

REVIEW

On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates

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Summary

1. Identifying priority areas for marine vertebrate conservation is complex because species of conservation concern are highly mobile, inhabit dynamic habitats and are difficult to monitor.
2. Many marine vertebrates are known to associate with oceanographic fronts – physical interfaces at the transition between water masses – for foraging and migration, making them important candidate sites for conservation. Here, we review associations between marine vertebrates and fronts and how they vary with scale, regional oceanography and foraging ecology.
3. Accessibility, spatiotemporal predictability and relative productivity of front-associated foraging habitats are key aspects of their ecological importance. Predictable mesoscale (10s–100s km) regions of persistent frontal activity ('frontal zones') are particularly significant.
4. Frontal zones are hotspots of overlap between critical habitat and spatially explicit anthropogenic threats, such as the concentration of fisheries activity. As such, they represent tractable conservation units, in which to target measures for threat mitigation.
5. Front mapping via Earth observation (EO) remote sensing facilitates identification and monitoring of these hotspots of vulnerability. Seasonal or climatological products can locate biophysical hotspots, while near-real-time front mapping augments the suite of tools supporting spatially dynamic ocean management.
6. *Synthesis and applications.* Frontal zones are ecologically important for mobile marine vertebrates. We surmise that relative accessibility, predictability and productivity are key biophysical characteristics of ecologically significant frontal zones in contrasting oceanographic regions. Persistent frontal zones are potential priority conservation areas for multiple marine vertebrate taxa and are easily identifiable through front mapping via EO remote sensing. These insights are useful for marine spatial planning and marine biodiversity conservation, both within Exclusive Economic Zones and in the open oceans.

Key-words: composite front mapping, foraging, habitat, marine protected areas, marine top predator, marine vertebrate, ocean front, oceanographic front, pelagic predator, remote sensing

Introduction

Accommodating the conservation needs of large marine vertebrates such as seabirds, turtles, cetaceans, pinnipeds

and sharks is a major challenge in marine management. These apex predators fulfil critical roles in ecosystem functioning (Heithaus *et al.* 2008), but are currently afforded only cursory or inadequate protection, particularly in the open oceans (Game *et al.* 2009). The combined effects of anthropogenic stressors (e.g. habitat degradation, over-exploitation, fisheries bycatch and climate variability) are

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negatively impacting marine vertebrate populations (Halpern *et al.* 2008; Maxwell *et al.* 2013; Lewison *et al.* 2014), and in some cases resulting in dramatic declines (e.g. rockfishes, Ralston 2002; seabirds, Croxall *et al.* 2012). However, effective conservation is problematic. Large marine vertebrates are highly mobile, ranging great distances over the course of their lives. For example, many migrate across entire ocean basins (e.g. leatherback turtle *Dermochelys coriacea*, Shillinger *et al.* 2008; Arctic tern *Sterna paradisaea*, Egevang *et al.* 2010; humpback whale *Megaptera novaeangliae*, Robbins *et al.* 2011), epitomizing the problems of conserving a moving target (Singh & Milner-Gulland 2011). Furthermore, the formation and propagation of pelagic foraging habitats is a function of complex oceanographic dynamics (see Hazen *et al.* 2013), so habitat in the marine context does not always refer to fixed geographical space, but preferentially used areas that may shift. Understanding how oceanographic processes influence marine vertebrate distributions is, therefore, crucial for effective conservation (Hooker *et al.* 2011).

Oceanographic conditions drive spatial structuring of predator abundance and diversity across the oceans. At a global scale, marine biodiversity is regulated by sea surface temperature, with diversity maxima occurring at mid-latitudes (Worm *et al.* 2005; Tittensor *et al.* 2010). At an ocean-basin scale, diversity is highest in productive zones associated with major water mass transitions, currents, upwellings and bathymetric features (Chavez & Messié 2009). Within these productive regions, meso- (10s - 100s km) and sub-mesoscale (*c.* 1 km) oceanographic dynamics lead to the formation of ecologically significant features such as fronts and eddies (see Godø *et al.* 2012). Here, we focus on fronts – physical interfaces between water bodies that manifest as steep gradients in temperature, salinity, density, turbidity or colour (Belkin, Cornillon & Sherman 2009) – as important habitats for mobile marine vertebrates.

Biophysical coupling at fronts can lead to the formation of pelagic foraging hotspots. Mixing and nutrient retention enhance primary productivity (Traganza, Redalije & Garwood 1987; Franks 1992a), while plankton and small nekton may become entrained in convergent surface flow (Le Fevre 1986; Franks 1992b; Genin *et al.* 2005). Convergences aggregate zooplankton advected from surrounding water masses, driving bottom-up processes across multiple trophic levels up to apex predators (Graham, Pages & Hamner 2001; Bakun 2006). However, the productivity and degree of bioaggregation along fronts varies according to physical characteristics such as spatiotemporal variability, gradient magnitude, type of front and properties of the surrounding water masses (Le Fevre 1986). Therefore, a holistic understanding of how biophysical mechanisms interact to influence the degree of bioaggregation at fronts, and their subsequent attractiveness to top predators, remains elusive.

A taxonomically diverse array of marine vertebrates have been shown to associate with fronts, and the scale,

nature and significance of these associations to vary according to regional oceanography and taxon-specific life-history characteristics. Ecologically significant features can range from ocean-basin scale, persistent frontal zones in the open oceans to fine-scale, ephemeral features in shelf seas (Le Fevre 1986; Belkin, Cornillon & Sherman 2009). Here, we review current understanding of associations between high trophic-level marine vertebrates and fronts, selecting key examples from contrasting oceanographic regions and highlighting important biophysical characteristics of ecologically significant frontal zones. We discuss implications for management and conservation, including overlap with anthropogenic threats, and highlight the potential role of front mapping via Earth observation (EO) remote sensing to inform threat mitigation.

Ecological importance of frontal zones

The mechanisms linking physical processes, prey dynamics and top predator foraging are complex and scale dependent (Fauchald 2009). Understanding these mechanisms is crucial to understanding what makes front-associated foraging opportunities attractive to high trophic-level consumers. Use of frontal zones is mediated bottom-up by the spatial scale, persistence and biophysical properties of fronts, and top-down by aspects of foraging ecology, including life-history mode (true pelagics vs. central-place foragers), physiological constraints (e.g. thermal range, diving capability), trophic level (planktivores vs. piscivores), foraging guild (near-surface vs. subsurface), foraging plasticity, ontogenetic stage and whether foraging is opportunistic or mediated by learning and memory (Vilchis, Ballance & Fiedler 2006).

OCEAN-BASIN SCALE (1000s KM)

Ocean-basin scale regions of intense mesoscale dynamics, such as those associated with the major water mass transitions discussed below, are ecologically significant features in the largely oligotrophic open oceans (Belkin, Cornillon & Sherman 2009). These regions are important foraging and migration habitats for pelagic marine vertebrates (Tittensor *et al.* 2010).

North Pacific Transition Zone (NPTZ)

This highly dynamic region delineates the boundary between warm, oligotrophic subtropical gyres and cold, productive subarctic gyres and is a marine biodiversity hotspot of global significance (Sydeman *et al.* 2006). Numerous marine vertebrates with contrasting life histories preferentially use areas of the NPTZ, including northern elephant seals *Mirounga angustirostris*, salmon shark *Lamna ditropis* and blue shark *Prionace glauca*, bluefin *Thunnus thynnus* and albacore tunas *Thunnus alalunga*, Laysan *Phoebastria immutabilis* and black-footed albatrosses *Phoebastria nigripes*, and loggerhead *Caretta*

caretta and olive ridley turtles *Lepidochelys olivacea* (Polovina *et al.* 2004; Kappes *et al.* 2010; Block *et al.* 2011; Robinson *et al.* 2012).

The NPTZ encompasses the transition zone chlorophyll front (TZCF), a surface convergence that extends over 8000 km (Polovina *et al.* 2001). While the wider NPTZ is predictable at broad scales, the position of the TZCF is strongly influenced by climate (Kappes *et al.* 2010), leading to spatial variability in foraging associations. Some near-surface foragers, such as loggerhead turtles, can track the southward movement of the TZCF in winter (Howell *et al.* 2010). Other taxa constrained to a central place, such as albatrosses breeding on the Hawaiian Islands, have experienced reproductive failure as a result of spatial deviation (Kappes *et al.* 2010). In contrast, elephant seals, which forage along the subsurface thermal boundary between gyres (Robinson *et al.* 2012), remain unaffected by the movement of surface features.

Equatorial Front (EF)

Manifesting between the equatorial upwelling to the South and warmer tropical waters to the North, the EF is a prominent feature of the tropical eastern Pacific, characterized by steep gradients in temperature, salinity and nutrients (Ballance, Pitman & Fiedler 2006). Planktivorous seabirds strongly associate with the EF, which entrains zooplankton in surface layers (Spear, Ballance & Ainley 2001). However, seabird densities are also closely coupled with climate-driven variability in frontal intensity.

Southern Ocean frontal zones

The major frontal zones of the Southern Ocean determine the distributions of pelagic prey species in the region (Rodhouse & Boyle 2010). A range of marine predators utilize the southern boundary of the Antarctic Circumpolar Current, the subtropical front and the Subantarctic Front (see Bost *et al.* 2009; Santora & Veit 2013). Penguins, albatrosses and seals travel from distant breeding colonies to forage along the subtropical and Polar Fronts (Xavier *et al.* 2003; Bailleul *et al.* 2007; Scheffer, Bost & Trathan 2012). Although distant from land, Southern Ocean frontal zones provide suitable foraging conditions for both near-surface and deep-diving foragers, but are accessible only to those species with the capacity to navigate across oceanic seascapes.

MESOSCALE (10s–100s KM) TO SUB-MESOSCALE (C. 1 KM)

Mesoscale and sub-mesoscale oceanographic processes drive front formation within large-scale transition zones and in regions associated with currents, upwellings and bathymetric features and appear to be of particular ecological importance. For example, hotspots of predatory fish diversity (tuna, billfish) are associated with mesoscale

fronts within warm waters (*c.* 25 °C) across all the major ocean basins (Worm *et al.* 2005).

Major currents

Bioaggregating thermal, colour and density fronts frequently form along the boundaries of major current systems (Fig. 1). Seabirds and neonate sea turtles associate strongly with fronts and eddies formed along the Gulf Stream (Haney 1986; Witherington 2002; Thorne & Read 2013) and the Kuroshio Current (Polovina *et al.* 2006). The peripheries of frontal eddies formed along these currents are also of ecological significance (Haney 1986; Bailleul, Cotté & Guinet 2010; Godø *et al.* 2012).

Upwelling fronts

Major Eastern boundary upwellings (e.g. Canary Current, Benguela Current, California Current, Humboldt Current) are hotspots of marine biodiversity (Chavez & Messié 2009) characterized by intense surface frontal activity. Mesoscale thermal and colour fronts mark the interface between cool, nutrient-rich upwelled water and warmer oligotrophic waters further offshore. Bioaggregation in upwelling-driven frontal structures attracts foragers from diverse foraging guilds (Nur *et al.* 2011;

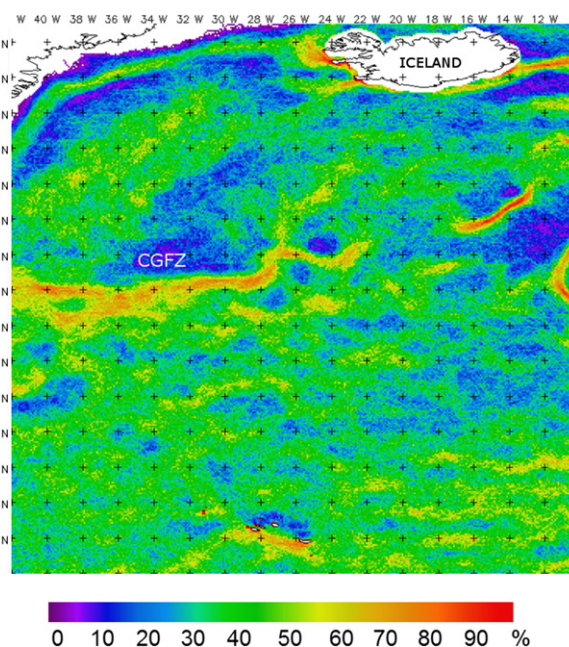


Fig. 1. Front mapping via Earth observation (EO) remote sensing. Example imagery: seasonal front frequency map, N. Atlantic (percentage time front detected in each 1 km pixel, March–May). Regions of intense mesoscale activity along the North Atlantic Current are highlighted, including that associated with the Charlie Gibbs Fracture Zone (CGFZ). Useful as part of a suite of tools for locating biophysical hot spots and their dynamics through time. Derived from merged microwave and infrared SST data, 2006–2011. Reproduced, with permission, from Miller, Read & Dale (2013).

Sabarro *et al.* 2013). For example, strong associations have been documented between cetaceans (Tynan *et al.* 2005), seabirds (Ainley *et al.* 2009) and upwelling fronts in the California Current. Similarly, coastal upwelling creates a persistent multiple trophic-level hotspot off Baja California, within which bioaggregating thermal fronts are utilized by subsurface predators, such as blue whales *Balaenoptera musculus*, green *Chelonia mydas* and loggerhead turtles (Etnoyer *et al.* 2006; Wingfield *et al.* 2011).

Strong convergent fronts also manifest at the peripheries of upwelling shadows, where water upwelled offshore meets coastal water masses sheltered by coastline irregularities (Chavez & Messié 2009). Large upwelling shadows in the Southern California Bight (Fiedler & Bernard 1987; Hunt & Schneider 1987) and off southern Peru (Acha *et al.* 2004) are known hotspots. However, upwelling intensity is often seasonal, varying under climatic and oceanographic influence, affecting the predictability of foraging opportunities in these regions (Thompson *et al.* 2012).

Shelf-edge frontal zones

Shelf-edge systems - at the transitions between the abyssal oceans and shelf seas - are zones of intense mixing, resulting in the manifestation of strong thermohaline fronts. Nutrient enrichment in shelf-edge fronts enhances primary production, attracting grazers such as copepods, fish larvae and planktivorous fish, and their predators (Le Fevre 1986). For example, the Celtic Sea shelf edge is an important overwintering habitat for basking sharks *Cetorhinus maximus* (Sims *et al.* 2003). Both surface-feeding and diving seabirds aggregate along shelf-edge fronts (Skov & Durinck 1998). Downwelling shelf slopes, such as those found at the Mid-Atlantic Bight (Ryan, Yoder & Cornillon 1999) and at the margins of the Bering Sea (Springer, McRoy & Flint 1996), are important seabird foraging areas. Shelf-edge fronts can also be significant habitat features for cetaceans, including deep-diving species that prey on squid and fish (Baumgartner 1997; Waring *et al.* 2001), rorquals (Azzellino *et al.* 2008) and some delphinids (Davis *et al.* 1998).

Mid-ocean bathymetrically-induced frontal zones

Mid-ocean bathymetric features generate persistent fronts that can produce predictable foraging grounds. For example, the interaction of the North Atlantic Current with the Mid-Atlantic Ridge around the Charlie-Gibbs Fracture Zone generates intense mesoscale frontal activity (Fig. 1; Miller, Read & Dale 2013), attracting surface and near-surface-foraging seabirds (Egevang *et al.* 2010; Frederiksen *et al.* 2012; Edwards *et al.* 2013). Piscivorous dolphins and whales also feed on mesopelagic fish and squid in this area (Doksæter *et al.* 2008; Skov *et al.* 2008).

Shelf-sea tidal mixing fronts

Tidal mixing fronts manifest in shelf seas between well-mixed and stratified waters (Pingree & Griffiths 1978). Nutrient retention and enhanced vertical mixing increase seasonal phytoplankton production (Pingree *et al.* 1975; Franks 1992a), attracting both pelagic and neritic foragers. For example, basking sharks forage for zooplankton at small-scale tidal fronts in UK waters (Sims & Quayle 1998), with sightings clustered around slicks indicative of convergent flow. Likewise, planktivorous ocean sunfish *Mola mola* are frequently encountered near fronts (Sims & Southall 2002). Similarly, strong associations have been observed between rorquals and tidal fronts in the Gulf of St. Lawrence (Doniol-Valcroze *et al.* 2007). On the European Continental Shelf, piscivorous cetaceans use both seasonally persistent tidal mixing fronts (Goold 1998; Weir & O'Brien 2000) and finer-scale fronts that manifest in tidal inlets (Pirota *et al.* 2013). In addition, numerous seabirds forage around mid-shelf fronts (Haney & McGillivray 1985; Hamer *et al.* 2009; Dean *et al.* 2012), sometimes in Multi-Species Foraging Associations (MSFAs; Camphuysen, Scott & Wanless 2006). Surface and near-surface-foraging birds are frequently observed near convergent fronts (Durazo, Harrison & Hill 1998; Hunt *et al.* 1999), whereas subsurface foragers tend to associate with strong, vertically structured fronts (Decker & Hunt 1996; Begg & Reid 1997).

Tidal topographic fronts

In neritic waters, tidal topographic interactions generate fine-scale, yet strongly bioaggregating fronts (Le Fevre 1986). For example, 'island wake' effects lead to the development of surface convergences and eddies (Wolanski & Hamner 1988). Marine mammals (Johnston & Read 2007) and surface-foraging seabirds (Schneider 1990) associate with island wake fronts. Similarly, offshore banks can initiate front development, increasing prey accessibility in surface layers (Stevick *et al.* 2008). Tidal-topographic fronts over banks can cause the formation of subsurface chlorophyll maxima (Franks 1992a), which are significant foraging areas for some diving predators (Scott *et al.* 2010). Tidal-topographic fronts are highly predictable and may be especially important for central-place marine vertebrates. However, at very fine scales (<1 km), other subsurface physical processes may mediate predator foraging over bank systems (Scott *et al.* 2010; Cox, Scott & Camphuysen 2013).

Estuarine plume and tidal intrusion fronts

Estuarine plume fronts are formed by interactions between tidal processes and river outflow. Entrainment of zooplankton (Govoni & Grimes 1992) attracts forage fish

(Kaltenberg, Emmett & Benoit-Bird 2010), making plume fronts significant nearshore foraging features. Large aggregations of piscivorous seabirds have been documented around some estuarine plume fronts (Skov & Prins 2001; Zamon, Phillips & Guy 2013).

KEY BIOPHYSICAL CHARACTERISTICS OF ECOLOGICALLY SIGNIFICANT FRONTAL ZONES

Current understanding indicates that accessibility, spatiotemporal predictability and relative productivity are central to the ecological importance of frontal zones (Hunt *et al.* 1999; Weimerskirch 2007). These insights are useful in predicting which taxa are likely to aggregate at frontal zones in different oceanographic regions, enhancing understanding of pelagic ecosystem function and identifying important at-sea habitats. For example, it is clear that large-scale frontal zones in the open oceans are often highly productive and persistent, and so predictable, yet are only really accessible to oceanic species and far-ranging central-place foragers (Bost *et al.* 2009; Tittensor *et al.* 2010). Predictable, productive mesoscale frontal zones associated with bathymetric features, currents and major upwellings attract marine vertebrates from diverse foraging guilds in contrasting oceanographic regions (Chavez & Messié 2009; Block *et al.* 2011). Persistent shelf-sea tidal mixing and tidal-topographic fronts create predictable foraging opportunities, accessible to coastal species such as colonial seabirds and some cetaceans. Recent work in the Celtic Sea highlights temporal persistence as a key component of frontal zones used as foraging features for a piscivorous seabird (Scales *et al.* 2014), presumably as persistence enhances both productivity and predictability.

The literature documenting associations between marine vertebrates and fronts has yielded valuable insights, yet many questions remain. For example, despite the implicit assumption that fronts generate suitable foraging conditions, the mechanisms linking physical processes and prey dynamics are not well understood (but see Cox, Scott & Camphuysen 2013). In many cases, it remains unclear how habitat utilization changes through the annual cycle, through ontogenetic development and through life cycle stages (i.e. breeding, migration; but see e.g. Votier *et al.* 2011). In addition, little is known about the ways in which many species perceive and respond to environmental cues (but see Nevitt & Bonadonna 2005; Tew Kai *et al.* 2009; Votier *et al.* 2013; Tremblay *et al.* 2014). Moreover, it is important to determine whether fronts are significant foraging features at the population level. This has not yet been achieved, to our knowledge, but is possible through estimation of the proportion of a population using a frontal zone, or the spatial range over which animals are attracted. Future work should address these questions, improving capacity to locate ecologically significant features.

Frontal zones as priority conservation areas

HOTSPOTS OF ANTHROPOGENIC THREAT

Frontal zones appear to be hot spots of overlap between potentially critical at-sea habitats and spatially explicit anthropogenic threats (e.g. fisheries), particularly in the coastal zone (Halpern *et al.* 2008). The major fisheries threats to marine vertebrates are bycatch (Gilman *et al.* 2008; Anderson *et al.* 2011; Žydelis, Small & French 2013; Lewison *et al.* 2014) and competition for resources (e.g. Bertrand *et al.* 2012). Comprehensive data are difficult to obtain, but industrialized fisheries, particularly pelagic long-lining fleets, target persistent frontal zones (Podestá, Browder & Hoey 1993; Hartog *et al.* 2011), generating significant risk of conflict with other apex consumers. Spatial overlap is particularly pronounced within the coastal zone, along shelf breaks and in upwelling regions (Halpern *et al.* 2008; Lewison *et al.* 2014), especially those around Africa and South America (Zeeberg, Corten & de Graaf 2006; Pichegru *et al.* 2009). Within these regions, frontal zones are logical areas in which to target measures for mitigation of fisheries threats. In addition, convergent fronts can concentrate pollutants and floating debris such as oil and plastics, potentially increasing exposure of marine vertebrates aggregating to forage (Bourne & Clark 1984; González Carman *et al.* 2014).

On the continental shelf, the expansion of marine renewable energy installations (MREIs) has the potential for direct and indirect effects on marine vertebrates (Inger *et al.* 2009; Grecian *et al.* 2010; Scott *et al.* 2014). MREIs that rely on tidal flow are likely to be concentrated in the vicinity of hydrographically dynamic tidal mixing fronts (Miller & Christodoulou 2014), altering habitat dynamics and displacing foraging effort. These impacts may be particularly pronounced for coastal central-place foragers (Scott *et al.* 2014). While more research is needed to determine whether MREIs have population-level effects, marine spatial planning can be improved by identification of vulnerability hotspots.

FRONT MAPPING TO IDENTIFY PRIORITY CONSERVATION AREAS

Technological innovations in remote sensing, biologging, autonomous marine vehicles and vessel monitoring hold promise for identification of priority conservation areas (Palacios *et al.* 2006; Grantham *et al.* 2011; Miller & Christodoulou 2014) and spatially dynamic, near-real-time threat management (Hobday *et al.* 2014). Front mapping via EO remote sensing (Fig. 1; Miller 2009) enables high-resolution, automated detection of frontal zones anywhere in the global ocean. Seasonal or climatological products are potentially useful for marine spatial planning, identifying priority areas for threat mitigation both on-shelf (Miller & Christodoulou 2014) and in areas beyond national jurisdiction (ABNJ; the

'high seas'). Moreover, near-real-time front mapping augments the suite of tools with potential to inform spatially dynamic ocean management (Hobday *et al.* 2014), enabling identification and monitoring of critical ephemeral habitats (Fig. 2).

Remotely sensed oceanographic data have been used to inform spatially dynamic fisheries management in several cases. For example, historical and near-real-time SST imagery, coupled with satellite telemetry and spatially explicit fisheries data, has been successfully used to reduce bycatch of loggerhead turtles along the TZCF north of Hawaii (Howell *et al.* 2008). The Australian Fisheries Management Authority has used a comparable approach using *in situ* sensors to regulate exploitation of southern bluefin tuna *Thunnus maccoyii* (Hobday & Hartmann 2006). Although there are few examples of such innovatively managed fisheries (Dunn, Boustany & Halpin 2011), similar methods are applicable to other species of conservation concern (Hobday & Hartmann 2006) and may be critical in mitigating future marine biodiversity loss.

Marine protected areas (MPAs) can regulate overlap between spatially explicit threats and critical at-sea habitats. MPAs are most tractable on-shelf, within Exclusive Economic Zones (EEZs), where anthropogenic threats to marine vertebrate populations, such as fisheries pressure, MREI development, noise and habitat degradation, are also concentrated (Maxwell *et al.* 2013). Spatially predictable biophysical hotspots, such as those associated with persistent tidal mixing, tidal-topographic and upwelling shadow fronts, are logical candidates for within-EEZ MPAs and easily identifiable. Indeed, hot spots associated with quasi-stationary frontal zones have been explicitly included in MPA design in the UK (Miller & Christodoulou 2014) and the Mediterranean (Panigada *et al.* 2008).

In the open oceans beyond EEZs, persistent frontal zones, such as that associated with the Charlie Gibbs Fracture Zone in the North Atlantic (Fig. 1), are also amenable to site-based management. However, effective

conservation of pelagic biodiversity in ABNJ rests not only upon the identification of vulnerability hotspots but also upon the capacity to track how these hotspots shift with changing oceanographic conditions (Hooker *et al.* 2011; Lascelles *et al.* 2012; Fig. 2). Spatially dynamic ocean management (Hobday *et al.* 2014) may be more effective in managing threats to marine vertebrate populations in some highly dynamic regions, and for increasing adaptability as pelagic ecosystems undergo changes related to climate variability. High-resolution front frequency maps, both near-real-time and seasonal/climatological (e.g. Fig. 1), coupled with real-time monitoring of anthropogenic activity and marine vertebrate habitat use (Fig. 2), present managers with data of value for more effective management of pelagic ecosystems.

CONCLUSIONS

Associations between marine vertebrates and oceanographic fronts vary spatially, temporally and between taxa, influenced by both the biophysical properties of fronts and taxon-specific foraging ecology (Hunt *et al.* 1999). Despite this variability, there now exists a considerable body of evidence indicating that persistent mesoscale frontal zones are ecologically significant across the oceans (e.g. Polovina *et al.* 2001; Bost *et al.* 2009). As areas of existing and potential overlap between critical habitats and anthropogenic threat, persistent frontal zones represent tractable conservation areas, in which to target threat mitigation measures. Continued integration between remote sensing science, spatial ecology, oceanography and fisheries management has potential to improve marine biodiversity conservation by (i) bridging the gaps in our understanding of the oceanographic drivers of marine vertebrate space use and (ii) feeding into systematic conservation planning through mapping and real-time monitoring of threat hot spots (Grantham *et al.* 2011; Hobday *et al.* 2014). Such integration is vital if we are to balance the competing demands of anthropogenic activities and biodiversity conservation in the vast and dynamic oceans.

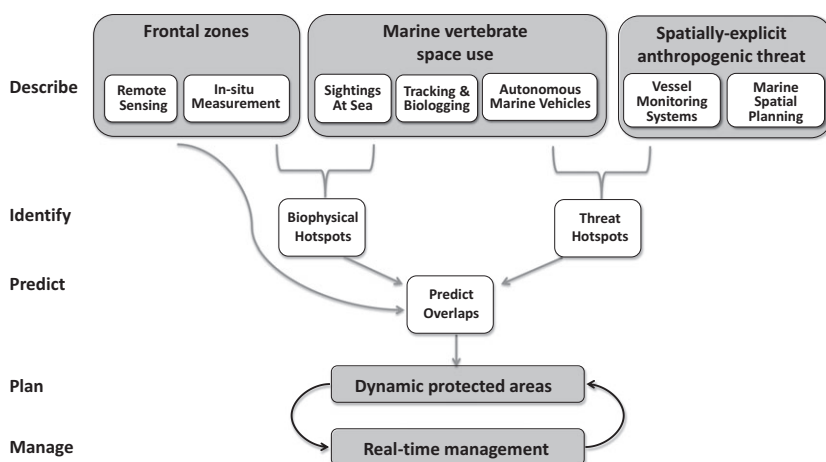


Fig. 2. Frontal zones as priority conservation areas for marine vertebrates. Understanding of associations between marine vertebrates and fronts can be enhanced using data describing (i) the oceanographic environment, obtainable from remote sensing or *in situ* measurement, and (ii) marine vertebrate space use, through at-sea sightings, tracking/biologging and autonomous marine vehicles. Insights can be fed forward into predictive habitat models, which can be used together with spatially explicit information describing anthropogenic threat to predict and monitor regions of overlap.

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