## Title Page

Title: Simulating Benefits, Costs, and Trade-offs of Spatial Management in Marine Social-Ecological Systems

Running Title: Spatial Social-Ecological Simulation

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## Abstract

Designing effective spatial management strategies is challenging because marine ecosystems are highly dynamic and opaque, and extractive entities such as fishing fleets respond endogenously to ecosystem changes in ways that depend upon ecological and policy context. We present a modeling framework, marlin, that can be used to efficiently simulate the bio-economic dynamics of marine systems in support of both management and research. We demonstrate marlin’s capabilities by focusing on two case studies on the conservation and food production impacts of marine protected areas (MPAs): a coastal coral reef and a pelagic tuna fishery. In the coastal coral reef example, we explore how heterogeneity in species distributions and fleet preferences can affect distributional outcomes of MPAs. In the pelagic case study, we show how our model can be used to assess the climate resilience of different MPA design strategies, as well as the climate sensitivity of different fishing fleets. This paper demonstrates how intermediate complexity simulation of coupled bio-economic dynamics can help communities predict and potentially manage trade-offs between conservation, fisheries yields, and distributional outcomes of management policies affected by spatial bio-economic dynamics.

## Keywords

bio-economic modeling conservation planning fisheries marine protected areas marine spatial planning spatio-temporal modeling

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## Introduction

Communities around the world are increasingly looking to spatial strategies for managing marine ecosystems . For example, the “30x30” movement calls for implementation of marine protected areas (MPAs), a form of spatial management, across 30% of the world’s oceans by the year 2030 (Grorud-Colvert et al., 2021 and references therein). Recent agreements such as the United Nations (UN) agreement on the conservation and sustainable use of marine biodiversity of areas beyond national jurisdiction (BBNJ) calls for expanded area-based management in the high seas. However, designing spatial management strategies to achieve desired objectives – which may include recovery and resilience of overfished species, increased food production and economic well being, and equitable distribution of benefits - is not straightforward. Different species have different resilience to fishing, distributions in space and time, and value to fishing fleets; fishing fleets themselves can have varying ranges of incentives and reactions to policy structures. These dynamics pose challenges even for single-species assessment and management strategies , which are only amplified when we consider management policies specifically designed around multiple species, fleets, and spatial features in the oceans (Field, Punt, Methot, & Thomson, 2006).

To illustrate, policies such as MPAs designed for both conservation and food production must consider factors such as the optimal size and placement of a protected area network given a wide array of life history, species distributions, exploitation levels, fleet dynamics, and policy-dependent behavior (Reimer, Abbott, & Wilen, 2017), all of which may fluctuate over time, particularly given the impacts of climate change. Efforts to effectively design spatial management strategies such as MPAs are further constrained by a lack of empirical evidence describing the size (Ovando, Caselle, et al., 2021) and time required (Nickols et al., 2019) for MPAs to produce substantial effects across a range of social-ecological settings (McClanahan, 2021).

Many models have been developed to support the theory and design of spatial management strategies (see Fulton et al. (2015) for a review). However, these models have tended to be either highly complex and tactical models designed for use in a specific location, or to be extremely stylized representations intended to provide theoretical insights with less relevance for specific applications. This lack of accessible models capable of representing reasonable amounts of complexity presents a challenge to stakeholders charged with marine spatial planning exercises. It also presents a barrier to the scientific community, wherein comparisons across spatial management simulation studies are clouded by discrepancies in underlying model structures beyond differences in the core phenomenon in question.

To help address this challenge, we present a bio-economic modeling tool called [marlin](https://danovando.github.io/marlin/) that allows for efficient simulation of spatio-temporal biological and economic dynamics. marlin allows users to simulate the impacts of marine management policies across a range of species targeted by various fleets across heterogeneous and dynamic seascapes. This model can help users seek Pareto-optimal solutions that produce win-wins or minimize trade-offs across multiple management objectives, such as food production and conservation (Sarah E. Lester et al., 2013).

Here we present the core methods and functionality of marlin, and demonstrate its use in two case-study applications; a coral reef system and a pelagic system. Our results show how interacting ecological, economic, and design attributes can affect the degree of benefits, costs, and trade-offs between conservation and food production outcomes of MPAs. More broadly, this paper demonstrates the functionality of our model and the critical need for considering sufficiently realistic coupled ecological and economic dynamics in policy evaluations.

## Methods

The model presented here focuses on representing the dynamics of heterogeneous habitats and movement dynamics, along with the simultaneous impacts of fishing fleets across multiple species (frequently called “technical interactions”). In its general form, marlin simulates the behavior of populations of spatially explicit biologically independent animal populations with age and subsequent size structure affected by one or more fishing fleets in time steps and a spatial resolution specified by the user.

The front end of the software package accompanying this paper, [marlin](https://danovando.github.io/marlin/), is written in R (R Core Team, 2021) to facilitate use, while the underlying population model is written in C++, integrated through the Rcpp package (Eddelbuettel & Balamuta, 2018), for speed. Users on standard computers should be able to simulate one age-structured population distributed across two-dimensional spatial surface represented by a ten by ten grid of cells over 20 years in fractions of a second.

While marlin does not simulate species interactions, fishing fleets in marlin are capable of targeting and affecting multiple species simultaneously. This allows the model to simulate processes such as fisheries bycatch or effort displacement in a way that accounts for how fleet behavior might affect multiple species in the system. The ability to track the impacts of fishing fleets across multiple species simultaneously is particularly important as very few fishing fleets are truly single species.

We define a few commonly used terms here. *Yields* refers to the volume of catch from fishing activity. *Spawning stock biomass* refers to the total biomass of reproductively mature fish in the water, a function of numbers, weight, fecundity, and sexual maturity at age. We measure the size of the population by the ratio of the *spawning stock biomass* (SSB) in a given time step relative to *unfished spawning stock biomass* (SSB0), SSB/SSB0. An SSB/SSB0 value of 1 means that the population is unfished, a SSB/SSB0 value of 0 means the population is extinct.

As a demonstration of the use of this modeling tool, we explore two general situations

1. Trade-offs and distributional outcomes for food production and multi-species biomass in a coastal coral reef fishery
2. Implications of climate-driven range shifts for MPA design in a pelagic fishery

We chose these two examples to illustrate the use of marlin in contrasting systems in which spatial management strategies such as MPAs are increasingly considered.

Below we provide a summary of the marlin model, as well as details of the case studies. We note that marlin is a complex software package with many options to control detailed behaviors. Given that these specific features will evolve over time, we do not describe in detail every option of the model here. Rather, we focus on the equations and methods describing the core foundations of our tool for efficiently simulating bio-economic dynamics in aquatic systems.

### Model Summary

marlin simulates the dynamics of one or more species, currently best representing fish-like species, using age-structured population dynamics. Ages are then converted to lengths using the von Bertalanffy growth equation with log-normally distributed variation in the length at age. Each time step, species move throughout the simulated seascape using both diffusion and “taxis” (active movement towards preferred habitat), experience natural and potentially fishing mortality, and if in a spawning season spawn using one of the possible forms of density dependence implemented in the model, with the potential to include auto-correlated stochastic deviations in the amount of offspring produced, generally called “recruitment deviates”.

These species can be caught by fishing fleets. A fishing fleet is defined in marlin by a set of fishers that have the same fishing skill, prices, and contact selectivity (Sampson, 2014) for individual species (each of which we denote as a *metier*). For example, both a longline and purse-seine fleet may capture bigeye (*Thunnus obesus*) and skipjack (*Katsuwonus pelamis*) tunas, but the longline fleet can be made much more likely to catch larger bigeye than skipjack, and *vice versa*. It is important to note that contact selectivity reflects the ability of the fishing method in question to capture fish of different sizes that come into “contact” with the gear. The contact selectivity of each of the specified *metiers* will then interact with the distribution of fish sizes and fishing effort in space simulated by marlin to produce a net “population” selectivity, which may differ from the individual contact selectivities of each of the *metiers* (Sampson, 2014; Waterhouse, Sampson, Maunder, & Semmens, 2014). Each fishing fleet distributes its fishing effort in space according to a specified spatial allocation rule (see *Spatial Allocation of Effort* section), for example in proportion to profit-per-unit-effort, conditional on management policies in places such as quotas and/or the presence of any spatial restrictions such as MPAs.

Unconstrained by management, the total amount of effort exerted by each fleet can follow one of two dynamics: open access or constant effort (see *Calculating Total Effort*). Under constant effort, the total amount of effort of each fleet is fixed over time, with the possible exception of attrition due to MPA placement. Under open access, the total amount of effort in a given time step is a function of the profitability of the fleet in the previous time step, evolving until a bionomic equilibrium of zero total profits is reached. Profitability is a function of the volume and price of each species caught, as well as the cost of the total amount of fishing effort per fleet and the travel costs as a function of distance from a port (see *Fleet Dynamics*).

The dynamics of each fleet can be modified by management in a variety of ways. Managers can impose size limits for individual species within each fleet. They can also impose total catch quotas for each species in each time step. When quotas are activated, if the total catch across all fleets for a given species under the model’s effort dynamics would exceed the allowable quota for that species, the total effort for each fleet is decreased proportional to its contribution to the total catch until the quota is satisfied. As an alternative to catch quotas, managers can set an effort cap per fleet, which prevents effort from exceeding a given amount under open access dynamics, though effort may be reduced below this cap if required by the profit equation (i.e. the fleet can choose to fish less than the quota or effort cap).

marlin also allows users to specify closed fishing seasons for one or more species in the system. When all species in a simulation share the same closed seasons, no fishing occurs in those seasons. When not all species share the same closed seasons, fishing still occurs in the closed seasons, but the fleet avoids catching the species for which fishing is closed in a given season, assuming no discard mortality. When closed seasons are in effect, the amount of effort in the next open season is a function of the effort and profits in the last open fishing season. Lastly, managers can specify locations of no-take MPAs, which can change in size and location if needed. When MPAs are implemented, fishing effort that used to operate inside the MPAs can either leave the fishery, or be redistributed outside the MPA (the default behavior).

Users can use the model to explore general properties of spatially explicit social-ecological systems, or can parameterize it to explore key uncertainties of more tactical applications. It is very important note that the parameters of this model cannot be fit to data directly within the marlin package; users must set model parameters themselves based on externally available data and their best judgement.

On the biological side, at a minimum users must for each species they wish to simulate supply the common or scientific name of the species in question, a measure of the level of fishing intensity the species is experiencing at the start of the simulation, and the diffusion rates for adult and larvae. Given a common or scientific name, the model will then input default life history parameters based on FishLife (internet connection required, Thorson, 2020), though users are encouraged to check these values and supply their own life history parameter values when possible.

On the fleet side, users must for each fleet they wish to simulate at a minimum specify the contact selectivity curves for each species caught by the fleet, as well relative price per unit weights greater than 0 for any target species. Species caught by but not targeted by the fleet can be represented by prices of 0 (not targeted) or below 0 (actively avoided).

### Fleet Dynamics

Each fishing fleet (*f*) generates catches or yield (*Y*), revenues (*R*), and costs (*C*) from fishing individual species (*s*) that it targets in a given time step (*t*) and patch (*p*). The fleet then makes decisions around fishing locations and intensity, subject to regulatory constraints, based on the total profitability across all species in space and time.

Revenues for each fleet in a time step are a function of the total amount of each species caught and its price (). The amount caught is a function of the contact selectivity at age of each species for each fleet (), the fishing efficiency of the fleet for that that species (also called “catchability”, *q*), the amount of fishing effort of the fleet in question in that patch in a given time step (*E*), and the total instantaneous fishing mortality (*u*) at age (*a*) (including all other fleets) for that particular species in that patch and time step.

Total catches or yield *Y* are calculated through the Baranov equation (Baranov, 1918), which accounts for the total instantaneous mortality (both fishing and natural, *z*) and divides the total amount of the population biomass (*b*) killed between natural (*m*) and fishing (*u*) sources, with the amount of biomass killed through fishing called “yield”.

Contact selectivity at age is modeled through either a logistic form or a dome-shaped form. The logistic form is based on the lengths *l* at which 50% of individuals are selected by the fishing gear, , and which is the difference between the length at 50% selectivity and the length at 95% selectivity.

We approximate the dome-shaped form as a normal distribution with mean and standard deviation . The normal density function is re-scaled such that the selectivity is 1 at .

Lastly *z* is total mortality, the sum of fishing mortality (*u*) and natural mortality (*m*).

This means that each species experiences a total mortality at age in a time step in a patch, individual fractions of which are portioned off as catches and subsequently revenues for each fleet. Given revenues *R*, we then calculate profits based on revenues and costs. Costs *C* are calculated as a function of base costs per unit effort () as well as potential additional costs per unit effort of fishing in particular patches () for fleet *f*. allows for the cost per unit effort effort to scale non-linearly. Travel costs () are calculated based on the Euclidean distance of each patch to the nearest port of a given fleet, and users can specify any number from zero to the number of patches of port locations. When no ports are specified, travel costs are zero.

#### Calculating Total Effort

marlin allows for two general modes of effort. The simplest is “constant effort”, in which the total effort of each fishing fleet remains constant over time.

The more complex option is “open access”. Under open access, the total amount of effort in a given time step for fleet *f* is a function of the profitability of that fleet in the proceeding time steps in which fishing was open, where controls the responsiveness of fleet *f* to the log of the ratio of total revenues *R* to total costs *C*, and approximates the proportional change in effort in response to a one unit changes in the log revenue to cost ratio.

This is essentially a Gompertz model for fishing effort, that has been used for other theoretical studies of fishing effort dynamics (Thorson, Minto, Minte-Vera, Kleisner, & Longo, 2013).

#### Tuning Fishing Fleet Parameters

The degree of fishing pressure exerted by a given set of fishing fleets on each species is a function of a range of parameters including the total amount of effort (*E*), the contact selectivity ogives (,the curve specifying the proportion of individuals at a given age or size that will be caught by a unit of fishing mortality), fishing cost (*C*), the spatial distribution of the species affected by the fleet, the relative prices across species (), and the catchability coefficient of each fleet for each species (). marlin provides a tuning option to help users achieve desired biological outcomes from their fleets.

Users can tune their fleets in one of two ways, conditional on the underlying population dynamics of the species in question. First, they can specify a target exploitation rate *u* for each species in their simulation. Taking all the other parameters of the model as given, marlin then adjusts the catchability coefficients for each fleet *f* and species *s* such that the equilibrium exploitation rate for each species matches the desired level. Second, they can specify a target total spawning stock biomass under fishing divided by total unfished spawning stock biomass, and the model will adjust the catchability coefficients for each fleet *f* and species *s* such that the equilibrium ratio of fished to unfished spawning biomass for each species matches the desired level.

Users can also tune the fleet dynamics by specifying the ratio of costs to revenues. Price data for use in the model can be obtained relatively simply through literature reviews, market surveys, or local experts, so long as they are converted to the same units of biomass used in the model. However, cost parameters are more complicated, as translating say cost per day of fishing into the same representation of fishing effort used in the model is not straight forward to accomplish. As an alternative, users can specify an equilibrium cost-to-revenue ratio for the fleet, essentially the profit margins of the fleet in question, and marlin will tune the cost parameter to achieve this desired cost to revenue ratio given the other parameters in the model (e.g. price and biomass of the target species). So for example, while users may not have access to exact cost parameters, they may have a general sense that when operating under ideal conditions a given fleet has a profit margin of 10%, i.e. the cost to revenue ratio is 90%. They can input the cost to revenue ratio as 0.9 then and allow marlin to tune the cost parameters accordingly.

#### Spatial Allocation of Effort

Each fishing fleet decides how to allocate its effort in space based on one of four possible spatial allocation strategies. The ideal free distribution (IFD) is the standard method for distributing fishing fleets in spaces (see Gillis (2003) and references therein). However, analytical solutions to the IFD present a number of complications for our model. Our model is capable of tracking multiple fleets at once. This means that the IFD for a single fleet would commonly be modeled as a Nash-equilibrium based on the actions of each of the individual fleet conditional on the actions of all other fleets. While possible to implement, this would slow down our model runs to the point of practically preventing large-scale evaluation of the spatial management policies.

As such we explored a series of “next best” fleet distribution algorithms. While not the IFD in any individual time step, over time they start to approximate the IFD, as each assumes that fleets base their decisions for the current time step on the outcomes in the prior timestep, meaning that the impacts of the actions of other fishing fleets are somewhat internalized. The timeline required for the fleets to reach an equilibrium distribution will vary and depend on factors such as the population dynamics of the species in question (e.g. movement, habitat heterogeneity, growth rates, density dependence) and the number and degree of competition across fleets. Users should explore different simulation times to ensure that any results they wish to use are not simply a reflection of the fleet dynamics fluctuating on their way to an equilibrium condition.

The four possible fleet distribution algorithms are

1. Revenue per unit effort (RPUE): The fleet distributes itself in space based on the realized revenue per unit effort in each patch in the preceding time step
2. Revenue: The fleet distributes itself in space based on the realized total revenue in each patch in the preceding time step
3. Profit per unit effort (PPUE): The fleet distributes itself in space based on the realized profit per unit effort in each patch in the preceding time step
4. Profit: The fleet distributes itself in space based on profit in each patch in the preceding time step

Revenue based spatial distribution is not likely to be very realistic; in general we would expect fishing fleets to respond to profits on some core level. However, due to the complexity of parameterizing cost functions, fleet dynamics are often evaluated based on yield or revenue alone, and so we include those scenarios here to allow users to evaluate the potential implications of this choice. The decision on whether to allocate the fleet based on absolute or relative (per unit effort) metrics is more complex. When effort represents the actions of separate and individual fishing actors (e.g. independent fishing vessels), a per-unit-effort strategy, in which fishers distribute themselves based on the expected catch of their individual efforts, may be more realistic (Hilborn & Walters, 1987). Conversely, a system defined by a sole owner seeking to maximize total profits might be better represented by a fleet model based on total profits.

### Population Model

The underlying population model used is an age structured single-species model in the manner of Ovando, Caselle, et al. (2021). The population model requires many parameters. However, if the user supplies either a scientific or common name for the species in question (scientific preferred), the model will supply default values for that species based on the values reported in FishLife (internet connection required, Thorson, 2020). FishLife provides estimates of core life history parameters for fish species based on a model integrating published values and evolutionary connections. FishLife provides reasonable default values for given species, but these default values should be not be taken as definitive and users should input best available parameters specific to the stock in question if they wish to best represent the dynamics of their specific system, and should check the plausibility of the default values prior to use. All of the life history values can be replaced with user-supplied values as needed and should be for more tactical applications; the default values simply ensure that reasonable and internally consistent values for the species in question are supplied as a starting point.

#### Movement

marlin’s movement dynamics are based on a continuous-time Markov chain (CTMC), as described in Thorson et al. (2021). Within this framework, the model allows for movement to be broken down into three components of *advection* (drifting with currents), *taxis* (active movement towards preferred habitat), and *diffusion* (essentially remaining variation in movement not explained by advection or taxis). For now, marlin focuses just on the diffusion and taxis components of this model, assuming that advection is zero, though future extensions could incorporate advection vectors from oceanographic models. In this way, marlin allows users to run anything from a simple Gaussian dispersal kernel up to a system governed by species that passively diffuse out from a core habitat defined by a dynamic thermal range. The model currently focuses on diffusion and taxis, which allows for general representation of animals following physical or oceanographic features, but research on the incorporation and importance of advective forces would be of value going forward.

We provide a brief overview of the the general CTMC method here (see Thorson et al. (2021) for a detailed description). Under this framework, movement of individuals from each patch to each other patch in the system in a given timestep *t* for life stage *a* of species *s* is defined by a movement matrix . is calculated as a function of diffusion and taxis matrices scaled by the width of the time step (e.g. one year) and the length of the edge of each patch (e.g. one kilometer) specified by the user. This parameterization allows users to set the effective area of the spatial domain through two avenues; the number of patches, which effectively scales the resolution of the model, and the area of each patch, which scales the spatial extent of the simulation.

The individual components (*M*) of the movement matrix () are filled based on an adjacency matrix, which defines whether two patches are both adjacent and water (as opposed to land or another physical barrier), a diffusion rate defined in units of area of a patch per unit of time, and a habitat preference function *H* in units of length of a side of a patch per unit time. For example, if we are defining the time units as years and the distance units as kilometers, for a tuna might be 1,000 . We then use parameters and parameters to translate the diffusion rate to match the time step and patch size used in a simulation. For example, if we were to run a model on a monthly timestep given time units of years, then . If one square patch in the simulation has an area of 100km2, then . This “scale free” parameterization means that appropriate value of can be identified for a species and then set, regardless of the time step or patch size used in the simulation model itself.

The taxis component of the movement process is a function of the difference in habitat quality *H*. The habitat preference function itself can take any form the user wishes. Exponentiating the difference in the habitat preference function between patches turns the taxis matrix into a multiplier of the diffusion rate *D*. As such, when creating habitat layers for simulation, users can tune the scale of the habitat gradient function to result in realistic multipliers of the diffusion rate. This parameterization ensures that the off-diagonal elements of the movement matrix are all non-negative, a requirement of the CTMC method.

For both the diffusion and taxis matrices, we allow for the inclusion of physical barriers to movement (i.e. land). Pairs of patches that are adjacent but in which one or both patches are a barrier to movement are set as non-adjacent. The CTMC model then produces movement dynamics that move around barriers rather than over them. This is different than setting habitat in a patch to zero; an animal will not preferentially move towards a patch with zero habitat all else being equal, but can move over a patch with zero habitat towards another better patch. An example might be a species that lives and feeds on coastal habitats transiting through a patch of open ocean to reach a new feeding ground. In contrast, a physical barrier represents something like a peninsula that an animal must move around to transit from one side to another.

The movement of individuals across patches is then calculated by matrix multiplication of the pre-movement vector of the number of individuals () of species *s* at age *a* in time step *t* across all patches *p* times the matrix exponential of the movement matrix

While this CTMC approach to movement simulation is to date not commonly seen in the marine modeling literature, it has numerous advantages that warrant its seeming complexity. First, the parameters of the model have interpretable biological meaning (e.g. the diffusion rate *D*). Second, when only diffusion is present, the model will generalize to the familiar dynamics of a Gaussian dispersal kernel at whatever spatial and temporal resolution the simulation is set to. Third, the taxis model allow for clearly parameterized active habitat choices by species, allowing us to simulate preferences of species in space and time efficiently. Lastly, the CTMC form has the advantage that its parameters are directly estimable from real data. So, if provided with for example spatial abundance data and a tagging study, users can estimate the diffusion and taxis movement parameters in the same manner as Thorson et al. (2021), and then pass their estimated parameters to marlin for simulation (so long as the estimating method uses the same functional form as the movement model in marlin).

#### Population Growth

For the population model, numbers *N* at time *t* for age *a* are a function of growth, death, and recruitment

where *BH* is the Beverton-Holt recruitment function (Beverton & Holt, 1957) and *SSB* is spawning-stock-biomass. Per convention, the model allows for a “plus group”, wherein rather than tracking numbers of every possible age, individuals greater than or equal to a given maximum age are grouped together.

Spawning stock biomass *SSB* is calculated by converting age to mean length at age, calculating weight at age, maturity at age, and then calculating spawning stock biomass as the sum of spawning potential at age in a given time step, taking into account the potential for hyperallometry in the manner of Marshall, Bode, Mangel, Arlinghaus, & Dick (2021). Age is converted to length through the von Bertalanffy growth equation given parameters asymptotic length (), growth (*k*) and theoretical age at length zero () assuming log-normally distributed variation *u* in the length at age with CV .

Users can manually supply a vector of of natural mortality at age (*m*). Or, they can supply one value of natural mortality which is then converted into mortality at age through one of two means. Under the default behavior, natural mortality at age given a target mean mortality across all ages is calculated using a length-inverse mortality function (Lorenzen, 2022).

Alternatively, users can set mortality at age to be constant

Biomass *B* at age is then given by the weight at length equation governed by a scaling coefficient and an exponent that controls the rate at which volume scales with length

The proportion of sexually mature individuals (*mat*) at a given age is then calculated as a logistic function where is the length at which on average 50% of individuals are sexually mature, and is the unit of length beyond at which on average 95% of fish are sexually mature.

Spawning stock biomass at time *t* is then calculated as a function of the numbers at age, the maturity at age, and the weight at age raised by a parameter . When is greater than 1, the species is said to experience hyperallometric fecundity, i.e. fecundity increases faster than weight.

#### Recruitment

Recruitment (i.e. the number of age 1 individuals entering the population) follows Beverton-Holt dynamics parameterized around steepness (*h*) with log-normally distributed recruitment deviates . When steepness is one recruitment is independent of spawning biomass. As steepness approaches 0.2 recruitment becomes a linear function of spawning biomass. marlin allows users to specify a target unfinished spawning stock biomass (), which will be achieved by tuning the total unfished recruitment (), given the remaining life history parameters and independent of any characteristics of the fishing fleets.

We allow for five variants in the timing of density dependent recruitment, building off of Babcock & MacCall (2011) :

1. Global density dependence: Density dependent recruitment is a function of the sum of spawning biomass across all patches, and recruits are then distributed according to habitat quality

where is is a vector of recruits under unfished conditions in a given patch.

1. Local density dependence: Density dependent recruitment occurs independently in each patch and recruits are retained in their home patch.

1. Local density dependence then disperse: Density dependent recruitment occurs independently in each patch and recruits are then dispersed.

where **dl** is the recruitment movement matrix

1. Post-dispersal density dependence: Larvae are distributed throughout the system, and then density dependent recruitment occurs based on the density of spawning biomass at the destination patch.

1. Global density dependence allocated by spawning biomass: Density dependence is a function of the sum of spawning biomass across all patches, and recruits are then distributed according to the distribution of spawning biomass

Log-normal recruitment deviates are calculated with the potential for autocorrelation defined with strength

And log recruitment deviates are converted to raw units using the bias correction factor

#### Reference Points

Fisheries management is often concerned with measuring stock status relative to maximum sustainable yield (MSY) based reference points, though the exact level of stock status relative to MSY reference points desired by management or societal objectives may vary widely. MSY based reference points present a problem for a multi-fleet and spatial-temporal model such as marlin. MSY and the fishing mortality rate that would produce MSY, , are a function of fishery selectivity. Fishery selectivity in this model can vary by fleet, and species can be distributed unevenly in both space and time. This means that the net effective fishing selectivity on a species can vary depending on the dynamics at a given moment, making the definition of an equilibrium concept such as MSY challenging (Berger et al., 2017 and references therein).

As such, we do not report MSY based reference points in the model by default, with the exception of the spawning stock biomass at MSY () which tends to be better conserved across selectivity patterns as it is primarily a function of the mortality and flow of recruits relative to the maturity ogive. There are many different strategies for estimating reference points in spatially explicit systems (Kapur et al., 2021). We leave it to users to define and find relevant reference point as required by their specific needs.

### Case Studies

We include two examples demonstrating how marlin can be used to support marine spatial planning. In the first, we show how marlin can be used to compare the total and distributional impacts of MPAs designed in a heavily fished coastal coral reef ecosystem. In the second, we demonstrate how marlin can be used to assess components of climate resilience of alternative MPA design strategies in a pelagic system.

Each of the case studies contains too many parameters and options to be succinctly presented in the text here, and we are concerned that attempting to duplicate all of the parameters of the model within the text would simply introduce errors and confusion. As such, and since these results are for illustrative purposes only, readers should consult the accompanying code to view the precise details of each simulation. Targeted applications must carefully consider and document all decisions made around model parameters.

#### MPA Design Strategies

We make use of three potential “rule of thumb” MPA design strategies in our case studies

1. *Rate*: MPAs are placed based on the pre-MPA SSB/SSB0 weighted catch relative to the total catch in a patch. So, patches with high rates of catch of depleted species relative to total catch are prioritized.
2. *Target Fishing*: MPAs locations are prioritized proportional to fishery catches. Patches with high total catches are prioritized over patches with low catches.
3. *Spawning Ground*: MPAs are centered on the grounds of a known spawning aggregation. This strategy is only used in the coral reef case study.

To our knowledge, MPAs are never randomly placed; their locations are decided based on stakeholder negotiation given available information and objectives. In theory, the design of MPA networks can be optimized through the use of a modeling framework, and depending on the validity of the model, this process is likely to produce better outcomes than manually-designed strategies (Rassweiler, Costello, Hilborn, & Siegel, 2014; Rassweiler, Costello, & Siegel, 2012). However, designing optimal MPA networks becomes increasingly difficult as the range of objectives and the complexity of the model increase. Therefore, we focus here on the design and performance of these more rule of thumb design strategies that may be more accessible to a wider range of users. We allow all MPAs to be designed in a mosaic fashion in these examples, but users can easily extend the analysis to compare outcomes between contiguous (MPA is made up of one continuously connected block) and mosaic (MPAs can be separated in space) MPA designs (Pons et al., 2022) by developing and passing their own MPA design algorithms to the model.

#### Coastal Coral Reef Fishery

In our coastal coral reef example, we model the dynamics of four tropical Pacific species: a grouper (*Epinephelus fuscoguttatus*), a shallow-reef snapper (*Lutjanus malabaricus*), a deep-reef snapper (*Pristipomoides filamentosus*), and a reef shark (*Carcharhinus amblyrhynchos*). The simulated groupers undergo a mass migration to a spawning aggregation once per year, followed by the sharks. Shallow-reef snappers stay in reefs closer to shore above a steep drop-off year-round, while deep-water snappers stay in the deeper reefs past the drop-off ([Figure 1](#fig-coral)).

These species are targeted by two different fleets. Fleet One primarily targets the grouper and near-shore snapper populations, but will land any incidentally captured sharks. Fleet One has a logistic selectivity pattern for all species, as they retain any fish caught for consumption or sale. Fleet One is totally dependent on fishing for their livelihood, meaning the local community takes advantage of every possible opportunity to fish, and as such we model it as a “constant effort” fishery. Due to having less efficient boats, Fleet One has a higher cost per distance coefficient than Fleet Two. Fleet One’s home port is located on near the site of the grouper spawning grounds.

Fleet Two is a more commercial fleet that primarily targets the snapper populations. This fleet primarily sells their catch to local restaurants and distributors where plate-sized fish are prized, and so for both snapper and grouper Fleet Two has a dome-shaped selectivity pattern (Kindsvater, Reynolds, Sadovy de Mitcheson, & Mangel, 2017). While plate-sized deep snapper are the primary target of Fleet Two, we model Fleet Two’s selectivity for deep snapper as logistic due to high levels of discard mortality for deep-water snapper resulting from barotrauma. Fleet Two catches groupers, though less than Fleet One, and receives no price for sharks due to the requirements of a certification program through which they sell their deep-water snapper. Accidental captures (bycatch) of sharks do occur, which results in mortality. Fleet Two operates under open-access dynamics, as fishing is not the only means of subsistence for this community; short-term effort expands and contracts in response to profitability of the primarily grouper-driven fishery. Fleet two’s home port is located in the northwest corner of the simulation space.

We used marlin to simulate the outcomes for both food production and conservation for each of the species and both of the fleets as a function of both MPA size and MPA design strategy. For this exercise, MPAs are placed with perfect information and have no design constraints for continuity (i.e. the selected MPA design can be as patchwork as dictated by the data). We ran the simulation for in quarter year time steps for 20 years () and set the area of each patch to be 5km2 (), using 144 patches for a total area of 2,000 KM2.

#### Pelagic Fishery

We model our pelagic case study loosely on the characteristics of the Western and Central Pacific Ocean (WCPO) tuna fisheries. Note that this is an illustrative example only and simulated stock status, species distributions, or outcome projections presented here should not be interpreted as a indicative of the current or future state of the WCPO. We simulate trajectories of 9 species commonly caught in the region, including both the highly abundant skipjack tuna and the heavily depleted oceanic whitetip shark (*Carcharhinus longimanus*) ([Figure 2](#fig-blue-ssb)). We use publicly available data on catch-per-unit-effort of each of these species from the WCPO as a very rough proxy for baseline habitat distributions, noting that where possible, fishery-independent abundance indices would be preferable ([Figure 3](#fig-blue)).

These pelagic species are caught by a longline fleet that primarily targets large adult tunas such as bigeye and yellowfin for high-grade consumption, and a purse-seine fishery that primarily targets skipjack tunas for bulk canning. Contact selectivities were modeled as logistic for the longline fleet, and dome-shaped for the purse-seine fleet, with selectivity values set to broadly match the patterns reported in relevant [stock assessments](https://oceanfish.spc.int/en/ofpsection/sam/sam/210-stock-assessment-input-and-result-files-) for each species. Both fleets operate under open-access dynamics with an effort cap. The effort cap was set at the level of effort that resulted in the desired levels of SSB/SSB0 for each species under open-access dynamics ([Figure 3](#fig-blue)), intended to simulate a scenario where managers step in to prevent further expansion of fishing effort in a fully developed fishery. For forward-simulation, open-access dynamics can result in effort decreasing in response to profitability, but cannot result in effort beyond the effort cap set for each fleet.

For this exercise, we focused on using marlin to assess resilience of the selected *Target Fishing* and *Rate* MPA design strategies to a climate-driven range shift. Specifically, we simulate an extreme example where the centroid of each population shifts northward at a rate of 0.2 patches per year over a 20 year time horizon ([Figure 2](#fig-blue-ssb)). We designed MPA networks given the conditions in the starting year, and then held that network constant over the years of the experiment, running one simulation with and another without the climate-drive range shift. We then compared the effects of this range shift on food production and conservation outcomes from MPA networks designed based on the pre-range shift world. We ran the pelagic simulation at a quarterly level ( = 1/4 year), and set the area of each cell to be roughly 97,000 KM2 across 144 patches each with a side length of roughly 311 KM, for a total area of 14,000,000 KM2, broadly commensurate with the area of the WCPO.

## Results

### Coastal Coral Reef Fishery

MPAs were capable of producing a range of positive and negative outcomes for food security and conservation in the coral reef case study depending on the design strategy used and the size of MPA implemented. Both of the MPA design strategies were capable of increasing fisheries yield for the more “industrial” Fleet Two, up to a value of 16%, even when MPAs covered more than 50% of the simulated area. However, the more “artisanal” Fleet One only benefited from MPAs under the *Spawning Ground* design strategy, with a maximum increase of 5%; the *Target Fishing* design strategy produced a roughly linear decrease in fishing yields as a function of increasing MPA size ([Figure 4](#fig-coral-results) A).

On the conservation front, MPAs were uniformly beneficial to the spawning biomass of all species under the *Target Fishing* design strategy, with the most rapid increases in spawning biomass for the deep snapper population. The *Spawning Ground* strategy primarily benefited the shallow snapper population, producing little change in the grouper population and decreasing spawning biomass of both the deep snapper and reef shark populations for MPA sizes covering less than 50% of the simulated area ([Figure 4](#fig-coral-results) B).

In total, the *Spawning Ground* strategy was capable or providing net increases in fishing yield (summed across both fleets) of up to roughly 7%, with positive net yield impacts up to network size of nearly 60% of the area. However, even MPAs covering 60% of the area only produced a maximum increase of roughly 5% in total SSB/SSB0 when designed around the spawning ground. Conversely, the *Target Fishing* design strategy was capable of producing a nearly 25% increase in total SSB/SSB0 for the same MPA size, but at a much greater cost to the total food production from the system’s fisheries ([Figure 4](#fig-coral-results) C).

### Pelagic Fishery

Yields of the purse-seine fleet were more resilient to the range shift under the *Rate* design strategy, while the longline fleet had the opposite result. Under the *Rate* strategy, longline yields were relatively stable across a large range of MPA sizes under the status quo conditions, but declined rapidly under the range shift conditions. For the purse-seine fleet, yields were more stable under the range shift conditions under the *Target Fishing* design scenario, but declined quickly as a function of MPA size under the status quo conditions ([Figure 5](#fig-blue-results) A). The *Target Fishing* strategy produced better yield outcomes for both fishing fleets under the range shift conditions, but the *Rate* strategy performed best under the status quo.

The primary tuna species (bigeye, skipjack, and yellowfin) were most sensitive to design strategy and climate scenario, with the *Target Fishing* strategies producing for example rapid conservation gains for bigeye and skipjack under the status quo, while the *Rate* strategy resulted in small net conservation losses for both species until the MPA became extremely large. However, under the range shift scenario the MPAs had little impact on many of the tuna populations until the MPA size became extremely large, due to movement of the primary fishing grounds outside of the current hotpots where the MPAs are placed based on status quo conditions. The 20 year time horizon simulated here was not enough to produce substantial gains for any of the shark species even with 100% closures except for the more rapidly growing blue shark ([Figure 5](#fig-blue-results) B).

## Discussion

Marine ecosystems are driven by complex social-ecological dynamics. Communities must often make decisions on how to manage these systems based on limited empirical evidence. Modeling tools such as the one presented here can help users answer scientific questions and design marine management policies informed by a better understanding of sensitivities to key uncertainties. In this paper we have documented the core system of equations underlying marlin, and demonstrated how marlin can be used to support marine resource management.

### Insights from Case Studies

The variation in both the magnitude and distribution of costs and benefits stemming from alternative design choices and states of nature shown in our case studies demonstrates the value in our method. For example, our coastal coral reef example illustrates both the potential for MPAs to benefit conservation and food production in these systems, and the potential for the same MPA to benefit some fleets and species while harming others when fishing fleets affected by an MPA do not share the same objectives and species are not uniformly distributed. Our pelagic case study illustrates how marlin can be used to assess the climate resiliency of spatial management strategies, and identify strategies that best meet the needs of both current and future conditions. Results from this type of work could be used to help prioritize communities and species at particular risk to climate change impacts.

Our coastal coral reef case study results show the sensitivity of conservation and food security outcomes of MPAs to alternative design scenarios, holding constant other social-ecological variables. The *Spawning Ground* MPA network was able to provide more equitable yield outcomes across the two fishing communities, whereas the *Target Fishing* MPA network only benefited Fleet Two ([Figure 4](#fig-coral-results) A). This is because Fleet One has two primary fishing grounds; the spawning grounds, and the offshore area where the deep snapper live. Fleet Two primarily fishes in the northern portions of the simulation grid. Under the *Spawning Ground* strategy, while Fleet One quickly losses fishing grounds on the spawning grounds, it can compensate for this by moving offshore and fishing the deep snapper population harder, while also being able to fish some of the spillover of snapper from the spawning ground closure. This displacement of Fleet One’s fishing effort is why biomass of deep snapper actually declines under the *Spawning Ground* strategy.

Conversely, most of the catch in the fishery comes from the nearshore and deep water snapper populations, which overlaps with both of Fleet One’s fishing grounds. The *Target Fishing* strategy then begins closing both the nearshore and offshore snapper fishing grounds, resulting in too much of a loss in fishing grounds for Fleet One to be offset by spillover from the MPAs. As a result of primarily placing MPAs on Fleet One’s fishing grounds, Fleet Two gains spillover benefits at little cost to their fishing grounds until the MPAs reach their fishing grounds once protection nears 100%.

By protecting both the spawning ground and the offshore areas, the *Target Fishing* network provides conservation benefits to all of the species, in contrast to the *Spawning Ground* strategy that only provides meaningful conservation gains to the snapper population up until very large MPA sizes. Our result that protection of a dedicated spawning ground did not provide substantially greater conservation outcomes for the species using that spawning ground (groupers and sharks) than an alternative design strategy is supported by other modeling studies that show that the impacts of spawning ground protection on conservation and yields may be highly variable, and that displacement of high levels fishing effort from the spawning grounds can offset potential conservation gains of the protection (Grüss, Robinson, Heppell, Heppell, & Semmens, 2014). That being said there is also evidence for the benefits of spawning aggregation protection (Erisman et al., 2015) , and our results are not nearly sufficiently resolved to provide any general statements as to the relative value of spawning aggregation protection relative to other design strategies. Further research could for example alter both the distribution of species in space and the susceptibility of the species to fishing gear when aggregated.

The two design strategies produced very different outcomes in terms of total changes in yield and conservation outcomes for the coral reef case study ([Figure 4](#fig-coral-results) C). Both MPA network design strategies were capable of producing net “win-win” outcomes in which both food security (as measured by change in total fisheries yields) and conservation (as measured by change in SSB/SSB0). However, in general for the same size MPA network the *Spawning Ground* design strategy produced better food security outcomes but worse conservation outcomes, and *vice* *versa* for the *Target Fishing* strategy. The coral reef case study shows how the modeling framework presented here can help stakeholders explore how different management strategies affect outcomes both in total ([Figure 4](#fig-coral-results) C) and across species ([Figure 4](#fig-coral-results) A) and fishing communities ([Figure 4](#fig-coral-results) B).

Turning to our Pelagic Ecosystem case study, the yield outcomes of the purse-seine fleet were much more sensitive to the presence of a range shift than the longline fleet, particularly under the *Target Fishing* design strategy. This is because the purse-seine fleet primarily targets skipjack tuna, which in this simulation are concentrated in a relatively narrow latitudinal band ([Figure 3](#fig-blue)), and the purse-seine fleet makes up a large portion of the total catch in the simulated fishery. So, the “Target Fishing” strategy starts by closing off the main purse-seine fishing grounds, which while only small part of the spatial domain of the model represents a large portion of the purse-seine fleet’s fishing grounds, resulting both in more rapid conservation gains and fishery losses under the status quo species distributions. The *Rate* strategy places more MPAs in areas that are of lesser importance fo the purse-seine fleet but overlap more with species such as oceanic whitetip shark. Conversely, the purse-seine fleet appears to do have better MPA yield outcomes under the range shift scenario, not because of rebuilding of the skipjack population, but due to future fishing grounds being essentially unprotected by smaller MPAs targeting the current skipjack distribution ( [Figure 5](#fig-blue-results) ).

The conservation outcomes of the skipjack, bigeye, and yellowfin tunas were among the most sensitive to range shifts, whereas even complete closure of the region was not sufficient to see significant increases in severely depleted species like oceanic whitetip sharks within the 20-year timeline of the simulation. Future research could be conducted then to see what sorts of timelines might be needed to see recovery of these species, and which design strategies result in the fastest recovery at the lowest cost to other objectives such as food security.

These case studies are intended to illustrate the capabilities of the model and the importance of considering the bio-economic dynamics represented in marlin; it is beyond the scope of this paper to provide broader conclusions about the performance of MPAs under different contexts or a comprehensive comparison of simulation and empirical results of MPAs around the world. That being said, the kinds of dynamics resulting in our case studies are well supported by both modeling and empirical studies. Our results support conceptual (Gaines, White, Carr, & Palumbi, 2010; Hilborn et al., 2004) and empirical (Ban et al., 2019) evidence that under the right conditions no-take MPAs can benefit fisheries and conservation. Rassweiler et al. (2014) demonstrated that the kinds of design choices presented in our case studies can greatly drive MPA outcomes.

MPAs based around coral-reef style ecosystems have been extensively studied around the world, with much of the empirical evidence of their performance centered on demonstrating higher metrics such as biomass densities inside protected areas relative to fished reference areas (“response ratios,” S. E. Lester et al., 2009). Our model predicts a similar rapid increase of the simple ratio of mean biomass inside MPAs relative to outside (Fig. S5, acknowledging that designing a proper response ratio would require controlling for habitat characteristics and MPA design criteria). However, despite producing clear response ratios, the net conservation and fishery outcomes of our simulated coral-reef ecosystem MPAs were not nearly as large or clear as the response ratio results ([Figure 4](#fig-coral-results)); this result is supported by works such as Ferraro, Sanchirico, & Smith (2018) an Ovando, Caselle, et al. (2021) showing that response ratios alone may be a poor indicator of the net causal impacts of MPAs at the population scale.

Studies such as Gilman, Chaloupka, Fitchett, Cantrell, & Merrifield (2020), Abbott & Haynie (2012), Tammy E. Davies et al. (2018) and Pons et al. (2022) provide empirical support for our case study results showing that MPAs can produce trade-offs across the conservation of different species and fleets when the spatial-temporal distributions and life history traits of affected species are heterogeneous, and MPAs result in some degree of effort displacement or concentration in the remaining fishing grounds. Hampton et al. (2023) supports our pelagic case study result showing that both conservation and fishery impacts of MPAs on the highly mobile species of the open oceans can be limited unless protected areas are very large. Brown et al. (2018) supports our result showing how heterogeneity in the behavior and objectives of fishing fleets sharing an ecosystem can affect the magnitude and equity of fishery reform outcomes. T. E. Davies, Maxwell, Kaschner, Garilao, & Ban (2017) discusses the importance of considering the potential of climate driven range shifts when assessing spatial management policies; our work builds on this by allowing users to not just simulate species distributions but also distribution of biomass and age composition of fish in space and time under climate change.

### Putting marlin In Context

The role of this paper is not to conduct a review of the many tools for spatial-temporal modeling available in the literature, each of which provide useful functionality for specific applications. However, we highlight here the specific gaps that we feel marlin fills in the modeling literature and in the policy support toolbox using some selected publications. More end-to-end models such as ATLANTIS (Audzijonyte et al., 2019) , OSMOSE (Shin & Cury, 2001), Ecopath with Ecosim (Christensen & Walters, 2004), POSEIDON (Bailey et al., 2019), DISPLACE (Bastardie, Nielsen, & Miethe, 2013), or SEAPODYM (Lehodey, Senina, & Murtugudde, 2008) are capable of representing tremendous amounts of complexity, but can be extremely time consuming to design and run. marlin allows some of the realism of these more end-to-end models while being simpler and faster to parameterize and run.

Tools such as virtualspecies (Leroy, Meynard, Bellard, & Courchamp, 2016), STEPS (Visintin et al., 2020), RangeShifter (Bocedi et al., 2014), and [SMS](https://www.aquaveo.com/software/sms-surface-water-modeling-system-introduction) can be efficiently constructed to model the dispersal and distribution of species in space and time as a function of environmental covariates. However, these typically require specifying a covariate-response curve without explicitly acknowledging how this arises from habitat-specific movement and demography (virtualspecies), or model movement using a dispersal kernel (RangeShifter, STEPS) or a least-cost path algorithm (SMS, STEPS). By contrast, marlin uses a continuous-time Markov chain movement model, which integrates multiple paths (including their path-dependent probability based on intervening habitat types and species preferences) while using scale-free parameters that can be measured experimentally in laboratory or tagging studies. In addition, marlin allows for simulating not only the distribution of the species but also biomass, age, and length structure in space and time.

Simplified bio-economic models such as those used in Hastings, Gaines, & Costello (2017), Sala et al. (2021), and Cabral et al. (2019) can be applied at scale and provide analytically tractable results, but as a result must abstract over many bio-economic dynamics that can be important for more tactical applications. Our results demonstrate how nuances in fleet dynamics and species distributions can dramatically impact MPA outcomes. marlin allows for more realistic representations of spatial social-ecological systems while maintaining processing speed.

marlin does not represent trophic interactions. Anthropgenic changes in species abundance can result in trophic cascades. However, studies such as Gilman et al. (2020), Ovando, Caselle, et al. (2021), Bruno, Côté, & Toth (2019) , and Malakhoff & Miller (2021) found no clear signs of MPA driven trophic cascades within the first decades of protection. Signals of trophic cascades may be masked by variations in the direction and strength of species interactions driven by environmental context (Liu & Gaines, 2022), or may simply take longer to develop detectable effects than the coverage of many time series of MPAs. While marlin does not incorporate trophic interactions, what empirical evidence we have does not suggest that management-mediated trophic cascades are so common and clear that they must be incorporated into any credible multi-species simulation model. There is value in capturing other dynamic bio-economic processes, as done here, even if that comes at the expense of modeling trophic interactions. However, research on the trophic impacts of spatial-temporal management actions is clearly of value and models like Atlantis (Audzijonyte et al., 2019), Ecopath with Ecosim (Christensen & Walters, 2004), and EASI-Fish (Griffiths, Kesner-Reyes, Garilao, Duffy, & Román, 2019) can help users explore those kinds of trophic processes, in the manner of Baskett, Micheli, & Levin (2007).

### General Recommendations for Use

Marine social-ecological systems are highly complex. The model presented here is designed to help users explore the impacts of different variables on policy outcomes. But, that freedom comes at a cost, namely that users have a large number of options at their disposal that they must decide on. Our recommended strategy is for users to try and narrow down a list of parameters that they feel are sufficiently “known” and another list of parameters that are highly uncertain and / or contentious which the users feel may impact results. Where possible, parameters from locally estimated stock assessment models can be used to provide a foundation around which sensitivity analyses around specific uncertainties of interest (Berger et al., 2017), though care should be taken interpreting population selectivity curves estimated from stock assessment as contact selectivity curves required as inputs to marlin (Sampson, 2014).

For example, a community seeking to a model a well-studied coastal coral reef ecosystem might leave as fixed the habitat distribution (as represented by reef locations) and general life history of the species in question (growth rates, age at maturity, etc). But, within those constraints, the users may wish to test the sensitivity of proposed MPA networks to key unknowns such as adult and larval dispersal rates or the the economic incentives and contact selectivity of the fishing fleets. As an example of this, we ran an alternative version of our coral reef case study in which Fleet Two was assigned logistic selectivity for the snapper and grouper species, rather than the dome-shaped selectivity presented in our main results. We found that the impacts of MPAs on conservation and food security were relatively insensitive to the form of contact selectivity specified for Fleet Two (Fig.S1). This does not mean that knowing the “correct” form of contact selectivity may not be extremely important in providing accurate assessment results (Waterhouse et al., 2014), but rather that in this case misspecifying the contact selectivity curve is projected to have little impact on the simulated outcomes of MPAs, conditional on holding other parameters constant.

Given a set of model runs, the choice of whether to use those results “strategically” or “tactically” will depend on the needs of the user. That being said, since. marlin is not fit to data directly it is more easily applied to strategic questions. For example, the two case studies presented in this paper provide general strategic insights into the sensitivity of outcomes to design choices range shifts. The extent to which users are comfortable using the outputs of marlin tactically will depend on the confidence they have in their parameterization of the model relative to the precision policy-makers require in order to make a decision.

marlin is just one model out of many that can be used to inform marine management. Other models may be better suited to address specific forms of complexity. Particularly for more tactical applications, we would encourage users to explore multiple modeling frameworks to help design policies that are likely to be robust to many different kinds of complexities.

At this time, marlin assumes that all evaluated policies are perfectly implemented; e.g. that MPAs are 100% no-take and perfectly enforced, that quotas and closed seasons are respected, that there is no discard mortality, etc. In reality no policy is perfectly implemented, and users should consider the extent to which the policies they simulate are actually feasible to implement. There is value though in being able to simulate and compare the outcomes of perfectly implemented policies to isolate the concept of the policy itself from its implementation. That being said, future work may add the capability for imperfect implementation to the model.

Fish populations often exhibit variation in demographic traits such as growth, maturation, and mortality across dimensions such as space, time, and sex. Models such as Stock Synthesis (Methot Jr. & Wetzel, 2013) capture these processes through the use of “morphs”. marlin does not currently allow for these kinds of processes explicitly, though users could simulate different populations of the same species with different life history traits as separate stocks. Users should be cautious interpreting simulation results from marlin for species in which these sorts of dynamics are likely to be particularly prevalent. For strongly sexually dimorphic species, we would recommend picking the sex most likely to drive the outcomes of management policies, which is often females given the general prevalence of eggs as the limiting reproductive material in marine ecosystems. Users should also proceed with caution using marlin for species with more complex reproductive biology, such as sex-changing fish (Kindsvater et al., 2017).

## Conclusions

marlin complements the existing spatial marine modeling literature by allowing scientists, decision makers, and other stakeholders to efficiently examine the impacts of realistic bio-economic dynamics on academic and applied problems. For example, scientists could use marlin to consider the relative importance of different biological variables in affecting policy outcomes. Managers could use marlin to assess the potential of proposed MPA networks to achieve stated objectives, such as maximizing conservation gains for a threatened species while minimizing or removing negative impacts to affected fishing fleets. We envision marlin being applicable to research on dynamic ocean management, range shifts, management strategy evaluation, policy interactions, and spatial stock assessment. marlin can help researchers generate data for further testing of the performance and design of spatially explicit integrated population models, in the manner of Bosley et al. (2022). In addition, the process-based movement model used in marlin can directly use empirical estimates of movement dynamics derived in the manner of Thorson et al. (2021), providing a link between empirical and simulation based approaches to marine resource management that has been challenging to implement in spatial simulations (Berger et al., 2017).

Fisheries models, assessments, management have often abstracted away many of the spatial-temporal complexities of marine social-ecological systems (Berger et al., 2017; Ovando, Liu, Molina, & Szuwalski, 2021). The modeling framework described here can help facilitate the science and application of spatial fisheries management by supporting the simulation of different spatial-temporal dynamics to aid in testing of various aspects of the marine resource management process.

Even the most complex marine model is a stylized cartoon of the true dynamics of ocean ecosystems. However, for all their limitations, models can help users understand factors that drive the performance of marine management strategies. The goal of this tool is to empower people to design policies based on evaluation of key uncertainties and trade-offs, and in doing so support more effective and equitable marine resource management.

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## Data Availability Statement

The code, novel code, data, and materials needed to reproduce the results and all aspects of this manuscript are publicly available at https://github.com/DanOvando/marlin-paper, with supporting novel code available at https://github.com/DanOvando/marlin/. Upon acceptance, all data, materials, code, and novel code needed to reproduce the results and all aspects of this manuscript will be publicly available via GitHub at https://github.com/DanOvando/marlin-paper and https://github.com/DanOvando/marlin/ and through figshare at https://figshare.com/articles/preprint/marlin-paper/21843582

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## Figure Legends

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| Figure 1: Distribution of fish spawning biomass (cell color, yellow = higher, blue = lower) each season (columns) under unfished conditions. The x-axis represents longitude, y-axis latitude. Numbers show the approximate location of each fleet’s (one or two) port. Columns indicate quarterly seasons that repeat each year. |

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| Figure 2: Spawning biomass divided by unfished spawning biomass in the time period prior to implementation of MPAs for the pelagic case study. Simulated species include skipjack tuna, yellowfin tuna (Thunnus albacares), bigeye tuna, shortfin mako (Isurus oxyrinchus), swordfish (Xiphias gladius), albacore tuna (Thunnus alalunga), blue shark (Prionace glauca), silky shark (Carcharhinus falciformis), and oceanic whitetip shark (Carcharhinus longimanus). |

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| Figure 3: Distribution of unfished spawning biomass in space under status quo (left column) and range-shifted (right column) conditions for blue-water simulation for each species. The x-axis represents longitude, the y-axis latitude. |

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| Figure 4: Percent change in yield per fleet (A) and SSB/SSB0 (spawning biomass divided by unfished spawning biomass) per species (B) as a function of MPA size and MPA design strategy for the coastal coral reef case study. Percent change in total yield across both fleets (y-axis) and total SSB/SSB0 across all species (x-axis) and placement strategies (line color) (C). Color of points along each line in panel C indicates the percent of the simulation area in an MPA. All results reflect outcomes after 20 years of simulated MPA protection. |

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| Figure 5: Change in yield (A) and SSB/SSB0 (spawning biomass divided by unfished spawning biomass) (B) as a function of MPA size and design strategy by fishing fleet and species. Blue lines indicate impacts of MPAs under status quo habitat, red impacts under climate-driven range shift. Results reflect the outcome of 20 years of simulated MPA protection. |