Title: **Ocean planning for species on the move provides substantial benefits and requires few tradeoffs**

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Teaser: Proactively preparing for climate change produces more effective ocean plans and imposes few tradeoffs.

Abstract:

Societies increasingly use multi-sector ocean planning as a tool to mitigate conflicts over space in the sea, but such plans can be highly sensitive to species redistribution driven by climate change or other factors. A key uncertainty is whether planning ahead for future species redistributions imposes high opportunity costs and sharp tradeoffs against current ocean plans. Here, we use more than 10,000 projections for marine animals around North America to test the impact of climate-driven species redistributions on the ability of ocean plans to meet their goals. We show that planning for redistributions can substantially reduce exposure to risks from climate change with little additional area set aside and with few tradeoffs against current ocean plan effectiveness. Networks of management areas are a key strategy. While climate change will severely disrupt many human activities, we find a strong benefit to proactively planning for long-term ocean change.

Introduction

The coastal ocean is a crowded landscape that supports diverse and expanding human uses, from fishing and recreation to energy development, transportation, aquaculture, and conservation (1–3). Governance that historically focused on individual activities or species has often allowed substantial and negative cumulative impacts on ocean ecosystems, including the decline of coral reefs and the collapse of both fishery and non-fishery species (1, 4, 5). In addition, many ocean and coastal uses impact and conflict with each other, such as scenic views and wind turbines or conservation and fishing (2, 6). As a result, ecosystem-based management (EBM) efforts to coordinate among marine activities have become common, often expressed as coastal and marine spatial planning (CMSP) or ocean planning (1, 2, 4, 7).

Ecological principles for ocean planning are built upon the spatial distribution of species, habitats, and ecological communities (8, 9). Even though species and biogenic habitats are rapidly shifting geographically as climate changes (10) and despite calls for greater consideration of these climate change impacts (7, 11), species redistributions are not a central consideration in the current principles, legal frameworks, or examples of ocean planning (7, 11, 12). A major impediment has been uncertainty about the difficulty of and tradeoffs required for incorporating long-term change into multi-sector ocean plans (3, 12).

Periodic revisions of ocean plans could enable climate adaptation over time, though revisions are challenging given the substantial negotiations among stakeholders inherent to ocean planning and the long-term legal agreements and impacts involved in offshore energy, mineral extraction, and other development or habitat-modifying activities (13). Alternatively, ocean plans could be designed around climate change impacts from the start (14), but the extent to which advance planning across multiple sectors can help in this regard remains unclear. One proposal in the context of conservation alone has been to identify areas that are likely to be consistently important through time (15). Even more importantly, it is unknown whether planning for the future requires setting aside substantially more area for ocean plans, or if there are strong tradeoffs between plans that are effective in the near-term versus those that are effective in the long-term. One heuristic approach for climate adaptation may be to designate networks of management areas that could act like stepping-stones as species shift (14). The extent to which networks can help in this regard, however, has not been quantified.

In this paper, we use nine regions on the continental shelves of North America (Fig. 1) to study these issues. Ocean planning efforts have occurred and are underway to varying degrees across this geography (6). We simulated the multi-sector ocean planning process to site zones for conservation, fishing, or energy development within each region. Inspired by the Convention on Biological Diversity's (CBD) Aichi Target 11, we designed conservation zones to protect at least 10% of the locations with occurrences of each species in a region. In contrast, we designed fishery zones to include locations that had, in sum, at least 50% of the biomass of each of the top ten fishery species in each region. Energy zones included at least 20% of the value from wind and wave energy resources, consistent with the ~20% of offshore energy potential proposed to be captured as part of a roadmap to 100% clean energy (16, 17).

Results and Discussion

We first developed myopic “present-only” plans that only considered species current geographic distributions for evaluating whether conservation and fishery zones met their goals through time. We then evaluated these plans against 11,776 projections of future species habitat distributions: 736 species across eight climate models following a low (RCP2.6) and a high (RCP8.5) greenhouse gas emissions scenario. This evaluation revealed substantial declines in effectiveness of the present-only plans that implied difficulty meeting societal targets for fishing and conservation (Fig. 2). By the middle of the 21st century (2041-2060), an average of 63% ± 16% (± 1 SD across climate models and scenarios) of goals were met (Fig. 2). Only 50% ± 18% of goals were met on average by the end of this century (2081-2100) under a high greenhouse gas emissions scenario (64% ± 16% under a low emissions scenario). Plans were especially sensitive to species habitat redistribution in the Eastern Bering Sea, Northeast U.S., and the Canadian Maritimes (Fig. 2), where plans met less than half of the goals by the end of this century.

We contrasted these results with a “proactive” approach that explicitly planned for future species redistributions. The plans were developed to meet the conservation, fishing, and energy goals both under current species habitat distributions and under future habitat distributions (see Methods). The species projections that were used for planning were not used for plan evaluation. Compared to present-only plans, proactive plans were substantially different and changed the zone designation for 22% ± 7% of the area across the nine regions (Fig. 3). However, proactive solutions included only marginally more area (0-7% more per region, mean 2% ± 0.07% standard error) in conservation, fishing, or energy zones than did present-only plans (Fig. 3). Ocean plans that require less area also leave more space (more opportunities) available for other ocean uses, both including and beyond the three activities we considered. The small increase in area required for the proactive plans implies that there was relatively little opportunity cost of planning for the future. In contrast, some ocean plans have high opportunity costs. An inefficient designation of marine conservation areas in South Australia, for example, has been described as an opportunity cost that may impede the expansion of marine conservation (18).

We then evaluated the proactive plans under 16 sets of redistribution projections (eight climate models across two emissions scenarios) that had not been used in planning. Despite this constraint, the plans met 75% ± 15% (± 1 SD) of goals by the middle of the century (Fig. 2). Under a high greenhouse gas emissions scenario, the plans met 64% ± 19% of goals by the end of the century, or 76% ± 14% under low emissions scenario (Fig. 2). This was significantly more goals met than the present-only plans (odds ratio 1.9 [95% confidence interval 1.86 - 1.97], $p = 2 \times 10^{-16}$, $n = 1440$, generalized linear mixed-effects model with binomial errors). Some conservation and fishing goals could not be met by the end of this century even with careful planning because species were expected to be extirpated from a region by then. Proactive plans, however, were also relatively robust to uncertainty in species redistributions across emissions scenarios and global climate models. With a proactive plan, we found a 42% chance of not meeting at least seven in every ten planning goals by the end of the 21st century across regions. In contrast, present-only plans had a 72% chance of not meeting at least seven in every ten planning goals by the end of this century.

Many of the benefits of proactive planning as compared to present-only plans appeared well before the end of this century (Fig. 2), consistent with substantial spread in species distribution projections under different global climate models in all time windows (19). Planning for long-term species redistribution therefore appears to have the added benefit of hedging against near-term uncertainty.

To more explicitly examine tradeoffs, we plotted tradeoff curves (6, 20) for ocean plans in terms of their ability to meet conservation (10% of all species' occurrences) and fishing (50% of fishery species biomass) goals in the present time vs. goals at the end of the century. Tradeoff curves, also called constraint envelopes or Pareto efficiency frontiers, are visualization tools from microeconomics that represent the maximum extent to which one goal can be met for a given value of another goal, and vice versa, subject to constraints like a limited budget (20). The shape of the curve indicates the type of tradeoff between two goals, which in our case are goals for the present and for the future (Fig. 4). A plan that designates larger conservation and fishing zones in effect costs more because it restricts ocean uses across a wider area, so we defined the budget in terms of the total area used for the ocean plan. For plotting the tradeoff curves, we then limited the plans to only use 75% of the total area that would have been needed to meet all of the ocean plan goals. The curves revealed little to no tradeoff between present and future (Fig. 4). In four regions (Gulf of Alaska, West Coast U.S., Maritimes, and Newfoundland), right-angle lines on the curves indicated that present and future goals did not interact (no tradeoff) and that plans could maximize both future and present goals at the same time. In the other five regions, small angled corners indicated a minimal tradeoff among future and present goals. The largest tradeoff was in the Northeast U.S., where 9% more future goals could be met in exchange for a 9% decrease in present goals met, or vice versa (Fig. 4). Tradeoff curves for plans with areas limited to 50% or 90% of the area needed to meet all goals revealed similarly small tradeoffs (Fig. S1).

We also examined the benefits of heuristic planning approaches such as designing management zones in spatial networks, a concept that has been applied to date through networks of protected areas (4, 14). We found that existing marine spatial management areas are expected to experience substantial change in species composition by the end of this century, including the extirpation of 29% ± 7% of existing species and overall 84% ± 2% species dissimilarity (Fig. 5) under a high greenhouse gas emissions scenario (RCP8.5). However, networks of management zones were expected to experience half the loss of species (16% ± 4%) and substantially less species turnover (11% ± 3% dissimilarity), as compared to individual management areas under the RCP8.5 scenario (Fig. 5, $p = 2 \times 10^{-16}$, paired Mann-Whitney U test, $n = 32$). Each network spanned a range of temperatures, and species often shifted within rather than into or out of a network. Simulated networks revealed that network size and thermal range were both important for minimizing turnover (Fig. S2). While corridors are central to conservation on land, stepping-stones of MPAs are important in the ocean because many species disperse as larvae in the water column.

While the reduction of local stressors can delay extirpation of local populations, such measures cannot maintain populations pushed far beyond their thermal tolerances. Instead, updating local conservation and management goals to adapt to change will often be necessary. Our results suggest that explicit consideration of future species distributions, even in static ocean plan designs, can be an effective approach to adapt to shifting species. In particular, our finding that proactive plans require little additional designated area suggests that proactive planning need not involve substantial tradeoffs for other ocean users or substantial opportunity costs in terms of additional ocean plan areas, thereby lowering potential barriers to implementation. An additional benefit of planning for long-term shifts in species distributions is that such plans may also be helpful for coping with seasonal, annual, and decadal shifts (21).

Our study tests the value of proactive planning from a biophysical perspective, but does not represent all relevant steps or considerations for ocean planning, including stakeholder interactions or adaptive management to learn from experience, to address non-climate-driven changes in ocean biodiversity, or to address changing societal goals, technologies, and ocean uses (2, 13). Our evaluation also considers only three of the many (and growing) human ocean activities (22), though we note that the value of ocean planning often increases as more activities are considered (6). Even with proactive planning, ecological and social surprises are inevitable and will require resilient and adaptive systems informed by ongoing monitoring, evaluation, and anticipation (13, 23, 24). For example, changes in ship traffic, water quality, habitat availability, population abundance, and other factors will also alter species ranges in the future, in addition to climate change impacts. Some of these may be predictable in a way that allows proactive planning similar to what we demonstrate for climate, while others will be surprises for which adaptive management, such as through dynamic ocean management, is the best or only realistic approach. We also note that the species habitat distribution projections that we used capture the major changes in biogeographic patterns that are expected in each region and exhibit good out-of-sample predictive skill (19), but do not reflect evolutionary processes, acclimation, or potential changes in species interactions that may cause species to occupy new thermal conditions or disappear from previously occupied conditions. The projections also do not consider changes in salinity, oxygen, acidification, or primary productivity that may further contract and fragment species geographic ranges (25). Global climate models do not resolve fine-scale oceanographic features that may be important for modulating oceanographic changes in some regions, particularly upwelling regions like the west coast of the U.S. (26). However, ensembles of global climate models help to bracket uncertainty in regional climate responses (26).

The ocean is changing rapidly, and warming is expected to continue (27). Climate change mitigation can substantially reduce the impact on ocean ecosystems and human activities, including the probability and magnitude of undesirable outcomes (27). However, major questions also surround how to adapt human activities—from coastal infrastructure to shipping, aquaculture, conservation, fisheries, and other uses—to expected changes over the coming decades. Resistance to proactive adaptation, however, can become the default when the benefits and costs are unclear. Our demonstration that ocean plans are more effective and can require few tradeoffs among ocean activities when they consider shifting species distributions is a timely contribution to ongoing adaptation efforts and the transition towards ecosystem-based management. While complete climate-proofing is impossible, proactively planning for long-term ocean change across a wide range of sectors is likely to provide substantial benefits.

Materials and Methods:

Our overall approach was to simulate the ocean planning process for conservation, fishery, and offshore energy goals, then evaluate these goals against future shifts in species habitat distributions. We conducted planning that only considered species' current distributions ("present-only") and planning that considered species current and future distributions ("proactive"). The sections below describe the input data (*Resource distribution data*), the planning and evaluation process (*Marine spatial planning*), and a comparison of networks of spatial management zones against shifts in species distributions (*Analysis of management area networks*).

Resource distribution data

Marine spatial planning integrates across sectors, and so our methods are by necessity interdisciplinary. For simulating the marine spatial planning process, we used information on species distributions and on the distribution of wave and wind energy resources. Species habitat distributions were used for conservation goals (species presence or absence) and for fisheries goals (species biomass), while wave and energy spatial distributions were used for energy goals.

Species habitat distributions

For species habitat distributions, we used an existing set of distribution projections for fish and invertebrates on the continental shelves of North America (19). The species habitat distribution models had been fit to species biomass data from 136,044 sampling events 1963-2015 during scientific surveys in Canada and the U.S. by considering seasonal bottom and surface temperatures, annual minimum and maximum temperatures, seafloor rugosity, and sediment grain size. Model selection procedures had been used to trim the number of explanatory variables used for each species. The models consisted of two parts: a first part that projected probability of species occurrence and a second part that projected species biomass conditional on presence. The product of the two parts provided projections of biomass (19).

The species distribution models had been projected at a grid size of 0.05 °longitude x 0.05 °latitude under a low and a high greenhouse gas emissions scenario (Representative Concentration Pathway RCP 2.6 and RCP 8.5) using ocean temperature projections from sixteen global climate models (19). We randomly selected eight of the climate models, averaged them into ensemble means for present (2007-2020, both RCP2.6 and RCP8.5) and end-of-century (2081-2100, only RCP8.5) time periods, and used the ensemble means for ocean planning (Table S1). We set aside projections under the other eight climate models across each of two RCPs for evaluating the ocean plans (Table S1).

To match the spatial scale of the projections to the 0.25 ° ocean planning grid, we averaged probabilities of occurrence (for conservation goals) or biomass (for fishery goals). We then converted probability of occurrence into projections of species presence and absence by applying a species-specific threshold that maximized Cohen's kappa (28). Kappa measures the extent to which the agreement between observed and projected values is higher than expected by chance alone, considering both omission and commission errors (28).

Wave and wind energy

We used the InVEST 3.7.0 toolkit (29) to calculate the spatial distribution of offshore wind and wave power in each region. InVEST is a decision-support tool for ecosystem services that was developed for and is commonly used in marine spatial planning efforts (12, 29), including for wave and wind energy (30–32).

The InVEST Offshore Wind Energy Production tool estimates wind power density from data on wind statistics (a probability density of wind speeds) at each location, then uses wind turbine characteristics (hub height, cut-in wind speed, cut-out wind speed, rated power, rated wind speed, etc.) to calculate the harvestable energy (30) (Table S3). We used global wind statistics at 30 arc-minute spatial resolution that are distributed with InVEST. These statistics were calculated from a global WAVEWATCH III hindcast reanalysis of winds globally for 1999-2012 (30). We did not consider changes in energy resources over the 21st century because the anthropogenic climate change signal appears small relative to natural variability (33).

Harvestable energy was calculated for wind farms composed of 16 turbines of 5.0 MW each. While wind farm designs can vary greatly in size and design (31), we chose a standard design to ensure comparability across different locations (Table S3). A size of sixteen turbines was chosen to achieve a density of approximately two per km^2, following proposals of this magnitude in the U.S. (6). Turbines were sited in locations 0 to 200 km from shore and 3 to 60 m depth using the ETOPO1 depth dataset (34) and a high resolution global shoreline dataset (35). We used the default turbine design parameters distributed with InVEST for a 5.0 MW turbine. Finally, installation and maintenance costs as well as electricity prices were used to calculate the net present value (NPV) of offshore wind at each location, following (31). The default costs included in InVEST were based on a detailed review of stated project costs from existing offshore wind development (31). Energy prices were set at $0.161/kWh to match approximate wholesale energy prices in the U.S., as has been used for other wind energy planning calculations (6). Overall, the offshore wind tool outputs a raster map of NPV across the continental shelf. The absolute values of these calculations are not of interest, but rather the relative value of one location compared to another so that areas particularly valuable to energy production can be designated for such uses.

Similarly, the InVEST Wave Energy Production tool estimates potential wave power from data on significant wave height and peak wave period, then calculates harvested wave energy from information on the performance of wave energy conversion devices (32, 36). We used global wave statistics at 30 arc-minute spatial resolution that are also distributed with InVEST and that had been calculated from a global WAVEWATCH III reanalysis (36). We then calculated harvested energy from wave farms composed of 100 attenuator-type Pelamis wave energy conversion devices (36) (Table S3). These devices are in a relatively advanced stage of development (36), and so they provide a consistent method for comparing wave energy potential across different locations. The number of devices was based on recommended densities in the literature (32). The tool then calculates the NPV of a wave energy conversion facility using information on the price of electricity, discount rate, and costs that had been derived for a wave energy planning project on the West Coast of Vancouver Island (36). Because no commercial-scale wave energy projects currently exist, the economic parameters are uncertain (32, 36). However, the calculations are useful for comparing the relative (not absolute) value of different ocean locations for wave energy capture, which is what we need for this ocean planning exercise.

Calculated NPV values for wind and wave energy were averaged separately within planning grid cells for incorporation into marine spatial planning. We then summed positive NPV values across wind and wave energy for a combined offshore energy NPV for each planning grid cell.

Marine spatial planning

Plan development

Marine spatial planning is a multi-stakeholder, multi-objective process by which areas of the ocean are designated for different uses. Here, we simulated that process by defining three types of planning zones for our North American case study: fishery, conservation, and energy development. Fishery, conservation, and energy zones each had their own planning goals. Our approach implicitly assumed that fishery, conservation, and energy development are mutually exclusive ocean uses, though in reality, not all ocean uses are incompatible (2). Our planning units consisted of 14,588 grid cells at 0.25 °latitude x 0.25 °longitude resolution across the continental shelves (Fig. 1). We divided these into nine regions (Fig. 1, Table S2), since ocean planning is typically conducted at a regional scale (2).

We set conservation zone goals to protect at least 10% of the occurrences of each species in a region, in line with the Convention on Biological Diversity's (CBD) Aichi Target 11 to protect at least 10% of coastal and marine areas by 2020. We set conservation goals for all species present in at least 5% of the area of each region, which resulted in 29 to 165 conservation goals per region (Table S2). We set fishery zone goals to protect at least 50% of the biomass of each of the top ten fishery species in each region, inspired by simple fisheries models which estimate maximum sustainable yield (MSY) at 50% of unfished biomass. We defined the top fishery species in each region using fishery landings for 1995-2014 by Large Marine Ecosystem (Table S4) (37). Large fishery landings are a useful indicator of importance to fisheries, but also identify species caught incidentally in large quantities, like Arrowtooth Flounder (*Atheresthes stomias*). In the energy zone, the goal was to include at least 20% of the total net present value (NPV) from wind and wave resources in each region. This goal was inspired by the projection that the U.S. needs 781 GW of offshore wind turbines installed (of 4200 GW potential, i.e., ~20%) as part of a roadmap to 100% clean energy (16, 17).

We simulated two different planning approaches. In the "present-only" approach, we developed plans that met our goals for the current distributions of marine animals. For consistency with our proactive approach (described next), we used species distributions (occurrence and biomass, see *Resource distribution data*) projected onto 2007-2020 temperatures as our current distributions. Occurrence information was used for conservation goals, biomass information was used for fishery goals, and the combined NPV of wind and wave energy was used for meeting energy goals.

In the "proactive" planning approach, we set goals for both the current (2007-2020) and the end-of-century (2081-2100) species distributions. We used ensemble projections under the RCP 8.5 greenhouse gas emissions scenario (a high emissions scenario). The proactive approach doubled the number of goals to be met in the conservation and fishery zones (i.e., both current and future distributions for each species). We kept the energy goals the same because we did not project future wind or wave conditions.

After defining the input data and goals, we then solved the 'minimum set problem' of allocating grid cells to conservation, fishery, or energy zones to meet the goals while minimizing the area of each zone. We solved the problem using prioritizr (38) in R v3.5.3 (39) with the Gurobi solver v8.1.1 (40). Prioritizr uses integer linear programming (ILP) techniques to solve spatial planning problems. It is guaranteed to find optimal solutions given sufficient time and supports multiple zones. We specified an efficiency gap of 1% (following the program's recommendations) and specified a uniform cost of including any planning grid cell in a zone. This choice was equivalent to assuming that the primary concern was minimizing the area included in conservation, fishing, or energy zones.

Plan evaluation

We then evaluated the present-only and the proactive marine spatial plans in each region by testing whether each zoning goal (species representation goals in conservation zones, percent of biomass in fishing zones, and percent of NPV in energy production zones) was met in future time-periods as species habitat distributions shifted. We evaluated each of the future climate scenarios in each time period independently against the same single set of goals (i.e., we tested whether each plan met conservation, fishing, and energy goals in a given time period). We considered a wide range of future scenarios in each region by using the 16 projected distributions for each species (i.e., for each of two RCPs in each of the eight global climate models reserved for testing, Table S1) for 2021-2040, 2041-2060, 2061-2080, and 2081-2100. This analysis approach allowed us to consider uncertainty in both emissions scenarios as well as in climate models.

We used a generalized linear mixed model (GLMM) with binomial errors to test whether the proactive planning approach met more goals than the present-only approach:

$$(numgoalsmet_{p,g,r,m,d},\ numtotalgoals_{p,g,r,m,d}) \sim plantype_p + region_g/rcp_r/model_m/period_d$$

The response variable was the proportion of goals met (coded as the number of goals met, *numgoalsmet*, and the total number of goals, *numtotalgoals*). The fixed effect was the planning approach (*plantype*). Random effects were time period (*period*) nested within climate model (*model*), nested within RCP (*rcp*), nested within region (*region*). We used the *lme4* package v1.1-21 in R 3.6.1 to fit the model (39, 41).

Tradeoff curves

We also calculated tradeoff curves (Pareto efficiency frontiers) (20) between present and future planning goals for conservation and fishing by setting a constrained plan area such that all present and future goals could not be met. We set the constrained area (the "budget") as 50%, 75%, or 90% of the total area needed to meet all conservation and fishing goals. The input data were the same as for the proactive planning approach described in section *Plan development*, though for simplicity we did not include energy goals. In other words, we used the ensemble mean species occurrence and biomass information for 2007-2020 and 2081-2100 (see *Species habitat distributions*).

We then used prioritizr to solve the 'fixed budget problem' of meeting as many goals as possible, subject to the constrained area. We ran prioritizr multiple times, each time applying a different set of weights to either future goals or present goals. The weights specified how important it was to meet future vs. present goals. Weights for present goals were varied from 0 (no attempt to meet present goals) to 100, while weights for future goals were set as 100 minus the weight assigned to present goals.

Analysis of management area networks

Existing management areas

To evaluate the climate sensitivity of existing marine spatial plans and the value of networks, we examined marine designations within the August 2019 version of the World Database on Protected Areas (WDPA) (42). These are not formal marine spatial plans, but they do represent areas of the ocean that have been set aside for particular purposes. The management areas included in this database have been designated for a wide range of purposes, including fisheries management or conservation. The Greater Farallones National Marine Sanctuary in California, for example, regulates construction, discharge, and research activities, but does not restrict fishing activities. The Great South Channel Restricted Gillnet Area in the Northeast U.S. restricts gillnet fishing gear in certain seasons, but allows other kinds of fishing. The full set of areas, therefore, provides an example of regions of the ocean set aside for spatial management and helps provide an example of existing (though largely uncoordinated) efforts towards marine spatial planning in North America.

We then compared ecological turnover within individual management areas and within networks of management areas driven by shifting species distributions. Within each management area, we evaluated the fraction of species habitats that were lost from the initial (2007-2020) to final (2081-2100) time period, the fraction gained, and Sørenson's similarity index between the initial and final species assemblages within each management area. Our input data were the high-resolution distribution projections described in *Species habitat distributions* above (0.05 x 0.05 ° for each global climate model and RCP).

We took a probability-based approach to these calculations to account for potential differences in scale between the projections and the reserves (43). We first calculated the probability ($p_{i,t}$) of each species i appearing in each management area in time period t, accounting for the fact that a given management area might span portions of multiple species projection grid cells:

$$p_{i,t} = 1 - \prod_{x=1}^{X} (1 - r_x p_{i,t,x})$$

where $p_{i,t,x}$ was the probability of species i being present in time period t in grid cell x, r_x was the fraction of grid cell x contained within the management area, and X was the total number of grid cells overlapping the management area. The logic of this equation combines two ideas. First, the probability of a species being present in an area smaller than a grid cell is equal to the proportion of the grid cell covered by the smaller area ($r_x p_{i,t,x}$) (43). Second, the combined probability of presence across multiple grid cells is the inverse of the probability that the species is not present in any of the grid cells.

To test this approach, we compared our calculations against data on whether or not species had been observed in each management area during bottom trawl surveys 2016-2018 (i.e., data that were not used to fit species distribution models by (19)). The trawl data were downloaded from OceanAdapt version March 25, 2019 (44). We calculated the fraction of management areas that were observed to have a species when it was predicted to be present (Positive Predictive Value, also called precision) and the fraction of management areas that were not observed to have a species when it was predicted to be absent (Negative Predictive Value) (28, 45). We bootstrapped across management areas and species to derive standard errors. We found relatively high values of both quantities, with PPV = 0.51 ± 0.007 (± 1 S.E.) and NPV = 0.81 ± 0.009. These values compare favorably to distribution models for phytoplankton (PPV 0.15 to 0.77 and NPV 0.7 to 1) and trees (PPV 0 to 0.6) (45, 46). Most management areas had only four or fewer sampling events (trawl tows) in our dataset (Fig. S3a), increasing the chance that some observed absences were in fact presences (i.e., false absences). When we trimmed out management areas with few sampling events, PPV increased towards 0.8, though NPV also decreased somewhat (Fig. S3b).

We then calculated the probabilistic number of species gained, lost, or shared within individual management areas between the first (2007-2020) and second (2081-2100) time-period:

$$n_{lost} = \sum_{i \in \{i | p_{i,2} < p_{i,1}\}} (p_{i,1} - p_{i,2})$$

$$n_{gained} = \sum_{i \in \{i | p_{i,2} > p_{i,1}\}} (p_{i,2} - p_{i,1})$$

$$n_{shared} = \sum_{i=1}^{n} p_{i,1} p_{i,2}$$

where n was the total number of species. From these, we then calculated the fraction of species lost, the fraction of species gained, and the Sørenson dissimilarity index:

$$f_{lost} = \frac{n_{lost}}{\sum_{i=1}^{n} p_{i,1}}$$

$$f_{gained} = \frac{n_{gained}}{\sum_{i=1}^{n} p_{i,2}}$$

$$S = 1 - \frac{2n_{shared}}{2n_{shared} + n_{gained} + n_{lost}}$$

We then repeated these calculations of turnover statistics (gain, loss, and similarity) for networks of management areas. We defined three networks from the WDPA database: 1) areas in California managed by the California Department of Fish and Game (n = 55), 2) areas in U.S. state waters east of 100°W (Atlantic Coast, n = 342), and 3) areas in Alaska state waters (Alaska, n = 35). The California areas are managed together as a network (4), while we defined the other networks as illustrative sets potentially connected through species dispersal or range shifts.

For a statistical test of similarity within networks and within the individual management areas of those networks, we first averaged similarity within each management area or network across the RCPs and climate models. We then conducted a non-parametric Mann-Whitney

(Wilcoxon two-sample signed rank) test of the null hypothesis that the two distributions share the same location with *wilcox.test()* in R 3.6.3 (39).

Simulated networks

Finally, we simulated management networks in each region by randomly choosing 0.25 ° x 0.25 ° grid cells within each region to designate. The simulated networks were constrained to cover only a designated area (eleven levels from 1% to 50% of the grid cells in each region) and to span a limited range of temperatures (eleven levels from 1% to 100% of the thermal range in a region). To define the thermal range and to guide site selection, we used the bottom temperature climatology for the North American continental shelf developed by (19). This climatology integrated data from the Simple Ocean Data Assimilation (SODA) reanalysis product (47). We repeated the process of randomly selecting areas with a network three times at each combination of area and thermal range constraints, for a total of 363 random networks in each of the nine regions. We then evaluated ecological similarity between the beginning and end of the 21st century following the procedure in section *Existing management areas*.

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Data and Code Availability:

Data and code from our analyses are available at https://doi.org/10.5281/zenodo.3991884.

Author Contributions:

Conceptualization: MLP; Methodology: MLP, LAR, JWM; Software: MLP, LAR, and JWM; Formal Analysis: MLP; Resources: TLF and JWM; Data Curation: MLP and JWM; Writing - Original Draft: MLP; Writing - Review & Editing: MLP, LAR, TLF, and JWM; Visualization: MLP; Project Administration: MLP; Funding Acquisition: MLP, TLF, JWM, LAR.

Competing Interests:

MLP serves as an Oceana science advisor and is a visiting research collaborator at Princeton University and a guest researcher at the University of Oslo.

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Figure Legends

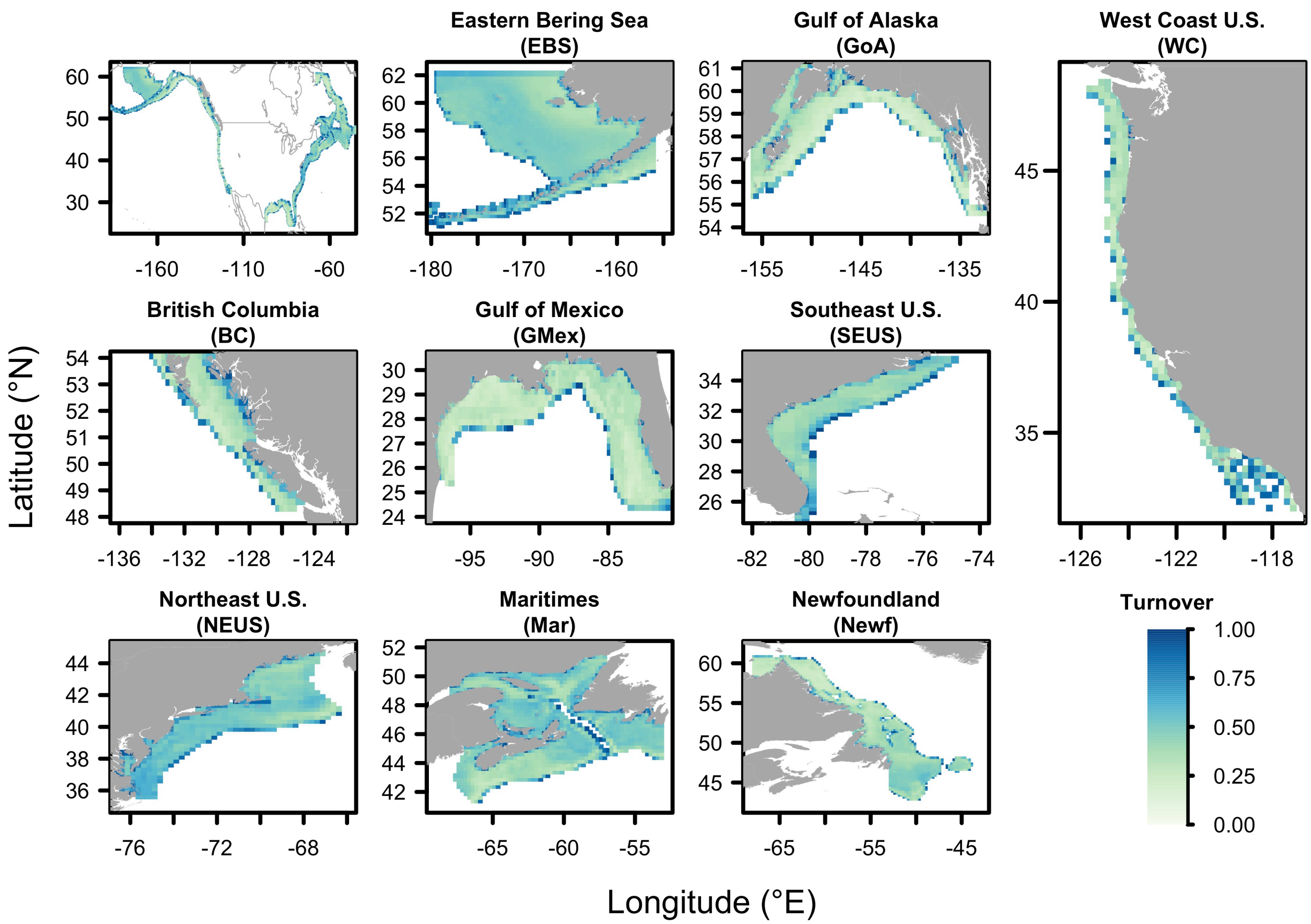
Fig. 1. Study areas for simulating the ocean planning process, shown with projected species turnover (Sørenson dissimilarity) 2007 to 2100 on the continental shelf.

Fig. 2. Comparison of “present-only” plans that only consider current conditions (orange) and “proactive” ocean plans that also consider species redistributions (purple). Success is expressed as the fraction of planning goals that are met by each plan at a given time. Thick lines show averages, thin lines show individual projections, and shading shows ± 1 standard deviation across the projections from eight global climate models used for testing and two greenhouse gas emissions scenarios (RCP2.6 and RCP8.5).

Fig. 3. Cost and impact on ocean plans that result from planning for future shifts in species distributions, as opposed to planning only for the present ocean state. a) Fraction of each region included in conservation, fishing, or energy zones for "proactive" plans (blue colors) is only slightly higher than under "present-only" plans (warm colors). b) Despite similar total areas, a substantial fraction of planning grids change zones between the two plans. Region abbreviations are defined in Fig. 1.

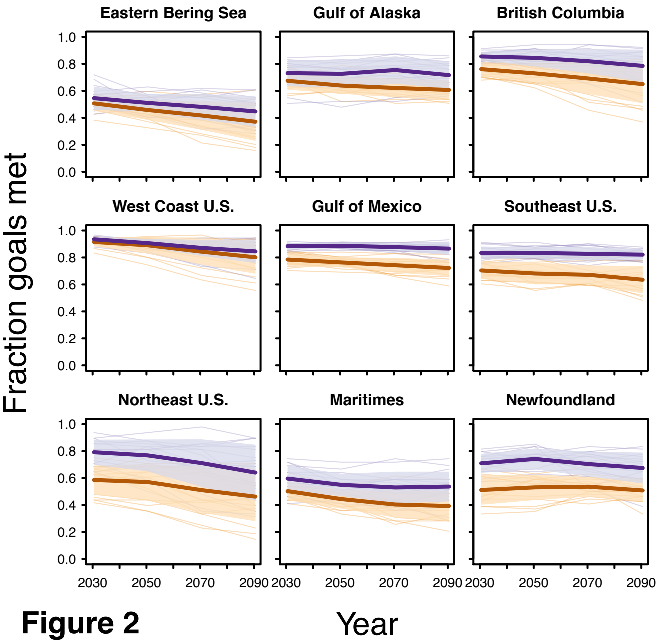
Fig. 4. Curves that delineate the tradeoff between the ability to meet planning goals in the present (x-axis) or in the future (y-axis). Left-hand images illustrate (from top to bottom) curves that have no tradeoff, a direct tradeoff, and a concave tradeoff (20). Main figure shows curves for the nine regions around North America. Points on each line are generated by weighting present vs. future goals to a greater or lesser extent with a limited total plan area (75% of the area needed to meet all present and future goals at once). The ends of each line indicate no attempt to meet one of the goal types. Areas of 50% or 90% are shown in Fig. S1.

Fig. 5. Average ecological turnover across existing individual management areas or in networks by 2081-2100, including a) fraction of species lost, b) fraction of species gained, and c) Sørenson dissimilarity. Beanplots show density distributions across projections from 16 global climate models under a low (RCP2.6) or a high (RCP8.5) emissions scenario. Thick lines show means within each group.



Eastern Bering Sea
(EBS)
Gulf of Alaska
(GoA)
West Coast U.S.
(WC)
British Columbia
(BC)
Gulf of Mexico
(GMex)
Southeast U.S.
(SEUS)
Northeast U.S.
(NEUS)
Maritimes
(Mar)
Newfoundland
(Newf)
Turnover
1.00
0.75
0.50
0.25
0.00
Latitude (°N)
Longitude (°E)

Figure 1



Eastern Bering Sea
Gulf of Alaska
British Columbia
West Coast U.S.
Gulf of Mexico
Southeast U.S.
Northeast U.S.
Maritimes
Newfoundland
Fraction goals met
1.0
0.8
0.6
0.4
0.2
0.0
2030
2050
2070
2090
Year

Figure 2

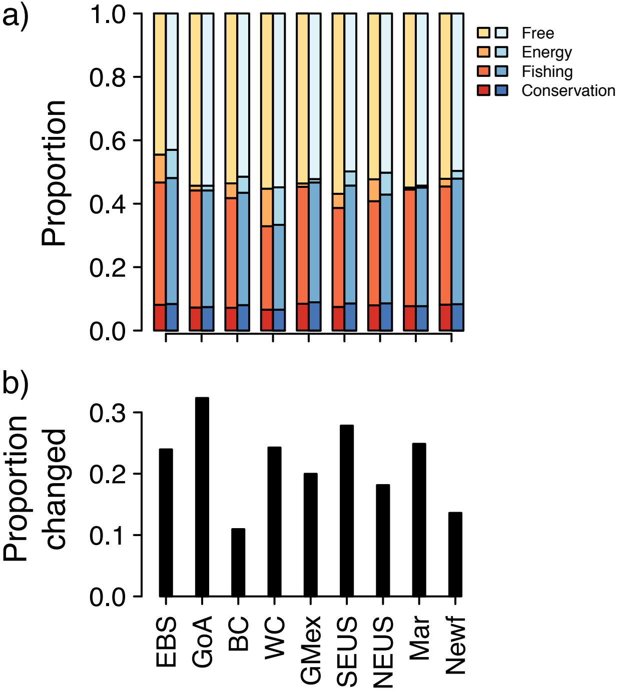
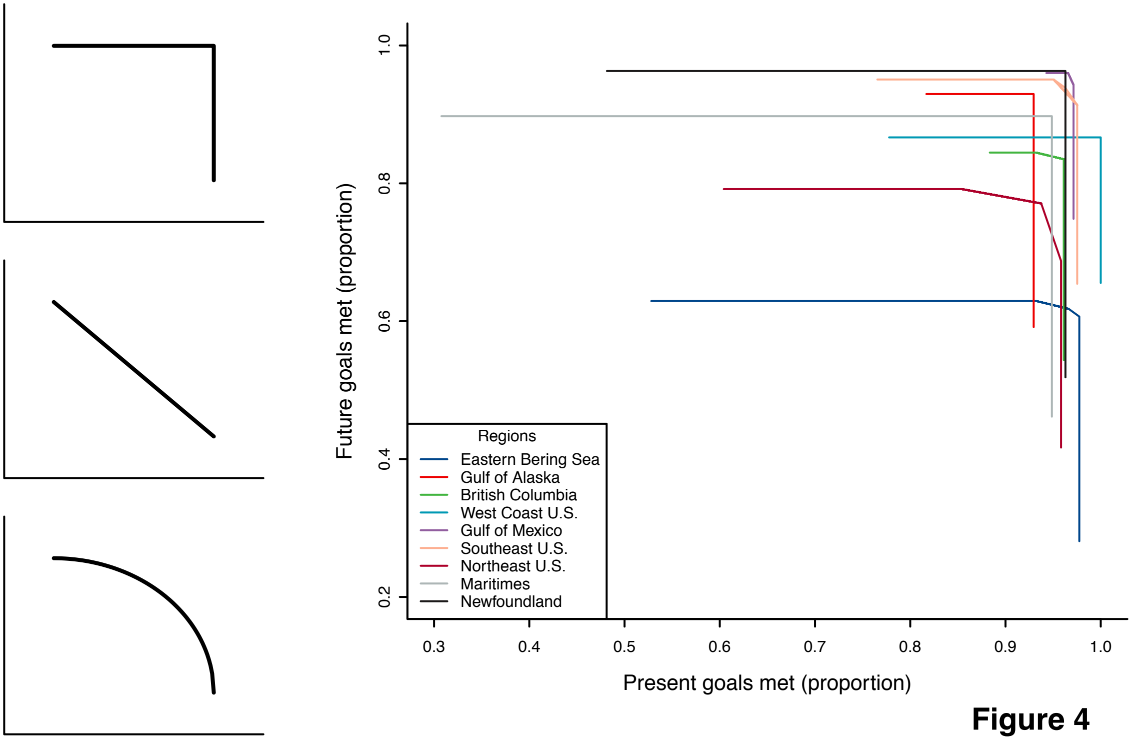

a)
1.0
0.8
0.6
0.4
0.2
0.0
Proportion
Free
Energy
Fishing
Conservation
b)
0.3
0.2
0.1
0.0
Proportion changed
EBS
GoA
BC
WC
GMex
SEUS
NEUS
Mar
Newf

Figure 3



Future goals met (proportion)
Present goals met (proportion)
1.0
0.8
0.6
0.4
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Regions
Eastern Bering Sea
Gulf of Alaska
British Columbia
West Coast U.S.
Gulf of Mexico
Southeast U.S.
Northeast U.S.
Maritimes
Newfoundland

Figure 4

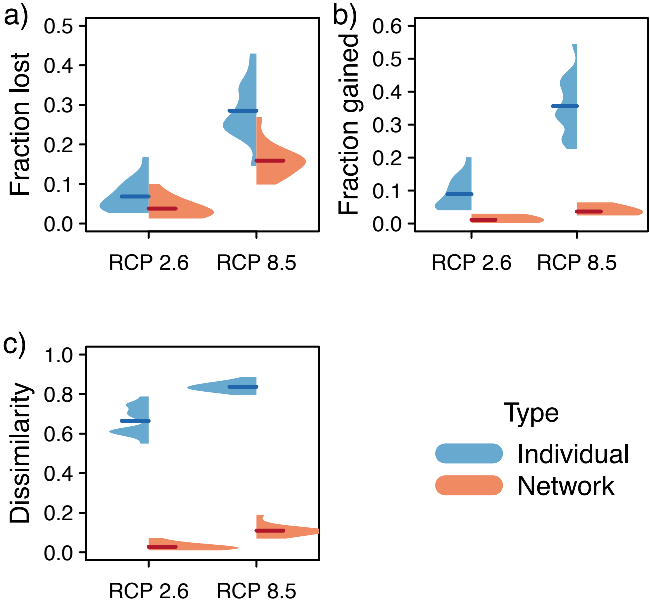

a)
Fraction lost
0.0
0.1
0.2
0.3
0.4
0.5
RCP 2.6
RCP 8.5
b)
Fraction gained
0.0
0.1
0.2
0.3
0.4
0.5
0.6
RCP 2.6
RCP 8.5
c)
Dissimilarity
0.0
0.2
0.4
0.6
0.8
1.0
RCP 2.6
RCP 8.5
Type
Individual
Network

Figure 5

Supplementary Materials:

Figures S1-S3

Tables S1-S4

Supplementary Materials for

Ocean planning for species on the move provides substantial benefits and requires few tradeoffs

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Supplementary Figures

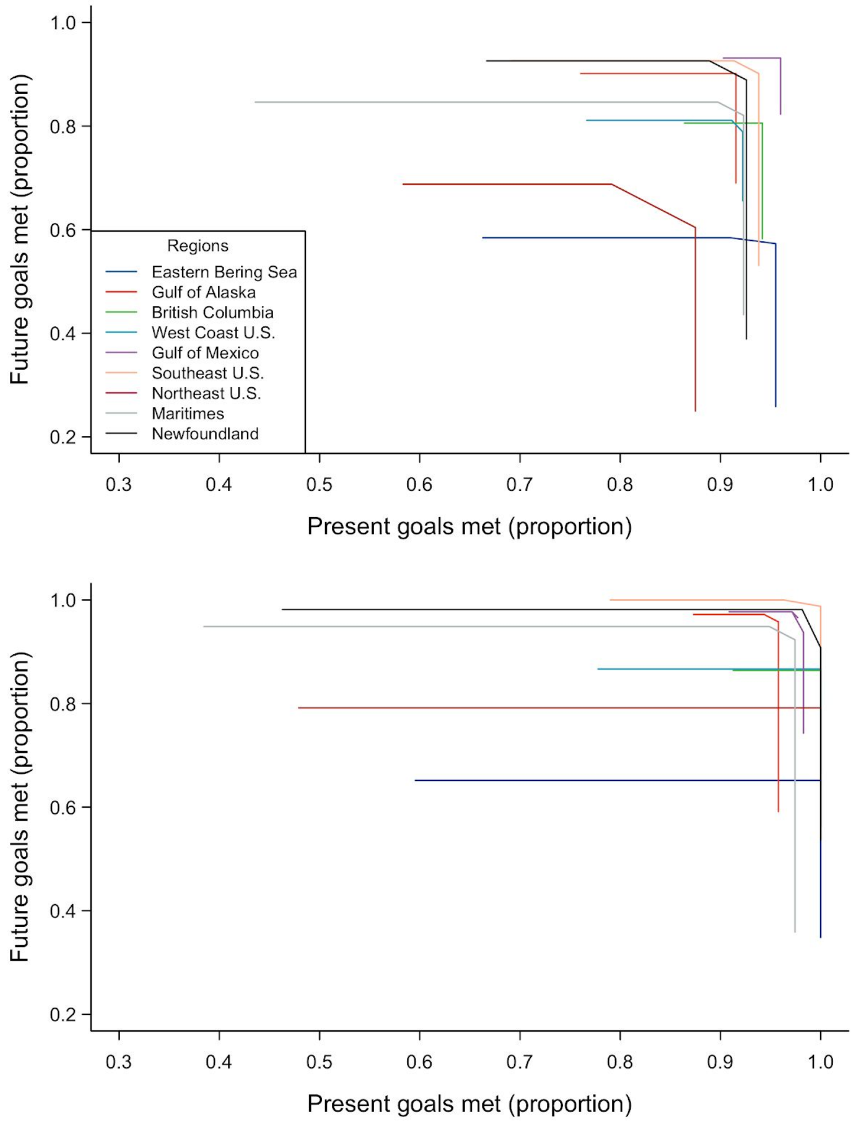

Figure S1. Tradeoff curves with constrained plan areas of 50% (top) or 90% (bottom). Compare to Fig. 4 with a 75% constrained plan area. Curves delineate the tradeoff between the ability to meet planning goals in the present (x-axis) or in the future (y-axis). Points on each line are generated by weighting present vs. future goals to a greater or lesser extent with a limited plan area (a percentage of the plan area that would be needed to meet all present and future goals at once). The ends of each line indicate no attempt to meet one of the goal types.

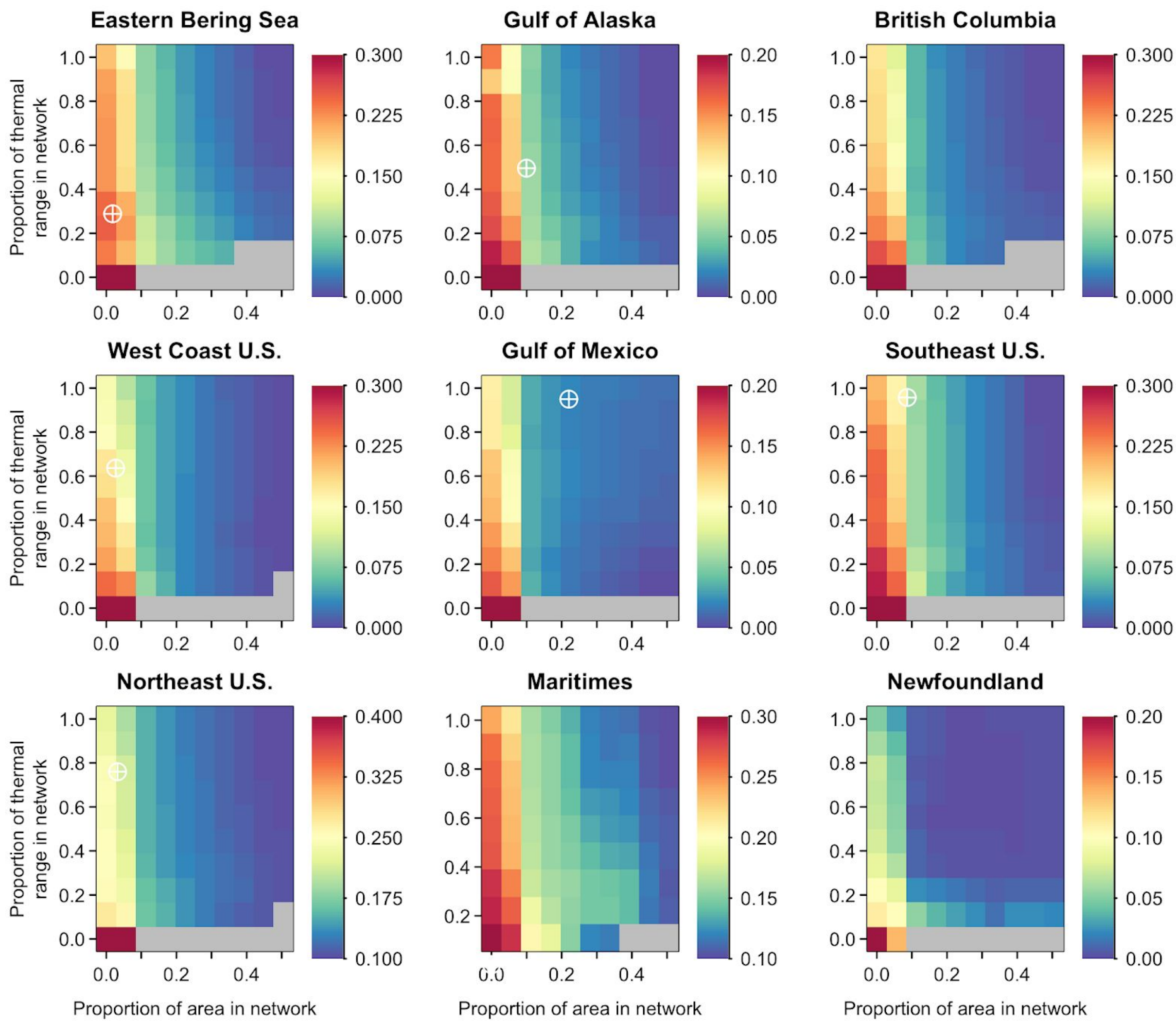

Figure S2. Ecological turnover expected in simulated management area networks. Networks vary in size (fraction of total cells selected in a region) and thermal range (fraction of total temperature range in a region selected within the network). Ecological turnover is expressed as the Sørenson dissimilarity index, where high numbers (red colors) indicate high species turnover between the beginning and end of the 21st century and low numbers (blue colors) indicate the opposite. The relative area and thermal ranges of the empirical networks examined in Fig. 5 are indicated with white symbols (California state, Alaska state, and Atlantic coast U.S. states).

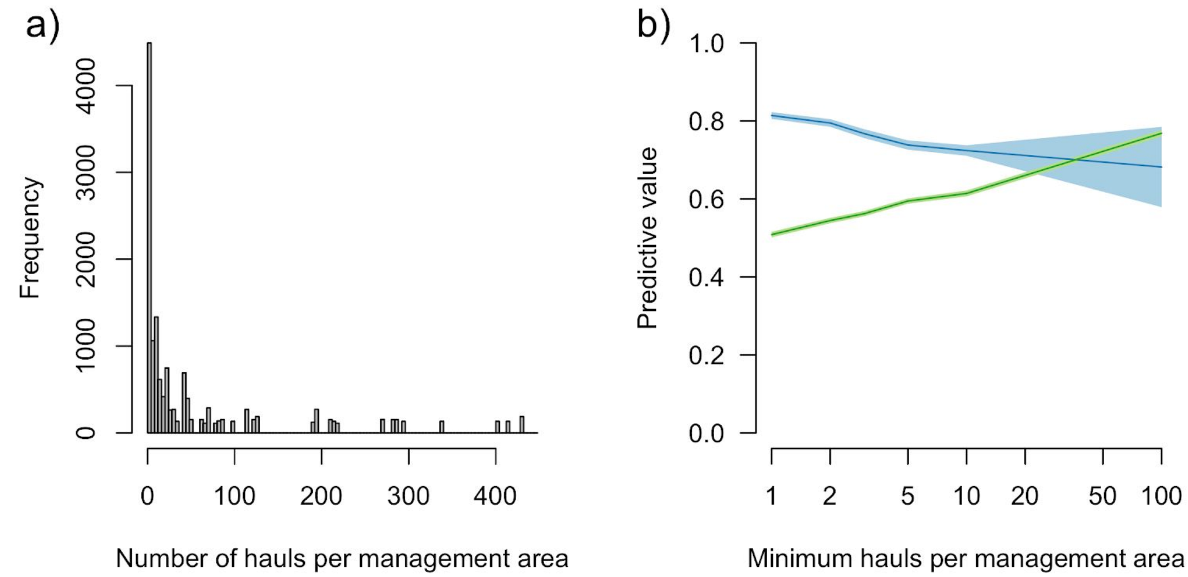

Figure S3. Comparison of species presence-absence projections in management areas against independent bottom trawl observations (2016-2018) in those same areas. a) Most management areas had few sampling events, as shown by a histogram of sampling events per management area with a bin size of four. b) Positive Predictive Value (green) and Negative Predictive Value (blue) after trimming out management areas with few sampling events. The x-axis shows the minimum number of hauls per management area retained in the dataset before calculating Positive and Negative Predictive Values. Shading shows standard errors.

Supplementary Tables

Table S1. Global climate models used in projections of surface and bottom temperatures over the 21st century. A randomly selected subset of half the models was used for simulated ocean planning, while the other half was used for testing the ocean plans.

Organization	Model	Use
Beijing Climate Center, China	bcc-csm1-1-m	Planning
Beijing Climate Center, China	bcc-csm1-1	Planning
Canadian Centre for Climate Modelling and Analysis, Canada	CanESM2	Planning
National Center for Atmospheric Research, USA	CCSM4	Planning
National Science Foundation, Department of Energy, National Center for Atmospheric Research, USA	CESM1-CAM5	Testing
Centre National de Recherches Météorologiques, France	CNRM-CM5	Testing
Geophysical Fluid Dynamics Laboratory, USA	GFDL-CM3	Testing
Geophysical Fluid Dynamics Laboratory, USA	GFDL-ESM2M	Planning
Geophysical Fluid Dynamics Laboratory, USA	GFDL-ESM2G	Planning
NASA Goddard Institute for Space Studies, USA	GISS-E2-R	Planning
NASA Goddard Institute for Space Studies, USA	GISS-E2-H	Testing
L'Institut Pierre-Simon Laplace, France	IPSL-CM5A-LR	Testing
L'Institut Pierre-Simon Laplace, France	IPSL-CM5A-MR	Testing
Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies, Japan	MIROC-ESM	Planning
Max-Planck-Institut für Meteorologie, Germany	MPI-ESM-LR	Testing
Norwegian Climate Centre, Norway	NorESM1-ME	Testing

Table S2. Area (number of grid cells) and number of species included in each region for meeting conservation goals or for meeting fishery goals.

Region	Area	Conservation	Fishery
Eastern Bering Sea	2195	79	10
Gulf of Alaska	661	61	10
British Columbia	237	93	10
West Coast	228	80	10
Gulf of Mexico	651	165	10
Southeast U.S.	269	71	10
Northeast U.S.	478	38	10
Maritimes	1131	29	10
Newfoundland	1444	44	10

Table S3. InVEST parameters for wind and wave energy net present value (NPV) calculations. Values marked as * are default for InVEST 3.7.0.

Parameter	**Value**	**Reference**
Discount rate	0.05	(6)
Wave model		
Wave data	WAVEWATCH III global	(36) *
Machine type	Pelamis	(36) *
Number of machines	100	(32)
Wind model		
Wind data	Global wind statistics derived from WAVEWATCH III reanalysis	(30) *
Minimum depth	3 m	*
Maximum depth	60 m	*
Minimum distance from shore	0 km	*
Maximum distance from shore	200 km	*
Turbines per farm	16	(6)
Energy price	0.161 $/kWh	(6)
Turbine rated power	5.0 MW	*

Table S4. Commercially important fishery species considered in each region for marine spatial planning.

Region	Species name	Common name
Eastern Bering Sea	*Gadus chalcogrammus*	Alaska pollock
Eastern Bering Sea	*Gadus macrocephalus*	Pacific cod
Eastern Bering Sea	*Limanda aspera*	Yellowfin sole
Eastern Bering Sea	*Pleurogrammus monopterygius*	Atka mackerel
Eastern Bering Sea	*Oncorhynchus keta*	Chum salmon
Eastern Bering Sea	*Hippoglossoides elassodon*	Flathead sole
Eastern Bering Sea	*Anoplopoma fimbria*	Sablefish
Eastern Bering Sea	*Glyptocephalus zachirus*	Rex sole
Eastern Bering Sea	*Atheresthes stomias*	Arrowtooth flounder
Eastern Bering Sea	*Sebastes alutus*	Pacific ocean perch
Gulf of Alaska	*Metacarcinus magister*	Dungeness crab
Gulf of Alaska	*Sebastes alutus*	Pacific ocean perch
Gulf of Alaska	*Merluccius productus*	North Pacific hake
Gulf of Alaska	*Gadus macrocephalus*	Pacific cod
Gulf of Alaska	*Gadus chalcogrammus*	Alaska pollock
Gulf of Alaska	*Clupea pallasii pallasii*	Pacific herring
Gulf of Alaska	*Hippoglossus stenolepis*	Pacific halibut
Gulf of Alaska	*Oncorhynchus keta*	Chum salmon
Gulf of Alaska	*Pleurogrammus monopterygius*	Atka mackerel
Gulf of Alaska	*Limanda aspera*	Yellowfin sole
British Columbia	*Metacarcinus magister*	Dungeness crab
British Columbia	*Sebastes alutus*	Pacific ocean perch
British Columbia	*Merluccius productus*	North Pacific hake
British Columbia	*Gadus macrocephalus*	Pacific cod
British Columbia	*Gadus chalcogrammus*	Alaska pollock
British Columbia	*Clupea pallasii pallasii*	Pacific herring
British Columbia	*Hippoglossus stenolepis*	Pacific halibut
British Columbia	*Oncorhynchus keta*	Chum salmon
British Columbia	*Pleurogrammus monopterygius*	Atka mackerel

British Columbia	*Limanda aspera*	Yellowfin sole
West Coast	*Merluccius productus*	North Pacific hake
West Coast	*Pandalus jordani*	Pink shrimp
West Coast	*Microstomus pacificus*	Dover sole
West Coast	*Anoplopoma fimbria*	Sablefish
West Coast	*Engraulis mordax*	California anchovy
West Coast	*Clupea pallasii pallasii*	Pacific herring
West Coast	*Sebastes entomelas*	Widow rockfish
West Coast	*Atheresthes stomias*	Arrowtooth flounder
West Coast	*Sardinops sagax*	Pacific sardine
West Coast	*Scomber japonicus*	Chub mackerel
Gulf of Mexico	*Penaeus setiferus*	Northern white shrimp
Gulf of Mexico	*Argopecten gibbus*	Atlantic calico scallop
Gulf of Mexico	*Penaeus aztecus*	Northern brown shrimp
Gulf of Mexico	*Scomberomorus maculatus*	Atlantic Spanish mackerel
Gulf of Mexico	*Brevoortia patronus*	Gulf menhaden
Gulf of Mexico	*Opisthonema oglinum*	Atlantic thread herring
Gulf of Mexico	*Penaeus duorarum*	Pink shrimp
Gulf of Mexico	*Scomberomorus cavalla*	King mackerel
Gulf of Mexico	*Sicyonia brevirostris*	Brown rock shrimp
Gulf of Mexico	*Xiphopenaeus kroyeri*	Atlantic seabob
Southeast U.S.	*Argopecten gibbus*	Atlantic calico scallop
Southeast U.S.	*Brevoortia tyrannus*	Atlantic menhaden
Southeast U.S.	*Callinectes sapidus*	Blue crab
Southeast U.S.	*Carcharhinus plumbeus*	Sandbar shark
Southeast U.S.	*Leiostomus xanthurus*	Spot
Southeast U.S.	*Micropogonias undulatus*	Atlantic croaker
Southeast U.S.	*Paralichthys dentatus*	Summer flounder
Southeast U.S.	*Penaeus setiferus*	Northern white shrimp
Southeast U.S.	*Placopecten magellanicus*	American sea scallop
Southeast U.S.	*Sicyonia brevirostris*	Brown rock shrimp

Northeast U.S.	*Placopecten magellanicus*	American sea scallop
Northeast U.S.	*Clupea harengus*	Atlantic herring
Northeast U.S.	*Homarus americanus*	American lobster
Northeast U.S.	*Brevoortia tyrannus*	Atlantic menhaden
Northeast U.S.	*Gadus morhua*	Atlantic cod
Northeast U.S.	*Merluccius bilinearis*	Silver hake
Northeast U.S.	*Doryteuthis pealeii*	Longfin inshore squid
Northeast U.S.	*Limanda ferruginea*	Yellowtail flounder
Northeast U.S.	*Melanogrammus aeglefinus*	Haddock
Northeast U.S.	*Scomber scombrus*	Atlantic mackerel
Maritimes	*Clupea harengus*	Atlantic herring
Maritimes	*Homarus americanus*	American lobster
Maritimes	*Gadus morhua*	Atlantic cod
Maritimes	*Chionoecetes opilio*	Snow crab
Maritimes	*Scomber scombrus*	Atlantic mackerel
Maritimes	*Melanogrammus aeglefinus*	Haddock
Maritimes	*Cancer irroratus*	Atlantic rock crab
Maritimes	*Mallotus villosus*	Capelin
Maritimes	*Pandalus borealis*	Pink shrimp
Maritimes	*Placopecten magellanicus*	American sea scallop
Newfoundland	*Chionoecetes opilio*	Snow crab
Newfoundland	*Homarus americanus*	American lobster
Newfoundland	*Mallotus villosus*	Capelin
Newfoundland	*Placopecten magellanicus*	American sea scallop
Newfoundland	*Clupea harengus*	Atlantic herring
Newfoundland	*Pandalus borealis*	Northern prawn
Newfoundland	*Gadus morhua*	Atlantic cod
Newfoundland	*Reinhardtius hippoglossoides*	Greenland halibut
Newfoundland	*Melanogrammus aeglefinus*	Haddock
Newfoundland	*Scomber scombrus*	Atlantic mackerel