

Optimizing marine spatial plans with animal tracking data¹

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Abstract: Marine user–environment conflicts can have consequences for ecosystems that negatively affect humans. Strategies and tools are required to identify, predict, and mitigate the conflicts that arise between marine anthropogenic activities and wildlife. Estimating individual-, population-, and species-scale distributions of marine animals has historically been challenging, but electronic tagging and tracking technologies (i.e., biotelemetry and biologging) and analytical tools are emerging that can assist marine spatial planning (MSP) efforts by documenting animal interactions with marine infrastructure (e.g., tidal turbines, oil rigs), identifying critical habitat for animals (e.g., migratory corridors, foraging hotspots, reproductive or nursery zones), or delineating distributions for fisheries exploitation. MSP that excludes consideration of animals is suboptimal, and animal space-use estimates can contribute to efficient and responsible exploitation of marine resources that harmonize economic and ecological objectives of MSP. This review considers the application of animal tracking to MSP objectives, presents case studies of successful integration, and provides a look forward to the ways in which MSP will benefit from further integration of animal tracking data.

Résumé : Les conflits entre les utilisateurs du milieu marin et l'environnement peuvent avoir des conséquences sur les écosystèmes qui, elles, ont des effets négatifs sur les humains. Des stratégies et outils sont nécessaires pour cerner, prédire et atténuer de tels conflits entre les activités humaines en mer et les espèces marines. L'estimation de la répartition d'animaux marins à l'échelle des individus, des populations et des espèces s'est avérée difficile par le passé, mais des technologies électroniques de marquage et de suivi (c.-à-d. la biotélémétrie et l'enregistrement de données biologiques) et des outils analytiques font leur apparition qui peuvent soutenir les efforts de planification de l'espace marin (PEM) en documentant les interactions d'animaux avec les infrastructures marines (p. ex. turbines marémotrices, plateformes pétrolières), en cernant les habitats essentiels d'animaux (p. ex. couloirs de migration, aires d'approvisionnement, de reproduction ou de croissance) ou en délimitant leurs répartitions pour les fins de la pêche. Une PEM qui n'intègre pas les animaux n'est pas optimale, et les estimations de l'utilisation de l'espace par les animaux peuvent contribuer à une exploitation efficiente et responsable des ressources marines qui répond à la fois aux objectifs économiques et écologiques de la PEM. La présente synthèse examine l'application du suivi d'animaux à la PEM, présente des études de cas d'intégrations réussies et se penche sur les avantages qu'entraînera pour la PEM l'intégration plus poussée de données de suivi d'animaux. [Traduit par la Rédaction]

Introduction

The marine realm is composed of highly diverse three-dimensional habitats with variation in depth and substrate, creating a heterogeneous aquascape for plants and animals. Humans are terrestrial animals but are reliant on these marine ecosystems, evidenced by the aggregation of settlements near coasts worldwide (Small and Nicholls 2003). There is an inherent cultural value of natural environments reflected in high property values of coastal real estate (Benson et al. 1998; Luttik 2000), and water has broad aesthetic appeal and recreational value for boating, beach-going, swimming, diving, and recreational fishing (Jennings 2007). Marine ecosystems are also direct sources of goods and services supporting a myriad of economic activities. Lucrative fisheries,

aquaculture sites, access to global trade, oil and gas deposits, tidal or offshore wind turbines, and cable and pipeline deployment are all examples of the extensive and intensive human use of the marine environment that continues to expand (Pimentel et al. 1997; Pagiola et al. 2004; e.g., Fedler 2013; Schwoerer et al. 2016; Haas et al. 2017). More indirect, but valuable, regulating services include climate moderation, flood regulation, coastal protection, carbon sinking, and oxygen production (Falkowski et al. 2000). To facilitate human activities within the oceans, the environment has been heavily modified by dredging harbours, constructing seawalls, excavating canals, and installing various infrastructure (Hinrichsen 1999). Now, growing human populations (Cohen 2003) and increasing pressure placed on ma-

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rine resources and ecosystems (Halpern et al. 2008; Crain et al. 2009) have rendered traditional reactive and sectoral approaches to marine management inadequate (White et al. 2012; Soininen and Hassan 2015).

Scientists and practitioners have advocated a more holistic approach to planning and management of spaces to achieve different societal objectives, from ecosystem protection to socioeconomic benefits (Young et al. 2007). Marine spatial planning (MSP) has emerged as an interdisciplinary field of law, economics, geography, and biology that seeks to provide a practical, efficient, and forward-looking framework to alleviate conflicts between human uses (user–user conflict), as well as conflicts between individual and cumulative human uses and coastal and marine environments (user–environment conflict; Soininen and Hassan 2015; Papageorgiou 2016). MSP has elsewhere been defined as the “public process of analyzing and allocating the spatial and temporal distribution of human activities in marine areas to achieve ecological, economic, and social objectives that usually have been specified through a political process” (Ehler and Douvère 2009). The overarching objective of MSP is “to create and establish a more rational use of marine space and the interactions between its uses, to balance demands for development with the need to protect the environment, and to achieve social and economic objectives in an open and planned way” (IOC-UNESCO [no date]). The key attribute of MSP is an explicit focus on, and allocation of, the spatial and temporal distribution of human activities and marine species and ecosystems; MSP is thus supported by spatial analysis and mapping tools and sometimes implemented through ocean zoning.

Ecological stakes have been underrepresented in marine spatial plans (Foley et al. 2010); demonstrating ecological importance to marine habitat is therefore essential to filling this need. Technological and analytical tools developed for tracking aquatic animal movement are providing crucial information about aquatic animal movement and distribution (Hussey et al. 2015) that can be integrated into management efforts by solving some of the mysteries of animal movement and testing hypotheses about impacts of human activities on the ecosystem (Allen and Singh 2016; Lennox et al. 2017). Although animal tracking may be conducted using a variety of tools, including visual identification or mark-recapture (Whitehead 2001), electronic animal tracking systems offer a lens through which to view the species–habitat and species–species interrelationships within ecosystems (Hussey et al. 2015). Animals affixed with electronic transmitter- or logger-type tags collect positional data that is relayed to analysts either directly (from loggers) or by receivers (e.g., satellites, acoustic receivers, PIT arrays; Lennox et al. 2017). Electronic tagging can even provide information about specific behaviours animals engage in, such as feeding and copulation (e.g., Whitney et al. 2010; Brownscombe et al. 2014; Whitlock et al. 2015). These tools have the potential to map animal movements and reveal important life history events and fundamental processes (e.g., migration, foraging behaviour).

Human activity is one of the greatest threats confronting marine ecosystems (McCauley et al. 2015). Increased pressure on marine resources and ecosystems (Halpern et al. 2008; Crain et al. 2009) demands tools that improve efficiency and satisfy multiple user groups in the ocean. MSP therefore requires tools that can assist with incorporating these ecological aspects to address user–environment conflicts (Crowder and Norse 2008; Foley et al. 2010). Understanding how movement ecology can inform management was purported to be a barrier to incorporation of ecological information into management by Ogburn et al. (2017). We interpret this as a knowledge gap in MSP; therefore, we discuss the potential applications of animal movement data collected by telemetry to MSP. First, we describe the relevant legal and policy framework that underlies the concept and authority of MSP, emphasizing obligations or recommendations to incorporate ecological considerations in comprehensive marine planning programs. Next, we identify the current and potential future contributions, as well as limitations, of electronic tagging and tracking tools to mobilize

knowledge and satisfy ecological dimensions of MSP. Finally, we discuss how our findings can be operationalized within MSP and the limitations that could impede the incorporation and adoption of these concepts.

Legal and policy framework for MSP

Early environmental law for marine protection had a marked sectoral approach, focused on single threats (e.g., pollution or fisheries) and the conservation of single species. Place-based measures were restricted to the protection of vulnerable ecosystems or the critical habitat of endangered species (Spalding et al. 2013). The 1982 Law of the Sea Convention (LOSC) (i.e., the “Constitution for the Oceans”; Koh 1982) reflects mostly this sectoral approach (Molenaar 2002). It is relevant for MSP in that it codifies various maritime zones for the use and allocation of marine resources and spaces and defines the rights, responsibilities, and obligations of States in each of these zones, thus forming the legal basis for MSP and marine zoning (Hassan and Soininen 2015; Kuokkanen 2015; Maes 2008). However, it does not establish obligations to introduce integrated, ecosystem- or area-based conservation, planning, or management (Molenaar 2002; Engler 2015) and does not refer to MSP (Maes 2008; Maes and Cliquet 2015).

Since the adoption of the LOSC, several international policy instruments have called for a shift towards holistic area-based management, with a particular emphasis on ecosystem approach to management, integrated management of marine and coastal areas, and marine protected areas (MPAs). Key instruments reflecting these trends include the United Nations (UN) Agenda 21 (UN 1992), the Johannesburg Plan of Implementation (UN 2002), the outcome document of the UN 2012 Conference on Sustainable Development “The Future We Want” (UN 2012), the Sustainable Development Goals (SDG; UN 2015), and the Programme of Work on Marine and Coastal Biodiversity (CBD 1998, 2004), and Aichi Biodiversity Targets (CBD 2010) adopted by the Conference of the Parties to the Convention on Biological Diversity (CBD). Although these instruments do not refer to MSP per se, in supporting area-based conservation and management approaches, they create a receptive policy landscape for MSP.

The international policy reflected in these instruments strongly endorses area-based conservation of marine biodiversity through ecologically representative and well-connected systems of marine protected areas (UN 2002; CBD 2010). The internationally agreed target is to conserve at least 10% of coastal and marine areas through MPAs and networks of MPAs by 2020 (CBD 2010; U.N. 2015). To support this international effort, the Conference of the Parties to the CBD approved scientific criteria for identifying Ecologically or Biologically Significant Areas (EBSAs) in open-ocean waters and deep-sea habitats, as well as scientific guidance for establishing a representative network of MPAs (CBD 2010; Decision IX/20). Several criteria for the identification of EBSAs rely on accurate information on animals’ residences, aggregations, migrations, or hotspots (e.g., areas of special importance for life history stages of species, areas containing habitat for the survival and recovery of endangered, threatened, or declining species, areas with substantial assemblages of such species) provided by animal tracking technologies, among other sources.

Progress towards the agreed target has been considerable but insufficient. Recent assessments estimate that 16% of marine areas under national jurisdiction have been protected (Protected Planet 2017), although concerns have been raised regarding the uneven geographic distribution (UNEP-WCMC and IUCN 2016) and uneven protection outcomes based on MPA design, management, and compliance (Edgar et al. 2014; Gill et al. 2017). Establishing MPAs in areas beyond national jurisdiction has been more difficult due to legal and governance challenges and sparsity of scientific information, including biology, ecology, and cross-boundary connectivity (Gjerde et al. 2016). To date, 12 MPAs have been designated in

the Northeast Atlantic region and Southern Ocean (Smith and Jabour 2018). The Ross Sea Region MPA under the Convention for the Conservation of Antarctic Marine Living Species (CCAMLR) is the most recent and important designation (CCAMLR 2016; but see Brooks et al. 2016). A new international, legally binding instrument under the LOSC on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction, currently under elaboration by an intergovernmental conference (UN General Assembly 2017), could remove legal challenges and further encourage MPAs and other area-based management tools in these areas (Gjerde et al. 2016).

Building on MPAs as a framework for ocean space planning (Secretariat of the CBD 2012), there is increasing acknowledgment of, and support for, comprehensive (rather than conservation-oriented) area-based planning tools to support ecosystem-based management approaches and sustainability goals. The CBD recognized the need for MPAs to be part of a broader marine and coastal management framework (CBD 1998, 2004). Aichi Biodiversity Target 11 explicitly states that MPAs need to be “integrated into the wider landscapes and seascapes”, thus reinforcing the need for MPAs to be understood as one element of a more holistic ecosystem-based management of marine and coastal areas, including through MSP (Spalding et al. 2013). More recently, the Conference of the Parties to the CBD has explicitly acknowledged MSP as a tool for achieving its objectives, facilitating the application of the ecosystem approach and expediting progress towards the achievement of Aichi Biodiversity Targets in marine and coastal areas (Decision X/29 para. 15, Decision XIII/9 para. 2). It has thus encouraged States Parties, and invited other governments, to apply MSP in marine and coastal areas under their jurisdiction or to enhance MSP initiatives (Decision XIII/9 para. 3, Decision X/29 para. 78). It has also encouraged the elaboration of studies and workshops that will support individual member States in these efforts (Decisions X/29, XI/18, XII/23, and XIII/9; see also Secretariat of CBD 2012; UNEP & GEF/STAP 2014; Maes and Cliquet 2015). Another forum, the UN Environment Assembly, has also called for MSP by requesting UN Environment Programme to step up its work, including through its Regional Seas Programme, on assisting countries and regions in the application of the ecosystem approach to managing the marine and coastal environment, including through MSP (UNEP 2016).

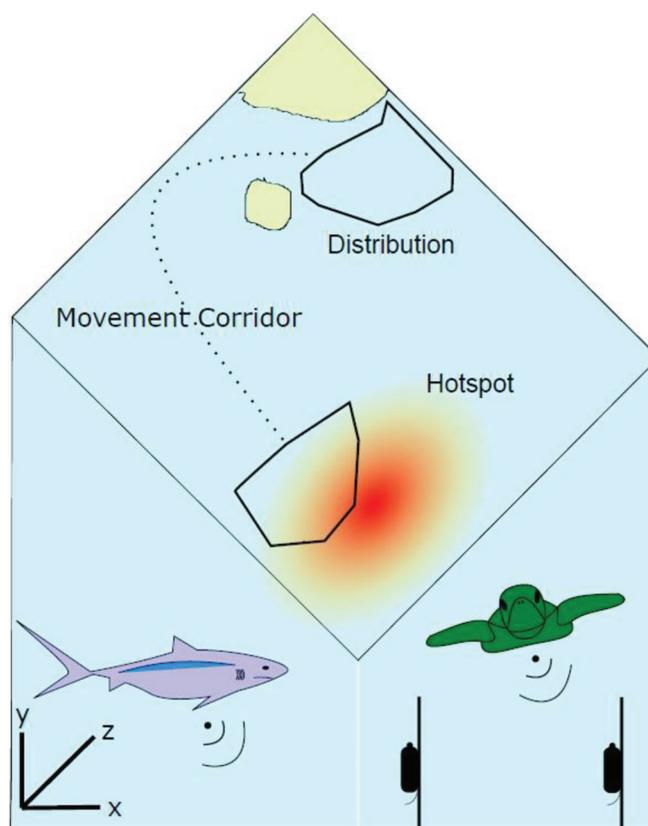
States' involvement in comprehensive MSP initiatives has grown considerably in the last decade. European countries are leading the development and implementation of integrated MSP, with Belgium, the Netherlands, Germany, and the UK being the pioneers (IOC-UNESCO 2017). This is partially the result of a supportive legal framework (the European Union Directive 2014/89/EU, establishing a framework for maritime spatial planning). But other States are following suit, in some cases even in the absence of a specific legal mandate. Globally, there are more than 60 MSP initiatives at different stages of development, including about 20 approved marine spatial plans (IOC-UNESCO 2017). Several stakeholders made voluntary commitments involving MSP initiatives within the framework of the 2030 Agenda and SDG 14 (UN 2017). The sustained assistance and support of IOC-UNESCO's MSP Programme has been an important factor of this development (IOC-UNESCO n.d.).

As States engage in MSP initiatives, it is timely to review how telemetry can inform and optimize the planning processes to ensure adequate protection of marine species, both in the context of area-based conservation for marine biodiversity (i.e., a representative network of MPAs) and in a wider coastal and marine planning framework for sustainable use of marine resources and marine space (Fig. A1).

Animal tracking and spatial planning

Although MSP requires coordinated efforts and government investment to be successful, it also requires data to create an evidence base with which to support decision-making and delin-

Fig. 1. Understanding how and why animals use certain areas of the ocean is integral to optimizing marine spatial planning. In the bottom panel we see generic illustrations of a fish and turtle transmitting position data to receivers moored to the bottom in an array designed to detect the tags in three dimensions (x, y, z). Animals use a mosaic of habitats based on biotic and abiotic habitat features, and detection data derived from animal tracking can be used to describe movement patterns (dashed line) and habitat requirements (solid lines). These are illustrated in the top panel, where we see a depiction of an individual's two-dimensional distribution (e.g., home range) and a movement corridor around an island or continent that it uses to reach a life history hotspot for conditioning or breeding where a new distribution is established. This information is necessary to optimize efforts to plan activities in the ocean to partition areas of the marine realm to maintain ecological integrity. [Colour online.]



ation. Marine ecologists are increasingly studying the habitat, life history, and spatial ecology of aquatic animals using electronic tagging and tracking equipment to investigate how individuals distribute within the marine environment, including where populations reside and move seasonally and ontogenetically, what the movement paths used by those populations are, and where core habitats or hotspots are located (Fig. 1; Hussey et al. 2015). These questions are of great relevance to ecologists for the comprehension of species' biology or ecosystem function and also hold great potential for informing the efforts of planners when developing or zoning territories in the ocean for development or activity. Spatial management actions such as time-area closures and MPAs have been widely used in the fields of fisheries management and conservation biology to protect particular life history stages or reduce bycatch of nontarget species (Roberts et al. 2005; Corrigan and Kershaw 2008; Game et al. 2009). These may be supported by direct observations such as spatial catch or catch rate data (e.g., Goodyear 1999; Grantham et al. 2008). However, in providing a more detailed, fisheries-independent perspective of habitat use, telemetry is becoming an indispensable

tool for identifying areas for closure or protection (e.g., Wetherbee et al. 2001; Ferraroli et al. 2004; Hobday and Hartmann 2006; Piatt et al. 2006). In this section, we discuss how electronic tracking technology can be applied for designing studies and transferring knowledge that can be used to design studies that inform MSP for sustainable use of the oceans.

Defining species distribution

Understanding the spatial patterns in species abundance is paramount to conservation, especially defining core and peripheries of the distribution and identifying source and sink habitats that sustain populations (Channell and Lomolino 2000). It is also relevant to delineate the responsibilities for species that may cross jurisdictional boundaries and identify stock complexes for co-management of fisheries (Afonso et al. 2017; Vaudo et al. 2017). The area needed by species to complete their life history and connectivity among populations is necessary to evaluate the extent of impacts conferred by ocean developments (e.g., Sequeira et al. 2012; Rosenbaum et al. 2014; Baudouin et al. 2015).

Movement within a core area delineates a home range, which is the space used by individuals for daily activities, particularly foraging and resting (Burt 1943; Kramer and Chapman 1999). For some animals, especially most aquatic species, the home range is three-dimensional (Fig. 1; Lee et al. 2017). Individual home range is influenced by a variety of factors, including habitat quality, prey availability, and shelter from predators (Speed et al. 2010). Distributions also have high degrees of intraspecific plasticity depending on size, metabolic rate, and age (March et al. 2010; Simpfendorfer et al. 2010; Welsh et al. 2013). Residency, a closely related concept to home range, measures the importance of a given habitat or zone by calculating the time or spatial overlap with species distributions, which can inform whether individuals remain in protected areas, live around aquaculture net pens, or are exposed to noise from drilling or boats (Glazer et al. 2003; Filous et al. 2017a). For example, Filous et al. (2017a) suggested that boat traffic in an MPA was altering the habitat use of an important predator (bluefin trevally, *Caranx melampygus*), suggesting that operations within the reserve would need to be modified to preserve ecological integrity (Fig. A2). Telemetry also provides evidence about the timing of occupancy as individuals may shift distributions. These measurements can be applied to investigate species-habitat relationships that reveal habitat demands and contribute to protecting critical areas (Jones et al. 2017). Patterns in individual movement and residency can also effectively be scaled to populations to evaluate population and species range boundaries (e.g., Allen et al. 2016).

The appropriate technology for characterizing animal distributions depends largely upon the animal (e.g., its size, morphology, anatomy, behaviours, physiology, natural history) and the environment in which it lives. Tracking data enables advanced estimation methods that can account for resource selection (Wilson et al. 2018) and depth use (Ballard et al. 2012; Lee et al. 2017) to calculate distribution. Acoustic tags require a tagged individual to move within the range of a compatible receiver and therefore cannot be used to accurately calculate the range of many vagile species (Heupel et al. 2006). Archival tags that estimate position based on environmental features such as sun position and temperature provide a relatively inexpensive method for obtaining long-term positional data, assuming the tag can be recovered (Schaefer and Fuller 2002). Satellite tags are also deployed on fishes, marine mammals, and turtles to collect movement data remotely. Although the cost and difficulty of attachment restricts their application to small sample sizes, short observation periods, and larger organisms, they can assist in discovering previously unknown areas of use, such as those used by humpback whales (*Megaptera novaeanglia*) in the Bearing Sea (Kennedy et al. 2014). Indeed, tracking is often limited to adults because tracking these early life stages for most species is not yet possible using electronic tagging

(Wikelski et al. 2007; Lennox et al. 2017), and alternative methods may be used to supplement electronic tagging and tracking data (e.g., particle simulations; Bonhommeau et al. 2009).

Optimizing development goals in the ocean can greatly benefit from knowledge of individual range, residency, and habitat use to evaluate and mitigate impacts. Insights into the space use of marine organisms, derived from tracking data, can be used to evaluate the efficacy of management measures to promote species conservation (Pecl et al. 2006; Chateau and Wantiez 2009; Hussey et al. 2017). Residency of sea turtles in shallows of Morton Bay, Australia, facilitated the recommendation of speed limits in areas of high use to protect turtles from ship strike (Shimada et al. 2017). Overlap between sea lion (*Otaria flavescens*) kernel distribution and Atlantic salmon (*Salmo salar*) aquaculture farms was used to predict conflicts, which could be used to inform mitigation measures that protect the investments (Sepúlveda et al. 2015). For species at risk, the extent of overlap between coastal development (Simpfendorfer et al. 2010) or contaminant exposure (Wolfe and Lowe 2015) can be quantified by tracking individual movements and home range relative to these stressors. Simpfendorfer et al. (2010) applied their tracking observations to recommend maintenance of natural shorelines in Australia from development to protect juvenile smalltooth sawfish (*Pristis pectinata*). Fisheries management also benefits from improved understanding of individual distributions (Crossin et al. 2017); the exchange rates of individuals on a fishing ground is relevant to demographics and sustainable rates of harvest through management measures such as quotas and can inform needs for spatial or temporal closures (Alós et al. 2016). Hussey et al. (2017) provided information on the distribution of Greenland halibut (*Reinhardtius hippoglossoides*) that led to the redrawing of a key management boundary and improvements in the fishery sustainability to improve fisheries management in the emerging arctic fishery.

Although MPAs are only one form of marine spatial planning, it is perhaps the most familiar example in which animal tracking data have been applied to evaluate or develop marine spatial plans (Fig. A2). The Ross Sea MPA was formally established in 2016 based on its ecological importance, which was detailed by Ballard et al. (2012), who described coexistence of a relatively unaltered mesopredator community. Meyer and Holland (2005) used active acoustic tracking to show that depth contours pose natural barriers to movement for bluespine unicorn fish (*Naso unicornis*), and MPA design could be enhanced by incorporating these contours into the protected area. Using habitat breaks to bound MPAs can reduce the spillover of adults and improve the potential of an MPA to retain these target species within its boundaries (Meyer et al. 2010). Tracking of deepwater *Centrophorus zeehaani* sharks in a protected area off Australia confirmed that it contained shark home ranges within the area, supporting the boundaries for the protected area, but suggested that protection may be stronger for females (Daley et al. 2015). Tracking can also reveal how redrawing boundaries can substantially alter the effectiveness of a protected area (Lea et al. 2018). A combination of electronic and conventional tagging showed that species that are well protected as juveniles, such as giant trevally (*Caranx ignobilis*), are often no longer protected by small MPAs as they mature (Wetherbee et al. 2004).

The marine environment is an open system, meaning that distributions are dynamic; indeed, many species are expected to shift their distributions under climate change scenarios (Perry et al. 2005; Hazen et al. 2013a). Changes to the timing (Sims et al. 2004; Otero et al. 2014) and expression (e.g., partial migration; Lea et al. 2018) of many key life history events will also shift the extent of interactions between animals and human infrastructure, necessitating ongoing research to monitor marine animals (Edwards and Richardson 2004; Krüger et al. 2018). Tracking these changes can inform MSP efforts, as many species that were historically rare in space or time may become more frequent in certain areas, for example expanding overlap between species at risk and fisheries

or infrastructure (Krüger et al. 2018). Continued efforts to characterize species distributions and understand mechanisms behind changes in spatial ecology will contribute to improved demographic modelling to generate records of natural mortality that can be used for assisting fisheries with setting quotas and ensuring sustainability of marine industries (Crossin et al. 2017).

Describing use of habitat mosaics and movement corridors

Although many marine animals maintain a core utilization area or home range during their lives, this may be dissolved at some point to find better quality habitat, begin a new stage in life (e.g., transition from juvenile to adult), or seek mating opportunities (Nathan et al. 2008). Indeed, fish use a mosaic of habitats at various times within their lives. Long-distance movements may be described as ranging or migration in many species and often occur in distinct pathways or corridors because of suitable habitats or currents that dictate movement paths (Fig. 1; Hays et al. 2014; Putman et al. 2016). Representatives of nearly all marine taxa (e.g., fishes, seabirds, cetaceans, turtles, cephalopods) undertake long-distance movements through the ocean between distinct habitats to achieve necessary life processes, including foraging, mating, and birthing. Movements between habitats can cover vast distances, such as the gray whale (*Eschrichtius robustus*) that travels between Russia and Mexico (Rugh et al. 2001) or Arctic terns (*Sterna paradisaea*) that travel >80,000 km (Egevang et al. 2010), but movements may equally be short or brief (Danylchuk et al. 2011; Moore et al. 2016). Movement corridors may also be vertical, as many species make daily vertical migrations (e.g., Aarestrup et al. 2009). Animals that make major movements through the ocean are in jeopardy of colliding with vessels, entanglement in fisheries, or disturbance by various auditory or visual distractions caused by human activities. The fitness of mobile marine species is entirely reliant on the individual's capacity to move, and the routes by which animals move are often consistent or predictable with appropriate data and models (Horton et al. 2017; Tucker et al. 2018); therefore, connectivity is essential to conservation and ecosystem management and must be considered if marine spatial plans are to be optimized for the protection of marine species (Beger et al. 2010).

Ascribing importance to movement corridors allows management to protect critical habitats and maintain connectivity in the ocean. Nearshore movements are logistically simpler than discovering the offshore movements of pelagic animals. Anadromous Arctic char (*Salvelinus alpinus*) that use shallow marine habitat during the summer are well understood by indigenous Inuit that use gill nets to capture them in the marine environment as they return to fresh water, but knowledge of their migrations can be supplemented by electronic tagging and tracking to manage fisheries (Moore et al. 2016). Many nearshore species may have cryptic behaviours that can be revealed by electronic tagging, such as bonefish (*Albula vulpes*), whose spawning migration off neritic flats was discovered by tracking tagged individuals to offshore spawning aggregations (Danylchuk et al. 2011), information necessary to restrict access to the areas at times when spawning could be disrupted. Satellite tagging has assisted in the discovery of migratory routes, including of pygmy blue whales (*Balaenoptera musculus brevicauda*; Double et al. 2014) and European eel (*Anguilla anguilla*; Aarestrup et al. 2009; Béguyer-Pon et al. 2015). Planning that maintains habitat connectivity and quality along these movement corridors is essential. For example, Double et al. (2014) suggested that management and industry could partner to reduce noise and traffic along pygmy blue whale migration routes. Morton and Routledge (2016) suggested that aquaculture facilities in British Columbia, Canada, be moved away from the migratory corridors used by sockeye salmon (*Oncorhynchus nerka*) to avoid transmission of pathogens from the farmed fish to the wild stocks. The impacts of other infrastructure such as subsea cables and turbines are emerging as potential barriers to animal movement (e.g.,

Westerberg and Lagenfelt 2008; Hastie et al. 2014) and provide an opportunity to use electronic tags to test hypotheses about impacts on the movements of marine animals and to plan the infrastructure to avoid critical habitat.

Better data quality and availability will continue to improve estimates of the space and times that animals use corridors in the ocean, separating predictable movements and important corridors from others that may be used more opportunistically. Intraspecific differences are relevant to population and species management, such as variation in individual humpback whale movements in the south Atlantic Ocean between populations and cohorts and in the northern Pacific Ocean (Rosenbaum et al. 2014; Fig. A3). Dynamic time-area closures can be used to avoid impacts as animals pass by along their migration, but impacts will be more difficult to mitigate for species with large ranges such as whale sharks (*Rhincodon typus*) when they are not at hotspots such as breeding grounds (Sequeira et al. 2012). Installing real-time monitoring systems to communicate the presence of animals to industries working in the marine environment will operationalize a valuable tool for MSP, allowing oceanic spatial resources to be more effectively shared and relieving some of the burden on industries ceasing operations (Hazen et al. 2016; Klimley et al. 2017). Shipping lanes can be rerouted, vessel behaviour changed (e.g., speeds below 14 km·h⁻¹ greatly reduce collisions with cetaceans), fishing closures implemented, or development restricted as deemed necessary, as actionable MSP solutions to conservation challenges are developed for ensuring connectedness of the ocean.

Identifying core habitats and hotspots

Ecosystem conservation and MSP demand understanding of which habitats are critical for species to complete their life cycles, termed biodiversity hotspots (Hazen et al. 2013b; Hays et al. 2016). Above, we discussed distributions and movement corridors, but for many species there are relatively few or small locations of high importance; often, these areas are used by multiple species, facilitating a holistic approach to ecosystem protection (Citta et al., in press). Marine habitats are highly heterogeneous in their temperature, salinity, oxygen concentration, depth, substrate, and nutrient and energy availability, meaning that certain areas of the ocean are highly productive hotspots, whereas others support little life (Worm et al. 2003; Hearn et al. 2010; Hazen et al. 2013a). The richest and most abundant aquatic communities tend to be found where physicochemical environments are most suitable (Tews et al. 2004; Gratwicke and Speight 2005). Hotspots may be areas that are important for key life history stages for a particular species (e.g., stopover sites for migrants; Silva et al. 2013; Whitlock et al. 2015) or areas of high productivity, trophic transfer, and biophysical coupling (Dower and Brodeur 2004; Sydeman et al. 2006; Santora and Veit 2013) and are therefore relevant areas to focus conservation efforts (Hays et al. 2016).

Hotspots in the ocean may be generic or more species-specific, potentially incorporating areas for settling or rearing in early life stages or foraging and reproduction for mature individuals. Many species have fidelity to spawning or foraging hotspots, returning to them periodically to complete their life histories. Consequently, the hotspots do not change within their lives or across generations. This is particularly true of spawning grounds, exemplified by European eels and American eels (*Anguilla rostrata*) that are only known to spawn in the Sargasso Sea (confirmed from satellite tagging of American eel; Béguyer-Pon et al. 2015). Tracking of movements has allowed the discovery of key foraging and breeding sites in a few short years in species with previously cryptic behaviours, revealing where animals aggregate, feed, and breed (e.g., Danylchuk et al. 2011; Rayner et al. 2015; Richardson et al. 2016; Soanes et al. 2016). Hotspots can also be dynamic for ranging species, especially pelagic predators following temperature isoclines (Eckert et al. 2006; Chittenden et al. 2013) or forage species (e.g., krill) requiring dynamic predictive modelling and

long-term tagging efforts to keep abreast of hotspots (e.g., Demer et al. 2012).

Integration of data collected using a variety of techniques and across scales is commonly used to identify marine hotspots. Remote sensing of ocean conditions (water temperature, primary production, etc.) provides broad spatial and temporal coverage from fine scales all the way to ocean basins to identify conditions conducive to hotspots, but such methods are limited to surface conditions and only provide a proxy for primary production via chlorophyll *a* concentrations (Palacios et al. 2006). Innovations in electronic tagging have advanced hotspot identification by providing high-resolution information on spatiotemporal distributions and movement (e.g., Ballard et al. 2012; Grecian et al. 2016; Citta et al., in press) and by permitting observations or inference of particular behaviours such as feeding (e.g., Brownscombe et al. 2014; Whitlock et al. 2015) or spawning (e.g., Whitney et al. 2010; Aranda et al. 2013) using biosensors and biologgers or animal-borne cameras (Struthers et al. 2015; Cooke et al. 2016). These tools to track animals and reveal places and times where key events are occurring can be used to identify risks of conflict (Queiroz et al. 2016), with the aim of mitigating those conflicts through MSP. Differential use of habitats is an emerging paradigm in the marine environment wherein habitat quality interfaces with activity and energy use with relevance to habitat selection and management. Brownscombe et al. (2015) quantified activity of queen conch (*Lobatus gigas*) on two coastal habitats and revealed activity deficits on seagrass, suggesting that preservation of more suitable rubble habitat could be an important step towards conservation.

Many species shift distribution as their needs transform along ontogenetic and seasonal axes, meaning that the potential for impacts changes over time (Afonso et al. 2017; Filous et al. 2017b). Optimum timing and location of marine activities therefore benefits from knowledge of hotspots that are revealed by animal tracking. Knowing the spatial and temporal dimensions of hotspots can allow dynamic opening or closure of certain areas during sensitive periods to avoid negative impacts such as over-exploitation of aggregations (Grafton and Kompas 2005). Tracking the movements of juvenile sharks to identify nursery areas can inform planning of potentially disruptive activities such as boating and dredging in coastal zones (Carlson et al. 2008). Likewise, identification of spawning hotspots for bluefin tuna (*Thunnus thynnus*; Hazen et al. 2016) provides the basis for future planning of offshore drilling and other activities in the Gulf of Mexico (Fig. A4). Knowing why animals are found where they are empowers management to ascribe importance to hotspots and make decisions to facilitate coexistence of animals and infrastructure in the ocean.

Prioritization is often a challenge for managing ecosystems. Although we largely discuss user–environment conflicts, environment–environment conflicts can arise in situations where habitats must be compared to find the most suitable site for development. Concepts of richness and diversity may prevail to protect hotspots of especially high ecological importance, but this may push activities into areas of high endemism towards rare species that would be disproportionately affected. Indeed, rare species are not necessarily found in areas of highest diversity (Williams et al. 1996), challenging conservation planning and necessitating careful consideration by marine spatial planners. As we have discussed above, marine animal tracking data can be used to determine the temporal and spatial requirements of individuals on given habitats (e.g., estuaries, reefs, seamounts) such that human activities in the ocean can circumvent interactions with these species.

Synthesis

The limitations of traditional sectoral oceans management led to a shift to a more integrated, comprehensive, and holistic place-based management that seeks to balance different soci-

etal objectives, from ecosystem protection to socioeconomic benefits (White et al. 2012). In recent years, MSP has emerged as one of the most widely endorsed tools for integrated ecosystem-based coastal and marine management. Effective mapping and spatially empowered data are central to the success of MSP. As we have shown, the spatial and temporal information that tracking systems provide about marine life habitats and processes, movement corridors, and hotspots is essential for MSP through diverse avenues of management, ranging from permanent, dynamic, spatial, temporal, or fishery-dependent methods of mitigation.

Constant oversight of marine life is now possible with advanced animal tracking tools (Hussey et al. 2015; Lennox et al. 2017). The mysteries of animal movements and distributions that once challenged managers' capacity to make informed decisions about the marine environment are now surmountable using electronic tagging and tracking tools to identify critical habitat and to predict and mitigate negative interactions with marine life. The result is the spatially empowered data that optimize marine planning such as marine traffic routes, dock locations, drilling timing, fisheries deployment, aquaculture, sites, turbine installation, and habitat restoration. Lacking technology to enumerate catches or map the distribution of fishing fleets, it would be logistically sub-optimal to determine the best routes for shipment, zone human activities, or distribute fishing efforts, especially in the multisectoral way championed by MSP. Access to digital maps and data are revolutionizing the ways in which ecosystems are planned and managed, including emerging sources for these data alongside animal movement data; for example, organizations such as Global Fishing Watch (www.globalfishingwatch.org) provide access to information necessary to evaluate impacts and improve decision-making (see Kroodsma et al. 2018). Tracking tagged fish has also provided insight into natural and fishing mortality, a substantial contribution to the species demographics that is necessary to prioritize conservation (Whitlock et al. 2012; Byrne et al. 2017; Vaudo et al. 2017). Distributional data can even be extended to evaluate impacts using energetics modelling to directly estimate the costs of interference with marine life, providing a currency with which to quantify impacts and baselines to test mitigation using MSP (Masden et al. 2010; Costa et al. 2016).

Many of the examples presented here are observational data discussed in the context of applications to MSP (direct integration is clearly limited; Fig. A5). However, there is potential for improved experimental approaches to test hypotheses about impacts. The effectiveness of protected areas or proposed reserves can be evaluated or predicted using tracking and, in many cases, assist in understanding of how these areas contribute to regional conservation while in the context of resource needs (Figs. A2, A3, A4). Setback distances for infrastructure can also be tested to evaluate various management options in an MSP framework (Cranmer et al. 2017). Tolerance to, and recovery from, disturbances can be measured; for example, Filous et al. (2017a) found that most marine predators except bluefin trevally were tolerant to boat noise in an MPA, and Russell et al. (2016) identified rapid recolonization of areas exposed to loud pile-driving by harbour seals (*Phoca vitulina*). Trade-offs may be necessary, and using protected areas to form source populations that spillover to adjacent, unprotected habitats may be necessary to facilitate long-term persistence of a population (Toonen et al. 2013; Friedlander et al. 2014). The technology required to obtain biologically significant data needed to make informed decision is becoming possible at nearly all scales and locations (Richardson et al. 2009; Siceloff and Howell 2013). There is also an emerging capacity to overlay multispecies data to map the most important areas of use within the ocean (Ballard et al. 2012; Pendoley et al. 2014).

Describing the distributions, movements, and hotspots used by marine animals is essential information to MSP so that various activities can be effectively organized within the oceans while minimizing impacts on biodiversity. Mitigative strategies can be

implemented to reduce conflicts, considering the behaviour of wild animals to keep them safe from interacting with fisheries, oil or gas prospecting, aquaculture, shipping, or other activities. Knowledge that marine turtles, cetaceans, sharks, seals, or other sensitive marine animals have the potential to be disturbed by industry provides the opportunity to evaluate protected areas. Scott et al. (2012) tracked green turtle (*Chelonia mydas*) residency within marine reserves to quantify their effectiveness for providing protection using satellite tracks of the turtles. Similarly, Chapman et al. (2005) used acoustic telemetry to quantify shark residency in a Caribbean MPA to evaluate its effectiveness for providing protection, recommending expansion for improved protection. There is also the potential to use tracking data to directly investigate mitigation measures such as offset distances of wind turbines (Cranmer et al. 2017) or sensory triggers that inform individuals to move away from fixed infrastructure such as tidal turbines, wind farms, aquaculture pens, etc.

Although we found that MSP is not yet well integrated within animal movement literature (and vice versa; Fig. A5), we posit that this integration is mutually beneficial to fields of biological sciences, planning, and policy. Electronic tracking is increasingly applied to determine the population structures and demographics of marine animals, which assist with conservation and particularly with fisheries that benefit from setting harvest quotas and regulations based on principles of reproduction and replacement (Heupel and Simpfendorfer 2002; Williams et al. 1996; Crossin et al. 2017). Tag return rates from fisheries can be used to determine the extent of exploitation and refine spatial plans, for example, keeping fisheries away from green turtle migration corridors (Baudouin et al. 2015) or blue shark (*Prionace glauca*) hotspots (Queiroz et al. 2016). Spatial plans can also be evaluated and modified after implementation to determine whether interventions are effective by tracking animal use. Effective MSP incorporating ecological theory will also consider smaller species that form the base of the food chain. Many of these species are presently too small to tag or track for long, a limitation that will hopefully be overcome in the future to track movement of larvae and juvenile fishes both in the open ocean and in local bays or harbours (Lennox et al. 2017). There are alternative methods to track the movement of larval species, including the use of stable isotopes, elemental chemistry, or echosounding, which can assist for filling in knowledge gaps (Gillanders 2005; Demer et al. 2012); indeed, comprehensive approaches to tracking animals are necessary to obtain an holistic perspective on space use and for effective ecosystem approaches to management and MSP. Although we focus on electronic tracking (both biologging and biotelemetry) in this paper, greater integration of technologies is needed to improve monitoring, particularly for the smallest and largest marine species. Passive acoustic monitoring is used to monitor the residency and movement corridors (e.g., Wingfield et al. 2017). Now, it is possible to extend monitoring into real time using bottom-mounted sonobuoys that can identify the presence of a whale and alert ships to its presence to avoid collisions (Laist et al. 2001). Sharing among technologies and data systems will increase physical and taxonomic coverage within the ocean. Implementing animal tracking to consider the environment ensures a true multisectoral approach to MSP and provides actionable solutions to potential user-environment conflicts that optimize use of the marine environment.

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Appendix A

Canada has abundant marine life (Fig. A1), but implementing MSP is challenging due to the complex jurisdictional framework for marine and coastal planning and management. Federal, provincial, and Indigenous peoples’ governments have exclusive or shared jurisdiction over different marine and coastal spaces and over different human activities that have taken place in the marine and coastal environments (e.g. Nowlan 2016). At the federal level, the key legislation is the Oceans Act (S.C. 1996 c. 31; refer to <http://laws-lois.justice.gc.ca/eng/acts/O-2.4/>), which committed the government to three main deliverables: a national oceans strategy (issued in 2002 and followed by an Oceans Action Plan; Government of Canada 2002, 2005); a national network of MPAs (Jessen 2011; Government of Canada 2005); and integrated management plans for five priority Large Ocean Management Areas (LOMAs; Government of Canada 2005). Although LOMAs integrated management plans could have provided an adequate policy platform for the development of MSP (Jessen 2011), progress was curtailed by the challenging implementation of the Oceans Act (Jessen 2011; Commissioner of the Environment and Sustainable Development 2012; Nowlan 2016). Integrated management plans were formally approved only for the Beaufort Sea (2010) and the Pacific North Coast (2017) and completed for the Eastern Scotian Shelf (2007), Gulf of St. Lawrence (2013), and Placentia Bay – Grand Banks (2012; Nowlan 2016; PNCIMA Initiative 2017). The federal government has reportedly moved “beyond the LOMA approach” to nationally defined marine bioregions (Fisheries and Oceans – Maritimes Region 2014), which provide the spatial planning framework for Canada’s national network of MPAs (Government of Canada 2011). The proposed amendments to the Oceans Act (Bill C-55) confirms the government’s focus on increasing protection for Canada’s marine and coastal waters in line with the CBD Aichi target. Although the need to embed MPAs in MSP frameworks has been highlighted (WCELA 2017), federal policies and priorities do not explicitly refer to MSP (e.g. Office of the Prime Minister 2016a, 2016b). Some MSP initiatives have advanced at the regional or local level (e.g. Marine Plan Partnership for the Pacific North Coast (MaPP); Nowlan 2016). It seems apparent, however, that strong and decisive federal stewardship for a nationwide, integrated, and comprehensive MSP is needed.

The Marine Life Conservation District (MLCD) program consists of a network of 11 MPAs in Hawaii. The MPAs were designed without movement data for species that occupy them, and replenishment of fisheries resources was not a principle objective (Friedlander et al. 2007). Hawaii’s fisheries managers have been advised to reverse these declines with biologically informed MSP

Fig. A1. National policies for marine spatial planning are required to protect marine life such as whales, pictured here.



Fig. A2. Acoustic telemetry revealed the residency of bluefin trevally (*Caranx melampygus*) within a small marine protected area in Hawaii.



Fig. A3. Humpback whales (*Megaptera novaeangliae*) are a highly migratory cetacean that use distinct pathways to access their breeding and feeding habitats. These corridors can be discovered and monitored using telemetry.



(Friedlander et al. 2014). Acoustic telemetry has proven to be an effective tool in evaluating the movements of fishes in the context of the protection provided by the State's MPAs (Holland et al. 1996; Meyer and Holland 2005; Meyer et al. 2007a, 2007b). Recent tracking data showed that bluefin trevally (*Caranx melampygus*) were well-protected by the Molokini MLCD (Fig. A2). However, giant trevally (*Caranx ignobilis*) were vulnerable during seasonal migrations outside of their home range to other islands, and the home range of green jobfish (*Aprion virescens*) was considerably larger than the MPA, evidenced by low residency and high recapture rate (Filous et al. 2017b). Further research indicated that noise from boating, an important nonextractive human use of the reserve, altered the distribution of bluefin trevally within the reserve (Filous et al. 2017a). This study provided the State's marine managers with new data on the efficacy of this MPA and range of potential management options that could enhance its effectiveness for an assemblage of predators that are heavily fished in the main Hawaiian Islands (Friedlander and DeMartini 2002).

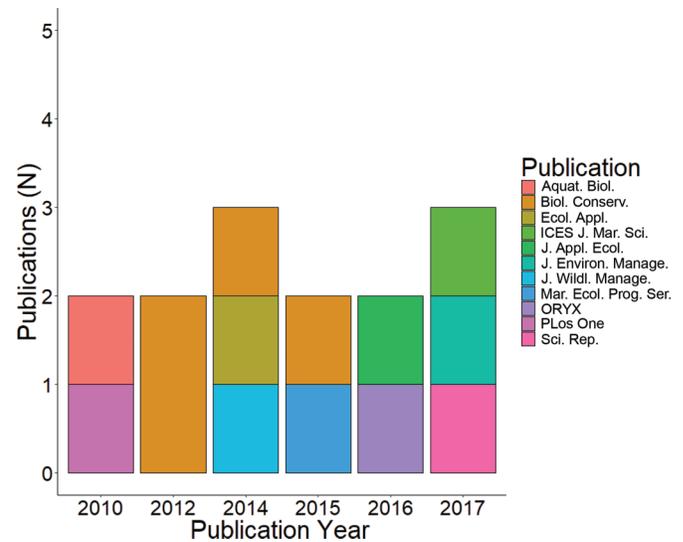
Whales make long-distance movements within the ocean between foraging and reproductive areas (Fig. A3). Exact movement routes and behavioural states of humpback whales (*Megaptera*

novaeangliae) were derived from satellite tags to measure the overlap between whales and anthropogenic stressors. State-space modelling was implemented to identify localized and transiting behaviours in the swimming of tagged individuals (Rosenbaum et al. 2014). Positions derived from the tracks confirmed that the migration route overlaps with important shipping lanes in the south Atlantic Ocean, and state-space modelling demonstrated



Fig. A4. Tuna such as this yellowfin (*Thunnus albacares*) can use entire ocean basins and understanding their range and movement patterns is challenging. Technology such as this satellite tag, attached in the dorsal musculature, provides information about the spatiotemporal movements of the oceans' wide-ranging species.

Fig. A5. Bibliometric search results for integration of marine spatial planning with telemetry literature. It was observed that overlap is relatively limited ($N = 14$), with the first articles integrating the term in 2010. All instances of overlap were in journals considered to be focused on biological sciences rather than policy-related publications. The journal *Biological Conservation* returned the most studies with overlap ($N = 4$). Scientific search engines Scopus and Web of Science were searched at the title, abstract, and keywords level for the search terms "marine spatial planning" also including "animal movement OR *telemetry" in scientific articles, where the asterisk is a wildcard to return variants including "biotelemetry". This figure was generated using ggplot2 (Wickham 2009) in R (R Core Team 2017). [Colour image available online only.]



novaeangliae) were derived from satellite tags to measure the overlap between whales and anthropogenic stressors. State-space modelling was implemented to identify localized and transiting behaviours in the swimming of tagged individuals (Rosenbaum et al. 2014). Positions derived from the tracks confirmed that the migration route overlaps with important shipping lanes in the south Atlantic Ocean, and state-space modelling demonstrated

that the overlap between human activity and whale breeding grounds may be extensive. Tracking also was used to calculate the relative potential impact to whales at different points in the migration based on the distribution of human activities in the ocean. Dominant stressors changed at different stages of the whale migration between Antarctica and the Gulf of Guinea, emphasizing the importance of the multisectoral approach championed by MSP. Individual variation in migratory routes will apparently challenge management, but most of the potential for impact was within national exclusive economic zones, meaning that national policy is necessary for humpback whale conservation but insufficient without cooperation among nations through which the whales pass along their migration. Future development of offshore infrastructure can incorporate knowledge of whale migration routes for mitigation.

Applications of electronic tagging technologies have allowed identification of life-history hotspots for tunas (*Thunnus* spp.), pav-

ing the way for spatially explicit management measures for these iconic species (Fig. A4). Electronic tagging of western Atlantic bluefin tuna (*Thunnus thynnus*) has provided new information on the seasonal utilisation of the Gulf of Mexico spawning grounds (Wilson et al. 2015), while putative spawning events have been identified using diving behaviours recorded by archival and PSAT tags, allowing characterisation of the oceanographic hotspots associated with spawning (Hazen et al. 2016). These studies enabled evaluation of the spatial overlap of spawning hotspots for bluefin in the Gulf of Mexico with seasonal closed areas, revealing that spawning hotspots are centred to the north of closed areas, well beyond their boundaries (Wilson et al. 2015). Identification of spawning hotspots also has implications for planning in coastal and offshore industries in the Gulf of Mexico, based on quantification of overlap with areas oiled by the 2010 *Deepwater Horizon* oil spill (Hazen et al. 2016).