

Planning for dynamic process: An assemblage-level surrogate strategy for species seasonal movement pathways

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ABSTRACT

1. Seasonally mobile species are globally prevalent and often provide vital ecosystem functions and services along their seasonal movement pathways. However, due to the challenges of planning for features that are spatially and temporally variable, mobile species are rarely accounted for in conservation planning. To protect this dynamic process, planners need a temporally explicit surrogate for species seasonal movements pathways. Because reserves networks typically aim to represent the full spectrum of biodiversity, these surrogates also need to capture the assemblage-level organization of species in order to preserve the full range of seasonal movement pathways that occur within a given planning region.
2. To this end, this study introduces a new assemblage-level surrogate strategy for species seasonal movements that preserves variation in biodiversity across the 12 months. Two monthly, assemblage-level attributes were integrated: discrete species assemblages and continuous assemblage suitability, thereby allowing planners to select complementary combinations of sites that achieve comprehensive assemblage coverage in each month.
3. As a marine case-study, this strategy was applied to the U.S. Mid-Atlantic, and a gap analysis was used to evaluate the ability of the Mid-Atlantic's current spatial management scheme to accommodate species' seasonal movements.
4. The results indicate that current protected areas in the Mid-Atlantic will be unable to meet even modest quantitative objectives for protecting seasonal movements, and priority conservation areas are identified for designing a reserve network that offers year-round protection.
5. Planning for processes remains a significant gap in conservation planning, and this study seeks to address this gap by proposing a surrogate strategy that will aid the incorporation of a wide-spread dynamic process into reserve design. This strategy uses public, predominantly global datasets that have terrestrial and marine counterparts, making it applicable to planning for species seasonal movements both on land and at sea.

Key words: fish, gap analysis, invertebrates, marine reserve, migration, ocean

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INTRODUCTION

Widespread decline of marine biodiversity and extensive loss of ecosystem functions and services underscore a growing need for systematic conservation planning (Halpern et al., 2008; Jackson 2008; Worm et al., 2006). Reserve networks, i.e. coordinated systems of zoned marine protected areas (MPAs), are important tools for mitigating threats while increasing the resilience and persistence of ecosystems (Ault et al., 2013; Halpern, 2003; Sackett et al., 2014). Empirical evidence has repeatedly demonstrated that embedded networks of no-take areas, i.e. MPAs that prohibit all extractive activities (IUCN categories Ia, Ib and II), can enhance biodiversity within their boundaries (Lester & Halpern 2008; Lester et al., 2009; Micheli, Halpern, Botsford, & Warner, 2004) and produce a wide range of “reserve effects” beyond their boundaries, e.g. spillover of adults and larvae and higher catch rates (da Silva, Hill, Shimadzu, Soares, & Dornelas, 2015; Rossetto, Micheli, Saenz-Arroyo, Montes, & De Ledo, 2015). However, effective design is critical to achieving the desired conservation benefits of reserve networks (Edgar et al., 2014; Lester et al., 2009).

A primary objective of reserve network design is to protect a representative and adequate portion of regional biodiversity, with the implication that that key ecosystem functions and services will also persist (Margules & Pressey, 2000). Most active reserve

networks were designed based on static patterns of regional biodiversity, for example snapshots of species distributions from one month or year, or generalizations across long-term average conditions (Brown, Smith, Lawton, & Anderson, 2011; Pressey, 2004; Pressey, Cabeza, Watts, Cowling, & Wilson, 2007). This is inherently problematic because patterns of biodiversity fluctuate in response to processes, or sequences of change in ecosystem components through time, e.g. hydrology (Lombard et al., 2007; Peñaflo, Skirving, Strong, Heron, & David, 2009), connectivity (Guichard, Levin, Hastings, & Seigel, 2004), and meta-community interactions (Guichard et al., 2004). Therefore, reserve networks that do not explicitly consider such processes risk becoming outdated if designed around snapshots in time, or ineffective during parts of the year when biodiversity features are at their extreme extents if designed around long-term average conditions.

To ensure that reserve networks remain relevant through time, there must be a paradigm shift towards planning for processes (Pressey et al., 2007). Many processes are dynamic by nature, meaning that they vary in their frequency, direction, and/or magnitude of change across time. Planning for dynamic processes requires novel surrogate strategies that are temporally explicit, i.e. that preserve how critical processes vary and affect biodiversity patterns at time-steps relevant to reserve design (e.g. weekly, monthly, yearly, etc.). In recent years the number and variety of temporally explicit surrogate strategies for dynamic processes has rapidly increased, e.g. for larval

connectivity (Magris, Treml, Pressey, & Weeks, 2015; Moilanen, Leathwick, & Elith, 2008), succession following disturbance (Thrush, Lundquist, & Hewitt, 2005), and species responses to climate change (Alagador, Cerdeira, & Araújo, 2016; Keppel et al., 2015; Mestre et al., 2015; Reside, VanDerWal, & Kutt, 2011; Williams et al., 2005). However, due to the paucity of data describing temporal aspects of biodiversity, surrogates for dynamic processes are still relatively uncommon in the literature, and are rarely accounted for in marine reserve design (Breen, Posen, & Righton, 2015; Martin et al., 2007; Runge et al., 2015).

For example, despite the prevalence and importance of species' seasonal movements, surrogates for this dynamic process are still rare (Green et al., 2015). A significant proportion of mobile marine species undertake large-scale cyclical movements driven by physiological, foraging, ontogenetic, and/or reproductive requirements (Breen et al., 2015; Dybala, Truan, & Engilis Jr, 2015; Green et al., 2015; Martin et al., 2007; Pérez-Ruzafa, Hegazi, Pérez-Ruzafa, & Marcos, 2008; Runge, Martin, Possingham, Willis, & Fuller, 2014). When considered at the assemblage-level, mobile species play an important role in driving seasonal fluctuations in biodiversity, and often provide important ecosystem functions and services along their movement pathways, e.g. the production of larvae, the delivery of nutrient inputs, and the regulation of prey abundances (Breen et al., 2015; Runge et al., 2014). Threats occurring during even brief periods of seasonal movements can significantly impact

populations, which can result in cascading shifts in species assemblages and/or critical disruptions to the provision of important functions and services (Runge et al., 2014, 2015). Therefore, surrogate strategies that allow planners to understand and provide adequate protection to species throughout their full movement pathway are central to effective reserve network design. Examples of such surrogates exist, but most focus only on one or two species of conservation or management interest (Hill, Tobin, Reside, Pepperell, & Bridge, 2015; Iwamura, Fuller, & Possingham, 2014; Klaassen, Bauer, Madsen, & Possingham, 2008; Martin et al., 2007; Mazor, Beger, McGowan, Possingham, & Kark, 2016; Phillips, Williams, Midgley, & Archer, 2008; Sheehy, Taylor, & Norris, 2011). Surrogate strategies that capture assemblage-level movements are still needed to allow planners to incorporate seasonal cycles of assembly into marine reserve design (Green et al., 2015).

In this regard, the following study presents a novel assemblage-level surrogate strategy for species seasonal movements. As a case study, the surrogate strategy was applied to the Mid-Atlantic region of the United States, which is almost completely covered by protected areas (NOS, 2015). Despite its extensive coverage, the Mid-Atlantic's current management scheme does not constitute a coordinated reserve network. Rather, protected areas were established in a piecemeal fashion, often to address goals for individual species or fisheries management plans and without consideration of systematic conservation and/or management (NOS, 2015).

Furthermore, most have lenient management plans (i.e. comparable to IUCN category V, which emphasizes intensive human use) and none are no-take areas (IUCN & UNEP-WCMC, 2016). An assemblage-level surrogate strategy for the Mid-Atlantic would be useful for both evaluating the effectiveness of Mid-Atlantic's current management scheme, and for guiding the establishment of a new systematic network of reserves that accommodates seasonal fluctuations in biodiversity.

The objectives of the study were 1) to define a surrogate that characterizes the assemblage-level seasonal movement pathways within the Mid-Atlantic, 2) to evaluate the ability of the Mid-Atlantic's current management scheme to accommodate such seasonal movements, and 3) to identify areas that will be important to protect within reserves to maintain the full suite of species seasonal movements. Because the surrogate strategy relies on publicly available datasets with predominantly global extents, it is not only useful for improving conservation schemes in the Mid-Atlantic, but is also widely applicable around the world.

METHODS

Broadly, this methodology can be described in three consecutive stages: model building, surrogate definition, and spatial management evaluation (Figure 1).

Study area

The study area extends roughly 150,000 km² along the north-eastern U.S. continental shelf from Cape Hatteras, North Carolina to Cape Cod, Massachusetts and stretches ~1km from shore out to the 450m contour (Figure 2). The study area—hereafter referred to as the Mid-Atlantic—largely consists of a flat and shallow continental shelf with sediments ranging from clay to gravel, with isolated natural rock deposits and man-made reefs (Steimle & Zetlin, 2000). The continental shelf is interrupted by deep canyons cutting towards the continental shelf break (Wilkinson, Wiken, Creel, Hourigan, & Agardy, 2009) – the largest of which is the Hudson Canyon extending south-east from the mouth of the Hudson River (Figure 2). The Mid-Atlantic has considerable seasonal and inter-annual variability in hydrological conditions, e.g. temperature, salinity, and ocean currents (Mountain, 2003; Steimle & Zetlin, 2000; Wilkinson et al., 2009).

Model building

To characterize seasonal movements at the species level, a habitat suitability modelling approach was employed. First, species records were obtained from the Northeast Fisheries Science Center's Bottom Trawl Survey (<http://www.nefsc.noaa.gov/epd/ocean/MainPage/ioos.html>) within the Mid-Atlantic from 2003-2015 for 434 species identified to the lowest taxonomic resolution possible. Species with less than 30 occurrences over the sampling period were removed to avoid

building inaccurate models (see Hernandez, Graham, Master, & Albert, 2006; Wisz et al., 2008), leaving 173 species for further analysis. Retained species spanned four broad categories of habitat preference: pelagic (n=18), i.e. species that primarily inhabit the water-column; benthic pelagic (n=13), i.e. species that live partly near the sea bed and partly within the water-column; demersal (n=122), i.e. species that live primarily near the sea bed; and epibenthic (n=20), i.e. species that live on the sea bed (Table S1).

Next, environmental variables that potentially affect the seasonal variation in the habitat suitability of marine taxa (Brown et al., 2011) were acquired from a variety of public sources (Table 1). To account for species that move within the water-column, variables were acquired (where available) at three depths: the surface, 10m and the bottom (maximum depth of 450m). To investigate how both short-term climate fluctuations and long-term trends might affect habitat suitability, variables were acquired at three temporal resolutions: static, real-time, and monthly. Static variables were assumed to be stationary over spatial and temporal scales relevant to spatial management (e.g. depth), whereas real-time variables fluctuated (e.g. temperature). Monthly climatological variables were the averages and standard deviations of real-time variables from 2003-2015 temporally binned by month. All variables were regridded in ArcGIS 10.3.1 to a resolution of 0.011° latitude and longitude and clipped to the study area using the Extract by Mask Tool.

Lastly, the habitat suitability of 173 species was modelled using Maxent (Phillips, Anderson, & Schapire, 2006) - a maximum-entropy algorithm for relating presence-only data to environmental variables. Models were built using static, real-time, and the standard deviation of monthly climatologic variables in order to preserve the temporally explicit responses of species to the environment. Then the models were projected onto static and monthly climatologic variables, producing 12 monthly layers of habitat suitability per species that captured seasonal variation in long-term habitat suitability (Figure 1). Model discriminant ability was evaluated using the area under the receiver operator characteristic curve (AUC). AUCs above or below 0.5 indicate better or worse than random discrimination between presences and pseudo-absences, respectively (Phillips & Dudik, 2008). Models with AUC values < 0.70 were removed to exclude low performance models (Reside et al., 2011; VanDerWal et al., 2013).

Surrogate definition

For each month, the habitat suitability layers were used to define two assemblage-level attributes that comprised the surrogate: 1) discrete, monthly species assemblages, and 2) continuous, monthly values of assemblage suitability (Figure 1). Species assemblages were defined for each month as groups of pixels with similar species composition based on habitat suitability. Assemblages were calculated through a progression of spatial analyses, beginning with a spatial principal components

analyses across all habitat suitability layers within each month to distill dominant movements pathways. Scree-plots were used to determine the number of principal components to retain in each month. Then, the retained principal components for each month were clustered into statistically discrete clusters using the Iso Unsupervised Classification Tool in ArcGIS. The initial number of clusters (hereafter: assemblages) for each month was set to 60, and was reduced following the reductions of inter-cluster distance within each monthly dendrogram. Assemblage success was evaluated using the Class Probability Tool in ArcGIS. If assemblages were successful, measured here in terms of distinctness, pixels had the highest probabilities of membership to the assemblage to which they were assigned during the unsupervised classification. A non-metric Multi-Dimensional Scaling ordination (nMDS) of the mean monthly habitat suitability of species within each monthly assemblage was also performed to examine the relative distinctness of assemblages within and between months (Clarke & Ainsworth, 1993). Assemblage suitability was defined as the average of monthly habitat suitability calculated across all species for a given month. Assemblage suitability served as an added measure of variation in assemblage-level habitat quality across species, in recognition that the species assemblages might contain internal heterogeneity in habitat suitability due to natural stochasticity in the environment.

Spatial management evaluation

A gap analysis was performed to evaluate the ability of the Mid-Atlantic's current spatial management scheme to meet a notional conservation objective for the representative and adequate protection of the surrogate (Figure 1). This objective is notional in that it is a starting point for discussion: concrete objectives for the Mid-Atlantic should ideally be informed by both ecological and social implications (e.g. Klein et al., 2013). For the purposes of this study, the following objective was evaluated: for each month, protect at least 10% of each assemblage, and at least 10% of pixels with above average assemblage suitability (following the Convention on Biological Diversity's recommendation; see CBD (2010)). This objective aimed to represent the portions of each assemblage that are most suitable for all associated species within reserves (e.g. Klein et al., 2013). Because the Mid-Atlantic currently does not contain a reserve network, the objective was evaluated across the most strictly protected areas: federal MPAs that restrict recreational and commercial fishing, and DeFacto MPAs (i.e. MPAs that were established for reasons other than conservation) that restrict all types of activities (Figure 2). These types of MPAs already represent the greatest opportunity costs to extractive users within the study area, and although new management plans might be necessary to coordinate protection, political and industry support will be more readily available for rezoning pre-existing MPAs than for proclaiming new ones.

The decision support tool Marxan (Ball, Possingham, & Watts, 2009) was used to identify priority conservation areas that will be important to protect in order to

accommodate the full suite of species seasonal movement pathways. Marxan is a systematic conservation planning software that identifies near-optimal reserve design solutions that meet biodiversity objectives while minimizing reserve cost and complexity. The simulated annealing algorithm followed by iterative improvement was used to find spatial solutions that met the objective for the protection of species seasonal movement pathways. The 0.011° grid of the environmental variables was used as planning units, and area was used as a cost metric. Based on the result of a sensitivity analysis of the trade-off between reserve boundary length and total area (Stewart & Possingham, 2005), a boundary length modifier of one was used. Marxan was run 100 times, with each run consisting of 10^7 iterations. Selection frequency, i.e. the number of times across all runs that each planning unit was selected in solutions, was used to identify priority conservation areas.

RESULTS

Habitat suitability models

AUCs for modelled species ranged from 0.49 in blue runner (*Caranx cyrsos*) to 0.99 in alligatorfish (*Aspidophoroides monopterygius*), although the majority of species produced high performing models (mean = 0.95, standard deviation= 0.06; Table S1). Two species had AUCs below the accepted threshold of 0.70 (*Caranx cyrsos* and

Lagodon rhomboides) and were subsequently removed, leaving 171 species for further analysis.

Surrogate Definition

Three dominant seasonal movement pathways emerged when examining the variation in habitat suitability across months for each species (Figure 3). The majority of species carried out either 'along-shelf' (55.5%) or 'across-shelf' (13.5%) movements. Species undertaking 'along-shelf' movements travelled seasonally between northern and southern locations, e.g. striped bass (*Morone saxatilis*; Figure 3A) and sandbar shark (*Carcharhinus plumbeus*; Figure S1). Species undertaking 'across-shelf' movements travelled seasonally between inshore and shelf-break locations, e.g. summer flounder (*Paralichthys dentatus*; Figure 3B). The remaining species (31%) exhibited restricted seasonal movements, e.g. sea scallop (*Placopecten magellanicus*; Figure 3C).

Eighty-five spatially discrete monthly species assemblages were identified within the Mid-Atlantic, ranging from five to eleven assemblages in each month (Figure 4, Table S2). Assemblages were generally oriented north-south along the shelf, and in all months except June there were disruptions to this orientation at the Hudson Shelf Valley. Across the shelf, there were distinct bands of inshore, midshelf and shelf-break assemblages in all months. Pixels had high probabilities of membership (> 83%) to their

assigned assemblage, indicating distinct species assemblages that were successfully defined by the cluster analysis (Table S3). Visual assessment of non-metric multidimensional scaling ordinations further demonstrated the distinctness of species assemblages both within- and between-months (e.g. Figure 5). Within each species assemblage, suitability varied internally, indicating areas of greater or lesser habitat quality across species (Figure 4; Figure S2).

Examination of the relative proportions of suitable habitat for each species within assemblages across months revealed how the surrogate preserved the dominant seasonal movement pathways (Figure 6). For example, the highest proportions of suitable habitat for striped bass were located in the inshore-north assemblage in September and in the southern assemblage in March, preserving this species 'along-shelf' movement pathway.

Spatial management evaluation

The strictest MPAs and Defacto MPAs in the Mid-Atlantic did not meet the objective for representative and adequate surrogate protection (i.e. for each month, protect at least 10% of each assemblage, and at least 10% of pixels with above average assemblage suitability). In no month was 10% of each assemblage protected (Table 2). However, in each month, over 30% of pixels with above average assemblage suitability were protected, exceeding the 10% target. The objective was met in all Marxan runs.

The reserve network solutions varied greatly between each run, with only 0.10% of planning units selected in more than 50 solutions (Figure 7). Generally, the planning units selected most frequently (e.g. in > 30 runs) were in patches distributed across northern, central and southern portions of the Mid-Atlantic at varied distances from shore (e.g. located inshore, and over the midshelf and shelf-break).

DISCUSSION

Marine reserve networks are unlikely to be effective at preventing biodiversity loss unless they maintain the key processes that dictate fluctuations in patterns of biodiversity. Dynamic processes cannot be incorporated into reserve networks without temporally explicit surrogates that preserve how processes vary and affect biodiversity through time. Surrogates for species seasonal movements remain a major gap in the conservation planning literature due to the challenges associated with mapping species habitat use through space and time (Game et al., 2009; Grantham et al., 2011; Green et al., 2015; Runge et al., 2014). However, this study seeks to fill this gap by presenting an assemblage-level surrogate strategy that allows planners to visualize and protect the full suite of seasonal movement pathways that occur within a given region. Because the surrogate is temporally explicit, it effectively preserves how species move and reassemble over the full annual cycle (Figure 3, Figure 6). The surrogate strategy combined two monthly assemblage-level attributes: species assemblages and

assemblage suitability (Figure 4, Figure S2), allowing planners to represent the portions of each assemblage that are most suitable for all associated species within reserve networks. Below, the broader applicability and implications of the surrogate strategy are discussed.

Seasonal movement pathways

The surrogate strategy is exclusively based on habitat suitability models (Figure 1). It is therefore critically important to evaluate models to ensure they contain useful information. The generally high AUC values indicate that the models are well fit for the Mid-Atlantic (Table S1). Empirical evidence from the literature (Callihan, Harris, & Hightower, 2015; Green et al., 2015; Moser & Shepherd, 2009) suggests that the dominant movement pathways captured by the surrogate are well-characterized in both the Mid-Atlantic and at other geographic locations, corroborating the ability of the surrogate strategy to represent real-world conditions. The pervasiveness of the pathways across varied taxa indicates that persistence of this widespread process will be important for effective conservation planning around the world.

'Along-shelf' movement pathways between northern and southern locations were most commonly captured by the surrogate (e.g. Figure 3A, Figure 6) and are well-documented in the literature (e.g. Callihan et al., 2015; Shepherd, Moser, Deuel, & Carlsen, 2006). This pathway is often associated with highly mobile species that are

energetically capable of travelling long distances (Anderson, Gurarie, Bracis, Burke, & Laidre, 2013; Chapman, Feldheim, Papastamatiou, & Hueter, 2015; Sousa, Queiroz, Mucientes, Humphries, & Sims, 2016). Globally, this pathway is most often coupled with the timing and latitudinal progression of seasonal environmental processes (e.g. changes in temperature, daylight, and productivity), as species shift to remain within thermal preferences (e.g. Sousa et al., 2016), to target seasonally-driven resources at higher latitudes (e.g. Hobday & Hartmann, 2006), or to reproduce in distant natal spawning grounds (Rose, 2005; Ramenofsky & Wingfield, 2007). 'Across-shelf' shelf movement pathways between inshore and shelf-break locations were also commonly captured by the surrogate (e.g. Figure 3B, Figure 6) and supported by the literature (e.g. Henderson, Fabrizio, & Lucy, 2014; Manderson, Palamara, Kohut, & Oliver, 2011; Moser & Shepherd, 2009). This pathway usually relates to the dynamics of environmental processes operating within and between coastal and shelf-break environments, i.e. the seasonal fluctuations of temperature, salinity, and water movement (Allen et al., 1983; Gabriel, 1992; Zhang & Gawarkiewicz, 2015), which drive species to move seasonally between environmentally regulated offshore winter spawning grounds and productive inshore summer foraging grounds (Block et al., 2011; Hunter, Metcalfe, Arnold & Reynolds, 2004; Loher, 2008). The remaining species captured by the surrogate had restricted movements (e.g. Figure 3C, Figure 6), exhibiting marginal shifts in distribution across months. This pathway is often associated

with species with either well-met habitat preferences, limited mobility capabilities, or smaller body sizes that make it energetically costly to move longer distances (Green et al., 2015; Kaiser et al., 2011).

Spatial prioritization of surrogates

Conservation objectives can help combat economic incentives to place reserves in areas that have little value to extractive users (Devillers et al., 2014). Over 30% of pixels with above average assemblage suitability were protected in each month, indicating that current management in the Mid-Atlantic protects waters that are highly suitable for associated species. However, only 36 out of 85 assemblages had 10% or more protection. This poor representation means that over half of the assemblages are currently left almost entirely exposed to extractive activities. This gap in protection indicates that the strictest MPAs and DeFacto MPAs currently in place are unable to meet even modest objectives for representative and adequate protection (i.e. the World Parks Congress recommended a 30% baseline target for representation of features within no-take areas to create a fully sustainable ocean; Wenzel, Laffoley, Caillaud, & Zuccarino-Crowe 2016; WPC 2014).

The gap analysis was applied to the strictest MPAs and DeFacto MPAs within the study area because there is currently no coordinated reserve network to evaluate. Therefore, there is an immediate need to consider a system of reserves for the Mid-

Atlantic region, especially given current plans for offshore wind, oil and gas developments (BOEM, 2015a, b). To meet objectives for species seasonal movements, protection will need to be coordinated across additional pre-existing protected areas, or new protected areas will need to be proclaimed. The Marxan solutions suggest that new protected areas will need to reflect the along- and across-shelf orientation of the assemblages, but the generally low selection frequency across runs indicates there is a high degree of spatial flexibility in their placement (Figure 7). This is desirable, because many additional factors need to be considered during reserve design, e.g. other key processes, special biodiversity areas that are important for species persistence (e.g. foraging areas; Lombard et al., 2007), the opportunity costs to extractive users (Ban & Klein, 2009); and connectivity between protected areas (e.g. Williams et al., 2005). However, setting conservation objectives based the representation of species assemblages and assemblage suitability could offer a starting point for considering new management schemes, providing two measures of confidence that assemblages are indeed present and highly suited to an area.

Future directions

Further work is needed to set meaningful objectives – a 10% representation target is essentially arbitrary. One solution is to augment objectives from a baseline percentage to reflect the level of protection required by each assemblage, for example

based on the irreplaceability and vulnerability of associated species (Pressey & Taffs, 2001), the function of each assemblage (Guillemot, Kulbicki, Chabanet, & Vigliola, 2011; Paterson & Whitfield, 2000), or the disturbance risk of each assemblage (Allison, Gaines, Lubchenco, & Possingham, 2003). However, area representation does not guarantee benefits to biodiversity. An ecosystem with extensive reserve coverage might still experience net biodiversity loss due to external threats, e.g. extractive activities or environmental stressors occurring beyond reserve boundaries. Biodiversity loss could be prevented more directly by setting objectives that limit how much threat or reduction in abundance can occur in each assemblage (Pressey, Visconti, & Ferraro, 2015). Additional information will be necessary to set these types of objectives, for example data on the spatial and temporal dimensions of threats, and adapted methods to integrate the surrogate and spatially-explicit stock models to predict future trends in abundance (e.g. Rassweiler, Costello, & Siegel, 2012). However, both of these types of objectives move reserve design beyond focusing on coverage, i.e. how much and what to protect, to focusing on outcome, i.e. how much biodiversity loss or threats to avoid.

Species do not recognize jurisdictional boundaries and for some, portions of their seasonal movement pathway will be outside the Mid-Atlantic, such as species that migrate seasonally between the Gulf of Maine and Florida, e.g. striped bass and bluefish, or the Caribbean, e.g. leatherback turtles (James, Andrea Ottensmeyer, & Myers, 2005). Threats to these species outside the Mid-Atlantic could compromise the

entire population (Martin et al., 2007), making a reserve network in the Mid-Atlantic ineffectual. Planning for species with large-scale seasonal movements will require management to be coordinated on both national and international scales. Although few examples of internationally coordinated management exist (Ardron, Gjerde, Pullen, & Tilot, 2008), the United States, Canada and Mexico already have a framework in place for developing a trinational network of reserves (NAMPAN, 2011), making these countries well-positioned to manage the large-scale movements of North American species.

Conservation planning concerns itself with future ecosystem state, and therefore reserve designs should be robust to both short-term climate variability and long-term climate change. The two assemblage-level surrogates were calculated across a time-series from 2003-2015, and therefore capture historical and contemporary variation in species seasonal movement pathways. The surrogates also provide some indication of variation in the near future, because variation in the near future is related to variation in the recent past (Ban et al., 2012). Ideally, however, reserve design would also incorporate long-term variation through the use of climate forecast models, e.g. GFDL CM 2.6 (Saba et al., 2016).

Wider applications

This surrogate strategy is widely applicable to the management of species seasonal movements anywhere in the world. It can be applied to direct the zonation of proposed reserve networks through conservation objectives, or to assess the ability of existing reserve networks to protect species over the full annual cycle by way of gap analysis. Without explicitly considering species seasonal movement during reserve design, this important and prevalent process is unlikely to be maintained by happenstance (e.g. Powell, Barborak, & Rodriguez, 2000), leading to biodiversity loss and changes in ecosystem function. The environmental variables used in this study are publicly available and predominantly global in extent, making them relevant to users in different locations and job sectors. The limiting factor of this strategy is the species records. The Northeast Fisheries Science Center's Bottom Trawl Survey is unparalleled in its utility: it is fisheries-independent, the sampling program was designed specifically for scientific analysis, and records are collected at a relatively fine spatial and temporal resolution. However, despite potential data limitations at other locations, there are ways forward. Maxent was designed for presence-only datasets which are more prevalent than presence-absence or abundance datasets; these relaxed data requirements increase the applicability of this surrogate strategy to data-poor regions. The Ocean Biogeographic Information System (<http://www.iobis.org/>) contains public, presence-only datasets for a wide variety of marine species, and has been the primary data source for many publications (e.g. Cheung, Brodeur, Okey, & Pauly, 2015; Strona et al., 2015).

Additionally, fishery-dependent datasets can be used as model inputs (e.g. Alabia et al., 2015). High quality species datasets take considerable time and resources to acquire, and in some locations they will not be available in time for spatial management to prevent significant biodiversity loss. Therefore it is important to move forward with the best data available, and to not cite data limitations as an excuse to delay conservation action (Avery, 2003).

Conclusion

Currently, 10.2% of national waters and only 0.25% of international waters are covered by marine protected areas (UNEP-WCMC & IUCN, 2016). Calls for more ocean protection (CBD 2010; WPC 2014) will likely cause these percentages to increase rapidly in the near future. While this could be good news for marine biodiversity, poorly planned reserves could in actuality have negative impacts by providing ineffectual protection while using up limited conservation resources and support, making it harder to proclaim new reserves in the future (Pressey, 2013). One component of successful reserve design will be the incorporation of processes to ensure that the patterns of biodiversity they generate and maintain and the processes themselves are not disrupted (Pressey et al., 2007). With the increased prevalence and longevity of remote sensing and species datasets, the tools are now available to do so, but a paradigm shift at the planning level is required. Moving from planning for pattern to planning for process will

require updated approaches to reserve design. Many processes have spatial extents that span multiple planning regions and Exclusive Economic Zones (e.g. Polovina et al., 2004; Welch, Pressey, Heron, Ceccarelli, & Hobday, 2015), and planning for these large-scale processes will require coordination between national and international management bodies. Static reserves designed to accommodate patterns might need to be replaced with temporally explicit designs to accommodate dynamic processes, e.g. seasonal reserves or real-time management (Hobday & Hartman, 2006). These approaches will be challenging to implement, yet necessary. We live in a fundamentally dynamic world and it is important that our approach to conservation planning reflects it.

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Supporting Information – short captions

Figure S1. Monthly habitat suitability layers for sandbar shark (*Carcharhinus plumbeus*).

Figure S2. The continuous values of assemblage suitability for each month.

Table S1. List of the 173 marine species used for habitat suitability modeling and their model AUC values.

Table S2. Results of the monthly principal component and cluster analyses.

Table S3. Results of the class probability analysis of cluster (assemblage) success.

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Tables

Table 1. Environmental variables used for the habitat suitability models. Three different categories of variables were used: static variables that are stationary in time/space; real-time variables that fluctuate on daily time scales; and monthly climatologic variables that are long-term monthly averages and standard deviations. SD, standard deviation; m, meters; PSU, Practical Salinity Unit; C, Celsius; m/s, meters/second; mg/m³, milligrams/cubic meter; CRM, Coastal Relief Model; HYCOM, Hybrid Coordinate Ocean Model; MODIS, Moderate Resolution Imaging Spectroradiometer; GHRSSST, The Group for High Resolution Sea Surface Temperature; BTM, Benthic Terrain Modeler: <http://coast.noaa.gov/digitalcoast/tools/btm>; NGDC, National Geophysical Data Center, <https://www.ngdc.noaa.gov/>; USGS, U.S. Geologic Survey, <http://walrus.wr.usgs.gov/usseabed/data.html>; MGET, Marine Geospatial Ecology Tools (Roberts *et al.*, 2010).

	Variable	Depth			Units	Source	Access	Usage	
		Surface	10m	Bottom				Model-building	Projection
Static (n=6)	Rugosity			x	m	CRM	BTM	x	x
	Bathymetry			x	m	CRM	NGDC	x	x
	Slope			x	Degree	CRM	BTM	x	x
	Gravel			x	%	usSEABED	USGS	x	x
	Mud			x	%	usSEABED	USGS	x	x
	Sand			x	%	usSEABED	USGS	x	x
Real-time (n=15)	Salinity	x	x	x	PSU	HYCOM	MGET	x	
	Temperature	x	x	x	C	HYCOM	MGET	x	
	Eastward water velocity	x	x	x	m/s	HYCOM	MGET	x	
	Northward water velocity	x	x	x	m/s	HYCOM	MGET	x	
	Chlorophyll a	x			mg/m ³	MODIS Aqua	MGET	x	
	Nighttime temperature	x			C	MODIS Aqua	MGET	x	
	Foundation temperature	x			C	GHRSSST	MGET	x	
Monthly Climatologic (n=30)	Mean salinity	x	x	x	PSU	HYCOM	MGET		x
	SD salinity	x	x	x	PSU	HYCOM	MGET	x	x
	Mean temperature	x	x	x	C	HYCOM	MGET		x
	SD temperature	x	x	x	C	HYCOM	MGET	x	x
	Mean eastward velocity	x	x	x	m/s	HYCOM	MGET		x

SD eastward velocity	x	x	x	m/s	HYCOM	MGET	x	x
Mean northward velocity	x	x	x	m/s	HYCOM	MGET		x
SD northward velocity	x	x	x	m/s	HYCOM	MGET	x	x
Mean chlorophyll a	x			mg/m-3	MODIS Aqua	MGET		x
SD chlorophyll a	x			mg/m-3	MODIS Aqua	MGET	x	x
Mean foundation temperature	x			C	GHRSSST	MGET		x
SD foundation temperature	x			C	GHRSSST	MGET	x	x
Mean nighttime temperature	x			C	MODIS Aqua	MGET		x
SD nighttime temperature	x			C	MODIS Aqua	MGET	x	x

Table 2. Evaluating the ability of the strictest marine protected areas (MPAs) and DeFacto MPAs in the Mid-Atlantic to accommodate species seasonal movements. One quantitative objective was evaluated: for each month, protect at least 10% of each assemblage, and at least 10% of pixels with above average assemblage suitability. The Mid-Atlantic's current management scheme did not meet the objective: only 36/85 assemblages had 10% or more protection (column A), although over 30% of pixels with above average assemblage suitability were protected in each month (column B).

	A. No. of assemblages with $\geq 10\%$ protection / total no. of assemblages	B. Percent of pixels protected with above average assemblage suitability
January	2 / 6	31.9%
February	2 / 7	33.0%
March	2 / 5	35.3%
April	4 / 7	33.3%
May	6 / 11	37.2%
June	5 / 7	38.2%
July	3 / 6	40.6%
August	4 / 7	39.5%
September	5 / 6	42.9%
October	3 / 5	39.4%
November	5 / 9	39.0%
December	4 / 9	33.8%

Figure captions

Figure 1. Flowchart of analysis. Broadly, the methodology consists of three stages: model building, surrogate definition, and spatial management evaluation. Grey shaded polygons indicate analyses and white-shaded polygons indicate products.

Figure 2. The study area – hereafter, the Mid-Atlantic (blue polygon), consists of waters between 42 and 35N, and between -76 and -69W (red bounding box) that are further than one kilometer from shore and within a minimum bounding polygon around the species records. The 450m contour (yellow line) forms the eastern boundary. Within the Mid-Atlantic, there are four marine protected areas (MPAs) under federal jurisdiction that restrict commercial and recreational fishing (green polygons); from north to south: the Great South Channel Sliver Restricted Area, the Nantucket Lightship Closed Area, the Carl N. Shuster, Jr. Horseshoe Crab Reserve, and in the south, a flynet closure; and several DeFacto MPAs that restrict all activities (yellow polygons). Together, these MPAs represent the strictest management within the Mid-Atlantic. A full list of MPAs and DeFacto MPAs are available respectively at: <http://marineprotectedareas.noaa.gov/dataanalysis/mpainventory/> and <http://marineprotectedareas.noaa.gov/dataanalysis/defacto/>.

Figure 3. The three dominant seasonal movement pathways (A-C) demonstrated across the monthly habitat suitability layers of three example species.

Figure 4. A temporally explicit surrogate strategy for species seasonal movements. The surrogate consists of discrete species assemblages (n=85) and continuous assemblage suitability in each month. Assemblages are numbered across months in reference to their 'along-shelf' and 'across-shelf' geographical positions. Northern (1-3) and southern (5-7) assemblages break to the north and south of the Hudson Shelf Valley (Figure 2), respectively; while midshelf, inshore and shelf-break assemblages (4, 8, 9) extend across the Hudson Shelf Valley. Assemblages that did not fit within the above geographic categories were numbered 10 (e.g. October 10 spans both north and shelf-break positions). When multiple assemblages in a given month occupy the same geographic position (e.g. the three midshelf-south assemblages in December), decimal places are used to indicate their sequence from shore (e.g.

December 7 is the midshelf-south assemblage closest to shore, December 7.2 is the midshelf-south assemblage furthest from shore).

Figure 5. Non-metric multidimensional scaling ordination of species assemblages for September (S; squares) and March (M; circles). Plot demonstrates the Bray-Curtis dissimilarity of species assemblages (in terms of species mean habitat suitability) within- and between-months. A stress value of 0.02 indicates a good representation in reduced dimensions. Numbers and colors of assemblages are consistent with Figure 4.

Figure 6. Relative proportions of suitable habitat for nine commercially important species across assemblages in September and March. Species seasonal movement pathways were preserved across assemblages, indicating that information on individual species is not lost by moving to a assemblage-level surrogate. Icons for a given species are assigned at 20% increments and calculated across assemblages within the same month. Assemblages are referenced by their numbers and geographic positions as defined in Figure 4.

Figure 7. Priority conservation areas for designing a reserve network that accommodates species seasonal movements. Selection frequency, i.e. the number of times across Marxan runs ($n=100$) that each planning unit (PU) was selected in solutions, indicates the relative protection priority of PUs for meeting the conservation objective (i.e. for each month, protect at least 10% of each assemblage, and at least 10% of pixels with above average assemblage suitability). The generally low selection frequency (99.9% of PUs were selected in $\leq 50\%$ of solutions) suggests a high degree of spatial flexibility in reserve design.

Supporting Information – full captions

Figure S1. Monthly habitat suitability layers for sandbar shark (*Carcharhinus plumbeus*), demonstrating an example of an 'along-shelf' seasonal movement pathway.

Figure S2. Continuous monthly values of assemblage suitability, defined as the average of habitat suitability across all species in a given month. Assemblage suitability provides a measure of confidence that an assemblage is present within a given area, in recognition that the discrete species assemblages will contain internal heterogeneity in habitat suitability across species due to the natural stochasticity of the environment.

Table S1. List of 173 marine species used for habitat suitability modeling. Records were collected by the Northeast Fisheries Science Center's Bottom Trawl Survey between 2003 and 2015, and include species from four broad categories of habitat preference: pelagic ($n=18$) – species that primarily inhabit the water column; benthic pelagic ($n=13$) – species that live partly near the seabed and partly within the water-column; demersal ($n=122$) – species that live primarily near the seabed; and epibenthic ($n=20$) – species that live on the seabed. Species that had models with areas under the receiver operator characteristic curve (AUCs) of less than 0.70 were removed from further analyses (denoted “**”, $n=2$).

Table S2. Monthly principal components and cluster analyses. For each month, the table shows the number of principal components (PCs) identified by the scree-plot, the percent of monthly variance in the habitat suitability distribution explained by the principal components, and the final number of clusters (i.e. assemblages).

Table S3. Class probability analysis of cluster success. Values indicate the spatial average of probability of membership calculated across pixels assigned to each cluster, +/- one spatial standard deviation. High average probabilities of membership indicate distinct clusters.

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