

# A framework for assessing the biodiversity and fishery aspects of marine reserves

Phillip S. Levin<sup>\*1</sup>, Isaac Kaplan<sup>1</sup>, Rikki Grober-Dunsmore<sup>2</sup>, Paul M. Chittaro<sup>1</sup>, Seichi Oyamada<sup>3</sup>, Kate Andrews<sup>3,4</sup> and Marc Mangel<sup>3</sup>

<sup>1</sup>Northwest Fisheries Science Center, NOAA Fisheries, 2725 Montlake Blvd E., Seattle, WA 98112, USA;

<sup>2</sup>National Marine Protected Areas Center Science Institute, NOAA, 100 Shaffer Road, Santa Cruz, CA 95060, USA;

<sup>3</sup>Department of Applied Mathematics and Statistics and Center for Stock Assessment Research, University of California, Santa Cruz, Santa Cruz, CA 95064, USA; and <sup>4</sup>Panama City Laboratory, Southeast Fisheries Science Center, NOAA Fisheries, Panama City, FL 32408, USA

## Summary

1. Resource management agencies are often charged with managing natural resources for economic and social goals, while also protecting and conserving biodiversity and ecosystem function. However, this may not always be possible. Ecosystem-based management is frequently suggested as a way to achieve multiple objectives in resource management and requires that trade-offs among conflicting objectives be identified and an effective means to utilize these trade-offs developed.

2. We examine the relationship between area and species richness in a diverse assemblage of fishes along the US West Coast and then use parameters from this relationship as input for a model that considers trade-offs between fisheries yield and the number of species protected by different management strategies.

3. The species–area relationship ( $S = cA^z$ ) for fishes along the US Pacific coast is well described by the relationship  $S = 16.18A^{0.226}$ .

4. There are nearly linear trade-offs between diversity and yield when fishing effort is low. However, the trade-offs become nonlinear as fishing effort increases and imposing MPAs increases both the conservation and fisheries value of the system when the system is overfished.

5. *Synthesis and applications.* Solving conflicts between fisheries and conservation requires attention as to how conservation benefits accrue as fishing effort is reduced. However, scientists often lack quantitative information about the trade-offs inherent in human activities such as fisheries. The approach we develop here can begin to help frame the questions to be posed and evaluate the likely consequences of different management options.

**Key-words:** California current, ecosystem-based management, fisheries management, marine protected area, species–area relationship

## Introduction

Widespread degradation of marine ecosystems and the apparent failure of existing governance structures to effectively deal with the demise of ocean resources have led to escalating calls for ecosystem-based approaches to management (Pew Oceans Commission 2003; US Commission on Ocean Policy 2004). Ecosystem-based management is an approach that considers the entire ecosystem, including humans, and differs from single-species or single-sector approaches in that it considers the

cumulative impacts of different sectors (McLeod *et al.* 2005). While ecosystem-based management is often identified as a solution to problems in the world's seas, its aims are often ill-defined and can differ widely among groups advocating it. For instance, resource agencies typically view marine resource use by humans as natural and believe that the desired outcome of ecosystem-based management is the production of goods and services for humans (e.g. Norway's policy on marine mammals, report no. 27, 2003; cf. Simberloff 1999). By contrast, conservation organizations frequently view human use as unnatural and envisage the goal of ecosystem-based management as maintaining biodiversity and/or ecosystem function

\*Correspondence author. E-mail: phil.levin@noaa.gov

(Pikitch *et al.* 2004). The different visions of marine ecosystem-based management are clearly illustrated in two high-level reports on the status of US marine ecosystems – the Pew Oceans Commission and the US Commission on Ocean Policy. The Pew Commission (Pew Oceans Commission 2003) emphasized the use of ecosystem-based management to maintain ocean resources for biodiversity and ecosystem function, while the government-mandated US Commission on Ocean Policy (US Commission on Ocean Policy 2004) highlighted the utility of ecosystem-based management for the sustainable use of ocean resources (Granek *et al.* 2005). We are left with a conflict (Simberloff 1999) – does ecosystem-based management protect and serve human needs or is it a means for humans to protect nature?

The central mission of the National Marine Fisheries Service (NMFS), the chief government agency charged with managing natural marine resources in US waters, is to manage fisheries to maintain economically viable harvest while also conserving 'healthy' ecosystems (NMFS 2004). Such an approach is akin to the philosophy of 'multiple use' adopted by the US Forest Service (Kessler *et al.* 1992). The sustainable management of resources for economic and social goals while also protecting and conserving the marine biodiversity and ecosystem functioning is laudable but may not always be possible (Zabel *et al.* 2003). As a consequence, the central aim of any ecosystem-based management approach must be to clearly identify trade-offs among conflicting objectives (Walters & Martell 2004) and to develop effective means to utilize these trade-offs (Mangel 2000c). In this paper, we use no-take marine protected areas (MPAs) to illustrate the potential trade-offs between consumptive (e.g. fisheries) and non-consumptive (e.g. existence of biodiversity) goals in marine ecosystems.

Marine protected areas are often highlighted as key tools for ecosystem-based management (e.g. Browman & Stergiou 2004) and are gaining increasing attention as conservation and fisheries management tools (Pew Oceans Commission 2003; Sissenwine & Murawski 2004). No-take MPAs eliminate fishing mortality and protect habitat from destructive fishing practices within reserve boundaries. As a consequence, fish abundance and diversity tend to be higher inside reserves than in unprotected areas (Halpern & Warner 2002; Halpern 2003). By contrast, the effects of MPAs on fishery yield is uncertain and controversial (Mangel 2000a; Willis *et al.* 2003; Hilborn *et al.* 2004). Obviously, there is no yield within an MPA, but fisheries benefits outside MPAs may be achieved if there is a spillover of adults from the MPA to adjacent areas (Murawski *et al.* 2005) or larvae are exported from protected areas. Whether these benefits exceed those realized through conventional fisheries management is unclear (NRC 2001). While the benefits of MPAs for protection of biodiversity are plain (NRC 2001; Halpern 2003), such gains may come at the expense of fisheries yields (Mangel 1998; Botsford *et al.* 2004; Botsford 2005). Consequently, the overall benefits of reserves can only be evaluated when biodiversity metrics are interposed with fisheries metrics (Halpern & Warner 2003; Hilborn *et al.* 2004).

Here, we focus on species richness as a biodiversity metric, as it is simple and transparent (Simberloff 1999). While species richness is not the only metric of biodiversity (e.g. Kareiva & Marvier 2003), it is an attribute upon which many stakeholders place high value (Simberloff 1999; Carter 2003). Consequently, species richness is often an important component of ecosystem approaches to resource management. We first examine the relationship between area and species richness in a diverse assemblage of fishes along the US West Coast, and then use parameters from these species–area relationships as key inputs into a model of the trade-off between fisheries yield and the number of species protected by different management strategies that involve MPA coverage and fishing mortality rates.

## Materials and Methods

### THE SPECIES–AREA RELATIONSHIP FOR A WEST COAST FISH ASSEMBLAGE

The tendency for the number of species to increase with area (the species–area relationship, SAR), is one of the oldest (Arrhenius 1921) and most robust (Rosenzweig 1999) empirical observations in ecology. While it has proved difficult to use the SAR to make inferences about the mechanisms structuring communities (Connor & McCoy 1979; Coleman *et al.* 1982; McGuinness 1984; Ney-Nifle & Mangel 2000), the SAR is a useful tool for estimating how species richness changes with area (Rosenzweig 1999; Williamson *et al.* 2001). Trade-offs between biodiversity in MPAs and fisheries yield depend fundamentally on how species richness changes with area. SARs therefore provide a useful starting point for understanding the conservation axis of this trade-off (Neigel 2003).

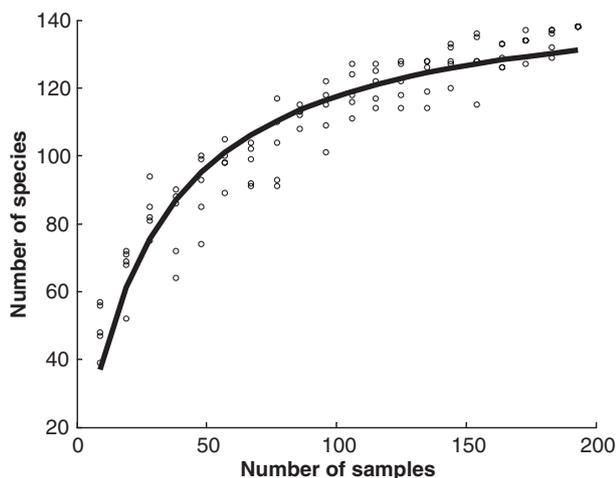
We used data on species richness from the 1999–2003 West Coast trawl survey conducted by the Northwest Fisheries Science Center, NMFS (e.g. Keller *et al.* 2007) to generate SARs for groups of species within the 'groundfish' assemblage (i.e. fish species typically associated with the sea floor). Trawl surveys extended from near Cape Flattery, Washington (48°27'N) to Point Conception, California (34°28'N) and ranged in depth from 35 to 1200 m. The survey was conducted during summer and consisted of 1786 tows using a 15-m-wide Aberdeen style net with a small (3.8-cm stretched measure or less) mesh liner in the cod end. Trawl duration was approximately 15 min of bottom contact at a speed of *c.* 2.2 knots. Bottom contact and acoustic instruments were attached to the nets to record aspects of mechanical performance and gear depth. Catches were sorted to species or the closest taxonomic level, counted and weighed. Complete details of the trawl survey are available from Keller *et al.* (2007). During 1786 tows, 213 species belonging to 61 families, 24 orders and 5 classes were sampled.

We generated SARs using the most common representation of the SAR,  $S = cA^z$ , where  $S$  is the species richness and  $A$  is the area. The constant,  $c$ , represents the height of the curve near the  $y$ -axis and the slope,  $z$ , is a scale-independent parameter that determines how steeply the curve rises. Traditional SAR studies often focus on  $z$  as a measure of the rate at which the natural logarithm of species richness increases with the natural logarithm of area (Rosenzweig 1995).

We fit the SAR to the West Coast groundfish assemblage using a simple Monte Carlo approach. We first generated 50 randomly placed boxes, each of which encompassed 5% of the latitude of the coast (4–6% of the area) and could overlap in space. We then estimated the total species richness within each of the boxes (see below).

This process was repeated for boxes of increasing size (5%, 10%, 15%, etc., up to 95% of the coast). The 19 unique box sizes, each with 50 replicates, yielded a total of 950 points. We natural logarithm transformed both the number of species and the area, and fit a linear regression to the 950 data points generated by this process. The parameter  $z$  was the slope of the regression and constant  $c$  was the exponential of the intercept of the regression.

This method required estimation of total species richness in each box. Simply counting the species present ignores potential sampling effects; larger boxes could display higher species richness solely because they are likely to contain more trawls. To control for this effect, species accumulation curves (Colwell & Coddington 1994) were constructed for each box by plotting species richness vs. number of trawls (e.g. Fig. 1) and estimating the true species richness as the asymptote of this curve, essentially asking the question, what would observed species richness be if there was unlimited sampling effort (Gotelli & Colwell 2001; Colwell *et al.* 2004)? We estimated the asymptote (true species richness) using the Michaelis Menten equation (cf. Colwell 2005). The main effect of this estimation procedure was for the 'true' species richness for small boxes (< 20% of the coast) to be larger than observed in the data. For most boxes that covered more than 20% of the coast, the asymptote was approximately equal to the maximum number of species observed in the data. The maximum number of species and slope were estimated by minimizing the sums of squares using the Nelder–Mead simplex method in MATLAB v. 6.1 (The Mathworks, Natick, MA, USA). One caveat of this approach is that it may slightly overestimate  $r^2$  and underestimate the confidence intervals of  $c$  and  $z$  because the SAR was fit to point estimates of the asymptotes of the species-accumulation curves, ignoring uncertainty in these estimates.



**Fig. 1.** An example of extrapolation to estimate true species richness for a box, controlling for the effect of sampling intensity (i.e. number of trawls). This example is for one box that represents 10% of the coast. The box contained 193 trawls, with a maximum observed species richness of 138. Five alternative sets of trawls (points) were generated for 20 different sampling intensities ( $x$ -axis) by sampling trawls randomly and without replacement within each set. The Michaelis Menten equation ( $S = S_{\max}n/[b + n]$ ) was fit to the data using the Nelder–Mead simplex method in MATLAB v. 6.1, where  $S_{\max}$  represents the true species richness,  $S$  is the observed species richness,  $n$  is the sampling intensity and  $b$  is a constant. Estimated true species richness ( $S_{\max}$ ) for this box was 150 species.

#### A MODEL FOR HABITAT, RESERVES AND SPECIES–AREA EFFECTS

The relationship between species richness and area provides an important tool that can be used to examine trade-offs between a non-consumptive value (e.g. biodiversity) of no-take MPAs and the potential cost in fisheries yield of such areas. We develop a model to illuminate the costs and benefits of an MPA, the number of species potentially protected by the MPA and the change in fisheries yield as a result of implementing the MPA. Although we use species richness as a metric of biodiversity, the approach we describe could use any biodiversity attribute that varies with area. The model we use is stylistic and simplified but is motivated by the US West Coast fish assemblage. In this system, a number of species are currently or have been individually targeted by fisheries (e.g. Pacific hake *Merluccius productus*, sablefish *Anoplopoma fimbria*, petrale sole *Eopsetta jordani*, widow rockfish *Sebastes entomelas*, market squid *Loligo opalescens* and Dungeness crab *Cancer magister*). At the same time, a number of fishery target (e.g. MacCall 2007; Stewart 2007) and non-target species (e.g., Levin *et al.* 2006; Mangel *et al.* 2006) have experienced precipitous declines in recent years and concern about this system has led to calls for the establishment of MPAs (Lubchenco *et al.* 2003). Thus, below we develop an example that focuses on how the fisheries yield of one species may be affected by MPAs established to conserve an entire suite of species.

We envision a domain that is divided into two areas, one open and the other closed, to fishing. In addition, we consider a category called 'untrawlable', which is open to fishing but experiences little fishing pressure due to bathymetry that makes the area nearly inaccessible to the fishery.

We model untrawlable habitat (indexed by 0) with area,  $A_0$ , logistic population growth, and fishing removing a small fraction,  $u_0$ , of the fish. Trawlable habitat (indexed by 1) has area  $A_1$ , logistic population growth, and proportion  $u_1$  of the fish population removed by fishing. Fishing also reduces habitat quality by an amount  $q$  in the trawlable habitat. For most model runs, we assumed that the untrawlable area was 30% of the total area (NOAA 2006). However, we also explored the consequence of different levels of untrawlable area. We assumed that a fraction  $\alpha$  of the trawlable habitat is set aside in an MPA.

In year  $t$ , biomass in the entire region is  $B(t)$ , partitioned into the untrawlable and trawlable habitats:

$$B(t) = B_0(t) + B_1(t) \quad \text{eqn 1}$$

Assuming an ideal free distribution (Fretwell 1972) of fish between the two habitats:

$$r_0 \left(1 - \frac{B_0(t)}{K_0}\right) = r_1 \left(1 - \frac{B_1(t)}{qK_1}\right) \quad \text{eqn 2}$$

where  $r_i$  is the maximum per capita reproduction in habitat  $i$ ,  $K_i$  is the carrying capacity and  $q$  scales the trawlable area to account for lower habitat quality. The maximum per capita reproduction  $r_i$  and carrying capacity  $K_i$  are independent of area.

An ideal free distribution is one in which individuals are distributed among habitats such that their fitness is maximized. Thus, individuals choose habitats based on the quality of the habitat and the density of conspecifics in the habitat. Therefore, individuals are distributed such that the ratio of density between any two patches will equal the ratio of resource levels in those patches. This pattern of density-dependent habitat selection has been used to explain patterns of habitat use by a wide range of marine fishes (Myers & Stokes 1989; MacCall 1990; Levin *et al.* 2000; Lindberg *et al.*

2006; Swain & Benoit 2006) and is a useful starting point for our work.

We solve eqn 2 to partition initial biomass at the start of year  $t$  ( $B_{\text{init}}$ ) into  $B_0(\text{init})$  and  $B_1(\text{init})$ :

$$B_0(\text{init}) = \frac{(r_0 - r_1) + \frac{r_1 B_{\text{init}}}{qK_1}}{\frac{r_1}{qK_1} + \frac{r_0}{K_0}} \quad \text{eqn 3}$$

$$B_1(\text{init}) = B_{\text{init}} - B_0(\text{init}) \quad \text{eqn 4}$$

We then define  $B'(t)$ , the biomass remaining in the trawlable habitat after fishing, as:

$$B'(t) = \alpha B_1(t) + (1 - u_1)(1 - \alpha)B_1(t) \quad \text{eqn 5}$$

Biomass in the next year is then:

$$B(t + 1) = (1 - u_0)B_0(t) + (1 - u_0)B_0(t)r_0 \left[ 1 - \frac{(1 - u_0)B_0(t)}{K_0} \right] + B'(t) + r_1 B'(t) \left( 1 - \frac{B'}{qK_1} \right) \quad \text{eqn 6}$$

after which partitioning of biomass across the habitats occurs.

The yield from the fishery during year  $t$ ,  $Y(t|x)$ , depends on the fraction of habitat in the MPA:

$$Y(t|x) = u_0 B_0(t) + u_1 (1 - \alpha) B_1(t) \quad \text{eqn 7}$$

The state yield was computed as a function of reserve fraction  $\bar{Y}(x)$ . We also calculated the effective area of the entire domain ( $A$ ) given the reserve fraction:

$$A_e = A_0 + \alpha A_1 + (1 - \alpha)qA_1 \quad \text{eqn 8}$$

so that the species richness is predicted to be:

$$S(x) = cA_e^z \quad \text{eqn 9}$$

Our approach makes the assumption that the slopes of the SARs are similar between trawlable and untrawlable habitat. While it is possible that this assumption is invalid, no data are available to test this assumption. Thus, for simplicity, we use a single SAR. However, as more data become available, total species richness could easily be generated as the sum of the number of species estimated by two (or more) different species–area relationships.

## Results

The power function fit the data well ( $r^2 = 0.87$ ; Fig. 2). The slope ( $z$ ) was estimated to be 0.226 (95% CI 0.221–0.231) and the intercept ( $c$ ) to be 16.18 (95% CI 15.34–17.07). Thus, the typical SAR for US West Coast groundfish is described by the relationship  $S = 16.18A^{0.226}$ . These parameters appear typical of those for marine fish and temperate marine communities (Appendix S1, Supporting Information).

The fishing mortality in the ‘trawlable’ habitat that produced maximum sustainable yield without MPAs was 0.09 (Fig. 3). The ‘untrawlable’ habitat serves as a buffer for yield in this system (see the results in Fig. 3 for very high levels of harvesting in trawlable habitat;  $u_1 > 0.17$ ). Moreover, the system-wide yield remains at stable levels due to the harvest ( $u_0 = 0.01$ ) of the high biomass in the untrawlable area even

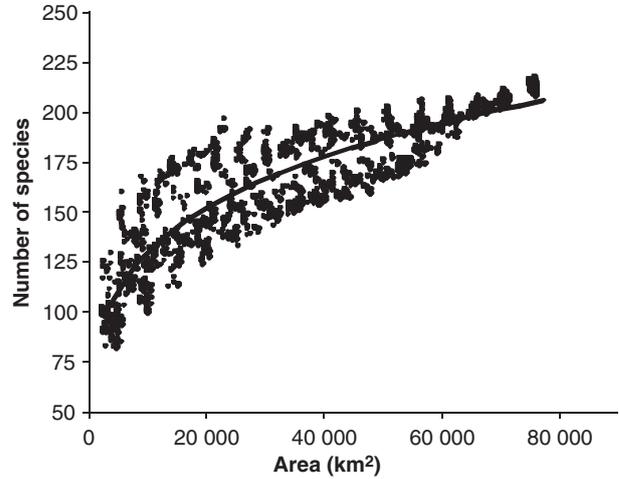


Fig. 2. Species–area relationship for fishes sampled along the US West Coast.

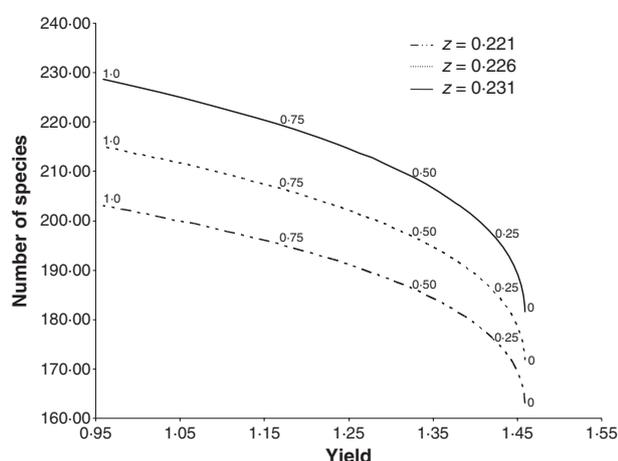
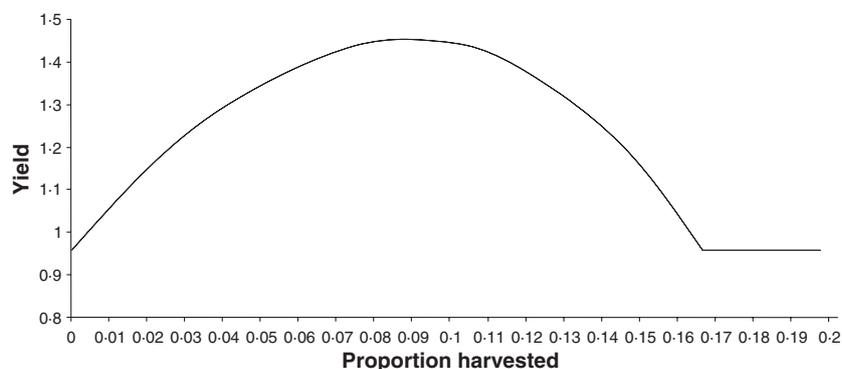
when the stock in trawlable habitat is extirpated and its yield is zero.

At sustainable levels of fishing ( $u_1 = 0.09$ ), there is a nonlinear, negative relationship between fisheries yield and species richness as the proportion of the trawlable area in the MPA increases from 0 to 1 when  $c = 16.18$  and  $z$  ranges from 0.221 to 0.231 (Fig. 4). The rate of species richness initially increases rapidly with little effect on yield as the proportion of the region in an MPA increases until the MPA is greater than about 25% of the total area. This relationship is not sensitive to the value of  $z$ , although changing  $z$  does change the number of species in the MPA (Fig. 4). Increasing habitat quality (i.e. higher  $q$ ) leads to higher yields when  $S = 16.18A^{0.226}$  and the fraction harvested is 0.09 (Fig. 5), although higher habitat quality and more potential yield in the trawlable habitat amplifies the nonlinear trade-off between species richness and yield.

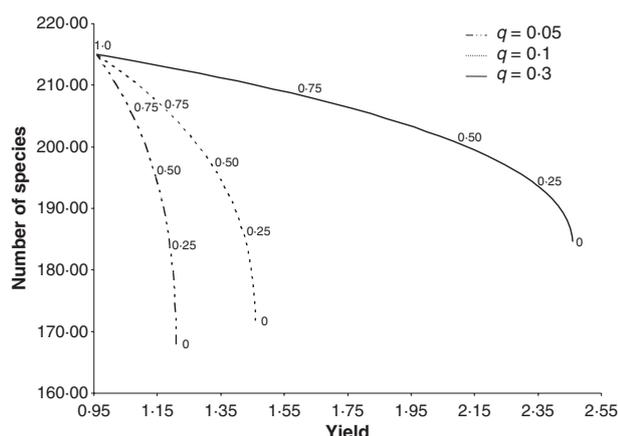
The effect of MPAs on the yield–species richness trade-off changes with  $u_1$  (Fig. 6; where  $S = 16.18 A^{0.226}$ ). There is a near-linear inverse relationship between fisheries yield and species richness as the proportion of the trawlable area in the MPA increase from 0 to 1 when  $u_1 = 0.03$  (Fig. 6a). The relationship becomes more nonlinear when the proportion of the population harvested increases to 0.09 (Fig. 6b). In this case, increasing the fraction of the area in the reserve has little effect on yield until the MPA comprises about 40% of the total area. Increases in MPA area result in declines in yield and increases in species richness once the MPA is 40% of the total area.

The situation is more complex when the population in the trawlable habitat is overfished (i.e.  $u_1 > 0.09$ ). When 15% of the population is harvested, initially there is a positive relationship between yield and species richness as the proportion of the region in the MPA increases (Fig. 6c). This occurs because the MPA eliminates overfishing, thus increasing productivity. As the proportion of the trawlable area in the MPA approaches 45%, the relationship reverses and yield begins to decline as species richness increases. The situation is similar when the proportion of the population harvested is 20% (Fig. 6d). For this case, there is no change in yield when less than 15% of the

**Fig. 3.** Fisheries yield (trawlable + untrawlable habitat) with MPA area set to 0 as a function of the proportion of the fish population harvested in the trawlable habitat ( $u_1$ ). Maximum sustainable yield was achieved with  $u_1 \approx 0.09$ . The harvest rate for the untrawlable habitat ( $u_0 = 0.01$ ) and its high biomass contributes approximately 0.95 units of catch.



**Fig. 4.** Species richness vs. yield as the proportion of the coast in MPAs (numbers above points) changes from 0 to 1 for three values for the slope of species–area relationship,  $z$ . In all cases the proportion of the fish stock harvested was set at 0.09, the level resulting in maximum sustainable yield.



**Fig. 5.** Species richness vs. yield as the proportion of the coast in MPAs (numbers above points) changes from 0 to 1. Species richness is given by  $S = 16.18A^{0.226}$ ,  $u_1$  is fixed at 0.09, and  $q$ , habitat quality in the trawled area relative to untrawled area, is 0.05, 0.1 or 0.3.

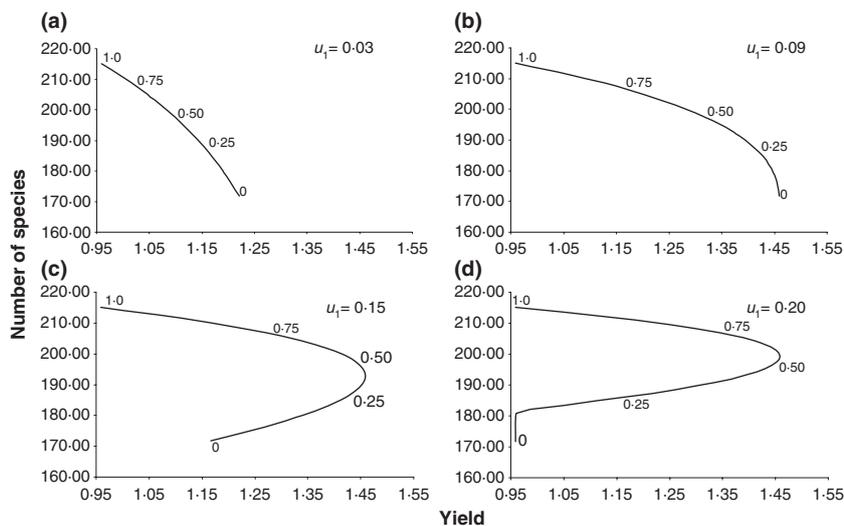
trawlable area is in the MPA because fishing mortality is still too high to sustain harvest. At MPA fractions  $> 0.15$ , the results for  $u_1 = 0.20$  mirror those for  $u_1 = 0.15$  – there is initially a positive relationship between yield and species

richness, and this shifts to a negative relationship when the MPA area is greater than *c.* 58% of the trawlable habitat. In all four of these harvesting scenarios, the 30% of habitat that is untrawlable stabilizes species richness and yield at moderate levels, even when the trawlable habitat is overfished and lacks an MPA. This is because we assigned high habitat quality and moderate fishing ( $u_0 = 0.01$ ) to the untrawlable habitat. As an example, equilibrium biomass with harvest  $u_1 = 0.09$  is 95.9 and 5.6 mt in the untrawlable and trawlable habitats respectively (Table 1). The equilibrium harvest for the untrawlable habitat is 0.96 mt and the maximum equilibrium harvest from the trawlable habitat is 0.50 mt when  $u_1 = 0.09$  and  $u_0 = 0.01$ . This may be an appropriate situation for rockfishes (*Sebastes* spp.) off the US West Coast which have high abundance in rocky habitat that can only be partially accessed by trawl gear.

The effect of the amount of trawlable habitat directly follows from eqns 8 and 9. It determines the areal extent of low habitat quality ( $q$ ) when the area is fished. This, in turn, has a direct effect on species richness. Thus, the amount of trawlable area influences the trade-off between species richness and yield. In particular, as trawlable area increases, the trade-off between yield and species richness is magnified (Fig. 7).

## Discussion

Ecosystem approaches to management attempt to explicitly consider multiple ecological and socioeconomic objectives. As resource managers adopt the precepts of ecosystem-based management, many decisions represent a crossroad where a potentially staggering array of choices faces policy makers. Decisions in natural resource management can be characterized by conflicts between those with a utilitarian, human-centred view vs. those with a biocentric view. While science cannot solve such conflicts, it can expose trade-offs between conservation and economic goals and thus clarify the consequences of decisions for managers. Fisheries management has long dealt with trade-offs such as those occurring among different fisheries targets, current vs. future harvest and abundance of target species vs. fishing effort (for a comprehensive discussion, see Walters & Martell 2004). However, examination of trade-offs between fisheries yield and conservation has been complex (Helvey 2004) because ecological and fisheries metrics are often drawn from different analytical frameworks. In this paper, we have illustrated an analytical approach that



**Fig. 6.** Species richness vs. yield as the proportion of trawlable area in the MPA (numbers above points) changes from 0 to 1.  $z$  was fixed at 0.226, and the proportion of stock harvested ( $u_1$ ) varies from 0.03 to 0.20.

**Table 1.** Parameters used in the model examining trade-offs between species richness and fisheries yield

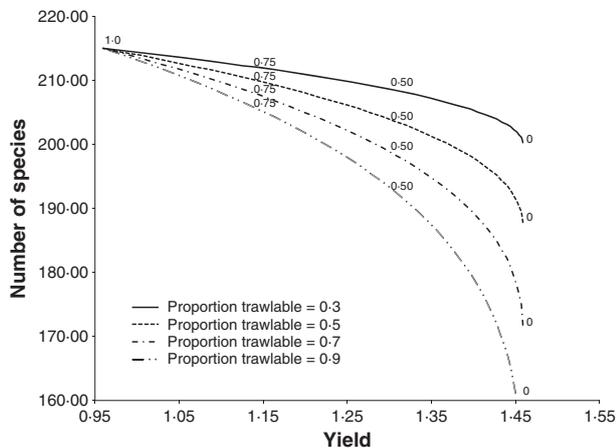
Symbol	Interpretation	Value
$c$	Constant from the species–area relationship	16.18 US West Coast groundfish
$z$	Slope from the species area curve	0.226 US West Coast groundfish 0.221, 0.231 Alternate simulations
$r_0$	Intrinsic rate of increase for fish in untrawlable habitat	0.20
$r_1$	Intrinsic rate of increase for fish in trawlable habitat	0.20
$K_0$	Area (as a proxy for carrying capacity) of untrawled habitat	100
$K_1$	Area (as a proxy for carrying capacity) of trawled habitat	100
$q$	Quality of trawled habitat relative to untrawled, in terms of effect on $K$	0.1
$A$	Total area in the system	93 559 km <sup>2</sup>
$A_0$	Proportion of the area that is untrawlable	0.30
$A_1$	Proportion of the area that is trawlable	0.70
$u_0$	Fraction harvested in untrawlable habitat	0.01
$u_1$	Fraction harvested in trawlable habitat	0.03–0.20
$B_{\text{start}}$	Total starting biomass in trawlable and untrawlable habitat combined	20
$B_0(\text{init})$	Initial biomass, untrawlable area	18.2
$B_1(\text{init})$	Initial biomass, trawlable area	1.8
$B_0(\text{equil})$	Equilibrium biomass, untrawlable area	95.9
$B_1(\text{equil})$	Equilibrium biomass, trawlable area	5.6 (when $u_1 = 0.09$ and no MPAs)
Yield <sub>0</sub> (equil)	Equilibrium yield, untrawlable area	0.96
Yield <sub>1</sub> (equil)	Equilibrium yield, trawlable area	0.50 (when $u_1 = 0.09$ and no MPAs)

integrates a basic biodiversity metric (species richness) with a fundamental fisheries measure (yield). Species richness is fundamentally associated with area and our analysis and review reveal that a slope of 0.226 in the SAR is a reasonable approximation for the rate at which richness increases with area for the groundfish assemblage along the US West Coast. We show that fisheries yield, as a function of area, is related to habitat quality, fish biomass and the area of the spatial domain in a marine reserve. Consequently, we can relate diversity to yield conditioned on habitat quality and stock biomass.

Models of MPAs often show that establishment of MPAs can be expected to increase yields when populations are overfished, but they will be unlikely to boost yields if stocks are lightly fished (e.g. Mangel 1998; Sladek Nowlis & Roberts 1999; Gerber *et al.* 2003; Hart 2006). Our modelling results agree with this generalization. In scenarios in which fishing mortality was greater than that which produces maximum sustainable yield, increases in the fraction of the region in

MPAs resulted in increases in yield as long as MPAs occupied less than 50–60% of the area. Additionally, increasing MPA area had no effect on yield when harvest was close to MSY. As a consequence, our model reveals that the relationship between species richness and fisheries is positive at MPA areas considered adequate for conservation by some (20–30%; e.g. Palumbi 2002). Thus, when a system is heavily fished, there may not be a trade-off between conservation and fisheries – both may benefit by the establishment of MPAs.

Setting aside areas in no-take MPAs reduces the area that can be fished and if an area is overfished this reduction in fishing may be analytically equivalent to reducing fishing mortality using traditional means (Botsford *et al.* 2003; Hilborn *et al.* 2004). However, a reduction in the size of fishing grounds can reduce yield if management limits fishing mortality to sustainable levels (which is, of course, the aim of fisheries managers). Thus, establishment of MPAs for conservation purposes may come at the expense of fisheries yield when fisheries management



**Fig. 7.** Species richness and yield as the proportion of the coast in the MPA (numbers above points) changes from 0 to 1. Species richness is given by  $S = 16.18A^{0.226}$ ,  $u_1$  is fixed at 0.09, and the proportion of habitat that is trawlable is 0.3, 0.5, 0.7 or 0.9.

operates as it is intended. Our conclusions are based on the assumption that yield in the area remaining open to fishing does not increase to make up for losses from the closed area. The degree to which MPAs contribute to fisheries yield outside the MPA is a highly contentious topic (Kareiva 2006) and is beyond the scope of this paper. Nonetheless, our approach could be modified to accommodate more complex models that incorporate various assumptions about adult movement, larval dispersal and fishing fleet dynamics (e.g. Mangel 2000b; Botsford 2005; Hilborn *et al.* 2006). Additionally, our work does not consider the costs of transitioning from one policy system to another, or the complete set of regulatory approaches available to managers. However, work defining the trade-off horizon is a necessary first step in more complex analyses which carefully integrate socioeconomic and policy considerations with biology.

*Scientists alone can establish the objectives of their research, but society, in extending support to science, must take account of its own needs.* (Kennedy 1963 in Woolley & Peters 2009)

The US National Oceanic and Atmospheric Administration (NOAA) has been challenged to develop a regional management and conservation approach to marine natural resource management. They have adopted an 'Integrated Ecosystem Assessment' (IEA) approach to meet this mandate (Levin *et al.* 2008, 2009). IEAs synthesize and quantitatively analyse information on relevant natural and socio-economic factors, in relation to specified ecosystem management objectives. A key challenge of the IEA approach is to transparently set ecosystem-scale management objectives. However, the varied objectives society wishes to achieve from ecosystems are often at odds. Science does not hold the power to make choices between conservation and extractive objectives, but science must clearly illuminate trade-offs where they exist so that informed decisions can be made (Ludwig *et al.* 2001). Unfortunately, ecologists and fisheries scientists often have little more than a qualitative feel for the trade-offs and interactions inher-

ent in human activities such as fisheries (Daily *et al.* 1996; Christensen & Walters 2004). The approach we develop here can begin to help frame the questions to be posed and evaluate the likely consequences of different management options. Ultimately, success in this endeavour rests on our ability to link separate theory and data in a single analytical framework that can be understood by policy makers.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

### Appendix S1. Species–area relationships for marine organisms

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