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Cox, SL

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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^{12+*}, Embling, CB¹, Hosegood, PJ², Votier, SC³ and Ingram, SN¹

5 ¹Marine Vertebrate Research Unit, University of Plymouth, Plymouth, PL4 8AA, UK

6 ²Marine Physics Research Group, University of Plymouth, Plymouth, PL4 8AA, UK

7 ³Environment and Sustainability Institute, University of Exeter, Penryn, TR10 9FE, UK

8 ⁺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 1.5ms^{-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 (Sharples 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.

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Figures

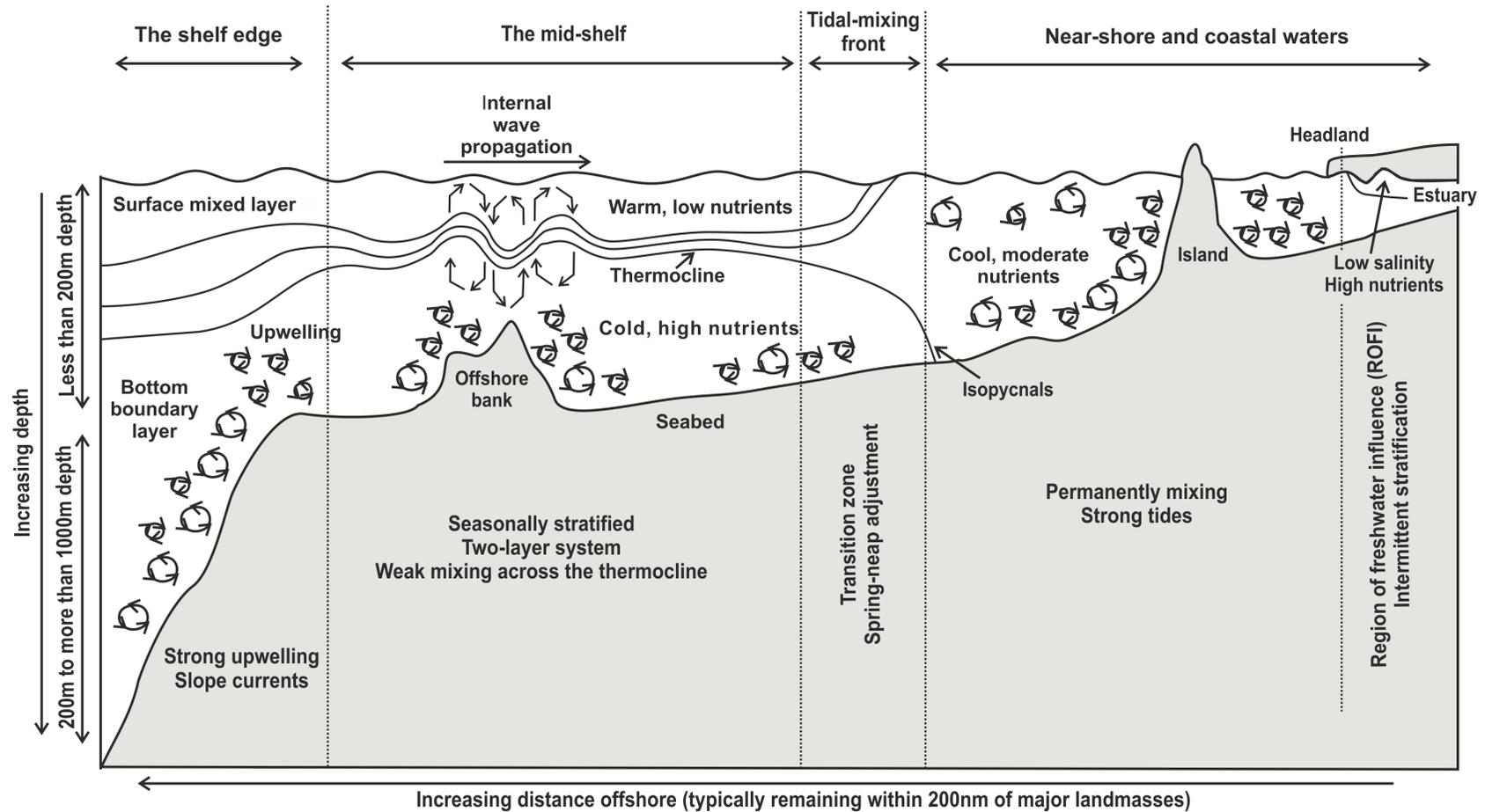


Figure 1. Cross shelf schematic giving an overview of the typical oceanographic structure of thermally stratified shelf-sea environments at mid-latitudes during the summer months. Adapted from Simpson and Sharples (2012). Black directional arrows show (1) turbulent mixing around the seabed, offshore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

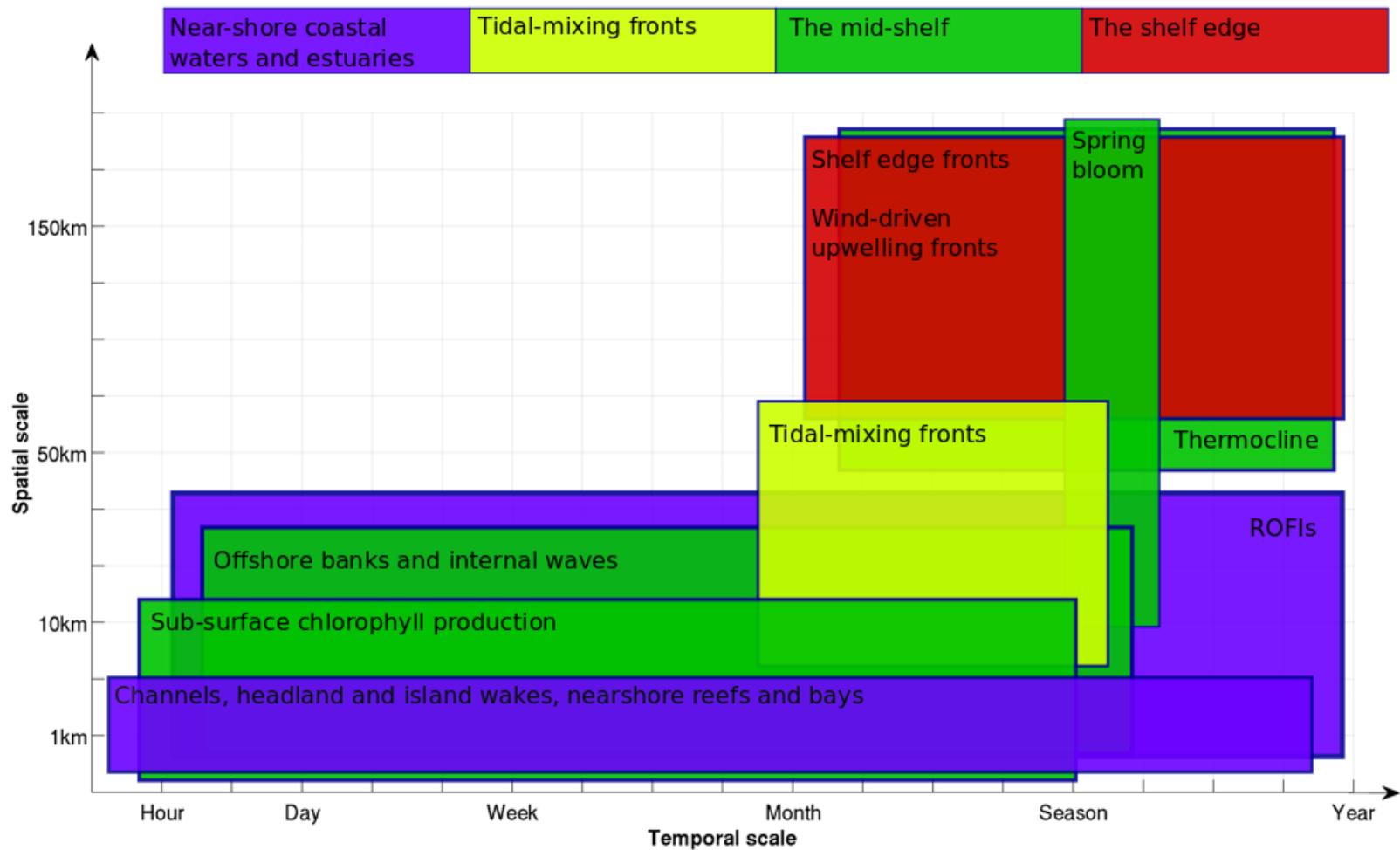


Figure 2. Overview of the typical spatio-temporal scales oceanographic structures across shelf-sea environments function over. Further details can be found in Table 1.

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 ² (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 ² (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 ² (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).