Conservation Biology

Contributed Paper

Decision-support tools for dynamic management

Heather Welch,[1,2]* Stephanie Brodie,[1,2] Michael G. Jacox,[1,2,3] Steven J. Bograd,[1,2] and Elliott L. Hazen[1,2]

[1]Institute of Marine Sciences, University of California Santa Cruz, 1156 High Street, Santa Cruz, CA 95064 U.S.A.
[2]Southwest Fisheries Science Center, National Oceanic and Atmospheric Administration, Suite 255A, 99 Pacific Street, Heritage Harbor, Monterey, CA 93940 U.S.A.
[3]Earth System Research Laboratory, National Oceanic and Atmospheric Administration, 325 Broadway Street, Boulder, CO 80305 U.S.A.

Abstract: Spatial management is a valuable strategy to advance regional goals for nature conservation, economic development, and human health. One challenge of spatial management is navigating the prioritization of multiple features. This challenge becomes more pronounced in dynamic management scenarios, in which boundaries are flexible in space and time in response to changing biological, environmental, or socioeconomic conditions. To implement dynamic management, decision-support tools are needed to guide spatial prioritization as feature distributions shift under changing conditions. Marxan is a widely applied decision-support tool designed for static management scenarios, but its utility in dynamic management has not been evaluated. EcoCast is a new decision-support tool developed explicitly for the dynamic management of multiple features, but it lacks some of Marxan's functionality. We used a hindcast analysis to compare the capacity of these 2 tools to prioritize 4 marine species in a dynamic management scenario for fisheries sustainability. We successfully configured Marxan to operate dynamically on a daily time scale to resemble EcoCast. The relationship between EcoCast solutions and the underlying species distributions was more linear and less noisy, whereas Marxan solutions had more contrast between waters that were good and poor to fish. Neither decision-support tool clearly outperformed the other; the appropriateness of each depends on management purpose, resource-manager preference, and technological capacity of tool developers.

Keywords: climate variability, ecosystem management, fisheries bycatch, Marxan, prioritization, reserve design, species distribution models

Herramientas de Apoyo para la Toma de Decisiones en el Manejo Dinámico

Resumen: El manejo espacial es una estrategia valiosa para llevar hacia adelante los objetivos regionales para la conservación de la naturaleza, el desarrollo económico y la salud humana. Uno de los retos del manejo espacial es la navegación a través de la priorización de múltiples caracteres. Este reto se vuelve más pronunciado dentro de los escenarios de manejo dinámico, en los cuales los límites son flexibles en el tiempo y en el espacio como respuesta a las cambiantes condiciones biológicas, ambientales o socioeconómicas. Para implementar el manejo dinámico, se necesitan herramientas de apoyo para la toma de decisiones para guiar a la priorización espacial conforme la distribución de los caracteres se modifica bajo condiciones cambiantes. Marxan es una herramienta de apoyo para la toma de decisiones utilizada ampliamente y diseñada para escenarios de manejo estático, pero su utilidad para el manejo dinámico no ha sido evaluada. EcoCast es una nueva herramienta de apoyo para la toma de decisiones desarrollada explícitamente para el manejo dinámico de múltiples caracteres, pero carece de algunas funcionalidades que tiene Marxan. Usamos un análisis de información retrospectiva para comparar la capacidad de estas dos herramientas para priorizar a cuatro especies marinas en un escenario de manejo dinámico con respecto a la sustentabilidad de las pesquerías. Configuramos exitosamente la herramienta Marxan para que operara dinámicamente con respecto a una escala diaria de tiempo y así se asemejara a EcoCast. La relación

*email heather.welch@noaa.gov
Article impact statement: Marxan can function as a decision-support tool for dynamic management scenarios in which boundaries are flexible in space and time.
Paper submitted January 24, 2019; revised manuscript accepted August 27, 2019.

Conservation Biology, Volume 34, No. 3, 589–599

DOI: 10.1111/cobi.13417

entre las soluciones de EcoCast y las distribuciones subyacentes de las especies fue más lineal y menos ruidosa, mientras que las soluciones de Marxan tuvieron un mayor contraste entre las aguas que eran buenas y aquellas que eran pobres para los peces. Ninguna de las dos herramientas de apoyo para la toma de decisiones tuvo un mejor desempeño que la otra; la pertinencia de cada una depende del propósito del manejo, la preferencia del administrador de los recursos y la capacidad tecnológica de quienes desarrollan la herramienta.

Palabras Clave: captura accesoria por pesquerías, diseño de reservas, manejo de ecosistemas, Marxan, modelos de distribución de especies, priorización, variabilidad climática

摘要: 空间管理是推动区域自然保护、经济发展和人类健康目标的重要战略, 它面临着多个特征物种优先保护决策的挑战。在管理的时空边界会随生物、环境和经济社会条件变化的动态管理情景中, 这样的挑战更加明显。随着特征物种的分布响应环境变化而变化, 为实现动态管理, 需要用决策支持工具来指导空间优先保护。Marxan 软件是为静态管理情景设计的一个应用广泛的决策支持工具, 但在动态管理中的实用性尚未得到评估。EcoCast 软件则是为多个特征物种的动态管理开发的新决策支持工具, 但却缺少 Marxan 软件的一些功能。我们用后报分析比较了这两个工具在渔业可持续性动态管理情景中为四种海洋生物设计优先保护方案的成效。我们通过配置 Marxan 软件, 成功使其像 EcoCast 软件一样在每日时间尺度上动态运作。 EcoCast 设计的决策方案和潜在物种分布的关系更符合线性, 模型噪声更小; 而 Marxan 的方案在适宜与不适宜捕鱼的水域之间差异更明显。这两种决策支持工具都没有压倒性优势, 其适用与否取决于管理目的、资源管理者偏好和工具开发者的技术能力。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 气候变异, 生态系统管理, 渔业副渔获, Marxan 软件, 优先保护, 保护区设计, 物种分布模型

Introduction

Spatial management strategies such as marine protected areas and national parks have been successfully applied to manage natural resources and disturbances (Margules & Pressey 2000). To implement spatial management, decisions must be made about which areas to prioritize for protection (Pressey et al. 2007). These decisions become more arduous when multiple features are managed under the same plan, for example, resources such as protected species and productive areas, and disturbances such as extractive operations and temperature anomalies. To help navigate spatial trade-offs, a suite of decision-support tools has been developed to allow for systematic decision-making about the value of areas toward meeting management priorities, for example, Marxan (Ball et al. 2009), C-Plan (Pressey et al. 2009), and Zonation (Moilanen et al. 2009). Recently, dynamic management—a subset of spatial management in which boundaries are automatically updated in space and time (Lewison et al. 2015)—has gained traction as a solution for managing features with changing distributions, such as highly migratory species (Eveson et al. 2015). To implement dynamic management, decision-support tools are needed to continuously balance spatial trade-offs as feature distributions shift under each new set of conditions.

Dynamic management has been applied in atmospheric (Sampson & Schrader 2000), marine (Hazen et al. 2017), and terrestrial (Quayle et al. 2004) ecosystems to manage features that vary too quickly (days to years), and over spatial scales that are too large (hundreds to thousands of kilometers) to be accommodated by traditional static management strategies. Operational dynamic management strategies function by acquiring data on current or forecasted biological, environmental, and socioeconomic conditions, then predicting and prioritizing target features in real-time or forecasted conditions, and last disseminating final products that communicate management recommendations (Welch et al. 2019). This entire process is automated to repeat at an appropriate temporal frequency, for example, daily, weekly, or monthly. Although static approaches require a 1-time prioritization of features, dynamic approaches must repeatedly navigate prioritization at each time step. Owing to the complexity of this task, most dynamic management strategies to date have focused on one target feature, for example, whales (Hazen et al. 2017), hurricanes (Sampson & Schrader 2000), or wildfires (Quayle et al. 2004).

EcoCast was one of the first examples of an applied multifeature dynamic management strategy (Hazen et al. 2018; Welch et al. 2019). Designed to improve the sustainability of a swordfish fishery off the U.S. West Coast, EcoCast aims to help fishers avoid bycatch of protected species while maintaining swordfish (*Xiphias gladius*) catch. Each day, EcoCast acquires the latest available data on ocean conditions, predicts the distributions of each species, and then prioritizes species using an algebraic algorithm to produce the final product, which is a continuous fishing suitability map that presents waters as relatively better and poorer to fish. Although other examples of operational dynamic fisheries management exist, they are often only applicable to single species management (Howell et al. 2008; Hazen et al. 2017), or require bycatch events to occur before management actions are initiated (e.g., move-on rules and grid-based closures) (Dunn et al. 2016). Hereafter, EcoCast refers to the algebraic algorithm used to prioritize multiple features, as opposed to the specific dynamic management scenario for the drift gillnet fishery.

The decision-support tool Marxan (Ball et al. 2009) was explicitly developed to find solutions to the type of multifeature trade-off problem EcoCast is trying to solve. Marxan uses a simulated annealing algorithm to identify complementary sets of areas that address management priorities while minimizing costs. Although Marxan was intended as a static management tool, its consideration of complementarity and overall solution costs might confer advantages over EcoCast when applied in dynamic management scenarios, as EcoCast does not explicitly incorporate these principles. Marxan has been frequently applied in fisheries contexts (Klein et al. 2010; Metcalfe et al. 2015), and has also been applied to find static solutions that accommodate dynamic features like frontal systems, upwelling, and highly migratory species (Lombard et al. 2007; Grantham et al. 2011; Roberson et al. 2017). However, using static solutions to manage dynamic features has drawbacks such as increased opportunity costs and larger area requirements (Dunn et al. 2016; Hazen et al. 2018), thus it is valuable to explore Marxan's utility as a decision-support tool for dynamic management.

By design, dynamic management strategies update their boundaries regularly to adapt to changing conditions. This built-in flexibility also allows dynamic strategies to be responsive to changing management priorities. Static management approaches require implementation phases to adjust to new priorities, whereas dynamic schemes can adopt changing priorities without requiring new management plans (Hazen et al. 2018). EcoCast was designed to be responsive to changing management priorities, which could reflect recent bycatch events, or new interaction risks as species shift in distribution. This responsiveness is achieved by adjusting species weightings in the algebraic algorithm, which affects the relative importance of each species in the final product (e.g., species X is twice as important as species Y). In Marxan managers can define targets for feature protection, for example, to protect 20% of each species' habitat, and these percentage targets could be updated as management priorities change. However, it is important to test tool performance under changing management priorities to ensure intended outcomes are achieved.

With improving computational capacity and data availability, management scenarios can incorporate increasing numbers of features. Static management scenarios routinely include tens (Fernandes et al. 2005; Roberson et al. 2017) to hundreds (Carroll et al. 2010; Welch & McHenry 2018) of features. The incorporation of additional features likely incurs costs, which may be direct monetary costs of implementation or indirect monetary costs of larger area requirements and the displacement of extractive operations. Incurred cost may also be measured in terms of efficiency, in which the inclusion of additional features reduces the ability to manage any individual feature, compromising the overall performance of the scenario and reducing return on investment (Laitila & Moilanen 2012). As dynamic management expands to explore multifeature prioritization, these costs and their variability in time must be quantified.

We compared the performance of 2 decision-support tools, EcoCast's algebraic algorithm and the simulated annealing algorithm underlying Marxan, to manage multiple marine species in a dynamic management scenario. Our aims were to configure Marxan to operate dynamically, evaluate the tools' abilities to respond to changing management priorities, and quantify the tools' efficiency costs of managing additional species. Assessing the performance of decision-support tools is a key step in developing dynamic management strategies that can accommodate climate variability and change.

Methods

Dynamic Management Scenario

The 2 decision-support tools were evaluated using a dynamic management scenario (see fig. 1 in Welch et al. [2019] for a procedural flowchart of dynamic management scenario development) designed to improve the sustainability of a U.S. swordfish fishery that experiences bycatch of protected leatherback turtles (*Dermochelys coriacea*), blue sharks (*Prionace glauca*), and California sea lions (*Zalophus californianus*) (Hazen et al. 2018). The dynamic management scenario aimed to identify areas that are better and poorer to fish each day, based on the distributions of swordfish and the bycatch species. To estimate species' distributions, boosted regression tree models with a binomial (presence–absence) response were built and validated for each of the 4 species, following the methods described in Brodie et al. (2018). Environmental covariates were obtained from a California Current System configuration of the Regional Ocean Modeling System with data assimilation (Neveu et al. 2016). Species data included fisheries observer data for swordfish and blue sharks, and satellite-tracking data for leatherback turtles, blue sharks, and sea lions (data described in Hazen et al. [2018]).

For the purpose of this analysis, species distributions were hindcast for 213 days in 3 periods that contained the majority of the species data used to fit the models: October–November 1997 ($\mu = 16.1$ °C), April 2003 ($\mu = 10.2$ °C), and August–November 2005 ($\mu = 17.9$ °C). These periods represent a range of sea surface temperatures in the study region, used here as a surrogate for ocean state (Supporting Information). For each day in the hindcast period, the species distribution models were predicted over the day's environmental covariates to produce real-time habitat suitability maps ranging from 1 to 0 (highest and lowest quality, respectively). These daily habitats were then prioritized as specified by management priorities using the EcoCast and Marxan decision-support tools (described below) to produce fishing suitability maps for each day. Management priorities for both tools were set using species weightings, which were decimal values between −1 and +1. Weightings for bycatch species were negative, and weightings for swordfish were positive.

EcoCast Decision-Support Tool

EcoCast uses an algebraic algorithm to prioritize the species habitat suitability maps. The habitat suitability map for each species was multiplied by its weighting, which determined each species' relative contribution to the final product. The absolute values of the weightings summed to one, such that in a management scenario with equal priority for 4 species, the 3 bycatch species would each be weighted −0.25 and swordfish would be weighted 0.25. The weighted habitat suitability maps were summed to produce a final product showing waters that were better and poorer to fish:

$$E = sp_1 \times w_1 + sp_2 \times w_2 + \cdots + sp_N \times w_N, \quad (1)$$

where E is the EcoCast output value, sp is the habitat suitability map for each of N species to be considered for management, and w is the respective weighting for each species.

Marxan Decision-Support Tool

We developed a dynamic configuration of Marxan that was responsive to changing management priorities and produced final products with values that varied continuously from low (poorer to fish) to high (better to fish) to align closely with the functionality of EcoCast. Marxan was run using the R package Marxan (https://github.com/jeffreyhanson/marxan), which is designed to bring the entire Marxan workflow into R.

The daily species habitat suitability maps were input as target features. For bycatch species, which need to be protected from fishing, the raw habitat suitability maps were used. For swordfish, which need to be available for fishing, the habitat suitability maps were subtracted from one such that the highest swordfish suitability had a value of 0 and the lowest swordfish suitability had a value of one. Swordfish were input as a target feature as opposed to a cost in order to allow for a consistent method of adjusting management priorities across all species by changing the percentage targets for species protection. To create planning units, the regular raster grid (0.1° × 0.1°) of the habitat suitability maps was converted into polygons. Planning-unit cost was the area of each polygon, which was consistent across the domain.

Marxan takes as input the percentage of each target feature to protect (i.e., the percentage of each species' habitat to protect from fishing). The decimal species weightings were converted into protection percentages (e.g., a weighting of −0.25 for bycatch species translated into 25% protection). The swordfish weightings were subtracted from one, and applied to the inverted habitat suitability surfaces (e.g., a weighting of 0.25 translated into protecting 75% of the least suitable swordfish habitat from fishing). A boundary length modifier of zero was used to ensure Marxan was prioritizing achieving weighting targets over solution compactness.

Marxan produces binary solutions in which planning units are either protected or unprotected. To generate final products with continuously varying fishing suitability, Marxan was run 1000 times for each day to produce maps of selection frequency in which planning units were valued between zero and 1000 (unimportant and critically important for meeting weighting targets, respectively). Selection frequency was multiplied by −1 so that waters that were better to fish had higher values (near 0) and waters that were poorer to fish had lower values (near -1000), consistent with the directionality of EcoCast.

Decision-Support Tool Comparison

The ability of the EcoCast and Marxan tools to respond to changing species management priorities was compared across 3 runs in which leatherback turtles and swordfish were weighted −0.3 and 0.7, −0.5 and 0.5, and −0.7 and 0.3, respectively, in both tools. Efficiency costs of managing additional species were evaluated between single-species runs (leatherback turtles only), 2-species runs (leatherback turtles and swordfish), 3-species runs (leatherback turtles, swordfish, and blue shark), and 4-species runs (leatherback turtles, swordfish, blue shark, and sea lion). For the multispecies configurations of EcoCast, the input species for each run were weighted equally, and for Marxan, input species were weighted at ±0.5. For each run and each hindcast day ($n = 213$), the EcoCast and Marxan algorithms were applied to prioritize the species habitat suitability maps to produce daily final products that indicated fishing suitability. Then, habitat suitability values for each input species and output values of fishing suitability from both tools were extracted at 3000 points distributed evenly in space and time across the hindcast period. To allow for comparison between EcoCast and Marxan, the output values for both were rescaled from 0 to 1 to match the scale of species habitat suitability.

Tool performance was evaluated based on the extracted relationships between habitat suitability for each species (species inputs) and fishing suitability in the final EcoCast and Marxan products (tool outputs). Relationships were evaluated within the scope of 3 management implications: predictability, interpretability, and the strength of management recommendation (Table 1 & Fig. 1). Predictability, or the strength of relationships between species inputs and tool outputs, was evaluated using R^2 values of generalized additive models (GAMs)

Table 1. Management implications based on the relationship between species inputs and decision-support tool outputs.

Management implication	*Performance metric**	*Definition*	*Interpretation*	*Optimal values*
Predictability	R^2 (GAM)	proportion of variance explained by the model	strength of relationship between tool outputs and species inputs	high
Interpretability	effective degrees of freedom (GAM)	number of values in final model that are free to vary	consistency of relationship between tool outputs and species inputs	low
Strength of management recommendation	slope (LM)	change in y for a given change in x	change in tool output for a given change in species input	bycatch species: negative and steep; swordfish: positive and steep
Strength of management recommendation	y intercept (LM)	y value when $x = 0$	tool output for a species input of 0	bycatch species and swordfish close to maximum and minimum tool output values, respectively

**Performance metrics derived from both nonlinear (generalized additive models [GAMs]) and linear (LM) fits.*

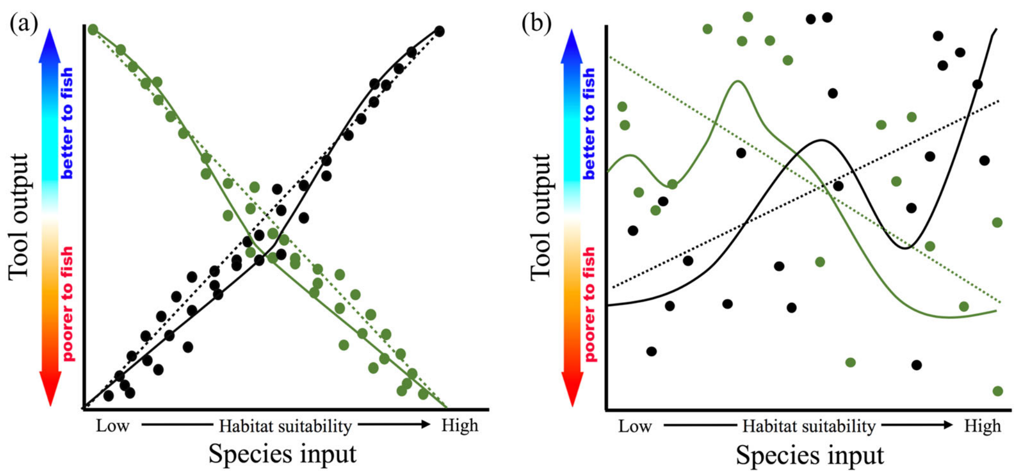

Figure 1. Two scenarios of potential relationships between species habitat suitability (species inputs) and fishing suitability in final EcoCast and Marxan tool outputs: (a) an optimal scenario characterized by high predictability (high R^2, from generalized additive model [GAM]), high interpretability (low df from GAM), and strong management recommendations (steep slopes and y intercepts close to maximum and minimum tool output values from linear model [LM]) and (b) a problematic scenario characterized by low predictability (low R^2 from GAM), low interpretability (high df from GAM), and weaker management recommendations (flatter slopes and moderate y intercepts far from potential maximum and minimum tool output values from LM). Data shown are simulated for an example bycatch species (green) and a target species (black) (solid lines, nonlinear fits from GAM; dotted lines, linear fits from LM).

(R package mgcv) fit between each tool output and each species input. High predictability (high R^2 values) gives managers confidence that species habitat suitability is strongly reflected in tool outputs. Interpretability, or the consistency of the relationship between species inputs and tool outputs, was evaluated using the effective degrees of freedom from the fitted GAM (Supporting Information). High interpretability (low degrees of freedom) means tool outputs responded in a consistent way to changes in species inputs, facilitating achievement of expected management outcomes. The strength of management recommendations, or the range of fishing suitability in the final product, was evaluated using the slopes and y-intercepts of linear regressions fit between each tool output and each species input. Stronger management recommendations (steeper slopes, extreme y-intercept values) mean there is more contrast between waters that are good and poor to fish, whereas lower ranges produce more ambiguity. Metrics from both nonlinear and linear fits were used in tandem because optimal relationships could be either nonlinear or linear.

All analyses were completed in R version 3.4.1. The R functions for running both EcoCast and Marxan and sample data are available at https://github.com/Heather-Welch/Decision-support-tools-for-dynamic-management.

Results

Qualitative Comparison

The dynamic configuration of Marxan produced fishing suitability maps that were spatially similar to those produced by EcoCast (Fig. 2). Both tools identified comparable waters to protect leatherback turtles from fishing and to maintain for fishing swordfish (Figs. 2b & 2c, maps 1 and 2). However, areas of overlapping distributions for swordfish and bycatch species (e.g., north of 40°N) were valued as neutral fishing suitability by EcoCast because the opposing weightings canceled out the contributions of each species. This did not occur in Marxan, which explicitly prioritized areas suitable for bycatch species and unsuitable for swordfish (Figs. 2b & 2c, map 3). An animation of EcoCast and Marxan outputs across the 213 hindcast days is available from https://heatherwelch.shinyapps.io/welch_et_al_algorithms/.

Responsiveness to Changing Management Priorities

Both tools were responsive to changing management priorities, which were reflected in the species weightings (Fig. 3). Slopes were always negative for bycatch species and positive for swordfish, meaning that waters deemed better to fish had lowest and highest leatherback turtle

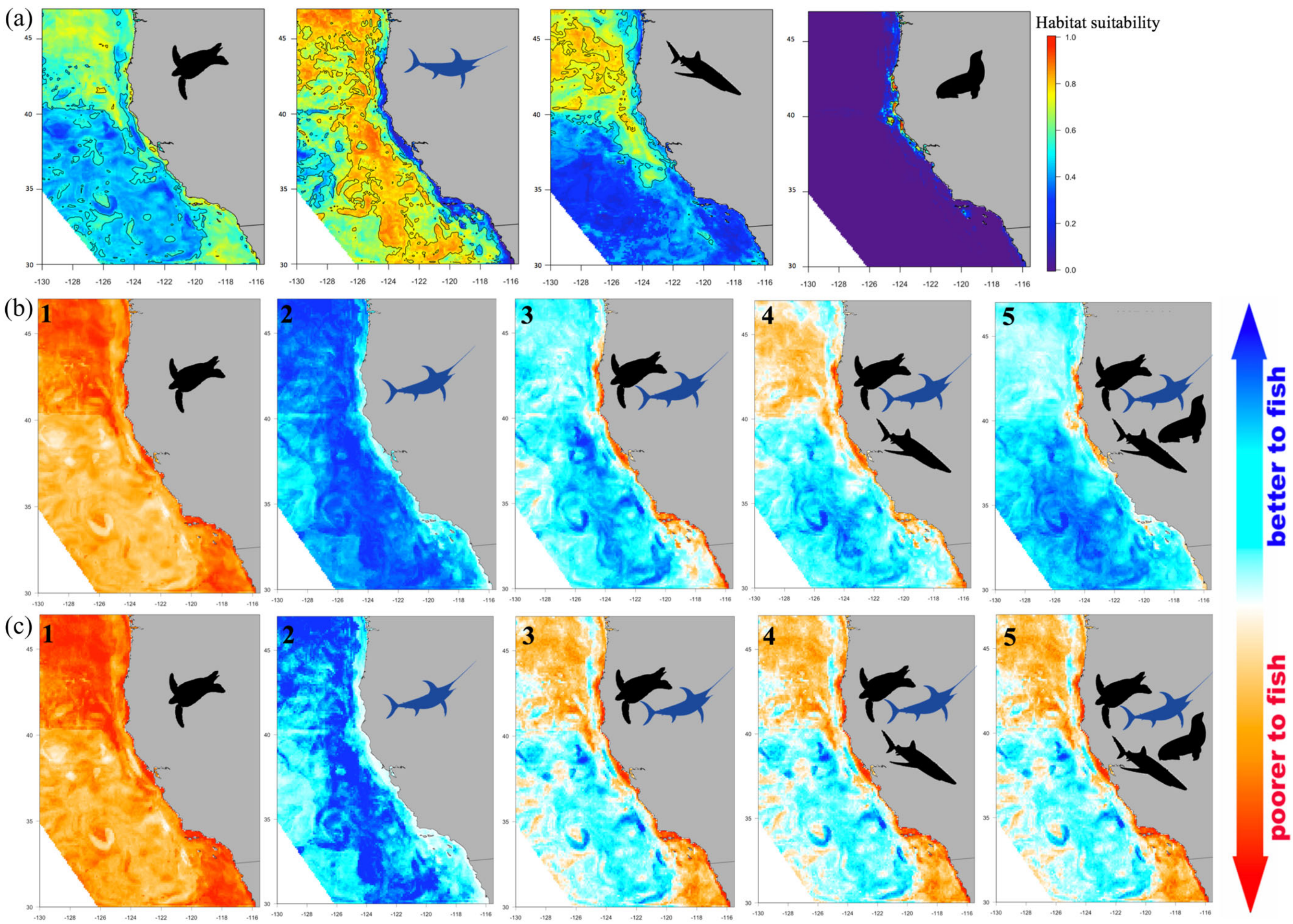

Figure 2. Predicted species distributions and EcoCast and Marxan solutions for an example day (10 January 1997): (a) habitat suitability layers for leatherback turtle, swordfish, blue shark, and California sea lion; (b) EcoCast outputs with equal weightings for each species; (c) Marxan outputs with ±0.5 weighting for each species. From left to right, (b) and (c) show weighting runs for 1–4 species. Icons show which species were input into the tools.

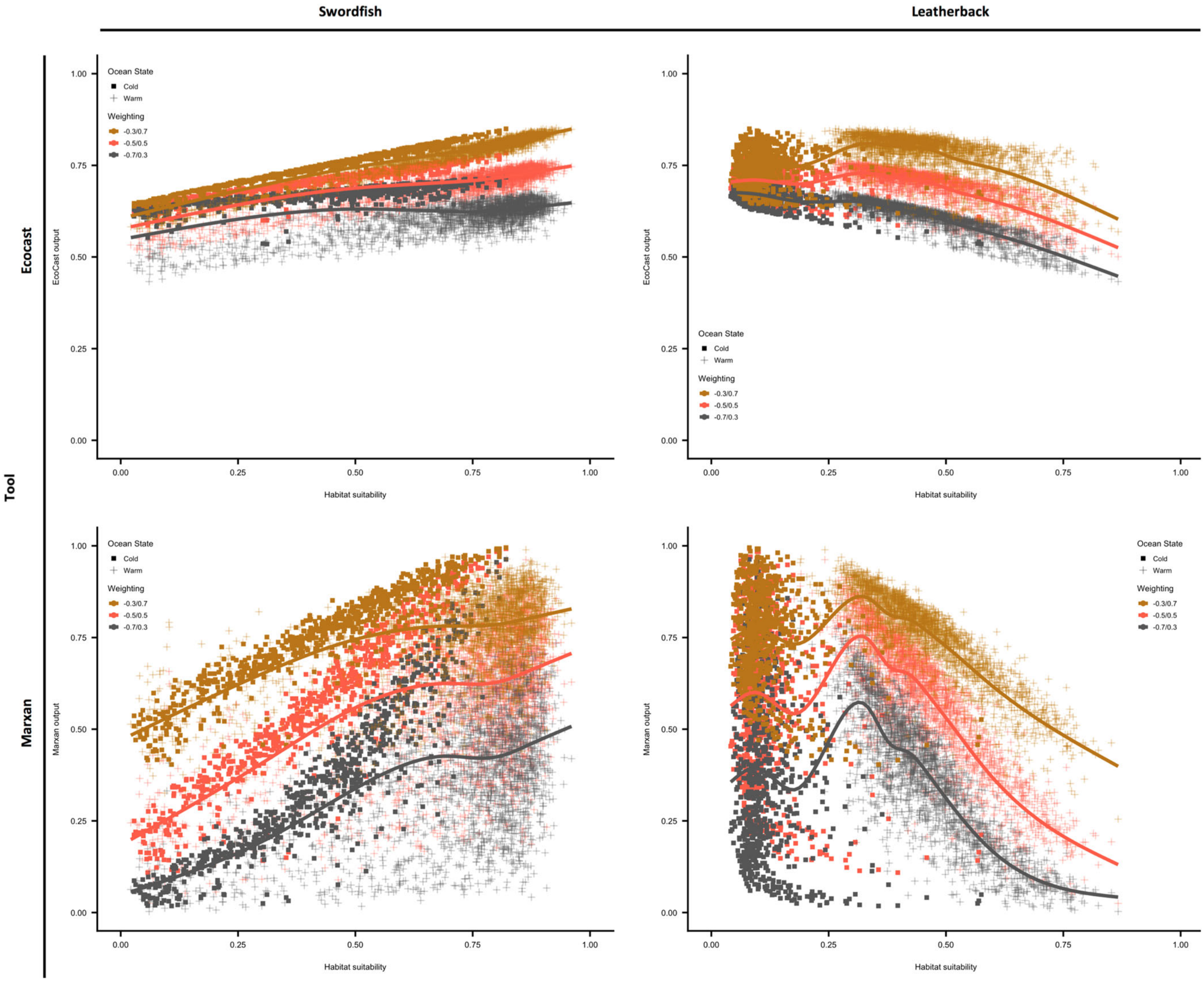

Figure 3. Effect of changing management priorities (i.e., weighting) for leatherback turtles and swordfish in EcoCast (top row) and Marxan (bottom row) tool outputs relative to species habitat suitability (weightings are indicated by paired numbers, which are negative for leatherback turtles and positive for swordfish; curves, generalized additive models fitted to each weighting run).

and swordfish suitability, respectively. Both tools were affected by changing ocean state, indicated by sea surface temperature. Relationships between species inputs and tool outputs were markedly different between warm and cold periods, though the difference was more pronounced in Marxan than in EcoCast (Fig. 3). The effect of ocean state was especially apparent in the relationship between Marxan and leatherback turtle habitat suitability, where it was most pronounced at extreme leatherback turtle weightings (−0.7). For EcoCast, changing species weightings primarily affected R^2 values; more extreme weightings for a given species increased the R^2 value for that species (Supporting Information). For Marxan changing weightings primarily affected the y-intercept; the more extreme the weightings, the more extreme the y-intercept (i.e., the y-intercept moved closer to y max [1] for leatherback turtles and y min [0] for swordfish).

Efficiency Costs of Managing Additional Species

When moving from one to 4 managed species, R^2 values averaged across input species for EcoCast and Marxan were reduced from 1.00 to 0.39 and 0.90 to 0.27, respectively (Supporting Information). In EcoCast, species are indirectly affected by the inclusion of species with which they are correlated. For example, leatherback turtles and swordfish had similar R^2 values (0.49 and 0.53, respectively) in the 2-species run. However when blue sharks were added, which are positively correlated with leatherback turtles ($r = 0.63$) (Supporting Information),

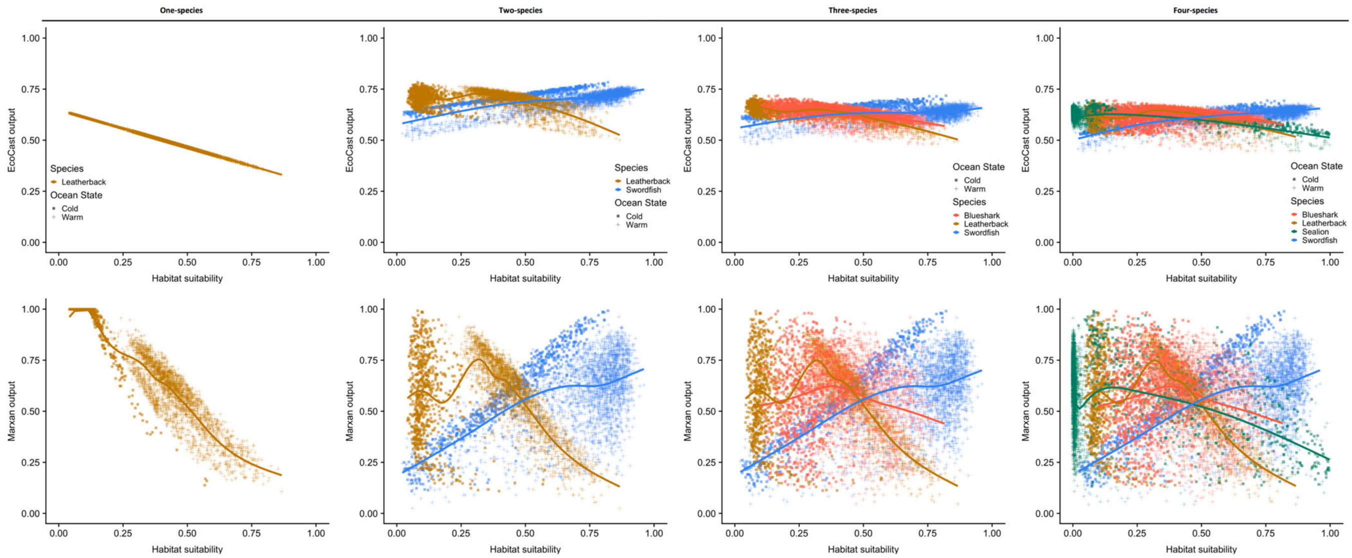

Figure 4. Effect of managing 1–4 species on EcoCast and Marxan tool outputs. Curves show generalized additive models fitted to each weighting run.

the swordfish R^2 decreased to 0.20, and the leatherback turtle R^2 increased to 0.63. In this EcoCast example, protecting blue sharks effectively increases the protection of leatherback turtles as well. When sea lions were added in the 4-species run, the inverse management priorities and inverse correlations between swordfish and sea lions ($r = -0.76$) (Supporting Information) translated into the 2 species having more combined contribution to the final product, ultimately decreasing the protection of leatherback turtles (an R^2 change from 0.63 to 0.36).

For Marxan, interspecies correlations are handled implicitly as the same habitat can satisfy management priorities for multiple species. Therefore, R^2 values for input species were unchanged among the 2-, 3-, and 4-species runs (Supporting Information). Weighting targets for blue sharks and sea lions were already met in the 2-species run (leatherback turtle and swordfish) due to the direct leatherback turtle–blue shark correlation and the inverse swordfish–sea lion correlation. Both tools displayed trends of decreasing spreads between the mean bycatch species y-intercept and the swordfish intercept and flattening mean slopes as additional species were added. This trend persisted for EcoCast when the 2-, 3-, and 4-species runs were rescaled from 0 to 1 to remove the effect of decreasing weighting magnitude (Supporting Information). Mean slope was always steeper and mean spread was always greater for Marxan across all weighting runs (Fig. 4 & Supporting Information).

Discussion

Decision-support tools provide a method of systematically navigating spatial prioritization, increasing the transparency and defensibility of management scenarios (Margules & Pressey 2000). Although decision-support tools are well established in the field of static management, comparable tools for dynamic management have not been explored, due in part to the infancy of the field. Although EcoCast was explicitly designed as a fisheries sustainability tool and Marxan is intended to be used as a conservation planning tool, Marxan has additional functionality that could confer advantages over EcoCast. Relationships between species habitat suitability (species input) and fishing suitability (tool output) were generally more predictable and interpretable in EcoCast, whereas Marxan produced stronger management recommendations. However, neither decision-support tool clearly outperformed the other. Therefore, the appropriateness of each tool depends on management purpose, resource manager preference, and the technological capacity of tool developers (Table 2).

For dynamic management scenarios that prioritize responsiveness to changing management priorities, EcoCast's algebraic algorithm may be a more appropriate tool. The range of useable species weightings was reduced in Marxan due to the effects of ocean state and species weightings on Marxan's selection frequency. Selection frequency is affected by the total amount of habitat available and patchiness of available habitat (Carwardine et al. 2007), both of which can vary significantly with ocean state. The effect of ocean state was most pronounced in Marxan (Fig. 3 & Supporting Information), especially under extreme species weightings and for leatherback turtles, which have markedly different distributions between warm and cold ocean states (Benson et al. 2011). The relationship between selection frequency and species inputs broke down when species

Table 2. Summary of decision-support tools' capabilities based on management purpose, manager preference, and technological capacity of tool developers.

		EcoCast	*Marxan*
Management purpose			
	predictability	high	low
	interpretability	high	low
	strength of management recommendation	weak	strong
	sensitivity to ocean state	low	high
	sensitivity to interspecies correlations	high	low
Manager preference			
	weighting interpretation	relative	absolute
	examples of applied use	many	few
Technological capacity of tool developers			
	run time (seconds)	3.2	156
	complexity	low	high
	flexibility	low	high

weightings were extreme (±0.9) or near 0. Under extreme weighting scenarios, Marxan must protect nearly all of a given species' habitat, leading to a wide range of habitat suitability values with high selection frequencies. Conversely, when species weightings were close to 0, there were many different possible solutions to meet weighting targets, causing low selection frequencies. The response of Marxan's selection frequency to ocean state and species weightings effectively caps the range of weightings beyond which decreased predictability and interpretability limit utility of the final product.

For dynamic management scenarios that aim to manage many features, Marxan may be a more appropriate tool, due to its increased ability to preserve contrast between waters that are better and poorer to fish and its implicit handling of interspecies correlations. The relationships between species inputs and tool outputs became compressed in EcoCast as more species were added, leading to a reduced range of fishing suitability and weaker management recommendations in the final product (Fig. 4 & Supporting Information). In contrast, Marxan, which operates on the principal of complementarity, preserved a larger range of fishing suitability as species were added, ultimately producing stronger management recommendations. EcoCast was more sensitive to interspecies correlations than Marxan, which could produce unintended management outcomes as additional species are managed. Not surprisingly, the performance of both tools for any one species was compromised as more species were added. Recently, efforts to manage biodiversity have moved away from single-species approaches toward holistic approaches that consider the interdependence of ecosystem components. Although this shift has many positive aspects, cautionary tales from disciplines as diverse as fisheries (Vinther et al. 2004), ESA listed species recovery (Clark & Harvey 2002), and conservation planning (Laitila & Moilanen 2012) indicate there may be a point of diminishing returns, beyond which the inclusion of additional features compromises management outcomes.

Resource manager preference will also affect decision-support tool selection. In Marxan management priorities are interpreted absolutely, such that managers can explicitly state how much of each species habitat is protected or maintained for extractive uses. In the EcoCast algorithm, the management priorities reflected in species weightings are interpreted relatively, such that managers must decide how much each species is prioritized in relation to other species. The EcoCast algorithm's relative interpretation of management priorities requires adjustments as new species are added because the absolute values of the species weightings sum to one. In contrast, management priorities can remain unchanged in Marxan as species are incrementally added, facilitating the uptake of new species data as it becomes available. Explicit criteria for setting meaningful management priorities are well explored in the Marxan literature (e.g., Pressey et al. 2015). Some criteria are only relevant to Marxan's absolute interpretation of management priorities; however, other criteria could be leveraged to inform EcoCast's relative interpretation of management priorities, such as scaling priorities relative to feature rarity, decline, or threat (Lieberknecht et al. 2010). The utility of setting relative versus absolute management priorities will depend on manager preference and their comfort interpreting the parameterization and outputs of different tools.

Resource managers may favor Marxan for its well-established track record in applied management. Marxan is the most widely applied decision-support tool for spatial prioritization and has been used to develop a variety of operational management scenarios such as integrated land-sea planning, terrestrial and marine protected areas, and conservation corridors (Fernandes et al. 2005; Smith et al. 2008; Adams et al. 2017). In contrast, the EcoCast algorithm is relatively new and has only one example of applied use (Hazen et al. 2018). Established practices frequently have significant inertia, and resource managers may prefer the Marxan algorithm for its greater familiarity.

Last, the technological capacity of tool developers will affect decision-support tool selection. The EcoCast algorithm is computationally simple, but this simplicity comes at a cost of reduced flexibility. Conversely, the Marxan algorithm is more complex to run, yet it has much greater flexibility. In Marxan tool developers can adjust parameters that control the cost of planning units, the penalties for missing weighting targets, and the compactness of solutions, which were not explored here. Run time may affect tool selection, which is greatly minimized in EcoCast (in our tests, 3.2 s per day to find a solution for a 4-species run vs. 156 seconds in Marxan).

Other decision-support tools that were developed for static applications, such as Zonation (Moilanen et al. 2009) and C-Plan (Pressey et al. 2009), could be explored in dynamic capacities and might provide functionalities beyond those offered by Marxan or EcoCast. Static conservation planning exercises that include dynamic features must first simplify feature variability, for example, by identifying persistent critical habitat areas such as breeding grounds (Game et al. 2009), or finding features' average distributions across time (Lombard et al. 2007; Grantham et al. 2011). However, these simplified representations can result in significant losses of information on feature variability. Applying the EcoCast algorithm or the dynamic configuration of Marxan in these scenarios can preserve variability by allowing scales of management to align with scales of feature variability, as opposed to forcing scales of feature variability to align with scales of management.

Acknowledgments

H.W. and S.B. were supported by the following: NASA Earth Science Division, Applied Sciences ROSES Program (NNH12ZDA001N-ECOF); NOAA Modeling, Analysis, Predictions and Projections MAPP Program (NA17OAR4310108); NOAA Coastal and Ocean Climate Application COCA Program (NA17OAR4310268); NOAA's Integrated Ecosystem Assessment program; NOAA Bycatch Reduction Engineering Program Funding Opportunity (NA14NMF4720312); NOAA NMFS Office of Science and Technology; and the California Sea Grant Program (NA140AR4170075).

Supporting Information

Sea surface temperature distribution over the analysis period (Appendix S1), a description of the calculation used for effective degrees of freedom (Appendix S2), a correlation matrix of species habitat suitabilities (Appendix S3), effects of changing management priorities and managing additional species for EcoCast and Marxan (Appendix S4), and evidence that the compression seen in EcoCast as the number of species increases represents biological insights, not mathematical artifacts (Appendix S5) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Adams VM, Tulloch VJ, Possingham HP. 2017. Land-sea conservation assessment for Papua New Guinea. University of Queensland, Brisbane, Australia. https://doi.org/10.13140/RG.2.2.26219.13606.

Ball IR, Possingham HP, Watts ME. 2009. Marxan and relatives: software for spatial conservation prioritisation. Pages 185–195 in Moilanen A, Wilson KA, Possingham HP, editors. Spatial conservation prioritization. Quantitative methods & computational tools. Oxford University Press, Oxford, United Kingdom.

Benson SR, et al. 2011. Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea*. Ecosphere **2**:1–27.

Brodie S, et al. 2018. Integrating dynamic subsurface habitat metrics into species distribution models. Frontiers in Marine Science **5**:219. https://doi.org/10.3389/fmars.2018.00219.

Carroll C, Dunk JR, Moilanen A. 2010. Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific Northwest, USA. Global Change Biology **16**:891–904.

Carwardine J, Rochester WA, Richardson KS, Williams KJ, Pressey RL, Possingham HP. 2007. Conservation planning with irreplaceability: Does the method matter? Biodiversity and Conservation **16**: 245–258.

Clark JA, Harvey E. 2002. Assessing multi-species recovery plans under the Endangered Species Act. Ecological Applications **12**:655–662.

Dunn DC, Maxwell SM, Boustany AM, Halpin PN. 2016. Dynamic ocean management increases the efficiency and efficacy of fisheries management. Proceedings of the National Academy of Sciences **113**:668–673.

Eveson JP, Hobday AJ, Hartog JR, Spillman CM, Rough KM. 2015. Seasonal forecasting of tuna habitat in the Great Australian Bight. Fisheries Research **170**:39–49.

Fernandes L, et al. 2005. Establishing representative no-take areas in the Great Barrier Reef: large-scale implementation of theory on marine protected areas. Conservation Biology **19**:1733–1744.

Game ET, Grantham HS, Hobday AJ, Pressey RL, Lombard AT, Beckley LE, Gjerde K, Bustamante R, Possingham HP, Richardson AJ. 2009. Pelagic protected areas: the missing dimension in ocean conservation. Trends in Ecology & Evolution **24**:360–369.

Grantham HS, et al. 2011. Accommodating dynamic oceanographic processes and pelagic biodiversity in marine conservation planning. PLOS ONE **6**(e16552) https://doi.org/10.1371/journal.pone.0016552.

Hazen EL, et al. 2017. WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current. Journal of Applied Ecology **54**:1415–1428.

Hazen EL, et al. 2018. A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. Science Advances **4**:eaar3001. https://doi.org/10.1126/sciadv.aar3001.

Howell EA, Kobayashi DR, Parker DM, Balazs GH, Polovina JJ. 2008. TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles Caretta caretta in the Hawaii-based pelagic longline fishery. Endangered Species Research **5**:267–278.

Klein CJ, Steinback C, Watts ME, Scholz AJ, Possingham HP. 2010. Spatial marine zoning for fisheries and conservation. Frontiers in Ecology and the Environment **8:**349–353.

Laitila J, Moilanen A. 2012. Use of many low-level conservation targets reduces high-level conservation performance. Ecological Modelling **247:**40–47.

Lewison R, et al. 2015. Dynamic ocean management: identifying the critical ingredients of dynamic approaches to ocean resource management. BioScience **65:**486–498.

Lieberknecht L, Ardron JA, Wells R, Ban NC, Lötter M, Gerhartz JL, Nicolson DJ. 2010. Addressing ecological objectives through the setting of targets. Marxan Good Practices Handbook **2:** 24–38.

Lombard AT, et al. 2007. Conserving pattern and process in the Southern Ocean: designing a marine protected area for the Prince Edward Islands. Antarctic Science **19:**39–54.

Margules CR, Pressey RL. 2000. Systematic conservation planning. Nature **405:**243–253.

Metcalfe K, Vaz S, Engelhard GH, Villanueva MC, Smith RJ, Mackinson S. 2015. Evaluating conservation and fisheries management strategies by linking spatial prioritization software and ecosystem and fisheries modelling tools. Journal of Applied Ecology **52:**665–674.

Moilanen A, Kujala H, Leathwick JR. 2009. The Zonation framework and software for conservation prioritization. Pages 196–210 in Moilanen A, Wilson KA, Possingham HP, editors. Spatial conservation prioritization. Quantitative methods & computational tools. Oxford University Press, Oxford, United Kingdom.

Neveu E, Moore AM, Edwards CA, Fiechter J, Drake P, Crawford WJ, Jacox MG, Nuss E. 2016. An historical analysis of the California Current circulation using ROMS 4D-Var: system configuration and diagnostics. Ocean Modelling **99:**133–151.

Pressey RL, Cabeza M, Watts ME, Cowling RM, Wilson KA. 2007. Conservation planning in a changing world. Trends in Ecology & Evolution **22:**583–592.

Pressey RL, Visconti P, Ferraro PJ. 2015. Making parks make a difference: poor alignment of policy, planning and management with protected-area impact, and ways forward. Philosophical Transactions of the Royal Society B: Biological Sciences **370:**20140280.

Pressey RL, Watts ME, Barrett TW, Ridges MJ. 2009. The C-Plan conservation planning system: origins, applications, and possible futures. Pages 211–234 in Moilanen A, Wilson KA, Possingham HP, editors. Spatial conservation prioritization. Quantitative methods & computational tools. Oxford University Press, Oxford, United Kingdom.

Quayle B, Sohlberg R, Descloitres J. 2004. Operational remote sensing technologies for wildfire assessment. Geoscience and Remote Sensing Symposium, 2004. IGARSS'04. Proceedings 2004 IEEE International **3:**2245–2247.

Roberson LA, Lagabrielle E, Lombard AT, Sink K, Livingstone T, Grantham H, Harris JM. 2017. Pelagic bioregionalisation using open-access data for better planning of marine protected area networks. Ocean & Coastal Management **148:**214–230.

Sampson CR, Schrader AJ. 2000. The automated tropical cyclone forecasting system (version 3.2). Bulletin of the American Meteorological Society **81:**1231–1240.

Smith RJ, et al. 2008. Designing a transfrontier conservation landscape for the Maputaland centre of endemism using biodiversity, economic and threat data. Biological Conservation **141:**2127–2138.

Vinther M, Reeves SA, Patterson KR. 2004. From single-species advice to mixed-species management: taking the next step. ICES Journal of Marine Science **61:**1398–1409.

Welch H, Hazen EL, Bograd SJ, Jacox MG, Brodie S, Robinson D, Scales KL, Dewitt L, Lewison R. 2019. Practical considerations for operationalizing dynamic management tools. Journal of Applied Ecology **56:**459–469. https://doi.org/10.1111/1365-2664.13281.

Welch H, McHenry J. 2018. Planning for dynamic process: an assemblage-level surrogate strategy for species seasonal movement pathways. Aquatic Conservation: Marine and Freshwater Ecosystems **28:**337–350.