Marine reserve networks for species that move within a home range

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ABSTRACT

Marine reserves are expected to benefit a wide range of species, but most models used to evaluate their effects assume that adults are sedentary, thereby potentially overestimating population persistence. Many nearshore marine organisms move within a home range as adults, and there is a need to understand the effects of this type of movement on reserve performance. We incorporated movement within a home range into a spatially explicit marine reserve model in order to assess the combined effects of adult and larval movement on persistence and yield in a general, strategic framework. We describe how the capacity of a population to persist decreased with increasing home range size in a manner that depended on whether the sedentary case was maintained by self persistence or network persistence. Self persistence declined gradually with increasing home range and larval dispersal distance, while network persistence decreased sharply to 0 above a threshold home range and was less dependent on larval dispersal distance. The maximum home range size protected by a reserve network increased with the fraction of coastline in reserves and decreasing exploitation rates outside reserves. Spillover due to movement within a home range contributed to yield moderately under certain conditions, although yield contributions were generally not as large as those from spillover due to larval dispersal. Our results indicate that for species exhibiting home range behavior, persistence in a network of marine reserves may be more predictable than previously anticipated from models based solely on larval dispersal, in part due to better knowledge of home range sizes. Including movement within a home range can change persistence results significantly from those assuming that adults are sedentary; hence it is an important consideration in reserve design.

Keywords: home range, adult movement, marine reserves, marine protected areas, fisheries, dispersal, dispersal per recruit, sustainability, spillover, yield

INTRODUCTION

Marine reserves are increasingly being used as a tool in fisheries management and biodiversity conservation. Many of the species that contribute to the biodiversity in protected areas are not completely sedentary, but exhibit movement in the larval, juvenile, and/or adult stage, and often these mobile species are direct targets for reserve protection (e.g. Fisher and Frank 2002, Parnell et al. 2005). Fifty years ago, Beverton and Holt (1957) pointed out the danger of ignoring adult fish movement in the evaluation of reserves. Sedentary adults inside reserves are fully protected from fishing mortality, but mobile adults may move from reserves into fished areas and therefore be less protected by reserves, potentially benefiting fisheries yield at the expense of population persistence. Properly accounting for and understanding the consequences of juvenile and adult movement is still a critical science gap in the design of marine reserves (Sale et al. 2005). Spatially explicit population models are commonly used to design reserve networks (Gerber et al. 2003), but such models have generally been focused on the effects of larval dispersal and have made the simplifying assumption that adults are sedentary. Modeling studies that assume sedentary adults run the risk of overestimating reserve effectiveness for persistence of mobile species. An increase in yield from “spillover” due to both larval dispersal and adult movement is often proposed as a benefit of reserves, but current models are inadequate for the task of capturing the potential tradeoffs between greater yield and decreased protection caused by spillover.

The few population models that explicitly included adult movement showed that large adult movement rates limit reserve efficacy by limiting gains in spawning stock biomass within reserve boundaries (references in Gerber et al. 2003, Gerber et al. 2005). A "moderate" level of adult movement was suggested as optimal for increasing spillover from reserves, and therefore yield, while protecting individuals sufficiently to lead to increases in egg production (Botsford et al. 2003, Gerber et al. 2003 and references therein). One commonality of these initial efforts is that adult movement is represented by diffusion. Diffusion involves a constant flux away from a source of individuals (e.g. Quinn and Deriso 1999). Intuitively, we would expect that animals that move diffusively are less likely to be protected in reserves than those that are sedentary or exhibit site fidelity, leading to more pessimistic results of the efficacy of reserves to protect species.

Home ranges, defined as the area an animal uses on a regular basis for its routine activities (Mace et al. 1983), are a common pattern of adult movement in the nearshore marine environment and can range in size from 1 meter to tens of kilometers in length (Lowe and Bray 2006). Because animals that move within a home range exhibit fidelity to a particular location, they are likely more suited to protection within reserves than those that move diffusively. Home range behavior is not well described by previous models that characterize movement as a transfer rate or diffusive, random movement. With diffusion, the movement of individuals from reserves into fished areas draws from the total abundance within the reserve, whereas with home range behavior individuals in a reserve only cross the boundary if they are located near the edge with their home range extending into fished area. Individuals with a home range spanning a reserve boundary will be exposed to fishing mortality for part of the time, even if its home range is centered within the reserve (Zeller and Russ 1998). Vulnerability of an individual to fishing mortality depends on the location of its home range relative to the location of reserve boundaries (Kramer and Chapman 1999), and only those individuals with their entire home range within the reserve will be fully protected from fishing. Empirical support for the importance of accounting for home range movement is found in Woodroffe and Ginsberg (1998). Their review of large terrestrial carnivores showed that populations that range widely are more likely to go extinct from small reserves than those with smaller home ranges, when conflict with humans on reserve borders is a major cause of mortality.

A second limitation of existing models that incorporate adult movement is their narrow focus on the boundary between a single reserve and an adjacent fished area (references in Gerber et al. 2003, Starr et al. 2004, Gerber et al. 2005, Kellner et al. 2008). Of the existing spatially explicit models that deal with multiple reserves, most are tactical, with movement rates parameterized for a particular species in a specific reserve network (Attwood and Bennett 1995, Guenette et al. 2000, Martell et al. 2000, Meester et al. 2001, Walters et al. 2007). They do not attempt to provide general conceptual understanding of the effects of both adult and larval movement on reserve effectiveness. Given the importance of larval dispersal to population persistence in reserve networks (Botsford et al. 2001), there is a need to understand the combined results of both larval and adult movement within entire reserve networks in a general, strategic framework.

Previous models that have revealed the effects of larval dispersal on persistence and yield for sedentary species provide a context within which new results for adult movement should be placed. In any marine population, population persistence requires that replenishment from larval stages be sufficient to offset benthic post-settlement mortality; i.e., that each adult replaces itself within its lifetime (Hastings and Botsford 2006). Studies of persistence with larval dispersal have shown two ways in which populations can persist in a system of reserves: (1) self persistence and (2) network persistence. In the self-persistent case, enough larvae return to the same reserve to maintain replacement. Replacement in network persistence occurs through multiple paths connecting reserves over several generations (Botsford et al. 2001, Hastings and Botsford 2006). Species with short larval dispersal distances are generally protected by self persistence in reserves, whereas species with long larval dispersal distances are protected by network persistence. An important practical difference is that network persistence is generally less predictable than self-persistence (Kaplan et al. 2009).

We incorporated adult movement within a home range into a spatially explicit marine reserve model in order to determine the effects on persistence and yield and to explore the interaction between larval dispersal and adult movement in a general, strategic framework. We first present results for a single cohort in order to reveal more clearly the effects of home range on eggs-per-recruit and yield-per-recruit. We then include recruitment and larval dispersal to form a complete population model, and examine the effects on settlement and yield and ultimately the interactions between adult movement and larval dispersal. We show the general results of adult movement in home ranges, its interaction with larval dispersal, and the differences in results depending on self persistence or network persistence. We demonstrate tactical application of this model by evaluating a reserve network on the California coast. We quantify how models that do not include adult movement will overestimate the capacity of the population to persist, in some cases even for species with home ranges an order of magnitude smaller than reserve size.

METHODS

Individuals have unique patterns of spatial use within their home ranges. The shape of an individual's home range can appear elongate or circular, Gaussian or multimodal (Eristhee and Oxenford 2001, Parsons et al. 2003, Topping et al. 2005, Jorgensen et al. 2006). Individuals may exhibit one or multiple core areas – areas within the home range where a disproportionate amount of time is spent (Eristhee and Oxenford 2001, Parsons et al. 2003, Jorgensen et al. 2006). Size and shape of the home range can be affected by habitat quality and shape (Matthews 1990, Eristhee and Oxenford 2001, Lowe et al. 2003, Topping et al. 2005), although we do not include this in the model for the sake of parsimony and because the knowledge of the habitat is typically not adequate for this level of detail.

We modeled home range as a probability density function (pdf) along a linear coastline with continuous habitat (cf. Meester et al. 2001). Our method is flexible in that it can accommodate any assumptions about the size and shape of the home range. Because home range shape varies among individuals in a population, and core areas can be found anywhere within the home range, any pdf is a simplification. Here we show results for the conservative estimate, a uniformly distributed pdf. We also ran the model for a normally distributed pdf and found that results are similar, but species are slightly more protected from fishing mortality. For each discrete point in space we calculated the fraction of the instantaneous fishing mortality rate experienced by an individual with its home range centered there. This vulnerability to fishing mortality (v_x) of individuals whose home range pdf is centered at x along a coastline equals the fraction of the home range that overlaps fished area:

$$v_x = \frac{1}{H}\sum_{i=-H/2}^{i=+H/2} c_{x+i} \tag{1a}$$

where H is the length of the home range pdf, and the coastline (c) is defined as:

$$c_x = \begin{cases} 0 & reserve \\ 1 & nonreserve \end{cases} \tag{1b}$$

Single cohort

The effects of fishing mortality on reproduction are expressed in terms of eggs-per-recruit (EPR), the number of eggs an average recruit produces over its reproductive lifespan (Goodyear 1993). For an age-structured population, EPR for an individual with its home range centered at x is the product of its survival to age a (l_a) and its fecundity at age a (m_a) summed over all ages above the age of maturity (a_{mat}):

$$\mathrm{EPR}_x = \sum_{a \geq a_{mat}} l_{a,x} m_a \tag{2a}$$

where survival ($l_{a,x}$) is a function of the instantaneous natural mortality rate (M), and the product of the instantaneous fishing mortality rate (F) and vulnerability to fishing mortality (v_x) for fish older than the age at first capture in the fishery (t_c):

$$l_{a,x} = \begin{cases} e^{-Ma} & a < t_c \\ l_{t_c} e^{-(M+v_x F)(a-t_c)} & a \geq t_c \end{cases} \tag{2b}$$

Vulnerability to fishing mortality (v_x) is incorporated into the survival term in a similar manner as age selectivity – it is a selectivity modification of F that is wholly dependent upon spatial location. Fishing mortality rate is assumed to be uniformly distributed outside reserves. Our goal is to evaluate population persistence and yield for species with varying adult and larval dispersal distances exposed to specified levels of fishing effort outside reserves. We are not comparing results before and after reserve implementation. Therefore, it is not necessary to include here the additional complexities of redistribution of fishing effort after reserve implementation. Fecundity at age increases with weight, as is the case for *Sebastes melanops* (black rockfish) (Bobko and Berkeley 2004)

$$m_a = \begin{cases} 0 & a < a_{mat} \\ (f + g w_a) w_a & a \geq a_{mat} \end{cases} \tag{2c}$$

where f and g are fecundity parameters. Weight at age (w_a);

$$w_a = d\, L_a{}^b \tag{2d}$$

is calculated from length at age (L_a), and weight at age parameters d and b. Length is defined by the von Bertalanffy growth equation:

$$L_a = L_\infty (1 - e^{-k(a - t_0)}) \tag{2e}$$

where L_∞ is asymptotic length, t_0 is the age at which an individual would have been length 0, and k is a von Bertalanffy growth parameter.

The fraction of natural eggs-per-recruit (FNEPR) at each location is the proportion of EPR relative to the natural EPR level (NEPR):

$$\text{FNEPR}_x = \frac{\text{EPR}_x}{\text{NEPR}} \tag{3a}$$

where NEPR is a calculation of EPR in the absence of fishing:

$$\text{NEPR} = \sum_{a \geq a_{mat}} l_a m_a \tag{3b}$$

with survival (l_a) depending only on natural mortality (M):

$$l_a = e^{-Ma} \tag{3c}$$

FNEPR here is essentially the same as the fraction of lifetime egg production (FLEP), a term used by O'Farrell and Botsford (2005), and the spawning potential ratio (SPR) commonly used in fisheries (Goodyear 1993).

Yield-per-recruit is the yield a recruit contributes to the fishery from the age of entry into the fishery (t_c) to its maximum age:

$$\mathrm{YPR}_x = \sum_{a \geq t_c} \frac{v_x F}{M + v_x F} (l_{a,x} - l_{a+1,x}) l_{a,x} w_a \tag{4}$$

Multiple cohort model with reproduction and larval dispersal

Because persistence in reserve networks ultimately depends on connectivity through the larval stage, larval dispersal and a stock-recruitment relationship are incorporated into the model. The stock-recruitment relationship is a description of the number of new recruits into a population that are produced from a given amount of egg production. In a single, non-spatial population the minimum value of EPR required for persistence is related to the form of the stock-recruitment relationship:

$$\mathrm{EPR} > \frac{1}{R'(0)} \tag{5}$$

where $R'(0)$ is the slope of the stock-recruitment curve at the origin (Sissenwine and Shepherd 1987, Goodyear 1993). If FNEPR is reduced by fishing so as to be less than $1/R'(0)$, the equilibrium population size will go to 0 and the population will collapse. Because of the difficulty in determining the shape of the stock-recruitment relationship at low population levels, the value of FNEPR required for sustainability is typically highly uncertain. Fishery biologists have found that values of FNEPR in the range of 35-60% avoid collapse for populations in which it has been studied (Mace and Sissenwine 1993, Myers et al. 1999, Clark 2002, Dorn 2002).

We used the numerical method developed by Kaplan et al. (2006) for evaluating persistence of marine reserve networks for spatial populations with dispersing larvae and sedentary adults. This equilibrium method, termed dispersal-per-recruit (DPR), is an extension of the ad-hoc approach taken in Botsford et al. (2001). DPR essentially determines population persistence by accounting for all pathways by which larvae can be dispersed to and returned from each point in space. It is a simplification of the full population model, and it reduces the problem of persistence to knowing just the distribution of EPR over space, larval dispersal, and the replacement level of the population. The larval dispersal pattern, which connects egg production at one location to post-larval settlement at another, is modeled here by a Laplacian distribution (a decaying exponential in both directions). Post-dispersal density-dependence is incorporated via the stock-recruitment relationship of a hockey-stick form, which increases linearly with egg production until a maximum value is reached and is then constant (Barrowman and Myers 2000). The slope of the hockey-stick function at low egg production was chosen to correspond to a threshold of 35% of natural EPR.

We incorporated adult movement into the DPR model by using the spatial distribution of EPR that accounts for movement of fish within home ranges (Eq. 2a). The iterative DPR approach was used to determine the equilibrium levels of settlement, recruitment and yield in space that would result from that spatial distribution of EPR. The iterative version of DPR finds the equilibrium distribution of recruitment and adult biomass more quickly than a full simulation model. Although the general results depend only on the spatial distribution of FNEPR, dispersal and the critical replacement level of the population, the same life history parameters were used throughout the results in order for the magnitude of yield-per-recruit and therefore yield to be comparable (Table 1).

We first evaluated persistence and yield for home ranging species along a linear coastline of infinite length and continuous habitat. An infinite coastline constructed from a repeating unit of coastline was used in order to avoid the idiosyncratic effects of larvae and adults being lost at the boundaries. We demonstrate the process with a single reserve, then show results for multiple reserves along a coastline. Finally, we show persistence and yield results in patchily distributed habitat for a network of marine protected areas along the California coast.

RESULTS

Single reserve

The vulnerability to fishing mortality was calculated for individuals with home ranges centered at each point along the coastline for several different home range sizes (Fig. 1a). For this illustration we assumed that fishing outside reserves reduced FNEPR to 0.2, a level that has been observed for some rockfish populations along the California coast (O'Farrell and Botsford 2006). For sedentary species (i.e. species with individuals that are contained in one discrete cell along the coastline), vulnerability to F (v_x) was simply 1 outside the reserve and 0 inside the reserve. For species that move within a home range, as the overlap of home range and fished area increased, either due to home range location or size, an individual's vulnerability to fishing mortality increased. Total protection from fishing mortality ($v_x = 0$) was possible only for individuals with home ranges entirely contained in the reserve. The effects of the reserve extended further into the fished area (and vice-versa) as home range size increased.

The resulting fraction of natural eggs-per-recruit (FNEPR) decreased with increasing vulnerability, and had lower values as home range increased, suggesting that the capacity of the population to persist in reserves decreases with increasing home range size (Fig. 1b). FNEPR was equivalent to the unfished level (FNEPR=1) for individuals with home ranges contained entirely within the reserve and decreased to the fully fished value (here FNEPR=0.2) for individuals with home ranges completely outside the reserve. When home range size was larger than reserve size, individuals at all locations experienced some fishing mortality, which led to FNEPR being less than 1 at all locations.

Individuals contributed to yield-per-recruit (YPR) if part of their home range overlapped fished area (Fig. 1c). For sedentary species, only those individuals in the fished area were caught by the fishery and contributed to YPR, but total YPR increased for species with larger relative home range sizes, indicating an increase in yield could occur if persistence was maintained.

To illustrate equilibrium results of the full model, including reproduction and larval dispersal, we continued this example for a single reserve in continuous habitat. We examined the case of self-persistence in a single reserve, in which mean larval dispersal distance is equal to the reserve length, a value for which the population without adult movement is just persistent (Fig. 2). Decreased egg production due to adult movement led to decreases in the fraction of natural larval settlement (FNLS). In this case, FNLS was adequate for persistence for species with sedentary adults, but as adult movement increased, the distribution of FNLS dropped to nonpersistent values (Fig. 2a). In this case, species that move in home ranges half the reserve size persisted, but species with home ranges as large or larger than the reserve did not. The fraction of natural larval recruitment

(FNLR) at each point along the coastline was then calculated from FNLS and the settlement-recruitment relationship (Fig. 2b). Where FNLS was greater than or equal to 0.35, recruitment was saturated at its maximum value. Yield is the product of YPR and FNLR, therefore only persistent populations can contribute yield to a fishery (Fig. 2c).

Coastline with multiple reserves

Persistence and yield were evaluated for combinations of mean larval dispersal distance and home range size in an infinite coastline with continuous habitat and periodically spaced, uniformly sized reserves in order to explore the interaction between larval dispersal and home range (Fig. 3). Three levels of reserve coverage were evaluated for a FNEPR of 0.2 outside reserves. The metric used to represent the persistence of a system of reserves was the fraction of unfished system-wide larval supply, which is the integral of FNLS over the entire coastline divided by natural larval settlement in the absence of fishing over the entire coastline (Fig. 3a-c). Yield was summed over a repeating unit of the coastline (Fig. 3d-f). Presenting the results as in Fig. 3 allows a scientist or decision maker to choose a fraction of coastline in reserves and a typical reserve size, then see the combinations of movement rates (larval dispersal distances and home range sizes) that will be protected. That will specify the mix of species protected, for those whose movement rates are known.

Results for sedentary species (i.e., those with home range length = 0) with varying larval dispersal distances were consistent with previous modeling results (e.g. Kaplan et al 2006, Kaplan et al. 2009). Species that do not disperse as larvae nor have adult movement (i.e.those at 0,0) persisted only in the fraction of coastline contained by reserves (Fig. 3a-c). Because these species were only persistent in the reserves and did not spillover into fished areas, there was no equilibrium yield available to the fishery (Fig. 3d-f). With 10% of the coastline in reserves, reserves protected sedentary species with mean larval dispersal distances up to 1.7 reserve lengths (Fig. 3a). In practical terms, the alongshore length of a 10 km^2 reserve (the upper size limit on most existing reserves (Halpern 2003)), is 3.16 km if we assume the reserves are square. Therefore 1.7 times this reserve length corresponds to a mean larval dispersal distance of 5.4 km. Sedentary species with any length larval dispersal distance were protected with 20% and 30% of the coastline in reserves, due to connectivity between reserves (the network effect) and non-zero reproductive capacity in fished areas (as in Botsford et al. (2001) and Kaplan et al. (2006)) (Fig. 3b-c).

Species that move within a home range (i.e., those with home range lengths > 0) were exposed to a larger proportion of fishing mortality, leading to less total larval supply than the sedentary case (Fig. 3a-c). As reserve coverage increased, species with greater dispersal distances (as both larvae and adults) were protected. An important distinction is that results differed between reserves that were self persistent in the sedentary case (persistence that would occur in a single reserve) and reserves that persisted because of a network effect in the sedentary case (persistence due to the connectivity between reserves in a network). Self-persistence protected species with larval dispersal distances similar in size or smaller than reserves (i.e., cases with mean larval dispersal less than 1-2 reserve widths in Fig. 3). For self-persistence in reserves, persistence declined gradually with increasing home range size. Network persistence protected species with larval dispersal distances several times larger than reserve size, but population collapse occurred beyond a specific threshold home range size. This threshold home range size depended on the fraction of coastline in reserves, but not on larval dispersal distance (Fig. 3a-c).

Yield was possible only when the population was persistent. In general, spillover due to increasing larval dispersal led to greater yield increases than spillover due to movement within a home range, which increased yield only in limited cases. Yield increased with home range size for very long larval dispersers (which were sustained by network persistence) and very short larval dispersers (which were sustained by self-persistence) because home range movement improved export beyond the reserve boundary.

Persistence and yield results are also sensitive to fishing intensity. We evaluated fishing mortality rates both higher and lower than the rate that leads to FNEPR of 0.2 outside reserves (see Appendix A in *Ecological Archives*). The largest home range size protected by network persistence for species with large larval dispersal distances (i.e. the threshold identified in Fig. 3) depended on both fishing mortality rate outside reserves and fraction of coastline in reserves (Fig. 4). The range of home range sizes protected by a reserve network increased with fraction of coastline in reserves and decreasing exploitation rates (shown as increasing FNEPR outside reserves). If species were not overfished (FNEPR ≥ 0.35), species with any size larval dispersal or home range were persistent with or without reserves (Fig. A3 in Appendix A).

The results in Figure 3 represent a best case scenario, in that every point along the coast is appropriate adult habitat. In reality, adult habitat is likely to be patchily distributed, decreasing total habitat and therefore total larval supply. Populations that occupy habitat that is patchily distributed have a reduced capacity for persistence in the model than populations that occupy more homogeneous habitat because many larvae disperse to unsuitable habitat patches and are lost from the system (Kaplan et al. 2009). For this reason, the results shown for continuous habitat (Fig. 3) should be interpreted as an upper limit for persistence; in order to evaluate specific marine networks it is necessary to incorporate habitat distribution.

Coastline with multiple reserves in heterogeneous habitat

A network of marine protected areas (MPAs) was recently implemented along the central coast of California from Pigeon Point to Point Conception (www.dfg.ca.gov/mlpa/ccmpas_list.asp) (Fig. 5a). This network covers nearly 18% of the coastline in that region, in MPAs ranging from about 1-20 km in alongshore length. Here we extended the results of Kaplan et al. (2009) who evaluated MPA networks proposed for this region for a range of larval dispersal distances for sedentary species. In this analysis we only considered species that inhabit rocky reefs, therefore outside of this habitat we assumed a fraction of natural eggs-per-recruit (FNEPR) of 0. For habitat in the fished area, we assumed fishing reduced FNEPR to 0.2 (gray bars in Fig. 5). FNEPR equaled 1 for individuals fully protected in an MPA in rocky reef habitat. We assumed that all MPAs allowed no take of the species being considered, but the method is flexible in this regard and can represent any amount of fishing in each MPA. Habitat north but not south of the study region was included in the model domain, as Point Conception to the south is considered a natural oceanographic break. We used the procedure described by Kaplan et al. (2009) for converting the California coastline into a one-dimensional domain.

The fraction of natural larval settlement (FNLS) was calculated along the coast for populations with different home range sizes (Fig. 5b). A range of larval dispersal distances was evaluated, but here we show only the results for 25 km, a reasonable mean larval dispersal distance for species with a pelagic larval phase (Kinlan and Gaines 2003). FNLS was highest near the middle of the central coast where the concentration of both rocky reef habitat and MPAs are high. FNLS was greatest for sedentary species and decreased for species with larger home ranges; species with home range lengths of 6 km or greater did not persist. Models that assume sedentary adults will overestimate the capacity for persistence for a species whose individuals move within a home range.

Yield along the coastline was highest for sedentary species and decreased for species with larger home ranges due to the reduction in recruitment (Fig. 5c). Yield came predominantly from individuals with home ranges centered in fished areas, but individuals centered in MPAs also contributed if their home ranges overlapped fished area.

Results are similar to those for uniformly distributed reserves in an infinite coastline (Fig. 3). The MPAs in the central coast have a mean alongshore length of 9 km, therefore a 25 km larval dispersal length is equal to 2.8 reserve lengths. In the infinite coastline in continuous habitat (Fig. 3b), species with a mean larval dispersal of 2.8 reserve lengths would experience population collapse with home ranges of 0.3 reserve lengths, or 2.7 km, which is similar to the point of collapse for the 5 km home range found in the central coast (Fig. 5). The greater protected home range size predicted in the central coast is most likely due to the variable size of MPAs; the central coast system includes a wide range of MPA sizes, including two large MPAs (~25 km combined length) near Cambria which likely increased the self-persistence of species with larger home ranges.

DISCUSSION

Empirical support for the general idea that reserve effectiveness depends on size comes from a recent meta-analysis of data from European marine reserves, in which population density in reserves increased with reserve size, implying that larger reserves protect a greater proportion of mobile fish (Claudet et al. 2008). Here we have provided a model framework for evaluating the performance of reserves for mobile species which exhibit home range behavior. Movement within a home range can change persistence results from those based on models assuming sedentary adults. For populations sustained within reserves by self persistence (i.e. populations with mean larval dispersal smaller than reserve length), persistence and yield decreases gradually as we attempt to protect species with greater home range sizes, while for network persistent populations (i.e. populations with mean larval dispersal larger than reserve length), there is a threshold home range size beyond which persistence is not possible. When species with any size larval dispersal distance were persistent due to the network effect, the size of adult home range beyond which the population would not persist did not vary with larval dispersal distance.

Larval dispersal distance and home range size have different effects on persistence and yield. Spillover of adults into fished areas led to a trade-off between persistence and yield. Increased spillover due to adults moving in a home range increased the exposure of the population to fishing mortality, which increased yield-per-recruit at the expense of total larval supply. This tradeoff differs from the predicted consequences of greater larval dispersal distance – if a certain minimum fraction of the coastline is contained in reserves, greater larval dispersal distance can cause increases in both persistence capacity (due to the network effect) and yield (due to spillover). Spillover due to movement within a home range contributed to yield moderately under certain conditions, although yield contributions were generally not as large as from spillover due to larval dispersal.

There will be a maximum home range size that can be protected by a given system of MPAs (Figs. 3 and 5), but the precise value of this threshold is likely to depend on a number of features that must be modeled carefully in a site-specific, tactical manner. This sensitivity will affect whether expectations are met after reserves are implemented. The relationship between the maximum home range protected and the percentage of coastline contained in reserves is sensitive to the level of fishing outside reserves and our assumption regarding a threshold FNEPR of 0.35. The sensitivity of persistence to the exploitation rate outside reserves requires knowledge of fishing levels that will be present after reserve implementation, and a lower value for the FNEPR threshold would lead to persistence at lower percent coverage. Finally, habitat configuration is also crucial to the spatial pattern of persistence (Kaplan et al. 2009), and this information is often available with greater certainty than information on FNEPR and the critical replacement threshold of the population.

In order to maximize yield for a single species, reserves should cover just enough coastline to lead to a persistent population, similar to the results for species that disperse only in the larval phase (Hastings and Botsford 2003). Attempting to maximize yield in this way would be risky in the face of uncertainty given that the highest yield is found at the edge of population collapse. Acknowledging that managers will be interested in outcomes for multiple species within a reserve network makes this problem much more complex. For example, increasing reserve coverage from 20% to 30% of the coastline led to protection of more species, but decreased yield for those with home ranges an order of magnitude smaller than reserve size (Fig. 3).

While the complexity of reserve design precludes quantitative rule-of-thumb guidelines, our results provide general insights. First, plots that display persistence results for many combinations of larval dispersal and home range size (such as Fig. 3) convey a sense of the diversity of species we may expect to persist, and therefore can be used to compare reserve network proposals directly. Results show that if a large enough fraction is contained in a network of reserves, species with any length larval dispersal distance are protected due to network persistence as long as their home range is below the threshold size (Fig. 4). Scientists, stakeholders or decision-makers could use such a figure to design a network of reserves to protect a broad range of species based on knowledge of quantifiable home range sizes, without having to know precisely the highly uncertain larval dispersal distances (as long as they were known to be long relative to reserve size).

Our example of an application of our approach to the MPA network along the central coast of California (Fig. 5), which is shown to demonstrate the tactical use of the model, differs from the results of Walters et al. (2007). They found that high rates of diffusive adult movement substantially reduced the efficacy of protected areas, leading to very pessimistic predictions of the use of MPAs along the central coast. Long-lived species that move diffusively as adults (by definition not site-attached) are not likely to spend much time in reserves, and therefore will be less protected by reserves than those that move within a home range. For the many nearshore species for which home range is a more accurate representation of adult movement than diffusion, our results show that MPAs can be an effective management tool.

The results we have shown assume that adult movement for all individuals in a population is described by a bounded home range of a certain size, and that individuals will always be found within the home range. Some species exhibit intraspecific variation in movement behavior, in which the movement of a portion of the population can be described by a home range while the rest of the population roams much more widely (Attwood and Bennett 1994, Egli and Babcock 2004). For these cases, or for species that move away from the home range seasonally, we could change the utilization rate of the home range to incorporate these types of behaviors. This would lead to decreased protection within reserves similar to increased home range size. Conversely, setting reserve boundaries at habitat breaks may reduce movement into fished areas (Barrett 1995, Chapman and Kramer 2000).

We assumed uniformly distributed fishing mortality outside reserves for ease of comparison with prior work and in order to more clearly reveal the effects of home range, but it may be more realistic to assume that fishing effort will be concentrated near reserve borders. Kellner et al. (2007) developed a spatial model that explored the consequences and optimality of fishing the reserve line. They found that fishing the line was the optimal effort distribution for targeting mobile species and led to depressed fish density inside and near the reserve more than if effort were uniformly distributed. This implies that fish with home ranges near reserve borders would be more vulnerable to fishing mortality, necessitating even larger reserves for protection than those predicted by uniform fishing effort.

Our results show that for species exhibiting home range behavior, persistence may be more predictable than previously anticipated from models based solely on larval dispersal. Results such as Figure 3 indicate a strong dependence on adult home range size with little dependence on larval dispersal distance, at least for species exhibiting network larval dispersal. This suggests greater predictability of reserve performance since adult movement is more straightforward to quantify than larval dispersal, and therefore more often known. Conversely, designing MPAs only on the basis of larval movement is likely to overestimate protection, in some instances even for species with home ranges an order of magnitude less than the reserve size.

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Table 1. *Sebastes melanops* (black rockfish) life history parameters used to generate figures.

Parameter	Value	Definition	Source
L_∞	44.2	Asymptotic von Bertalanffy length (cm)	(Bobko and Berkeley 2004)
k	0.33	von Bertalanffy growth parameter	(Bobko and Berkeley 2004)
t_0	0.75	Age at which individual would be length 0	(Bobko and Berkeley 2004)
a_{mat}	7	Age at 50% maturity	(Bobko and Berkeley 2004)
Max age	50	Maximum age	(Love et al. 2002)
d	1.677×10^{-5}	Coefficient in weight at length (kg)	(Ralston and Dick 2003)
b	3	Exponent in weight at length	(Ralston and Dick 2003)
f	289,406	Parameter in weight-fecundity relationship	(Ralston and Dick 2003)
g	103,076	Parameter in weight-fecundity relationship	(Ralston and Dick 2003)
M	0.14	Natural mortality rate	(Ralston and Dick 2003, Sampson 2007)
t_c	7	Age at first capture in fishery	We chose this to correspond with a_{mat}

Figure legends:

Figure 1. (a) Vulnerability to fishing mortality (v_x), (b) fraction of natural eggs-per-recruit (FNEPR), and (c) yield-per-recruit (YPR) for varying home range lengths and a single reserve (gray area). Home range lengths are in units of reserve length.

Figure 2. (a) Fraction of natural larval settlement (FNLS), (b) fraction of natural larval recruitment (FNLR) and (c) yield for varying home range lengths and a single reserve (gray area). The dashed line in (a) is the persistence criterion. Home range lengths are in units of reserve length. Fraction of natural eggs-pre-recruit (FNEPR) outside the reserve equals 0.2. The mean larval dispersal distance is equal to the reserve length. Yield is in arbitrary but consistent biomass units

Figure 3. The fraction of natural unfished larval supply along an infinite coastline for (a) 10% of the coastline in reserves, (b) 20% of the coastline in reserves, and (c) 30% of the coastline in reserves for varying larval dispersal and home range lengths. Total yield along an infinite coastline for (d) 10% of the coastline in reserves, (e) 20% of the coastline in reserves, and (f) 30% of the coastline in reserves. Population persistence occurs when the fraction of natural unfished larval supply > 0. Mean larval dispersal and home range lengths are in units of reserve length. Reserves are spaced periodically along the coast. Fraction of natural eggs-per-recruit (FNEPR) outside reserves equals 0.2. Total yield is in arbitrary but consistent biomass units.

Figure 4. The largest home range sizes (in units of reserve size) protected by network persistence for species with large mean larval dispersal distances relative to reserve size. Reserves are uniformly distributed in an infinite coastline. When network persistence occurs, home range sizes persistent in the reserves are determined by the exploitation level outside reserves (FNEPR) and the fraction of coastline contained in reserves. 0 indicates network persistence does not occur.

Figure 5. Application of the model to the implemented network of MPAs along the central coast of California. (a) Linearization of all MPAs (red) and hard bottom habitat (green) at a depth of 0-30m. (b) The equilibrium fraction of natural larval settlement (FNLS) along the coastline that results from several home range lengths. The dashed line is the persistence criterion. FNEPR for sedentary species is shown in gray bars for reference. A population with a home range length of 6 km is not persistent. (c) Yield along the coastline for several home range lengths. Yield for a population with home range length of 6 km is 0 everywhere. The mean larval dispersal distance is 25 km. Total yield is in arbitrary but consistent biomass units.

Figure 1.

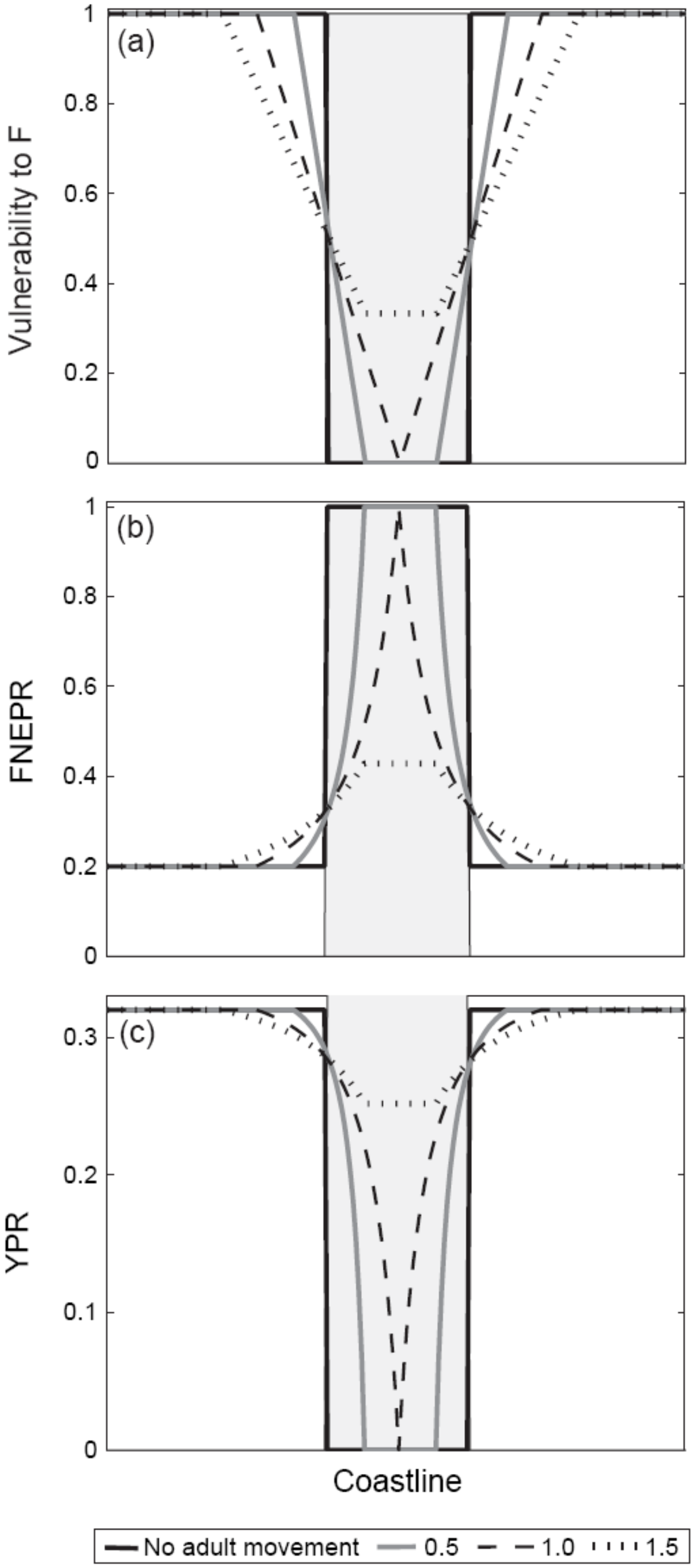

(a)
Vulnerability to F
1
0.8
0.6
0.4
0.2
0
(b)
FNEPR
1
0.8
0.6
0.4
0.2
0
(c)
YPR
0.3
0.2
0.1
0
Coastline
No adult movement
0.5
1.0
1.5

Figure 2.

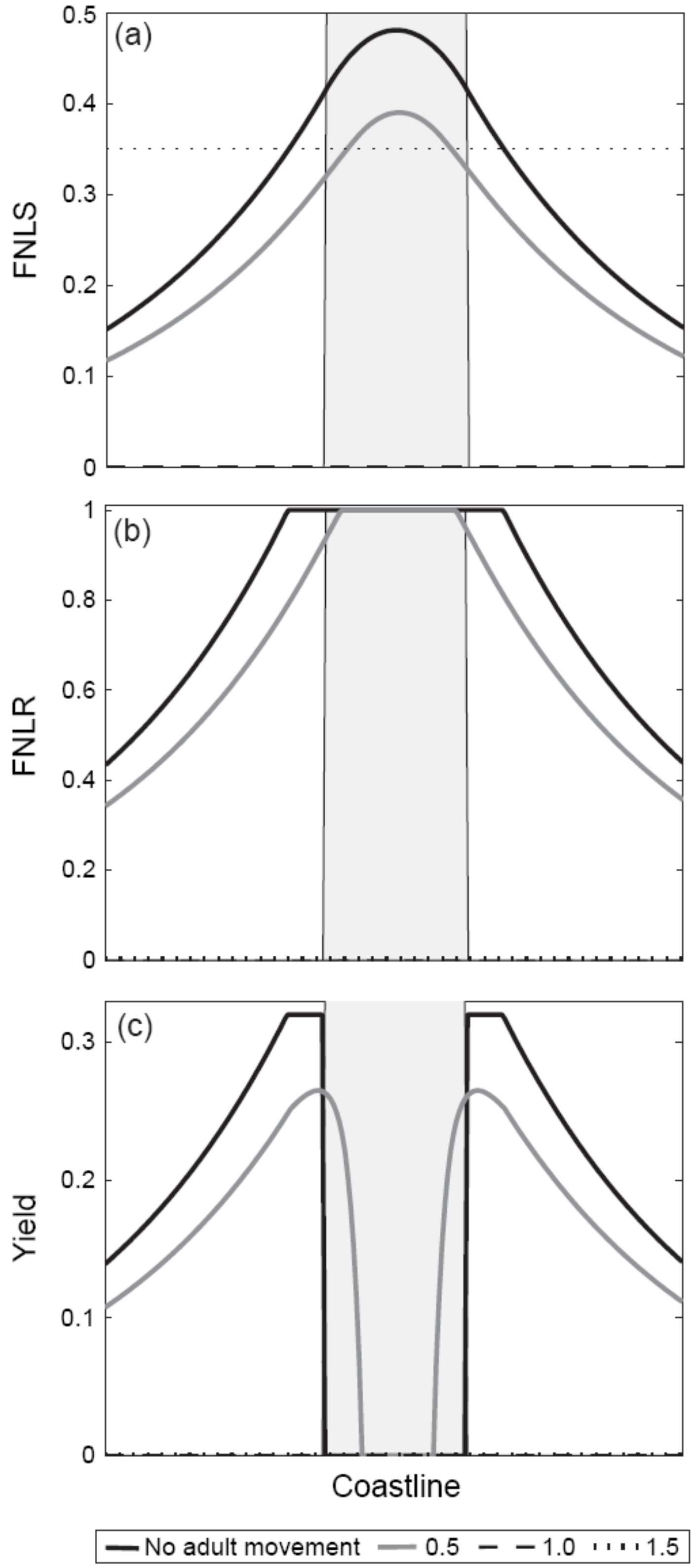

(a)
FNLS
0.5
0.4
0.3
0.2
0.1
0
(b)
FNLR
1
0.8
0.6
0.4
0.2
0
(c)
Yield
0.3
0.2
0.1
0
Coastline
No adult movement
0.5
1.0
1.5

Figure 3.

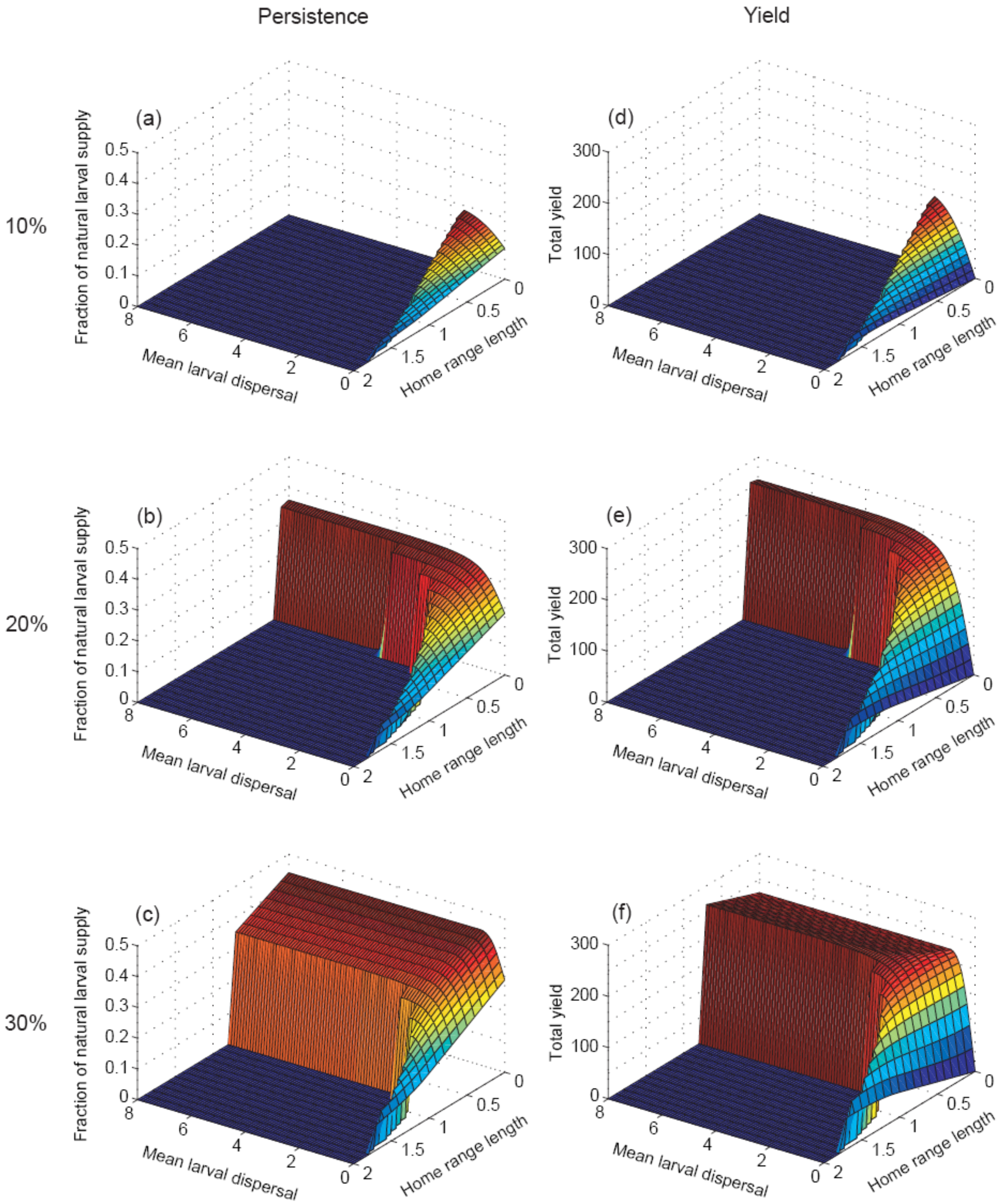

Persistence
Yield
10%
20%
30%
(a)
(b)
(c)
(d)
(e)
(f)
Fraction of natural larval supply
0
0.1
0.2
0.3
0.4
0.5
Total yield
0
100
200
300
Mean larval dispersal
8
6
4
2
0
Home range length
2
1.5
1
0.5
0

Figure 4.

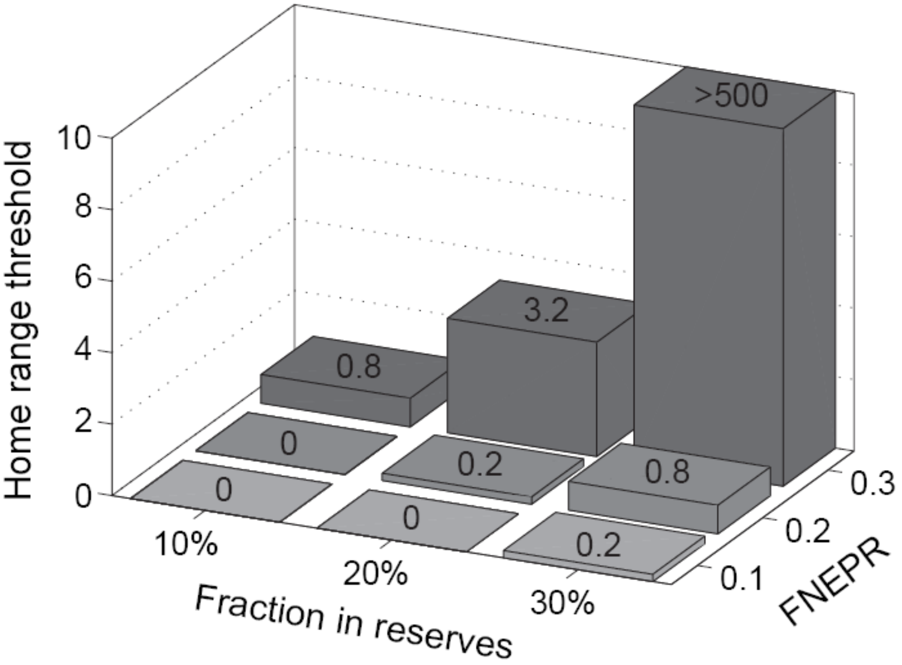
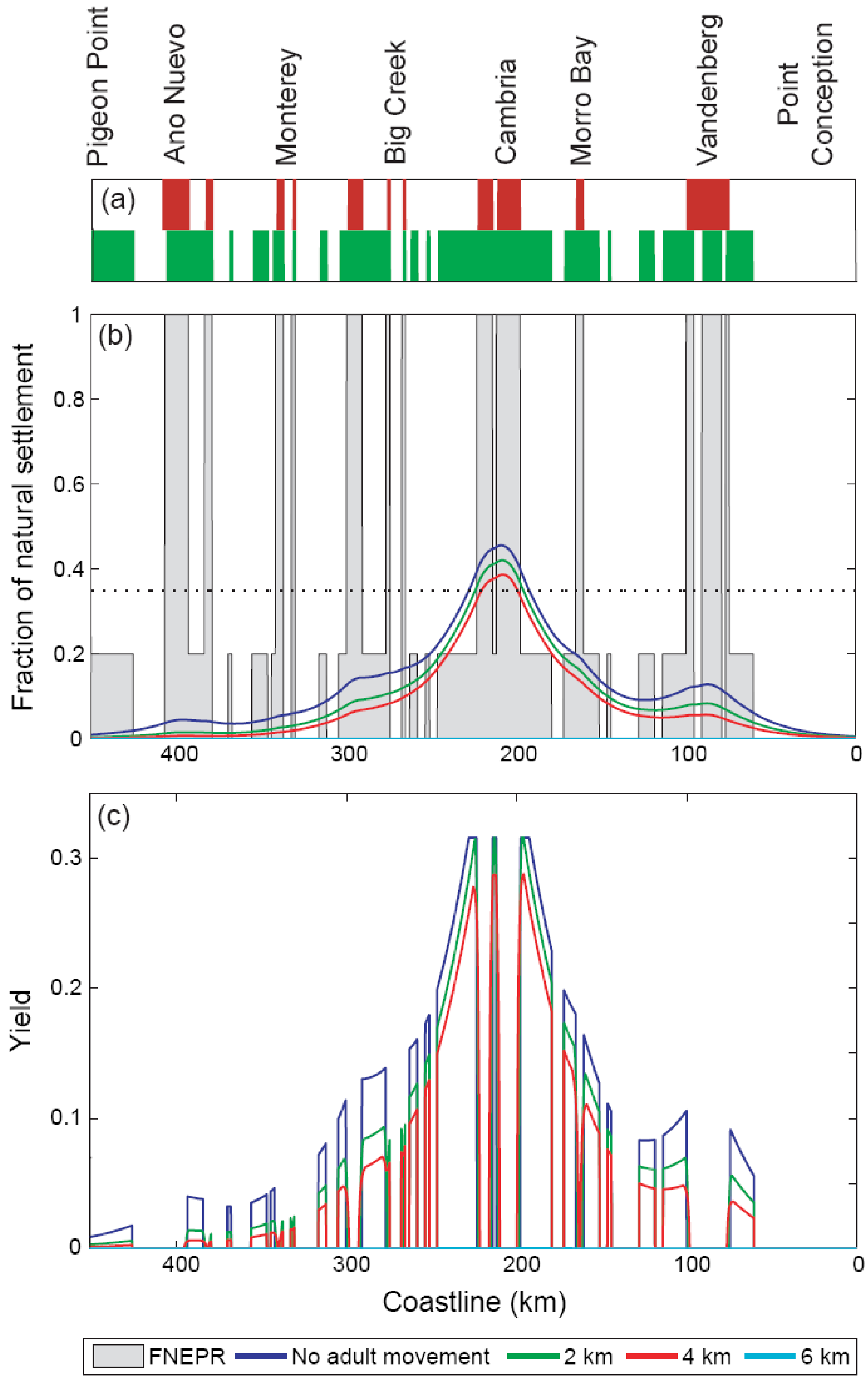

Home range threshold
0
2
4
6
8
10
0
0
0.8
0
0.2
3.2
0.2
0.8
>500
10%
20%
30%
Fraction in reserves
0.1
0.2
0.3
FNEPR

Figure 5.


Pigeon Point
Ano Nuevo
Monterey
Big Creek
Cambria
Morro Bay
Vandenberg
Point Conception
(a)
(b)
Fraction of natural settlement
1
0.8
0.6
0.4
0.2
0
400
300
200
100
0
(c)
Yield
0.3
0.2
0.1
0
400
300
200
100
0
Coastline (km)
FNEPR
No adult movement
2 km
4 km
6 km

Persistence and yield plots at varying exploitation rates outside reserves

Here we show persistence and yield results for combinations of mean larval dispersal distance and home range size for several exploitation rates outside reserves. The coastline is infinite with continuous habitat and periodically spaced reserves similar to Figure 4. We evaluated exploitation rates greater than and less than the rate shown in Figure 4 (FNEPR=0.2).

Persistence and yield for FNEPR of 0.10 in fished areas is shown in Figure A1. At this greater level of overfishing, a smaller range of dispersal distances were protected compared to the case where fishing reduced FNEPR to 0.2 in fished areas. Reserves exhibit self-persistence for species with larval dispersal distances of the same order of magnitude as the reserve size and with home ranges less than 1.2 times reserve length. For reserves of 10 km^2, this is a 3.8 km home range. Network persistence occurred if 30% of the coastline was in reserves, at which point sedentary species with any distance larval dispersal were persistent (Fig. A1c). With 30% reserve coverage, only species with home ranges less than 1/5 the reserve size persisted for all larval dispersal distances, which for 10 km^2 reserves is a home range of 0.6 km. Similar to previous results, yield was at a maximum just before population collapse (Fig. A1d-f).

Persistence and yield results for a less severe level of overfishing (FNEPR=0.3) are shown in Figure A2. A broader range of dispersal distances were persistent than for the previously described results for greater rates of overfishing outside reserves. Network persistence occurred if 10% or greater of the coastline was in reserves. With 10% reserve coverage, network persistence occurs for species with large larval dispersal distances and home ranges 0.7 times the reserve length or smaller (Fig. A2a). For 10 km^2 reserves, this corresponds to a home range of 2.2 km. With 20% of the coastline in reserves, network persistence occurs for species with large larval dispersal distances and home ranges 3.1 times the reserve length or smaller, which for 10 km^2 reserves is a 9.8 km home range (Fig A2b). With 30% of coastline in reserves all combinations of larval dispersal and home range size were persistent (a range of dispersal distances up to 500 times the reserve size were evaluated but not shown) (Fig. A2c). Yield was at a maximum for the largest dispersal distances that were persistent (Fig. A2d-f).

When overfishing did not occur and populations were managed sustainably (FNEPR$\geq$0.35), all populations were persistent with or without reserves (Fig. A3). The fraction of natural larval supply (FNLS) decreased with increasing home range size, and increased with greater reserve coverage (Fig. A3a-c). Because FNLS was always above the persistence criterion, the fraction of natural larval recruitment (FNLR) did not vary with larval dispersal distance, so the equilibrium FNLS varied only with the spatial distribution of FNEPR, and therefore home range size. Similarly, because FNLR equaled one everywhere, yield followed the distribution of YPR and varied with home range size (Fig. A3d-f). Increasing reserve coverage resulted in decreases in yield. For populations that are not subject to overfishing, there is a direct trade-off between persistence and yield. Reserves may increase FNLS, but because they are not necessary for population persistence, by protecting part of the population that could be fished sustainably, they lead to decreased yield.

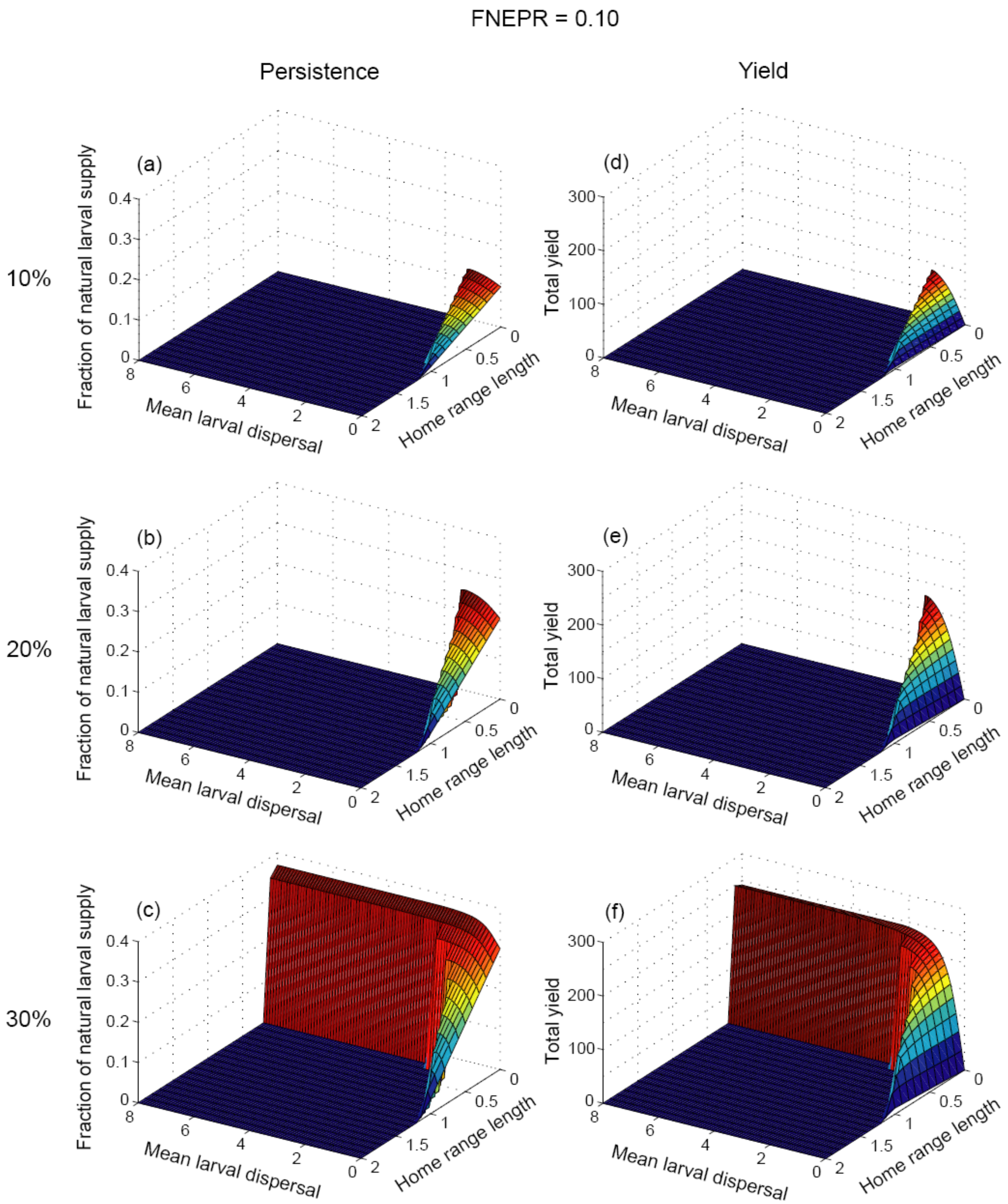


Figure A1. The fraction of natural unfished larval supply along an infinite coastline for (a) 10% of the coastline in reserves, (b) 20% of the coastline in reserves, and (c) 30% of the coastline in reserves for varying larval dispersal and home range lengths. Total yield along an infinite coastline for (d) 10% of the coastline in reserves, (e) 20% of the coastline in reserves, and (f) 30% of the coastline in reserves. Mean larval dispersal and home range lengths are in units of reserve length. Reserves are spaced periodically along the coast. Fraction of natural eggs-per-recruit (FNEPR) outside reserves is 0.1 (populations are intensely overfished). Total yield is in arbitrary but consistent biomass units.

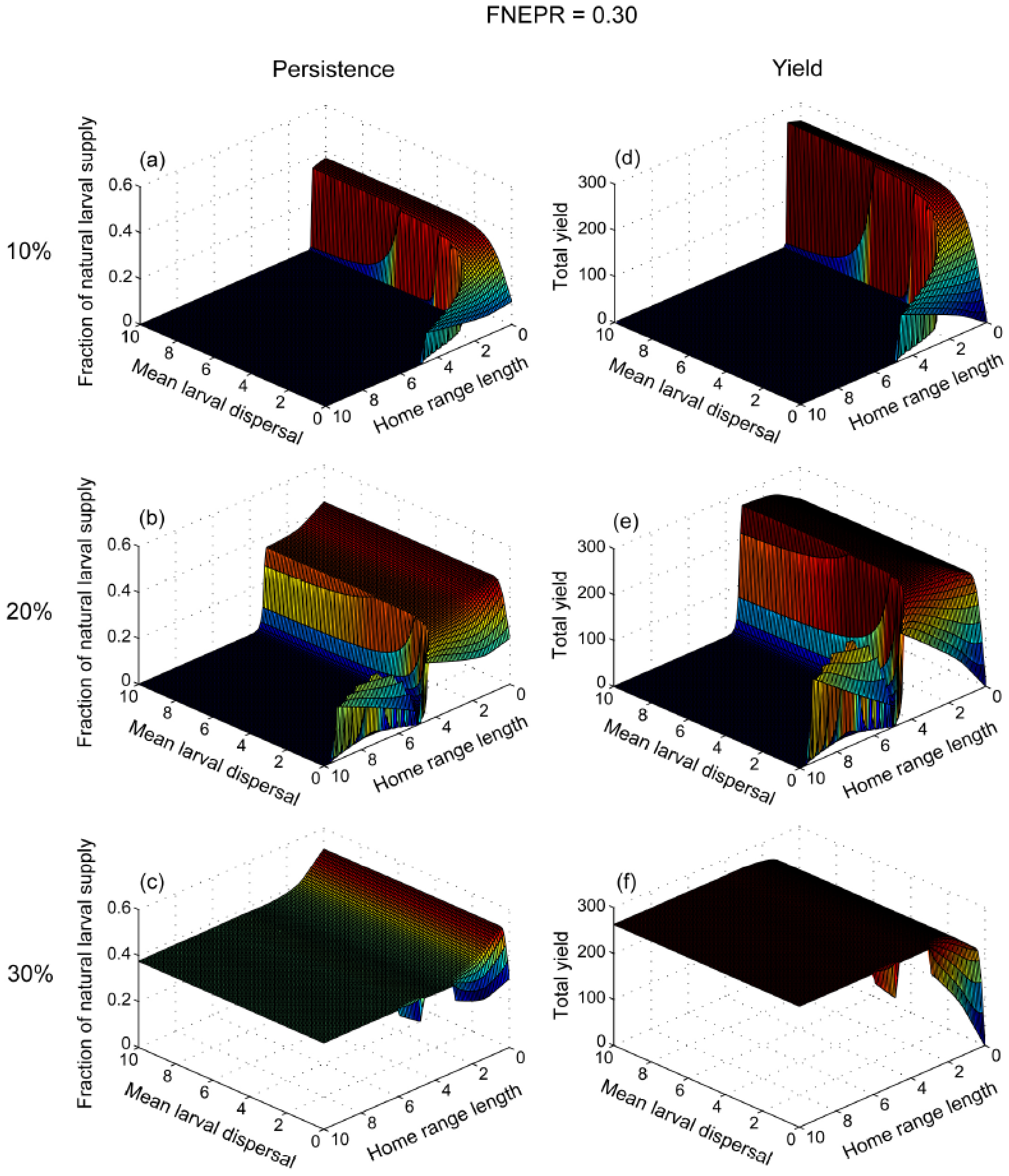


Figure A2. The fraction of natural unfished larval supply along an infinite coastline for (a) 10% of the coastline in reserves, (b) 20% of the coastline in reserves, and (c) 30% of the coastline in reserves for varying larval dispersal and home range lengths. Total yield along an infinite coastline for (d) 10% of the coastline in reserves, (e) 20% of the coastline in reserves, and (f) 30% of the coastline in reserves. Mean larval dispersal and home range lengths are in units of reserve length. Reserves are spaced periodically along the coast. Fraction of natural eggs-per-recruit (FNEPR) outside reserves is 0.3 (populations are slightly overfished). Total yield is in arbitrary but consistent biomass units.

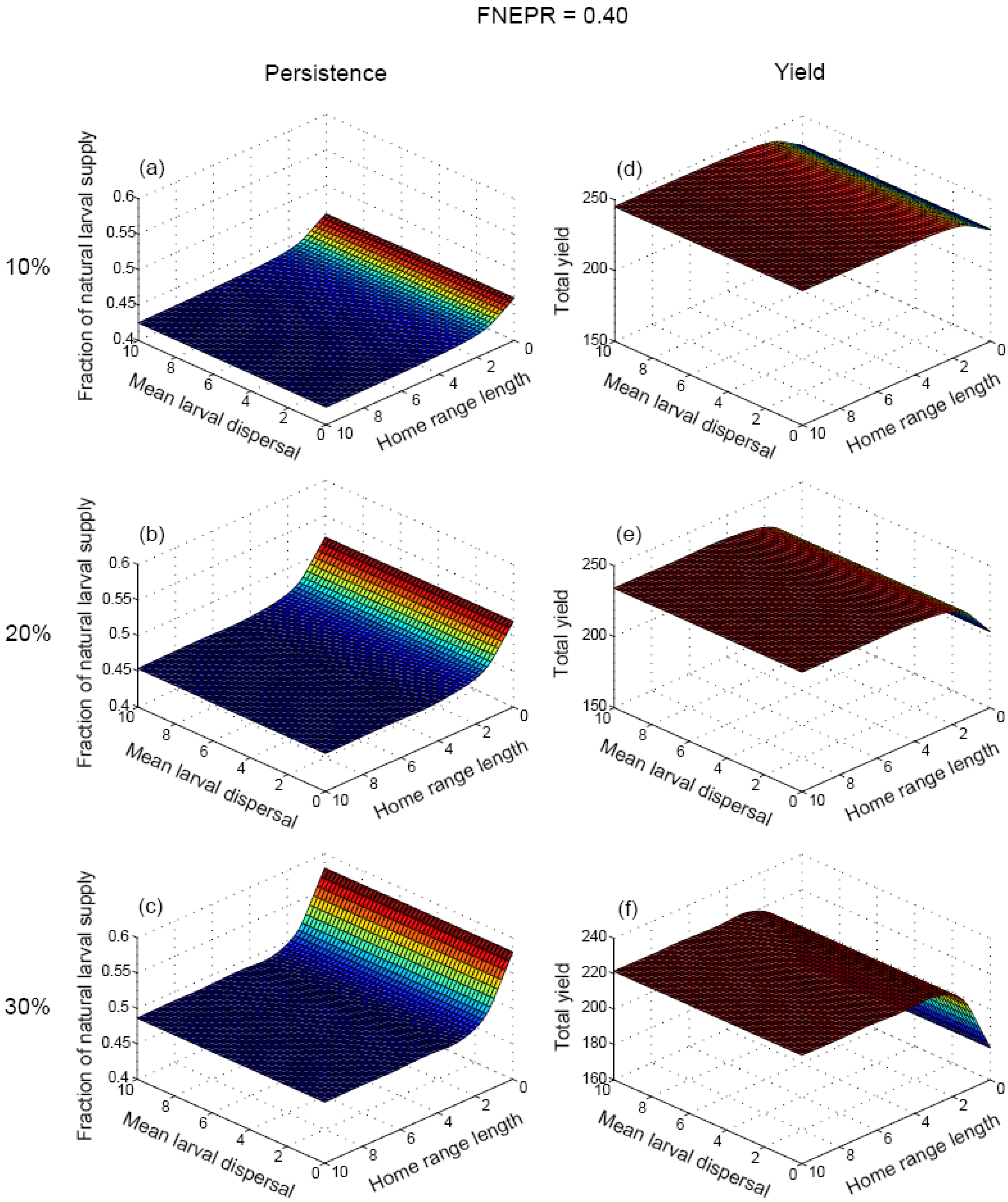


Figure A3. The fraction of natural unfished larval supply along an infinite coastline for (a) 10% of the coastline in reserves, (b) 20% of the coastline in reserves, and (c) 30% of the coastline in reserves for varying larval dispersal and home range lengths. Total yield along an infinite coastline for (d) 10% of the coastline in reserves, (e) 20% of the coastline in reserves, and (f) 30% of the coastline in reserves. Mean larval dispersal and home range lengths are in units of reserve length. Reserves are spaced periodically along the coast. Fraction of natural eggs-per-recruit (FNEPR) outside reserves is 0.4 (populations are not overfished). Total yield is in arbitrary but consistent biomass units.