with negative consequences for ecosystem functioning. Across mid-latitude shelf-seas,  
15 marine mammals and seabirds are known to forage at a number of oceanographic habitats that  
16 structure the spatio-temporal distributions of prey. Knowledge of these and the bio-physical  
17 mechanisms driving such associations are needed to improve marine management and policy. Here,  
18 we provide a concise and easily accessible guide for both researchers and managers of marine systems  
19 on the predominant oceanographic habitats that are favoured for foraging by marine mammals and  
20 seabirds across mid-latitude shelf seas. We (1) identify and describe key discrete physical features  
21 present across the continental shelf, working inshore from the shelf-edge to the shore line, (2) provide  
22 an overview of findings relating to associations between these habitats and marine mammals and

23 seabirds, (3) identify areas for future research and (4) discuss the relevance of such information to  
24 conservation management. We show that oceanographic features preferentially foraged at by marine  
25 mammals and seabirds include shelf-edge fronts, upwelling and tidal-mixing fronts, offshore banks  
26 and internal waves, regions of stratification, and topographically complex coastal areas subject to  
27 strong tidal flow. Whilst associations were variable across taxa and through space and time, in the  
28 majority of cases interactions between bathymetry and tidal currents appear to play a dominant role,  
29 alongside patterns in seasonal stratification and shelf-edge upwelling. We suggest that the ecological  
30 significance of these bio-physical structures stems from a capacity to alter the densities, distributions  
31 (both horizontally and vertically) and behaviours of prey in a persistent and/or predictable manner  
32 that increases accessibility for predators, and likely enhances foraging efficiency. Future  
33 conservation management should aim to preserve and protect these habitats. This will require  
34 adaptive and holistic strategies that are specifically tailored to the characteristics of an oceanographic  
35 feature, and where necessary evolve through space and time. Improved monitoring of animal  
36 movements and bio-physical conditions across shelf-seas would aid in achieving this. Areas for  
37 future research include multi- disciplinary/trophic studies of the mechanisms linking oceanographic  
38 habitats, prey and marine mammals and seabirds (which may also elucidate the importance of lesser  
39 studied features such as bottom fronts and Langmuir circulation cells), alongside a better  
40 understanding of how predators perceive their environment and develop foraging strategies during  
41 immature/juvenile stages. Estimates of the importance of bio-physical processes at a population level  
42 should also be obtained. Such information is vital to ensuring the future health of these complex  
43 ecosystems, and can be used to assess how anthropogenic activities and changes in the environment  
44 will impact the functioning and spatio-temporal dynamics of these bio-physical features and their use  
45 by marine predators.

46 **KEYWORDS: Habitat selection · Foraging ecology · Bio-physical coupling · Conservation**  
47 **management · Marine mammals · Oceanography · Seabirds**

## 48 **1 Introduction**

49 Mid-latitude ( $\sim 30\text{-}60^\circ$ ) seasonally stratifying shelf seas cover less than 8% of the world's oceans, yet  
50 account for  $\sim 15\%$  of marine global productivity (Muller-Karger *et al.*, 2005; Simpson and Sharples,  
51 2012). These regions support high abundances of species above the base of the food web, which  
52 includes a diversity of marine predators such as marine mammals and seabirds. However, they are  
53 currently going through a period of rapid alteration, driven by the combined and cumulative effects  
54 of a range of anthropogenic activities and impacts such as climate change, fisheries and the  
55 development of marine renewables (Walther *et al.*, 2002; Frid *et al.*, 2005; Witt *et al.*, 2012; Avila *et*  
56 *al.*, 2018; Kroodsmas *et al.*, 2018). As a result, many populations of marine mammals and seabirds in  
57 shelf-seas have shifted in distribution (Bertrand *et al.*, 2012; Hazen *et al.*, 2013) or suffered severe  
58 declines (Cury *et al.*, 2011; McCauley *et al.*, 2015; Paleczny *et al.*, 2015), which has negatively  
59 impacted the functioning of these systems as a whole (Heithaus *et al.*, 2008). Addressing this issue  
60 represents a major environmental conservation challenge requiring response at the policy level  
61 alongside informed management practices.

62 Marine mammals and seabirds meet their requirements for survival, growth and reproduction through  
63 the exploitation of prey resources from their surrounding environment. Whilst typically these animals  
64 are highly mobile and capable of ranging vast distances (Block *et al.*, 2011), foraging efforts are often  
65 concentrated over localised spatio-temporal scales (Hastie *et al.*, 2004; Sydeman *et al.*, 2006;  
66 Weimerskirch, 2007). Such heterogeneity in distributions is expected to match the organisation of  
67 prey, but this has proved surprisingly challenging to demonstrate (Logerwell *et al.*, 1998; Fauchald  
68 and Erikstad, 2002; Gremillet *et al.*, 2008; Torres *et al.*, 2008), particularly at finer scales which may  
69 be impacted by confounding factors (Schneider and Piatt, 1986; Hunt *et al.*, 1992; Mehlum *et al.*,  
70 1999; Swartzman and Hunt, 2000; Vlietstra, 2005; Fauchald, 2009). Increasing evidence suggests the  
71 behavioural patterns of marine predators (particularly those feeding on plankton and/or forage and  
72 pelagic fish) are linked to bio-physical oceanographic processes that structure the accessibility and

73 availability of these lower trophic level food sources (Cox *et al.*, 2013; Bertrand *et al.*, 2014;  
74 Woodson and Litvin, 2015; McInnes *et al.*, 2017), and thus influence foraging efficiency/success  
75 (Boyd *et al.*, 2016). Across shelf-sea environments, a number of discrete habitat features have been  
76 identified as important locations that host enhanced foraging opportunities, including fronts, offshore  
77 banks where internal waves propagate and tidally dependent island wakes (Hunt and Schneider, 1987;  
78 Hunt *et al.*, 1999; Bost *et al.*, 2009; Bertrand *et al.*, 2014; Scales *et al.*, 2014a; Benjamins *et al.*, 2015).  
79 Given the tight energy constraints of many marine mammals and seabirds (Cairns, 1988), these  
80 structures can be thought of as critical habitat features.

81 Knowledge of the bio-physical processes that underlie links between oceanographic habitat features  
82 and marine mammal and seabird foraging is vital to obtaining a comprehensive understanding of  
83 marine ecosystem functioning. This will prove invaluable as we move towards implementing holistic  
84 management methods, that consider ecosystems in their entirety and aim to incorporate more  
85 precautionary conservation measures (Arkema *et al.*, 2006; Hooker *et al.*, 2011). Early syntheses  
86 and reviews have outlined the prominent bio-physical processes occurring across ocean environments  
87 and how these are linked to the spatio-temporal distributions of seabirds (e.g. Hunt, 1990, 1991, 1997;  
88 Hunt *et al.*, 1999), but no known equivalent review exists for marine mammals. Over the past 10-15  
89 years, methodological and technological advances have substantially improved the way in which the  
90 marine environment is studied, both in terms of how we collect data (Cooke *et al.*, 2004; Hunt and  
91 Wilson, 2012; Brown *et al.*, 2013; Waggitt and Scott, 2014; Photopoulou *et al.*, 2015; Benoit-Bird  
92 and Lawson, 2016; Macaulay *et al.*, 2017) and quantitatively analyse it (Redfern *et al.*, 2006;  
93 Wakefield *et al.*, 2009; Brown *et al.*, 2013; Carter *et al.*, 2016; Bennison *et al.*, 2017). As such, our  
94 knowledge of links between oceanographic habitats and marine predators has substantially improved,  
95 and a more mechanistic understanding of how these features aid marine mammal and seabird  
96 foraging, and function as dynamic habitats is being attained. Although, more recent regional and/or  
97 feature specific reviews have been published (e.g. fronts; Scales *et al.*, 2014a, southern ocean fronts

98 and eddies; Acha *et al.*, 2004; Bost *et al.*, 2009, and tidal stream environments; Benjamins *et al.*,  
99 2015), as of yet, a paper which encompasses links between both marine mammals and seabirds with  
100 the full range of oceanographic habitat features that occur across mid-latitude, seasonally stratifying  
101 shelf-seas as a whole is lacking. Such knowledge is still yet to be fully integrated into studies  
102 examining behavioural patterns and habitat use by marine predators alongside marine management  
103 strategies (Tremblay *et al.*, 2009; Fourcade *et al.*, 2018), and so it is particularly pertinent that this is  
104 addressed, not least because the diverse human use of shelf-seas is accelerating impacts on these  
105 ecosystems. We feel it important to synthesise the broad and diverse habitat features present in this  
106 environment to facilitate conservation management and ecological research, and drive a policy  
107 response to this crisis.

108 In light of this, we provide a concise and easily accessible guide for both researchers and managers  
109 of marine systems on the predominant oceanographic habitats that are favoured for foraging by  
110 marine mammals and seabirds across mid-latitude shelf seas. We identify and describe key discrete  
111 physical features present across the continental shelf, working inshore from the shelf-edge to the  
112 shore line (Figures 1 & 2, Table 1), and discuss links to marine mammals and seabirds. We then  
113 highlight the key characteristics of these features that make them attractive as foraging habitats. We  
114 identify areas where knowledge is lacking and make recommendations for the direction of future  
115 research. Finally, we discuss how these insights can be used to improve the conservation management  
116 of shelf-sea environments. Our aim is to provide a concise overview, in a format that is broken down  
117 into feature specific sections accessible to non-oceanographers. In doing so we hope to encourage  
118 both researchers and conservation managers of marine systems to move towards the identification,  
119 bio-physical characterisation and incorporation of discrete oceanographic habitat structures that  
120 promote prey availability into future studies and management strategies.

## 121 **2 The shelf edge**

122 The shelf edge marks the transition zone from the comparatively shallow (usually less than 200m)  
123 waters of the continental shelf to the deep abyssal plains (where depths exceed 2000m) of the open  
124 ocean (Simpson and Sharples, 2012). This region is relatively narrow, with a typical lateral distance  
125 of around 50km, and so generally characterised by a steep sloping profile (e.g. the European  
126 continental shelf-edge). Along the shelf edge, dependent upon geographical location (e.g. bordering  
127 a major eastern boundary current), shelf-edge fronts and wind-driven upwelling fronts support high  
128 levels of primary and secondary productivity which attract a diversity of marine mammals and  
129 seabirds.

### 130 **2.1 Shelf-edge fronts**

131 Shelf-edge fronts (also shelf-break and shelf-slope fronts) occur at the interface between on-shelf and  
132 open-ocean waters (Figure 1), and are marked by strong gradients in salinity, and sometimes  
133 temperature. As currents, pushed onto the shelf via tidal forcing, are interrupted by the steep sloping  
134 topographic profiles of these regions, upwelling pushes the surface mixed layer above the critical  
135 depth for phytoplankton growth (Fournier *et al.*, 1979), whilst simultaneously facilitating exchange  
136 with the nutrient rich waters of the open-ocean's bottom boundary layer (Springer *et al.*, 1996; Ryan  
137 *et al.*, 1999). High levels of primary productivity are typically sustained, sometimes perennially  
138 (Fournier *et al.*, 1979), attracting planktivorous grazers alongside large numbers of pelagic fish  
139 (Podesta *et al.*, 1993; Sabatés and Olivar, 1996; Springer *et al.*, 1996; Genin, 2004; Greer *et al.*, 2015).  
140 Dependent upon the lateral extent and topography of the adjacent continental shelf, these features  
141 may be far from land, and so relatively inaccessible to those foragers constrained to land-based  
142 colonies (e.g. breeding seabirds and some seals). Links to marine predators are dominated by those  
143 taxa capable of performing far-ranging foraging trips (e.g. black petrel *Procellaria parkinsoni*, fork-  
144 tailed storm petrel *Oceanodroma furcate*, northern fulmar *Fulmarus glacialis* and short-tailed  
145 albatross *Phoebastria albatrus*; Schneider, 1982; Stone *et al.*, 1995; Piatt *et al.*, 2006; Freeman *et al.*,  
146 2010) or that are not restricted to a central location for breeding (e.g. Cuvier's beaked whale *Ziphius*

147 *cavirostris*, Risso's dolphin *Grampus griseus*, sperm whale *Physeter microcephalus* and spotted  
148 dolphin *Stenella attenuata*; Baumgartner, 1997; Waring *et al.*, 2001; Pinedo *et al.*, 2002; Azzellino  
149 *et al.*, 2008; Scott and Chivers, 2009). Where the shelf edge is nearer to land (e.g. the Skagerrak),  
150 shorter ranging breeding species may forage at these features (e.g. little auk *Alle alle*; Skov and  
151 Durinck, 1998). Shelf-edge fronts may also be important to non-breeding individuals in the late  
152 summer, autumn and winter, when constraints to a central land-based breeding location no longer  
153 apply (e.g. Cory's shearwater *Calonectris borealis* and little auk; Haney and McGillivray, 1985a;  
154 Brown, 1988).

## 155 **2.2 Wind-driven upwelling fronts**

156 Along the major eastern boundary currents of western North America (the California current), Peru  
157 (the Humboldt current) and west Africa (the Benguela, Canary and Somali currents), strong cross  
158 winds in combination with Coriolis forcing and Ekman transport form intense upwelling systems,  
159 which sustain some of the highest levels of primary and secondary productivity globally (Longhurst  
160 *et al.*, 1995). In other regions, similarly structured upwelling systems may occur (e.g. the southern  
161 shelf of Australia and along the eastern boundary of the Labrador Current; Kinsella *et al.*, 1987;  
162 Kampf *et al.*, 2004), albeit on a smaller and less impressive spatio-temporal scale.

163 Along, or immediately inshore of the shelf-edge, upwelling fronts mark where these systems meet  
164 on-shelf coastal waters. Strong convergent flows accumulate and retain the phytoplankton biomass  
165 and small nekton generated by adjacent upwelling systems (Bjorkstedt *et al.*, 2002), which attracts  
166 large numbers of pelagic and forage fish (Ainley *et al.*, 2005; Reese *et al.*, 2011; Watson *et al.*, 2018).  
167 Due to the typically narrow extent of adjacent shelves (e.g. western Africa and western America's),  
168 upwelling fronts are often proximate to land. As such, the prey aggregating effects of these features  
169 are exploited by a diverse range of marine predators (Bourne and Clark, 1984; Forney and Barlow,  
170 1998; Hoefler, 2000; Camphuysen and van der Meer, 2005; Croll *et al.*, 2005; Tynan *et al.*, 2005;



171 Ainley *et al.*, 2009) that includes those individuals constrained to land-based colonies or a shoreward  
172 distribution (e.g. lactating New Zealand fur seals *Arctocephalus forsteri* and Northern elephant seals  
173 *Mirounga angustirostris* alongside numerous breeding seabirds such as Cape gannet *Morus capensis*,  
174 common guillemot *Uria aalge*, Humboldt penguin *Spheniscus humboldti*, kelp gull *Larus*  
175 *dominicanus*, Peruvian booby *Sula variegata*, rhinoceros auklet *Cerorhinca monocerata* and a  
176 number of phalarope species; Briggs *et al.*, 1984; Croll, 1990; Weichler *et al.*, 2004; Ainley *et al.*,  
177 2005; Crocker *et al.*, 2006; Baylis *et al.*, 2008; Sabarros *et al.*, 2014).

178 The intensities of upwelling systems and their associated fronts can vary seasonally and/or inter-  
179 annually with climatic conditions and wind patterns (Kinsella *et al.*, 1987; Bograd *et al.*, 2009a),  
180 which can substantially impact the structuring of surrounding ecosystems with concomitant  
181 consequences for marine mammals and seabirds (Schneider and Methven, 1988; Schneider, 1994;  
182 McGowan *et al.*, 1998; Abraham and Sydeman, 2004; Wolf *et al.*, 2009; Black *et al.*, 2011; Woodson  
183 and Litvin, 2015). For example, in years when decreased upwelling intensity reduces the availability  
184 of high quality foraging habitats around frontal zones (e.g. with the El Nino Southern Oscillation;  
185 ENSO), breeding seabirds along the west coast of the America's display signs of reduced body  
186 condition (e.g. common guillemots; Croll, 1990), whilst others (e.g. Cassin's Auklet *Ptychoramphus*  
187 *aleuticus*, Humboldt penguins and marbled murrelet *Brachyramphus marmoratus*) extend their  
188 foraging trips, which may result in reduced reproductive success (Becker and Beissinger, 2003;  
189 Hennenke and Culik, 2005; Bertram *et al.*, 2017).

### 190 **3 The mid-shelf: from the shelf-edge to near-shore coastal waters**

191 The mid-shelf extends from the shelf-edge to near-shore coastal waters (Figure 1) with topographic  
192 depths typically ranging from around 50m to 200m. In mid-latitude, temperate zones this region  
193 stratifies seasonally between late spring and autumn when increased solar irradiation heats surface  
194 waters sufficiently to increase buoyancy levels and overcome tidal and wind-driven mixing (Pingree,

195 1975; Pingree *et al.*, 1976; Simpson and Sharples, 2012). A two-layer system is formed, characterised  
196 by a surface mixed layer of warm, nutrient deficient water and a bottom boundary layer of dense,  
197 cold nutrient rich water (Figure 1). This structuring underlies a number of oceanographic processes  
198 that appear important to marine mammals and seabirds, particularly in areas where the spatial extent  
199 of the continental on-shelf region is large and tidal ranges considerable (e.g. the Canadian, European,  
200 northeast USA continental shelf and the eastern Bering Sea Shelf).

### 201 **3.1 The annual spring bloom**

202 The development/onset of stratification in the spring drives a significant annual phytoplankton bloom  
203 (Pingree *et al.*, 1976; Sambrotto *et al.*, 1986; Sharples *et al.*, 2006). The timing of this bloom varies  
204 annually as a result of climatic fluctuations in air temperature/solar irradiation and wind stress  
205 (Sharples *et al.*, 2006), which can lead to a temporal mismatch between fish spawning and plankton  
206 production (match-mismatch hypothesis; Cushing, 1975). This can have bottom-up impacts at higher  
207 trophic levels by influencing fish recruitment (Beaugrand and Kirby, 2010; Sigler *et al.*, 2016) and  
208 food availability (Durant *et al.*, 2007), and has been shown to effect the breeding success of a number  
209 of seabirds including Atlantic puffin *Fratercula arctica*, black-legged kittiwake *Rissa tridactyla*,  
210 common guillemot and rhinoceros auklet off the coast of British Columbia, and across the North and  
211 Norwegian Seas (Durant *et al.*, 2006; Scott *et al.*, 2006; Borstad *et al.*, 2011). Such impacts  
212 sometimes occur at a lag of 1-2 years to underlying shifts in environmental conditions (Zador *et al.*,  
213 2013). Changes in prey availability have also been linked to spatial variability in the distribution of  
214 the spring bloom alongside the oceanographic conditions within which it occurs (Table 2). For  
215 example, across the eastern Bering Sea, in years when the spring bloom occurs in warmer offshore  
216 waters (due to earlier sea ice retreat; Hunt and Stabeno, 2002), changes in the abundance,  
217 composition, distribution and survival of predominant plankton and juvenile fish species results in  
218 shifts in the diets and distributions of several seabird populations (Springer *et al.*, 2007; Renner *et al.*,

219 2016; Hunt *et al.*, 2018), which can result in demographic impacts (Satterthwaite *et al.*, 2012; Zador  
220 *et al.*, 2013).

### 221 ***3.2 Vertical interfaces in offshore stratified regions (the pycnocline) and sub-surface productivity***

222 Following the spring bloom, productivity within the mid-shelf region redistributes and is maintained  
223 by a number of oceanographic processes (Richardson *et al.*, 2000; Weston *et al.*, 2005). An important  
224 feature is the vertical interface between the low nutrient, warm surface mixed layer and the cool,  
225 dense, high nutrient bottom boundary layer, where steep vertical gradients in density form a  
226 pycnocline, which can alternatively be referred to as the thermocline (when vertical density gradients  
227 are temperature driven) or the halocline (when vertical density gradients are driven by changes in  
228 salinity). This structure acts as a barrier between surface and bottom boundary waters by inhibiting  
229 the vertical transport of nutrients and plankton (Stepputtis *et al.*, 2011). In some instances, the  
230 pycnocline may be composed of both a thermocline and halocline. Alternatively, the effects of  
231 vertical changes in temperature and salinity can cancel each other out, resulting in no pycnocline.  
232 Across shelf-seas, offshore seasonal summer stratification is predominantly thermally driven (with a  
233 temperature driven pycnocline; Simpson and Sharples, 2012), although in regions subject to high  
234 levels of freshwater input (e.g. the Skagerrak between the North and Baltic Seas; Skov and Durinck,  
235 2000) saline gradients may also be important. The majority of studies investigating interactions  
236 between marine predators and the pycnocline have focused on links with temperature delineated  
237 thermoclines (e.g. Takahashi *et al.*, 2008; Kokubun *et al.*, 2010; Pelletier *et al.*, 2012; Nordstrom *et*  
238 *al.*, 2013; ven Eeden *et al.*, 2016).

239 High levels of sub-surface primary productivity often concentrate around the pycnocline, and can  
240 account for over 50% of water column productivity (Weston *et al.*, 2005), alongside ~30% of total  
241 annual productivity (Richardson and Christoffersen, 1991). This is maintained through the summer  
242 months by two sources of episodic mixing events, each of which results in an influx of nutrients from

243 the bottom boundary layer that enhance productivity. First, increased tidal currents during spring  
244 tides generate turbulent dissipation (due to friction with the sea bed), that may extend up through the  
245 bottom boundary layer temporarily eroding the base of the pycnocline (Sharples, 1999, 2008;  
246 Sharples *et al.*, 2001; Allen *et al.*, 2004). Second, wave and wind driven surface mixing (due to  
247 changes in wave/wind direction and/or velocity with prevailing weather conditions) may partially  
248 break down vertical stratification (Sharples and Tett, 1994; Rippeth *et al.*, 2005; Williams *et al.*,  
249 2013). Shear boundaries (strong vertical gradients in horizontal currents) around the pycnocline may  
250 additionally aid in the retention of small organisms such as phytoplankton (Franks, 1995; Durham *et*  
251 *al.*, 2009; Cheriton *et al.*, 2010), whilst a synchronous accumulation of zooplankton (McManus *et al.*,  
252 2005) can result in a propagation of food supply across multiple trophic levels.

253 Sub-surface productivity at and around the pycnocline has been linked to foraging by a number of  
254 marine predators, such as little auk, northern fulmar, northern gannet *Morus bassanus* and grey seal  
255 *Halichoerus grypus* (Skov and Durinck, 2000; Scott *et al.*, 2010). In diving species, individuals may  
256 repetitively descend to the pycnocline (e.g. African penguin *Spheniscus demersus*, northern fur seal  
257 *Callorhinus ursinus*, northern right whale *Eubalaena glacialis*, rhinoceros auklet and thick-billed  
258 murre *Uria lomvia*; Baumgartner and Mate, 2003; Matsumoto *et al.*, 2008; Takahashi *et al.*, 2008;  
259 Kuhn, 2011; ven Eeden *et al.*, 2016), where peaks in prey density (Hansen *et al.*, 2001; Baumgartner  
260 and Mate, 2003) increase foraging efficiency (Pelletier *et al.*, 2012). In years when a pycnocline is  
261 absent or highly dispersed, foraging success tends to decrease, with concomitant consequences for  
262 seabird breeding success (Ropert-Coudert *et al.*, 2009a). Alternatively, individuals (e.g. thick-billed  
263 murre in the southeastern Bering Sea) may expand the range of habitats foraged at (both in terms of  
264 horizontal extent and dive depth; Kokubun *et al.*, 2010).

265 The depth of the pycnocline is also an important determinant of foraging habitat suitability (Hunt *et*  
266 *al.*, 1993; Skov and Durinck, 2000; Nordstrom *et al.*, 2013). Increased light attenuation with depth  
267 means productivity around shallower pycnoclines is likely enhanced compared with deeper

268 pycnoclines (Skov and Durinck, 2000). Moreover, for near-surface feeders (e.g. northern fulmar) a  
269 shallower pycnocline may make prey available at more accessible depths (Skov and Durinck, 2000),  
270 and for those that dive from the surface (e.g. least auklet *Aethia pusilla*), reduce foraging energetic  
271 costs (Hunt *et al.*, 1990; Haney, 1991; Skov and Durinck, 2000; Langton *et al.*, 2011). In thermally  
272 stratified waters, exothermic prey may redistribute themselves near the surface in an attempt to avoid  
273 unfavourable cool bottom boundary waters below the pycnoline (e.g. mackerel *Scomber scombrus*;  
274 Grégoire, 2006).

### 275 **3.3 Internal waves and offshore banks**

276 Internal waves form within stratified regions when tidal currents are interrupted by areas of abrupt,  
277 raised and/or uneven topography (Figure 1; Mann and Lazier, 2006), and commonly occur in  
278 proximity to the shelf edge (Bertrand *et al.*, 2014) and around offshore banks (Palmer *et al.*, 2013),  
279 reefs and rock pinnacles (Moum and Nash, 2000). Resultant locally induced upwelling causes an  
280 oscillation in the pycnocline that can exceed an amplitude of 30m and approach ~50% of local water  
281 depth (Witman *et al.*, 1993; Palmer *et al.*, 2013). Nutrient fluxes across the pycnocline sustain  
282 exceptionally high levels of sub-surface productivity (Richardson *et al.*, 2000; Tweddle *et al.*, 2013),  
283 whilst the simultaneous creation of a number of convergent (aggregating) and divergent (dispersing)  
284 zones (Figure 1) can alter the vertical distributions of plankton and small nekton (Lennert-Cody and  
285 Franks, 1999; McManus *et al.*, 2005; Bertrand *et al.*, 2008), forcing large aggregations of prey to the  
286 surface (Embling *et al.*, 2013) that are foraged at by a range of marine predators (Moore and Lien,  
287 2007; Stevick *et al.*, 2008; Scott *et al.*, 2013; Bertrand *et al.*, 2014). These features appear to be  
288 especially important to those taxa that near-surface feed on plankton and/or forage fish such as black-  
289 legged kittiwake, humpback whale *Megaptera novaeangliae* and several species of petrel and  
290 shearwater (Haney, 1987; Stevick *et al.*, 2008; Hazen *et al.*, 2009; Embling *et al.*, 2012). The  
291 generation of internal waves is tidally mediated (Pineda *et al.*, 2015), and patterns in the occurrence  
292 of surface prey aggregations alongside marine mammal and seabird foraging regularly reflect this

293 (Hazen *et al.*, 2009; Embling *et al.*, 2012). Further complexities in the shape of a topographic  
294 structure (e.g. steep-sided crests and mounts) may enhance the density of surface aggregations by  
295 concentrating tidal currents whilst simultaneously moderating the passage of internal waves to  
296 increase upwelling flows and surface convergence (Stevick *et al.*, 2008).

#### 297 **4 Tidal-mixing fronts**

298 Tidal-mixing fronts mark the transition zones between the seasonally stratifying waters of the mid-  
299 shelf and mixing coastal waters (Simpson and Hunter, 1974; Pingree and Griffiths, 1978; Schumacher  
300 *et al.*, 1979), and are marked by strong horizontal surface temperature gradients (Miller, 2009). Their  
301 positions are dependent upon the ability of tidal currents and wind stress to overcome the buoyant  
302 effects of surface heat fluxes and mix the entire water column (Fearnhead, 1975; Franks, 1992a; Acha  
303 *et al.*, 2004). This is a function of water column depth, and so the position of a tidal-mixing front can  
304 be roughly predicted from the ratio of total water depth ( $h$ ) to tidal velocity ( $u$ ) -  $h/u^3$  (the Simpson-  
305 Hunter parameter; Simpson and Hunter, 1974; Simpson and Sharples, 2012). Once established,  
306 variation in a tidal-mixing front's position occurs (Figure 2, Table 2), in response to changes in the  
307 strength of tidal currents with the spring-neap cycle (Sharples and Simpson, 1996; Simpson and  
308 Sharples, 2012), as well as from variation in heat flux and wind-driven mixing (Kachel *et al.*, 2002;  
309 Nahas *et al.*, 2005; Pisoni *et al.*, 2015).

310 Tidal-mixing fronts are often associated with elevated and persistent primary productivity that has  
311 the potential to propagate across multiple trophic levels (Coyle and Cooney, 1993; Munk *et al.*, 1995;  
312 Gregory Lough and Manning, 2001). Where the pycnocline of stratified offshore waters shallows to  
313 meet inshore mixing waters, increased light exposure supplemented with runoff nutrients (of coastal  
314 waters) alongside those mixed up from the bottom boundary layer results in productivity levels  
315 several orders of magnitude higher than in surrounding waters (Pingree *et al.*, 1975; Simpson *et al.*,  
316 1979; Franks, 1992a). Additional convergent flows (Pingree *et al.*, 1974) may redistribute the

317 horizontal and vertical distributions of weak or passively swimming organisms (e.g. plankton grazers  
318 attracted to the high productivity levels of the front; Coyle *et al.*, 1998), resulting in near-surface  
319 retention and accumulation (Franks, 1992b; Epstein and Beardsley, 2001).

320 A diverse range of marine predators forage around tidal-mixing fronts (Haney and McGillivray,  
321 1985b; Begg and Reid, 1997; Goold, 1998; Hunt *et al.*, 1999; Weir and O'Brien, 2000). Associations  
322 are particularly prominent in colonial seabirds, and land-based breeding sites are often located in  
323 proximity to these features (Hunt, 1997). Large numbers of near-surface feeding planktivores, such  
324 as least auklet and short-tailed shearwater *Puffinus tenuirostris*, forage at and around tidal-mixing  
325 fronts in concordance with patches of increased zooplankton abundance (Hunt *et al.*, 1996; Jahneke  
326 *et al.*, 2005), which are often concentrated near the sea's surface (Harrison *et al.*, 1990; Hunt and  
327 Harrison, 1990; Russell *et al.*, 1999). These features may also attract large cetacean species including  
328 a number of lunge-feeding rorquals (e.g. blue whale *Balaenoptera musculus*, fin whale *Balaenoptera*  
329 *physalus* and humpback whale; Doniol-Valcroze *et al.*, 2007; Dalla Rosa *et al.*, 2012). Piscivores,  
330 such as black-legged kittiwake, common dolphin *Delphinus delphis*, common guillemot, Magellanic  
331 penguin *Spheniscus magellanicus* and northern gannet, also frequently forage at tidal-mixing fronts  
332 (Kinder *et al.*, 1983; Durazo *et al.*, 1998; Goold, 1998; Boersma *et al.*, 2009; Scales *et al.*, 2014b;  
333 Cox *et al.*, 2016, 2017), likely because the aggregating effects of these features on plankton  
334 predictably attract high densities of forage and pelagic fish (Hansen *et al.*, 2001; Alemany *et al.*,  
335 2009; Brigolin *et al.*, 2018). Across the southeastern Bering Sea, individuals present at these features  
336 have been directly linked to high density patches of fish prey (Decker and Hunt, 1996; Kokubun *et*  
337 *al.*, 2008), where capture rates were increased (Vlietstra *et al.*, 2005). For both piscivores and  
338 planktivores, fronts with strong surface flow gradients may be particularly attractive, possibly due to  
339 additional aggregative effects on small biomass (Schneider *et al.*, 1987). Reduced productivity at  
340 frontal zones alongside geographical shifts in typical locations (in years of abnormal oceanographic

341 conditions; e.g. ENSO events) have been linked to increases in short-tailed shearwater mortality rates  
342 (Napp and Hunt, 2001).

### 343 **5 Near-shore coastal waters and estuaries**

344 On the shoreward side of a tidal-mixing front, turbulence generated through friction between tidal  
345 currents and the seabed extends the entire water column (due to shallow depths), and prevents thermal  
346 stratification (Simpson and Sharples, 2012). As such, the majority of this region remains permanently  
347 mixed throughout the year. Concentrated patches of primary productivity are generally limited to  
348 regions of fresh water influence (ROFIs) around estuarine systems, where salinity driven stratification  
349 may occur. Other notable areas of interest to marine mammals and seabirds, such as those associated  
350 with tidally driven turbulence around topographic structures, likely function by mechanically altering  
351 the behaviours and distributions of zooplankton and fish prey, as indicated by periodicity in their use  
352 (Zamon, 2002, 2003). Unlike the mid-shelf, where the seasonal development of thermal stratification  
353 plays a dominant role in the formation of foraging habitat, features occurring in near-shore coastal  
354 waters may persist throughout the year and, in some cases, are targeted perennially by marine  
355 predators (Skov and Prins, 2001).

#### 356 **5.1 Channels, headland and island wakes, nearshore reefs and bays**

357 In near-shore coastal regions, marine mammals and seabirds frequently forage within tidally active  
358 areas (Nol and Gaskin, 1987; Marubini *et al.*, 2009; Anderwald *et al.*, 2012; Benjamins *et al.*, 2015;  
359 Warwick-Evans *et al.*, 2016; Waggitt *et al.*, 2018), resulting in distinct regularities in their  
360 distributions and behaviours that coincide with particular tidal phases (Becker *et al.*, 1993; Hunt *et*  
361 *al.*, 1998; Irons, 1998; Isojunno *et al.*, 2012; De Boer *et al.*, 2014; Ijsseldijk *et al.*, 2015). Specifically,  
362 areas such as narrow channels, headlands, islands, reefs and bays often function as periodic foraging  
363 hotspots, where interactions between strong tidal currents (often exceeding  $1.5\text{ms}^{-1}$ ) and complex  
364 topography create prosperous foraging opportunities for marine predators (Cairns and Schneider,



365 1990; Coyle *et al.*, 1992; Zamon, 2003; Benjamins *et al.*, 2015; Couperus *et al.*, 2016). In some  
366 instances, several of these features may occur in close proximity to one another (Bailey and  
367 Thompson, 2010).

#### 368 5.1.1 Channels and narrow passes

369 Channels, corridors and narrow passes are typical of estuaries, fjords and island groups. During  
370 strong tidal flows, these features may act as bottlenecks creating predictable and exploitable  
371 concentrations of zooplankton and fish prey advected from adjacent areas (Zamon, 2001, 2002;  
372 Couperus *et al.*, 2016), which are exploited by a number of marine mammals and seabirds (Thompson  
373 *et al.*, 1991; Lescrauwaet *et al.*, 2000; Zamon, 2001; Holm and Burger, 2002; Hastie *et al.*, 2004,  
374 2016; Ladd *et al.*, 2005; Bailey and Thompson, 2010). Rapid currents and turbulence along these  
375 passages (Nimmo Smith *et al.*, 1999) may additionally disorientate fish and break down shoal  
376 cohesion (Liao, 2007), increasing catchability (Zamon, 2001, 2003; Crook and Davoren, 2014). The  
377 fine scale foraging distributions of several piscivorous alcids, cetaceans and pinnipeds (e.g. Atlantic  
378 puffin, common guillemot, harbour porpoise *Phocoena phocoena* and harbour seal *Phoca vitulina*)  
379 across channels and narrow passes are known to concentrate in central and/or narrow areas where  
380 current flows are maximised (Pierpoint, 2008; Hastie *et al.*, 2016; Waggitt *et al.*, 2016a). However,  
381 it should be noted that due to the energetics of navigating turbulent flows (Wilson *et al.*, 2001; Heath  
382 and Gilchrist, 2010), some individuals may forage around the periphery of these currents where  
383 speeds are reduced (Pierpoint, 2008; Wilson *et al.*, 2013; Cole *et al.*, 2018), or avoid such areas  
384 completely (Wilson *et al.*, 2001; Embling *et al.*, 2010; Waggitt *et al.*, 2016b).

385 In some cases, the steep sides of a channel, corridor or narrow pass may additionally provide a barrier  
386 suitable for prey herding (Heimlich-Boran, 1988), and cetaceans that employ complex group foraging  
387 strategies (Simila and Ugarte, 1993; Fertl and Wilson, 1997; Duffy-Echevarria *et al.*, 2008) are  
388 frequently observed at these features (Heimlich-Boran, 1988; Hastie *et al.*, 2004; Bailey and

389 Thompson, 2010). Where the edge of a channel or pass acts as a barrier to tidal currents (e.g. in the  
390 presence of shallow banks and/or meanders), resultant upwelling and current circulation can force  
391 advected zooplankton, and sometimes small nekton (e.g. forage fish), into dense aggregations  
392 (Simard *et al.*, 1986; Lavoie *et al.*, 2000; Davies *et al.*, 2013) that may be driven towards the surface  
393 (Simard *et al.*, 2002), making these features additionally attractive to both bulk-feeding baleen whales  
394 (Cotté and Simard, 2005) and surface feeding birds (e.g. a number of auklet species alongside  
395 Bonaparte's *Larus Philadelphi*a and Mew *Larus canus* gull; Vermeer *et al.*, 1987; Hunt *et al.*, 1998).  
396 In some instances, ephemeral features, known as Langmuir circulation cells, form convergent zones  
397 at the sea's surface (over scales of a few to a couple of hundred metres; Barstow, 1983). These can  
398 further entrain plankton and small nekton (Hamner and Schneider, 1986), which near-surface/surface  
399 foraging seabirds (e.g. northern fulmars and prions *Pachyptila spp*) have been observed exploiting  
400 (Goss *et al.*, 1997; Ladd *et al.*, 2005). Where fast currents pour down into a channel, or where  
401 previous upwelled waters descend (Hunt *et al.*, 1998), downwelling structures may form (Hunt *et al.*,  
402 1998; Waggitt *et al.*, 2016a). Whilst these features have been linked to the foraging distributions of  
403 two benthic/demersal feeders (black guillemot *Cepphus grille* and European shag *Phalacrocorax*  
404 *aristotelis*; Waggitt *et al.*, 2016a) alongside one upper-water column feeder (least auklet; Hunt *et al.*,  
405 1998), the exact mechanisms driving these interactions are unclear, but appear to be site and species  
406 specific (Hunt *et al.*, 1998; Waggitt *et al.*, 2017).

#### 407 5.1.2 Headland and island wakes

408 When headland and island features interrupt the passage of strong tidal current flows, a leeward wake  
409 (or eddy) may form. At the interface with non-wake waters, shear induced hydrographic fronts  
410 (Wolanski and Hamner, 1988; Johnston and Read, 2007) may accumulate zooplankton which become  
411 retained within the calm waters of the wake (Alldredge and Hamner, 1980). In addition, turbulent  
412 flows around these structures may disorientate fish prey that use the wake to forage, or seek refuge  
413 from adjacent strong tidal currents (Liao, 2007; Robinson *et al.*, 2007; Tarrade *et al.*, 2008). For

414 example, in the Bay of Fundy (Canada), harbour porpoise, fin and minke *Balaenoptera acutorostrata*  
415 whale exploit dense patches of euphausiids *Meganyctiphanes norvegica* and herring *Clupea harengus*  
416 along the edge of an island wake during flood tides (Johnston *et al.*, 2005b, 2005a; Ingram *et al.*,  
417 2007). Bottlenose dolphins in the Moray Firth (UK) concentrate foraging activity along the surface  
418 signatures of hydrographic fronts, that form during specific tidal conditions in proximity to a headland  
419 on the edge of a deep, steep-sided channel (Bailey and Thompson, 2010), while across Glacier Bay  
420 and Icy Strait in southeastern Alaska, humpback whale distributions are disproportionately distributed  
421 within the leeward waters of several headlands (Chenoweth *et al.*, 2011). Where fish actively avoid  
422 turbulent flows (Nichol and Somerton, 2002), hydrographic fronts may act as a barrier to their  
423 movements, and so some predators (e.g. bottlenose dolphin and killer whale) may use these features  
424 for prey herding (Heimlich-Boran, 1988; Benjamins *et al.*, 2015). However, as of yet this has not  
425 been directly explored.

#### 426 5.1.3 Nearshore reefs, banks and ridges

427 Where current flows run across nearshore topographically complex structures such as reefs, banks  
428 and ridges, under specific tidal conditions friction can generate shear instabilities, turbulence and  
429 upwelling (Coyle *et al.*, 1992; Jones *et al.*, 2014). Peaks in common guillemot, harbour porpoise,  
430 phalaropes and thick-billed murre occurrence, corresponding to the locations and times at which these  
431 hydrographic features manifest, likely reflect changes in plankton and fish prey distributions that aid  
432 capture (Brown and Gaskin, 1986; Coyle *et al.*, 1992; Skov and Thomsen, 2008; Jones *et al.*, 2014).  
433 Further offshore where tidal currents are less pronounced (but still within boundaries of near-coastal  
434 regions), bathymetric features such as reefs and ridges may also act to trap plankton and small  
435 biomass during downward migration, which may be particularly attractive to planktivorous species  
436 foraging upon euphausiids, such as the short-tailed shearwater (Hunt *et al.*, 1996).

#### 437 5.1.4 Bays

438 Where the curvature of a headland or series of small islands results in the formation of a bay, complex  
439 tidal circulation patterns (enforced by the curved profile of the bay) may accumulate plankton and  
440 small nekton through advection and retention (Gomez-Gutierrez and Robinson, 2006; Rogachev *et*  
441 *al.*, 2008). In bays characterised by the presence of steep topographic barriers and ledges, interactions  
442 with these circulation patterns can generate localised upwelling. This can force accumulated biomass  
443 into dense surface aggregations, which appear to provide important foraging opportunities for a  
444 number of planktivorous species that either surface feed (e.g. black-legged kittiwake and red-necked  
445 phalarope *Phalaropus lobatus*; Drew *et al.*, 2013; Thorne and Read, 2013) and/or bulk feed (e.g.  
446 bowhead whale *Balaena mysticetus* and North Atlantic right whale; Jiang *et al.*, 2007; Rogachev *et*  
447 *al.*, 2008).

#### 448 **5.2 Regions of freshwater influence (ROFIs): Estuarine plume and tidal intrusion fronts**

449 Within and around estuarine systems, typical circulation patterns, forcing dense water below less  
450 dense water, promote the two-layer stratification of outflowing nutrient rich freshwater and intruding  
451 saline waters (Simpson and Sharples, 2012). Where this stratification meets coastal mixing waters,  
452 high horizontal gradients in salinity and density mark the position of either a tidal intrusion front  
453 (dense saline coastal water intruding into the estuary) or a plume front (brackish water discharging  
454 out of the estuary; Simpson and Nunes, 1981; Lewis, 1984). Stratification increases stability in the  
455 water column, and allows plankton to redistribute and settle at or above the salinity driven pycnocline  
456 (halocline) where waters are nutrient rich and light exposure increased. Resultant productivity levels  
457 are high (Cloern, 1991), and attract large numbers of zooplankton and forage fish (Govoni *et al.*,  
458 1989; Kingsford and Suthers, 1994; Kaltenberg *et al.*, 2010; Phillips *et al.*, 2017), which may be  
459 concentrated at the surface signature of the front due to additional convergent flows (Govoni *et al.*,  
460 1989). A number of piscivores, such as black and red throated diver *Gavia stellata/arctica*, bottlenose  
461 dolphin, common guillemot, little penguin, northern fur seal and sooty shearwater *Ardenna grisea*,  
462 forage at estuarine plume and tidal intrusion fronts (Skov and Prins, 2001; Mendes *et al.*, 2002;

463 Pelland *et al.*, 2014; Zamon *et al.*, 2014; Kowalczyk *et al.*, 2015a; Phillips *et al.*, 2017). The location,  
464 occurrence and strength of these features may be tidally mediated and/or dependent upon local current  
465 patterns, rainfall and wind events (Sharpley and Simpson, 1993; Kingsford and Suthers, 1994; Choi  
466 and Wilkin, 2007; Schlacher *et al.*, 2008). Such variability may further impact the abundance and  
467 distribution of zooplankton and forage fish, alongside the behaviours of marine mammals and  
468 seabirds that forage at these feature (Mendes *et al.*, 2002; Schlacher *et al.*, 2008; Kowalczyk *et al.*,  
469 2015b; Lin *et al.*, 2015; Phillips *et al.*, 2018). For example, bottlenose dolphin foraging at a tidal  
470 intrusion front in the Moray Firth (UK), did so only during flood tide conditions when the front was  
471 most pronounced (Mendes *et al.*, 2002), whilst sooty shearwater and common guillemots have been  
472 shown to spatially track the boundary of the Columbia River plume (USA) as it evolves through time  
473 (Phillips *et al.*, 2018). In Port Phillip Bay (Australia), little penguin breeding success has been linked  
474 to the occurrence and intensity of rainfall events, and subsequent changes in the dynamics of a local  
475 estuarine plume front and prey availability (Kowalczyk *et al.*, 2015b).

## 476 **6 Oceanographic habitats and the facilitation of foraging**

477 It is evident that bio-physical processes strongly influence habitat choice by a diversity of marine  
478 mammals and seabirds that feed upon plankton and/or forage and pelagic fish, and across shelf-seas  
479 a range of oceanographic features are favoured for foraging. Such associations appear attributable to  
480 predictable increases in prey accessibility and availability that stem from changes in the abundance  
481 and density, depth distribution, behaviour and/or patch persistence of prey, which together likely  
482 facilitate trophic transfer and enhance foraging efficiency (Pelletier *et al.*, 2012; Boyd *et al.*, 2016).  
483 For example, notable declines in the reproductive success of some marine predator populations have  
484 mirrored a change/reduction in the availability of prey enhancing oceanographic habitats following  
485 environmental changes with prevailing climatic and weather conditions (Hennicke and Culik, 2005;  
486 Scott *et al.*, 2006; Boersma and Rebstock, 2009; Ropert-Coudert *et al.*, 2009a; Wolf *et al.*, 2009;  
487 Borstad *et al.*, 2011). The importance of difference aspects of prey availability (e.g. prey abundance

488 versus depth distribution, versus predictability) will depend upon species specific foraging strategies  
489 (e.g. surface feeder versus diver, available search time, differences in prey type; Hunt *et al.*, 1999;  
490 Langton *et al.*, 2011), alongside individual energetic requirements (Hennicke and Culik, 2005;  
491 Goldbogen *et al.*, 2011). For central place foragers constrained to land (e.g. many breeding seabirds  
492 and seals), some features may be inaccessible due to their proximity and limitations on an individuals  
493 foraging range (e.g. shelf-edge fronts; Thaxter *et al.*, 2012).

#### 494 **6.1 Increased abundance and density of prey**

495 Sites where prey are abundant in dense aggregations allow individuals to reduce foraging effort while  
496 maintaining sufficient yields (Enstipp *et al.*, 2007; Benoit-Bird *et al.*, 2013; Goldbogen *et al.*, 2015;  
497 Thaxter *et al.*, 2016). Behavioural changes alongside increases in prey capture rates at a number of  
498 oceanographic features (Vlietstra *et al.*, 2005; Rogachev *et al.*, 2008; Cox *et al.*, 2016) reflect the  
499 presence of abundant and densely concentrated prey (Decker and Hunt, 1996; Vlietstra *et al.*, 2005;  
500 Stevick *et al.*, 2008), suggesting these habitats can aid individuals in maximising foraging efficiency  
501 (Ropert-Coudert *et al.*, 2009a; Goldbogen *et al.*, 2011; Pelletier *et al.*, 2012). This typically occurs  
502 in tandem with increases in primary and secondary productivity (e.g. around shelf-edge fronts,  
503 upwelling fronts and tidal-mixing fronts; Decker and Hunt, 1996; Ainley *et al.*, 2005; Jahncke *et al.*,  
504 2005) or specific flow characteristics (e.g. convergent zones at offshore banks subject to the passage  
505 of internal waves; Embling *et al.*, 2012, 2013), and may be particularly important for those individuals  
506 with especially high energetic needs (e.g. chick provisioning seabirds; Hennicke and Culik, 2005)  
507 and/or whose foraging strategies are particularly costly (Green *et al.*, 2009; Goldbogen *et al.*, 2011).

#### 508 **6.2 Depth distribution of prey**

509 Depth distribution plays a key role in prey accessibility, particularly for those taxa that feed at or near  
510 the surface and/or have limited dive capabilities (Embling *et al.*, 2012; Boyd *et al.*, 2015). Surface  
511 convergent zones at shelf-edge fronts, upwelling fronts and tidal-mixing fronts are frequently used

512 by these foragers, as are localised upwelling structures related to interactions between topography  
513 and tidal currents (e.g. at offshore banks and around the coast). In such areas, individuals have been  
514 directly linked to shallow prey aggregations (Russell *et al.*, 1999; Stevick *et al.*, 2008; Embling *et al.*,  
515 2012). For air-breathing diving predators, changes in the depth distributions of their prey may reduce  
516 the energetic costs of capture by either allowing individuals to concentrate search activity within a  
517 restricted proportion of the water column, or reducing overall dive depths from the surface (Ropert-  
518 Coudert *et al.*, 2009b; Benoit-Bird *et al.*, 2011). For example, the foraging efficiencies of some diving  
519 seabirds appear to be tied to the presence of vertical prey aggregating features such as the pycnocline  
520 (Ropert-Coudert *et al.*, 2009a; Pelletier *et al.*, 2012).

### 521 **6.3 Prey behaviour**

522 Bio-physical conditions and processes may elicit a change in prey behaviour that further alters  
523 densities and depth distributions to increase vulnerability to predation by marine mammals and  
524 seabirds. The breakdown of fish school cohesion likely makes individual prey items easier to catch  
525 (Crook and Davoren, 2014; Kilian *et al.*, 2015; Hastie *et al.*, 2016), as may the formation of prey  
526 concentrations in areas of reduced current speeds (e.g. around island wakes) as fish attempt to avoid  
527 such disruptions (Liao, 2007; Robinson *et al.*, 2007; Benjamins *et al.*, 2015). Alternatively, the  
528 temperature preferences of some prey mean they may redistribute themselves to aggregate in warmer,  
529 near surface waters (Grégoire, 2006).

### 530 **6.4 Persistence and predictability**

531 The oceanographic features favoured for foraging by marine mammals and seabirds typically occur  
532 in a persistent and/or predictable manner. If individuals can learn and remember the locations at  
533 which encountering accessible prey is more probable (Hunt *et al.*, 1999; Gende and Sigler, 2006;  
534 Weimerskirch, 2007; Davoren, 2013; Regular *et al.*, 2013; Grecian *et al.*, 2018), concentrated search  
535 effort (Hamer *et al.*, 2009; Pettex *et al.*, 2010; Dragon *et al.*, 2012; Patrick *et al.*, 2014) can increase

536 foraging efficiency (Stephens and Krebs, 1986). Targeted search patterns have been shown to  
537 coincide with the occurrence of a number of oceanographic habitats that are repetitively visited  
538 (Bailey and Thompson, 2010; Sabarros *et al.*, 2014; Scales *et al.*, 2014b). Moreover, these behaviours  
539 have been shown to develop as individuals mature, suggesting they are beneficial (Grecian *et al.*,  
540 2018). In some cases, the scales across which targeted search effort occur are tied to those of  
541 corresponding physical processes. For example, gannets foraging around tidal-mixing fronts restrict  
542 search behaviours over scales of between 2km to 10km (Hamer *et al.*, 2009; Scales *et al.*, 2014b)  
543 reflective of those over which the locations of these features vary with tidal- and wind- driven events  
544 (Nahas *et al.*, 2005; Pisoni *et al.*, 2015). Bottlenose dolphins foraging around topographically  
545 controlled tidal structures display highly localised search behaviours over 100's of metres, which  
546 mirrors the similarly scaled predictability of these features (Bailey and Thompson, 2010).

## 547 **7 Future research directions**

548 Whilst associations between marine predators and bio-physical processes have been documented  
549 across numerous studies, there are a number of areas in which improvements are still necessary.  
550 Concurrent measurements of sub-surface oceanography, low- to mid- trophic level prey distributions  
551 and marine mammal and seabird behaviours around many discrete physical features are lacking (e.g.  
552 tidal stream environments), or limited to a specific set of locations and sites (e.g. the Bering Sea,  
553 British Isles and Canadian Continental Shelf). Moreover, fine-scale three-dimensional measurements  
554 of marine mammal and seabird movements are rarely integrated, which would allow for estimates of  
555 prey capture attempts and energetic expenditure to be calculated and used to evaluate foraging  
556 effort/efficiency (Viviant *et al.*, 2010; Watanabe and Takahashi, 2013; Richard *et al.*, 2016).  
557 Achieving this would greatly increase our understanding of how physical habitats impact prey  
558 availability for marine predators and facilitate trophic transfer (Embling *et al.*, 2012), whilst also  
559 elucidating site and species specificity (Waggitt *et al.*, 2017) alongside the drivers of spatio-temporal  
560 variability in marine mammal and seabird distributions (Certain *et al.*, 2007). Such efforts may also



561 reveal the importance of other, lesser studied structures. For example, to our knowledge, the  
562 ecological significance of bottom fronts (which may be important to deeper diving predators) is yet  
563 to be investigated (Hill *et al.*, 2008). In addition, despite some evidence suggesting Langmuir  
564 circulation cells are exploited by surface feeding seabirds in near-coastal regions (Goss *et al.*, 1997;  
565 Ladd *et al.*, 2005), the importance of these features further offshore is yet to be explored (Barstow,  
566 1983). Distinguishing the way in which individuals perceive their environment via knowledge  
567 transfer (Machovsky-Capuska *et al.*, 2014), learning and memory (Regular *et al.*, 2013; Grecian *et*  
568 *al.*, 2018), sight (Bodey *et al.*, 2014; Tremblay *et al.*, 2014; Bairos-Novak *et al.*, 2015) and smell  
569 (Savoca and Nevitt, 2014) would also be beneficial, as would an increased knowledge of  
570 immature/juvenile foraging behaviours and how these develop through time (de Grissac *et al.*, 2017;  
571 Votier *et al.*, 2017; Grecian *et al.*, 2018). Further inter-taxa research (e.g. marine mammals versus  
572 seabirds, planktivores versus piscivores, and surface feeders versus divers) would compliment this,  
573 and provide additional insight of the selection pressures that have shaped the evolution of the at-sea  
574 behaviours of these animals, and driven the necessary adaptations required for foraging in dynamic  
575 waters. Such investigations may also be useful for assessing the potential of these taxa to adapt in  
576 response to climate change. Finally, there is a distinct lack of studies determining the importance of  
577 oceanographic habitat features at a population level, which should be addressed. Future research  
578 should aim to fill these gaps if we are to improve our understanding of habitat use by marine mammals  
579 and seabirds across shelf-seas. However, achieving this will require novel methodological  
580 techniques. Adaptive survey designs (Embling *et al.*, 2012; Suberg *et al.*, 2014; Waggitt and Scott,  
581 2014; Waggitt *et al.*, 2016a; Benjamins *et al.*, 2017) that incorporate active and passive acoustics  
582 (Williamson *et al.*, 2015; Benoit-Bird and Lawson, 2016; Macaulay *et al.*, 2017; Malinka *et al.*, 2018)  
583 alongside underwater videography (Machovsky-Capuska *et al.*, 2011; Crook and Davoren, 2014) may  
584 prove particularly useful, as will animal borne biologging via the attachment of accelerometers  
585 (Viviant *et al.*, 2010; Watanabe and Takahashi, 2013), cameras (Votier *et al.*, 2013; Watanabe and

586 Takahashi, 2013; Tremblay *et al.*, 2014), GPS loggers (Yoda *et al.*, 2014), oceanographic sensors  
587 (Charrassin *et al.*, 2008) and satellite relay systems (e.g. the Argos satellite system; Photopoulou *et*  
588 *al.*, 2015; CLS, 2016; Cox *et al.*, 2018). Moreover, outputs from remote-sensing and oceanographic  
589 modelling can be used to initially identify discrete features of interest (Scales *et al.*, 2014a; Waggitt  
590 *et al.*, 2016a), and/or provide data over extended areas/time-spans/retrospectively. This may require  
591 novel processing and analytical routines, that can characterise and link bio-physical processes to  
592 information on animal behaviour and movement (d'Ovidio *et al.*, 2004; Miller, 2009; Embling *et al.*,  
593 2012; Boyd *et al.*, 2014; Bayle *et al.*, 2015; Mattei *et al.*, 2018; Pirotta *et al.*, 2018), with particular  
594 attention paid towards the spatio-temporal scales of investigations (Figure 2, Table 1; Mannocci *et*  
595 *al.*, 2017; Scales *et al.*, 2017). Ideally, multiple approaches should be combined and integrated with  
596 demographic data, which would yield an overview of ecosystem dynamics unprecedented in detail  
597 (Boyd *et al.*, 2015; Barbraud *et al.*, 2017; Carroll *et al.*, 2017), and can later be used to force individual  
598 and population based models to determine the adaptability of these environments to future change  
599 (e.g. anthropogenic or climatically driven; Boyd *et al.*, 2016; Barbraud *et al.*, 2017).

## 600 **8 Applications to conservation management**

601 Over the last 20-30 years, marine management and policy has started to evolve from single species  
602 based protocols and strategies (typically tailored to a specific fishery/sector), to more holistic methods  
603 that consider ecosystems in their entirety, and incorporate more precautionary conservation measures  
604 (e.g. the European Marine Strategy Framework Directive 2008/56/EC; Pikitch *et al.*, 2004; Arkema  
605 *et al.*, 2006; Curtin and Prellezo, 2010). Key to this is the preservation of core shelf-sea habitats,  
606 such as those oceanographic features identified here as favourable for foraging by marine mammals  
607 and seabirds (Hooker and Gerber, 2004; Taylor *et al.*, 2005; Heithaus *et al.*, 2008; Game *et al.*, 2009;  
608 Dickey-Collas *et al.*, 2017; Sherley *et al.*, 2017). However, achieving adequate protection is  
609 complicated by the diverse nature of such structures, which occur over a range of spatio-temporal  
610 scales (Figure 2 and Table 1), and function via a variety of bio-physical mechanisms that may impact

611 prey availability in different ways (e.g. through inducing changes in depth distribution, persistent,  
612 predictability, abundance and/or behaviour; see section 6). A sophisticated understanding of these  
613 dynamics can be used to effectively implement appropriate and customised conservation management  
614 strategies (Authier *et al.*, 2017).

615 For example, initial implementations of holistic management have focused on fixed area based  
616 protection through the designation of marine protected areas (MPAs; Hyrenbach, 2000; Hooker and  
617 Gerber, 2004). Here, the aim is to reduce overlap with spatially explicit threats (e.g. commercial  
618 fisheries, marine renewables and maritime traffic) that may cause direct mortality and/or disrupt  
619 accessibility to favoured habitats (e.g. through prey depletion or displacement; Pichegru *et al.*, 2010;  
620 Gormley *et al.*, 2012). However, while persistent and predictable bathymetrically tied tidal features  
621 (e.g. offshore banks, channels and island wakes) may be particularly well suited to such measures, to  
622 accommodate individuals relying on habitats that are variable through space and time (e.g. upwelling  
623 and tidal-mixing fronts), adaptive approaches are required. A recent solution to this is dynamic ocean  
624 management (DOM), defined as management that is adjustable through space and time in response  
625 to the shifting nature of the ocean and its users (Hobday *et al.*, 2014; Lewison *et al.*, 2015; Maxwell  
626 *et al.*, 2015). Such methods can thus allow for geographical changes in habitat locations with, for  
627 example, prevailing environmental conditions (e.g. position in spring-neap cycle alongside short term  
628 weather events, seasonal trends and longer term climatic changes; Nahas *et al.*, 2005; Bograd *et al.*,  
629 2009a; Pisoni *et al.*, 2015). However, implementing DOM requires multidisciplinary and novel  
630 monitoring approaches, so as boundaries are effectively designated and modified (Hazen *et al.*, 2018).  
631 Moreover, attention needs to be paid towards the spatio-temporal scales over which data is acquired  
632 and protection implemented, which should reflect the characteristics and spatio-temporal variability  
633 of an oceanographic feature (Figure 2, Table 2; Mannocci *et al.*, 2017; Scales *et al.*, 2017). Satellite  
634 remote-sensing can aid in this by allowing oceanographic features to be tracked both instantaneously  
635 in near real time and over longer periods, although this is only applicable where a distinct surface

636 signature is presented (Miller, 2009; Scales *et al.*, 2014a). Sensors deployed on diving animals  
637 autonomous/unmanned survey vehicles and/or moorings may compliment such information  
638 (Charrassin *et al.*, 2008; Suberg *et al.*, 2014; Photopoulou *et al.*, 2015), as can outputs from  
639 oceanographic and statistical modelling (Brodie *et al.*, 2018; Mattei *et al.*, 2018). Where stationary  
640 management is preferred, long-term time series data may be used to develop buffer zones that extend  
641 the boundaries of a fixed MPA, such that fluctuations in the spatio-temporal occurrence of a habitat  
642 feature is captured (e.g. the entire spring-neap/weather dependent range of a tidal-mixing front; Nahas  
643 *et al.*, 2005; Grantham *et al.*, 2011; Pisoni *et al.*, 2015). Such strategies should still be evaluated at  
644 regular intervals to assess potential geographical shifts in response to climate change (Queiros *et al.*,  
645 2016).

646 A shift towards management strategies than consider habitat hydrology in addition to geography is  
647 also beneficial to ensuring that the functioning of oceanographic features favoured for foraging is  
648 maintained (Dickey-Collas *et al.*, 2017). For example, anthropogenically generated structural  
649 changes to the marine environment (e.g. marine renewable energy installations; MREIs) may alter  
650 the bio-physical and spatio-temporal characteristics of oceanographic environments (e.g.  
651 interruptions to near coastal current regimes may alter and/or manifest tidally driven features such as  
652 hydrographic fronts, wakes and localised upwelling systems; Brostrom, 2008; Shields *et al.*, 2011;  
653 Benjamins *et al.*, 2015; Fraser *et al.*, 2018). This may cause shifts in the geographical locations at  
654 which these structures occur and impact prey availability (e.g. depth distribution and predictability;  
655 Becker and Beissinger, 2003), and thus should be carefully considered during the planning stages of  
656 development projects. Impact assessments at sites where oceanographic features favoured for  
657 foraging are present need to consider how variability in the dynamics of such structures influence  
658 patterns in area use by marine mammals and seabirds, and thus the validity of associated evaluations  
659 (Benjamins *et al.*, 2017; Cox *et al.*, 2017). Climate change impacts will likely also alter the  
660 functioning of these habitats. Increases in the frequency and intensity of extreme climatic (e.g. ENSO

661 associated changes in upwelling; Cai *et al.*, 2014) and weather (e.g. storm induced turbulent mixing;  
662 Young *et al.*, 2011) events may again, modify the dynamics and geographical locations of critical  
663 oceanographic features (Hazen *et al.*, 2013; Sherley *et al.*, 2017), such as upwelling fronts, the  
664 pycnocline and tidal-mixing fronts (Ropert-Coudert *et al.*, 2009a; Pisoni *et al.*, 2015). For example,  
665 decreases in the reproductive outputs of a number of seabirds have been linked to changes in the  
666 availability of oceanographically generated foraging habitats following irregularities in prevailing  
667 climatic and weather conditions (Hennicke and Culik, 2005; Durant *et al.*, 2006; Scott *et al.*, 2006;  
668 Ropert-Coudert *et al.*, 2009a). Minimising the impacts of this will require adaptive, innovative and  
669 precautionary management strategies that minimise cumulative stressors (Field and Francis, 2006;  
670 Lester *et al.*, 2010; Sherley *et al.*, 2017), particularly since our understanding of how ecosystems will  
671 cope and respond to such alterations is largely unknown. Again, MPAs and DOM informed by  
672 studies on the dynamics of oceanographic features favoured for foraging will likely play an important  
673 role in this (Halpern *et al.*, 2010; Grantham *et al.*, 2011; Briscoe *et al.*, 2016; Dickey-Collas *et al.*,  
674 2017).

## 675 **9 Conclusions**

676 A range of oceanographic features are favoured for foraging by marine mammals and seabirds across  
677 shelf-seas in mid-latitude temperate zones. Whilst associations are diverse and variable in nature  
678 (both between sites and across species), in the majority of cases intricate interactions between  
679 bathymetry and tidal currents play a dominant role, alongside patterns in seasonal stratification and  
680 shelf-edge upwelling. The attractiveness of a favoured oceanographic feature appears to stem from  
681 persistent and/or predictable increases in prey accessibility which facilitates foraging. Changes in  
682 prey abundance and density, behaviour and depth distribution are fundamental to this, and in a number  
683 of cases have been shown to improve foraging efficiencies. However, our knowledge of interactions  
684 between marine predators and oceanographic features favoured for foraging is far from complete, and  
685 future work should aim to further our understanding of the functional mechanisms linking bio-

686 physical processes, prey and marine mammals and seabirds. In many instances, detailed and  
687 simultaneous three-dimensional measurements of sub-surface oceanography, prey densities and  
688 distributions alongside marine predator behaviours (across three-dimensions) are lacking, and this  
689 should be addressed. Such efforts may also elucidate the importance of lesser studied features such  
690 as bottom fronts and Langmuir circulation cells. A better understanding of how predators perceive  
691 their environment and develop foraging strategies during immature/juvenile stages would also be  
692 beneficial, as would comparative inter-taxa research and estimates of the importance of  
693 oceanographic habitat features at a population level. Knowledge of the bio-physical processes that  
694 underlie habitat use by marine mammals and seabirds across shelf-seas should be used to inform  
695 future conservation management and policy. This will require improvements in the monitoring of  
696 oceanographic conditions such that adaptive strategies can be implemented which, where necessary,  
697 can evolve through space and time in response to the dynamic nature of the ocean. This would aid  
698 the preservation and protection of oceanographic features that facilitate trophic transfer, and are thus  
699 critical to the functioning of shelf-sea environments. Such holistic approaches are vital to ensuring  
700 the future health of these complex ecosystems.

## 701 **Acknowledgements**

702 This work was funded by a PhD studentship to SLC by the Natural Environment Research Council  
703 (NERC; NE/J500380/1). We thank GL Hunt and one anonymous reviewer for comments on earlier  
704 versions of this manuscript.

## **References**

- Abraham, C. L., and Sydeman, W. J. 2004. Ocean climate, euphausiids and auklet nesting: inter-annual trends and variation in phenology, diet and growth of a planktivorous seabird, *Ptychoramphus aleuticus*. *Marine Ecology Progress Series*, 274: 235–250.
- Acha, E. M., Mianzan, H. W., Guerrero, R. A., Favero, M., and Bava, J. 2004. Marine fronts at the continental shelves of austral South America: physical and ecological processes. *Journal of Marine Systems*, 44: 83–105.

- Ainley, D. G., Spear, L. B., Tynan, C. T., Barth, J. A., Pierce, S. D., Ford, R. G., and Cowles, T. J. 2005. Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. *Deep-Sea Research II*, 52: 123–143.
- Ainley, D. G., Dugger, K. D., Ford, R. G., Pierce, S. D., Reese, D. C., Brodeur, R. D., Tynan, C. T., *et al.* 2009. Association of predators and prey at frontal features in the California Current: Competition, facilitation, and co-occurrence. *Marine Ecology Progress Series*, 389: 271–294.
- Aleman, D., Acha, E. M., and Iribarne, O. 2009. The relationship between marine fronts and fish diversity in the Patagonian Shelf Large Marine Ecosystem. *Journal of Biogeography*, 36: 2111–2124.
- Allredge, A. L., and Hamner, W. M. 1980. Recurring aggregation of zooplankton by a tidal current. *Estuarine and Coastal Marine Science*, 10: 31–37.
- Allen, J. I., Siddorn, J. R., Blackford, J. C., and Gilbert, F. J. 2004. Turbulence as a control on the microbial loop in a temperature seasonally stratified marine systems model. *Journal of Sea Research*, 52: 1–20.
- Anderwald, P., Evans, P. G. H., Dyer, R., Dale, A., Wright, P. J., and Hoelzel, A. R. 2012. Spatial scale and environmental determinants in minke whale habitat use and foraging. *Marine Ecology Progress Series*, 450: 259–274.
- Arkema, K. K., Abramson, S. C., and Dewsbury, B. M. 2006. Marine ecosystem-based management: From characterisation to implementation. *Frontiers in Ecology and the Environment*, 4: 525–532.
- Authier, M., Spitz, J., Blanck, A., and Ridoux, V. 2017. Conservation science for marine megafauna in Europe: historical perspectives and future directions. *Deep-Sea Research II*, 141: 1–7.
- Avila, I. C., Kaschner, K., and Dormann, C. F. 2018. Current global risks to marine mammals: taking stock of the threats. *Biological Conservation*, 221: 44–58.
- Azzellino, A., Gaspari, S., Airoidi, S., and Nani, B. 2008. Habitat use and preferences of cetaceans along the continental slope and the adjacent pelagic waters in the western Ligurian Sea. *Deep-Sea Research I*, 55: 296–323.
- Bailey, H., and Thompson, P. 2010. Effect of oceanographic features on fine-scale foraging movements of bottlenose dolphins. *Marine Ecology Progress Series*, 418: 223–233.
- Bairos-Novak, K. R., Crook, K. A., and Davoren, G. K. 2015. Relative importance of local enhancement as a search strategy for breeding seabirds: An experimental approach. *Animal Behaviour*, 106: 71–78.
- Barbraud, C., Bertrand, A., Bouchon, M., Chaigneau, A., Delord, K., Demarcq, H., Gimenez, O., *et al.* 2017. Density dependence, prey accessibility and prey depletion by fisheries drive Peruvian seabird population dynamics. *Ecography*, 000: 1–10.
- Barstow, S. F. 1983. The ecology of Langmuir circulation: a review. *Marine Environmental Research*, 9: 211–236.
- Baumgartner, M. F. 1997. The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the Northern Gulf of Mexico. *Marine Mammal Science*, 13: 614–638.

- Baumgartner, M. F., and Mate, B. R. 2003. Summertime foraging ecology of North Atlantic right whales. *Marine Ecology Progress Series*, 264: 123–135.
- Bayle, S., Monestiez, P., Guinet, C., and Nerini, D. 2015. Moving towards finer scales in oceanography: predictive linear functional model of Chlorophyll *a* profile from light data. *Progress in Oceanography*, 134: 221–231.
- Baylis, A. M. M., Page, B., and Goldsworthy, S. D. 2008. Effect of seasonal changes in upwelling activity on the foraging locations of a wide-ranging central-placed forager, the New Zealand fur seal. *Canadian Journal of Zoology*, 86: 774–789.
- Beaugrand, G., and Kirby, R. R. 2010. Climate, plankton and cod. *Global Change Biology*, 16: 1268–1280.
- Becker, B. H., and Beissinger, S. R. 2003. Scale-dependent habitat selection by a nearshore seabird, the marbled murrelet, in a highly dynamic upwelling system. *Marine Ecology Progress Series*, 256: 243–255.
- Becker, P. H., Frank, D., and Sudmann, S. R. 1993. Temporal and spatial pattern of common tern (*Sterna hirundo*) foraging in the Wadden Sea. *Oecologia*, 93: 389–393.
- Begg, G. S., and Reid, J. B. 1997. Spatial variation in seabird density at a shallow sea tidal mixing front in the Irish Sea. *ICES Journal of Marine Science*, 54: 552–565.
- Benjamins, S., Dale, A., Hastie, G. D., Waggitt, J. J., Lea, M. A., Scott, B. E., and Wilson, B. 2015. Confusion reigns? A review of marine megafauna interactions with tidal-stream environments. *Oceanography and Marine Biology: An Annual Review*, 53: 1–54.
- Benjamins, S., van Geel, N., Hastie, G., Elliott, J., and Wilson, B. 2017. Harbour porpoise distribution can vary at small spatiotemporal scales in energetic habitats. *Deep-Sea Research Part II*, 141: 191–202.
- Bennison, A., Bearhop, S., Bodey, T. W., Votier, S. C., Grecian, W. J., Wakefield, E. D., Hamer, K. C., *et al.* 2017. Search and foraging behaviours from movement data: a comparison of methods. *Ecology and Evolution*.
- Benoit-Bird, K. J., Kuletz, K., Heppell, S., Jones, N., and Hoover, B. 2011. Active acoustic examination of the diving behaviour of murrelets foraging on patchy prey. *Marine Ecology Progress Series*, 443: 217–235.
- Benoit-Bird, K. J., Battaile, B. C., Heppell, S. A., Hoover, B., Irons, D., Jones, N., Kuletz, K. J., *et al.* 2013. Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PLoS ONE*, 8: e53348.
- Benoit-Bird, K. J., and Lawson, G. L. 2016. Ecological insights from pelagic habitats acquired using active acoustic techniques. *Annual Review of Marine Science*, 8: 21.1-21.28.
- Bertram, D. F., Mackas, D. L., Welch, D. W., Boyd, W. S., Ryder, J. L., Galbraith, M., Hedd, A., *et al.* 2017. Variation in zooplankton prey distribution determines marine foraging distributions of breeding Cassin's Auklet. *Deep-Sea Research I*, 129: 32–40.



- Bertrand, A., Gerlotto, F., Bertrand, S., Gutiérrez, M., Alza, L., Chipollini, A., Diaz, E., *et al.* 2008. Schooling behaviour and environmental forcing in relation to anchoveta distribution: An analysis across multiple spatial scales. *Progress in Oceanography*, 79: 264–277.
- Bertrand, A., Grados, D., Colas, F., Bertrand, S., Capet, X., Chaigneau, A., Vargas, G., *et al.* 2014. Broad impacts of fine-scale dynamics on seascape structure from zooplankton to seabirds. *Nature communications*, 5.
- Bertrand, S., Joo, R., Smet, C. A., Tremblay, Y., Barbraud, C., and Weimerskirch, H. 2012. Local depletion by a fishery can affect seabird foraging. *Journal of Applied Ecology*, 49: 1168–1177.
- Bjorkstedt, E. P., Rosenfeld, L. K., Grantham, B. A., Shkedy, Y., and Roughgarden, J. 2002. Distributions of larval rockfishes *Sebastes* spp. across nearshore fronts in a coastal upwelling region. *Marine Ecology Progress Series*, 242: 215–228.
- Black, B. A., Schroeder, I. D., Sydeman, W. J., Bograd, S. J., Wells, B. K., and Schwing, F. B. 2011. Winter and summer upwelling modes and their biological importance in the California Current Ecosystem. *Global Change Biology*, 17: 2536–2545.
- Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., Hazen, E. L., *et al.* 2011. Tracking apex marine predator movements in a dynamic environment. *Nature*, 475: 86–90.
- Bodey, T. W., Jessopp, M. J., Votier, S. C., Gerritsen, H. D., Cleasby, I. R., Hamer, K. C., Patrick, S. C., *et al.* 2014. Seabird movement reveals the ecological footprint of fishing vessels. *Current Biology*, 24: 514–515.
- Boersma, P. D., Rebstock, G. A., Frere, E., and Moore, S. E. 2009. Following the fish: Penguins and productivity in the South Atlantic. *Ecological Monographs*, 79: 59–76.
- Boersma, P. D., and Rebstock, G. A. 2009. Foraging distance affects reproductive success in Magellanic penguins. *Marine Ecology Progress Series*, 375: 263–275.
- Bograd, S. J., Schroeder, I., Sarkar, N., Qiu, X., Sydeman, W. J., and Schwing, F. B. 2009a. Phenology of coastal upwelling in the California Current. *Geophysical Research Letters*, 36: L01602.
- Bograd, S. J., Schroeder, I., Sarkar, N., Qiu, X., Sydeman, W. J., and Schwing, F. B. 2009b. Phenology of coastal upwelling in the California Current. *Geophysical Research Letters*, 36: L01602.
- Borstad, G., Crawford, W., Hipfner, J. M., Thomson, R., and Hyatt, K. 2011. Environmental control of the breeding success of rhinoceros auklets at Triangle Island, British Columbia. *Marine Ecology Progress Series*, 424: 285–302.
- Bost, C. A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J. B., Guinet, C., Ainley, D. G., *et al.* 2009. The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems*, 78: 363–376.
- Bourne, W. R. P., and Clark, G. C. 1984. The occurrence of birds and garbage at the Humboldt front off Valparaiso, Chile. *Marine Pollution Bulletin*, 15: 34–344.

- Boyd, C., Punt, A. E., Weimerskirch, H., and Bertrand, S. 2014. Movement models provide insights into variation in the foraging effort of central place foragers. *Ecological Modelling*, 286: 13–25.
- Boyd, C., Castillo, R., Hunt, G. L., Punt, A. E., VanBlaricom, G. R., Weimerskirch, H., and Bertrand, S. 2015. Predictive modelling of habitat selection by marine predators with respect to the abundance and depth distribution of pelagic prey. *Journal of Animal Ecology*, 84: 1575–1588.
- Boyd, C., Grunbaum, D., Hunt Jr, G. L., Punt, A. E., Weimerskirch, H., and Bertrand, S. 2016. Effects of variation in the abundance and distribution of prey on the foraging success of central place foragers. *Journal of Applied Ecology*.
- Briggs, K. T., Dettman, K. F., Lewis, D. B., and Tyler, W. B. 1984. Phalarope feeding in relation to autumnal upweeling off California. *In* *Marine birds: their feeding ecology and commercial fisheries relationships*, pp. 51–64. Ed. by D. N. Nettleship, G. A. Sanger, and P. A. Springer. Canadian Wildlife Service Special Publications, Ottawa, Canada.
- Brigolin, D., Girardi, P., Miller, P. I., Xu, W., Nachite, D., Zucchetto, M., and Pranovi, F. 2018. Using remote sensing indicators to investigate the association of landings with fronts: applications to the Alboran Sea (western Mediterranean Sea). *Fisheries Oceanography*: 1–9.
- Briscoe, D. K., Maxwell, S. M., Kudela, R., Crowder, L. B., and Croll, D. 2016. Are we missing important areas in pelagic marine conservation? Redefining conservation hotspots in the ocean. *Endangered Species Research*, 39: 229–237.
- Brodie, S., Jacox, M. G., Bograd, S. J., Welch, H., Dewar, H., Scales, K. L., Maxwell, S. M., *et al.* 2018. Integrating dynamic subsurface habitat metrics into species distribution models. *Frontiers in Marine Science*: In press.
- Brostrom, G. 2008. On the influence of large wind farms on the upper ocean circulation. *Journal of Marine Systems*, 74: 585–591.
- Brown, D. D., Kays, R., Wikelski, M., Wilson, R., and Klimley, A. P. 2013. Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry*: 1:20.
- Brown, R. G. B., and Gaskin, D. E. 1986. The pelagic ecology of the Grey and Red-necked Phalaropes *Phalaropus fulicarius* and *P. lobatus* in the Bay of Fundy, eastern Canada. *IBIS*, 130: 234–250.
- Brown, R. G. B. 1988. Oceanographic factors as determinants of the winter range of the Dovekie (*Alle alle*) off Atlantic Canada. *Colonial Waterbirds*, 11: 176–180.
- Cai, W., Borlace, S., Languagne, M., Van Rensch, P., Collins, M., Vecchi, G., Timmermann, A., *et al.* 2014. Increasing frequency of extreme El Nino events due to greenhouse warming. *Nature Climate Change*, 4: 111–116.
- Cairns, D. K. 1988. Seabirds as indicators of marine food supplies. *Biological Oceanography*, 5: 261–271.
- Cairns, D. K., and Schneider, D. C. 1990. Hot spots in cold water: feeding habitat selection by Thick-billed Murres. *Studies in Avian Biology*, 14: 52–60.

- Cairns, J. L., and LaFond, E. C. 1966. Periodic motions of the seasonal thermocline along the southern Californian coast. *Journal of Geophysical Research*, 71: 3903–3914.
- Camphuysen, C. J., and van der Meer, J. 2005. Wintering seabirds in West Africa: Foraging hotspots off Western Sahara and Mauritania driven by upwelling and fisheries. *African Journal of Marine Science*, 27: 427–437.
- Capet, X., McWilliams, J. C., Molemaker, M. J., and Shchepetkin, A. F. 2008. Mesoscale to submesoscale transition in the California Current System. Part II. Frontal processes. *Journal of Physical Oceanography*, 38: 44–64.
- Carroll, G., Cox, M., Harcourt, R., Pitcher, B. J., Slip, D., and Jonsen, I. 2017. Hierarchical influences of prey distribution on patterns of prey capture by a marine predator. *Functional Ecology*.
- Carter, M. I. D., Bennett, K. A., Embling, C. B., Hosegood, P., and Russell, D. J. F. 2016. Navigating uncertain waters: a critical review of inferring foraging behaviour from location and dive data in pinnipeds. *Movement Ecology*, 4.
- Certain, G., Bellier, E., Planque, B., and Bretagnolle, V. 2007. Characterising the temporal variability of the spatial distribution of animals: an application to seabirds at sea. *Ecography*, 30: 695–708.
- Charrassin, J. B., Hindell, M., Rintoul, S. R., Roquet, F., Sokolov, S., Biuw, M., Costa, D., *et al.* 2008. Southern Ocean frontal structure and sea-ice formation rates revealed by elephant seals. *PNAS*, 105: 11634–11639.
- Chenoweth, E. M., Gabriele, C. M., and Hill, D. F. 2011. Tidal influences on humpback whale habitat selection near headlands. *Marine Ecology Progress Series*, 423: 279–289.
- Cheriton, O. M., McManus, M. A., Holliday, D. V., Greenlaw, C. F., Donaghay, P. L., and Cowles, T. J. 2007. Effects of mesoscale physical processes on thin zooplankton layers at four sites along the west coast of the U.S. *Estuaries and Coasts*, 30: 575–590.
- Cheriton, O. M., McManus, M. A., Steinbeck, J. V., Stacey, M. T., and Sullivan, J. M. 2010. Towed vehicle observations of thin layer structure and a low-salinity intrusion in Northern Monterey Bay, CA. *Continental Shelf Research*, 30: 39–49.
- Choi, B.-J., and Wilkin, J. L. 2007. The effect of wind on the dispersal of the Hudson river plume. *Journal of Physical Oceanography*, 37: 1878–1897.
- Cloern, J. E. 1991. Tidal stirring and phytoplankton bloom dynamics in an estuary. *Journal of Marine Research*, 49: 203–221.
- CLS. 2016. Argos user's manual: worldwide tracking and environmental monitoring by satellite.
- Cole, E.-L., Waggitt, J. J., Hedenstrom, A., Piano, M., Holton, M. D., Borger, L., and Shepard, E. L. C. 2018. The ornithodolite as a tool to quantify animal space use and habitat selection: a case study with birds diving in tidal waters. *Integrative Zoology*: In press.
- Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G., and Butler, P. J. 2004. Biotelemetry: A mechanistic approach to ecology. *Trends in Ecology and Evolution*, 19: 334–343.

- Cotté, C., and Simard, Y. 2005. Formation of dense krill patches under tidal forcing at whale feeding hot spots in the St. Lawrence Estuary. *Marine Ecology Progress Series*, 288: 199–210.
- Couperus, B., Gastauer, S., Fassler, S. M. M., Tulp, I., van der Veer, H. W., and Poos, J. J. 2016. Abundance and tidal behaviour of pelagic fish in the gateway to the Wadden Sea. *Journal of Sea Research*, 109: 42–51.
- Cox, S. L., Scott, B. E., and Camphuysen, C. J. 2013. Combined spatial and temporal processes identify links between pelagic prey species and seabirds. *Marine Ecology Progress Series*, 479: 203–221.
- Cox, S. L., Miller, P. I., Embling, C. B., Scales, K. L., Bicknell, A. W. J., Hosegood, P., Morgan, G., *et al.* 2016. Seabird diving behaviour reveals the functional significance of shelf-sea fronts as foraging hotspots. *Royal Society Open Science*, 3: 160317.
- Cox, S. L., Witt, M. J., Embling, C. B., Godley, B. J., Hosegood, P., Miller, P. I., Votier, S. C., *et al.* 2017. Temporal patterns in habitat use by small cetaceans at an oceanographically dynamic marine renewable energy test site in the Celtic Sea. *Deep-Sea Research Part II*, 141: 178–190.
- Cox, S. L., Orgeret, F., Gesta, M., Rodde, C., Heizer, I., Weimerskirch, H., and Guinet, C. 2018. Processing of acceleration and dive data on-board satellite relay tags to investigate diving and foraging performance in free-ranging marine predators. *Methods in Ecology and Evolution*, 9: 64–77.
- Coyle, K. O., Hunt, G. L., Decker, M. B., and Weingartner, T. J. 1992. Murre foraging, epibenthic sound scattering and tidal advection over shoal near St. George Island, Bering Sea. *Marine Ecology Progress Series*, 83: 1–14.
- Coyle, K. O., and Cooney, R. T. 1993. Water column sound scattering and hydrography around the Pribilof Islands, Bering Sea. *Continental Shelf Research*, 13: 803–827.
- Coyle, K. O., Weingartner, T. J., and Hunt, G. L. 1998. Distribution of acoustically determined biomass and major zooplankton taxa in the upper mixed layer relative to water masses in the western Aleutian Islands. *Marine Ecology Progress Series*, 165: 95–108.
- Crocker, D. E., Costa, D. P., Le Boeuf, B. J., Webb, P. M., and Houser, D. S. 2006. Impact of El Nino on the foraging behaviour of female northern elephant seals. *Marine Ecology Progress Series*, 309: 1–10.
- Croll, D. A. 1990. Physical and biological determinants of the abundance, distribution and diet of the common murre in Monterey Bay, California. *Studies in Avian Biology*, 14: 139–148.
- Croll, D. A., Marinovic, B., Benson, S., Chavez, F. P., Black, N., Ternullo, R., and Tershy, B. R. 2005. From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology Progress Series*, 289: 117–130.
- Crook, K. A., and Davoren, G. K. 2014. Underwater behaviour of common murre foraging on capelin: Influences of prey density and antipredator behaviour. *Marine Ecology Progress Series*, 501: 279–290.

- Curtin, R., and Prellezo, R. 2010. Understanding marine ecosystem based management: a literature review. *Marine Policy*, 34: 821–830.
- Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R. W., Mills, J. A., *et al.* 2011. Global seabird response to forage fish depletion - One-third for the birds. *Science*, 334: 1703–1706.
- Cushing, D. H. 1975. *Marine ecology and fisheries*. Cambridge University Press.
- d'Ovidio, F., Fernandez, V., Hernandez-Garcia, E., and Lopez, C. 2004. Mixing structures in the Mediterranean Sea from finite-size Lyapunov exponents. *Geophysical Research Letters*, 31: L17203.
- Dalla Rosa, L., Ford, J. K. B., and Trites, A. W. 2012. Distribution and relative abundance of humpback whales in relation to environmental variables in coastal British Columbia waters. *Continental Shelf Research*, 36: 89–104.
- Davies, K. T. A., Ross, T., and Taggart, C. T. 2013. Tidal and subtidal currents affect deep aggregations of right whale prey, *Calanus* spp., along a shelf-basin margin. *Marine Ecology Progress Series*, 479: 263–282.
- Davoren, G. K. 2013. Distribution of marine predator hotspots explained by persistent areas of prey. *Marine biology*, 160: 3043–3058.
- De Boer, M. N., Simmonds, M. P., Reijnders, P. J. H., and Aarts, G. 2014. The influence of topographic and dynamic cyclic variables on the distribution of small cetaceans in a shallow coastal system. *PLoS ONE*, 9: e86331.
- de Grissac, S., Bartumeus, F., Cox, S. L., and Weimerskirch, H. 2017. Early-life foraging: behavioural responses of newly fledged albatrosses to environmental conditions. *Ecology and Evolution*, in press.
- Decker, M. B., and Hunt, G. L. 1996. Foraging by murre ( *Uria* spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. *Marine Ecology Progress Series*, 139: 1–10.
- Dickey-Collas, M., McQuatters-Gollop, A., Bresnan, E., Kraberg, A. C., Manderson, J. P., Nash, R. D. M., Otto, S. A., *et al.* 2017. Pelagic habitat: exploring the concept of good environmental status. *ICES Journal of Marine Science*.
- Doniol-Valcroze, T., Berteaux, D., Larouche, P., and Sears, R. 2007. Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. *Marine Ecology Progress Series*, 335: 207–216.
- Dragon, A., Bar-Hen, A., Monestiez, P., and Guinet, C. 2012. Horizontal and vertical movements as predictors of foraging success in a marine predator. *Marine Ecology Progress Series*, 447: 243–257.
- Drew, G. S., Piatt, J. F., and Hill, D. F. 2013. Effects of currents and tides on fine-scale use of marine bird habitats in a Southeast Alaska hotspot. *Marine Ecology Progress Series*, 487: 275–286.
- Duffy-Echevarria, E. E., Connor, R. C., and St Aubin, D. J. 2008. Observations of strand-feeding behaviour by bottlenose dolphins (*Tursiops truncatus*) in Bull creek, South Carolina. *Marine Mammal Science*, 24: 202–206.

- Durant, J. M., Anker-Nilssen, T., and Stenseth, N. C. 2006. Ocean climate prior to breeding affects the duration of the nestling period in the Atlantic puffin. *Biology Letters*, 2: 628–631.
- Durant, J. M., Hjermann, D. O., Ottersen, G., and Stenseth, N. C. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33: 271–283.
- Durazo, R., Harrison, N. M., and Hill, A. E. 1998. Seabird observations at a tidal mixing front in the Irish Sea. *Estuarine, Coastal and Shelf Science*, 47: 153–164.
- Durham, W. M., Kessler, J. O., and Stocker, R. 2009. Disruption of vertical motility by shear triggers formation of thin phytoplankton layers. *Science*, 323: 1067–1070.
- Embling, C. B., Gillibrand, P. A., Gordon, J., J. S., Stevick, P. T., and Hammond, P. S. 2010. Using habitat models to identify suitable sites for marine protected areas for harbour porpoises (*Phocoena phocoena*). *Biological Conservation*, 143: 267–279.
- Embling, C. B., Illian, J., Armstrong, E., Van der Kooij, J., Sharples, J., Camphuysen, C. J., and Scott, B. E. 2012. Investigating fine-scale spatio-temporal predator-prey patterns in dynamic marine ecosystems: A functional data analysis approach. *Journal of Applied Ecology*, 49: 481–492.
- Embling, C. B., Sharples, J., Armstrong, E., Palmer, M. R., and Scott, B. E. 2013. Fish behaviour in response to tidal variability and internal waves over a shelf sea bank. *Progress in Oceanography*, 117: 106–117.
- Enstipp, M. R., Grémillet, D., and Jones, D. R. 2007. Investigating the functional link between prey abundance and seabird predatory performance. *Marine Ecology Progress Series*, 331: 267–279.
- Epstein, A. W., and Beardsley, R. C. 2001. Flow-induced aggregation of plankton at a front: A 2-D Eulerian model study. *Deep-Sea Research II*, 48: 395–418.
- Fauchald, P., and Erikstad, K. E. 2002. Scale-dependent predator-prey interactions: The aggregative response of seabirds to prey under variable prey abundance and patchiness. *Marine Ecology Progress Series*, 231: 279–291.
- Fauchald, P. 2009. Spatial interaction between seabirds and prey: Review and synthesis. *Marine Ecology Progress Series*, 391: 139–151.
- Fearnhead, P. G. 1975. On the formation of fronts by tidal mixing around the British Isles. *Deep-Sea Research*, 22: 311–321.
- Fertl, D., and Wilson, B. 1997. Bubble use during prey capture by a lone bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals*, 23: 113–114.
- Field, J. C., and Francis, R. C. 2006. Considering ecosystem-based fisheries management in the California Current. *Marine Policy*, 30: 552–569.
- Forney, K. A., and Barlow, J. 1998. Seasonal patterns in the abundance and distribution of California cetaceans, 1991-1992. *Marine Mammal Science*, 14: 460–489.

- Fourcade, Y., Besnard, A. G., and Secondi, J. 2018. Paintings predict the distribution of species, or the challenge of selection environmental predictors and evaluation statistics. *Global Ecology and Biogeography*, 27: 245–256.
- Fournier, R. O., van Det, M., Wilson, J. S., and Hargreaves, N. B. 1979. Influence of the shelf-break front off Nova Scotia on Phytoplankton standing stock in winter. *Journal of the Fisheries Research Board of Canada*, 36: 1128–1237.
- Franks, P. J. S. 1992a. Phytoplankton blooms at fronts: Patterns, scales and physical forcing mechanisms. *Reviews in Aquatic Science*, 6: 121–137.
- Franks, P. J. S. 1992b. Sink or swim: Accumulation of biomass at fronts. *Marine Ecology Progress Series*, 82: 1–12.
- Franks, P. J. S. 1995. Thin layers of phytoplankton: A model of formation by near-inertial wave shear. *Deep-Sea Research I*, 42: 75–91.
- Fraser, S., Williamson, B. J., Nikora, V., and Scott, B. E. 2018. Fish distribution in a tidal channel indicate the behavioural impact of a marine renewable energy installation. *Energy Reports*, 4: 65–69.
- Freeman, R., Dennis, T., Landers, T., Thompson, D., Bell, E., Walker, M., and Guilford, T. 2010. Black petrels (*Procellaria parkinsoni*) patrol the ocean shelf-break: GPS tracking of a vulnerable procellariiform seabird. *PLoS ONE*, 5: e9236.
- Frid, C., Paramor, O., and Scott, C. 2005. Ecosystem-based fisheries management: Progress in the NE Atlantic. *Marine Policy*, 29: 461–469.
- Game, E. T., Grantham, H. S., Hobday, A. J., Pressey, R. L., Lombard, A. T., Beckley, L. E., Gjerde, K., *et al.* 2009. Pelagic protected areas: The missing dimension in ocean conservation. *Trends in Ecology and Evolution*, 24: 360–369.
- Gende, S. M., and Sigler, M. F. 2006. Persistence of forage fish ‘hot spots’ and its association with foraging Stellar sea lions (*Eumetopias jubatus*) in southeast Alaska. *Deep-Sea Research II*, 53: 432–441.
- Genin, A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems*, 50: 3–20.
- Goldbogen, J. A., Calambokidis, J., Oleson, E., Potvin, J., Pyenson, N. D., Schorr, G., and Shadwick, R. E. 2011. Mechanics, hydrodynamics and energetics of blue whale lunge feeding: Efficiency dependence on on krill density. *The Journal of Experimental Biology*, 214: 131–146.
- Goldbogen, J. A., Hazen, E. L., Friedlaender, A. S., Calambokidis, J., DeRuiter, S. L., Stimpert, A. K., and Southall, B. L. 2015. Prey density and distribution drive the three-dimensional foraging strategies of the largest filter feeder. *Functional Ecology*, 29: 951–961.
- Gomez-Gutierrez, J., and Robinson, C. J. 2006. Tidal current transport on epibenthic swarms of the euphausiid *Nyctiphanes simplex* in a shallow, sub-tropical bay on Baja California peninsula, Mexico. *Marine Ecology Progress Series*, 320: 215–231.

- Goold, J. C. 1998. Acoustic assessment of populations of common dolphin off the west Wales coast, with perspectives from satellite infrared imagery. *Journal of the Marine Biological Association of the United Kingdom*, 78: 1353–1364.
- Gormley, A. M., Slooten, E., Dawson, S., Barker, R. J., Rayment, W., du Fresne, S., and Brager, S. 2012. First evidence that marine protected areas can work for marine mammals. *Journal of Applied Ecology*, 49: 474–480.
- Goss, C., Bone, D. G., Peck, J. M., Everson, I., Hunt, G. L., and Murray, A. W. A. 1997. Small-scale interactions between prions *Pachyptila* spp. and their zooplankton prey at an inshore site near Bird Island, South Georgia. *Marine Ecology Progress Series*, 154: 41–51.
- Govoni, J. J., Hoss, D. E., and Colby, D. R. 1989. The spatial distribution of larval fishes about the Mississippi River plume. *Limnology and Oceanography*, 34: 179–187.
- Grantham, H. S., Game, E. T., Lombard, A. T., Hobday, A. J., Richardson, A. J., Beckley, L. E., Pressey, R. L., *et al.* 2011. Accommodating dynamic oceanographic processes and pelagic biodiversity in marine conservation planning. *PLoS ONE*, 6: e16552.
- Grecian, W. J., Lane, J. V., Michelot, T., Wade, H. M., and Hamer, K. C. 2018. Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *Journal of the Royal Society Interface*, 15: 20180084.
- Green, J. A., White, C. R., Bunce, A., Frappell, P. B., and Butler, P. J. 2009. Energetic consequences of plunge diving in gannets. *Endangered Species Research*, 10: 269–279.
- Greer, A. T., Cowen, R. K., Guigand, C. M., and Hare, J. A. 2015. Fine-scale planktonic habitat partitioning at a shelf-slope front revealed by a high-resolution imaging system. *Journal of Marine Systems*, 142: 111–125.
- Grégoire, F. 2006. Vertical distribution of the midwater trawl catches of Atlantic mackerel (*Scomber scombrus* L.) in relation with water temperature. Research document. DFO Canadian Science Advisory Secretariat.
- Gregory Lough, R., and Manning, J. P. 2001. Tidal-front entrainment and retention of fish larvae on the southern flank of Georges Bank. *Deep-Sea Research II*, 48: 631–644.
- Gremillet, D., Lewis, S., Drapeau, L., van Der Lingen, C. D., Huggett, J. A., Coetzee, J. C., Verheye, H. M., *et al.* 2008. Spatial match-mismatch in the Benguela upwelling zone: Should we expect chlorophyll and sea-surface temperature to predict marine predator distributions. *Journal of Applied Ecology*, 45: 610–621.
- Halpern, B. S., Lester, S. E., and McLeod, K. L. 2010. Placing marine protected areas onto the ecosystem-based management seascape. *Proceedings of the National Academy Science*, 107: 18312–18317.
- Hamer, K. C., Humphreys, E. M., Magalhaes, M. C., Garthe, S., Hennenke, J., Peters, G., Gremillet, D., *et al.* 2009. Fine-scale foraging behaviour of a medium-ranging marine predator. *Journal of Animal Ecology*, 78: 880–889.



- Hamner, W. M., and Schneider, D. 1986. Regularly spaced rows of medusae in the Bering Sea: role of Langmuir circulation. *Limnology and Oceanography*, 31: 171–177.
- Haney, J. C., and McGillivray, P. A. 1985a. Aggregations of cory's shearwaters (*Calonectris diomedea*) at Gulf Stream fronts. *Wilson Bulletin*, 97: 191–200.
- Haney, J. C., and McGillivray, P. A. 1985b. Midshelf fronts in the South Atlantic Bight and their influence on seabird distribution and seasonal abundance. *Biological Oceanography*, 3: 401–430.
- Haney, J. C. 1987. Ocean internal waves as sources of small-scale patchiness in seabird distributions on the Blake Plateau. *The Auk*, 104: 129–133.
- Haney, J. C. 1991. Influence of pycnocline topography and water-column structure on marine distributions of alcids (Aves: Alcidae) in Anadyr Strait, Northern Bering Sea, Alaska. *Marine Biology*, 110: 419–435.
- Hansen, J. E., Martos, P., and Madirolas, A. 2001. Relationship between spatial distribution of the Patagonian stock of Argentine anchovy, *Engraulis anchoita*, and sea temperatures during late spring to early summer. *Fisheries Oceanography*, 10: 193–206.
- Harrison, N. M., Hunt, G. L., and Cooney, R. T. 1990. Front affecting the distribution of seabirds in the northern Bering Sea. *Polar Research*, 8: 29–31.
- Hastie, G. D., Wilson, B., Wilson, L. J., Parsons, K. M., and Thompson, P. M. 2004. Functional mechanisms underlying cetacean distribution patterns: Hotspots for bottlenose dolphins are linked to foraging. *Marine Biology*, 144: 397–403.
- Hastie, G. D., Russell, D. J. F., Benjamins, S., Moss, S., Wilson, B., and Thompson, D. 2016. Dynamic habitat corridors for marine predators: intensive use of a coastal channel by harbour seals is modulated by tidal currents. *Behavioural Ecology and Sociobiology*.
- Hazen, E. L., Friedlaender, A. S., Thompson, M. A., Ware, C. R., Weinrich, M. T., Halpin, P. N., and Wiley, D. N. 2009. Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaeangliae*. *Marine Ecology Progress Series*, 395: 75–89.
- Hazen, E. L., Jorgensen, S. J., Rykaczewski, R. R., Bograd, S. J., Foley, D. G., Jonsen, I. D., Shaffer, S. A., *et al.* 2013. Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change*, 3: 234–238.
- Hazen, E. L., Scales, K. L., Maxwell, S. M., Briscoe, D. K., Welch, D. W., Bograd, S. J., Bailey, H., *et al.* 2018. A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. *Science Advances*, 4: eaar3001.
- Heath, J. P., and Gilchrist, H. G. 2010. When foraging becomes unprofitable: energetics of diving in tidal currents by common eiders wintering in the Arctic. *Marine Ecology Progress Series*, 403: 279–290.
- Heimlich-Boran. 1988. Behavioural ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. *Canadian Journal of Zoology*, 66: 565–578.

- Heithaus, M. R., Frid, A., Wirsing, A., and Worm, B. 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution*, 23: 202–210.
- Hennicke, J., and Culik, B. M. 2005. Foraging performance and reproductive success of Humboldt penguins in relation to prey availability. *Marine Ecology Progress Series*, 296: 173–181.
- Henson, S. A., Dunne, J. P., and Sarmiento, J. L. 2009. Decadal variability in North Atlantic phytoplankton blooms. *Journal of Geophysical Research*, 114: C0403.
- Hill, A. E., and Simpson, J. H. 1989. On the interaction of thermal and haline fronts: The Islay front revisited. *Estuarine, Coastal and Shelf Science*, 28: 495–505.
- Hill, A. E., Brown, J., Fernand, L., Holt, J., Horsburgh, K. J., Proctor, R., Raine, R., *et al.* 2008. Thermohaline circulation of shallow tidal seas. *Geophysical Research Letters*, 35.
- Hobday, A. J., Maxwell, S. M., Forgie, J., McDonald, J., Darby, M., Seto, K., Bailey, H., *et al.* 2014. Dynamic ocean management: integrating scientific and technological capacity with law, policy and management. *Stanford Environmental Law Journal*, 33: 125–168.
- Hoefler, C. J. 2000. Marine bird attraction to thermal fronts in the California Current System. *The Condor*, 102: 423–427.
- Holligan, P. M., Aarup, T., and Groom, S. B. 1989. The North Sea: satellite colour atlas. *Continental Shelf Research*, 9: 667–765.
- Holm, K. J., and Burger, A. E. 2002. Foraging behaviour and resource partitioning by diving birds during winter in areas of strong tidal currents. *Waterbirds*, 25: 312–325.
- Hooker, S. K., and Gerber, L. R. 2004. Marine reserves as a tool for ecosystem-based management: The potential importance of megafauna. *BioScience*, 54: 27–39.
- Hooker, S. K., Canadas, A., Hyrenbach, K. D., Corrigan, C., Polovina, J. J., and Reeves, R. R. 2011. Making marine protected area networks effective for marine top predators. *Endangered Species Research*, 13: 203–218.
- Hunt, G. L., and Schneider, D. C. 1987. Scale-dependent processes in the physical and biological environment of marine birds. *In* *Seabird Feeding Ecology*, pp. 7–41. Ed. by J. P. Croxall. Cambridge University Press.
- Hunt, G. L. 1990. The pelagic distribution of marine birds in a heterogeneous environment. *Polar Research*, 8: 43–54.
- Hunt, G. L., Harrison, N. M., and Cooney, R. T. 1990. The influence of hydrographic structure and prey abundance on foraging of least auklets. *Studies in Avian Biology*, 14: 7–22.
- Hunt, G. L., and Harrison, N. M. 1990. Foraging habitat and prey taken by least auklets at King Island, Alaska. *Marine Ecology Progress Series*, 65: 141–150.
- Hunt, G. L. 1991. Occurrence of polar seabirds at sea in relation to prey concentrations and oceanographic factors. *Polar Research*, 10: 553–560.

- Hunt, G. L., Heinemann, D., and Everson, I. 1992. Distributions and predator-prey interactions of macaroni penguins, Antarctic fur seals, and Antarctic krill near Bird Island, South Georgia. *Marine Ecology Progress Series*, 86: 15–30.
- Hunt, G. L., Harrison, N. M., and Piatt, J. F. 1993. Foraging ecology as related to the distribution of planktivorous auklets in the Bering Sea. *In* The status, ecology and conservation of marine birds in the North Pacific, pp. 18–25. Ed. by K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey. Ottawa: Canadian Wildlife Service Special Publication.
- Hunt, G. L., Coyle, K. O., Hoffman, S., Decker, M. B., and Flint, E. N. 1996. Foraging ecology of short-tailed shearwaters near the Pribilof Islands, Bering Sea. *Marine Ecology Progress Series*, 141: 1–11.
- Hunt, G. L. 1997. Physics, zooplankton, and the distribution of least auklets in the Bering sea- a review. *ICES Journal of Marine Science*, 54: 600–607.
- Hunt, G. L., Russell, R. W., Coyle, K. O., and Weingartner, T. 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Marine Ecology Progress Series*, 167: 241–259.
- Hunt, G. L., Mehlum, F., Russell, R. W., Irons, D. B., Decker, M. B., and Becker, P. H. 1999. S34.3: Physical processes, prey abundance, and the foraging ecology of seabirds. *In* Proceedings of the 22nd International Ornithological Congress. Adams, N. J. & Slotow, R. H., Durban.
- Hunt, G. L., and Stabeno, P. J. 2002. Climate change and the control of energy flow in the southeastern Bering Sea. *Progress in Oceanography*, 55: 5–22.
- Hunt, G. L., and Wilson, R. 2012. The coming of age of marine ornithology. *Marine Ecology Progress Series*, 451: 227–229.
- Hunt, G. L., Renner, M., Kuletz, K. J., Salo, S., Eisner, L., Ressler, P. H., Ladd, C., *et al.* 2018. Timing of sea-ice retreat affects the distribution of seabirds and their prey in the southeastern Bering Sea. *Marine Ecology Progress Series*, in press.
- Hyrenbach, K. D. 2000. Marine protected areas and ocean basin management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 10: 437–458.
- Ijsseldijk, L. L., Camphuysen, K. C. J., Nauw, J. J., and Aarts, G. 2015. Going with the flow: tidal influence on the occurrence of the harbour porpoise (*Phocoena phocoena*) in the Marsdiep area, The Netherlands. *Journal of Sea Research*, 103: 129–137.
- Irons, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology*, 79: 647–655.
- Isojunno, S., Matthiopoulos, J., and Evans, P. G. H. 2012. Harbour porpoise habitat preferences: Robust spatio-temporal inferences from opportunistic data. *Marine Ecology Progress Series*, 448: 155–170.
- Jahncke, J., Coyle, K. O., Zeeman, S. I., Kachel, N. B., and Hunt, G. L. 2005. Distribution of foraging shearwaters relative to inner front of SE Bering Sea. *Marine Ecology Progress Series*, 305: 219–233.

- Jiang, M., Brown, M. W., Turner, J. T., Kenney, R. D., Mayo, C. A., Zhang, Z., and Zhou, M. 2007. Springtime transport and retention of *Calanus finmarchicus* in Massachusetts and Cape Cod Bays, USA, and implications for right whale foraging. *Marine Ecology Progress Series*, 349: 183–197.
- Johnston, D. W., and Read, A. J. 2007. Flow-field observations of a tidally driven island wake used by marine mammals in the Bay of Fundy, Canada. *Fisheries Oceanography*, 16: 422–435.
- Jones, A. R., Hosegood, P., Wynn, R. B., De Boer, M. N., Butler-Cowdry, S., and Embling, C. B. 2014. Fine-scale hydrodynamics influence the spatio-temporal distribution of harbour porpoises at a coastal hotspot. *Progress in Oceanography*, 128: 30–48.
- Kachel, N. B., Hunt, G. L., Salo, S. A., Schumacher, J. D., Stabeno, P. J., and Whitley, T. E. 2002. Characteristics and variability of the inner front of the southeastern Bering Sea. *Deep-Sea Research II*, 49: 5889–5909.
- Kahru, M., Di Lorenzo, E., Manzano-Sarabia, M., and Mitchell, B. G. 2012. Spatial and temporal statistics of sea surface temperature and chlorophyll fronts in the California Current. *Journal of Plankton Research*, 34: 749–760.
- Kaltenberg, A. M., Emmett, R. L., and Benoit-Bird, K. J. 2010. Timing of forage fish seasonal appearance in the Columbia River plume and link to ocean conditions. *Marine Ecology Progress Series*, 419: 171–184.
- Kampf, J., Doubell, M., Griffin, D., Matthews, R. L., and Ward, T. M. 2004. Evidence of a large seasonal coastal upwelling system along the southern shelf of Australia. *Geophysical Research Letters*, 31.
- Kilian, M., Dehnhardt, G., and Hanke, F. D. 2015. How harbor seals *Phoca vitulina* pursue schooling herring. *Mammalian Biology*, 80: 385–389.
- Kinder, T. H., Hunt, G. L., Schneider, D., and Schumacher, J. D. 1983. Correlations between seabirds and oceanic fronts around the Pribilof, Islands, Alaska. *Estuarine, Coastal and Shelf Science*, 16: 309–319.
- Kingsford, M. J., and Suthers, I. M. 1994. Dynamic estuarine plumes and fronts: importance to small fish and plankton in coastal waters of NSW, Australia. *Continental Shelf Research*, 14: 655–672.
- Kinsella, E. D., Hay, A. E., and Denner, W. W. 1987. Wind and topographic effects on the Labrador Current at Carson Canyon. *Journal of Geophysical Research*, 92: 10853–10869.
- Kokubun, N., Iida, K., and Mukai, T. 2008. Distribution of murre ( *Uria* spp.) and their prey south of St. George Island in the southeastern Bering Sea during the summers of 2003-2005. *Deep-Sea Research II*, 55: 1827–1836.
- Kokubun, N., Takahashi, A., Ito, M., Matsumoto, K., Kitaysky, A. S., and Watanuki, Y. 2010. Annual variation in the foraging behaviour of thick-billed murre in relation to upper-ocean thermal structure around St. George Island, Bering Sea. *Aquatic Biology*, 8: 289–298.
- Kowalczyk, N. D., Reina, R. D., Preston, T. J., and Chiaradia, A. 2015a. Selective foraging within estuarine plume fronts by an inshore resident seabird. *Frontiers in Marine Science*, 2.

- Kowalczyk, N. D., Reina, R. D., Preston, T. J., and Chiaradia, A. 2015b. Environmental variability drives shifts in the foraging behaviour and reproductive success of an inshore seabird. *Oecologia*, 178: 967–979.
- Kroodsmas, D. A., Mayorga, J., Hochberg, T., Miller, N. A., Boerder, K., Ferretti, F., Wilson, A., *et al.* 2018. Tracking the global footprint of fisheries. *Science*, 359: 904–908.
- Kuhn, C. E. 2011. The influence of subsurface thermal structure on the diving behaviour of northern fur seals (*Callorhinus ursinus*) during the breeding season. *Marine Biology*, 158: 649–663.
- Ladd, C., Jahncke, J., Hunt, G. L., Coyle, K. O., and Stabeno, P. J. 2005. Hydrographic features and seabird foraging in Aleatian Passes. *Fisheries Oceanography*, 14: 178–195.
- Langton, R., Davies, I. M., and Scott, B. E. 2011. Seabird conservation and tidal stream and wave power generation: Information needs for predicting and managing potential impacts. *Marine Policy*, 35: 623–630.
- Lavoie, D., Simard, Y., and Saucier, F. J. 2000. Aggregation and dispersion of krill at channel heads and shelf edges: The dynamics in the Saguenay - St. Lawrence Marine Park. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 1853–1869.
- Lennert-Cody, C. E., and Franks, P. J. S. 1999. Plankton patchiness in high-frequency internal waves. *Marine Ecology Progress Series*, 186: 59–66.
- Lescrauwaet, A. K., Gibbons, J., Guzman, L., and Schiavini, A. 2000. Abundance estimation of Commersons dolphin in the eastern area of the Strait of Magellan - Chile. *Revista Chilena de Historia Natural*, 73: 473–478.
- Lester, S. E., McLeod, K. L., Tallis, H., Ruckelshaus, M., Halpern, B. S., Levin, P. S., Chavez, F. P., *et al.* 2010. Science in support of ecosystem-based management for the US West Coast and beyond. *Biological Conservation*, 143: 576–587.
- Letelier, J., Pizarro, O., and Nunez, S. 2009. Seasonal variability of coastal upwelling and the upwelling front off central Chile. *Journal of Geophysical Research*, 114: C12009.
- Lewis, R. E. 1984. Circulation and mixing in estuary outflows. *Continental Shelf Research*, 3: 201–214.
- Lewison, R. L., Hobday, A. J., Maxwell, S. M., Hazen, E. L., Hartog, J. R., Dunn, D. C., Briscoe, D., *et al.* 2015. Dynamic ocean management: Identifying the critical ingredients of dynamic approaches to ocean resource management. *BioScience*.
- Liao, J. C. 2007. A review of fish swimming mechanics and behaviour in altered flows. *Philosophical Transactions of the Royal Society of London B*, 362: 1973–1993.
- Lin, T.-H., Akamatsu, T., and Chou, L.-S. 2015. Seasonal distribution of Indo-Pacific humpback dolphins at an estuarine habitat: influences of upstream rainfall. *Estuaries and Coasts*, 38: 1376–1384.
- Linder, C. A., and Gawarkiewicz, G. 1998. A climatology of the shelfbreak front in the Middle Atlantic Bight. *Journal of Geophysical Research*, 103: 12405–12423.

- Logerwell, E. A., Hewitt, R. P., and Demer, D. A. 1998. Scale-dependent spatial variance patterns and correlations of seabirds and prey in the southeastern Bering Sea as revealed by spectral analysis. *Ecography*, 21: 212–223.
- Longhurst, A., Platt, T., and Caverhill, C. 1995. An estimate of global primary production in the ocean from satellite radiometer data. *Journal of Plankton Research*, 17: 1245–1271.
- Macaulay, J., Gordon, J., Gillespie, D., Malinka, C., and Northridge, S. 2017. Passive acoustic methods for fine-scale tracking of harbour porpoises in tidal rapids. *The Journal of the Acoustical Society of America*, 141: 1120–1132.
- Machovsky-Capuska, G. E., Vaughn, R. L., Wursig, B., Katzir, G., and Raubenheimer, D. 2011. Dive strategies and foraging effort in the Australasian gannets *Morus serrator* revealed by underwater videography. *Marine Ecology Progress Series*, 442: 255–261.
- Machovsky-Capuska, G. E., Hauber, M. E., Libby, E., Amiot, C., and Raubenheimer, D. 2014. The contribution of private and public information in foraging by Australasian gannets. *Animal Cognition*, 17: 849–858.
- Malinka, C., Gillespie, D., Macaulay, J. D. J., Joy, R., and Sparling, C. 2018. First *in situ* passive acoustic monitoring for marine mammals during operation of atidal turbine in Ramsey Sounds, Wales. *Marine Ecology Progress Series*, 590: 247–266.
- Mann, K. H., and Lazier, J. R. N. 2006. *Dynamics of marine ecosystems: Biological-physical interactions in the ocean*. Blackwell Publishing.
- Mannocci, L., Boustany, A. M., Roberts, J. J., Palacios, D. M., Dunn, D. C., Halpin, P. N., Viehman, S., *et al.* 2017. Temporal resolutions in species distribution models of highly mobile marine animals: recommendations for ecologists and managers. *Diversity and Distributions*, 23: 1098–1109.
- Marubini, F., Gimona, A., Evans, P. G. H., Wright, P. J., and Peirce, G. J. 2009. Habitat preferences and interannual variability in occurrence of the harbour porpoise *Phocoena phocoena* off northwest Scotland. *Marine Ecology Progress Series*, 381: 297–310.
- Matsumoto, K., Deguchi, T., Wada, A., Kato, A., Saitoh, S., and Watanuki, Y. 2008. Estimating foraging area of Rhinoceros Auklets by simultaneous sampling of water temperature profiles using bird-borne data-loggers. *Ornithological Science*, 7: 37–46.
- Mattei, F., Franceschini, S., and Scardi, M. 2018. A depth-resolved artificial neural network model of marine phytoplankton primary production. *Ecological Modelling*, 382: 51–62.
- Maxwell, S. M., Hazen, E. L., Lewison, R. L., Dunn, D. C., Bailey, H., Bograd, S. J., Briscoe, D. K., *et al.* 2015. Dynamic ocean management: Defining and conceptualising real-time management of the ocean. *Marine Policy*, 58: 42–50.
- McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H., and Warner, R. R. 2015. Marine defaunation: Animal loss in the global ocean. *Science*, 347: 12556411–12556417.
- McGowan, J. A., Cayan, D. R., and Dorman, L. M. 1998. Climate-ocean variability and ecosystem response in the northeast Pacific. *Science*, 281: 210–217.

- McInnes, A. M., Ryan, P. G., Lacerda, M., Deshayes, J., Goschen, W. S., and Pichegru, L. 2017. Small pelagic fish responses to fine-scale oceanographic conditions: implications for the endangered African penguin. *Marine Ecology Progress Series*, 569: 187–203.
- McManus, M. A., Cheriton, O. M., Drake, P. J., Holliday, D. V., Storlazzi, C. D., Donaghay, P. L., and Greenlaw, C. F. 2005. Effects of physical processes on structure and transport of thin zooplankton layers in the coastal ocean. *Marine Ecology Progress Series*, 301: 199–214.
- Mehlum, F., Hunt, G. L., Klusek, Z., and Decker, M. B. 1999. Scale-dependent correlations between the abundance of Brunnich's guillemots and their prey. *Journal of Animal Ecology*, 68: 60–72.
- Mendes, S., Turrell, W., Lütkebohlehle, T., and Thompson, P. 2002. Influence of the tidal cycle and a tidal intrusion front on the spatio-temporal distribution of coastal bottlenose dolphins. *Marine Ecology Progress Series*, 239: 221–229.
- Miller, P. 2009. Composite front maps for improved visibility of dynamics sea-surface features on cloudy SeaWiFS and AVHRR data. *Journal of Marine Systems*, 78: 327–336.
- Mills, D. K., Tett, P. B., and Novarino, G. 1994. The spring bloom in the south western North Sea in 1989. *Netherlands Journal of Sea Research*, 33: 65–80.
- Moore, S. E., and Lien, R. 2007. Pilot whales follow internal solitary waves in the South China Sea. *Marine Mammal Science*, 23: 193–196.
- Moum, J. N., and Nash, J. D. 2000. Topographically induced drag and mixing at a small bank on the continental shelf. *Journal of Physical Oceanography*, 30: 2049–2054.
- Muller-Karger, F. E., Varela, R., Thunell, R., Luerssen, R., Hu, C., and Walsh, J. J. 2005. The importance of continental margins in the global carbon cycle. *Geophysical Research Letters*, 32: L01602.
- Munk, P., Larsson, P. O., Danielsen, D., and Moksness, E. 1995. Larval and small juvenile cod *Gadus morhua* concentrated in the highly productive areas of a shelf break front. *Marine Ecology Progress Series*, 125: 21–30.
- Nahas, E. L., Pattiaratchi, C. B., and Ivey, G. N. 2005. Processes controlling the positions of frontal systems in Shark Bay, Western Australia. *Estuarine, Coastal and Shelf Science*, 65: 463–474.
- Napp, J. M., and Hunt, G. L. 2001. Anomalous conditions in the south-eastern Bering Sea 1997: linkages among climate, weather, ocean, and biology. *Fisheries Oceanography*, 10: 61–68.
- Nichol, D. G., and Somerton, D. A. 2002. Diurnal vertical migration of the Atka mackerel *Pleurogrammus monopterygius* as shown by archival tags. *Marine Ecology Progress Series*, 239: 193–207.
- Nimmo Smith, W. A. M., Thorpe, S. A., and Graham, A. 1999. Surface effects of bottom-generated turbulence in a shallow tidal sea. *Nature*, 400: 251–253.
- Nol, E., and Gaskin, D. E. 1987. Distribution and movements of Black Guillemots (*Cepphus grylle*) in coastal waters of the southwestern Bay of Fundy, Canada. *Canadian Journal of Zoology*, 65: 2682–2689.

- Nordstrom, C. A., Battaile, B. C., Cotté, C., and Trites, A. W. 2013. Foraging habitat of lactating northern fur seals are structured by thermocline depths and submesoscale fronts in the eastern Bering Sea. *Deep-Sea Research II*, 88–89: 78–96.
- Paleczny, M., Hammill, E., Karpouzi, V., and Pauly, D. 2015. Population trend of the world's monitored seabirds, 1950-2010. *PLoS ONE*, 10: e0129342.
- Palmer, M. R., Inall, M. E., and Sharples, J. 2013. The physical oceanography of Jones Bank: A mixing hotspot in the Celtic Sea. *Progress in Oceanography*, 117: 9–24.
- Patrick, S. C., Bearhop, S., Grémillet, D., Lescroel, A., Grecian, W. J., Bodey, T. W., Hamer, K. C., *et al.* 2014. Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos*, 123: 33–40.
- Pelland, N. A., Sterling, J. T., Lea, M. A., Bond, N. A., Ream, R. R., Lee, C. M., and Eriksen, C. C. 2014. Fortuitous encounters between seagliders and adult northern fur seals (*Callorhinus ursinus*) off the Washington (USA) coast: upper ocean variability and links to a top predator behaviour. *PLoS ONE*, 9: e101268.
- Pelletier, L., Kato, A., Chiaradia, A., and Ropert-Coudert, Y. 2012. Can thermoclines be a cue to prey distribution for marine top predators? A case study with little penguins. *PLoS ONE*, 7: e31768.
- Pettex, E., Bonadonna, F., Enstipp, M. R., Siorat, F., and Grémillet, D. 2010. Northern gannets anticipate the spatio-temporal occurrence of their prey. *The Journal of Experimental Biology*, 213: 2365–2371.
- Phillips, E. M., Horne, J., and Zamon, J. E. 2017. Predator-prey interactions influenced by a dynamic river plume. *Canadian Journal of Fisheries and Aquatic Sciences*: 1–16.
- Phillips, E. M., Horne, J. K., Adams, J., and Zamon, J. E. 2018. Selective occupancy of a persistent yet variable coastal river plume by two seabird species. *Marine Ecology Progress Series*, 594: 245–261.
- Photopoulou, T., Fedak, M. A., Matthiopoulos, J., McConnell, B., and Lovell, P. 2015. The generalized data management and collection of protocol for Conductivity-Temperature-Depth Satellite Relay Data Loggers. *Animal Biotelemetry*, 3: 1–10.
- Piatt, J., Wetzel, J., Bell, K., Degange, A., Balogh, G., Drew, G., Geernaert, T., *et al.* 2006. Predictable hotspots and foraging habitat of the endangered short-tailed albatross (*Phoebastria albatrus*) in the North Pacific: Implications for conservation. *Deep-Sea Research II*, 53: 387–398.
- Pichegru, L., Grémillet, D., Crawford, R. J. M., and Ryan, P. G. 2010. Marine no-take zone rapidly benefits endangered penguin. *Biology Letters*, 6: 498–501.
- Pierpoint, C. 2008. Harbour porpoise (*Phocoena phocoena*) foraging strategy at a high energy, near-shore site in south-west Wales, UK. *Journal of the Marine Biological Association of the United Kingdom*, 88: 1167–1173.
- Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., *et al.* 2004. Ecosystem-based fishery management. *Science*, 305: 346–347.



- Pineda, J., Starczak, V., Silva, J. C. B., Helfrich, K., Thompson, M., and Wiley, D. 2015. Whales and waves: Humpback whale foraging response and the shoaling of internal waves at Stellwagen Bank. *Journal of Geophysical Research: Oceans*, 120: 2555–2570.
- Pinedo, M. C., Polacheck, T., Barreto, A. S., and Lammardo, M. P. 2002. A note on vessel of opportunity sighting surveys for cetaceans in the shelf edge region off the southern coast of Brazil. *Journal of Cetacean Research and Management*, 4: 323–329.
- Pingree, R. D., Forster, G. R., and Morrison, G. K. 1974. Turbulent convergent tidal fronts. *Journal of the Marine Biological Association of the United Kingdom*, 54: 469–479.
- Pingree, R. D. 1975. The advance and retreat of the thermocline on the continental shelf. *Journal of Marine Biological Association UK*, 55: 965–974.
- Pingree, R. D., Pugh, P. R., Holligan, P. M., and Forster, G. R. 1975. Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature*, 258: 672–677.
- Pingree, R. D., Holligan, P. M., Mardell, G. T., and Head, R. N. 1976. The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea. *Journal of Marine Biological Association UK*, 56: 845–873.
- Pingree, R. D., and Griffiths, D. K. 1978. Tidal fronts on the shelf seas around the British Isles. *Journal of Geophysical Research*, 83: 4615–4622.
- Pingree, R. D., Mardell, G. T., and Cartwright, D. E. 1981. Slope turbulence, internal waves and phytoplankton growth at the Celtic Sea shelf-break. *Philosophical Transactions of the Royal Society of London A*, 302: 663–682.
- Pirotta, E., Edwards, E. W. J., New, L., and Thompson, P. M. 2018. Central place foragers and moving stimuli: a hidden-state model to discriminate the processes affecting movement. *Journal of Animal Ecology*: In press.
- Pisoni, J. P., Rivas, A. K., and Piola, A. R. 2015. On the variability of tidal fronts on a macrotidal continental shelf, Northern Patagonia, Argentina. *Deep-Sea Research II*, 119: 61–68.
- Podesta, G. P., Browder, J. A., and Hoey, J. J. 1993. Exploring the association between swordfish catch rates and thermal fronts on U.S. longline grounds in the western North Atlantic. *Continental Shelf Research*, 13: 253–277.
- Queiros, A. M., Huebert, K. B., Keyl, F., Fernandes, J. A., Stolte, W., Maar, M., Kay, S., *et al.* 2016. Solutions for ecosystem-level protection of ocean systems under climate change. *Global Change Biology*.
- Redfern, J. V., Ferguson, M. C., Becker, E. A., Hyrenbach, K. D., Good, C., Barlow, J., Kaschner, K., *et al.* 2006. Techniques for cetacean-habitat modelling. *Marine Ecology Progress Series*, 310: 271–295.
- Reese, D. C., O'Malley, R. T., Brodeur, R. D., and Churnside, J. H. 2011. Epipelagic fish distributions in relation to thermal fronts in a coastal upwelling system using high-resolution remote-sensing techniques. *ICES Journal of Marine Science*, 68: 1865–1874.

- Regular, P. M., Hedd, A., and Montevecchi, W. A. 2013. Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird. *Animal Behaviour*, 86: 545–552.
- Renner, M., Salo, S., Eisner, L. B., Ressler, P. H., Ladd, C., Kuletz, K. J., Santora, J. A., *et al.* 2016. Timing of sea ice retreat alters seabird abundances and distributions in the southeast Bering Sea. *Biology Letters*, 12: 20160276.
- Richard, G., Cox, S. L., Picard, B., Vacquie-Garcia, J., and Guinet, C. 2016. Southern elephant seals replenish their lipid reserves at different rates according to foraging habitat. *PLoS ONE*, 11: e0166747.
- Richardson, K., and Christoffersen, A. 1991. Seasonal distribution and production of phytoplankton in the southern Kattegat. *Marine Ecology Progress Series*, 78: 217–227.
- Richardson, K., Visser, A. W., and Pedersen, F. B. 2000. Subsurface phytoplankton blooms fuel pelagic production in the North Sea. *Journal of Plankton Research*, 22: 1663–1671.
- Rippeth, T. P., Palmer, M. R., Simpson, J. H., Fisher, N. R., and Sharples, J. 2005. Thermocline mixing in summer stratified continental shelf seas. *Geophysical Research Letters*, 32: L05602.
- Robinson, S. J., Gomez-Aguirre, S., and Gomez-Gutierrez, J. 2007. Pacific sardine behaviour related to tidal current dynamics in Bahia Magdalena, Mexico. *Journal of Fish Biology*, 71: 200–218.
- Rogachev, K. A., Carmack, E. C., and Foreman, M. G. G. 2008. Bowhead whales feed on plankton concentrated by estuarine and tidal currents in Academy Bay, Sea of Okhotsk. *Continental Shelf Research*, 28: 1811–1826.
- Ropert-Coudert, Y., Kato, A., and Chiaradia, A. 2009a. Impact of small-scale environmental perturbations on local marine food resources: A case study of a predator, the little penguin. *Proceedings of the Royal Society of Biological Sciences*, 276: 4105–4109.
- Ropert-Coudert, Y., Daunt, F., Kato, A., Ryan, P. G., Lewis, S., Kobayashi, K., Mori, Y., *et al.* 2009b. Underwater wingbeats extend depth and duration of plunge dives in northern gannets *Morus bassanus*. *Journal of Avian Biology*, 40: 380–387.
- Russell, R. W., Harrison, N. M., and Hunt, G. L. 1999. Foraging at a front: Hydrography, zooplankton, and avian planktivory in the northern Bering Sea. *Marine Ecology Progress Series*, 182: 77–93.
- Ryan, J. P., Yoder, J. A., and Cornillon, P. C. 1999. Enhanced chlorophyll at the shelfbreak of the Mid-Atlantic Bight and Georges Bank during the spring transition. *Limnology and Oceanography*, 44: 1–11.
- Sabarros, P. S., Grémillet, D., Demarcq, H., Moseley, C., Pichegru, L., Mullers, R. H. E., Stenseth, N. C., *et al.* 2014. Fine-scale recognition and use of mesoscale fronts by foraging Cape gannets in the Benguela upwelling region. *Deep-Sea Research II*, 107: 77–84.
- Sabatés, A., and Olivar, M. P. 1996. Variation of larval fish distributions associated with variability in the location of the shelf-slope front. *Marine Ecology Progress Series*, 135: 11–20.

- Sambrotto, R. N., Niebauer, H. J., Goering, J. J., and Iverson, R. L. 1986. Relationships among vertical mixing, nitrate uptake, and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. *Continental Shelf Research*, 5: 161–198.
- Satterthwaite, W. H., Kitaysky, A. S., and Mangel, M. 2012. Linking climate variability, productivity and stress to demography in a long-lived seabird. *Marine Ecology Progress Series*, 454: 221–235.
- Savoca, M. S., and Nevitt, G. A. 2014. Evidence that dimethyl sulfide facilitates a tritrophic mutualism between marine primary producers and top predators. *PNAS*, 111: 4157–4161.
- Scales, K. L., Miller, P. I., Hawkes, L. A., Ingram, S. N., Sims, D. W., and Votier, S. C. 2014a. On the front line: Frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, 51: 1575–1583.
- Scales, K. L., Miller, P. I., Embling, C. B., Ingram, S. N., Pirotta, E., and Votier, S. C. 2014b. Mesoscale fronts as foraging habitats: Composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *Journal of the Royal Society Interface*, 11: 20140679.
- Scales, K. L., Hazen, E. L., Jacox, M. G., Edwards, C. A., Boustany, A. M., Oliver, M. J., and Bograd, S. J. 2017. Scale of inference: on the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. *Ecography*, 49: 210–220.
- Schlacher, T. A., Skillington, A. J., Connolly, R. M., Robinson, W., and Gaston, T. F. 2008. Coupling between marine plankton and freshwater flow in the plumes off a small estuary. *International Review of Hydrobiology*, 93: 641–658.
- Schneider, D. 1982. Fronts and seabird aggregations in the southeastern Bering Sea. *Marine Ecology Progress Series*, 10: 101–103.
- Schneider, D. C., and Piatt, J. F. 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. *Marine Ecology Progress Series*, 32: 237–246.
- Schneider, D. C., Harrison, N. M., and Hunt, G. L. 1987. Variation in the occurrence of marine birds at fronts in the Bering Sea. *Estuarine, Coastal and Shelf Science*, 25: 135–141.
- Schneider, D. C., and Methven, D. A. 1988. Response of capelin to wind-induced thermal events in the southern Labrador Current. *Journal of Marine Research*, 46: 105–118.
- Schneider, D. C. 1994. Distribution of capelin (*Mallotus villosus*) in relation to coastal upwelling in the Avalon Channel. *Journal of Northwest Atlantic Fishery Science*, 17: 23–31.
- Schumacher, J. D., Kinder, T. H., Pashinski, D. J., and Charnell, R. L. 1979. A structural front over the continental shelf of the eastern Bering Sea. *Journal of Physical Oceanography*, 9: 79–87.
- Scott, B. E., Sharples, J., Wanless, S., Ross, O. N., Frederiksen, M., and Daunt, F. 2006. The use of biologically meaningful oceanographic indices to separate the effects of climate and fisheries on seabird breeding success. *In* Top predators in marine ecosystems: Their role in monitoring and management. Ed. by I. L. Boyd, S. Wanless, and C. J. Camphuysen. Cambridge University Press.
- Scott, B. E., Sharples, J., Ross, O. N., Wang, J., Pierce, G. J., and Camphuysen, C. J. 2010. Sub-surface hotspots in shallow seas: Fine-scale limited locations of top predator foraging habitat

- indicated by tidal mixing and sub-surface chlorophyll. *Marine Ecology Progress Series*, 408: 207–226.
- Scott, B. E., Webb, A., Palmer, M. R., Embling, C. B., and Sharples, J. 2013. Fine scale bio-physical oceanographic characteristics predict the foraging occurrence of contrasting seabird species; Gannet (*Morus bassanus*) and storm petrel (*Hydrobates pelagicus*). *Progress in Oceanography*, 117: 118–129.
- Scott, M., and Chivers, S. 2009. Movements and diving behavior of pelagic spotted dolphins. *Marine Mammal Science*, 25: 137–160.
- Sharples, J., and Simpson, J. H. 1993. Periodic frontogenesis in a region of freshwater influence. *Estuaries*, 16: 74–82.
- Sharples, J., and Tett, P. 1994. Modelling the effect of physical variability on the midwater chlorophyll maximum. *Journal of Marine Research*, 52: 219–238.
- Sharples, J., and Simpson, J. H. 1996. The influence of the Springs-Neaps Cycle on the position of Shelf Fronts. *In* Buoyancy effects on coastal and estuarine dynamics, pp. 71–82. Ed. by D. G. Aubrey and C. T. Friedrichs. American Geophysical Union, Washington.
- Sharples, J. 1999. Investigating the seasonal vertical structure of phytoplankton in shelf seas. *Marine Models*, 1: 3–38.
- Sharples, J., Moore, C. M., Rippeth, T. P., Holligan, P. M., Hydes, D. J., Fisher, N. R., and Simpson, J. H. 2001. Phytoplankton distribution and survival in the thermocline. *Limnology and Oceanography*, 46: 486–496.
- Sharples, J., Ross, O. N., Scott, B. E., Greenstreet, S. P. R., and Fraser, H. 2006. Inter-annual variability in the timing of stratification and the spring bloom in the North-western North Sea. *Continental Shelf Research*, 26: 733–751.
- Sharples, J. 2008. Potential impacts of the spring-neap tidal cycle on shelf sea primary production. *Journal of Plankton Research*, 30: 186–197.
- Sherley, R. B., Ludynia, K., Dyer, B. M., Lamont, T., Makhado, A. B., Roux, J. P., Scales, K. L., *et al.* 2017. Metapopulation tracking juvenile penguins reveals an ecosystem-wide ecological trap. *Current Biology*, 27: 563–568.
- Shields, M. A., Woolf, D. K., Grist, E. P. M., Kerr, S. A., Jackson, A. C., Harris, R. E., Bell, M. C., *et al.* 2011. Marine renewable energy: The ecological implications of altering the hydrodynamics of the marine environment. *Ocean and Coastal Management*, 24: 2–9.
- Sigler, M. F., Napp, J. M., Stabeno, P. J., Heintz, R., Lomas, M. W., and Hunt, G. L. 2016. Variation in the annual production of copepods, euphausiids, and juvenile walleye pollock in the southeastern Bering Sea. *Deep-Sea Research Part II*, 134: 223–234.
- Simard, Y., Ladurantaye, R., and Therriault, J.-C. 1986. Aggregation of euphausiids along a coastal shelf in an upwelling environment. *Marine Ecology Progress Series*, 32: 203–215.

- Simard, Y., Lavoie, D., and Saucier, F. J. 2002. Channel head dynamics: Capelin (*Mallotus villosus*) aggregation in the tidally driven upwelling system of the Saguenay - St Lawrence Marine Park's whale feeding ground. *Canadian Journal of Fisheries and Aquatic Sciences*, 59: 197–210.
- Simila, T., and Ugarte, F. 1993. Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology*, 71: 1494–1499.
- Simpson, J. H., and Hunter, J. R. 1974. Fronts in the Irish Sea. *Nature*, 250: 404–406.
- Simpson, J. H., Edelsten, D. J., Edwards, A., Morris, N. C. G., and Tett, P. B. 1979. The Islay front: Physical structure and phytoplankton distribution. *Estuarine and Coastal Marine Science*, 9: 713–726.
- Simpson, J. H., and Nunes, R. A. 1981. The tidal intrusion front: An estuarine convergence front. *Estuarine, Coastal and Shelf Science*, 13: 257–266.
- Simpson, J. H., and Sharples, J. 2012. Introduction to the physical and biological oceanography of shelf seas. Cambridge University Press. 424 pp.
- Skov, H., and Durinck, J. 1998. Constancy of frontal aggregations of seabirds at the shelf break in the Skagerrak. *Journal of Sea Research*, 39: 305–311.
- Skov, H., and Durinck, J. 2000. Seabird distribution in relation to hydrography in the Skagerrak. *Continental Shelf Research*, 20: 169–187.
- Skov, H., and Prins, E. 2001. Impact of estuarine fronts on the dispersal of piscivorous birds in the German Bight. *Marine Ecology Progress Series*, 214: 279–287.
- Skov, H., and Thomsen, F. 2008. Resolving fine-scale spatio-temporal dynamics in the harbour porpoise *Phocoena phocoena*. *Marine Ecology Progress Series*, 373: 173–186.
- Springer, A. M., McRoy, C. P., and Flint, M. V. 1996. The Bering Sea Green Belt: Shelf-edge processes and ecosystem production. *Fisheries Oceanography*, 5: 205–223.
- Springer, A. M., Vernon Byrd, G., and Iverson, S. J. 2007. Hot oceanography: planktivorous seabirds reveal ecosystem responses to warming of the Bering Sea. *Marine Ecology Progress Series*, 352: 289–297.
- Stephens, D. W., and Krebs, J. R. 1986. Foraging theory. *Monographs in Behaviour and Ecology*. Princeton University Press.
- Stepputtis, D., Hinrichsen, H., Bottcher, U., Gotze, E., and Mohrholz, V. 2011. An example of meso-scale hydrographic features in the central Baltic Sea and their influence on the distribution and vertical migration of sprat, *Sprattus sprattus balticus* (Schn.). *Fisheries Oceanography*, 20: 82–88.
- Stevick, P. T., Incze, L. S., Kraus, S. D., Rosen, S., Wolff, N., and Baukus, A. 2008. Trophic relationships and oceanography on and around a small offshore bank. *Marine Ecology Progress Series*, 363: 15–28.
- Stone, C. J., Webb, A., and Tasker, M. L. 1995. The distribution of auks and Procellariiformes in north-west European waters in relation to depth of sea. *Bird Study: The Journal of the British Trust for Ornithology*, 42: 50–56.

- Suberg, L., Wynn, R. B., Van der Kooij, J., Fernand, L., Fielding, S., Guihen, D., Gillespie, D., *et al.* 2014. Assessing the potential of autonomous submarine gliders for ecosystem monitoring across multiple trophic levels (plankton to cetaceans) and pollutants in shallow shelf-seas. *Methods in Oceanography*, 10: 70–89.
- Swartzman, G., and Hunt, G. 2000. Spatial association between murre (*Uria* spp.), puffins (*Fratercula* spp.) and fish shoals near Pribilof Islands, Alaska. *Marine Ecology Progress Series*, 206: 297–309.
- Sydeman, W. J., Brodeur, R. D., Grimes, C. B., Bychkov, A. S., and McKinnell, S. 2006. Marine habitat ‘hotspots’ and their use by migratory species and top predators in the North Pacific Ocean: Introduction. *Deep-Sea Research II*, 53: 247–249.
- Takahashi, A., Matsumoto, K., Hunt, G. L., Schultz, M. T., Kitaysky, A. S., Sato, K., Iida, K., *et al.* 2008. Thick-billed murre use different diving behaviors in mixed and stratified waters. *Deep-Sea Research II*, 55: 1837–1845.
- Tarrade, L., Texier, A., David, L., and Larinier, M. 2008. Topologies and measurements of turbulent flow in vertical slot fishways. *Hydrobiologia*, 609: 177–188.
- Taylor, M. F. J., Suckling, K. F., and Rachlinski, J. J. 2005. The effectiveness of the endangered species act: A quantitative analysis. *BioScience*, 55: 360–367.
- Thaxter, C. B., Lascelles, B., Sugar, K., Cook, A. S. C. P., Roos, S., Bolton, M., Langston, R. H. W., *et al.* 2012. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biological Conservation*, 156: 53–61.
- Thaxter, C. B., Daunt, F., Grémillet, D., Harris, M. P., Benvenuti, S., Watanuki, Y., Hamer, K. C., *et al.* 2016. Modelling the effects of prey size and distribution on prey capture rates of two sympatric marine predators. *PLoS ONE*, 8: e79915.
- Thompson, P. M., Pierce, G. J., Hislop, J. R. G., Miller, D., and Diack, J. S. W. 1991. Winter foraging by common seals (*Phoca vitulina*) in relation to food availability in the Inner Moray Firth, N. E. Scotland. *Journal of Animal Ecology*, 60: 283–294.
- Thorne, L. H., and Read, A. J. 2013. Fine-scale biophysical interactions drive prey availability at a migratory stopover site for *Phalaropus* spp. in the Bay of Fundy, Canada. *Marine Ecology Progress Series*, 487: 261–273.
- Torres, L. G., Read, A. J., and Halpin, P. 2008. Fine-scale habitat modelling of a top marine predator: Do prey data improve predictive capacity? *Ecological Applications*, 18: 1702–1717.
- Townsend, D. W., and Spinrad, R. W. 1986. Early spring phytoplankton blooms in the Gulf of Maine. *Continental Shelf Research*, 6: 515–529.
- Tremblay, Y., Bertrand, S., Henry, R. W., Kappes, M. A., Costa, D. P., and Shaffer, S. A. 2009. Analytical approaches to investigating seabird-environment interactions: A review. *Marine Ecology Progress Series*, 391: 153–163.

- Tremblay, Y., Thiebault, A., Mullers, R., and Pistorius, P. 2014. Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. *PLoS ONE*, 9: e88424.
- Tweddle, J. F., Sharples, J., Palmer, M. R., Davidson, K., and McNeil, S. 2013. Enhanced nutrient fluxes at the shelf sea seasonal thermocline caused by stratified flow over a bank. *Progress in Oceanography*, 117: 37–47.
- Tynan, C. T., Ainley, D. G., Barth, J. A., Cowles, T. J., Pierce, S. D., and Spear, L. B. 2005. Cetacean distributions relative to ocean processes in the northern California Current System. *Deep-Sea Research II*, 52: 145–167.
- van Eeden, R., Ryan, P. G., and Pichegru, L. 2016. Fine-scale foraging cues for African penguins in a highly variable marine environment. *Marine Ecology Progress Series*, 543: 257–271.
- Vermeer, K., Szabo, I., and Greisman, P. 1987. The relationship between plankton-feeding Bonaparte's and Mew Gulls and tidal upwelling at Active Pass, British Columbia. *Journal of Plankton Research*, 9: 483–501.
- Viviant, M., Trites, A. W., Rosen, D. A. S., Monestiez, P., and Guinet, C. 2010. Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. *Polar Biology*, 33: 713–719.
- Vlietstra, L. 2005. Spatial association between seabirds and prey: effects of large-scale prey abundance on small-scale distribution. *Marine Ecology Progress Series*, 291: 275–287.
- Vlietstra, L., Coyle, K. O., Kachel, N. B., and Hunt, G. L. 2005. Tidal front affects the size of prey used by a top marine predator, the short-tailed shearwater (*Puffinus tenuirostris*). *Fisheries Oceanography*, 14: 196–211.
- Votier, S. C., Bicknell, A., Cox, S. L., Scales, K. L., and Patrick, S. 2013. A bird's eye view of discard reforms: Bird-borne cameras reveal seabird/fishery interactions. *PLoS ONE*, 8: e57376.
- Votier, S. C., Fayet, A. L., Bearhop, S., Bodey, T. W., Clark, B. L., Grecian, W. J., Guilford, T., *et al.* 2017. Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proceedings of the Royal Society B*, in press.
- Waggitt, J. J., and Scott, B. E. 2014. Using a spatial overlap approach to estimate the risk of collisions between deep diving seabirds and tidal stream turbines: A review of potential methods and approaches. *Marine Policy*, 44: 90–97.
- Waggitt, J. J., Cazenave, P. W., Torres, R., Williamson, B. J., and Scott, B. E. 2016a. Quantifying pursuit-diving seabirds' association with fine-scale physical features in tidal stream environments. *Journal of Applied Ecology*, In press.
- Waggitt, J. J., Cazenave, P. W., Torres, R., Williamson, B. J., and Scott, B. E. 2016b. Predictable hydrodynamic conditions explain temporal variations in the density of benthic foraging seabirds in a tidal stream environment. *ICES Journal of Marine Science*.

- Waggitt, J. J., Robbins, A. M. C., Wade, H. M., Masden, E. A., Furness, R. W., Jackson, A. C., and Scott, B. E. 2017. Comparative studies reveal variability in the use of tidal stream environments by seabirds. *Marine Policy*, 81: 143–152.
- Waggitt, J. J., Dunn, H. K., Evans, P. G. H., Hiddink, J. G., Holmes, L. J., Keen, E., Murcott, B. D., *et al.* 2018. Regional-scale patterns in harbour porpoise occupancy of tidal stream environments. *ICES Journal of Marine Science*, 75: 701–710.
- Wakefield, E. D., Phillips, R. A., and Matthiopoulos, J. 2009. Quantifying habitat use and preferences of pelagic seabirds using individual movement data: A review. *Marine Ecology Progress Series*, 391: 165–182.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., *et al.* 2002. Ecological responses to recent climate change. *Nature*, 416: 389–395.
- Waring, G., Hamazaki, T., Sheehan, D., Wood, G., and Baker, S. 2001. Characterization of beaked whale (Ziphiidae) and sperm whale (*Physeter macrocephalus*) summer habitat in shelf-edge and deeper waters off the northeast U.S. *Marine Mammal Science*, 17: 703–717.
- Warwick-Evans, V. C., Atkinson, P. W., Robinson, L. A., and Green, J. A. 2016. Predictive modelling to identify near-shore, fine-scale seabird distributions during the breeding season. *PLoS ONE*, 11: e0150592.
- Watanabe, Y. Y., and Takahashi, A. 2013. Linking animal-borne video to accelerometers reveals prey capture variability. *Proceedings of the National Academy Science*, 110: 2199–2204.
- Watson, J. R., Fuller, E. C., Castruccio, F. S., and Samhuri, J. F. 2018. Fisherman follow fine-scale physical ocean features for finance. *Frontiers in Marine Science*, 5: 1–13.
- Weichler, T., Garthe, S., Luna-Jorquera, G., and Moraga, J. 2004. Seabird distribution on the Humboldt Current in northern Chile in relation to hydrography, productivity, and fisheries. *ICES Journal of Marine Science*, 61: 148–154.
- Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? *Deep-Sea Research Part II*, 54: 211–223.
- Weir, C. R., and O'Brien, S. H. 2000. Association of the harbour porpoise (*Phocoena phocoena*) with the Western Irish sea front. *In* Proceedings of the fourteenth annual conference of the European cetacean society, pp. 61–65. Cork, Ireland.
- Weston, K., Fernand, L., Mills, D. K., Delahunty, R., and Brown, J. 2005. Primary production in the deep chlorophyll maximum of the central North Sea. *Journal of Plankton Research*, 27: 909–922.
- Williams, C., Sharples, J., Mahaffey, C., and Rippeth, T. 2013. Wind-driven nutrient pulses to the subsurface chlorophyll maximum in seasonally stratified shelf seas. *Geophysical Research Letters*, 40: 5467–5472.
- Williamson, B. J., Blondel, P., Armstrong, E., Bell, P. S., Hall, C., Waggitt, J. J., and Scott, B. E. 2015. A self-contained subsea platform for acoustic monitoring of the environment around marine



- renewable energy devices - Field deployments at wave and tidal energy sites in Orkney, Scotland. *IEEE Journal of Oceanic Engineering*, 41: 67–81.
- Wilson, B., Benjamins, S., and Elliott, J. 2013. Using drifting passive echolocation loggers to study harbour porpoises in tidal-stream habitats. *Endangered Species Research*, 22: 125–143.
- Wilson, R. P., Locca, R., Scolaro, J. A., Laurenti, S., Upton, J., Gallelli, H., Frere, E., *et al.* 2001. Magellanic penguins *Spheniscus magellanicus* commuting through San Julian Bay: do current trends induce tidal tactics. *Journal of Avian Biology*, 32: 82–89.
- Witman, J. D., Leichter, J. J., Genovese, S. J., and Brooks, D. A. 1993. Pulsed phytoplankton supply to the rocky subtidal zone: Influence of internal waves. *Proceedings of the National Academy Science*, 90: 1686–1690.
- Witt, M. J., Sheenan, E. V., Bearhop, S., Broderick, A. C., Conley, D. C., Cotterell, S. P., Crow, E., *et al.* 2012. Assessing wave energy effects on biodiversity: The Wave Hub experience. *Philosophical Transactions of the Royal Society*, 370: 502–529.
- Wolanski, E., and Hamner, W. M. 1988. Topographically controlled fronts in the ocean and their biological influence. *Science*, 241: 177–181.
- Wolf, S. G., Sydeman, W. J., Hipfner, J. M., Abraham, C. L., Tershy, B. R., and Croll, D. A. 2009. Range-wide reproductive consequences of ocean climate variability for the seabird Cassin's Auklet. *Ecology*, 90: 742–753.
- Woodson, C. B., and Litvin, S. Y. 2015. Ocean fronts drive marine fishery production and biogeochemical cycling. *Proceedings of the National Academy Science*, 112: 1710–1715.
- Yoda, K., Shiomi, K., and Sato, K. 2014. Foraging spots of streaked shearwaters in relation to ocean surface currents as identified using their drift movements. *Progress in Oceanography*, 122: 54–64.
- Young, I. R., Zieger, S., and Babanin, A. V. 2011. Global trends in wind speed and wave height. *Science*, 332: 451–455.
- Zador, S., Hunt, G. L., TenBrink, T., and Aydin, K. 2013. Combined seabird indices show lagged relationships between environmental conditions and breeding activity. *Marine Ecology Progress Series*, 485: 245–258.
- Zamon, J. E. 2001. Seal predation on salmon and forage fish schools as a function of tidal currents in the San Juan Islands, Washington, USA. *Fisheries Oceanography*, 10: 353–366.
- Zamon, J. E. 2002. Tidal changes in copepod abundance and maintenance of a summer *Coscinodiscus* bloom in the southern San Juan Channel, San Juan Islands, USA. *Marine Ecology Progress Series*, 226: 193–210.
- Zamon, J. E. 2003. Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. *Marine Ecology Progress Series*, 261: 243–255.

Zamon, J. E., Phillips, E. M., and Guy, T. J. 2014. Marine bird aggregations associated with the tidally-driven plume and plume fronts of the Columbia River. *Deep-Sea Research Part II*, 107: 85–95.

## Figures

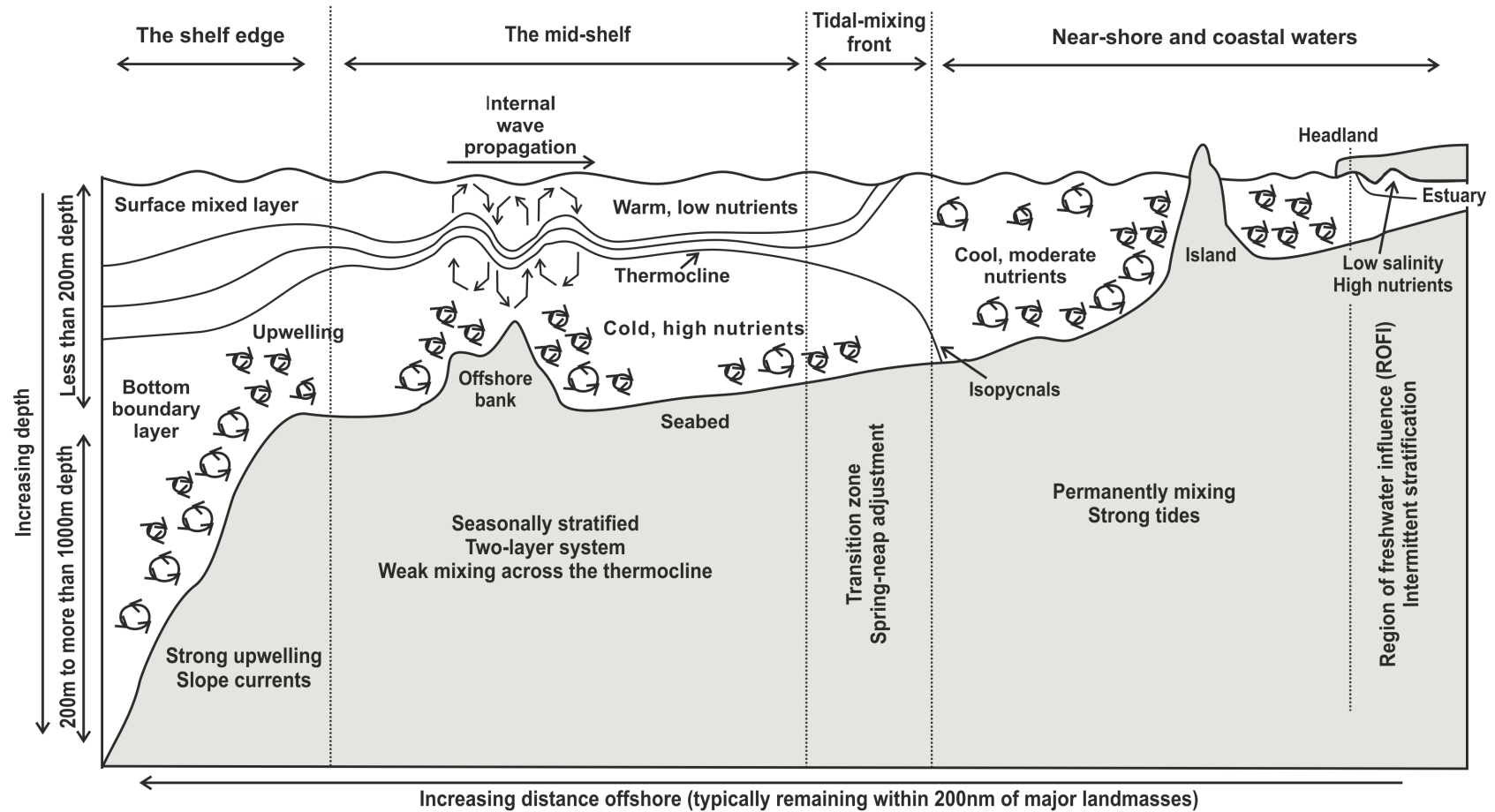


Figure 1. Cross shelf schematic giving an overview of the typical oceanographic structure of thermally stratified shelf-sea environments at mid-latitudes during the summer months. Adapted from Simpson and Sharples (2012). Black directional arrows show (1) turbulent mixing around the seabed, offshore banks and islands (circular arrows), and (2) convergent and divergent upwelling and downwelling currents associated with the passage of internal waves (angled arrows).

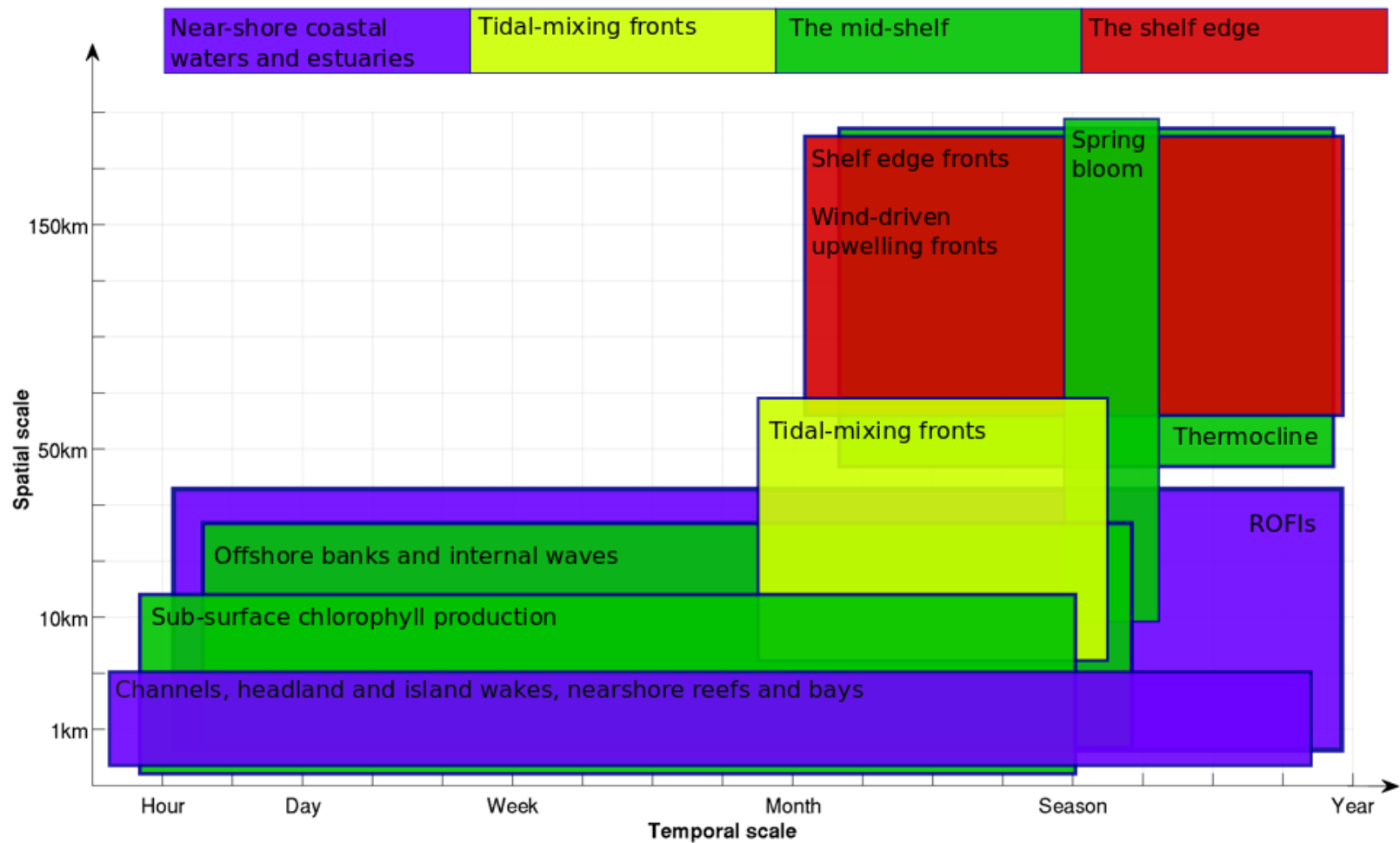


Figure 2. Overview of the typical spatio-temporal scales oceanographic structures across shelf-sea environments function over. Further details can be found in Table 1.

706 Table 1. Details of the generalised spatio-temporal scales over which oceanographic features favoured for foraging across shelf-seas function. Columns  
 707 from left to right list a features name, the spatial and temporal extent its expanse covers respectively, and finally the spatio-temporal scales over which  
 708 variation may occur. References are provided for specific examples of features functioning in this manner. Note that regional and site specific differences  
 709 in physical forcing mean there is variation around these generalisations in spatio-temporal scale, which should be assessed.

BIO-PHYSICAL HABITAT FEATURE	SPATIAL EXTENT	TEMPORAL EXTENT	SPATIO-TEMPORAL VARIATION
Shelf-edge fronts	Lateral extent of 10's - ~100km. Length may exceed 100's km's (e.g. Celtic shelf break and along the edge of the continental shelf of the Bering Sea; Pingree <i>et al.</i> , 1981; Springer <i>et al.</i> , 1996).	Typically persist perennially, although strength and associated productivity may vary seasonally (Fournier <i>et al.</i> , 1979; Ryan <i>et al.</i> , 1999).	Geographical location may shift 10's km's with prevailing meteorological conditions, seasonal changes and climatic fluctuations (Linder and Gawarkiewicz, 1998). Intensity may also vary over similar temporal scales (e.g. the strength of frontal interfaces as determined by horizontal gradients in sea surface temperature), and inter-annually with impacts on associated productivity (Fournier <i>et al.</i> , 1979).
Wind-driven upwelling fronts	Lateral extent of 10's to ~100km. Length may exceed 100's km's (e.g. along the California and Humbolt Currents; Acha <i>et al.</i> , 2004; Letelier <i>et al.</i> , 2009; Kahru <i>et al.</i> , 2012).	Generally display some seasonality in occurrence in response to upwelling intensity with current flows wind events (Kampf <i>et al.</i> , 2004; Bograd <i>et al.</i> , 2009b; Letelier <i>et al.</i> , 2009). Once established, may persist for several months.	Geographical location may shift 10-100's km's seasonally and inter-annually with climatic fluctuations in upwelling intensity, which may also impact frontal intensity and productivity levels (Bograd <i>et al.</i> , 2009b; Letelier <i>et al.</i> , 2009). Surface convergences and instabilities within these zones may be more ephemeral in occurrence, and linked to local meteorological conditions (Capet <i>et al.</i> , 2008).
Spring bloom	Can extend across stratified section of the shelf-sea, encompassing areas exceeding 100's km <sup>2</sup> (e.g. Celtic & North Seas; Pingree <i>et al.</i> , 1976; Holligan <i>et al.</i> , 1989).	Seasonally occurring in spring for a period lasting no more than a month (typically around 1-2 weeks; Pingree <i>et al.</i> , 1976; Townsend and Spinrad, 1986; Mills <i>et al.</i> , 1994).	Initial date may vary with the spring-neap cycle alongside changes in climatic conditions (Hunt and Stabeno, 2002; Mann and Lazier, 2006; Sharples <i>et al.</i> , 2006), which can also impact magnitude of productivity (Sambrotto <i>et al.</i> , 1986). Regional variation in initial start date also occurs (e.g. latitudinally; Henson <i>et al.</i> , 2009). Smaller scaled shifts in geographical occurrence may also occur inter-annually (e.g. across the Bering Sea; Hunt and Stabeno, 2002).
Vertical interfaces in stratified regions (i.e. the pycnocline)	Vertical extent of 10 cm's to a few metres (Simpson and Sharples, 2012). Horizontally extends across offshore stratified section of shelf-sea, which may encompass 100's km <sup>2</sup> (Pingree, 1975; Holligan <i>et al.</i> , 1989).	In offshore waters may be persistent perennially, although depth and inshore extent varies seasonally, and is most prominent during spring, summer and early autumn (Pingree, 1975).	Inshore extent and depth can vary inter-annually, seasonally, and on short time-scales (days to weeks), with climatic variation, weather events and tidal currents, as can the intensity of the pycnocline (i.e. gradient of change in density; Cairns and LaFond, 1966; Skov and Durinck, 2000; Ropert-Coudert <i>et al.</i> , 2009; Kokubun <i>et al.</i> , 2010). As the pycnocline approaches tidal-mixing fronts at the boundaries of coastal mixing waters, its depth shallows (Pingree, 1975). Around offshore banks, reduced depths are observed with internal wave passage and localised upwelling (Stevick <i>et al.</i> , 2008; Embling <i>et al.</i> , 2012).
Sub-surface productivity	May occur over a larger area exceeding 10's km's (Weston <i>et al.</i> , 2005), or locally in concentrated patches of 100's m's to km's (Scott	Can occur across a season, or ephemerally for a few days/weeks (Richardson and Christoffersen, 1991; Sharples <i>et al.</i> , 2001;	Productivity and entrainment may be highest when the water column stabilises, following a period of tidal and wave induced vertical mixing (McManus <i>et al.</i> , 2005; Cheriton <i>et al.</i> , 2007;

	<i>et al.</i> , 2010). Productivity is generally vertically concentrated within a few m's of the pycnocline (Sharples <i>et al.</i> , 2001).	Sharples, 2008).	Durham <i>et al.</i> , 2009). May be particularly elevated around offshore banks where internal waves propagate or there is localised upwelling (Lennert-Cody and Franks, 1999; Richardson <i>et al.</i> , 2000; Embling <i>et al.</i> , 2012).
Offshore banks & internal waves	Spatially predictable and tied to topographic features generally occurring over 1-10's km <sup>2</sup> (e.g. Jones bank; (Palmer <i>et al.</i> , 2013).	Appear to be seasonal features linked to thermal stratification between late spring and early autumn. May function intermittently with specific tidal conditions (Embling <i>et al.</i> , 2012, 2013; Palmer <i>et al.</i> , 2013)	Closely tied to bathymetric structures. Propagation of internal waves may vary with spring-neap modulation and storms (Embling <i>et al.</i> , 2013; Palmer <i>et al.</i> , 2013). Those associated with the shelf edge (e.g. within the Humboldt current; Bertrand <i>et al.</i> , 2008), may be influenced by changes in upwelling intensity.
Tidal-mixing fronts	Small lateral extent of typically 100's m's to 10's km (Schumacher <i>et al.</i> , 1979; Decker and Hunt, 1996; Durazo <i>et al.</i> , 1998). Length may exceed 10's km's (e.g. tidal mixing fronts around the British Isles; Fearnhead, 1975; Pingree and Griffiths, 1978; Miller, 2009).	Seasonally occurring from late spring to early autumn (e.g. Fearnhead, 1975; Pingree and Griffiths, 1978; Kachel <i>et al.</i> , 2002; Acha <i>et al.</i> , 2004).	Locations are coarsely predictable and typically tied to a ratio of total water depth ( $h$ ) and tidal velocity ( $u$ ) - $h/u^3$ (Simpson and Hunter, 1974). Inshore/offshore shifts may occur over scales of 10's km's, in response to changes in current strength with the spring-neap cycle, alongside surface induced mixing during wind events and decreased solar irradiance (Kachel <i>et al.</i> , 2002; Nahas <i>et al.</i> , 2005; Pisoni <i>et al.</i> , 2015). This may follow seasonal patterns (Hill and Simpson, 1989). Small scale variation (100's m's to km's) in the surface signature of a front may occur throughout the tidal cycle and due to prevailing wind conditions (Durazo <i>et al.</i> , 1998).
Channels, headland & island wakes, nearshore reefs & bays	Predictable, topographically tied localised features, occurring over 100's m's to a few km's (Zamon, 2002; Johnston and Read, 2007; Bailey and Thompson, 2010; Jones <i>et al.</i> , 2014). Some channels, bays and passes may extend across 10's km's (e.g. Academy Bay, Sea of Okhotsk, and passes between Aleutian Islands; Ladd <i>et al.</i> , 2005; Rogachev <i>et al.</i> , 2008).	May occur perennially, although only at specific times in the tidal cycle (Zamon, 2003; Johnston and Read, 2007; Bailey and Thompson, 2010; Waggitt <i>et al.</i> , 2016).	Functionality may vary with strength and direction of water currents across diurnal and bi-weekly tidal cycles (Johnston and Read, 2007; Bailey and Thompson, 2010; Jones <i>et al.</i> , 2014). Local wind patterns may temporarily intensify surface convergences (e.g. occurrence of Langmuir circulation cells; Goss <i>et al.</i> , 1997; Ladd <i>et al.</i> , 2005).
ROFI's: estuarine plume & tidal intrusion fronts	May be localised over 100's m's (e.g. Moray Firth fronts; Mendes <i>et al.</i> , 2002) or larger encompassing 10's to 100's of km's (e.g. Columbine Estuarine & Mississippi River Plume Fronts; Govoni <i>et al.</i> , 1989; Phillips <i>et al.</i> , 2018).	Occur perennially, sometimes periodically with the tidal cycle (Simpson and Nunes, 1981; Mendes <i>et al.</i> , 2002; Phillips <i>et al.</i> , 2018).	Occurrence may be linked to specific phases of the tidal cycle (e.g. Mendes <i>et al.</i> , 2002). Geographical location and strength may vary with tidal cycle and experience spatial variation with spring-neap changes in current strength. Local weather conditions and climate will also impact geographical location, occurrence and strength (e.g. rainfall and wind; Kowalczyk <i>et al.</i> , 2015b; Phillips <i>et al.</i> , 2018). Productivity blooms may follow such cycles (Cloern, 1991).