

## Fisheries and biodiversity benefits of using static versus dynamic models for designing marine reserve networks

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**Abstract.** Marine reserves are widely used to manage for the potentially conflicting objectives of conserving biodiversity and improving fisheries. The fisheries and conservation benefits of alternative reserve designs would ideally be assessed using dynamic models, which consider spillover of fish and larvae to fished areas, and the displacement of fishers to unprotected sites. In practice, however, decisions about the location of marine reserves generally rely on cheaper and faster static models. Static models analyze only spatial patterns in habitats, and typically assume fisheries profits are reduced by the amount that was generated in areas designated as reserves. To help determine the benefits of developing dynamic fisheries models, we assessed how well static models estimate costs of reserve systems to fisheries and how outcomes from reserves designed using either static or dynamic models differ. We tested these questions in two case studies, the network of marine protected areas in southern California, USA and the proposed Tun Mustapha Marine Park in Malaysia. Static models could either under or over-estimate the cost of reserve plans to fisheries, depending on the relative importance of fisher movement and larval dispersal dynamics. Despite the inaccuracy of static models for estimating costs, reserves designed using static models were similar to those designed with dynamic models if fisheries were well managed; or larval dispersal networks were simple. If larval networks were complex or there was overfishing, dynamic models generated substantially different reserve networks from static models, which improved conservation outcomes by up to 10% and fishing profits by up to 20%. The time-scale of management was also important, because only dynamic models accounted for larval dispersal, so could find reserves that maximized the long-term benefits of larval spillover. Our case studies provide quantitative support for the assertion that static models can be useful for planning marine reserves for short-term objectives in well managed fisheries, but are not reliable for evaluating the relative costs of reserves to fisheries.

**Key words:** conservation planning; fishery behavior; marine protected area; model complexity; spatial population model.

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## INTRODUCTION

Fisheries are a globally significant source of income and sustenance (Smith et al. 2010*b*), but they are also a major threat to marine biodiversity (Jackson et al. 2001). Networks of no-take marine reserves offer a mechanism to help balance fisheries and conservation objectives (e.g., Klein et al. 2009). Reserve networks may recover the biomass of fished populations (Abesamis et al. 2014; Brown et al. 2015), and provide benefits to fisheries through spillover of large fish and larval export (Halpern et al. 2009, Harrison et al. 2012). However, reserves may also displace fishing effort, potentially increasing fishing pressure elsewhere (Smith and Wilen 2003, Hilborn et al. 2004, Horta e Costa et al. 2013). The implications of reserves to fisheries and conservation will therefore be a balance between the effects of build-up of fish biomass inside of reserves and increased pressure and competition among fishers outside of reserves. Accounting for these ecological and socio-economic dynamics in response to reserves is thus key to designing effective reserves (e.g., Kaplan et al. 2009, Costello et al. 2010, Little et al. 2011, Rassweiler et al. 2014) and communicating the impact of reserves to stakeholders (e.g., Dowling et al. 2012, White et al. 2013).

In practice, reserve designs are often developed using static models that assess reserve placement based on patterns of status-quo profits and species or habitat distributions (Klein et al. 2008, Collie et al. 2013). For example, a widely used static reserve design tool is the Marxan software. Marxan searches for reserve designs that minimize lost fishing opportunities to achieve representation of habitats within the reserves (e.g., Klein et al. 2009, Watts et al. 2009). Users of software like Marxan usually assume the opportunity cost of a site is the revenue or harvest currently taken from that site. Thus, Marxan does not consider the displacement of fishing effort or spillover of fish to fished

areas. In contrast, more realistic, and thus more likely effective, reserve designs can be achieved using dynamic models that account for ecological processes and fishery behavior (e.g., Kaplan et al. 2009, Costello et al. 2010, Little et al. 2011). For instance, models that account for complex patterns of larval dispersal produce reserve designs with greater improvements in fisheries profits (Costello et al. 2010) and conservation (White et al. 2014).

Static models are often used in practice because the development of dynamic models is computationally intensive and constrained by data, time, budgets and staff expertise (Stelzenmüller et al. 2013). Even when these constraints can be overcome, static models are faster to develop and may allow managers to quickly respond to new environmental regulations, with greater immediate benefits for biodiversity (Grantham et al. 2009). Thus, managers and scientific advisors must decide whether the additional time and investment in gaining accuracy through developing dynamic models for their region is worthwhile. For instance, when used to evaluate a reserve proposal, dynamic and static models predicted similar relative profit losses for fisheries, but only for overfished fisheries (White et al. 2013). Further, simple rules about reserve size and spacing provide inferior outcomes for fisheries and conservation when compared to reserves designed using dynamic models (Rassweiler et al. 2014). The extent that reserve networks can be designed to provide better outcomes for fisheries and conservation when using dynamic models over static models, like Marxan, has not been evaluated.

We compared the outcomes for fisheries and conservation when using dynamic versus static models for planning optimized marine reserve networks. We aim to answer two questions: (Q1) How accurate are static models for estimating relative losses in profits for fisheries from reserve systems? (Q2) How do outcomes for fisheries and conservation differ if using either static or

dynamic models to design reserves? We address our questions using two case studies, chosen to represent two common approaches to reserve design. For both case studies we compare static and dynamic models for designing marine reserves. While the case-studies are for different types of fisheries, similarities in the results suggest there are generalities in the value of dynamic models. The key innovation here is that we investigate how much worse static models are than dynamic models in an applied setting. We aim to inform decisions about the inherent tradeoff between more accurate, expensive dynamic models and easier but less accurate static models.

The first case study is the proposed Tun Mustapha Marine Park in Sabah, Malaysia. A marine protected area system is currently being planned and implemented in the Sabah province. It aims to protect tropical marine habitats and improve multiple, mostly artisanal, fisheries. It is likely that many species in the region are overfished (Teh and Sumaila 2007), so the aim of the reserve system is to assist in recovering the fish species biomass and harvests. Further, destructive fishing practices have damaged critical habitats, so the conservation objective of the reserve system is to protect habitats and limit destructive fishing. These management objectives are typically addressed using software that optimizes static models (e.g., Marxan; Klein et al. 2008), so we use a static model formulated to represent the basic components of Marxan, and then used this model as the starting point to develop the dynamic model for comparison.

The second case study is the red sea urchin (*Strongylocentrotus franciscanus*) fishery in the Southern California Bight, USA. The Southern California Bight recently underwent an extensive marine reserve design process that was informed by the analysis of dynamic bio-economic models estimating fish conservation and fishery economic implications for proposed marine reserve designs (White et al. 2013). The red sea urchin fishery is one of the key commercial fisheries in the region. The fishery is limited-entry and managed via harvest effort regulations. The management objective is to maximize the biomass of fished species (the conservation objective) while maximising fishery profits (the fishery objective). Such an objective has been addressed

in other fisheries using dynamic models of fish populations with an embedded fleet model (e.g., Kaplan et al. 2009, Little et al. 2009, Rassweiler et al. 2012). Typically, dynamic models are used to assess competing reserve designs (e.g., Kaplan et al. 2009, Little et al. 2009), rather than being used in an optimization of reserve design, because of computational challenges (but see Rassweiler et al. 2012). Thus for the California case study, we use a dynamic model as the starting point to develop a comparable static model.

## METHODS

### *General approach*

For each question, we generated trade-off curves, or pareto efficiency frontiers, that represent the most efficient reserve designs for achieving a range of outcomes from conservation-focused to fisheries-focused. Points on the trade-off curve indicate designs where one outcome cannot be increased without decreasing the other outcome (Lester et al. 2013). Trade-off curves inform and illustrate the nature of the tradeoff between two possible management objectives (in this case, fisheries vs. conservation). Our interest here is less on the nature of the tradeoff between these objectives, and instead on the difference in the location and shape of these curves derived from dynamic versus static models. In other words, differences in the curves generated using static or dynamic models describe the value of dynamic over static modeling.

To examine if static models can reliably assess the relative loss in profits (Q1), we compared two scenarios: a naïve static scenario with a realistic static scenario. The naïve static scenario is the static model's estimate of the effects of the reserve design it generated (i.e., the reserve design and its effect perceived by a manager using a static model only). The realistic static scenario used a static model to find reserve designs, but the outcomes were evaluated using the dynamic model (Fig. 1). The realistic static scenario represented the predicted outcome of using static models for designing reserves. Thus, the two scenarios used the same model to design reserves (static), but different models to evaluate their outcomes (static versus dynamic). We compared relative loss in profits from the two scenarios, so that they were on a standardized scale (e.g.,

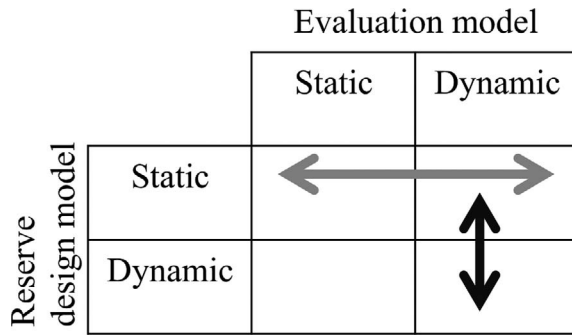


Fig. 1. Model comparisons used to ask how well static models estimate costs of reserve to fisheries (Q1, grey arrow) and how outcomes of reserves designed using static or dynamic models differ (Q2, black arrow).

White et al. 2013). If the naïve trade-off curve is different from the realistic static trade-off curve, then static models inaccurately represent the relative cost of alternate reserve proposals to fisheries.

To examine how much can be gained for fisheries and conservation using dynamic over static models (Q2), we compared the realistic static scenario with a further scenario, the best-case scenario (Fig. 1). The best-case scenario used a dynamic model to find reserve designs and evaluate their success, which represented the highest outcomes for profits and conservation that could be achieved using marine reserves to manage the fisheries. Thus, the two scenarios used different models to design reserves (static versus dynamic), but the same model to evaluate the outcomes of reserve designs (dynamic). If the trade-off curve for the best-case scenario can achieve greater fishing profits for a given conservation value (or vice-versa), then there is a benefit from dynamic models.

The details of each model were tailored to the case studies, but for each we followed the same sequence of simulations. (1) The dynamic models were simulated under status-quo management until equilibrium conditions were reached (profits and biomass were stable across time and space). The equilibrium state represented the initial condition. (2) The initial spatial patterns in profits and biomass were taken for the optimization of the static models. The static optimization used these patterns to find reserves designs

that minimized the loss of fishing profits, but maximized biomass or habitat protection. The outcome is the naïve static outcome. (3) The optimal static reserve designs were evaluated using the dynamic model—the realistic static outcome. (4) The dynamic model was used to find optimal reserves designs—the best case outcome.

The effects of reserve on fisheries are be sensitive to the time-horizon for management (Brown et al. 2015), so we modeled all scenarios for short and long-term (equilibrium) planning horizons. The Malaysia model was more computationally efficient to run, so we explored additional scenarios for variations in fishing effort and larval dispersal (Table 1).

#### Tun Mustapha Park case study

We focused our analysis on coral reef habitats and the coral trout (*Plectropomus leopardus*) fishery in the northern region of the park. Our aim was to represent eight general types of coral reef habitat within reserves (Appendix: Table A1), while maximizing profits from coral trout fishing. Coral trout is a highly sought-after predator species in the artisanal catch (e.g., Teh and Sumaila 2007) and a species with well-known life history parameters (e.g., Little et al. 2009). Adult fish generally move within relatively small home range area, so flux of adults between reserved and unreserved areas is likely to be small (Zeller and Russ 1998). Coral trout larvae disperse over larger areas and studies of similar species have found larvae from reserves can make a significant contribution to recruitment in unreserved areas (Harrison et al. 2012).

The dynamic fishery model for Tun Mustapha Park was divided into two components, a fish population model, and a model of fishing effort (e.g., Rassweiler et al. 2012). The fish population model was an age-structured discrete time (annual time-step) and discrete space model of coral trout. Within each time-step, processes occurred in this order: (1) total fishing effort is distributed across planning units; (2) harvest, natural mortality, age increase and allometric growth; (3) spawning; (4) larval dispersal; (5) intra-cohort density dependent recruitment. Recruitment was varied by habitats to reflect observations that coral trout densities are higher in more exposed environments, which is likely a



Table 1. Scenarios that were evaluated for each question and case study.

Scenario	Q1: Are static models accurate?		Q2: Value of dynamic models	
	Malaysia	California	Malaysia	California
Timespan				
Equilibrium	yes	yes	yes	yes
Short-term discounted	discounted at 10% p.a.	discounted at 5% p.a.	discounted at 10% p.a.	discounted at 5% p.a.
Fishing effort				
Optimal profits	yes, optimized without reserves	yes, optimized with reserves	yes, optimized without reserves	yes, optimized with reserves
Overfished	$2 \times$ optimal effort	not simulated	$2 \times$ optimal effort	not simulated
Larval dispersal				
Base larval dispersal scenario	39% retention	from oceanographic model	39% retention	from oceanographic model
Equal mixing	not simulated	not simulated	yes	not simulated
Short	not simulated	not simulated	86% retention	not simulated

consequence of recruit selection for exposed habitats (Kingsford 2009). Specifically, the maximum recruitment rate was varied by habitat exposure (Appendix: Eq. A8, Table A1) and is the number of age 1 fish that recruit to the population when larval supply is high. Larval supply was determined by a simple distance based dispersal model, where the proportion of larvae leaving one planning unit and arriving at another declined exponentially with the over-water distance between planning units (Appendix: Eq. A6). We assessed the sensitivity of our results to different assumptions about larval dispersal distances.

The fishery model distributed fishing effort according to the cost of travel and a preference for fishing in high profit areas (online supplement). We set the total annual fishing effort relative to the effort that gave the maximum sustainable profits (found through simulation). This allowed us to explore the effects of different levels of effort on the value of dynamic models.

The area modeled for reserve design was divided into a spatial grid (Table 2), where each grid cell is a single planning unit that can be selected for inclusion in a reserve system. We did not model habitat dynamics, so the area of each habitat type was constant over time and independent of reserve designation and fishing effort. The distribution of coral reef habitats across planning units was estimated from habitat maps (online supplement).

The objective for our planning algorithm was to maximize profits from coral trout harvest subject to the constraint that a fixed proportion of

each coral reef habitat type was represented within marine reserves. The objective function was the same for static and dynamic approaches

$$\begin{aligned}
 & \max \sum_t^T \left( \sum_{i=1}^n P_{t,i} / (1+D)^t \right) \\
 & \text{subject to } \sum_{i=1}^n a_{i,j} x_i \geq b_j p \\
 & \text{with } x_i \in \{0, 1\}
 \end{aligned} \tag{1}$$

where  $P_{t,i}$  is the profits from harvest in planning unit  $i$  ( $i, \dots, n$ ) at time  $t$  and  $D$  is the discount rate and  $T$  is the time-horizon for planning. The area of coral reef habitat  $j$  in planning unit,  $i$ , is  $a_{i,j}$ .  $x_i$  indicates reserve designation,  $b_j$  is the area of habitat  $j$  in the planning region and  $p$  is the target percentage representation for coral reef habitat conservation, which was the same for all habitat types. The difference between the dynamic and static models was that  $P_{t,i}$  was calculated using simulations of the dynamic model over time, whereas for the static model,  $P_{t,i}$  was always the initial profits ( $P_{t,i} = P_{0,i}$ ). A greedy algorithm, with multiple random starting points, was applied to optimize the objective function for the static and dynamic models (online supplement).

Both planning horizons were evaluated for two plausible levels of fishing effort: the optimal effort level that maximized profits and, to represent a scenario with overfishing, twice the optimal effort level (biomass at 18% of unfished; Table 1). The dynamic model is expected to be sensitive to the planning horizon, whereas the static approach is insensitive to the time-horizon

Table 2. Characteristics of each case study, highlighting key differences and similarities.

Case study	Tun Mustapha Park	Southern California Bight
Site details		
Fishery species	coral trout ( <i>Plectropomus leopardus</i> )	red sea urchin ( <i>Strongylocentrotus franciscanus</i> )
Status-quo fishing effort	(1) level that maximizes equilibrium profits (2) overfished	level that maximizes equilibrium profits
Fishery objective	maximize fishery profit	maximize fishery profit
Conservation objective	represent a percentage (ranging from 0-90%) of each of 8 coral reef habitats in reserves	maximize wild biomass of red sea urchin
Trade-off between fisheries and conservation generated by:	varying target for representation of habitats	varying relative importance of biomass over profits
Fishery objective modeled as dynamic?	yes, in dynamic model	yes, in dynamic model
Conservation objective modeled as dynamic?	no	yes, in dynamic model
Time horizons	(1) 30 yrs at 10% discounting, (2) equilibrium	(1) 30 yrs at 5% discounting, (2) equilibrium
Model details		
Number of planning units	929	135
Area modeled	~4000 km <sup>2</sup>	~10,000 km <sup>2</sup>
Model resolution	1-km <sup>2</sup> planning units	5-km radius planning units

because it does not generate time-varying responses to reserves. For the static approach, annual fishery profit in unreserved sites ( $P_{t,i}$ ) was calculated as the equilibrium profits in the dynamic model run with status quo conditions. This approach gives the static model the benefit of the doubt by assuming that a manager building the model has available spatially explicit empirical data on current fish population density and fishery profit across the study domain.

For the dynamic scenario, at the long-term planning horizon,  $P_{t,i}$  was calculated by simulating the dynamics of fishery harvest and profits with a given reserve design until the dynamics reached equilibrium. For the short-term planning horizon, the fishery objective was to maximize the net present value (NPV) of profits. The model began at equilibrium fishing conditions with no reserves. A reserve system was then implemented and the model was run for 30 years. Annual profits were discounted at a rate of 10%, a high value, but realistic for private discount rates in many artisanal coral reef fisheries (Teh et al. 2013). Thus, the NPV results were intended to represent the level of opposition from individual fishers, rather than public benefits (Smith et al. 2010a). Discounted profits were summed over a 30 year time-horizon to calculate NPV of profits. The effect of a high discount rate was to cause the dynamic model to avoid short-term profit losses

from reserve implementation.

#### *Southern California Bight case study*

Here we constructed a bio-economic fishery and fish conservation model following the form and parameter values used by Rassweiler et al. (2012; see Appendix for more details) in the southern California Bight. Our model had 135 coastal patches (planning units), 11 of which have existing reserves that we did not change in this study (Table 2).

Similar to the Malaysia case study, the urchin population model accounted for dynamics in population size, individual fish/urchin growth, larval dispersal and fishing effort (full details in Appendix and Rassweiler et al. 2012). Dispersal of urchin larvae was determined using a larval dispersal kernel previously developed for the species and region using simulation of Lagrangian particles in a hydrodynamic model (Mitarai et al. 2009, Rassweiler et al. 2012). The number of patches in the dispersal kernel (135) was used to set the number of planning units in our model. Maximum recruitment rate was in proportion to the area of habitat within a planning unit, so that potential abundance of adult urchins was larger in planning units that contained more habitat. The fishery was modeled as a limited entry fishery with a minimum size limit. Management rules controlled the total allowable fishing effort

(TAE) to be expended annually by the fishery. The annual effort level was optimized to maximize total regional profit. Spatial allocation of that effort by the fishery was modeled using an ideal free distribution (Fretwell and Lucas 1970) fleet model, such that average profits (profit per unit effort) were equal among all fishable (i.e., non-MPA) patches. Note that this behavioral model of fleet dynamics, while potentially representative of the actual relationship between vessel and resource distributions in commercial fisheries (Gillis 2003, Branch et al. 2006), is not necessarily expected to produce the optimal pattern of spatial effort distribution (e.g., by a sole owner or fishery cooperative) that maximizes the total value of the fishery (Costello and Polasky 2008).

For both the static and dynamic models, the objective was to maximize the sum of weighted fishery and conservation NPVs in the system. Fishery and conservation NPVs were calculated as the profit and biomass, respectively, discounted annually and summed over a set time horizon. Weighting of NPVs (determined by  $\alpha$ ; see below) was used because there is a trade-off between profits and biomass that prevents maximizing both metrics simultaneously (Rassweiler et al. 2012). The overall objective function was thus

$$Obj = \max \left( \alpha \sum_t^T \left( \sum_{i=1}^n B_{t,i} / (1+D)^t \right) + (1-\alpha) \sum_t^T \left( \sum_{i=1}^n P_{t,i} / (1+D)^t \right) \right) \quad (2)$$

where  $B_{t,i}$  and  $P_{t,i}$  are urchin biomass and urchin fishery profit in planning unit  $i$  in year  $t$ . The objective function was maximized using a genetic search algorithm that varied which planning units were reserved, thus reserve status of a planning unit was the control variable (see Appendix). We maximized the objective function across weighting parameter values from  $\alpha = 0-1$  to generate an efficiency frontier of optimal solutions representing the set of marine reserve designs where profits (or biomass) could not be increased without reducing biomass (or profits).

In the static model, urchin biomass and fishery profit were calculated using the initial condition. Profit in a planning unit ( $P_{t,i}$ ) was simply set as the existing profit under status quo conditions, or zero if the planning unit was converted into a

marine reserve. Similarly, biomass in a fished planning unit was set to the level observed in the planning unit. The biomass increase from designating a reserve was estimated from the relationship between habitat area and biomass in the existing eleven reserves, and then used to interpolate biomass in the new reserve given its habitat area (Appendix). Biomass and profits were assumed by the static model to be constant across all future years in the analysis.

For both dynamic and static models, a discount rate of zero was used for the long-term planning horizon, and in practice NPV was calculated using the final year because over the long-term annual fishery and conservation metrics were constant. For the short-term planning horizon, a discount rate of 5% was used, a reasonable rate for environmental policies (White et al. 2012), and values were assessed over a 30-year time horizon.

#### Case study differences

There were some important differences between the two case study models (Table 2). Total fishing effort was optimized each time a new reserve system was used in the (dynamic) California model; whereas the Malaysia model assumed fishing effort was fixed regardless of the reserve system. The fishery and conservation objectives in the California model were unconstrained and we found solutions that maximized profits and urchin biomass for a given weighting value. Further, for the California model, both conservation (fish biomass) and fishery (NPV) values were dynamic. In contrast, in the Malaysia model the conservation objective was constrained and static, so we found the maximal fishery profits for a given percentage of habitats protected. Finally, detailed larval dispersal modeling was available to parameterize the California model, whereas such modeling was not available for Malaysia model, so we made simple assumptions about the likely distance of dispersal (Appendix).

## RESULTS

### *Can static models accurately estimate losses in profits for fisheries from reserves?*

Plans evaluated using the naïve static scenario can only decrease fishery profits from the

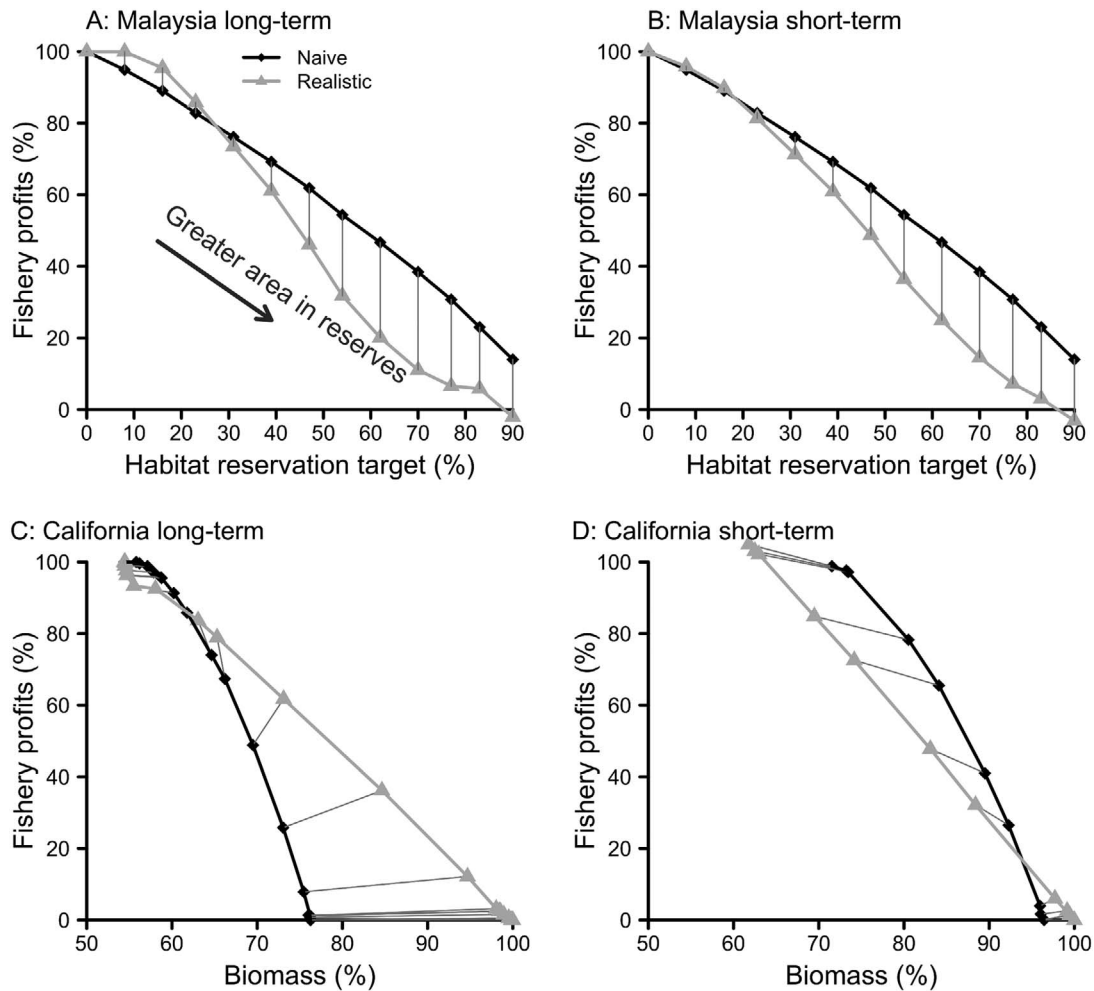


Fig. 2. Comparison of naïve static and realistic static scenarios for Malaysia (A, B) and California (C, D), in the long-term (A, C) and short-term (B, D). Connecting lines indicate naïve and informed scenarios for a given conservation target (Malaysia model) or weighting parameter value (Californian model, i.e.,  $\alpha$ ). The difference between connected points indicates the error when using static estimates of cost.

baseline, whereas it is possible for realistic static and dynamic scenarios to increase profits. For both case studies, the naïve static and realistic static scenarios predicted lower fishery profits when larger areas of the seascape were reserved (Fig. 2). However, there were large differences between the naïve and realistic trade-off curves between the two case studies.

For the Malaysia case study with over-fishing, the naïve scenario slightly underestimated fishery profits for small conservation targets, and greatly over-estimated profit for large reserves (Fig. 2A, B). The overestimation occurred because the naïve static estimate did not account for the

concentration of fishing effort outside of reserves and the resulting lower profits from harvesting smaller fish at lower densities. If the fishery was fished at the optimal effort level, naïve and realistic profit predictions were similar (results not shown).

For the California model and the long-term planning horizon, naïve and realistic predictions for profit and biomass were similar if small areas of the seascape were reserved (Fig. 2C). For larger areas reserved, the naïve prediction grossly under-estimated biomass and profit outcomes (Fig. 2C), because it did not account for the synergistic effects of larval connectivity



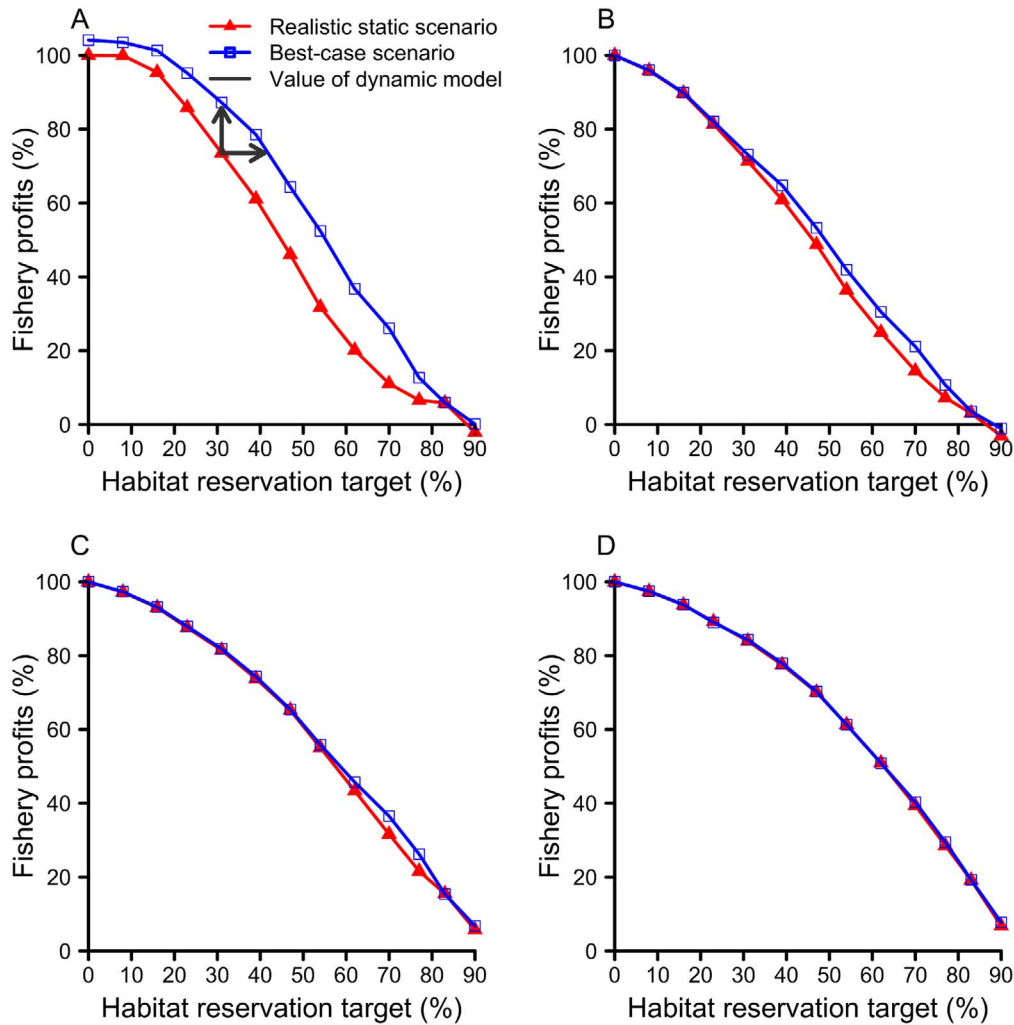


Fig. 3. Value of dynamic models in marine reserve planning over static models in the Malaysia model. Comparison of the best-case and realistic static scenarios in the long-term (A, C) and short-term (B, D) and when there is overfishing (A, B) or fishing effort is optimally managed with no marine reserves (C, D). The difference between the curves indicates the error when using static estimates of cost.

among marine reserves. For the short-term planning horizon, the naïve static model tended to underestimate profits and in particular overestimate biomass (Fig. 2D). This model behavior resulted because over the short-term time horizon (30 years), the dynamic build-up of biomass was as yet unable to reach the level predicted by the naïve static model, which was calculated in relation to the observed equilibrium biomass levels in the pre-existing 11 reserves.

#### *How do outcomes for fisheries and conservation differ if using either static or dynamic models to design reserves?*

For the Malaysia case study, the best-case scenario had noticeably greater profits and habitat protection than the realistic static scenario if there was overfishing (Fig. 3A, B). The difference between the best-case and realistic static scenarios was further enhanced if profits were assessed in the long-term (Fig. 3A), rather than the short-term (Fig. 3B). In the long-term with overfishing, protected planning units in the static

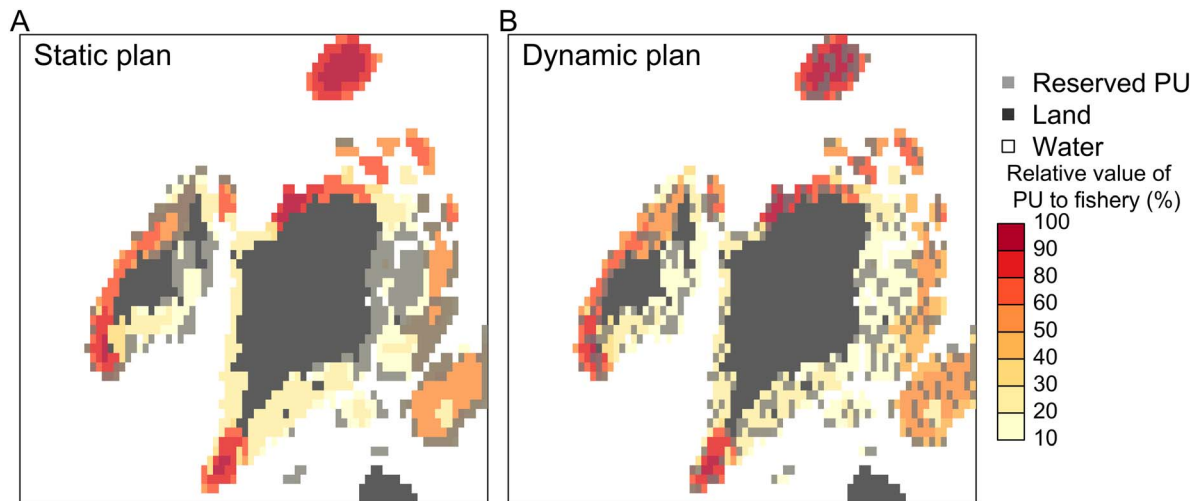


Fig. 4. Examples of reserve designed in the (A) static and (B) dynamic scenarios for the Malaysia model, with overfishing. Colors indicate the value of a planning unit to the fishery before reserve implementation. Both scenarios protected 30% of each habitat type within reserves and aimed to maximize equilibrium fishing profits. Equilibrium fishing profits were 14% higher in the dynamic scenario.

scenario were clumped together into large reserves, which were positioned in places with low value for fisheries (Fig. 4A; Appendix: Fig. A4A). For the best-case scenario, the reserve systems consisted of many small reserves, some of which were placed in planning units that had high status-quo profits (Fig. 4B). If fishing effort was optimal, the two model types created similar reserve networks with similar outcomes (Fig. 3C, D). The static model could design reserve networks with outcomes similar to the best-case dynamic model because the optimal strategy was to avoid profitable fishing areas, even though the static model was inaccurate in estimating the effects of reserves.

The differences between the realistic static and best case scenarios tended to be greater when the objective was for a compromise between the maximal fisheries profits and habitat protection (up to 20% higher profits for the same area habitat protection, or 10% greater habitat protection for the same profit).

Analysis of different larval dispersal scenarios in the Malaysia case study indicated that the benefits of dynamic models were greater if larval dispersal was shorter (Appendix: Fig. A5B). It was more important to place reserves in high profit planning units when larval dispersal was short, to ensure some spillover to fisheries. In

contrast, if larvae were well mixed across the region, dynamic models only had a benefit for very small conservation targets (Appendix: Fig. A5C). For small conservation targets, the dynamic scenario reserved more area than necessary to represent all habitat types in reserves, because the extra reserves provided spillover benefits.

For the California case study, the best-case scenario improved profits over the realistic static scenario in both the short and long-term (Fig. 5), but more so in the long-term scenario as was found in the Malaysia case study. The difference was small in the short-term because both models targeted protection of sites with initially high biomass and/or low profit (depending on the weighted factor in the objective function), even though the static model was inaccurate at estimating the outcome (Fig. 2). In the long-term the best-case scenario had up to 14% higher profits and 12% higher biomass than the realistic static scenario (Appendix: Fig. 5A). The best-case scenario consistently used fewer reserves than the realistic static scenario (Appendix: Fig. A6). The best-case scenario could achieve greater biomasses for fewer reserves because it reserved planning units connected by larval dispersal, so higher biomasses in each reserve contributed to building larval supply at other reserves.

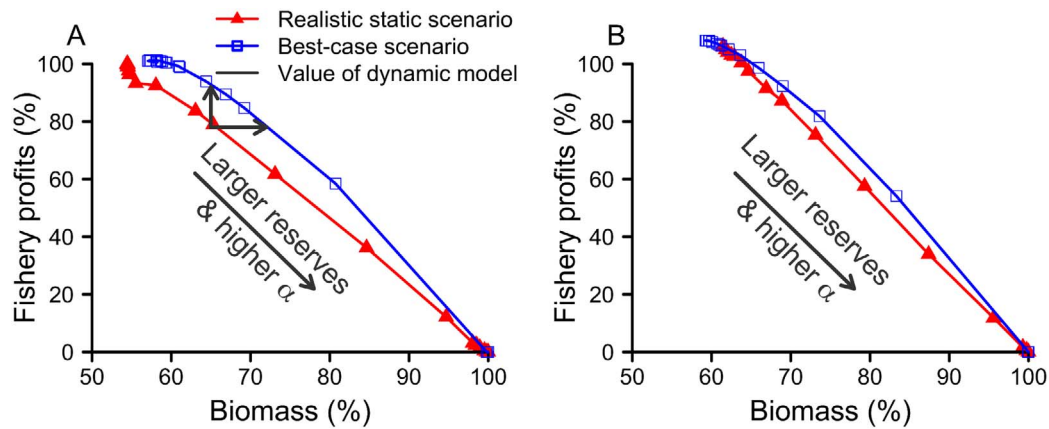


Fig. 5. Value of dynamic models in the California model. Comparison of realistic static and best-case scenarios in the long (A) and short term (B). The difference between the curves indicates the error when using static estimates of cost.

As with the Malaysia case study, the benefit of the best-case scenario over the realistic static scenario was greatest when the objective was a compromise between the maximal conservation and fishery outcome (Fig. 5). Compromise objectives require reserving moderate areas of the total seascape (i.e., ~30–60% of total area), which resulted in the largest number of alternative reserve designs to choose from when compared to very small or large reserve areas, and thus the greatest scope for flexible strategic planning.

## DISCUSSION

Our results provide practical illustrations of the relative value of using dynamic and static models for designing marine reserves, and identify conditions under which pattern-based (static) versus process-based (dynamic) models are warranted. The first question we posed was whether static models can accurately estimate losses of fishery profit under different reserve design proposals. We evaluated this question by comparing the outcomes expected if a static reserve design is evaluated using the static model (naïve static outcome) or dynamic model (realistic static outcome). Earlier studies have suggested that the naïve static scenario, which represents an estimate of opportunity cost, provides an estimate of the maximum relative cost of reserves to fisheries (White et al. 2013). We found this was

not necessarily the case. The sign of the difference between naïve and realistic scenarios depended on the relative importance of both dynamic movements in fishing effort and the synergistic effects of dispersal dynamics on biomass in reserves. Static opportunity should therefore not be used to assess compensation amounts to fishing groups that are affected by marine reserves.

We found dynamic process models could improve reserve designs for fisheries and conservation when reserves could provide spillover to fisheries that offset some of the lost fishing grounds. The time-scale over which outcomes were assessed was critical. Predicting the long-term outcomes of reserve networks requires modeling dynamic increases in fish biomass and spillover of larvae from reserves. In the short-term, reserves tend to cause profit losses to fisheries, because fishers lose fishing grounds and spillover benefits do not develop for several years (Smith et al. 2010a). Thus, the static model reasonably approximates the relative value of planning units to fisheries in the short-term. The static models can be nearly as effective as dynamic models for curtailing losses to fishers in the short-term, even if they estimate those losses poorly.

Fishery management outside reserves is important for determining how reserves perform (Hilborn et al. 2004, White et al. 2013). If effort is optimal, reserves designed using static models,

which avoid high profit areas, conserve the most biomass and habitats at the lowest cost to fisheries (Klein et al. 2008). An exception occurs when directional patterns of larval dispersal generate source-sink dynamics that can be leveraged by strategically sited reserves (Costello et al. 2010, Rassweiler et al. 2012). Thus, in the California model where such source-sink dynamics exist, the dynamic model provides additional benefits to the fishery even though fishing effort was optimized for profits both with and without reserves. If a fishery is overfished, appropriate reserve placement can further benefit the fishery (e.g., Abesamis and Russ 2005, Halpern et al. 2009), increasing the importance of using dynamic models to evaluate the implications of alternative reserve designs. Dynamic models are also more beneficial over simple spacing guidelines when there is overfishing (Rassweiler et al. 2014). This conclusion is best exemplified by the Malaysia model, which had non-directional larval dispersal patterns; in this case dynamic models were beneficial only if there was overfishing.

A major advantage of static models is that they are computationally efficient and can consider multiple species, habitats, fisheries and other socioeconomic constraints in a straightforward manner. In comparison, dynamic approaches can be computationally expensive (for instance, solving the California objective function for each  $\alpha$  value took >6 hours on a typical 2013 desktop) and difficult to formulate for representing multiple, interacting species. Complexity partly explains why static tools for designing marine reserves, such as Marxan, have been widely applied (e.g., Klein et al. 2008). One compromise is to include greater process detail into static models, such as maps of larval connectivity (White et al. 2014) or sensitivity of habitats to climate change (Mumby et al. 2011). Static reserve algorithms that incorporate more process details can provide better outcomes for conservation and fisheries without the additional expense of dynamic models.

There are many types of dynamic processes that we did not consider in the analysis. For instance, loss of habitat by climate change may occur irrespective of reserve designation, so it is important to use predictions of climate change impacts in reserve planning (Mumby et al. 2011).

Interactions between reserve design and enforcement will also be important to consider. The dynamic Malaysia model placed many small reserves in areas that were close to and far from ports, so there was spillover of larvae to potentially valuable fishing grounds. Enforcement of many small reserves may be more costly, so the relative costs of enforcing reserves of different sizes could be incorporated into reserve design models (Kritzer 2004). We also assumed that fishing effort was constant over time. In reality, fishing effort could vary year to year, for instance, due to fishers behavioral responses to reserves and changes in fish price (Stevenson et al. 2013). Accounting for changes in effort when using dynamic models for reserve planning may also increase their benefits over static models.

A future challenge for dynamic reserve design tools is to model multiple fishery species simultaneously. Multiple species and fisheries can be more easily considered in static models, which at least consider the spatial patterns representative of multiple species (Klein et al. 2008). However, dynamics, like differences in dispersal distance among species, affect how reserves are designed to meet goals for both conserving fish populations and benefit fisheries (White et al. 2010). The benefits of small reserves for increasing biomass are greater for species with shorter dispersal distances (e.g., White et al. 2010). For species with shorter dispersal, we found dynamic models were necessary to design reserves that provide substantial spillover to fisheries. Further investigation is needed to determine how multi-species conservation and fisheries objectives can be traded-off using reserves.

Managers and scientific advisors should consider the ecological and economic context when making a choice between static and dynamic models. We predict dynamic models will provide significantly better outcomes if: reserves must meet a compromise between the best possible outcomes for conservation and fisheries, the time-scale of management interest is long-term, the fishery is over-fished, or there is potential for highly directional larval dispersal. These results also provide cautionary lessons for reserve designs where static models must be used, such as when there is inadequate time to develop dynamic models. The appropriate choice of models and consideration of model assumptions



will ultimately assist decision makers to propose reserve designs that better meet objectives for conservation and fisheries.

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## SUPPLEMENTAL MATERIAL

### ECOLOGICAL ARCHIVES

The Appendix and the Supplement are available online: <http://dx.doi.org/10.1890/14-00429.1.sm>