

1 **Title Page**

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

4 Running Title: Spatial Social-Ecological Simulation

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20 **Abstract**

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

36 **Keywords**

37 Bio-economic modeling; Conservation planning; Fisheries; Marine protected areas; Marine
38 spatial planning; Spatio-temporal modeling

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57 **Introduction**

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

73 To illustrate, policies such as MPAs designed for both conservation and food production must
74 consider factors such as the optimal size and placement of a protected area network given a
75 wide array of life history, species distributions, exploitation levels, fleet dynamics, and policy-
76 dependent behavior (Reimer et al., 2017), all of which may fluctuate over time, particularly
77 given the impacts of climate change. Efforts to effectively design spatial management strate-
78 gies such as MPAs are further constrained by a lack of empirical evidence describing the size
79 (Ovando, Caselle, et al., 2021) and time required (Nickols et al., 2019) for MPAs to produce

80 substantial effects across a range of social-ecological settings (McClanahan, 2021).

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

90 To help address this challenge, we present a bio-economic modeling tool called `marlin` that
91 allows for efficient simulation of spatio-temporal biological and economic dynamics. `marlin`
92 allows users to simulate the impacts of marine management policies across a range of species
93 targeted by various fleets across heterogeneous and dynamic seascapes. This model can help
94 users seek Pareto-optimal solutions that produce win-wins or minimize trade-offs across mul-
95 tiple management objectives, such as food production and conservation (Lester et al., 2013).

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

102 **Methods**

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

109 The front end of the software package accompanying this paper, `marlin`, is written in R (R
110 Core Team, 2021) to facilitate use, while the underlying population model is written in C++,
111 integrated through the `Rcpp` package (Eddelbuettel & Balamuta, 2018). Users on standard
112 computers should be able to simulate one age-structured population distributed across two-
113 dimensional spatial surface represented by a ten by ten grid of cells over 20 years in fractions
114 of a second. It is very important to note that the parameters of this model cannot be fit to data
115 directly within the `marlin` package; users must set model parameters themselves based on
116 externally available data and their best judgement.

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

123 We define a few commonly used terms here. *Yields* refers to the volume of catch from fishing

124 activity. *Spawning stock biomass* refers to the total biomass of reproductively mature fish in
125 the water, a function of numbers, weight, fecundity, and sexual maturity at age. We measure
126 the size of the population by the ratio of the *spawning stock biomass* (SSB) in a given time
127 step relative to *unfished spawning stock biomass* (SSB₀), SSB/SSB₀. An SSB/SSB₀ value
128 of 1 means that the population is unfished, a SSB/SSB₀ value of 0 means the population is
129 extinct.

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

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

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

136 Below we provide a summary of the `marlin` model, as well as details of the case studies.

137 **Model Summary**

138 `marlin` simulates the dynamics of one or more species, currently best representing fish-like
139 species, using age-structured population dynamics. Ages are then converted to lengths using
140 the von Bertalanffy growth equation with log-normally distributed variation in the length at
141 age. Each time step, species move throughout the simulated seascape using both diffusion
142 and “taxis” (active movement towards preferred habitat), experience natural and potentially
143 fishing mortality, and potentially spawn using one of the possible forms of density dependence

144 implemented in the model, with the ability to include auto-correlated stochastic deviations in
145 the amount of offspring produced, generally called “recruitment deviates”.

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

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

168 fleet and the travel costs as a function of distance from a port (see *Fleet Dynamics*).

169 The dynamics of each fleet can be modified by management in a variety of ways. Managers
170 can impose size limits for individual species within each fleet. They can also impose total catch
171 quotas for each species in each time step. When quotas are activated, if the total catch across
172 all fleets for a given species under the model's effort dynamics would exceed the allowable
173 quota for that species, the total effort for each fleet is decreased proportional to its contribution
174 to the total catch until the quota is satisfied. As an alternative to catch quotas, managers can
175 set an effort cap per fleet, which prevents effort from exceeding a given amount under open
176 access dynamics, though effort may be reduced below this cap if required by the profit equation
177 (i.e. the fleet can choose to fish less than the quota or effort cap). `marlin` also allows users
178 to specify closed fishing seasons for one or more species in the system. Lastly, managers can
179 specify locations of no-take MPAs, which can change in size and location if needed. When
180 MPAs are implemented, fishing effort that used to operate inside the MPAs can either leave
181 the fishery, or be redistributed outside the MPA (the default behavior).

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

189 On the fleet side, users must for each fleet they wish to simulate at a minimum specify the
190 contact selectivity curves for each species caught by the fleet, as well relative price per unit

191 weights greater than 0 for any target species. Species caught by but not targeted by the fleet
 192 can be represented by prices of 0 (not targeted) or below 0 (actively avoided).

193 **Fleet Dynamics**

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

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

$$R_{t,p,f} = \sum_s^{N_s} \sum_a^{N_a} \Pi_{s,f} \frac{\alpha_{a,s,f} q_{s,f} E_{t,p,f}}{u_{t,p,s,a}} \times Y_{t,p,s,a} \quad (1)$$

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

$$Y_{t,p,s,a} = \frac{u_{t,p,s,a}}{z_{t,p,s,a}} \times b_{t,p,s,a} \times (1 - e^{-z_{t,p,s,a}}) \quad (2)$$

$$u_{t,p,s,a} = \sum_{f=1}^{N_f} \alpha_{a,s,f} q_{s,f} E_{t,p,f} \quad (3)$$

208 Contact selectivity at age α is modeled through either a logistic form or a dome-shaped form.
 209 The logistic form is based on the lengths l at which 50% of individuals are selected by the
 210 fishing gear, l^{sel} , and δ which is the difference between the length at 50% selectivity and the
 211 length at 95% selectivity.

$$\alpha_{a,s,f} = \frac{1}{(1 + e^{-\log(19) \times \frac{l_{a,s} - l^{sel}}{\delta_{s,f}}})} \quad (4)$$

212 We approximate the dome-shaped form as a normal distribution with mean l^{sel} and standard
 213 deviation σ . The normal density function is re-scaled such that the selectivity is 1 at l^{sel} .

$$\alpha_{a,s,f} = \frac{1}{\sigma_{s,f} \sqrt{2\pi}} e^{-0.5 \left(\frac{l_{a,s} - l^{sel}}{\sigma_{s,f}} \right)^2} \quad (5)$$

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

$$z_{t,p,s,a} = u_{t,p,s,a} + m_{s,a} \quad (6)$$

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

$$\phi_{t,p,f} = R_{t,p,f} - C_{t,p,f} \quad (7)$$

$$C_{t,p,f} = \gamma_f \left(E_{t,p,f}^{\beta_f} + \eta_{f,p} E_{t,p,f} \right) \quad (8)$$

223 **Calculating Total Effort**

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

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

$$E_{t+1,f} = E_{t,f} \times e^{\theta_f \log(R_{t,f}/C_{t,f})} \quad (9)$$

231 This is essentially a Gompertz model for fishing effort, that has been used for other theoretical
 232 studies of fishing effort dynamics (Thorson et al., 2013).

233 **Tuning Fishing Fleet Parameters**

234 The degree of fishing pressure exerted by a given set of fishing fleets on each species is a
 235 function of a range of parameters including the total amount of effort (E), the contact selectivity
 236 ogives (α), fishing cost (C), the spatial distribution of the species affected by the fleet, the
 237 relative prices across species (Π), and the catchability coefficient of each fleet for each species
 238 (q). `marlin` provides a tuning option to help users achieve desired biological outcomes from
 239 their fleets.

240 Users can tune their fleets in one of two ways, conditional on the underlying population dy-
 241 namics of the species in question. First, they can specify a target exploitation rate u for each
 242 species in their simulation. Taking all the other parameters of the model as given, `marlin` then
 243 adjusts the catchability coefficients $q_{f,s}$ for each fleet f and species s such that the equilibrium
 244 exploitation rate for each species matches the desired level. Second, they can specify a target
 245 total spawning stock biomass under fishing divided by total unfished spawning stock biomass,
 246 and the model will adjust the catchability coefficients $q_{f,s}$ for each fleet f and species s such
 247 that the equilibrium ratio of fished to unfished spawning biomass for each species matches the
 248 desired level.

249 Users can also tune the fleet dynamics by specifying the ratio of costs to revenues. Price data
250 for use in the model can be obtained relatively simply through literature reviews, market sur-
251 veys, or local experts. However, cost parameters are more complicated, as translating say cost
252 per day of fishing into the same representation of fishing effort used in the model is not straight
253 forward to accomplish. As an alternative, users can specify an equilibrium cost-to-revenue ra-
254 tio for the fleet, essentially the profit margins of the fleet in question, and `marlin` will tune
255 the cost parameter to achieve this desired cost to revenue ratio given the other parameters in
256 the model.

257 **Spatial Allocation of Effort**

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

266 As such we explored a series of “next best” fleet distribution algorithms. While not the IFD
267 in any individual time step, over time they start to approximate the IFD, as each assumes
268 that fleets base their decisions for the current time step on the outcomes in the prior timestep,
269 meaning that the impacts of the actions of other fishing fleets are eventually accounted for.
270 The timeline required for the fleets to reach an equilibrium distribution will vary and depend

271 on factors such as the population dynamics of the species in question and the number and
272 degree of competition across fleets. Users should explore different simulation times to ensure
273 that any results they wish to use are not simply a reflection of the fleet dynamics fluctuating
274 on their way to an equilibrium condition.

275 The four possible fleet distribution algorithms are

- 276 1. Revenue per unit effort (RPUE): The fleet distributes itself in space based on the realized
277 revenue per unit effort in each patch in the preceding time step
- 278 2. Revenue: The fleet distributes itself in space based on the realized total revenue in each
279 patch in the preceding time step
- 280 3. Profit per unit effort (PPUE): The fleet distributes itself in space based on the realized
281 profit per unit effort in each patch in the preceding time step
- 282 4. Profit: The fleet distributes itself in space based on profit in each patch in the preceding
283 time step

284 Revenue based spatial distribution is not likely to be very realistic; in general we would ex-
285 pect fishing fleets to respond to profits on some core level. However, due to the complexity
286 of parameterizing cost functions, fleet dynamics are often evaluated based on yield or rev-
287 enue alone, and so we include those scenarios here to allow users to evaluate the potential
288 implications of this choice. The decision on whether to allocate the fleet based on absolute or
289 relative (per unit effort) metrics is more complex. When effort represents the actions of sepa-
290 rate and individual fishing actors (e.g. independent fishing vessels), a per-unit-effort strategy,
291 in which fishers distribute themselves based on the expected catch of their individual efforts,
292 may be more realistic (Hilborn & Walters, 1987). Conversely, a system defined by a sole

293 owner seeking to maximize total profits might be better represented by a fleet model based on
294 total profits.

295 **Population Model**

296 The underlying population model used is an age structured single-species model in the manner
297 of Ovando, Caselle, et al. (2021). The population model requires many parameters. However,
298 if the user supplies either a scientific or common name for the species in question (scientific
299 preferred), the model will supply default values for that species based on the values reported in
300 FishLife (Thorson, 2020). FishLife provides estimates of core life history parameters for fish
301 species based on a model integrating published values and evolutionary connections. FishLife
302 provides reasonable default values for given species, but these default values should be not
303 be taken as definitive and users should check the default values and input best available pa-
304 rameters specific to the stock in question if they wish to best represent the dynamics of their
305 specific system.

306 **Movement**

307 `marlin`'s movement dynamics are based on a continuous-time Markov chain (CTMC), as de-
308 scribed in Thorson et al. (2021). Within this framework, the model allows for movement to be
309 broken down into three components of *advection* (drifting with currents), *taxis* (active move-
310 ment towards preferred habitat), and *diffusion* (essentially remaining variation in movement
311 not explained by advection or taxis). For now, `marlin` focuses just on the diffusion and taxis
312 components of this model, assuming that advection is zero, though future extensions could
313 incorporate advection vectors from oceanographic models. In this way, `marlin` allows users

314 to run anything from a simple Gaussian dispersal kernel up to a system governed by species
315 that passively diffuse out from a core habitat defined by a dynamic thermal range. The model
316 currently focuses on diffusion and taxis, which allows for general representation of animals
317 following physical or oceanographic features, but research on the incorporation and impor-
318 tance of advective forces would be of value going forward.

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

328 The individual components (M) of the movement matrix (\mathbf{M}) are filled based on an adjacency
329 matrix, which defines whether two patches are both adjacent and water (as opposed to land or
330 another physical barrier), a diffusion rate D defined in units of area of a patch per unit of time,
331 and a habitat preference function H in units of length of a side of a patch per unit time. For
332 example, if we are defining the time units as years and the distance units as kilometers, for a
333 tuna D might be $1,000 \frac{KM^2}{Year}$. We then use parameters Δ_t and Δ_d parameters to translate the
334 diffusion rate D to match the time step and patch size used in a simulation. For example, if we
335 were to run a model on a monthly timestep given time units of years, then $\Delta_t = 1/12years$.
336 If one square patch in the simulation has an area of $100km^2$, then $\Delta_d = 10KM$. This “scale
337 free” parameterization means that appropriate value of D can be identified for a species and

338 then set, regardless of the time step or patch size used in the simulation model itself.

339 The taxis component of the movement process is a function of the difference in habitat quality
 340 H . The habitat preference function itself can take any form the user wishes. Exponentiating
 341 the difference in the habitat preference function between patches turns the taxis matrix into a
 342 multiplier of the diffusion rate D . As such, when creating habitat layers for simulation, users
 343 can tune the scale of the habitat gradient function to result in realistic multipliers of the dif-
 344 fusion rate. This parameterization ensures that the off-diagonal elements of the movement
 345 matrix $\mathbf{M}_{t,s,a}$ are all non-negative, a requirement of the CTMC method.

$$M_{p1,p2,t,s,a} = \begin{cases} = \frac{\Delta_t}{\Delta_d^2} D e^{\frac{\Delta_t(H(p2,t,s,a)-H(p1,t,s,a))}{\Delta_d}} & \text{if } p2 \text{ and } p1 \text{ are adjacent} \\ = - \sum_{p' \neq p1} M_{p1,p2,t,s,a} & \text{if } p1 = p2 \\ = 0 & \text{otherwise.} \end{cases} \quad (10)$$

346 For both the diffusion and taxis matrices, we allow for the inclusion of physical barriers to
 347 movement (i.e. land). Pairs of patches that are adjacent but in which one or both patches are
 348 a barrier to movement are set as non-adjacent. The CTMC model then produces movement
 349 dynamics that move around barriers rather than over them.

350 The movement of individuals across patches is then calculated by matrix multiplication of the
 351 pre-movement vector of the number of individuals (\mathbf{n}) of species s at age a in time step t across
 352 all patches p times the matrix exponential of the movement matrix \mathbf{M}

$$\mathbf{n}_{t+1,s,a} = \mathbf{n}_{t,s,a} e^{\mathbf{M}_{t,s,a}} \quad (11)$$

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

365 **Population Growth**

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

$$N_{t,p,s,a} = \begin{cases} = BH(SSB_{t-1,p,s,a}) & \text{if } a = 1 \\ = N_{t-1,p,s,a-1}e^{-(z_{t-1,p,s,a-1})}, & \text{if } 1 < a < \max(\text{age}) \\ = N_{t-1,p,s,a}e^{-(z_{t-1,p,s,a})} + N_{t-1,a-1}e^{-(z_{t-1,p,s,a-1})}, & \text{if } a = \max(a) \end{cases} \quad (12)$$

368 where BH is the Beverton-Holt recruitment function (Beverton & Holt, 1957) and SSB is

369 spawning-stock-biomass. Per convention, the model allows for a “plus group”, wherein rather
 370 than tracking numbers of every possible age, individuals greater than or equal to a given max-
 371 imum age are grouped together.

372 Spawning stock biomass SSB is calculated by converting age to mean length at age, calculat-
 373 ing weight at age, maturity at age, and then calculating spawning stock biomass as the sum of
 374 spawning potential at age in a given time step, taking into account the potential for hyperal-
 375 lometry in the manner of Marshall et al. (2021). Age is converted to length through the von
 376 Bertalanffy growth equation given parameters asymptotic length (l_∞), growth (k) and theo-
 377 retical age at length zero (a_0) assuming log-normally distributed variation u in the length at
 378 age with CV σ_s .

$$l_{a,s} = l_{\infty,s} (1 - e^{-k_s(a-a_0_s)}) e^{u_s} \quad (13)$$

$$u_s \sim N(0, \sigma_s) \quad (14)$$

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

$$minv_{s_a} = \left(\frac{l_{s,a}}{l_{\infty,s}}\right)^{-1} \quad (15)$$

$$m_{s,a} = \frac{minv_{s,a}}{mean(minv_{s,a})} m_s \quad (16)$$

383 Alternatively, users can set mortality at age to be constant

$$m_{s,a} = m_s \quad (17)$$

384 Biomass B at age is then given by the weight at length equation governed by a scaling coeffi-
 385 cient Ω_s and an exponent Φ_s that controls the rate at which volume scales with length

$$B_{a,s} = \Omega_s \times l_{a,s}^{w_b} \quad (18)$$

386 The proportion of sexually mature individuals (mat) at a given age is then calculated as a
 387 logistic function where l_{mat} is the length at which on average 50% of individuals are sexually
 388 mature, and δ_{mat} is the unit of length beyond l_{mat} at which on average 95% of fish are sexually
 389 mature.

$$mat_{a,s} = \frac{1}{\left(1 + e^{-\log(19) \times \frac{l_{a,s} - l_{mat_s}}{\delta_{mat_s}}}\right)} \quad (19)$$

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

$$SSB_{t,p,s} = \sum_{a=1}^{N_a} w_{a,s,t}^{\gamma_s} mat_{t,a} N_{t,p,s,a} \quad (20)$$

394 Recruitment

395 Recruitment (i.e. the number of age 1 individuals entering the population) follows Beverton-
 396 Holt dynamics parameterized around steepness (h) with log-normally distributed recruitment
 397 deviates ϵ . When steepness is one recruitment is independent of spawning biomass. As steep-
 398 ness approaches 0.2 recruitment becomes a linear function of spawning biomass. marlin
 399 allows users to specify a target unfinished spawning stock biomass ($SSB0$), which will be
 400 achieved by tuning the total unfished recruitment ($r0$), given the remaining life history pa-
 401 rameters and independent of any characteristics of the fishing fleets.

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

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

$$N_{t,p,s,a=1} = \left(\frac{0.8 \times \sum_{p=1}^P r0_{p,s} \times h_s \times \sum_{p=1}^P SSB_{t-1,p,s}}{0.2 \times \sum_{p=1}^P SSB0_{p,s} \times (1 - h_s) + (h_s - 0.2) \times \sum_{p=1}^P SSB_{t-1,p,s}} \right) \times \frac{r0_{p,s}}{\sum_p r0_{p,s}} \times \epsilon_{t,s} \quad (21)$$

407 where r_0 is a vector of recruits under unfished conditions in a given patch.

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

$$n_{t,p,s,a=1} = \left(\frac{0.8 \times r_{0,p,s} \times h_s \times SSB_{t-1,p,s}}{0.2 \times SSB_{0,p,s} \times (1 - h_s) + (h_s - 0.2) \times SSB_{t-1,p,s}} \right) \times \epsilon_{t,s} \quad (22)$$

410 3. Local density dependence then disperse: Density dependent recruitment occurs inde-
411 pendently in each patch and recruits are then dispersed.

$$n_{t,p,s,a=1} = \left(\frac{0.8 \times r_{0,p,s} \times h_s \times SSB_{t-1,p,s}}{0.2 \times SSB_{0,p,s} \times (1 - h_s) + (h_s - 0.2) \times SSB_{t-1,p,s}} \right) \times \mathbf{d}_s^l \times \epsilon_{t,s} \quad (23)$$

412 where \mathbf{d}^l is the recruitment movement matrix

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

$$larv_{t,p,s} = SSB_{t-1,p,s} \times \mathbf{d}_s^l \quad (24)$$

$$n_{t,a=1,p,s} = \left(\frac{0.8 \times r0_{p,s} \times h_s \times larv_{t,p,s}}{0.2 \times SSB0_{p,s} \times (1 - h_s) + (h_s - 0.2) \times larv_{t,p,s}} \right) \times \epsilon_{t,s} \quad (25)$$

416 5. Global density dependence allocated by spawning biomass: Density dependence is a
 417 function of the sum of spawning biomass across all patches, and recruits are then dis-
 418 tributed according to the distribution of spawning biomass

$$n_{t,p,s,a=1} = \left(\frac{0.8 \times \sum_{p=1}^P r0_{p,s} \times h_s \times \sum_{p=1}^P SSB_{t-1,p,s}}{0.2 \times \sum_{p=1}^P SSB0_{p,s} \times (1 - h_s) + (h_s - 0.2) \times \sum_{p=1}^P SSB_{t-1,p,s}} \right) \times \frac{SSB_{t-1,p,s}}{\sum_{p=1}^P SSB_{t-1,p,s}} \times \epsilon_{t,s} \quad (26)$$

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

$$v_{t,s} \sim \begin{cases} N(0, \sigma_{r,s}), & \text{if } t = 1 \\ \rho_s v_{t-1,s} + \sqrt{1 - \rho_s^2} N(0, \sigma_{r,s}), & \text{if } t > 1 \end{cases} \quad (27)$$

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

$$\epsilon_{t,s} = e^{v_{t,s} - \sigma_{r,s}^2/2} \quad (28)$$

422 **Reference Points**

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

432 As such, we do not report MSY based reference points in the model by default. There are
433 many different strategies for estimating reference points in spatially explicit systems (Kapur
434 et al., 2021). We leave it to users to define and find relevant reference points as required by
435 their specific needs.

436 **Case Studies**

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

442 Each of the case studies contains too many parameters and options to be succinctly presented
443 in the text here. Readers should consult the accompanying code to view the precise details
444 of each simulation. Targeted applications must carefully consider and document all decisions
445 made around model parameters.

446 **MPA Design Strategies**

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

448 1. *Rate*: MPAs are placed based on the pre-MPA SSB/SSB0 weighted catch relative to the
449 total catch in a patch. So, patches with high rates of catch of depleted species relative
450 to total catch are prioritized.

451 2. *Target Fishing*: MPAs locations are prioritized proportional to fishery catches. Patches
452 with high total catches are prioritized over patches with low catches.

453 3. *Spawning Ground*: MPAs are centered on the grounds of a known spawning aggrega-
454 tion. This strategy is only used in the coral reef case study.

455 In theory, the design of MPA networks can be optimized through the use of a modeling frame-
456 work, and depending on the validity of the model, this process is likely to produce better
457 outcomes than manually-designed strategies (Rassweiler et al., 2012, 2014). However, de-
458 signing optimal MPA networks becomes increasingly difficult as the range of objectives and
459 the complexity of the model increase. Therefore, we focus here on the design and performance
460 of these more rule of thumb design strategies that may be more accessible to a wider range of
461 users. We allow all MPAs to be designed in a mosaic fashion in these examples, but users can
462 easily extend the analysis to compare outcomes between contiguous (MPA is made up of one

463 continuously connected block) and mosaic (MPAs can be separated in space) MPA designs
464 (Pons et al., 2022).

465 **Coastal Coral Reef Fishery**

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

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

481 Fleet Two is a more commercial fleet that primarily targets the snapper populations. This fleet
482 primarily sells their catch to local restaurants and distributors where plate-sized fish are prized,
483 and so for both snapper and grouper Fleet Two has a dome-shaped selectivity pattern (Kinds-
484 vater et al., 2017). While plate-sized deep snapper are the primary target of Fleet Two, we

485 model Fleet Two's selectivity for deep snapper as logistic due to high levels of discard mor-
486 tality for deep-water snapper resulting from barotrauma. Fleet Two catches groupers, though
487 less than Fleet One, and receives no price for sharks due to the requirements of a certification
488 program through which they sell their deep-water snapper. Accidental captures (bycatch) of
489 sharks do occur, which results in mortality. Fleet Two operates under open-access dynamics,
490 as fishing is not the only means of subsistence for this community; short-term effort expands
491 and contracts in response to profitability of the primarily grouper-driven fishery. Fleet two's
492 home port is located in the northwest corner of the simulation space.

493 We used `marlin` to simulate the outcomes for both food production and conservation for each
494 of the species and both of the fleets as a function of both MPA size and MPA design strategy.
495 For this exercise, MPAs are placed with perfect information and have no design constraints
496 for continuity. We ran the simulation for in quarter year time steps for 20 years ($\Delta_t = 1/4$)
497 and set the area of each patch to be 5km^2 ($\Delta_p = \sqrt{5}$), using 144 patches for a total area of
498 $2,000 \text{ KM}^2$.

499 **Pelagic Fishery**

500 We model our pelagic case study loosely on the characteristics of the Western and Central
501 Pacific Ocean (WCPO) tuna fisheries. Note that this is an illustrative example only and sim-
502 ulated stock status, species distributions, and projections presented here should not be inter-
503 preted as a indicative of the current or future state of the WCPO. We simulate trajectories of
504 9 species commonly caught in the region, including both the highly abundant skipjack tuna
505 and the heavily depleted oceanic whitetip shark (*Carcharhinus longimanus*, Carcharhinidae)
506 (Figure 2). We use publicly available data on catch-per-unit-effort of each of these species

507 from the WCPO as a very rough proxy for baseline habitat distributions, noting that where
508 possible, fishery-independent abundance indices would be preferable (Figure 3).

509 These pelagic species are caught by a longline fleet that primarily targets large adult tunas such
510 as bigeye and yellowfin (*Thunnus albacares*, Scombridae) for high-grade consumption, and a
511 purse-seine fishery that primarily targets skipjack tunas for bulk canning. Contact selectivities
512 were modeled as logistic for the longline fleet, and dome-shaped for the purse-seine fleet. Both
513 fleets operate under open-access dynamics with an effort cap. The effort cap was set at the
514 level of effort that resulted in the desired levels of SSB/SSB0 for each species under open-
515 access dynamics (Figure 3), intended to simulate a scenario where managers step in to prevent
516 further expansion of fishing effort in a fully developed fishery. For forward-simulation, open-
517 access dynamics can result in effort decreasing in response to profitability, but cannot result
518 in effort beyond the effort cap set for each fleet.

519 For this exercise, we focused on using `marlin` to assess resilience of the selected *Target Fish-*
520 *ing* and *Rate* MPA design strategies to a climate-driven range shift. Specifically, we simulate
521 an extreme example where the centroid of each population shifts northward at a rate of ~62km
522 per year over a 20 year time horizon (Figure 2). We designed MPA networks given the condi-
523 tions in the starting year, and then held that network constant over the years of the experiment,
524 running one simulation with and another without the climate-drive range shift. We then com-
525 pared the effects of this range shift on food production and conservation outcomes from MPA
526 networks designed based on the pre-range shift world. We ran the pelagic simulation at a
527 quarterly level ($\Delta_t = 1/4$ year), and set the area of each cell to be roughly 97,000 KM² across
528 144 patches each with a side length of roughly 311 KM, for a total area of 14e6 KM², broadly
529 commensurate with the area of the WCPO.

530 **Results**

531 **Coastal Coral Reef Fishery**

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

539 MPAs were uniformly beneficial to the spawning biomass of all species under the *Target Fish-*
540 *ing* design strategy, with the most rapid increases in spawning biomass for the deep snapper
541 population. The *Spawning Ground* strategy primarily benefited the shallow snapper popula-
542 tion, producing little change in the grouper population and decreasing spawning biomass of
543 both the deep snapper and reef shark populations for MPA sizes covering less than 50% of the
544 simulated area (Figure 4 B).

545 In total, the *Spawning Ground* strategy was capable of providing net increases in fishing yield
546 (summed across both fleets) of up to roughly 7%, with positive net yield impacts up to network
547 size of nearly 60% of the area. However, even MPAs covering 60% of the area only produced
548 a maximum increase of roughly 5% in total SSB/SSB₀ when designed around the spawning
549 ground. Conversely, the *Target Fishing* design strategy was capable of producing a nearly
550 25% increase in total SSB/SSB₀ for the same MPA size, but at a much greater cost to the total
551 food production from the system's fisheries (Figure 4 C).

552 **Pelagic Fishery**

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

561 The primary tuna species (bigeye, skipjack, and yellowfin) were most sensitive to design strat-
562 egy and climate scenario, with the *Target Fishing* strategies producing for example rapid con-
563 servation gains for bigeye and skipjack under the status quo, while the *Rate* strategy resulted
564 in small net conservation losses for both species until the MPA became extremely large. How-
565 ever, under the range shift scenario the MPAs had little impact on many of the tuna populations
566 until the MPA size became extremely large, due to movement of the primary fishing grounds
567 outside of the current hotspots where the MPAs are placed based on status quo conditions. The
568 20 year time horizon simulated here was not enough to produce substantial gains for any of
569 the shark species even with 100% closures except for the more rapidly growing blue shark
570 (Figure 5 B).

571 **Discussion**

572 Marine ecosystems are driven by complex social-ecological dynamics. Communities must
573 often make decisions on how to manage these systems based on limited empirical evidence.
574 Modeling tools such as the one presented here can help users answer scientific questions and
575 design marine management policies informed by a better understanding of sensitivities to key
576 uncertainties.

577 **Insights from Case Studies**

578 Our coastal coral reef example illustrates both the potential for MPAs to benefit conservation
579 and food production in these systems, and the potential for the same MPA to benefit some
580 fleets and species while harming others when fishing fleets affected by an MPA do not share
581 the same objectives and species are not uniformly distributed. Our pelagic case study illustrates
582 how marlin can be used to assess the climate resiliency of spatial management strategies, and
583 identify strategies that best meet the needs of both current and future conditions. Results from
584 this type of work could be used to help prioritize communities and species at particular risk to
585 climate change impacts.

586 Holding constant other social-ecological variables in the coral reef example, the *Spawning*
587 *Ground* MPA network was able to provide more equitable yield outcomes across the two fish-
588 ing communities, whereas the *Target Fishing* MPA network only benefited Fleet Two (Figure 4
589 A). This is because Fleet One has two primary fishing grounds; the spawning grounds, and the
590 offshore area where the deep snapper live. Fleet Two primarily fishes in the northern portions
591 of the simulation grid. Under the *Spawning Ground* strategy, while Fleet One quickly losses

592 fishing grounds on the spawning grounds, it can compensate for this by moving offshore and
593 fishing the deep snapper population harder, while also being able to fish some of the spillover
594 of snapper from the spawning ground closure. This displacement of Fleet One's fishing effort
595 is why biomass of deep snapper actually declines under the *Spawning Ground* strategy.

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

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

616 species to fishing gear when aggregated.

617 The two design strategies produced very different outcomes in terms of total changes in yield
618 and conservation outcomes for the coral reef case study (Figure 4 C). Both MPA network de-
619 sign strategies were capable of producing net “win-win” outcomes in which both food security
620 and conservation. However, in general for the same size MPA network the *Spawning Ground*
621 design strategy produced better food security outcomes but worse conservation outcomes, and
622 *vice versa* for the *Target Fishing* strategy. The coral reef case study shows how the modeling
623 framework presented here can help stakeholders explore how different management strate-
624 gies affect outcomes both in total (Figure 4 C) and across species (Figure 4 A) and fishing
625 communities (Figure 4 B).

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

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

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

655 MPAs based around coral-reef style ecosystems have been extensively studied around the
656 world, with much of the empirical evidence of their performance centered on demonstrat-
657 ing higher metrics such as biomass densities inside protected areas relative to fished reference
658 areas (“response ratios,” Lester et al., 2009). Our model predicts a similar rapid increase of
659 the simple ratio of mean biomass inside MPAs relative to outside (Fig. S5, acknowledging
660 that designing a proper response ratio would require controlling for habitat characteristics and
661 MPA design criteria). However, despite producing clear response ratios, the net conservation
662 and fishery outcomes of our simulated coral-reef ecosystem MPAs were not nearly as large or
663 clear as the response ratio results (Figure 4); this result is supported by works such as Ferraro

664 et al. (2018) and Ovando, Caselle, et al. (2021) showing that response ratios alone may be a
665 poor indicator of the net causal impacts of MPAs at the population scale.

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

680 **Putting marlin In Context**

681 The role of this paper is not to conduct a review of the many tools for spatial-temporal modeling
682 available in the literature, each of which provide useful functionality for specific applications.
683 However, we highlight here the specific gaps that we feel marlin fills in the modeling litera-
684 ture and in the policy support toolbox using some selected publications. More end-to-end mod-
685 els such as ATLANTIS (Audzijonyte et al., 2019) , OSMOSE (Shin & Cury, 2001), Ecopath

686 with Ecosim (Christensen & Walters, 2004), POSEIDON (Bailey et al., 2019), DISPLACE
687 (Bastardie et al., 2013), or SEAPODYM (Lehodey et al., 2008) are capable of representing
688 tremendous amounts of complexity, but can be time consuming to design and run. `marlin`
689 allows some of the realism of these more end-to-end models while being simpler and faster to
690 parameterize and run.

691 Tools such as `virtualespecies` (Leroy et al., 2016), STEPS (Visintin et al., 2020), RangeShifter
692 (Bocedi et al., 2014), and SMS can be efficiently constructed to model the dispersal and distri-
693 bution of species in space and time as a function of environmental covariates. However, these
694 typically require specifying a covariate-response curve without explicitly acknowledging how
695 this arises from habitat-specific movement and demography (`virtualespecies`), or model move-
696 ment using a dispersal kernel (RangeShifter, STEPS) or a least-cost path algorithm (SMS,
697 STEPS). By contrast, `marlin` uses a continuous-time Markov chain movement model, which
698 integrates multiple paths (including their path-dependent probability based on intervening
699 habitat types and species preferences) while using scale-free parameters that can be measured
700 experimentally in laboratory or tagging studies. In addition, `marlin` allows for simulating not
701 only the distribution of the species but also biomass, age, and length structure in space and
702 time.

703 Simplified bio-economic models such as those used in Hastings et al. (2017), Sala et al.
704 (2021), and Cabral et al. (2019) can be applied at scale and provide analytically tractable
705 results, but as a result must abstract over many bio-economic dynamics that can be important
706 for more tactical applications. Our results demonstrate how nuances in fleet dynamics and
707 species distributions can dramatically impact MPA outcomes. `marlin` allows for more realis-
708 tic representations of spatial social-ecological systems while maintaining processing speed.

709 `marlin` does not represent trophic interactions. Anthropogenic changes in species abundance
710 can result in trophic cascades. However, studies such as Gilman et al. (2020), Ovando, Caselle,
711 et al. (2021), Bruno et al. (2019) , and Malakhoff & Miller (2021) found no clear signs of
712 MPA driven trophic cascades within the first decades of protection. Signals of trophic cascades
713 may be masked by variations in the direction and strength of species interactions driven by
714 environmental context (Liu & Gaines, 2022), or may simply take longer to develop detectable
715 effects than the coverage of many time series of MPAs. While `marlin` does not incorporate
716 trophic interactions, what empirical evidence we have does not suggest that management-
717 mediated trophic cascades are so common and clear that they must be incorporated into any
718 credible multi-species simulation model. However, research on the trophic impacts of spatial-
719 temporal management actions is clearly of value and models like Atlantis (Audzijonyte et al.,
720 2019), Ecopath with Ecosim (Christensen & Walters, 2004), and EASI-Fish (Griffiths et al.,
721 2019) can help users explore those kinds of trophic processes, in the manner of Baskett et al.
722 (2007).

723 **General Recommendations for Use**

724 The model presented here is designed to help users explore the impacts of different variables
725 on policy outcomes. But, that freedom means that users have a large number of options at their
726 disposal that they must decide on. Our recommended strategy is for users to try and narrow
727 down a list of parameters that they feel are sufficiently “known” and another list of parameters
728 that are highly uncertain and / or contentious which the users feel may impact results. Where
729 possible, parameters from locally estimated stock assessment models can be used to provide a
730 foundation around which sensitivity analyses around specific uncertainties of interest (Berger
731 et al., 2017), though care should be taken interpreting population selectivity curves estimated

732 from stock assessment as contact selectivity curves required as inputs to `marlin` (Sampson,
733 2014).

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

748 Given a set of model runs, the choice of whether to use those results “strategically” or “tacti-
749 cally” will depend on the needs of the user. Since `marlin` is not fit to data directly it is more
750 easily applied to strategic questions. The extent to which users are comfortable using the out-
751 puts of `marlin` tactically will depend on the confidence they have in their parameterization of
752 the model relative to the precision policy-makers require in order to make a decision. Other
753 models may be better suited to address specific forms of complexity. Particularly for more
754 tactical applications, we would encourage users to explore multiple modeling frameworks to
755 help design policies that are likely to be robust to many different kinds of complexities.

756 At this time, `marlin` assumes that all evaluated policies are perfectly implemented; e.g. that
757 MPAs are 100% no-take and perfectly enforced, that quotas and closed seasons are respected,
758 that there is no discard mortality, etc. In reality no policy is perfectly implemented, and users
759 should consider the extent to which the policies they simulate are actually feasible to imple-
760 ment. There is value though in being able to simulate and compare the outcomes of perfectly
761 implemented policies to isolate the concept of the policy itself from its implementation.

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

772 **Conclusions**

773 `marlin` complements the existing spatial marine modeling literature by allowing scientists,
774 decision makers, and other stakeholders to efficiently examine the impacts of realistic bio-
775 economic dynamics on academic and applied problems. We envision `marlin` being applicable
776 to research on dynamic ocean management, range shifts, management strategy evaluation,
777 policy interactions, and spatial stock assessment. `marlin` can help researchers generate data

778 for further testing of the performance and design of spatially explicit integrated population
779 models, in the manner of Bosley et al. (2022). In addition, the process-based movement
780 model used in `marlin` can directly use empirical estimates of movement dynamics derived in
781 the manner of Thorson et al. (2021), providing a link between empirical and simulation based
782 approaches to marine resource management that has been challenging to implement in spatial
783 simulations (Berger et al., 2017).

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

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

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798 **Data Availability Statement**

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

806 **References**

- 807 Abbott, J. K., & Haynie, A. C. (2012). What are we protecting? Fisher behavior and the
808 unintended consequences of spatial closures as a fishery management tool. *Ecological*
809 *Applications*, 22(3), 762–777. <https://doi.org/https://doi.org/10.1890/11-1319.1>
- 810 Audzijonyte, A., Pethybridge, H., Porobic, J., Gorton, R., Kaplan, I., & Fulton, E. A. (2019).
811 Atlantis: A spatially explicit end-to-end marine ecosystem model with dynamically inte-
812 grated physics, ecology and socio-economic modules. *Methods in Ecology and Evolution*,
813 10(10), 1814–1819. <https://doi.org/10.1111/2041-210X.13272>
- 814 Babcock, E. A., & MacCall, A. D. (2011). How useful is the ratio of fish density outside versus
815 inside no-take marine reserves as a metric for fishery management control rules? *Canadian*
816 *Journal of Fisheries and Aquatic Sciences*, 68(2), 343–359. <https://doi.org/10.1139/F10->
817 [146](https://doi.org/10.1139/F10-146)
- 818 Bailey, R. M., Carrella, E., Axtell, R., Burgess, M. G., Cabral, R. B., Drexler, M., Dorsett,
819 C., Madsen, J. K., Merkl, A., & Saul, S. (2019). A computational approach to manag-

820 ing coupled human–environmental systems: The POSEIDON model of ocean fisheries.
821 *Sustainability Science*, 14(2), 259–275. <https://doi.org/10.1007/s11625-018-0579-9>

822 Ban, N. C., Gurney, G. G., Marshall, N. A., Whitney, C. K., Mills, M., Gelcich, S., Bennett,
823 N. J., Meehan, M. C., Butler, C., Ban, S., Tran, T. C., Cox, M. E., & Breslow, S. J. (2019).
824 Well-being outcomes of marine protected areas. *Nature Sustainability*, 2(6), 524. <https://doi.org/10.1038/s41893-019-0306-2>
825

826 Baranov, T. I. (1918). On the question of the biological basis of fisheries. Nauchnyi issle-
827 dovatelskii ikhtiologicheskii institut isvestia 1 (1): 81–128. *Reports from the Division of*
828 *Fish Management and Scientific Study of the Fishing Industry.](English Translation by*
829 *WE Ricker, 1945. Mimeographed.)*

830 Baskett, M. L., Micheli, F., & Levin, S. A. (2007). Designing marine reserves for interacting
831 species: Insights from theory. *Biological Conservation*, 137(2), 163–179. [https://doi.org/](https://doi.org/10.1016/j.biocon.2007.02.013)
832 [10.1016/j.biocon.2007.02.013](https://doi.org/10.1016/j.biocon.2007.02.013)

833 Bastardie, F., Nielsen, J. R., & Miethe, T. (2013). DISPLACE: A dynamic, individual-based
834 model for spatial fishing planning and effort displacement — integrating underlying fish
835 population models. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(3), 366–386.
836 <https://doi.org/10.1139/cjfas-2013-0126>

837 Berger, A. M., Goethel, D. R., Lynch, P. D., Quinn, T., Mormede, S., McKenzie, J., & Dunn, A.
838 (2017). Space oddity: The mission for spatial integration. *Canadian Journal of Fisheries*
839 *and Aquatic Sciences*, 74(11), 1698–1716. <https://doi.org/10.1139/cjfas-2017-0150>

840 Beverton, R. J. H., & Holt, S. J. (1957). *On the Dynamics of Exploited Fish Populations*.
841 Springer.

842 Bocedi, G., Palmer, S. C. F., Pe'er, G., Heikkinen, R. K., Matsinos, Y. G., Watts, K., & Travis,
843 J. M. J. (2014). RangeShifter: A platform for modelling spatial eco-evolutionary dynamics
844 and species' responses to environmental changes. *Methods in Ecology and Evolution*, 5(4),

845 388–396. <https://doi.org/10.1111/2041-210X.12162>

846 Bosley, K. M., Schueller, A. M., Goethel, D. R., Hanselman, D. H., Fenske, K. H., Berger,
847 A. M., Deroba, J. J., & Langseth, B. J. (2022). Finding the perfect mismatch: Evaluat-
848 ing misspecification of population structure within spatially explicit integrated population
849 models. *Fish and Fisheries*, 23(2), 294–315. <https://doi.org/10.1111/faf.12616>

850 Brown, C. J., Althor, G., Halpern, B. S., Iftekhar, M. S., Klein, C. J., Linke, S., Pryde, E.
851 C., Schilizzi, S., Watson, J. E. M., Twohey, B., & Possingham, H. P. (2018). Trade-offs
852 in triple-bottom-line outcomes when recovering fisheries. *Fish and Fisheries*. [https://doi.](https://doi.org/10.1111/faf.12240)
853 [org/10.1111/faf.12240](https://doi.org/10.1111/faf.12240)

854 Bruno, J. F., Côté, I. M., & Toth, L. T. (2019). Climate change, coral loss, and the curious case
855 of the parrotfish paradigm: Why don't marine protected areas improve reef resilience? *An-*
856 *ual Review of Marine Science*, 11(1), 307–334. [https://doi.org/10.1146/annurev-marine-](https://doi.org/10.1146/annurev-marine-010318-095300)
857 [010318-095300](https://doi.org/10.1146/annurev-marine-010318-095300)

858 Cabral, R. B., Halpern, B. S., Lester, S. E., White, C., Gaines, S. D., & Costello, C. (2019).
859 Designing MPAs for food security in open-access fisheries. *Scientific Reports*, 9(1), 8033.
860 <https://doi.org/10.1038/s41598-019-44406-w>

861 Christensen, V., & Walters, C. J. (2004). Ecopath with ecosim: Methods, capabilities and lim-
862 itations. *Ecological Modelling*, 172(2–4), 109–139. [https://doi.org/10.1016/j.ecolmodel.](https://doi.org/10.1016/j.ecolmodel.2003.09.003)
863 [2003.09.003](https://doi.org/10.1016/j.ecolmodel.2003.09.003)

864 Davies, T. E., Epstein, G., Aguilera, S. E., Brooks, C. M., Cox, M., Evans, L. S., Maxwell, S.
865 M., Nenadovic, M., & Ban, N. C. (2018). Assessing trade-offs in large marine protected
866 areas. *PLOS ONE*, 13(4), e0195760. <https://doi.org/10.1371/journal.pone.0195760>

867 Davies, T. E., Maxwell, S. M., Kaschner, K., Garilao, C., & Ban, N. C. (2017). Large marine
868 protected areas represent biodiversity now and under climate change. *Scientific Reports*,
869 7(1), 1–7. <https://doi.org/10.1038/s41598-017-08758-5>

- 870 Eddelbuettel, D., & Balamuta, J. J. (2018). Extending extitR with extitC++: A Brief Intro-
871 duction to extitRcpp. *The American Statistician*, 72(1), 28–36. [https://doi.org/10.1080/](https://doi.org/10.1080/00031305.2017.1375990)
872 [00031305.2017.1375990](https://doi.org/10.1080/00031305.2017.1375990)
- 873 Erisman, B., Heyman, W., Kobara, S., Ezer, T., Pittman, S., Aburto-Oropeza, O., & Nemeth,
874 R. S. (2015). Fish spawning aggregations: where well-placed management actions can
875 yield big benefits for fisheries and conservation. *Fish and Fisheries*. [https://doi.org/10.](https://doi.org/10.1111/faf.12132)
876 [1111/faf.12132](https://doi.org/10.1111/faf.12132)
- 877 Ferraro, P. J., Sanchirico, J. N., & Smith, M. D. (2018). Causal inference in coupled human
878 and natural systems. *Proceedings of the National Academy of Sciences*, 201805563. <https://doi.org/10.1073/pnas.1805563115>
- 879 [//doi.org/10.1073/pnas.1805563115](https://doi.org/10.1073/pnas.1805563115)
- 880 Field, J. C., Punt, A. E., Methot, R. D., & Thomson, C. J. (2006). Does MPA mean “major
881 problem for assessments”? Considering the consequences of place-based management
882 systems. *Fish and Fisheries*, 7(4), 284–302. [https://doi.org/10.1111/j.1467-2979.2006.](https://doi.org/10.1111/j.1467-2979.2006.00226.x)
883 [00226.x](https://doi.org/10.1111/j.1467-2979.2006.00226.x)
- 884 Fulton, E. A., Bax, N. J., Bustamante, R. H., Dambacher, J. M., Dichmont, C., Dunstan, P. K.,
885 Hayes, K. R., Hobday, A. J., Pitcher, R., Plagányi, É. E., Punt, A. E., Savina-Rolland, M.,
886 Smith, A. D. M., & Smith, D. C. (2015). Modelling marine protected areas: insights and
887 hurdles. *Phil. Trans. R. Soc. B*, 370(1681), 20140278. [https://doi.org/10.1098/rstb.2014.](https://doi.org/10.1098/rstb.2014.0278)
888 [0278](https://doi.org/10.1098/rstb.2014.0278)
- 889 Gaines, S. D., White, C., Carr, M. H., & Palumbi, S. R. (2010). Designing ma-
890 rine reserve networks for both conservation and fisheries management. *Pro-*
891 *ceedings of the National Academy of Sciences*, 107(43), 18286–18293. <https://doi.org/10.1073/pnas.0906473107>
- 892 [//doi.org/10.1073/pnas.0906473107](https://doi.org/10.1073/pnas.0906473107)
- 893 Gillis, D. M. (2003). Ideal free distributions in fleet dynamics: A behavioral perspective on
894 vessel movement in fisheries analysis. *Canadian Journal of Zoology*, 81(2), 177–187.

895 <https://doi.org/10.1139/z02-240>

896 Gilman, E., Chaloupka, M., Fitchett, M., Cantrell, D. L., & Merrifield, M. (2020). Ecological
897 responses to blue water MPAs. *PLOS ONE*, *15*(7), e0235129. [https://doi.org/10.1371/
898 journal.pone.0235129](https://doi.org/10.1371/journal.pone.0235129)

899 Griffiths, S. P., Kesner-Reyes, K., Garilao, C., Duffy, L. M., & Román, M. H. (2019).
900 Ecological Assessment of the Sustainable Impacts of Fisheries (EASI-Fish): a
901 flexible vulnerability assessment approach to quantify the cumulative impacts of
902 fishing in data-limited settings. *Marine Ecology Progress Series*, *625*, 89–113.
903 <https://doi.org/10.3354/meps13032>

904 Grorud-Colvert, K., Sullivan-Stack, J., Roberts, C., Constant, V., Horta e Costa, B., Pike, E.
905 P., Kingston, N., Laffoley, D., Sala, E., Claudet, J., & al., et. (2021). The MPA guide: A
906 framework to achieve global goals for the ocean. *Science*, *373*(6560), eabf0861. [https://
907 //doi.org/10.1126/science.abf0861](https://doi.org/10.1126/science.abf0861)

908 Grüss, A., Robinson, J., Heppell, S. S., Heppell, S. A., & Semmens, B. X. (2014). Conserva-
909 tion and fisheries effects of spawning aggregation marine protected areas: What we know,
910 where we should go, and what we need to get there. *ICES Journal of Marine Science*,
911 *71*(7), 1515–1534. <https://doi.org/10.1093/icesjms/fsu038>

912 Hampton, J., Lehodey, P., Senina, I., Nicol, S., Scutt Phillips, J., & Tiamere, K. (2023).
913 Limited conservation efficacy of large-scale marine protected areas for pacific skipjack
914 and bigeye tunas. *Frontiers in Marine Science*, *9*. [https://www.frontiersin.org/articles/10.
915 3389/fmars.2022.1060943](https://www.frontiersin.org/articles/10.3389/fmars.2022.1060943)

916 Hastings, A., Gaines, S. D., & Costello, C. (2017). Marine reserves solve an important bycatch
917 problem in fisheries. *Proceedings of the National Academy of Sciences*, 201705169. [https://
918 //doi.org/10.1073/pnas.1705169114](https://doi.org/10.1073/pnas.1705169114)

919 Hilborn, R., Stokes, K., Maguire, J.-J., Smith, T., Botsford, L. W., Mangel, M., Orensanz, J.,

- 920 Parma, A., Rice, J., Bell, J., & al., et. (2004). When can marine reserves improve fisheries
921 management? *Ocean & Coastal Management*, 47(3–4), 197–205. [https://doi.org/10.1016/
922 j.ocecoaman.2004.04.001](https://doi.org/10.1016/j.ocecoaman.2004.04.001)
- 923 Hilborn, R., & Walters, C. J. (1987). A general model for simulation of stock and fleet dy-
924 namics in spatially heterogeneous fisheries. *Canadian Journal of Fisheries and Aquatic
925 Sciences*, 44(7), 1366–1369. <https://doi.org/10.1139/f87-163>
- 926 Kapur, M. S., Siple, M. C., Olmos, M., Privitera-Johnson, K. M., Adams, G., Best, J., Castillo-
927 Jordán, C., Cronin-Fine, L., Havron, A. M., Lee, Q., & al., et. (2021). Equilibrium refer-
928 ence point calculations for the next generation of spatial assessments. *Fisheries Research*,
929 244, 106132. <https://doi.org/10.1016/j.fishres.2021.106132>
- 930 Kindsvater, H. K., Reynolds, J. D., Sadovy de Mitcheson, Y., & Mangel, M. (2017). Selectivity
931 matters: Rules of thumb for management of plate-sized, sex-changing fish in the live reef
932 food fish trade. *Fish and Fisheries*, 18(5), 821–836. <https://doi.org/10.1111/faf.12208>
- 933 Lehodey, P., Senina, I., & Murtugudde, R. (2008). A spatial ecosystem and populations dy-
934 namics model (SEAPODYM) – modeling of tuna and tuna-like populations. *Progress in
935 Oceanography*, 78(4), 304–318. <https://doi.org/10.1016/j.pocean.2008.06.004>
- 936 Leroy, B., Meynard, C. N., Bellard, C., & Courchamp, F. (2016). Virtualspecies, an r package
937 to generate virtual species distributions. *Ecography*, 39(6), 599–607. [https://doi.org/10.
938 1111/ecog.01388](https://doi.org/10.1111/ecog.01388)
- 939 Lester, S. E., Costello, C., Halpern, B. S., Gaines, S. D., White, C., & Barth, J. A. (2013).
940 Evaluating tradeoffs among ecosystem services to inform marine spatial planning. *Marine
941 Policy*, 38, 80–89. <https://doi.org/10.1016/j.marpol.2012.05.022>
- 942 Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S.
943 D., Airamé, S., & Warner, R. R. (2009). Biological effects within no-take marine reserves:
944 A global synthesis. *Marine Ecology Progress Series*, 384, 3346.

- 945 Liu, O. R., & Gaines, S. D. (2022). Environmental context dependency in species interactions.
946 *Proceedings of the National Academy of Sciences*, 119(36), e2118539119. [https://doi.org/](https://doi.org/10.1073/pnas.2118539119)
947 [10.1073/pnas.2118539119](https://doi.org/10.1073/pnas.2118539119)
- 948 Lorenzen, K. (2022). Size- and age-dependent natural mortality in fish populations: Biol-
949 ogy, models, implications, and a generalized length-inverse mortality paradigm. *Fisheries*
950 *Research*, 255, 106454. <https://doi.org/10.1016/j.fishres.2022.106454>
- 951 Malakhoff, K. D., & Miller, R. J. (2021). After 15 years, no evidence for trophic cascades
952 in marine protected areas. *Proceedings of the Royal Society B: Biological Sciences*,
953 288(1945), 20203061. <https://doi.org/10.1098/rspb.2020.3061>
- 954 Marshall, D. J., Bode, M., Mangel, M., Arlinghaus, R., & Dick, E. J. (2021). Reproductive
955 hyperallometry and managing the world's fisheries. *Proceedings of the National Academy*
956 *of Sciences*, 118(34). <https://doi.org/10.1073/pnas.2100695118>
- 957 McClanahan, T. R. (2021). Marine reserve more sustainable than gear restriction in maintain-
958 ing long-term coral reef fisheries yields. *Marine Policy*, 128, 104478. [https://doi.org/10.](https://doi.org/10.1016/j.marpol.2021.104478)
959 [1016/j.marpol.2021.104478](https://doi.org/10.1016/j.marpol.2021.104478)
- 960 Methot Jr., R. D., & Wetzel, C. R. (2013). Stock synthesis: A biological and statistical frame-
961 work for fish stock assessment and fishery management. *Fisheries Research*, 142, 86–99.
962 <https://doi.org/10.1016/j.fishres.2012.10.012>
- 963 Nickols, K. J., White, J. W., Malone, D., Carr, M. H., Starr, R. M., Baskett, M. L., Hast-
964 ings, A., & Botsford, L. W. (2019). Setting ecological expectations for adaptive man-
965 agement of marine protected areas. *Journal of Applied Ecology*, 56(10), 2376–2385.
966 <https://doi.org/https://doi.org/10.1111/1365-2664.13463>
- 967 Ovando, D., Caselle, J. E., Costello, C., Deschenes, O., Gaines, S. D., Hilborn, R., & Liu,
968 O. (2021). Assessing the population-level conservation effects of marine protected areas.
969 *Conservation Biology*, 35(6). <https://doi.org/10.1111/cobi.13782>

970 Ovando, D., Liu, O., Molina, R., & Szuwalski, C. (2021). Models of marine protected ar-
971 eas must explicitly address spatial dynamics. *Proceedings of the National Academy of*
972 *Sciences*, 118(23). <https://doi.org/10.1073/pnas.2025958118>

973 Pons, M., Watson, J. T., Ovando, D., Andraka, S., Brodie, S., Domingo, A., Fitchett, M.,
974 Forselledo, R., Hall, M., Hazen, E. L., & al., et. (2022). Trade-offs between bycatch
975 and target catches in static versus dynamic fishery closures. *Proceedings of the National*
976 *Academy of Sciences*, 119(4). <https://doi.org/10.1073/pnas.2114508119>

977 R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation
978 for Statistical Computing. <https://www.R-project.org/>

979 Rassweiler, A., Costello, C., Hilborn, R., & Siegel, D. A. (2014). Integrating scientific guid-
980 ance into marine spatial planning. *Proceedings of the Royal Society B: Biological Sciences*,
981 281(1781), 20132252. <https://doi.org/10.1098/rspb.2013.2252>

982 Rassweiler, A., Costello, C., & Siegel, D. A. (2012). Marine protected areas and the value
983 of spatially optimized fishery management. *Proceedings of the National Academy of Sci-*
984 *ences*, 109(29), 11884–11889. <https://doi.org/10.1073/pnas.1116193109>

985 Reimer, M. N., Abbott, J. K., & Wilen, J. E. (2017). Fisheries production: Management insti-
986 tutions, spatial choice, and the quest for policy invariance. *Marine Resource Economics*,
987 32(2), 143–168. <https://doi.org/10.1086/690678>

988 Sala, E., Mayorga, J., Bradley, D., Cabral, R. B., Atwood, T. B., Auber, A., Cheung, W.,
989 Costello, C., Ferretti, F., Friedlander, A. M., & al., et. (2021). Protecting the global
990 ocean for biodiversity, food and climate. *Nature*, 1–6. [https://doi.org/10.1038/s41586-](https://doi.org/10.1038/s41586-021-03371-z)
991 [021-03371-z](https://doi.org/10.1038/s41586-021-03371-z)

992 Sampson, D. B. (2014). Fishery selection and its relevance to stock assessment and fishery
993 management. *Fisheries Research*, 158, 5–14. [https://doi.org/10.1016/j.fishres.2013.10.](https://doi.org/10.1016/j.fishres.2013.10.004)
994 [004](https://doi.org/10.1016/j.fishres.2013.10.004)

- 995 Shin, Y.-J., & Cury, P. (2001). Exploring fish community dynamics through size-dependent
996 trophic interactions using a spatialized individual-based model. *Aquatic Living Resources*,
997 *14*(02), 65–80. [https://doi.org/10.1016/S0990-7440\(01\)01106-8](https://doi.org/10.1016/S0990-7440(01)01106-8)
- 998 Thorson, J. T. (2020). Predicting recruitment density dependence and intrinsic growth rate for
999 all fishes worldwide using a data-integrated life-history model. *Fish and Fisheries*, *21*(2),
1000 237–251. <https://doi.org/10.1111/faf.12427>
- 1001 Thorson, J. T., Barbeaux, S. J., Goethel, D. R., Kearney, K. A., Laman, E. A., Nielsen, J. K.,
1002 Siskey, M. R., Siwicke, K., & Thompson, G. G. (2021). Estimating fine-scale movement
1003 rates and habitat preferences using multiple data sources. *Fish and Fisheries*, *22*(6), 1359–
1004 1376. <https://doi.org/10.1111/faf.12592>
- 1005 Thorson, J. T., Minto, C., Minto-Vera, C. V., Kleisner, K. M., & Longo, C. (2013). A new role
1006 for effort dynamics in the theory of harvested populations and data-poor stock assessment.
1007 *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(12), 1829–1844. [https://doi.org/](https://doi.org/10.1139/cjfas-2013-0280)
1008 [10.1139/cjfas-2013-0280](https://doi.org/10.1139/cjfas-2013-0280)
- 1009 Visintin, C., Briscoe, N. J., Woolley, S. N. C., Lentini, P. E., Tingley, R., Wintle, B. A., &
1010 Golding, N. (2020). Steps: Software for spatially and temporally explicit population simu-
1011 lations. *Methods in Ecology and Evolution*, *11*(4), 596–603. [https://doi.org/10.1111/2041-](https://doi.org/10.1111/2041-210X.13354)
1012 [210X.13354](https://doi.org/10.1111/2041-210X.13354)
- 1013 Waterhouse, L., Sampson, D. B., Maunder, M., & Semmens, B. X. (2014). Using areas-as-
1014 fleets selectivity to model spatial fishing: Asymptotic curves are unlikely under equilib-
1015 rium conditions. *Fisheries Research*, *158*, 15–25. [https://doi.org/10.1016/j.fishres.2014.](https://doi.org/10.1016/j.fishres.2014.01.009)
1016 [01.009](https://doi.org/10.1016/j.fishres.2014.01.009)

1017 **Figure Legends**

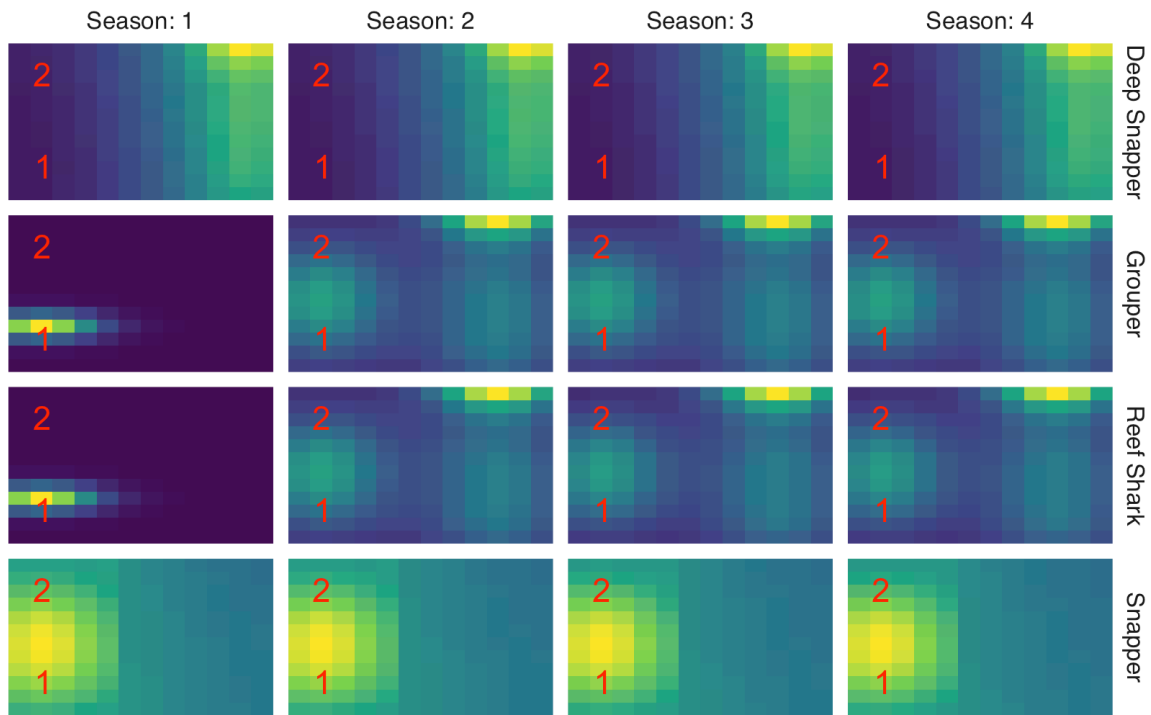


Figure 1: Distribution of fish spawning biomass (cell color, yellow = higher, blue = lower) each season (columns) under unfished conditions. The x-axis represents longitude, y-axis latitude. Numbers show the approximate location of each fleet's (one or two) port. Columns indicate quarterly seasons that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

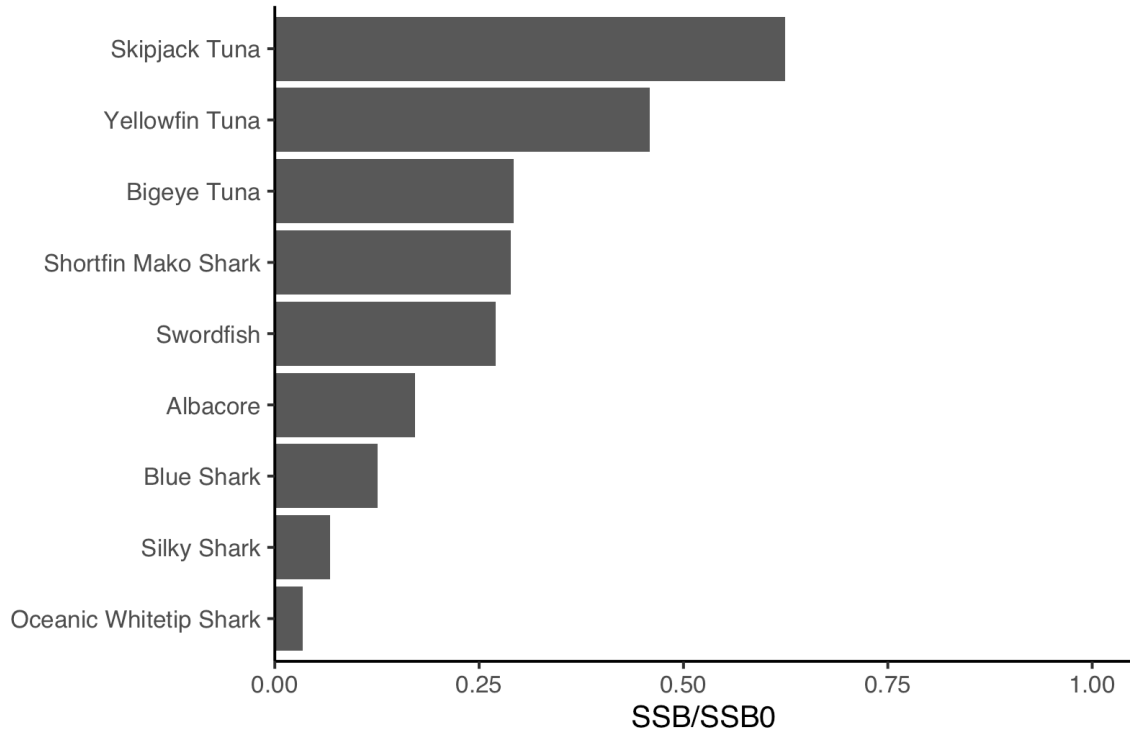
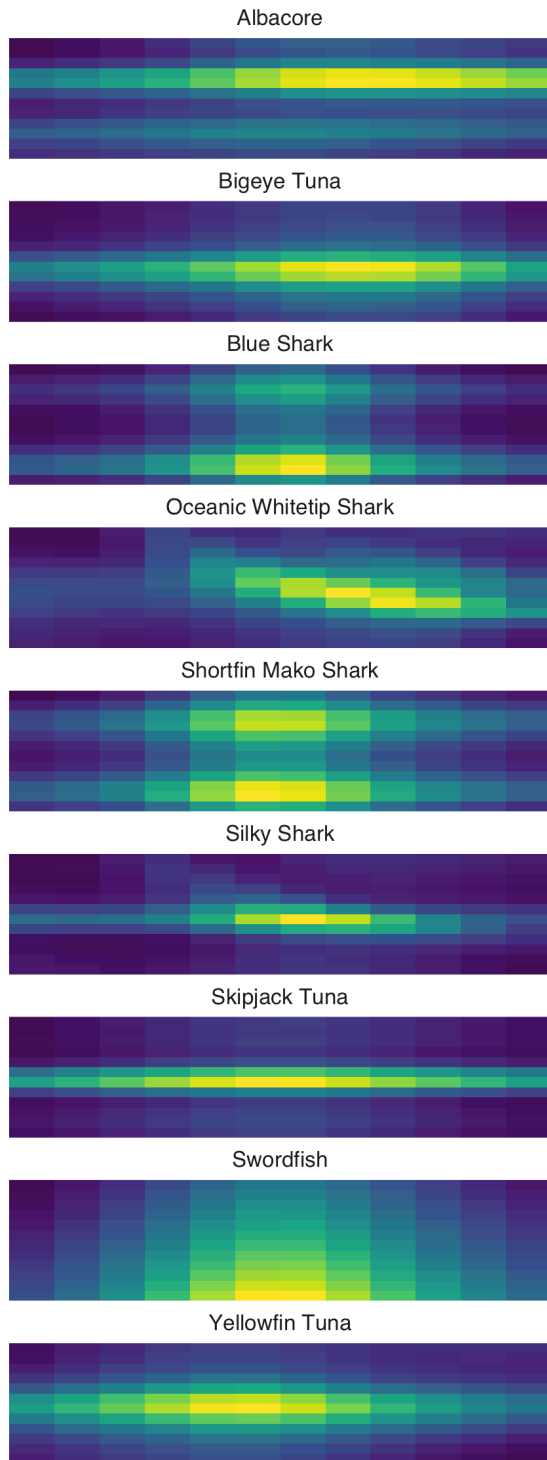


Figure 2: Spawning biomass divided by unfished spawning biomass in the time period prior to implementation of MPAs for the pelagic case study. Simulated species include skipjack tuna, yellowfin tuna, bigeye tuna, shortfin mako (*Isurus oxyrinchus*, Lamnidae), swordfish (*Xiphias gladius*, Xiphiidae),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

Status Quo



Range Shift

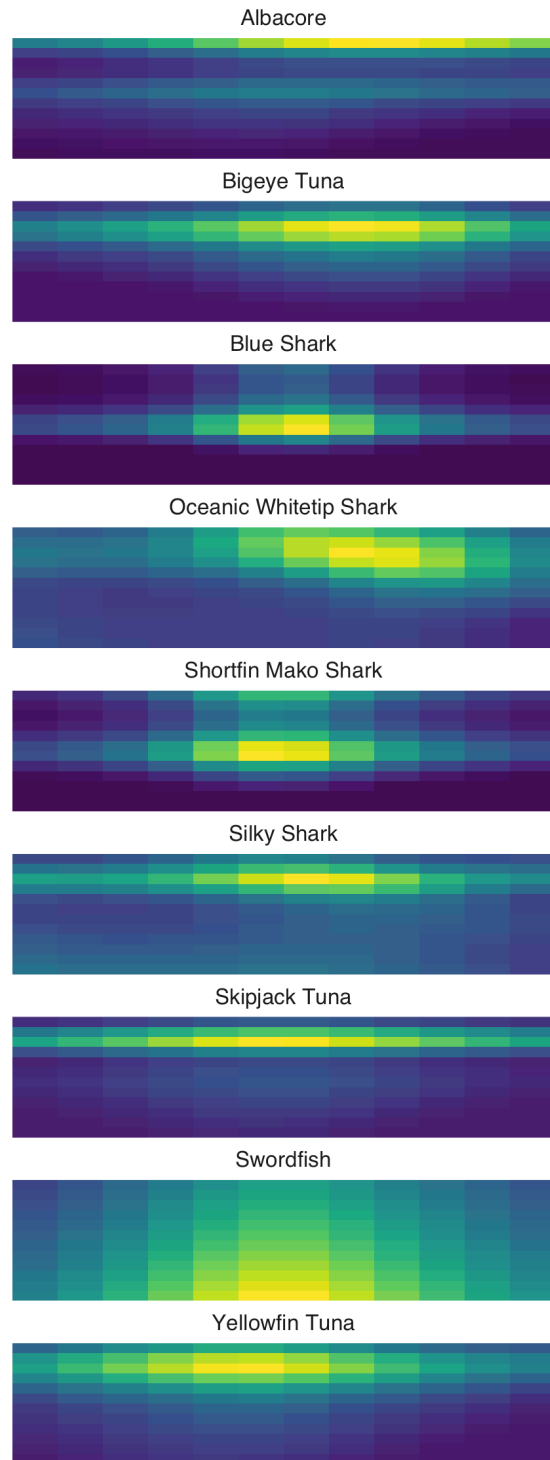


Figure 3: Distribution of unfished spawning biomass in space under status quo (left column) and range-shifted (right column) conditions for blue-water simulation for each species. The x-axis represents longitude, the y-axis latitude.

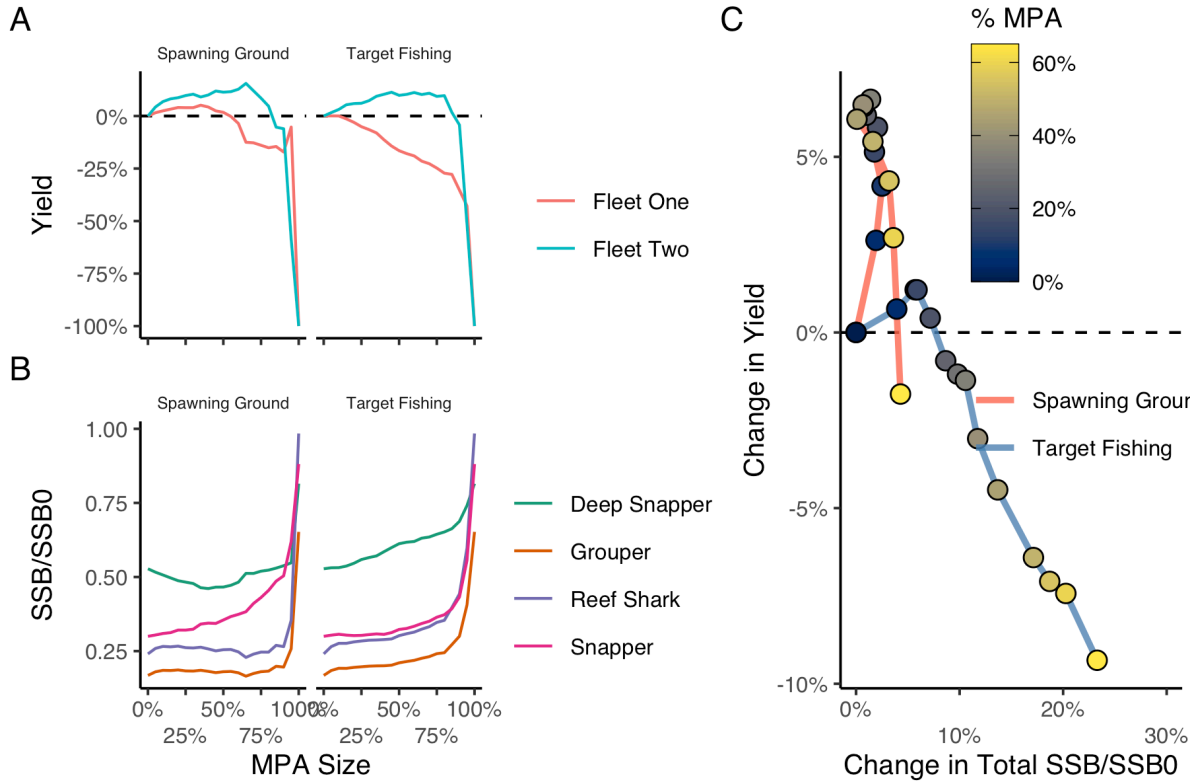


Figure 4: Percent change in yield per fleet (A) and SSB/SSB0 (spawning biomass divided by unfished spawning biomass) per species (B) as a function of MPA size and MPA design strategy for the coastal coral reef case study. Percent change in total yield across both fleets (y-axis) and total SSB/SSB0 across 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.

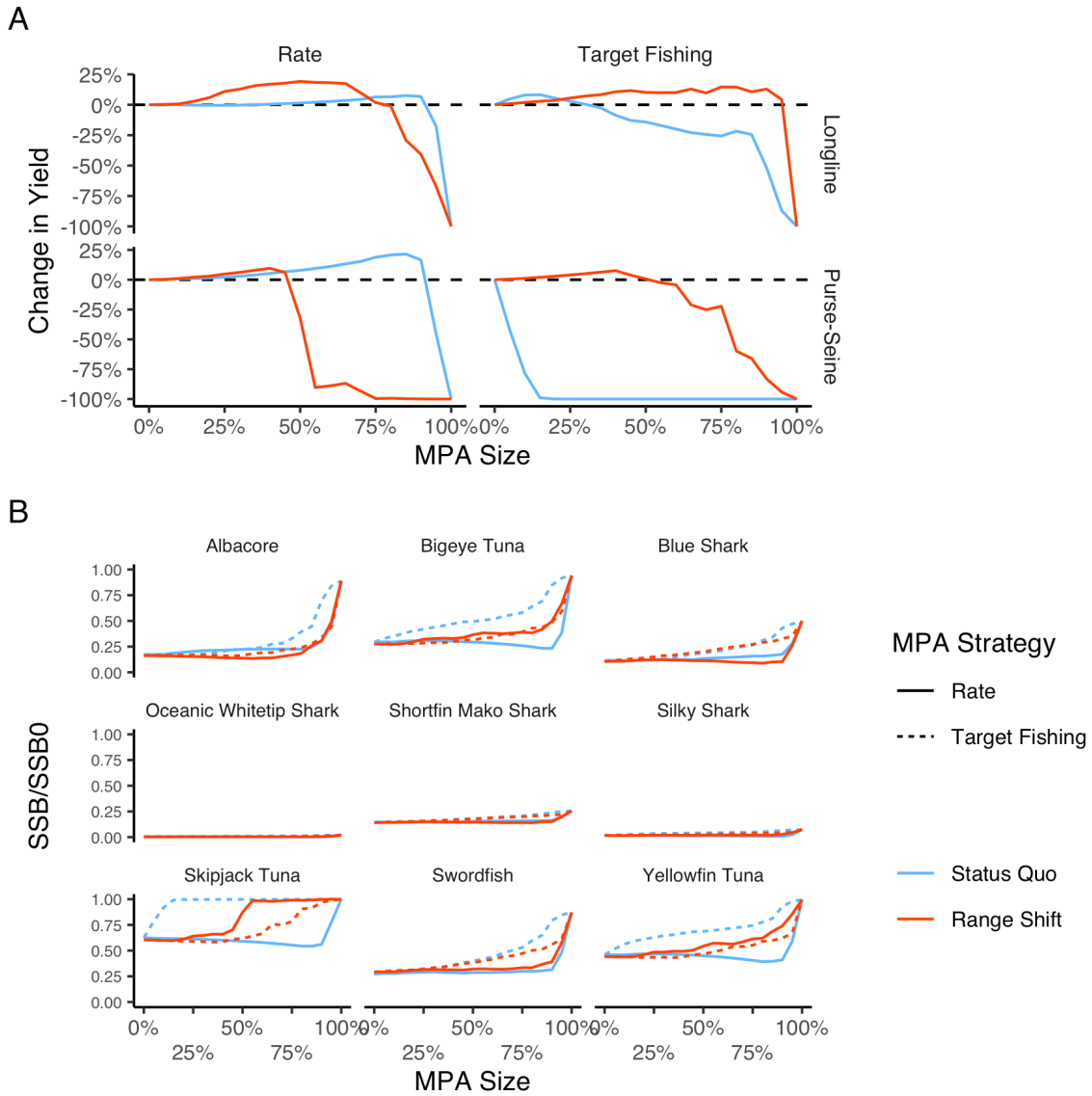


Figure 5: Change in yield (A) and SSB/SSB0 (spawning biomass divided by unfished spawning biomass) (B) as a function of MPA size and design strategy by fishing fleet and species. Blue lines indicate impacts of MPAs under status quo habitat, red impacts under climate-driven range shift. Results reflect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