

Regime, phase and paradigm shifts: making community ecology the basic science for fisheries

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Modern fishery science, which began in 1957 with Beverton and Holt, is *ca.* 50 years old. At its inception, fishery science was limited by a nineteenth century mechanistic worldview and by computational technology; thus, the relatively simple equations of population ecology became the fundamental ecological science underlying fisheries. The time has come for this to change and for community ecology to become the fundamental ecological science underlying fisheries. This point will be illustrated with two examples. First, when viewed from a community perspective, excess production must be considered in the context of biomass left for predators. We argue that this is a better measure of the effects of fisheries than spawning biomass per recruit. Second, we shall analyse a simple, but still multi-species, model for fishery management that considers the alternatives of harvest regulations, inshore marine protected areas and offshore marine protected areas. Population or community perspectives lead to very different predictions about the efficacy of reserves.

Keywords: population ecology; community ecology; marine reserves; excess production; paradigm shift

1. INTRODUCTION

The decline of the world's fisheries has been the subject of much recent attention in the media and in the scientific literature (e.g. Botsford *et al.* 1997; Pauly *et al.* 2002; Myers & Worm 2003). Historically, overfishing was viewed as declines of single species or stocks, but in recent years, there has been increasing recognition of the importance of the marine communities within which fisheries are prosecuted. We explore the different implications of viewing fishery problems from the perspective of population ecology or from the perspective of community ecology. By population ecology, we mean a view of the world that focuses on the dynamics of a single stock or species. This view may recognize interactions, but considers that the interactions are all one-way (Mangel 1988), i.e. that the wider ecosystem affects the stock, but not vice versa. By contrast, community ecology explicitly recognizes and takes account of interactions between different stocks and species. For example, the simplest models of predator–prey, competitive or mutualistic interactions are community ecology according to this definition, rather than population ecology. Shelford (1929, cited in Morin (1999)), in fact, considered that studies without community interactions were not the domain of ecology at all.

Although the importance of interspecific interactions was widely appreciated by some of the earliest fishery scientists (Smith 1994), fishery science developed very much with a focus on population ecology as we have defined it.

There are at least two reasons for this. First, as late as 1970, there was a general view by fishery scientists and managers, and by many ecologists, that communities were stable, closed, internally regulated and behaved in a more or less deterministic manner. This view was probably rooted in a nineteenth century mechanistic view of the world. Between the 1970s and the new century, however, this view changed and most fishery scientists and managers currently recognize that communities are dynamic, open, often regulated by processes external to the community, may exist in multiple alternative steady states and behave in a more or less stochastic manner. That is, communities are probabilistic and multi-causal, rather than deterministic and homeostatic (see the Appendix in Mangel *et al.* (1996) for further details and examples).

As a result of recognizing this change, there now exists a greater appreciation of the unintended effects of fishing (often called an 'ecosystem based approach to fishery management'). For example, Hughes (1994) describes a disease-induced phase shift in a Caribbean coral reef. In its simplest description, the ecosystem consisted of coral, algae, urchins and parrotfish. The urchins and parrotfish preyed on the algae, which competed with the coral. The parrotfish were overfished by the 1960s and biomass was reduced to *ca.* 20% of the unfished biomass. An epizootic then decimated the urchin population (with *ca.* 99% mortality rate). Thus, the natural catastrophe coupled with overfishing left essentially no predators to control the algae, which then overgrew the coral.

Greer (1995) describes cases in which opossum shrimp *Mysis relicata* have been added to lakes as a supplemental food source for adult trout and charr. However, the shrimp

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shared the same prey items with juvenile salmonids, and outcompeted them; this caused the collapse of a number of important fisheries for charr and salmon. Greer (1995, p. 36) notes 'Who would have predicted fish being out-competed by their own food'? It is one thing, however, to recognize the potential for unintended consequences, and quite another to devise how to do something about it.

The second issue is computational complexity. Even the simplest fishery problems are hard, may have complex non-linear behaviour, and rarely have analytical solutions. At the time of their classic work, Beverton & Holt (1957) struggled with computational and graphical issues that would be straightforward to today's undergraduates.

The single-species view continues to be developed today. For example, recent work using diffusion approximations to derive management rules (Engen *et al.* 1997, 2002; Ratner & Lande 2001) or risk analysis (McClure *et al.* 2003) relies on single-species models.

However, we have now reached a point in which computational tools allow us to move beyond single-species/population approaches. Fishery problems require us to deal with dynamically complicated worlds and a network of interactions. We shall use a mixture of general concepts and specific models to illustrate how community ecology can become the science underlying fishery management. In § 2, we explore in a general way community ecology as the fishery paradigm for the twenty-first century and then discuss (in § 3) how the concept of 'excess production', a cornerstone of management based on population ecology, changes when one views it from the perspective of community ecology. In § 4, we consider marine reserves in a community perspective, using a specific model. We close the paper by looking forward 30 years hence and asking what we will conclude from that vantage point about fishery management in the first third of the twenty-first century.

2. COMMUNITY ECOLOGY AS THE FISHERY PARADIGM FOR THE TWENTY-FIRST CENTURY: INTERACTIONS AND UNEXPECTED EFFECTS ARE THE KEY

Communities are assemblages of species in varying proportions doing different things, and have properties that are the amalgam of the properties of individual populations and interactions among populations. Indeed, it is the interactions that make communities more than the sum of their parts. Fisheries scientists who are rooted in population ecology tend to focus on the dynamics of individual fish populations. While much can be learned from this approach, the structure of communities and thus the dynamics of fish populations within communities cannot be understood by focusing only on single species. It may even be that studies of pairwise interactions (as we do here) between exploited fishes and their prey, competitors or predators may be inadequate. For instance, we might expect the removal of a predator to result in an increase of its prey, and often this occurs (Sih *et al.* 1985). However, elimination of predators may lead to decreases in prey biomass (perhaps by increasing the biomass of a competitor). Such indirect effects appear to be common in nature—about one-third of the experimental studies of predation reviewed by Sih *et al.* (1985) showed some result that could

not be predicted by studying only pairwise interactions. Fisheries typically begin by targeting higher-order predators (Pauly *et al.* 1998), and thus human exploitation of fishes could be considered a massive predator removal experiment. In common with smaller-scale ecological manipulations, the prosecution of fisheries is likely to produce changes to the community and to the target species that could not be predicted by investigating the ecology of target populations alone.

The potential unanticipated effects of species removals in concert with changes in the trophic level, species, or even phyla targeted by fisheries requires a shift to community-level thinking if we are to understand or predict effects of fishing. The almost 90% decline of predatory fishes in the Northwest Atlantic over the past century (Christensen *et al.* 2003) with the concomitant shifts in target species provide a useful case study (Steneck *et al.* 2002). Cod and other large groundfish were abundant and apparently stable, components of coastal zones throughout the Northwest Atlantic for thousands of years (Steneck 1997). Predation by these fishes upon the dominant subtidal grazer, the green sea urchin (*Strongylocentrotus droebachiensis*), reduced herbivory sufficiently to allow abundant kelp forests in coastal zones throughout the region (Steneck *et al.* 2002). Because coastal kelp forests appear to be important nursery habitats for cod and other fishes (Tupper & Boutilier 1995; Levin *et al.* 1997), the presence of large numbers of groundfish may have increased the survival of juveniles by sustaining nursery habitats. Increased fishing effort and efficiency in the mid-1900s led to rapid declines of cod abundance and size (Steneck 1997; Jackson *et al.* 2001), the expansion of sea urchin populations, and the regional demise of kelp beds (Steneck *et al.* 2002).

In the late 1980s, an urchin fishery developed in the Gulf of Maine; within a decade urchin populations crashed, and kelp forests recovered (Vavrinec 2003). Kelp is also an important juvenile habitat for crabs (*Cancer* spp.), and with the loss of fish predators, crabs have settled in large numbers to Gulf of Maine kelp beds (Steneck *et al.* 2002). These crabs are voracious predators of juvenile and adult urchins, and thus crabs now serve as an apex predator with functionally the same impact that cod and other fish predators had had in the past.

Even with drastic reductions in fishing pressure, cod populations have not recovered (Hutchings 2000, 2001). While Allee effects may be playing a role in the slow recovery of cod (Walters & Kitchell 2001), the loss of important nursery grounds, once created by the presence of cod themselves, may also be playing a role in the slow recovery of cod. In that case, the increase in the number of crabs and their indirect positive effects on kelp forests should have resulted in an increase in the quality of cod nursery habitat. However, recent increased effort in the crab fishery appears to be leading to a decline in crab numbers and kelp (Vavrinec 2003). Thus, to the extent that coastal macroalgal habitat is important to cod, the fate of the cod fishery in the Gulf of Maine may lie not only in the hands of cod fishermen, but also urchin and crab fishermen.

Fishing activities may disturb entire communities, and subsequent recovery of communities is essentially an example of secondary succession. By focusing on populations, fishery scientists may be making implicit assumptions about the mechanisms underlying succession in

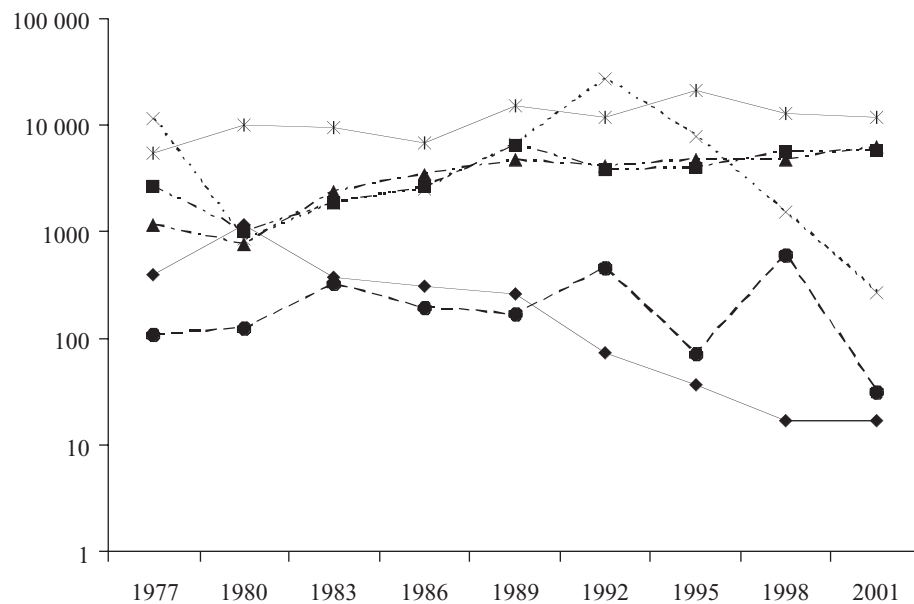


Figure 1. Indices of larval abundance of rockfish (*Sebastes* spp.) along the US Pacific Coast for the period 1977–2001. Shorter-lived rockfishes such as greenstriped (filled triangles) and splitnose have greatly increased in abundance, while longer-lived species (e.g. canary and bocaccio (filled diamonds)) have declined. This decline occurred simultaneously with a regime shift around 1977 and the passage of the Magnuson–Stevens Fishery Conservation and Management Act (which led to the development of US fleets) in 1976. (Chilipepper, filled squares; shortbelly, crosses; striptail, stars; widow, filled circles.)

marine communities. For example, after overexploitation, the foundation of models predicting the time to rebuild the stock to acceptable levels may be simple population models (i.e. Ricker or Beverton–Holt stock recruitment curves). Consequently, we are assuming that (i) the succession of the community and thus the rebuilding of its exploited constituents occurs in a predictable manner without interference from the remaining members of the disturbed community (that is, there is no hysteresis) and (ii) the inhibition model of succession (Connell & Slatyer 1977) is not applicable to fished communities. However, if inhibitory interactions in fish communities are important, they could slow or prevent recovery of overfished stocks. This situation could exist in the southern oceans, where the recovery of smaller (e.g. minke) whales may have inhibited the recovery of the great whales.

Consider a fish assemblage in which all species are good colonists and essentially equal competitors. If several species are able to invade gaps and can successfully hold the gaps against potential competitors, classic succession after fishing is not expected. Instead, the community will reflect chance colonization events by larval fishes (cf. Sale 1977). By reducing the biomass of target species, fishing could alter the composition of the larval pool, thus promoting a shift in the community species not targeted by fisheries (Kaiser & Jennings 2001). If prior residency implies great advantage in competitive interactions, individuals occupying habitat, no matter which species, are competitively dominant (e.g. Shulman *et al.* 1983); even after fishing mortality is reduced and population models predict a rapid increase in biomass, recovery cannot occur.

The composition of a number of exploited fish communities has recently shifted, with shorter-lived species becoming more prevalent. Along the Pacific coast of the US, for example, shorter-lived rockfishes (such as greenstriped and splitnose) have greatly increased in abundance, while

longer-lived species (such as canary and bocaccio) have declined (figure 1). Because smaller species of rockfish may be able to consume or outcompete recruiting juveniles of larger species, and since many rockfishes overlap greatly in their patterns of resource use, it is possible that together environmental change (something we do not control) and fishing (something we do control) have created a perturbation that has shifted the rockfish assemblage to an alternative stable state. If such an alternative stable state has been reached, even severe reductions in fishing pressure may not result in recovery of overfished larger species. Similarly, in the Northeastern Atlantic, Dulvy *et al.* (2000) showed a dramatic shift in the assemblage of skates harvested over a 40 year period. Large-bodied species with long generation times have declined, whereas smaller species have increased in abundance. Dulvy *et al.* (2000) argued that larger skates historically outcompeted smaller species for food, and that overfishing of larger species released the small skates from competition. Fogarty & Murawski (1998) also suggested that competitive release resulted in a phase-shift from teleost-dominated to elasmobranch-dominated populations in the Northwestern Atlantic.

The magnitude of disturbance that can be absorbed by a community before it shifts from one state to another (i.e. its resilience) may be affected the degree to which disturbed sites are linked to undisturbed areas (Duncan & Chapman 1999). Organisms that move among communities provide ecological memory (*sensu* Scheffer *et al.* 2001) external to the disturbed system that may rapidly restore the lost function resulting from disturbance, thus increasing the resilience of the system (Lundberg & Moberg 2003). Although the importance of material and energetic flows between distinct communities has received much recent attention by ecologists (e.g. Polis *et al.* 1997), the significance of such inputs is often overlooked in population-based fisheries assessments.

Pacific salmon fisheries in the Columbia River Basin in the northwestern US illustrate the consequences of altering links between systems. Salmon runs in the Columbia River once supported a thriving fishery, but overfishing and construction of dams led to the decline of many salmon populations; many are now listed under the US Endangered Species Act (Levin & Schiewe 2001). Because more than 95% of the body mass of salmon is accumulated while fish are in the sea (Pearcy 1992), the return of adult salmon results in a transfer of nutrients from marine to freshwater habitats. These marine-derived nutrients are now recognized to play an important role in the ecology of riparian habitats in the Pacific Northwest (Gresh *et al.* 2000); consequently, the recent dramatic reduction in salmon abundance has resulted in a nutrient deficit in spawning and rearing streams (Kline *et al.* 1990; Bilby *et al.* 1998; Wipfli *et al.* 1999). Thus, in this system, fishing not only lowers spawning biomass, it also lowers carrying capacity for juveniles (Achord *et al.* 2003). As a result of community-level changes in the rearing habitat, juvenile salmon now experience density-dependent mortality even though populations are more than 90% lower than historical levels (Achord *et al.* 2003). Recovery of these populations, therefore, does not depend solely on reduction in adult mortality, but also depends critically on changes throughout stream communities that ultimately increase carrying capacity to its previous levels.

3. EXCESS PRODUCTION IN A COMMUNITY CONTEXT

Fishery science has, at its core, the concept that we can sustainably harvest fish populations by reducing abundances below unfished biomass levels and then harvest fishes at a rate equal to the population growth rate. Classical fisheries science is thus based on the compensatory response of fish populations to reductions in density of conspecifics (Rose *et al.* 2001). Such an approach (i) ignores the potential for nonlinearities that may produce thresholds for phase shifts; (ii) implicitly assumes intraspecific interactions are more important to population dynamics than interspecific interactions; and (iii) disregards potential ecosystem-level problems of removing large quantities of fish biomass from marine communities. Each of these issues requires us to extend the traditional view of 'excess production' of fisheries population models to include a more community-level perspective.

The classical view of excess production assumes that the strength of interspecific competitive interactions is negligible compared to the magnitude of intraspecific interactions (Hilborn & Walters 1992). However, from elementary ecology we know that in even the simplest case of Lotka–Volterra two species competition, steady states in which both species persist are determined by both interspecific and intraspecific parameters. A complication arises, as we discussed above, because competitive ability may not always be a function of species identity, but could be a function of which individual arrives at a site first because of prior residency advantage (Sale 1978). Additionally, within guilds of fishes, the strength of intraspecific and interspecific competitive interactions may be similar. If this is true, then a compensatory response of a population to fishing is not solely a function of the

reduction of conspecifics, but also a function of the density of potential competitors. In this case, ignoring simple interspecific interactions will result in overestimates of compensatory ability and thus the surplus biomass available for harvest. It is quite simple to construct multi-species analogues to traditional fishery models (Hilborn & Walters 1992), and a number of multi-species approaches have been recently reviewed by Hollowed *et al.* (2000). Although such multi-species models appear to be an improvement over single-species approaches, practitioners of multi-species approaches typically focus on static and linear trophic interactions, with competitors considered only weakly or not at all.

At a larger scale, the absolute limit on the sustainable rate of harvest is determined by the rate of production of energy by primary producers. This energy is dissipated as it is assimilated into higher trophic levels. If energy removed from the global system by harvest represents a substantial proportion of the energy available from primary producers, the system is potentially unstable. Pauly & Christensen (1995) estimated that in commercially valuable regions of the oceans, the proportion of primary production necessary to sustain global fisheries was 25.1% for upwelling zones, 24.2% for tropical coastal shelves, and an extraordinary 35.3% for temperate coastal shelves. It is thus possible that we are close to the ultimate limit on sustainable harvest and no simple increase in fishing efficiency or management practice will allow a significant increase in the global exploitation of marine resources. Unlike other predators, fisheries do not recycle energy back into the ecosystem from which it was obtained. We have little understanding of the long-term effect of the transfer of huge amounts of biomass out of marine ecosystems.

What, then, is the excess production of fish populations in a community context? Zabel *et al.* (2003) proposed a shift in our thinking from maximum sustainable yield to ESY, defined as the maximum yield of fish that an ecosystem can sustain without shifting states. Other community-level metrics such as species richness, evenness or community resiliency could also be used as ESY targets. Here we come to a general ecological problem. While communities change in response to natural processes in ways that we do not fully understand, and we can never predict the behaviour of communities with absolute certainty, we can and should improve our understanding of the bounds of expected community behaviour and define ESY within the limits of their predictability.

4. MARINE RESERVES IN THE COMMUNITY PERSPECTIVE

No-take marine reserves (or marine protected areas) are gaining increasing attention as conservation and management tools. Rather than provide a comprehensive review here, we point readers to recent issues of the *Bulletin of Marine Science* 66(3), 2000 (Conover *et al.* 2000) and *Ecological Applications* 13(1(Suppl)), 2003 (Lubchenco *et al.* 2003). A summary of these is this: there is general agreement that no-take marine reserves are likely to be effective tools for conservation, but it is still not clear if they will enhance fishery catches, either in the short-term or the long-term (Mangel 1998, 2000a,b; Botsford *et al.* 2001; Lockwood *et al.* 2002).

In this section, we explore how the different perspectives (population versus community) can change the assessment of the effectiveness of a reserve. We use a specific model to illuminate the general issues. The model that we use is highly stylistic and simplified but motivated by lingcod (*Ophiodon elongates*) and bocaccio (*Sebastes paucispinis*) off the west coast of North America; the ideas will apply to systems that are considerably different (e.g. Fanshawe *et al.* 2003). For simplicity, we shall refer to the two species as predator and prey, since this is a conceptual model, not an application tool (*sensu* Mangel *et al.* 2001).

We envision a wide-ranging, omnivorous inshore species, with population biomass at the start of year t denoted by $L(t)$, that is a predator for the juveniles of a second species (population biomass of the juveniles of the prey species denoted by $\mathcal{J}(t)$). The juveniles are spawned offshore, have a pelagic phase and then move inshore for a developmental period, after which they move back offshore as adults. The biomass of adults offshore is denoted by $B(t)$. There are fisheries for adults of both species inshore and offshore, and incidental take of juveniles inshore.

We assume logistic dynamics for the inshore predator, Beverton–Holt recruitment for the offshore species, and for simplicity a discrete time formulation. The dynamics of the inshore predator are

$$L(t+1) = L(t) + r_L L(t) \left(1 - \frac{L(t)}{K_L + \gamma \mathcal{J}(t)} \right) - f(t) H_L^*. \quad (4.1)$$

In this equation, r_L is the maximum *per capita* growth rate of the predator population, K_L is the carrying capacity of the predator population determined by sources of food other than the juveniles of the second species, γ is a parameter measuring the contribution of those juveniles to carrying capacity of the predator, $f(t)$ is the fraction of MSY of the predator taken in year t and H_L^* is the MSY of that species, based solely on r_L and K_L . The relative sizes of K_L and γ determine the nature of the links between predator and prey. If γ is relatively small, then the link is one-way (Mangel 1988): the predator affects the prey but the prey has little effect on predator. If γ is larger, then the linkage is two-way.

The dynamics of the juveniles inshore are given by

$$\mathcal{J}(t+1) = \frac{\alpha B(t)}{1 + \beta B(t)}, \quad (4.2)$$

where α is the maximum juvenile production per adult at low adult population size and β is a measure of density dependence (when $B(t) = 1/\beta$, juvenile recruitment is reduced to half of its maximum value). Finally, the dynamics of the offshore stock are

$$B(t+1) = B(t) \exp(-M - F_{iA}(t) - F(t)) + \mathcal{J}(t) \exp\left(-M_{\mathcal{J}} - F_{i\mathcal{J}}(t) - \rho \frac{L(t)}{K_L}\right), \quad (4.3)$$

where M is the natural mortality, $F_{iA}(t)$ is the incidental fishing mortality, and $F(t)$ is the directed fishing mortality on the adult, offshore stock; $M_{\mathcal{J}}$ is natural mortality, $F_{i\mathcal{J}}(t)$ the incidental fishing mortality, and ρ is the intensity of predation on the juvenile inshore stock. The choice of scaling this predation intensity by the fraction of carrying

Table 1. Parameters used in the marine reserves model. (Although these parameters are intended for a stylistic model, they are chosen to match, as closely as possible, what is known about the characteristics of the motivating species (e.g. Smith 1985; Adams & Howard 1996).)

symbol	interpretation	value
r_L	maximum <i>per capita</i> growth rate of predator	0.08
K_L	carrying capacity of predator population independent of focal prey	800 Mt
γ	contribution of prey towards predator carrying capacity	0.002
α	maximum prey <i>per capita</i> reproduction at low population size	5 mt Mt ⁻¹
β	density-dependent parameter in recruitment	0.0033 Mt ⁻¹
ρ	predator mortality on juveniles when inshore	0.9
M	offshore adult mortality	0.2
$M_{\mathcal{J}}$	inshore juvenile mortality	0.5

capacity of the predator is arbitrary (that is ρ and K_L can clearly be combined into one parameter).

Were we to ignore the community aspects of this stylized system, we would work with a single species population model of the form

$$\begin{aligned} \mathcal{J}(t+1) &= \frac{\alpha B(t)}{1 + \beta B(t)} \\ B(t+1) &= B(t) \exp(-M - F_{iA}(t) - F(t)) \\ &\quad + \mathcal{J}(t) \exp(-M_{\mathcal{J}} - F_{i\mathcal{J}}(t)). \end{aligned} \quad (4.4)$$

Although the differences between equations (4.1)–(4.3) and (4.4) are slight (indeed, the only difference is that juvenile natural mortality and incidental fishing mortality are redefined), the consequences may be profound. Parameter values are shown in table 1. With these parameters, in the absence of fishing the populations stabilize at steady states of ca. 800 and 1750 mt for the predator and prey, respectively.

We will now compare predictions concerning the efficacy of marine reserves based on equations (4.1)–(4.3) (the community perspective) or equation (4.4) (the population perspective). To do this, we begin with fishing populations assumed to be at the steady state and fish the populations down to a small fraction of the unexploited biomass. We then introduce a no take marine reserve and examine the ‘predicted’ behaviour of the system using the population perspective and the ‘actual’ behaviour using the underlying community dynamics.

Over a period of 100 years, the fraction of MSY of the predator taken is 100% (so that this stock is not overfished), the incidental mortality on inshore juveniles and offshore adults of the prey are set at 0.65 and 0.05, respectively, and directed mortality on the offshore adults increases from 0 to 0.8 during a 20-year period. The consequence of this pattern of fishing (figure 2a) is a considerable decline of the prey species over the next 30 year period, to less than 10% of its pre-exploitation value. We can obtain a very good fit of equation (4.4) to the data generated by equations (4.1)–(4.3) (figure 2a).

We now embark on a rebuilding programme for the prey species, by considering three options: (i) stop all directed

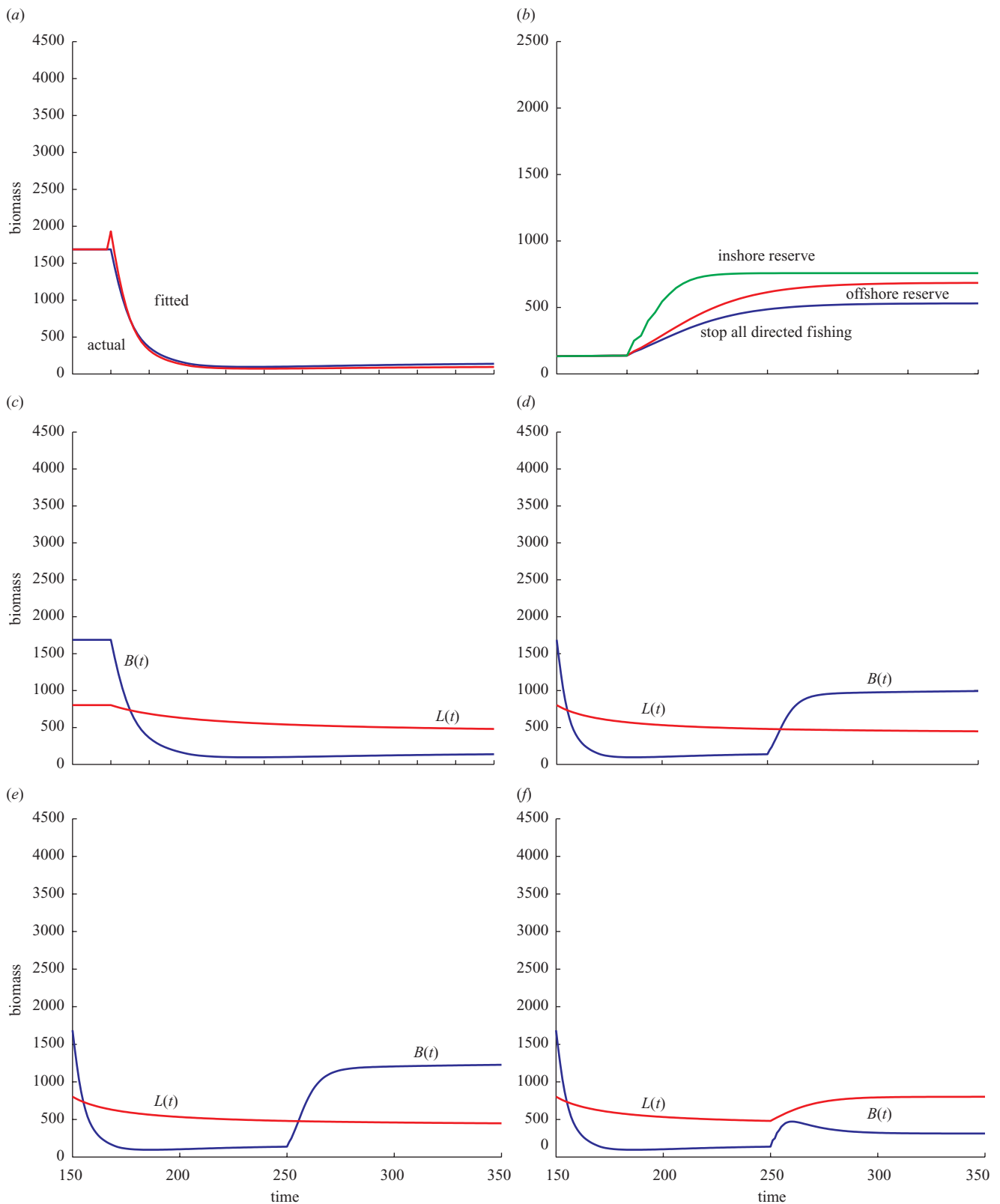


Figure 2. (a) The actual and fitted dynamics for the prey only (equation (4.4)), using the data generated by the full model (equations (4.1)–(4.3)). (b) Using equation (4.4), one predicts that the inshore reserve will be the most effective tool for recovery of the stock. (c) The actual dynamics of both prey and predator. An inshore reserve also releases the predator from fishing pressure so that either ceasing directed take (d) or an offshore reserve (e) are effective conservation tools while an inshore reserve is not (f).

fishing offshore, (ii) create an offshore reserve, or (iii) create an inshore reserve. These options have the obvious effects on the fishing mortality terms in equations (4.1)–(4.4).

Based on equation (4.4), we predict that although all three options improve the state of the stock, the inshore

reserve is predicted to be the most effective, both in terms of the speed of recovery and of the size at recovery (figure 2b).

However, equation (4.4) does not describe the actual biological dynamics. During the fishing period, both the prey species and predator decline due to fishing (figure 2c).

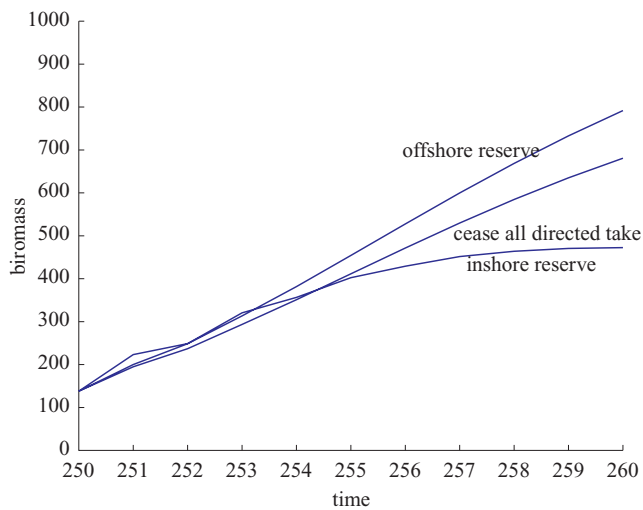


Figure 3. For the first 5 years after the creation of a reserve, the trajectory of the prey population is indistinguishable according to management action.

When the community aspects—in this case the predator population dynamics—are taken into account, quite a different story emerges. In this case, ceasing all directed fishing offshore (figure 2*d*) as well as an offshore reserve (figure 2*e*) led to recovery of the prey, with the offshore reserve being slightly more effective (because both directed and incidental mortality are eliminated). However, the inshore reserve (figure 2*f*) is predicted to be highly ineffective. The reason is clear: creating an inshore reserve both removes indirect fishing pressure on the prey species and direct fishing pressure on the predator. Note too that the trajectory of $B(t)$ in figure 2*f* shows an increase and then a decline; one might conclude that the reserve was not working. However, it was indeed working—perhaps only too well! Furthermore, within the first 5 years of the establishment of a reserve (either inshore or offshore) or ceasing of directed take, the trajectories of the prey are indistinguishable (figure 3). Process or observation uncertainty (*sensu* Hilborn & Mangel 1997) will make it even more difficult to distinguish the trajectories even 10 years afterwards. Consequently, early management evaluation of the inshore reserve may be favourable, but such positive assessments would prove incorrect as predator biomass accumulates and leads to the subsequent decline of the prey.

A full sensitivity analysis is beyond the scope of this paper, but we make one point about sensitivity. As the parameter γ increases, the prey are increasingly an important component of the predator carrying capacity (although the predator is still assumed to be omnivorous). One consequence of this is that for moderate values of γ (here greater than *ca.* 0.1), all management actions lead to trajectories similar to figure 2*f* in which the prey begins a recovery but then population size peaks and the prey begins to decline. This pattern will be unintelligible from a population perspective, but sensible from a community perspective: as the prey population recovers, the predator population follows with the consequence of higher levels of predation on the prey.

5. LOOKING BACKWARD FROM 2033: PREDICTION IS ALWAYS DIFFICULT, ESPECIALLY ABOUT THE FUTURE (Y. BERRA)

Futurists face a daunting task because a prediction can follow the arrow of time in only one direction and because the future represents only one of many sample paths. (This is more than a mathematical platitude; it means, for example, that in a management situation we can do everything right and still end up with a bad result because of stochastic effects.) Given this constraint of prediction, we shall try to look backwards from 30 years hence.

6. MOVING FROM POPULATION TO COMMUNITY ECOLOGY

While computational tools have allowed us to begin to move beyond single-species approaches, changes in computational power in the next 30 years will be awesome and will truly allow us to explore the dynamically complicated communities within which fisheries exist. The question is then: what will be done with that awesome computational power? Each of the possibilities that we now suggest already has antecedents.

(a) *BRPs will be determined in a multispecies context (Collie & Gislason 2001; Tsou & Collie 2001)*

BRPs are the benchmarks against which the current status of a fish stock is measured. Most of the common BRPs are based on a single stock/population ecology approach to management of human intervention in ecosystems. But these can, and will, be generalized to include interactions. For example, biomass needed for MSY (and MSY itself) or ‘surplus production’ will be modified to account for the needs of predators and competitors. Fishing mortality for MSY will recognize the different role that numbers of predators play in the dynamics of a prey species (Fowler & Hobbs 2002), and all reference points will recognize the potential for the short-term evolution of life-history parameters in response to natural or anthropogenic change (Mangel *et al.* 1996; Conover & Munch 2002), as has been done for many years by the Commission for the Conservation of Antarctic Marine Living Resources.

(b) *Overfishing will be defined from an ecosystem perspective (Murawski 2000)*

Population ecology leads us to describe single stocks as overfished when the biomass is less than that which would produce MSY. Thus, for example, a single stock can be sustainably overfished, if we remove only the production, but not the spawning biomass, at the overfished level.

Community ecology causes us to think about a variety of indices that could indicate the harmful effects of fishing. These include biomasses and population trajectories of a number of species, not just those that are targets for the fishery; species richness and diversity; the variability of the system and whether it exceeds a natural range; species composition and demographic parameters of target and non-target species.

Focusing on such a variety of indicators will also force us to both embrace uncertainty and avoid false precision. This may require us to forgo the hope of finely tuned management plans, opting instead for a series of indicators that can be broadly categorized. For example, Caddy (2002)

describes a 'basket' of indicators, each of one of which is associated with a yes/no question:

- (i) is total mortality in excess of the optimal mortality for the stock?
- (ii) is spawning stock biomass less than 20% of the estimated value in the unfished case?
- (iii) is fishing mortality larger than a specified multiple of natural mortality?
- (iv) is recruitment much less than average recruitment?
and
- (v) is fishing mortality more than $2/3$ of F_{MSY} (or $F_{0.1}$)?

Each answer that is 'yes' produces a 'red' traffic light. The decision rule is that five red lights lead to closure of the fishery, and 1–4 lights lead to an open fishery with decreasing levels of fishing effort (75%, 60%, 40% and 20% of F_{MSY}). What is noteworthy here is that although the standard quantitative measures are evaluated, they are used in a non-standard way. This particular traffic light approach is clearly single species/population ecology, but we predict the development of multi-species versions focused on community ecology.

(c) *Development of a theory of the metrics of community structure and fishing*

Rice (2000) reviewed a variety of metrics of community structure through which the ecosystem impacts of fisheries could be evaluated. These included diversity indices, ordination methods and correspondence analysis, number or biomass size spectra, dominance curves, and metrics that emerge out of ecological models such as the stability of food webs and mean trophic level. He concluded that none of these metrics can be endorsed without reservation and that progress in the development of a theory linking community metrics to fishing has been slow, but is essential because without a conceptual framework that provides unambiguous predictions one is unable to test hypotheses.

7. MSE

To some extent, our example is artificial in that we constructed the situation so that a single-species model would make the wrong prediction. It would be equally easy to construct a model in which the single species made the correct prediction. However, actual ecosystems are complex, with a wide range of dynamical behaviour, and the near-shore ecosystem that motivated our example has competitors and predators of both lingcod and bocaccio. Thus, in the future we expect that a wide range of models, focusing on the community and ecosystem and basically viewed as multiple working hypotheses (Hilborn & Mangel 1997) will be compared and robust management strategies sought out. One way to do this is through MSE (Smith *et al.* 1999).

In its most general use, MSE involves assessing the performance of a range of (possibly adaptive) management strategies, and evaluating the trade-offs across a range of management objectives. The approach involves explicitly testing the robustness of each strategy to a range of uncertainties. The method tests the performance of each strategy against a simulated 'real' world, called an operating model. In the case where a single-species harvest strategy is being evaluated, the operating model will include a model of the stock dynamics embedded within the community ecology and the fishery as

well as an 'observation' model that simulates the monitoring process in the fishery. The operating model will usually seek to incorporate more of the perversities of the world than are generally included in stock assessment models. The data generated by the operating model are fed into the assessment model, which in turn feeds into the harvest control rule. The allocation rules that result from applying the harvest control rule to these inputs drives the fishery management decisions for the next year, and the application of the harvest strategy continues for a specified number of years. The performance is evaluated against the outcomes in the operating model. This approach captures (albeit in a simulation) all aspects of the application of a harvest strategy (monitoring, assessment, control rule and implementation). It differs from the types of projections that are often undertaken in a stock assessment, which assume some fixed sequence of catches or fishing mortality rates into the future, but which do not capture the feedback nature of the decision-making process.

The aim here is to test the robustness of a harvest strategy that uses an assessment model (preferably at the community level) that is quite different from the representation of the actual dynamics in the operating model, which should include many more of the complexities and error sources that function in the world. The potential benefit of an MSE approach is to provide further confidence to decision-makers and the public that the strategy is a robust one. Hilborn & Walters (1992) have argued that all harvest strategies should be tested in this way; a terrestrial example is given by Milner-Gulland *et al.* (2001).

8. IMPROVING THE NATURE OF DATA UNDERLYING FISHERY MANAGEMENT

No matter how rigorous the modelling and how scrupulous the conceptual and philosophical framework underlying the models, ultimately, models are only as good as the data used to parameterize them. Inadequate monitoring and poor data accessibility are common problems in the management of endangered species, and surprisingly the same problems afflict the management of some fisheries. For example, management of Pacific salmon in the US relies heavily on coded expert opinion (Ruckelshaus *et al.* 2002). Similarly, expert opinion is relied upon when designating 'essential fish habitat' in the USA. While expert opinion is clearly a practical necessity, a problem occurs when expert opinion is substituted for real data when making a management decision, and the urgency to actually gather the data wanes after the decision is made. Expediency often dictates that we rely on expert opinion; even so, pleas for rigorous empirical data to remedy gaps in our understanding must be unrelenting.

Fisheries scientists have collected vast amounts of detailed data. In some cases, these databases have been extensively mined and have provided immense insight into the factors affecting the dynamics of fish populations. However, data without relationship to precisely formulated hypotheses, have limited use. Passive science, in which 'historical' or 'pattern' data are periodically used to parameterize models, prevents the resolution of uncertainties (Walters 1986). Well-formulated experiments with clearly stated hypotheses are more likely to bring us rapidly to an understanding of how management actions can best be applied to recover populations than alternative approaches

(Simberloff 1980). Experiments on exploited fishes are often difficult to conduct; however, management activities provide opportunities to conduct such experiments. While such management experiments may lack the elegance of basic ecology, they provide important opportunities to unravel key mechanisms underlying the patterns illuminated by monitoring activities. As fisheries science moves to the community level such experiments become even more critical. For instance, careful monitoring might reveal an inverse relationship between the abundance of two species, and it would be possible to conclude that these two species compete for limited resources. However, the same pattern could be generated if these two species share a predator (Holt & Lawton 1994), and the existence of such indirect effects would be clearly illuminated by carefully planned experiments.

In summary, Hughes (1994) described a catastrophic phase shift in the Caribbean ecosystem that was the unintended result of overfishing a target species but that affected the entire community, target and non-target species alike. At least in the North Pacific, regime shifts are now recognized as an underlying physical forcing of the biological system (Mantua *et al.* 1997; Chavez *et al.* 2003; Francis 2003). To use a somewhat tired and inexact phrase, here we call for a paradigm shift (Kuhn 1970) in which community ecology becomes the working framework for fishery science. The time is right for a Kuhnian revolution because the ingredients are there: we have an accumulated body of experience that shows the population perspective is limited and limiting and (this is crucial) we have an alternative view with the tools to make it operational. The work is just beginning.

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GLOSSARY

- BRP: biological reference point
ESY: ecologically sustainable yield
MSE: management strategy evaluation
MSY: maximum sustainable yield