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

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[12+*], Embling, CB[1], Hosegood, PJ[2], Votier, SC[3] and Ingram, SN[1]

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

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

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

[+]Current address: UMR MARBEC SÈTE, Avenue Jean Monnet, CS 30171, 34203, Sète, FRANCE.

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

ABSTRACT

Mid-latitude (~30-60^o) seasonally stratifying shelf-seas support a high abundance and diversity of marine predators such as marine mammals and seabirds. However, anthropogenic activities and climate change impacts are driving changes in the distributions and population dynamics of these animals, with negative consequences for ecosystem functioning. Across mid-latitude shelf-seas, marine mammals and seabirds are known to forage at a number of oceanographic habitats that structure the spatio-temporal distributions of prey. Knowledge of these and the bio-physical mechanisms driving such associations are needed to improve marine management and policy. Here, we provide a concise and easily accessible guide for both researchers and managers of marine systems on the predominant oceanographic habitats that are favoured for foraging by marine mammals and seabirds across mid-latitude shelf seas. We (1) identify and describe key discrete physical features present across the continental shelf, working inshore from the shelf-edge to the shore line, (2) provide an overview of findings relating to associations between these habitats and marine mammals and seabirds, (3) identify areas for future research and (4) discuss the relevance of such information to conservation management. We show that oceanographic features preferentially foraged at by marine mammals and seabirds include shelf-edge fronts, upwelling and tidal-mixing fronts, offshore banks and internal waves, regions of stratification, and topographically complex coastal areas subject to strong tidal flow. Whilst associations were variable across taxa and through space and time, in the majority of cases interactions between bathymetry and tidal currents appear to play a dominant role, alongside patterns in seasonal stratification and shelf-edge upwelling. We suggest that the ecological significance of these bio-physical structures stems from a capacity to alter the densities, distributions (both horizontally and vertically) and behaviours of prey in a persistent and/or predictable manner that increases accessibility for predators, and likely enhances foraging efficiency. Future conservation management should aim to preserve and protect these habitats. This will require adaptive and holistic strategies that are specifically tailored to the characteristics of an oceanographic feature, and where necessary evolve through space and time. Improved monitoring of animal movements and bio-physical conditions across shelf-seas would aid in achieving this. Areas for future research include multi- disciplinary/trophic studies of the mechanisms linking oceanographic habitats, prey and marine mammals and seabirds (which may also elucidate the importance of lesser studied features such as bottom fronts and Langmuir circulation cells), alongside a better understanding of how predators perceive their environment and develop foraging strategies during immature/juvenile stages. Estimates of the importance of bio-physical processes at a population level should also be obtained. Such information is vital to ensuring the future health of these complex ecosystems, and can be used to assess how anthropogenic activities and changes in the environment will impact the functioning and spatio-temporal dynamics of these bio-physical features and their use by marine predators.

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

1 Introduction

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

Marine mammals and seabirds meet their requirements for survival, growth and reproduction through the exploitation of prey resources from their surrounding environment. Whilst typically these animals are highly mobile and capable of ranging vast distances (Block *et al.*, 2011), foraging efforts are often concentrated over localised spatio-temporal scales (Hastie *et al.*, 2004; Sydeman *et al.*, 2006; Weimerskirch, 2007). Such heterogeneity in distributions is expected to match the organisation of prey, but this has proved surprisingly challenging to demonstrate (Logerwell *et al.*, 1998; Fauchald and Erikstad, 2002; Gremillet *et al.*, 2008; Torres *et al.*, 2008), particularly at finer scales which may be impacted by confounding factors (Schneider and Piatt, 1986; Hunt *et al.*, 1992; Mehlum *et al.*, 1999; Swartzman and Hunt, 2000; Vlietstra, 2005; Fauchald, 2009). Increasing evidence suggests the behavioural patterns of marine predators (particularly those feeding on plankton and/or forage and pelagic fish) are linked to bio-physical oceanographic processes that structure the accessibility and availability of these lower trophic level food sources (Cox *et al.*, 2013; Bertrand *et al.*, 2014; Woodson and Litvin, 2015; McInnes *et al.*, 2017), and thus influence foraging efficiency/success (Boyd *et al.*, 2016). Across shelf-sea environments, a number of discrete habitat features have been identified as important locations that host enhanced foraging opportunities, including fronts, offshore banks where internal waves propagate and tidally dependent island wakes (Hunt and Schneider, 1987; Hunt *et al.*, 1999; Bost *et al.*, 2009; Bertrand *et al.*, 2014; Scales *et al.*, 2014a; Benjamins *et al.*, 2015). Given the tight energy constraints of many marine mammals and seabirds (Cairns, 1988), these structures can be thought of as critical habitat features.

Knowledge of the bio-physical processes that underlie links between oceanographic habitat features and marine mammal and seabird foraging is vital to obtaining a comprehensive understanding of marine ecosystem functioning. This will prove invaluable as we move towards implementing holistic management methods, that consider ecosystems in their entirety and aim to incorporate more precautionary conservation measures (Arkema *et al.*, 2006; Hooker *et al.*, 2011). Early synthesises and reviews have outlined the prominent bio-physical processes occurring across ocean environments and how these are linked to the spatio-temporal distributions of seabirds (e.g. Hunt, 1990, 1991, 1997; Hunt *et al.*, 1999), but no known equivalent review exists for marine mammals. Over the past 10-15 years, methodological and technological advances have substantially improved the way in which the marine environment is studied, both in terms of how we collect data (Cooke *et al.*, 2004; Hunt and Wilson, 2012; Brown *et al.*, 2013; Waggitt and Scott, 2014; Photopoulou *et al.*, 2015; Benoit-Bird and Lawson, 2016; Macaulay *et al.*, 2017) and quantitatively analyse it (Redfern *et al.*, 2006; Wakefield *et al.*, 2009; Brown *et al.*, 2013; Carter *et al.*, 2016; Bennison *et al.*, 2017). As such, our knowledge of links between oceanographic habitats and marine predators has substantially improved, and a more mechanistic understanding of how these features aid marine mammal and seabird foraging, and function as dynamic habitats is being attained. Although, more recent regional and/or feature specific reviews have been published (e.g. fronts; Scales *et al.*, 2014a, southern ocean fronts and eddies; Acha *et al.*, 2004; Bost *et al.*, 2009, and tidal stream environments; Benjamins *et al.*, 2015), as of yet, a paper which encompasses links between both marine mammals and seabirds with the full range of oceanographic habitat features that occur across mid-latitude, seasonally stratifying shelf-seas as a whole is lacking. Such knowledge is still yet to be fully integrated into studies examining behavioural patterns and habitat use by marine predators alongside marine management strategies (Tremblay *et al.*, 2009; Fourcade *et al.*, 2018), and so it is particularly pertinent that this is addressed, not least because the diverse human use of shelf-seas is accelerating impacts on these ecosystems. We feel it important to synthesise the broad and diverse habitat features present in this environment to facilitate conservation management and ecological research, and drive a policy response to this crisis.

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

2 The shelf edge

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

2.1 Shelf-edge fronts

Shelf-edge fronts (also shelf-break and shelf-slope fronts) occur at the interface between on-shelf and open-ocean waters (Figure 1), and are marked by strong gradients in salinity, and sometimes temperature. As currents, pushed onto the shelf via tidal forcing, are interrupted by the steep sloping topographic profiles of these regions, upwelling pushes the surface mixed layer above the critical depth for phytoplankton growth (Fournier *et al.*, 1979), whilst simultaneously facilitating exchange with the nutrient rich waters of the open-ocean's bottom boundary layer (Springer *et al.*, 1996; Ryan *et al.*, 1999). High levels of primary productivity are typically sustained, sometimes perennially (Fournier *et al.*, 1979), attracting planktivorous grazers alongside large numbers of pelagic fish (Podesta *et al.*, 1993; Sabatés and Olivar, 1996; Springer *et al.*, 1996; Genin, 2004; Greer *et al.*, 2015). Dependent upon the lateral extent and topography of the adjacent continental shelf, these features may be far from land, and so relatively inaccessible to those foragers constrained to land-based colonies (e.g. breeding seabirds and some seals). Links to marine predators are dominated by those taxa capable of performing far-ranging foraging trips (e.g. black petrel *Procellaria parkinsoni*, fork-tailed storm petrel *Oceanodroma furcate*, northern fulmar *Fulmarus glacialis* and short-tailed albatross *Phoebastria albatrus*; Schneider, 1982; Stone *et al.*, 1995; Piatt *et al.*, 2006; Freeman *et al.*, 2010) or that are not restricted to a central location for breeding (e.g. Cuvier's beaked whale *Ziphius* *cavirostris*, Risso's dolphin *Grampus griseus*, sperm whale *Physeter microcephalus* and spotted dolphin *Stenella attenuata*; Baumgartner, 1997; Waring *et al.*, 2001; Pinedo *et al.*, 2002; Azzellino *et al.*, 2008; Scott and Chivers, 2009). Where the shelf edge is nearer to land (e.g. the Skagerrak), shorter ranging breeding species may forage at these features (e.g. little auk *Alle alle*; Skov and Durinck, 1998). Shelf-edge fronts may also be important to non-breeding individuals in the late summer, autumn and winter, when constraints to a central land-based breeding location no longer apply (e.g. Cory's shearwater *Calonectris borealis* and little auk; Haney and McGillivary, 1985a; Brown, 1988).

2.2 Wind-driven upwelling fronts

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

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

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

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

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

The mid-shelf extends from the shelf-edge to near-shore coastal waters (Figure 1) with topographic depths typically ranging from around 50m to 200m. In mid-latitude, temperate zones this region stratifies seasonally between late spring and autumn when increased solar irradiation heats surface waters sufficiently to increase buoyancy levels and overcome tidal and wind-driven mixing (Pingree, 1975; Pingree *et al.*, 1976; Simpson and Sharples, 2012). A two-layer system is formed, characterised by a surface mixed layer of warm, nutrient deficient water and a bottom boundary layer of dense, cold nutrient rich water (Figure 1). This structuring underlies a number of oceanographic processes that appear important to marine mammals and seabirds, particularly in areas where the spatial extent of the continental on-shelf region is large and tidal ranges considerable (e.g. the Canadian, European, northeast USA continental shelf and the eastern Bering Sea Shelf).

3.1 The annual spring bloom

The development/onset of stratification in the spring drives a significant annual phytoplankton bloom (Pingree *et al.*, 1976; Sambrotto *et al.*, 1986; Sharples *et al.*, 2006). The timing of this bloom varies annually as a result of climatic fluctuations in air temperature/solar irradiation and wind stress (Sharples *et al.*, 2006), which can lead to a temporal mismatch between fish spawning and plankton production (match-mismatch hypothesis; Cushing, 1975). This can have bottom-up impacts at higher trophic levels by influencing fish recruitment (Beaugrand and Kirby, 2010; Sigler *et al.*, 2016) and food availability (Durant *et al.*, 2007), and has been shown to effect the breeding success of a number of seabirds including Atlantic puffin *Fratercula arctica*, black-legged kittiwake *Rissa tridactyla*, common guillemot and rhinoceros auklet off the coast of British Columbia, and across the North and Norwegian Seas (Durant *et al.*, 2006; Scott *et al.*, 2006; Borstad *et al.*, 2011). Such impacts sometimes occur at a lag of 1-2 years to underlying shifts in environmental conditions (Zador *et al.*, 2013). Changes in prey availability have also been linked to spatial variability in the distribution of the spring bloom alongside the oceanographic conditions within which it occurs (Table 2). For example, across the eastern Bering Sea, in years when the spring bloom occurs in warmer offshore waters (due to earlier sea ice retreat; Hunt and Stabeno, 2002), changes in the abundance, composition, distribution and survival of predominant plankton and juvenile fish species results in shifts in the diets and distributions of several seabird populations (Springer *et al.*, 2007; Renner *et al.*, 2016; Hunt *et al.*, 2018), which can result in demographic impacts (Satterthwaite *et al.*, 2012; Zador *et al.*, 2013).

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

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

High levels of sub-surface primary productivity often concentrate around the pycnocline, and can account for over 50% of water column productivity (Weston *et al.*, 2005), alongside ~30% of total annual productivity (Richardson and Christoffersen, 1991). This is maintained through the summer months by two sources of episodic mixing events, each of which results in an influx of nutrients from the bottom boundary layer that enhance productivity. First, increased tidal currents during spring tides generate turbulent dissipation (due to friction with the sea bed), that may extend up through the bottom boundary layer temporarily eroding the base of the pycnocline (Sharples, 1999, 2008; Sharples *et al.*, 2001; Allen *et al.*, 2004). Second, wave and wind driven surface mixing (due to changes in wave/wind direction and/or velocity with prevailing weather conditions) may partially break down vertical stratification (Sharples and Tett, 1994; Rippeth *et al.*, 2005; Williams *et al.*, 2013). Shear boundaries (strong vertical gradients in horizontal currents) around the pycnocline may additionally aid in the retention of small organisms such as phytoplankton (Franks, 1995; Durham *et al.*, 2009; Cheriton *et al.*, 2010), whilst a synchronous accumulation of zooplankton (McManus *et al.*, 2005) can result in a propagation of food supply across multiple trophic levels.

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

The depth of the pycnocline is also an important determinant of foraging habitat suitability (Hunt *et al.*, 1993; Skov and Durinck, 2000; Nordstrom *et al.*, 2013). Increased light attenuation with depth means productivity around shallower pcynoclines is likely enhanced compared with deeper pcynoclines (Skov and Durinck, 2000). Moreover, for near-surface feeders (e.g. northern fulmar) a shallower pycnocline may make prey available at more accessible depths (Skov and Durinck, 2000), and for those that dive from the surface (e.g. least auklet *Aethia pusilla)*, reduce foraging energetic costs (Hunt *et al.*, 1990; Haney, 1991; Skov and Durinck, 2000; Langton *et al.*, 2011). In thermally stratified waters, exothermic prey may redistribute themselves near the surface in an attempt to avoid unfavourable cool bottom boundary waters below the pycnoline (e.g. mackerel *Scomber scombrus*; Grégoire, 2006).

3.3 Internal waves and offshore banks

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

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

4 Tidal-mixing fronts

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

Tidal-mixing fronts are often associated with elevated and persistent primary productivity that has the potential to propagate across multiple trophic levels (Coyle and Cooney, 1993; Munk *et al.*, 1995; Gregory Lough and Manning, 2001). Where the pycnocline of stratified offshore waters shallows to meet inshore mixing waters, increased light exposure supplemented with runoff nutrients (of coastal waters) alongside those mixed up from the bottom boundary layer results in productivity levels several orders of magnitude higher than in surrounding waters (Pingree *et al.*, 1975; Simpson *et al.*, 1979; Franks, 1992a). Additional convergent flows (Pingree *et al.*, 1974) may redistribute the horizontal and vertical distributions of weak or passively swimming organisms (e.g. plankton grazers attracted to the high productivity levels of the front; Coyle *et al.*, 1998), resulting in near-surface retention and accumulation (Franks, 1992b; Epstein and Beardsley, 2001).

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

5 Near-shore coastal waters and estuaries

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

5.1 Channels, headland and island wakes, nearshore reefs and bays

In near-shore coastal regions, marine mammals and seabirds frequently forage within tidally active areas (Nol and Gaskin, 1987; Marubini *et al.*, 2009; Anderwald *et al.*, 2012; Benjamins *et al.*, 2015; Warwick-Evans *et al.*, 2016; Waggitt *et al.*, 2018), resulting in distinct regularities in their distributions and behaviours that coincide with particular tidal phases (Becker *et al.*, 1993; Hunt *et al.*, 1998; Irons, 1998; Isojunno *et al.*, 2012; De Boer *et al.*, 2014; Ijsseldijk *et al.*, 2015). Specifically, areas such as narrow channels, headlands, islands, reefs and bays often function as periodic foraging hotspots, where interactions between strong tidal currents (often exceeding $1.5 ms^{-1}$) and complex topography create prosperous foraging opportunities for marine predators (Cairns and Schneider, 1990; Coyle *et al.*, 1992; Zamon, 2003; Benjamins *et al.*, 2015; Couperus *et al.*, 2016). In some instances, several of these features may occur in close proximity to one another (Bailey and Thompson, 2010).

5.1.1 Channels and narrow passes

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

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

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

5.1.2 Headland and island wakes

When headland and island features interrupt the passage of strong tidal current flows, a leeward wake (or eddy) may form. At the interface with non-wake waters, shear induced hydrographic fronts (Wolanski and Hamner, 1988; Johnston and Read, 2007) may accumulate zooplankton which become retained within the calm waters of the wake (Alldredge and Hamner, 1980). In addition, turbulent flows around these structures may disorientate fish prey that use the wake to forage, or seek refuge from adjacent strong tidal currents (Liao, 2007; Robinson *et al.*, 2007; Tarrade *et al.*, 2008). For example, in the Bay of Fundy (Canada), harbour porpoise, fin and minke *Balaenoptera acutorostrata* whale exploit dense patches of euphasiids *Meganyctiphanes norvegica* and herring *Clupea harengus* along the edge of an island wake during flood tides (Johnston *et al.*, 2005b, 2005a; Ingram *et al.*, 2007). Bottlenose dolphins in the Moray Firth (UK) concentrate foraging activity along the surface signatures of hydrographic fronts, that form during specific tidal conditions in proximity to a headland on the edge of a deep, steep-sided channel (Bailey and Thompson, 2010), while across Glacier Bay and Icy Strait in southeastern Alaska, humpback whale distributions are disproportionately distributed within the leeward waters of several headlands (Chenoweth *et al.*, 2011). Where fish actively avoid turbulent flows (Nichol and Somerton, 2002), hydrographic fronts may act as a barrier to their movements, and so some predators (e.g. bottlenose dolphin and killer whale) may use these features for prey herding (Heimlich-Boran, 1988; Benjamins *et al.*, 2015). However, as of yet this has not been directly explored.

5.1.3 Nearshore reefs, banks and ridges

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

5.1.4 Bays

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

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

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

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

6 Oceanographic habitats and the facilitation of foraging

It is evident that bio-physical processes strongly influence habitat choice by a diversity of marine mammals and seabirds that feed upon plankton and/or forage and pelagic fish, and across shelf-seas a range of oceanographic features are favoured for foraging. Such associations appear attributable to predictable increases in prey accessibility and availability that stem from changes in the abundance and density, depth distribution, behaviour and/or patch persistence of prey, which together likely facilitate trophic transfer and enhance foraging efficiency (Pelletier *et al.*, 2012; Boyd *et al.*, 2016). For example, notable declines in the reproductive success of some marine predator populations have mirrored a change/reduction in the availability of prey enhancing oceanographic habitats following environmental changes with prevailing climatic and weather conditions (Hennicke and Culik, 2005; Scott *et al.*, 2006; Boersma and Rebstock, 2009; Ropert-Coudert *et al.*, 2009a; Wolf *et al.*, 2009; Borstad *et al.*, 2011). The importance of difference aspects of prey availability (e.g. prey abundance versus depth distribution, versus predictability) will depend upon species specific foraging strategies (e.g. surface feeder versus diver, available search time, differences in prey type; Hunt *et al.*, 1999; Langton *et al.*, 2011), alongside individual energetic requirements (Hennicke and Culik, 2005; Goldbogen *et al.*, 2011). For central place foragers constrained to land (e.g. many breeding seabirds and seals), some features may be inaccessible due to their proximity and limitations on an individuals foraging range (e.g. shelf-edge fronts; Thaxter *et al.*, 2012).

6.1 Increased abundance and density of prey

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

6.2 Depth distribution of prey

Depth distribution plays a key role in prey accessibility, particularly for those taxa that feed at or near the surface and/or have limited dive capabilities (Embling *et al.*, 2012; Boyd *et al.*, 2015). Surface convergent zones at shelf-edge fronts, upwelling fronts and tidal-mixing fronts are frequently used by these foragers, as are localised upwelling structures related to interactions between topography and tidal currents (e.g. at offshore banks and around the coast). In such areas, individuals have been directly linked to shallow prey aggregations (Russell *et al.*, 1999; Stevick *et al.*, 2008; Embling *et al.*, 2012). For air-breathing diving predators, changes in the depth distributions of their prey may reduce the energetic costs of capture by either allowing individuals to concentrate search activity within a restricted proportion of the water column, or reducing overall dive depths from the surface (Ropert-Coudert *et al.*, 2009b; Benoit-Bird *et al.*, 2011). For example, the foraging efficiencies of some diving seabirds appear to be tied to the presence of vertical prey aggregating features such as the pycnocline (Ropert-Coudert *et al.*, 2009a; Pelletier *et al.*, 2012).

6.3 Prey behaviour

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

6.4 Persistence and predictability

The oceanographic features favoured for foraging by marine mammals and seabirds typically occur in a persistent and/or predictable manner. If individuals can learn and remember the locations at which encountering accessible prey is more probable (Hunt *et al.*, 1999; Gende and Sigler, 2006; Weimerskirch, 2007; Davoren, 2013; Regular *et al.*, 2013; Grecian *et al.*, 2018), concentrated search effort (Hamer *et al.*, 2009; Pettex *et al.*, 2010; Dragon *et al.*, 2012; Patrick *et al.*, 2014) can increase foraging efficiency (Stephens and Krebs, 1986). Targeted search patterns have been shown to coincide with the occurrence of a number of oceanographic habitats that are repetitively visited (Bailey and Thompson, 2010; Sabarros *et al.*, 2014; Scales *et al.*, 2014b). Moreover, these behaviours have been shown to develop as individuals mature, suggesting they are beneficial (Grecian *et al.*, 2018). In some cases, the scales across which targeted search effort occur are tied to those of corresponding physical processes. For example, gannets foraging around tidal-mixing fronts restrict search behaviours over scales of between 2km to 10km (Hamer *et al.*, 2009; Scales *et al.*, 2014b) reflective of those over which the locations of these features vary with tidal- and wind- driven events (Nahas *et al.*, 2005; Pisoni *et al.*, 2015). Bottlenose dolphins foraging around topographically controlled tidal structures display highly localised search behaviours over 100's of metres, which mirrors the similarly scaled predictability of these features (Bailey and Thompson, 2010).

7 Future research directions

Whilst associations between marine predators and bio-physical processes have been documented across numerous studies, there are a number of areas in which improvements are still necessary. Concurrent measurements of sub-surface oceanography, low- to mid- trophic level prey distributions and marine mammal and seabird behaviours around many discrete physical features are lacking (e.g. tidal stream environments), or limited to a specific set of locations and sites (e.g. the Bering Sea, British Isles and Canadian Continental Shelf). Moreover, fine-scale three-dimensional measurements of marine mammal and seabird movements are rarely integrated, which would allow for estimates of prey capture attempts and energetic expenditure to be calculated and used to evaluate foraging effort/efficiency (Viviant *et al.*, 2010; Watanabe and Takahashi, 2013; Richard *et al.*, 2016). Achieving this would greatly increase our understanding of how physical habitats impact prey availability for marine predators and facilitate trophic transfer (Embling *et al.*, 2012), whilst also elucidating site and species specificity (Waggitt *et al.*, 2017) alongside the drivers of spatio-temporal variability in marine mammal and seabird distributions (Certain *et al.*, 2007). Such efforts may also reveal the importance of other, lesser studied structures. For example, to our knowledge, the ecological significance of bottom fronts (which may be important to deeper diving predators) is yet to be investigated (Hill *et al.*, 2008). In addition, despite some evidence suggesting Langmuir circulation cells are exploited by surface feeding seabirds in near-coastal regions (Goss *et al.*, 1997; Ladd *et al.*, 2005), the importance of these features further offshore is yet to be explored (Barstow, 1983). Distinguishing the way in which individuals perceive their environment via knowledge transfer (Machovsky-Capuska *et al.*, 2014), learning and memory (Regular *et al.*, 2013; Grecian *et al.*, 2018), sight (Bodey *et al.*, 2014; Tremblay *et al.*, 2014; Bairos-Novak *et al.*, 2015) and smell (Savoca and Nevitt, 2014) would also be beneficial, as would an increased knowledge of immature/juvenile foraging behaviours and how these develop through time (de Grissac *et al.*, 2017; Votier *et al.*, 2017; Grecian *et al.*, 2018). Further inter-taxa research (e.g. marine mammals versus seabirds, planktivores versus piscivores, and surface feeders versus divers) would compliment this, and provide additional insight of the selection pressures that have shaped the evolution of the at-sea behaviours of these animals, and driven the necessary adaptations required for foraging in dynamic waters. Such investigations may also be useful for assessing the potential of these taxa to adapt in response to climate change. Finally, there is a distinct lack of studies determining the importance of oceanographic habitat features at a population level, which should be addressed. Future research should aim to fill these gaps if we are to improve our understanding of habitat use by marine mammals and seabirds across shelf-seas. However, achieving this will require novel methodological techniques. Adaptive survey designs (Embling *et al.*, 2012; Suberg *et al.*, 2014; Waggitt and Scott, 2014; Waggitt *et al.*, 2016a; Benjamins *et al.*, 2017) that incorporate active and passive acoustics (Williamson *et al.*, 2015; Benoit-Bird and Lawson, 2016; Macaulay *et al.*, 2017; Malinka *et al.*, 2018) alongside underwater videography (Machovsky-Capuska *et al.*, 2011; Crook and Davoren, 2014) may prove particularly useful, as will animal borne biologging via the attachment of accelerometers (Viviant *et al.*, 2010; Watanabe and Takahashi, 2013), cameras (Votier *et al.*, 2013; Watanabe and

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

8 Applications to conservation management

Over the last 20-30 years, marine management and policy has started to evolve from single species based protocols and strategies (typically tailored to a specific fishery/sector), to more holistic methods that consider ecosystems in their entirety, and incorporate more precautionary conservation measures (e.g. the European Marine Strategy Framework Directive 2008/56/EC; Pikitch *et al.*, 2004; Arkema *et al.*, 2006; Curtin and Prellezo, 2010). Key to this is the preservation of core shelf-sea habitats, such as those oceanographic features identified here as favourable for foraging by marine mammals and seabirds (Hooker and Gerber, 2004; Taylor *et al.*, 2005; Heithaus *et al.*, 2008; Game *et al.*, 2009; Dickey-Collas *et al.*, 2017; Sherley *et al.*, 2017). However, achieving adequate protection is complicated by the diverse nature of such structures, which occur over a range of spatio-temporal scales (Figure 2 and Table 1), and function via a variety of bio-physical mechanisms that may impact prey availability in different ways (e.g. through inducing changes in depth distribution, persistent, predictability, abundance and/or behaviour; see section 6). A sophisticated understanding of these dynamics can be used to effectively implement appropriate and customised conservation management strategies (Authier *et al.*, 2017).

For example, initial implementations of holistic management have focused on fixed area based protection through the designation of marine protected areas (MPAs; Hyrenbach, 2000; Hooker and Gerber, 2004). Here, the aim is to reduce overlap with spatially explicit threats (e.g. commercial fisheries, marine renewables and maritime traffic) that may cause direct mortality and/or disrupt accessibility to favoured habitats (e.g. through prey depletion or displacement; Pichegru *et al.*, 2010; Gormley *et al.*, 2012). However, while persistent and predictable bathymetrically tied tidal features (e.g. offshore banks, channels and island wakes) may be particularly well suited to such measures, to accommodate individuals relying on habitats that are variable through space and time (e.g. upwelling and tidal-mixing fronts), adaptive approaches are required. A recent solution to this is dynamic ocean management (DOM), defined as management that is adjustable through space and time in response to the shifting nature of the ocean and its users (Hobday *et al.*, 2014; Lewison *et al.*, 2015; Maxwell *et al.*, 2015). Such methods can thus allow for geographical changes in habitat locations with, for example, prevailing environmental conditions (e.g. position in spring-neap cycle alongside short term weather events, seasonal trends and longer term climatic changes; Nahas *et al.*, 2005; Bograd *et al.*, 2009a; Pisoni *et al.*, 2015). However, implementing DOM requires multidisciplinary and novel monitoring approaches, so as boundaries are effectively designated and modified (Hazen *et al.*, 2018). Moreover, attention needs to be paid towards the spatio-temporal scales over which data is acquired and protection implemented, which should reflect the characteristics and spatio-temporal variability of an oceanographic feature (Figure 2, Table 2; Mannocci *et al.*, 2017; Scales *et al.*, 2017). Satellite remote-sensing can aid in this by allowing oceanographic features to be tracked both instantaneously in near real time and over longer periods, although this is only applicable where a distinct surface signature is presented (Miller, 2009; Scales *et al.*, 2014a). Sensors deployed on diving animals autonomous/unmanned survey vehicles and/or moorings may compliment such information (Charrassin *et al.*, 2008; Suberg *et al.*, 2014; Photopoulou *et al.*, 2015), as can outputs from oceanographic and statistical modelling (Brodie *et al.*, 2018; Mattei *et al.*, 2018). Where stationary management is preferred, long-term time series data may be used to develop buffer zones that extend the boundaries of a fixed MPA, such that fluctuations in the spatio-temporal occurrence of a habitat feature is captured (e.g. the entire spring-neap/weather dependent range of a tidal-mixing front; Nahas *et al.*, 2005; Grantham *et al.*, 2011; Pisoni *et al.*, 2015). Such strategies should still be evaluated at regular intervals to assess potential geographical shifts in response to climate change (Queiros *et al.*, 2016).

A shift towards management strategies than consider habitat hydrology in addition to geography is also beneficial to ensuring that the functioning of oceanographic features favoured for foraging is maintained (Dickey-Collas *et al.*, 2017). For example, anthropogenically generated structural changes to the marine environment (e.g. marine renewable energy installations; MREIs) may alter the bio-physical and spatio-temporal characteristics of oceanographic environments (e.g. interruptions to near coastal current regimes may alter and/or manifest tidally driven features such as hydrographic fronts, wakes and localised upwelling systems; Brostrom, 2008; Shields *et al.*, 2011; Benjamins *et al.*, 2015; Fraser *et al.*, 2018). This may cause shifts in the geographical locations at which these structures occur and impact prey availability (e.g. depth distribution and predictability; Becker and Beissinger, 2003), and thus should be carefully considered during the planning stages of development projects. Impact assessments at sites where oceanographic features favoured for foraging are present need to consider how variability in the dynamics of such structures influence patterns in area use by marine mammals and seabirds, and thus the validity of associated evaluations (Benjamins *et al.*, 2017; Cox *et al.*, 2017). Climate change impacts will likely also alter the functioning of these habitats. Increases in the frequency and intensity of extreme climatic (e.g. ENSO associated changes in upwelling; Cai *et al.*, 2014) and weather (e.g. storm induced turbulent mixing; Young *et al.*, 2011) events may again, modify the dynamics and geographical locations of critical oceanographic features (Hazen *et al.*, 2013; Sherley *et al.*, 2017), such as upwelling fronts, the pycnocline and tidal-mixing fronts (Ropert-Coudert *et al.*, 2009a; Pisoni *et al.*, 2015). For example, decreases in the reproductive outputs of a number of seabirds have been linked to changes in the availability of oceanographically generated foraging habitats following irregularities in prevailing climatic and weather conditions (Hennicke and Culik, 2005; Durant *et al.*, 2006; Scott *et al.*, 2006; Ropert-Coudert *et al.*, 2009a). Minimising the impacts of this will require adaptive, innovative and precautionary management strategies that minimise cumulative stressors (Field and Francis, 2006; Lester *et al.*, 2010; Sherley *et al.*, 2017), particularly since our understanding of how ecosystems will cope and respond to such alterations is largely unknown. Again, MPAs and DOM informed by studies on the dynamics of oceanographic features favoured for foraging will likely play an important role in this (Halpern *et al.*, 2010; Grantham *et al.*, 2011; Briscoe *et al.*, 2016; Dickey-Collas *et al.*, 2017).

9 Conclusions

A range of oceanographic features are favoured for foraging by marine mammals and seabirds across shelf-seas in mid-latitude temperate zones. Whilst associations are diverse and variable in nature (both between sites and across species), in the majority of cases intricate interactions between bathymetry and tidal currents play a dominant role, alongside patterns in seasonal stratification and shelf-edge upwelling. The attractiveness of a favoured oceanographic feature appears to stem from persistent and/or predictable increases in prey accessibility which facilitates foraging. Changes in prey abundance and density, behaviour and depth distribution are fundamental to this, and in a number of cases have been shown to improve foraging efficiencies. However, our knowledge of interactions between marine predators and oceanographic features favoured for foraging is far from complete, and future work should aim to further our understanding of the functional mechanisms linking bio-physical processes, prey and marine mammals and seabirds. In many instances, detailed and simultaneous three-dimensional measurements of sub-surface oceanography, prey densities and distributions alongside marine predator behaviours (across three-dimensions) are lacking, and this should be addressed. Such efforts may also elucidate the importance of lesser studied features such as bottom fronts and Langmuir circulation cells. A better understanding of how predators perceive their environment and develop foraging strategies during immature/juvenile stages would also be beneficial, as would comparative inter-taxa research and estimates of the importance of oceanographic habitat features at a population level. Knowledge of the bio-physical processes that underlie habitat use by marine mammals and seabirds across shelf-seas should be used to inform future conservation management and policy. This will require improvements in the monitoring of oceanographic conditions such that adaptive strategies can be implemented which, where necessary, can evolve through space and time in response to the dynamic nature of the ocean. This would aid the preservation and protection of oceanographic features that facilitate trophic transfer, and are thus critical to the functioning of shelf-sea environments. Such holistic approaches are vital to ensuring the future health of these complex ecosystems.

Acknowledgements

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

Alemany, 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.

Alldredge, 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., Airoldi, 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., Giminez, 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 murres 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 foarging 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 strcuture 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 Wildelife Service Special Publications, Ottawa, Canada.

Brigolin, D., Girardi, P., Miller, P. I., Xu, W., Nachite, D., Zucchetta, 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., Langaigne, 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 souther 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 humpabck 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., Steinbuck, 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 murres 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 murres (*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., Hennicke, 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 McGillivary, P. A. 1985a. Aggregations of cory's shearwaters (*Calonectris diomedea*) at Gulf Stream fronts. Wilson Bulletin, 97: 191–200.

Haney, J. C., and McGillivary, 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 forgaing. 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.

Hoefer, 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 foarging ecology of seabirds. *In* Proceedings of the 22nd Internatioanl 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 Whitledge, 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 murres (*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 murres 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.

Kroodsma, 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 Magallan - 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 foarging 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., Lütkebohleohle, 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 Noth Pacific: Implications for conservation. Deep-Sea Research II, 53: 387–398.

Pichegru, L., Gremillet, 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 whlae 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 vessle 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 teh 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 demongraphy 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 instrusion 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 murres (*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 murres 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.

ven Eeden, R., Ryan, P. G., and Pichegru, L. 2016. Fine-scale foraging cues for African penguins in ahighly 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 rick 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 Samhouri, J. F. 2018. Fisherman follow fine-scale physcial 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

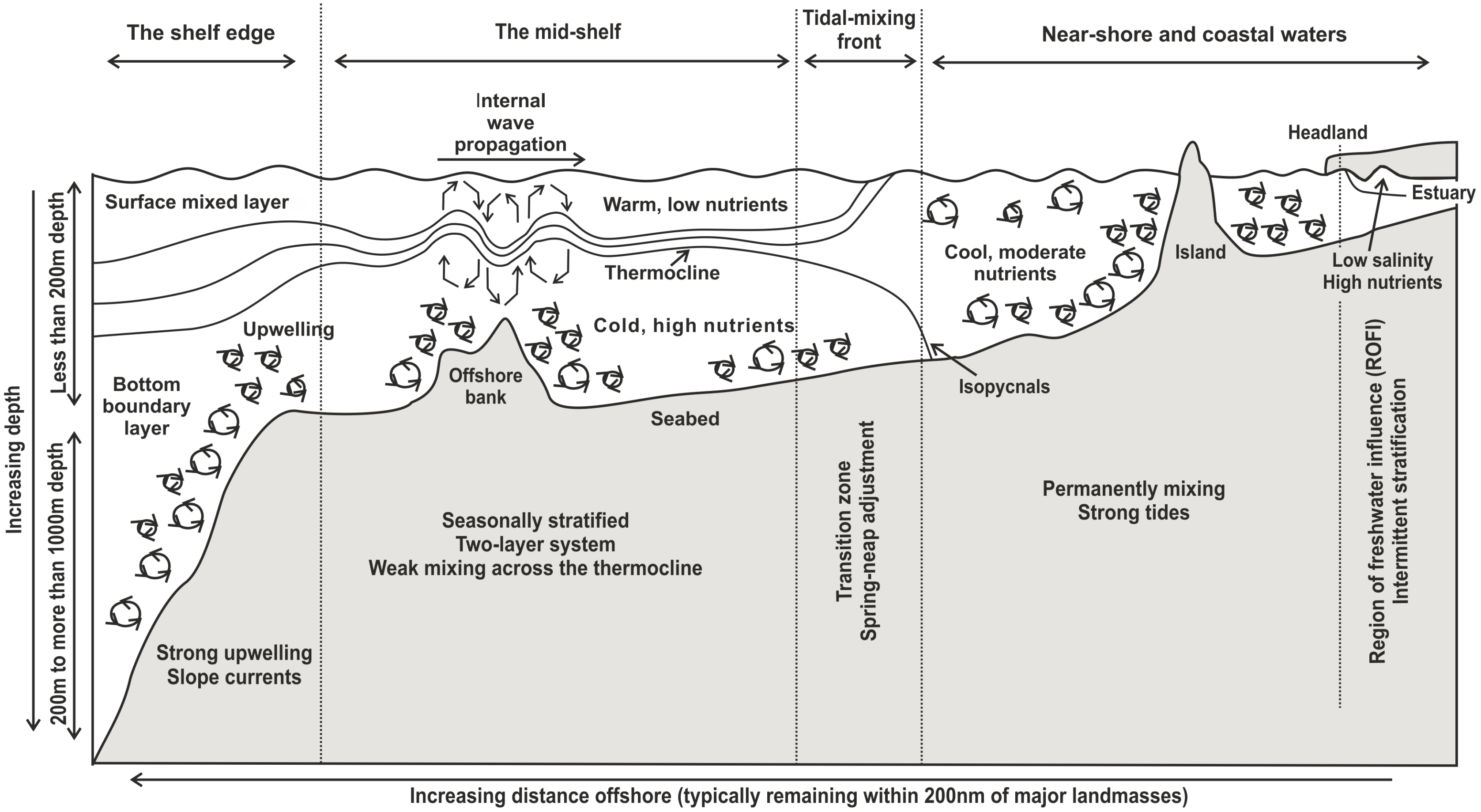

Figure 1. Cross shelf schematic giving an overview of the typical oceanographic structure of thermally stratified shelf-sea environments at mid-latitudes during the summer months. Adapted from Simpson and Sharples (2012). Black directional arrows show (1) turbulent mixing around the seabed, offshore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

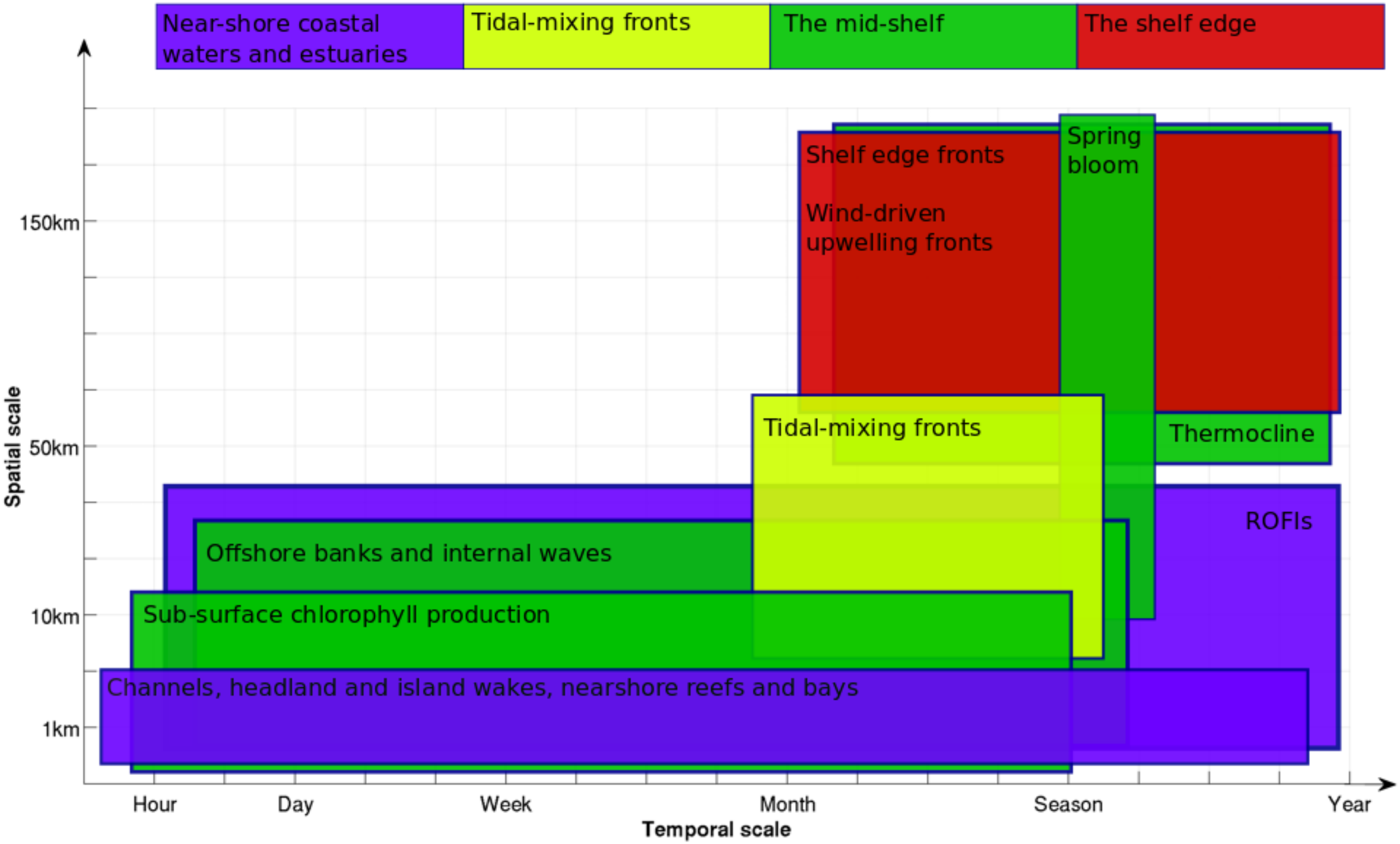

Figure 2. Overview of the typical spatio-temporal scales oceanographic structures across shelf-sea environments function over. Further details can be found in Table 1.

Table 1. Details of the generalised spatio-temporal scales over which oceanographic features favoured for foraging across shelf-seas function. Columns 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 variation may occur. References are provided for specific examples of features functioning in this manner. Note that regional and site specific differences 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 *et al.*, 1981; Springer *et al.*, 1996).	Typically persist perennially, although strength and associated productivity may vary seasonally (Fournier *et al.*, 1979; Ryan *et al.*, 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 *et al.*, 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 *et al.*, 2004; Letelier *et al.*, 2009; Kahru *et al.*, 2012).	Generally display some seasonality in occurrence in response to upwelling intensity with current flows wind events (Kampf *et al.*, 2004; Bograd *et al.*, 2009b; Letelier *et al.*, 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 *et al.*, 2009b; Letelier *et al.*, 2009). Surface convergences and instabilities within these zones may be more ephemeral in occurrence, and linked to local meteorological conditions (Capet *et al.*, 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 *et al.*, 1976; Holligan *et al.*, 1989).	Seasonally occurring in spring for a period lasting no more than a month (typically around 1-2 weeks; Pingree *et al.*, 1976; Townsend and Spinrad, 1986; Mills *et al.*, 1994).	Initial date may vary with the spring-neap cycle alongside changes in climatic conditions (Hunt and Stabeno, 2002; Mann and Lazier, 2006; Sharples *et al.*, 2006), which can also impact magnitude of productivity (Sambrotto *et al.*, 1986). Regional variation in initial start date also occurs (e.g. latitudinally; Henson *et al.*, 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 *et al.*, 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 *et al.*, 2009; Kokubun *et al.*, 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 *et al.*, 2008; Embling *et al.*, 2012).
Sub-surface productivity	May occur over a larger area exceeding 10's km's (Weston *et al.*, 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 *et al.*, 2001;	Productivity and entrainment may be highest when the water column stabilises, following a period of tidal and wave induced vertical mixing (McManus *et al.*, 2005; Cheriton *et al.*, 2007;

	et al., 2010). Productivity is generally vertically concentrated within a few m's of the pycnocline (Sharples *et al.*, 2001).	Sharples, 2008).	Durham *et al.*, 2009). May be particularly elevated around offshore banks where internal waves propagate or there is localised upwelling (Lennert-Cody and Franks, 1999; Richardson *et al.*, 2000; Embling *et al.*, 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 *et al.*, 2013).	Appear to be seasonal features linked to thermal stratification between late spring and early autumn. May function intermittently with specific tidal conditions (Embling *et al.*, 2012, 2013; Palmer *et al.*, 2013)	Closely tied to bathymetric structures. Propagation of internal waves may vary with spring-neap modulation and storms (Embling *et al.*, 2013; Palmer *et al.*, 2013). Those associated with the shelf edge (e.g. within the Humboldt current; Bertrand *et al.*, 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 *et al.*, 1979; Decker and Hunt, 1996; Durazo *et al.*, 1998). Length may exceed 10's km's (e.g. tidal mixing fronts around the Bristish 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 *et al.*, 2002; Acha *et al.*, 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 *et al.*, 2002; Nahas *et al.*, 2005; Pisoni *et al.*, 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 *et al.*, 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 *et al.*, 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 *et al.*, 2005; Rogachev *et al.*, 2008).	May occur perennially, although only at specific times in the tidal cycle (Zamon, 2003; Johnston and Read, 2007; Bailey and Thompson, 2010; Waggitt *et al.*, 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 *et al.*, 2014). Local wind patterns may temporarily intensify surface convergences (e.g. occurrence of Langmuir circulation cells; Goss *et al.*, 1997; Ladd *et al.*, 2005).
ROFI's: estuarine plume & tidal intrusion fronts	May be localised over 100's m's (e.g. Moray Firth fronts; Mendes *et al.*, 2002) or larger encompassing 10's to 100's of km's (e.g. Columbine Estuarine & Mississippi River Plume Fronts; Govoni *et al.*, 1989; Phillips *et al.*, 2018).	Occur perennially, sometimes periodically with the tidal cycle (Simpson and Nunes, 1981; Mendes *et al.*, 2002; Phillips *et al.*, 2018).	Occurrence may be linked to specific phases of the tidal cycle (e.g. Mendes *et al.*, 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 *et al.*, 2015b; Phillips *et al.*, 2018). Productivity blooms may follow such cycles (Cloern, 1991).