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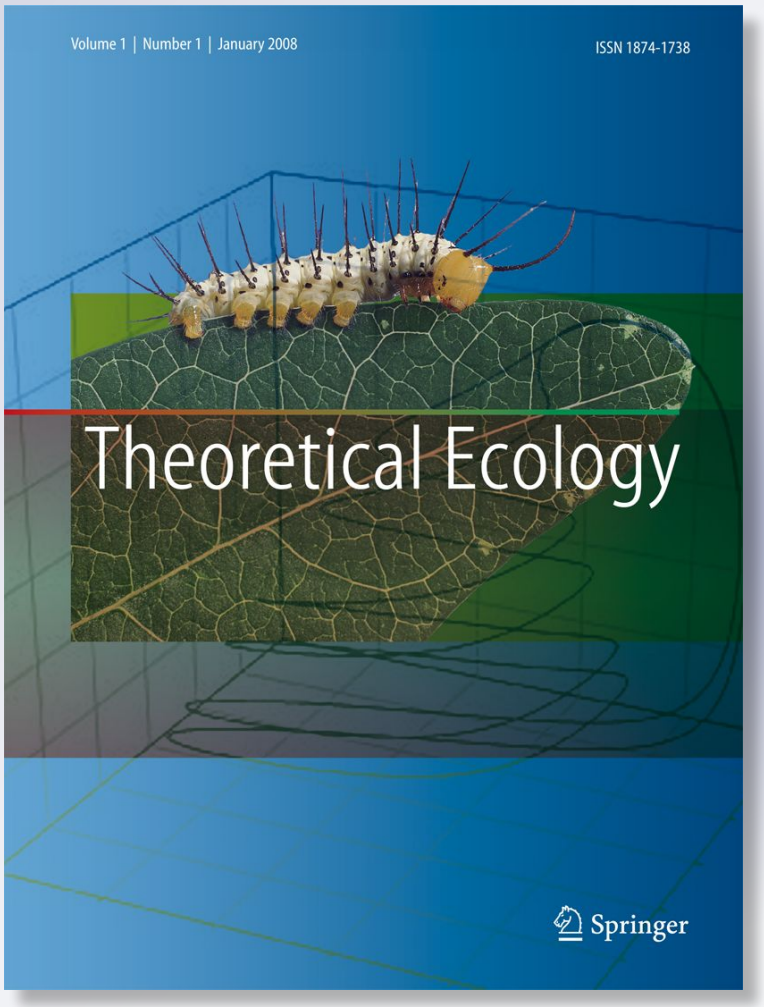

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REVIEW PAPER

Marine fisheries as ecological experiments

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Abstract There are many examples of ecological theory informing fishery management. Yet fisheries also provide tremendous opportunities to test ecological theory through large-scale, repeated, and well-documented perturbations of natural systems. Although treating fisheries as experiments presents several challenges, few comparable tests exist at the ecosystem scale. Experimental manipulations of fish populations in lakes have been widely used to develop and test ecological theory. Controlled manipulation of fish populations in open marine systems is rarely possible, but fisheries data provide a valuable substitute for such manipulations. To highlight the value of marine fisheries data, we review leading ecological theories that have been empirically tested using such data. For example, density dependence has been examined through meta-analysis of spawning stock and recruitment data to show that compensation (higher population growth) occurs commonly when populations are reduced to low levels, while depensation (the Allee effect) is rare. As populations decline, spatial changes typically involve populations contracting into high-density core habitats while abandoning less productive habitats. Fishing down predators may result in trophic cascades, possibly shifting entire ecosystems into alternate stable states, although alternate states can be maintained by both ecological processes and continued fishing pressure. Conversely, depleting low trophic level groups may affect central-place foragers, although these bottom–up effects rarely appear to impact fish—perhaps because many fish populations have been reduced to the point that they are no longer prey limited. Fisheries provide empirical tests for diversity–stability relations: catch data suggest that more diverse systems recover faster and provide more stable returns than less diverse systems. Fisheries have also provided examples of the tragedy of the commons, as well as counter-examples where common property resources have been managed successfully. We also address two barriers to use of fisheries data to answer ecological questions: differences in terminology for similar concepts and misuse of records of fishery landings (catch data) as a proxy for biomass trends.

Keywords Alternative stable states · Density dependence · Depensation · Resilience · Stability · Trophic cascades

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Introduction

Fisheries are ecosystem-scale ecological experiments. Sometimes, as with adaptive management (Walters 1986), they are explicitly recognized as such, but more often they are not (Walters 2007) and a learning opportunity is wasted. While much fisheries research has focused on single species, there has been a growing realization that fisheries management must broaden its focus from population dynamics of single species to ecological interactions among species and between species and their environment (Pikitch et al. 2004; Marasco et al. 2007). Recent calls for ecosystem-based fishery management include a mandate

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to better incorporate ecological theory into management decision making, which makes sense since fishery management can clearly be improved through better understanding of the ecology of exploited ecosystems (Mangel and Levin 2005). At the same time, fisheries can and have been used to help refine our understanding of population, community, and ecosystem dynamics (Magnuson 1991), although Larkin (1978) and Frank and Leggett (1994) lamented the limited infusion of fisheries knowledge into ecology. Since their papers, much progress has been made, but there are still untapped opportunities for ecologists to utilize data from exploited marine populations, communities, and ecosystems.

Compared with other types of human disturbance, fisheries are a highly targeted perturbation. Most methods of fishing, such as hook and line, pot and trap fishing, purse seining, and mid-water trawling, involve the removal of many individuals of a few species, with relatively little confounding impact on physical habitat. Some forms of fishing, like bottom trawling, can significantly modify habitat at a large-scale, stirring up sediments, reducing structural complexity, and releasing nutrients (Jennings and Kaiser 1998; NRC 2002). However, in comparison to terrestrial disturbances of similar scale like agriculture, urbanization, and clear-cut logging, even these fisheries are relatively selective.

Fisheries are also—for an unplanned experiment conducted by millions of people working independently—often meticulously well documented over long time periods. For example, catch and effort data are available since the 1950s from Japanese longliners fishing throughout the Atlantic, Pacific, and Indian Oceans. Stock assessments (population models applied to fishery data and used in management) typically include more than 20 years of data, and in some places (e.g., the US West Coast and Gulf of Mexico) time series of fish catches longer than 70 years are common. For many demersal ecosystems, there are long-term research surveys. In a short space of time, for example, we compiled 29 separate long-term trawl surveys from 14 different ecosystems, with results reported in Worm et al. (2009) and Branch et al. (2010).

Fished systems differ from the traditional focus of ecologists on the study of pristine systems, where the workings of nature untouched by the hand of man can be revealed. There are advantages to studying undisturbed ecosystems, of course, but for understanding dynamics, a system at steady equilibrium is a poor teacher. Even long-term observations of a population near its carrying capacity tell us little about how fast that population can grow, whether it exhibits compensatory changes in growth, survival or fecundity, and whether there is a threshold size below which the population cannot recover. There is simply too much noise and not enough signal. Furthermore, when ecologists are asked to solve real-life problems, these rarely involve pristine ecosystems; instead, they typically involve questions about the impact of humans on biological diversity (Sutherland et al. 2009) or dynamics at small population sizes. Such questions are hard to solve without large-scale experimental manipulation of the kind provided by fisheries.

Our goal here is not to polish the record of fisheries management by suggesting that there is a bright side to the collapse of fished stocks. Many fisheries have been failures by almost any measure one could choose, providing valuable lessons about how to better manage fisheries in the future (Beddington et al. 2007; Hilborn 2007). Instead of focusing on these failures, we wish to highlight recent work that has sought to learn from these mistakes about the dynamics of populations, communities and ecosystems. Thus, we hope to encourage ecologists to take a page from recession politics and "never let a crisis go to waste."

Freshwater fish populations in ponds or small lakes are more easily subjected to experimental manipulations than fish in open marine ecosystems. As a result, there is a substantial literature on ecosystem-scale studies of fish in lakes (Leavitt et al. 1989; Hecky et al. 1994; Carpenter and Kitchell 1996; Carpenter et al. 1996; Post et al. 1999) and a less pressing need to recognize and use freshwater fisheries as data sources. Long-term data from freshwater fisheries are also less common because, in many developed countries where resources for monitoring might otherwise be available, the largest freshwater fisheries are recreational. Long-term quantitative data on recreational fisheries are rare (Post et al. 2002). For these reasons, we limit our review to marine fisheries examples.

As our focus here is on empirical lessons that can be learnt from fisheries, we try to avoid studies that rely solely on theoretical models or simulations. Nevertheless, almost everything that we "know" about fisheries comes from applying some sort of mathematical model to observations of the fishery. We thus include abundance trends and species interactions derived from such empirical models. The "fisheries" we examine include the hunting of whales and other marine mammals, such as seals and sea otters, and the fishing or gathering of marine invertebrates. Heavily exploited marine ecosystems have become ubiquitous, and as such, comparisons with unfished locations (e.g., marine reserves and remote unfished sites) have taken on critical importance, forming a valuable part of our review. The topic we have chosen is, of course, exceptionally broad and our citations to the literature are necessarily incomplete with a focus on revealing hidden gems: fisheries publications that offer interesting insights relevant to the broader ecological literature. We organize our review within three main themes: population dynamics, community and ecosystem dynamics, and social–ecological systems.

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Population dynamics

Fisheries data are highly informative about the dynamics of individual fished populations. Across 267 fished populations in the RAM Legacy stock assessment database (Worm et al. 2009; Ricard et al. 2012), the median value of maximum observed mature adult biomass (spawning stock biomass (SSB)) relative to minimum SSB is 4.6 and more than 50 of these populations showed an order of magnitude range in biomass, i.e., $SSB_{max}/SSB_{min}>10$ (Fig. 1). Drastically reducing the size of a population through measured removals while simultaneously recording changes in relative abundance, is one of the best ways to learn about the original carrying capacity of the environment and the intrinsic growth rate of the population. Fisheries record exactly this information: measured removals (catches) and an index of relative abundance. Ideally, the index of abundance comes from scientific research surveys, but often it comes simply from catch divided by fishing effort (although this latter measure often fails, for reasons discussed below). Nevertheless, fisheries data have taught us a great deal about the density dependence of vital biological parameters and of habitat use.

Density dependence: evidence for compensation

Compensation occurs when individual growth and survival increase as populations are reduced to low levels. In fisheries, we can test for the presence of compensatory density dependence by examining whether survival (for example) increases when populations are fished down. Across a wide range of adult abundance, the absolute number of surviving offspring is only weakly related to the abundance of spawners, a pattern attributed to compensatory increases in juvenile survival. The most common way that compensation is examined in fisheries is through the use of "stock–recruitment" curves, which compare the relative abundance of young fish (recruitment, R) this year to the abundance of mature adults (the spawning stocks) that produced this cohort some years in the past. Studying such relationships has been a mainstay of fisheries ecology but is relatively rare in other branches of ecology (Hughes et al. 2000). Some of the jargon and conventions used by fisheries scientists obscure the fact that stock–recruit relationships are related to the intrinsic population growth rate (r). The most common fisheries measure of compensation, steepness (h), is defined as the recruitment produced by a spawning biomass at 20% of unfished levels (S_0), relative to the recruitment (R_0) produced by unfished spawning biomass (Mace and Doonan 1988), or to put it another way: how much does recruitment decline when spawning biomass is reduced by 80%? Steepness is an arbitrary metric but relates directly to r by integrating several different aspects of the reproductive biology of fish stocks (Mangel et al. 2010) and is also correlated with a variety of life-history traits (Denney et al. 2002). For the Beverton and Holt (1957) stock–recruit model:

$$R = \frac{0.8R_0\,hS}{0.2S_0(1-h)+S(h-0.2)}. \tag{1}$$

If it is assumed that S_0 is equal to the carrying capacity (K) of a logistic model, then (Quinn and Deriso 1999):

$$r = \ln\left(\frac{4h}{1-h}\right) \tag{2}$$

Meta-analysis of more than 700 stock–recruit datasets (Myers et al. 1999) shows that steepness is relatively constant within species and remarkably constrained across all populations examined. The median value of steepness, based on the Ricker (1954) stock–recruit model, across their collection of fish species is 0.67: i.e., fully 67% of the maximum recruitment is produced by 20% of the unfished spawning stock. The relative constancy of steepness within taxonomic groups has lead to the expanding use of stock–recruit meta-analysis to develop informative priors on steepness for poorly known species (Punt and Hilborn 1997; Myers et al. 2002; Dorn 2002). Use of informative empirical Bayesian priors (Myers et al. 2002) has become relatively common in fisheries stock assessment, but remains less common in ecology as a whole. One of the drawbacks of this trend is that more recent fisheries population models (stock assessments) are influenced by

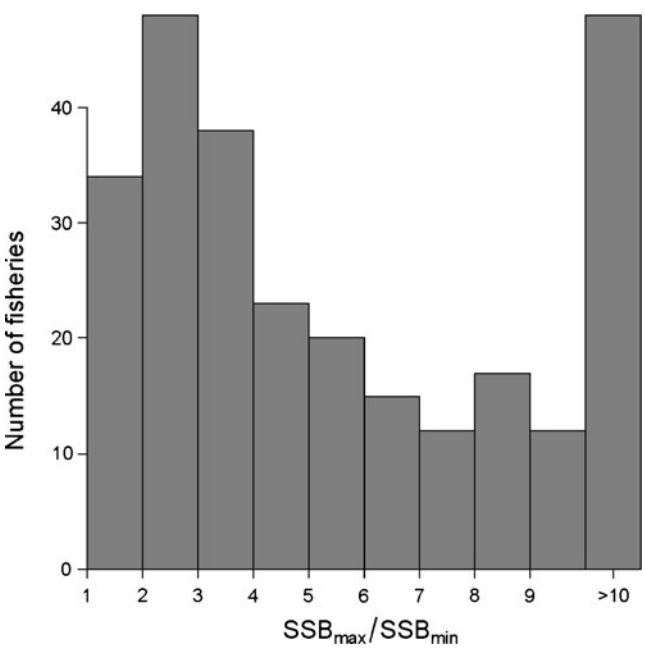

Fig. 1 Ratio of maximum spawning stock biomass (SSB_{max}) to minimum spawning stock biomass (SSB_{min}) for 267 fish stocks from the RAM Legacy stock assessment database (Ricard et al. 2012)

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such priors thus complicating their use in future meta-analyses (Minte-Vera et al. 2005).

The Beverton–Holt stock–recruit model is one of the more popular explanations for stock–recruit relationships. The main alternative is the Ricker (1954) stock–recruit model, which generally provides lower (more conservative for management purposes) steepness estimates than the Beverton–Holt model (Myers et al. 2002; Walters and Martell 2004). The Ricker model, however, predicts a dome in recruitment at intermediate spawning biomass, implicitly assuming that there will be some type of overcompensatory change in reproductive rate or juvenile survival, i.e., at high spawner abundance, the decrease in juvenile survival has more impact on recruitment than the increase in spawner abundance. The mechanisms that have been suggested for this overcompensation (cannibalism, nest site destruction, and density-dependent disease spread) are common in many salmon populations. However, empirical evidence shows that recruitment is usually high when spawners are high, and low when spawners are low (Myers and Barrowman 1996), thus overcompensation is likely rare or weak for most species other than salmon. Use of the Ricker model for estimating the slope at the origin of the stock–recruitment curve is complicated by the fact that, because of the limited flexibility of this two-parameter model, observations at high stock size can have a large impact on the estimated slope at the origin (Myers et al. 1997).

That recruitment remains remarkably constant across a wide range of spawner abundance does not mean that recruitment is never a limiting factor in population growth. Larkin (1978) wrote about the possibility of recruitment overfishing—reducing the abundance of spawners to such an extent that recruitment is reduced. With the benefit of many more years of observation at low stock size, we now know that despite high variability, recruitment in fish populations is predictably lower at low spawner abundance (Myers and Barrowman 1996). Even highly fecund broadcast-spawning mollusks show evidence of reduced recruitment (Peterson and Summerson 1992; Hobday et al. 2001). To combine their two main findings (recruitment is constant over a wide range of biomass but declines at low biomass), Barrowman and Myers (2000) proposed another stock–recruit model, termed the hockey stick model, which combines a linear relationship between spawners and recruits at low spawner levels with constant recruitment at moderate and high spawner levels. The Beverton–Holt, Ricker, and hockey stick models all make slightly different assumptions, but in practice, recruitment data are so variable that there is rarely strong empirical support for one model over another (Dorn 2002; Zhou 2007).

Reduction in spawner abundance to low levels is frequently accompanied not just by a reduction in recruitment but by an increase in recruitment variability (e.g., Hsieh et al. 2006; Minto et al. 2008; Nash et al. 2009). Anderson et al. (2008) attribute this increased variability to an increase in nonlinear behavior of fished populations at low spawner abundance, rather than to any direct effect of variable fishing mortality.

The intrinsic population growth rate (r) can also be estimated from population models applied to time series of fishery removals (catch (C)) and an index of relative abundance from surveys or biomass (B) estimates from stock assessments. One of the simplest of these models is the well-known logistic model:

$$B_{t+1} = B_t + rB_t\left(1 - \frac{B_t}{K}\right) \tag{3}$$

where the subscript t refers to time in years. Equation 3 can be fit to time series of catch and biomass from stock assessments using Schaefer's (1954) surplus production model parameterization:

$$\widehat{P}_t = \frac{4mB_t}{K} - 4m\left(\frac{B_t}{K}\right)^2 \tag{4}$$

where parameters m (maximum sustainable yield) and K are generally estimated by minimizing some function (sum of squares or the negative log likelihood) of the difference between estimated surplus production $\left(\widehat{P}_t\right)$ and "observed" surplus production (P_t):

$$P_t = B_{t+1} - B_t + C_t \tag{5}$$

The intrinsic rate of increase (r) from Eq. 3 is: r=4 m/K. Applying Eq. 4 to catch and biomass time series from 170 marine fish stocks in the RAM Legacy stock assessment database (Worm et al. 2009; Ricard et al. 2012), yields estimates of r ranging from 0.06 to 1.33 with a mean of 0.38 (Fig. 2). That is, at very low biomass, growth of fish populations ranges widely from 6% to 133%/year.

Density dependence: evidence for depensation

Compensation occurs when populations grow faster at lower densities because of decreased competition; depensation (or the Allee effect) is the opposite process, when per-capita population growth rates actually decline at low densities, and is a concern because this may result in a minimum population size below which the population will decline to extinction (Liermann and Hilborn 2001). Trivially, at extremely low population sizes, per-capita recruitment will decrease (zero spawners will produce zero recruits), but more generally, there is little evidence for widespread depensation in fishes. Myers et al. (1995) found significant depensation in only 3 out of 128 fish stocks in the Myers stock–recruit database, although only 26 of these stocks had high enough power (>0.95) to detect depensation. Similarly, Liermann and

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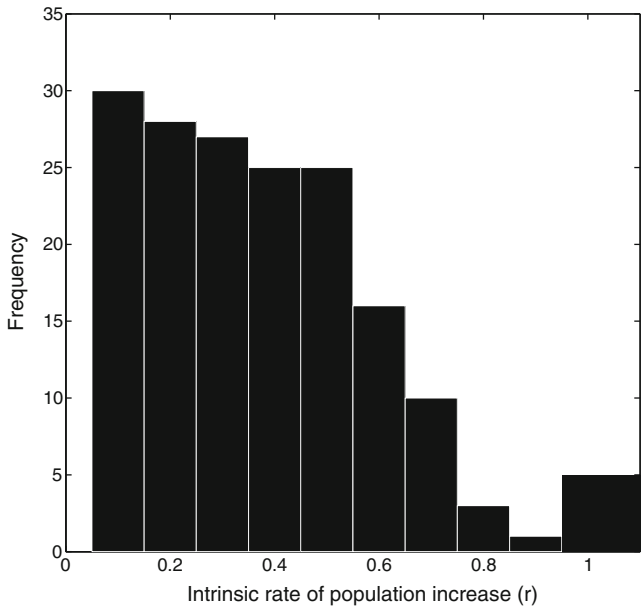

Fig. 2 Estimates of the intrinsic rate of population growth (*r*) from the logistic model for 170 fish populations from the RAM Legacy stock assessment database (Ricard et al. 2012). The *right-most bar* contains all values of >1; maximum, 1.33

Hilborn (1997) applied a hierarchical Bayesian approach to the same database, and found a broad posterior distribution for their depensation parameter, neither confirming nor ruling out the possibility of depensation for many stocks; in only one taxon (Pleuronectiformes, flatfishes) was depensation more likely than not. A broader review of population dynamics of fish (including many fisheries time series), mammals, birds, and insects found that Allee effects were "rare if present at all" (Sibly et al. 2005). Simulation models, however, caution that stock–recruit data derived from multiple sub-populations can show no evidence of depensation even when each of the sub-populations has a depensatory stock–recruit relationship (Frank and Brickman 2000), and it can often be hard to determine whether sub-populations exist except when fisheries occur on the breeding grounds. Environmental and demographic variability may also obscure evidence of depensation, particularly at the low population sizes where depensation would be seen (Liermann and Hilborn 2001).

While there is little evidence for widespread depensation from meta-analysis of stock–recruit time series, some populations, particularly Atlantic cod in Eastern Canada, have failed to recover following serious declines and a major reduction in fishing pressure. Hutchings (2000a) looked at changes over time in the biomass of spawning-age adults in 90 fish populations and found that only 8% of stocks had completely recovered after they had experienced their greatest 15-year percentage decline, with most of the fully recovered stocks being clupeids (herring and sprat). Hutchings' analysis was criticized for failing to include changes in fishing mortality as a predictor of recovery—recovery presumably cannot occur until the high fishing levels that caused the declines is reduced. Further work revealed that recovery is indeed more common when exploitation is reduced, although there was no relation between the magnitude of the reduction in fishing intensity and the probability of recovery (Hutchings 2001; Hutchings and Reynolds 2004). This lack of recovery speaks to a major debate in fisheries: is fishing pressure or the environment the main driver of population change? Empirical examination of fishery productivity across a range of populations shows that indeed, reductions in productivity preceded many population declines (Walters et al. 2008). This not to say that overfishing did not contribute to these declines, but it does explain why some fisheries fail to recover after reductions in fishing effort. In particular, an examination of nine cod stocks in the North–West Atlantic shows that four of the nine would increase in abundance if fishing mortality were sufficiently reduced, while the other five show negative surplus production (population change expected in the absence of fishing, i.e., biomass in the current year less biomass in the previous year plus the catch in the previous year) and thus would not be expected to increase even if all fishing was halted (Hilborn and Litzinger 2009). Past studies on the effects of depensation would benefit greatly from a re-examination, given recent examples of increases in abundance following reductions in fishing mortality (Mace 2004), and substantial reductions in fishing mortality in many ecosystems (Worm et al. 2009) since the early 1990s when the original Myers's database was last updated. A recent update and expansion of this database (Ricard et al. 2012) provides a foundation for revisiting questions about depensation and population recovery. Depensation can be strongly influenced, or even caused by, interspecific interactions, and dispersal and use of refugia can moderate the effects of depensatory community interactions. These processes are discussed in more detail in the section on Community and ecosystem dynamics, below.

Density dependence: influence on spatial distribution

Fisheries offer many insights into changes in spatial distribution as populations decline. Frequently, declines in fish and marine invertebrate populations result in a reduction in the area occupied by the population (Shackell et al. 2005). Observations of density-dependent range contraction in sardines and anchovies (MacCall 1976; Radovich 1976, 1982; Csirke 1980) lead to the development of the basin model of density-dependent habitat use (MacCall 1990), a variation on the ideal free distribution (Fretwell and Lucas 1970; Gillis 2003). The basin model holds that as numbers of fish decline, population distribution will contract, reducing densities in marginal habitats

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while maintaining high densities in core habitat areas. Density-dependent habitat or distributional changes have also been observed in a wide range of other fish populations reduced in abundance by fishing or environmental shifts, including Atlantic herring (Winters and Wheeler 1985) and Atlantic menhaden (Schaaf 1980), as well as invertebrates such as squid (Lange 1991) and blue crab (Jensen and Miller 2005). Studies that have looked for density dependence in habitat use for several ages or life stages of fishes (Gibson et al. 2008; Schneider et al. 1997) have often found that this effect is limited to just one or a couple stages.

The importance of density-dependent habitat changes in fisheries is that it can lead to a break-down in the critical assumption that catch-per-unit-effort (catch divided by fishing effort, or CPUE) is proportional to abundance, an assumption that is used in models of many fisheries (and populations of other organisms), discussed in more depth later in this review. A classic example is the relatively high cod catches off Newfoundland taken right up to the point of collapse, a phenomenon explained by the range of the population contracting as abundance declined (Hutchings 1996; Rose and Kulka 1999). Trawl fishermen were able to maintain high CPUE even as the population declined, because the most rapid changes in abundance occurred at the edges of the population, while fishermen concentrated on exploiting the still-dense population center. The conflict between declining scientific trawl survey indices and the CPUE from the fishery contributed to uncertainty, management inaction, and ultimately, collapse (deYoung and Rose 1993; Rose and Leggett 1991; Hutchings et al. 1997). While the collapse of northern cod was unique in its scope (annual catches of 250,000 mt worth US $115 million, Schrank 2005), the general phenomenon of range contraction accompanying population decline is widespread.

Community and ecosystem dynamics

While population dynamics has long been the de facto basic science underlying fisheries management (for better or worse, Hutchings 2000b), there is a strong movement toward greater consideration of community ecology and ecosystem processes (Pikitch et al. 2004; Mangel and Levin 2005). Fisheries data are informative about many of the theories and debates that have dominated the ecological literature, including keystone predators, trophic cascades, alternate stable states, top–down vs. bottom–up control, and the relationship between diversity and stability.

The role of keystone species and top–down effects

A classic keystone predator facilitates the coexistence of two or more interacting species by reducing the abundance of the species which would otherwise dominate (Paine 1966, 1969; Power et al. 1996). In some regions, such as the Northwest Atlantic, fisheries have had a disproportionate impact on higher trophic level species (Pauly et al. 1998; Essington et al. 2006), providing a strong test for keystone predators and, more generally, for top–down effects. Sea otters are, of course, one of the best known keystone predators, and were hunted to near extirpation by the late 1800s throughout much of their North American range. Their keystone role in controlling herbivorous sea urchins was discovered through comparison of islands where they remained absent with islands where they had started to recover (Estes and Palmisano 1974; Simenstad et al. 1978). There are few other empirical studies that explicitly use fisheries data to test for classic keystone predators; however, there have been observations of prey fish increases following declines in pelagic predators. For example, increased biomass of small pelagic species (Ward and Myers 2005) and skipjack tuna (Sibert et al. 2006) have been observed following fishery-induced declines in the abundance and mean size of yellowfin tuna and other top predators throughout the Pacific. Even though yellowfin tuna are not considered overfished, the fishery in the eastern Pacific has still reduced their predation rate on other species by 67% (Essington et al. 2002), a reminder of the large ecological impact of fisheries even when they are meeting their management goals.

Studies comparing fished and unfished coral reefs or gradients of fishing intensity provide evidence of strong top–down effects, but rarely identify a keystone predator. Fish biomass on unfished coral reefs appears to be dominated by apex predators (e.g., large jacks, groupers, and sharks), creating inverted trophic pyramids (Friedlander and DeMartini 2002; Sandin et al. 2008). Top predators on coral reefs have the greatest effect on trophic structure where they control the abundance of key grazers. It is these grazers, including sea urchins (Hughes et al. 1987; Carpenter 1988, 1990), herbivorous reef fish (Hay 1984; Hixon and Brostoff 1996; Hughes et al. 2007), and coral-eating crown-of-thorns starfish (Birkeland and Lucas 1990), rather than their predators which have been most commonly identified as keystone species on coral reefs. Gradients of fishing pressure in the Fijian Islands revealed an association between the loss of top predators and outbreaks of coral-eating crown-of-thorns starfish that decimated reef-building corals (Dulvy et al. 2004). Comparison of fished areas and marine reserves on the Great Barrier Reef show a similar link between fishing on higher trophic level species and outbreaks of crown-of-thorns starfish (Sweatman 2008). In general, the great diversity of coral reef predator assemblages combined with substantial diet overlap, makes it uncommon for a single predator species to play a keystone role, although McClanahan (2000) provides an exception.

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He compared fished and protected areas of East African coral reefs and found that a single triggerfish species played a keystone role in controlling the dominant sea urchin species. Other than this example, we conclude that fishing reveals few individual fish species that are classic keystone predators, but when top predators are considered as a group, there are many examples of cascading effects following their removal.

Trophic cascades

Trophic cascades (Hairston et al. 1960; Carpenter et al. 1985) in marine systems have been revealed through overfishing of predators and through predator recovery in marine reserves. Many of these cascades involve declines in predators that were controlling the abundance of herbivores, such as urchins or herbivorous fish, on rocky bottoms or coral reefs (Pinnegar et al. 2000). For example, a trophic cascade involving sea urchin predators (spiny lobster and a demersal fish), sea urchins, and kelp has been described by comparing fished and unfished rocky reefs in New Zealand (Babcock et al. 1999; Shears and Babcock 2002). Overfishing of predators allowed urchins to dominate to the point that they created urchin barrens nearly devoid of kelp. Although the presence of this cascade requires specific conditions of depth and wave exposure (Shears et al. 2008), it has the potential to not only change the abundance of kelp, but alter carbon flow (Salomon et al. 2008). Similar trophic cascades involving fishing of sea urchin predators have been suggested from other studies of fished and protected areas (e.g., Clemente et al. 2009). In coral reefs, where the control of benthic macroalgae is necessary to maintain the reef (Pandolfi et al. 2005), it has been argued that restoring the abundance of large predators within marine reserves can have a negative impact on grazing; however, this effect is offset if herbivores are also protected from fishing (Mumby et al. 2006).

While fishery-induced trophic cascades are more commonly reported for hard-bottom benthic food webs (Pinnegar et al. 2000), they have also been observed in pelagic food webs (Frank et al. 2005), soft-bottom continental shelf ecosystems (Myers et al. 2007), and in the open ocean (Baum and Worm 2009; Essington 2010a). Frank et al. (2005) used fishery landings and scientific survey data to demonstrate a cascading effect of the collapse of cod and other large-bodied predatory fish species on the Scotian Shelf. The collapse of cod was correlated not only with an increase in small pelagic fish, crabs, and shrimp but also a decline in large-bodied (i.e., predation sensitive) zooplankton and an increase in phytoplankton. Whether the changes observed at lower trophic levels are the result of a top–down cascade or climate shifts (Greene and Pershing 2007), remains a subject of debate. Myers et al. (2007) combined research surveys with experimental results to show that the declines of large sharks throughout the US East Coast allowed smaller elasmobranchs, especially cownose rays, to increase, and this in turn led to a massive increase in predation on bay scallops, ending the long-sustainable bay scallop fishery.

As a counterpoint to these findings, other studies have found little effect of fishing on apex predators. For example, Jennings et al. (1995) looked at patterns of fish abundance along a gradient of fishing intensity in the Seychelles. They found that while the abundance of targeted species (piscivores and invertebrate feeders) declined with higher fishing intensity, there was no apparent pattern among the unfished species. Similarly, Jennings and Polunin (1997) found little evidence of indirect effects of fishing along a gradient of fishing intensity in Fiji. Once again, declines in the abundance of targeted species showed little relationship to the diversity or biomass of their prey species. This lack of a cascading effect from fishery-induced depletion of piscivores has been observed in other studies of coral reefs (Bohnsack 1982; Russ 1985) and may be related to the high diversity and complex food web structure of these ecosystems. Thus, examples from exploited marine ecosystems provide support to the idea that trophic cascades should be particularly strong in systems with relatively simple linear food webs with low intraguild predation (Polis and Strong 1996; Borer et al. 2005). Essington (2010a) suggests that lack of spatial and temporal overlap between production and consumption may be an additional factor limiting the strength of trophic cascades in open marine systems, while model results (Andersen and Pedersen 2010) provide evidence that fishing at lower trophic levels can mask increases in productivity that would otherwise be apparent following declines in top predator abundance.

Regime shifts and multiple stable states

Phase or regime shifts and alternative stable states describe a situation in which an ecosystem abruptly shifts from one discrete state to another. A return to the original state requires more than a simple restoration of the environmental conditions that prevailed before the switch, i.e., the system exhibits hysteresis (Scheffer et al. 2001). Such regime shifts can involve ontogenetic or predator–prey role reversals; for example Barkai and McQuaid (1988) report on two adjacent islands, one of which is dominated by rock lobsters preying on whelks (*Burnupena* spp., Gastropoda), while the other is dominated by whelks which rapidly overwhelm and consume translocated rock lobsters. One example of a fishery-induced regime shift in the marine environment is the alteration in the Northwest Atlantic from an ecosystem dominated by cod to one dominated by small sharks (particularly spiny dogfish) and invertebrates

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(shrimp, crab, and lobsters) (Mayo et al. 1992; Fogarty and Murawski 1998; Worm and Myers 2003). Many have suggested that the failure of some cod stocks to recover, despite reductions in fishing mortality, is related to the increased abundance of species that eat or compete with cod juveniles (e.g., Overholtz and Tyler 1986; Murawski 1991). Under the "cultivation–depensation" hypothesis (Walters and Kitchell 2001) or the "prey-to-predator loop" (Bakun and Weeks 2006), adult cod are able to cultivate a productive environment by suppressing predators and competitors of their juveniles. When adult cod are reduced by fishing, these predators and competitors are able to increase in abundance to the point where they reduce cod recruitment, thus maintaining an alternate ecosystem state. While certainly plausible, the evidence for a cultivation–depensation effect in the Northwest Atlantic is mixed. Although some cod stocks do show depensatory stock–recruit curves that are consistent with this hypothesis (Walters and Kitchell 2001), there is little evidence to suggest that this is the result of predation by elasmobranchs (Link et al. 2002). Apparent geographic shifts in elasmobranch distributions also complicate the idea that predatory release is responsible for the rise in elasmobranch populations (Frisk et al. 2008). Another system where a cultivation–depensation effect has been proposed involves cod and sprat in the Baltic Sea (Möllmann et al. 2008; Casini et al. 2009), although continued high fishing mortality rates on Baltic Sea cod stocks suggest that low cod biomass at that time was simply being maintained by fishing (Hilborn and Litzinger 2009).

Other kinds of regime shifts involving dramatic increases in the abundance of gelatinous zooplankton (jellyfish and ctenophores) have been reported in several heavily fished ecosystems (Mills 2001), including the Northeast U.S. shelf (Link and Ford 2006), the eastern Bering Sea (Brodeur et al. 2002), the Benguela current (Lynam et al. 2006), the northern Gulf of Mexico (Graham 2001), and the Black Sea (Zaitsev and Mamaev 1997). It has been suggested that jellyfish increases could be a result of competitive release following declines in planktivorous fish (Brodeur et al. 2002) or in the Black Sea from a combination of eutrophication and reduced predation due to overfishing of jellyfish predators such as mackerel (Mills 2001; Oguz and Gilbert 2007; Daskalov et al. 2007). Once dominant in a system, gelatinous zooplankton can be important predators on fish eggs and larvae. Cowan and Houde (1993) estimated that they could consume 20–40% of bay anchovy eggs and larvae per day in Chesapeake Bay, while Lynam et al. (2005) suggested that jellyfish may limit herring recruitment in the North Sea. The Benguela Current, Namibia, offers up an interesting story. Traditionally this system was dominated by huge biomasses of sardines and anchovies, but these collapsed due to overfishing and jellyfish have proliferated to the point where they now greatly exceed the combined biomass of fish in the system (Lynam et al. 2006). Surprisingly, bearded goby thrives in this alternate state despite being the favored prey of seabirds, mammals and other fish, because they feed on jellyfish while finding refuge on the anoxic ocean floor where their predators cannot follow (Utne-Palm et al. 2010).

As with the Baltic Sea cod example, however, the proposed mechanism for the shift between fish and jellyfish is only weakly supported by data: there is little evidence that predation by fish or competition over zooplankton controls jellyfish populations (Purcell and Arai 2001), while the oft-cited Black Sea example is complicated by the fact that the currently dominant ctenophore, *Mnemiopsis leidyi*, is an exotic invader (Daskalov et al. 2007). Furthermore, climate changes and eutrophication (and not overfishing) may play a leading role both in jellyfish increases and fish declines (Brodeur et al. 2008; Oguz and Gilbert 2007; Purcell et al. 2007).

Bottom–up and middle-out effects

Fisheries operate at all levels of marine food webs, including the lower trophic levels, potentially providing evidence of bottom–up effects. One reason given for the move toward ecosystem-based management is concern that fisheries are overfishing forage fish species that are prey for many marine predators (Alder et al. 2008), thus subjecting predators to both direct fishing pressure and indirect pressure through declines in their prey. This concern is echoed by large-scale crashes and recoveries of many important forage fish stocks, including Peruvian anchoveta (the single most important species by weight in global fish landings), California sardines and anchovy, and Japanese sardine (Schwartzlose et al. 1999). Large removals of primary consumers provide unique ecosystem-level tests of bottom–up effects on apex predators. What do they tell us?

Clear bottom–up effects emerge from central-place foragers such as nesting seabirds and pinnipeds at rookeries, many of which have declined when fishing locally depleted their food resources. For example, a developing fishery for sand eels off Scotland in the 1990s depleted the sand eel population, reducing the breeding success of nesting kittiwakes (Rindorf et al. 2000). While climate shifts have also been implicated in the decline of sand eels, together with fishing, the bottom–up effect of sand eel abundance on kittiwakes appears clear (Frederiksen et al. 2004). Similarly, fishery-induced declines in sardine and anchovy populations in the Benguela upwelling off south–western Africa have been linked to declines of African

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Penguin, Cape Gannet, and Cape Cormorant (Crawford 2007). The evidence for a bottom–up effect led to reductions in total allowable catches of sardine and anchovy in South Africa to ensure that sufficient local food was present for African Penguins (Crawford 2004). Similar declines in seabirds off of Peru since the mid-1960s appear to be related to the depletion of anchoveta by the commercial fishery (Jahncke et al. 2004); there was a strong negative correlation ($r=-0.85$) between fishery landings and seabird productivity (Duffy 1983). As for nesting seabirds, pinnipeds in rookeries also feed on fish and invertebrate species targeted by commercial fisheries (Kaschner et al. 2001), and fishing of prey species has been implicated by some in the decline of Steller sea lions (reviewed by Trites and Donnelly 2003). However, the role of fishing and the quantity and quality of food in the decline of Steller sea lions is debated, and other studies have found no evidence of a fishery effect (NRC 2003; Dillingham et al. 2006). Thus central-place foragers appear to be more vulnerable to bottom–up effects arising from local depletion of prey species than wide-ranging seabirds and marine mammals, although the overrepresentation of central-place foragers in bottom–up studies may also be because they are easier to monitor.

In contrast to central-place foragers, there is surprisingly little evidence of bottom–up effects on predatory fish species, perhaps because many apex predator populations have themselves been reduced to the point that they are no longer resource limited. For example, severe reductions of herring abundance in the Georgia Strait and the West Coast of Vancouver Island during the 1960s did not measurably alter piscivore abundance (Walters et al. 2005). Similarly, Micheli (1999) found little evidence for effects of zooplankton abundance on zooplanktivores in 20 heavily fished marine ecosystems. Instead, correlations between planktivorous pelagic fishes and zooplankton were generally negative, a result interpreted as top–down control of zooplankton by fish predation. One of the few examples of empirical evidence for bottom–up effects on predatory fish is in the Barents Sea where the sequential collapse of the two dominant forage fish species, herring and capelin (Hjermann et al. 2004), appears to have contributed to declines in productivity, and eventual collapse, of cod stocks (Hamre 1994).

The general lack of clear evidence for effects on higher trophic level fish is perhaps surprising given that many marine ecosystems are thought to be "wasp-waisted" (Bakun 1996; Cury et al. 2000; Bakun 2006), where energy flow from low trophic levels to high trophic levels funnels through a small number of zooplanktivores, often small pelagic fish. However, the picture is complicated because energy flow may not be as constrained as a focus on small zooplanktivorous fish would suggest. For example, cephalopods are extremely abundant, though poorly sampled, in many continental shelf ecosystems and contribute substantially to global fish production through their role as prey for commercially harvested fish (Hunsicker et al. 2010). Larvae and juveniles of other abundant fish, such as jack mackerels (*Trachurus* spp.), may also represent an alternative pathway for energy flow from zooplankton to higher trophic levels. In some marine ecosystems a pair of dominant small pelagic fish groups, anchovies and sardines, show out of phase oscillations in abundance (Schwartzlose et al. 1999; Bakun and Broad 2003; Chavez et al. 2003). This pattern can somewhat dampen interannual variability in the total abundance of all small pelagic fishes, although large fluctuations may still be evident. In other cases, a relatively less abundant zooplanktivore may increase in abundance following a decline in the dominant species, for example sand lance increased on Georges Bank when herring collapsed in the 1970s (Sherman et al. 1981; Fogarty et al. 1991; Murawski et al. 2010). A final reason for the lessened impact of prey removal in wasp-waist systems is that many predators of small pelagic fishes, such as tunas, are highly mobile and opportunistic, and therefore less vulnerable to food limitation from local depletion of one or even a few prey species. Larkin's (1978) caution against expectations that the removal of a single predator or prey species would result in dramatic change, appears to be borne out in many cases.

The relation between diversity and stability

The ongoing debate in ecology about the relation between diversity and stability (McCann 2000; Ives and Carpenter 2007) has many parallels with recent findings in fisheries research. Worm et al. (2006) examined 12 coastal ecosystems in Europe, North America and Australia, finding that increasing species richness was associated with lower percentages of collapsed fish and invertebrate stocks. They found similar patterns in catch data from large marine ecosystems: more diverse ecosystems had higher rates of recovery for depleted species and lower interannual variability in catch (Worm et al. 2006). As with most diversity–stability relationships (Ives and Carpenter 2007), the mechanisms generating these patterns are not clear, but may be related to human behavior as well as ecology. Greater diversity in fishing opportunities may encourage the redirection of fishing effort away from depleted populations; given a choice, fishermen target stocks that are more abundant (Sethi et al. 2010). Fisheries scientists are increasingly recognizing that maintaining diversity within individual populations provides a crucial buffer against changes in the environment (e.g., Hilborn et al.

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2003a). For sockeye salmon in Bristol Bay, Alaska, stocks are at all time high levels, but interestingly, the individual populations that are currently highly productive were only minor players in previous decades. Maintaining diversity at multiple levels also enables the portfolio effect to occur, where the sum of catches and profits from many diverse individual stocks is more stable than catches and profits from each individual stock (Ruzzante et al. 2006); an effect that has been examined in ecology in the context of metapopulation dynamics (Doak et al. 1998; Tilman et al. 1998). For Bristol Bay sockeye salmon stocks, for example, the portfolio effect ensures that variability in catches is 2.2 times lower than it would be if the hundreds of diverse individual populations were replaced by a single population, reducing by tenfold the probability of fisheries closures to protect spawning salmon (Schindler et al. 2010).

Stability is also observed at the level of functional guilds within fish communities. For example, Auster and Link (2009) examined patterns in the abundance of feeding guilds from planktivores to piscivores on the northeast U.S. continental shelf and found that, despite fluctuations in the abundance of individual species, the overall abundance of 5 of the 7 guilds showed "remarkable stability." Similar results were found for a simple food web model based on biomass time series for 35 species on heavily exploited Georges Bank, where interannual variability in the entire community was substantially lower than the sum of variability over individual species (Gifford et al. 2009). Duplisea and Blanchard (2005) also found evidence from Georges Bank that competitive interactions among species within trophic guilds served to buffer variability, both natural and fishery induced. Finally, Worm et al. (2009) found that total biomass in long-term trawl surveys compiled from around the world was on average quite stable. These multiple definitions of stability are a reminder that conclusions about stability-diversity relationships can be strongly dependent on how stability is defined and measured (Ives and Carpenter 2007).

Fisheries therefore provide substantial evidence that higher diversity, both within and among species, is associated with greater stability in abundance and harvest. Remarkably, even in heavily fished systems, total consumer biomass of exploited marine ecosystems is often quite stable, although abundance of individual species can fluctuate dramatically.

Social–ecological systems

> *"Just as the whole of ecology must treat man as part of an ecosystem, so must fisheries science."* (Larkin 1978)

A narrow ecological view of fisheries would be constrained to interactions between fisheries and the aquatic environment. But this would fail to capture the important role that social systems, economics, and governments play in the failure or success of fisheries (e.g., Gelcich et al. 2010). Stable biological systems are difficult to maintain in the absence of stable and resilient social systems, and there are many lessons that can be learnt from the repeated failures (and occasional successes) in constraining fishing and maintaining healthy fisheries and ecosystems.

Tragedy of the commons

The "tragedy of the commons," coined by Hardin (1968), describes the case of common resources where each user will gain the entire benefit of using more of the resource, while only sharing the negative effects of this extra use among all users. These problems had previously been analyzed for fisheries by Gordon (1954) and Scott (1955). The tragedy of the commons results in incentives that lead each user to increase their use of the resource until it is exhausted, whereas if the users could agree to limit their exploitation, they would all benefit. In fisheries this situation is frequently observed in open-access fisheries, where there are no barriers to entry and no limits on catches, or where monitoring and enforcement is so inadequate that a de facto open-access situation arises. Each fisherman can increase income by catching more, while the costs of resource depletion are shared among all fishers. This inevitably results in ever-increasing fishing effort until the resource is depleted to the point, termed the bionomic equilibrium, where the economic rent is dissipated (i.e. profits are no more than could be obtained from alternative livelihoods). It has long been understood that greater profits could be obtained if the fishers could instead mutually agree to reduce their fishing effort and maintain fish stocks at a higher level (Gordon 1954; Scott 1955).

There are numerous examples of the depletion of open-access fisheries: Antarctic whale populations (Hilborn et al. 2003b), Atlantic bluefin tuna (Fromentin and Powers 2005), and sea urchin fisheries around the world (Berkes et al. 2006). Nevertheless, the inevitability of the tragedy of the commons in fisheries has been questioned by many authors (McCay 1978; Berkes et al. 1989; Feeny et al. 1990, 1996; Ostrom et al. 1999). They point out that most fisheries are not actually open access but are common property resources governed by a specified group of people, and in many cases are managed to maintain sustainability and reduce resource degradation. For example, Hardin does not account for the possibility that some users may be able to exclude other users, that there are institutional constraints on fishing effort, and that users can choose to cooperate with each other to improve their common interests and deter free riders. These authors argue that the solution to the tragedy of the commons

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espoused by Hardin—"mutual coercion mutually agreed upon"—is actually quite widespread.

What fisheries have taught us about the tragedy of the commons is that although there are caveats to its widespread applicability in the most dire sense (open access will lead to inevitable ruin), there are aspects of the underlying incentives (benefits accrue to individuals but costs are shared by all) that must be accounted for when designing fisheries systems. One example is given by Norway's blue whiting (*Micromesistius poutassou*) fishery within a small fishing community (Gezelius 2007). Government-set total quotas were far in excess of sustainable levels, and the fishers showed good understanding that current fishing levels would result in resource depletion. Yet, despite good communication and cooperation among fishers, there was no attempt to restrain fishing effort. Instead, each boat competed to see who could catch the most fish in the shortest possible time, in order to maximize their prestige within the community. In fact, communication and cooperation fostered rapid spread of technological innovations and sharing of current hot fishing locations, greatly improving the efficiency of the fleet while not leading to any reductions of fishing to sustainable levels. The author concludes that "in the absence of state regulation to ensure collective action, no one will reduce his effort individually." The Norwegian blue whiting fishery provides an example of the tragedy of the commons operating at an international level. The reason that total allowable catch is so high is that each of the European countries managing the shared resource has unilaterally increased quotas or removed quotas altogether. Higher catches increase benefits to each country, while the costs of lower fishery size are shared among all the countries. Therefore each individual country is unwilling to reduce catch limits and all countries suffer the consequences of overfishing.

Thus fisheries have provided numerous confirmations of the tragedy of the commons, although this pattern is not inevitable and there are also many examples of self-organization to limit exploitation of common pool resources.

Incentives in modifying human behavior

The oft-cited solution to the tragedy of the commons is sole or private ownership (Gordon 1954; Scott 1955; Hardin 1968), which manifests in fisheries in the form of individual transferable quotas, catch shares, co-operatives and other forms of dedicated access (Christy 1973; Moloney and Pearse 1979; Hilborn 2007). The idea is to limit entry and allocate a share of the total allowable catch to each participant; this right (or privilege) can be transferred or leased to others. Owners of quota therefore have an economic incentive not only to maximize short-term revenue, but also to protect the long-term value of their quota by maintaining viable fisheries. Catch data suggest that in fisheries managed under catch shares, the probability of stock collapse is dramatically lower and has decreased over time, in contrast with fisheries not managed using catch shares (Costello et al. 2008). A paired case–control analysis of a smaller number of fisheries shows that catch share fisheries also lead to reduced interannual variability in the ratio of actual catch to the target catch (Essington 2010b). This increased stability and predictability of harvest rates can have benefits of its own, for example allowing processors to more efficiently allocate resources in advance of a fishing season. However, many of the ecological benefits of catch shares are a result of instituting hard caps on the total annual catch (Bromley 2009; Melnychuk et al. 2012), with catch shares simply being one method of allocating this catch. The different forms of property rights discussed above need not be implemented from above, but in many cases arise from self-organization by resource users to limit overexploitation (Ostrom et al. 1999), such as methods of marine tenure in parts of Oceania (Johannes 1978, 2002).

Forms of private ownership do not necessarily eliminate incentives for overexploitation. When the discount rate is higher than the natural productivity of the resource, a sole owner would make more money by catching the entire resource and investing the money elsewhere, than by harvesting sustainably (Clark 1973). The oft-cited example is Antarctic blue whales, which were harvested unsustainably during the twentieth century because of their high value, resulting in their near extinction by the 1960s (Branch et al. 2004). When Clark's idea is applied to fisheries though, it turns out to be hard to find cases where private owners have liquidated their resources. Why the contradiction? When dealing with a single species, it is rarely optimal to fish the stock to extinction because the cost of catching fish rises steeply as abundance declines. In fact, calculated maximum economic yield (which incorporates costs and discount rates) is nearly always, or perhaps always, achieved at higher biomass than the maximum sustainable biological yield, even for very long-lived and unproductive species like orange roughy (*Hoplostethus atlanticus*) (Grafton et al. 2007). In this light, the Antarctic blue whale example cited by Clark is both misleading and illuminating. First, there was never any private ownership of catch shares for Antarctic blue whale quota: the quotas were pooled for all species, and the quotas were always set at levels much greater than the maximum sustainable yield, encouraging the tragedy of the commons. Second, catches of blue whales continued not because it was profitable to target them, but because the whaling industry could remain profitable while targeting other species, particularly fin whales, while catching blue whales incidentally. Whaling

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would have ceased much earlier if blue whales were the sole target species. More generally, it can be entirely rational for a private owner to over-exploit incidental species in a multispecies complex, if this maximizes overall economic yield from the system (Hilborn et al. 2004a; Branch et al. 2006), which explains the serious overexploitation and depletion of many incidental species in multispecies fisheries, such as skates and sharks (Brander 1981; Baum et al. 2003).

Challenges in treating fisheries as experiments

Fishing is rarely a designed experiment

Fisheries provide experimental results from large numbers of whole ecosystems but violate many ideals of experimental design, namely that the system should be divided into a large number of independent experimental units (replication); randomization should be used to allocate units to the untouched (control) and manipulated units; and treatments and controls should be interspersed to ensure that no environment gradients could influence the results (Hurlbert 1984). Clustering of experimental and control units is a common form of pseudoreplication, making it impossible to infer that differences between experimental units are the result of the manipulation rather than site-specific differences (Hurlbert 1984). Although large-scale fishing experiments have been proposed which would conform to these ideals, reviewed by McAllister and Peterman (1992), few have ever been implemented (Walters 2007). When viewed in the light of this kind of ideal experimental design, fisheries fall short in being able to definitively ascribe patterns to causes.

Fisheries have been conducted in so many areas that obtaining some type of replication is usually possible. Ecosystems ranging from coral reefs to muddy bottom, from intertidal nearshore fisheries to the open ocean, from freshwater to estuaries to the ocean, and from demersal to pelagic, have been extensively fished. In addition, the existence of multiple stocks of the same species can sometimes provide replication within a species, though care must be taken to ensure that the stocks represent independent populations. Fisheries therefore provide a range of ecosystems and taxonomic groups against which theory can be tested. Analysis of multiple fisheries datasets is not replication in the classic experimental design framework as substantial differences exist among populations and the ecosystems in which they are embedded. Patterns or results that persist despites such differences, however, suggest broader generality (though often at the cost of mechanistic understanding) than results from carefully controlled experiments.

In fact, fisheries provide so many examples of manipulated ecosystems (Jackson et al. 2001; Hilborn et al. 2003b) that the main problem is finding unfished control ecosystems. Even more rare are time series of data starting in the unfished state because managers typically start collecting data after fishing commences. There are a few systems that remain unfished, namely marine protected areas, remote coral reefs, and inaccessible grounds such as those around wrecks, oil rigs or where the bottom topography is too rocky to allow fishing. Whether these unfished areas can act as reasonable controls depends on the system and questions to be addressed. There are, however, many informative cases where fishing was temporarily halted. For example, in European waters, fishing was drastically reduced during both World Wars. This hiatus provided a glimpse into the capacity for fish stocks to recover (Beverton and Holt 1957; Beare et al. 2010). Similarly, the establishment of 200-nm exclusive economic zones by many coastal countries in the mid-1970s led to drastic short-term reductions in fishing effort as domestic fishing capacity built up or international fishing access agreements were negotiated. Such de facto closures have resulted in increases of 6–22% in some exploited fish populations during closures of 2 to 4 years duration (Jensen et al. 2010). In other cases, a staircase design may exist, i.e., where fishing started in separate years in a number of regions. If the observed effects on each region follow the sequence of fishery development, this provides evidence that the effects were caused by fishing (Walters et al. 1988). Finally, effects can be inferred where there is a spatial gradient of fishing intensity, even if there are few unfished controls (Jennings et al. 1995; Jennings and Polunin 1997).

Randomization of fishing "treatment" is almost never possible in reality. Fisheries operate based on economic concerns, which are driven by accessibility, value of the fish, and available technology (Sethi et al. 2010). It is rare indeed for management authorities to protect some randomly chosen areas from fishing when new fisheries start. One possible exception is New Zealand where some seamounts have been closed to fishing and remain unfished; although the distribution of fishing intensity among fished seamounts is heavily influenced by the presence of orange roughy and other valuable species (O'Driscoll and Clark 2005). Randomization is particularly rare for the distribution of marine protected areas (MPAs), which are almost never randomly selected from all potential sites. For this reason, fishing effects are better addressed using before–after comparisons in newly protected MPAs than comparisons with areas that remain fished, especially if the MPAs displace fishing effort, increasing pressure outside their boundaries (Hilborn et al. 2004b). On the other hand, if the question being asked is whether adding protected areas

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increases fishing yields, then catches from the entire region need to be examined, because there is no control system.

Fisheries rarely achieve the ideal of interspersion of fished and unfished sites to guard against environmental gradients and chance events that affect only part of the study area, leading to pseudoreplication (Hurlbert 1984). The difficulties in overcoming pseudoreplication in fisheries data are illustrated by Krkošek et al. (2007). They showed that pink salmon from 128 populations in northern British Columbia were not declining while 14 populations in southern British Columbia exposed to sea lice infestation from salmon farms were declining and concluded that sea lice mortality on juvenile pink salmon migrating out to sea past the salmon farms was the root cause of the population declines. Pseudoreplication occurs because all of their control populations were in the north, while the treatment populations were in the south. Thus Krkošek et al. (2007) could not rule out the possibility that a chance event or environmental factor affected only the southern populations and not the northern populations. However, the authors were able to strengthen their argument by making use of temporal changes in salmon farm management: in 1 year the farms were laid fallow, halting declines in those populations. Additionally, pink salmon populations to the south in Washington State did not experience any declines, showing how important it is to bolster conclusions with evidence from additional sources. Convinced of the possible harm to wild pink salmon, farm management was altered to greatly reduce sea lice numbers, and pink salmon in the affected populations rapidly rebounded to high levels. However, they rebounded in all areas, from Washington to northern British Columbia, not just the areas formerly affected by salmon farms, further complicating the picture since it is possible that the recovery was driven by environmental conditions and not changes in salmon farm management.

Catch surrogates for abundance are often misleading

The best long-term fishery datasets are time series of catches, but catches are a misleading proxy of current status and trends in abundance. For example, Worm et al. (2006) inferred biomass collapses when catches declined below 10% of the historical maximum, and then extrapolated the trend in percent collapsed to predict that all fisheries would be collapsed by 2048. This reasoning is problematic. Catches can decline for many reasons, including changes in taxonomic classification and regulations to prevent overfishing (Murawski et al. 2007; de Mutsert et al. 2008); different ways of analyzing the data and extrapolating into the future produce very different results (Hölker et al. 2007; Jaenike 2007; Branch 2008); and the same apparent trend in collapses is found when this method is applied to randomly generated catch data that is fluctuating around a constant mean (Wilberg and Miller 2007; Branch et al. 2011). When biomass data for fisheries are examined, there are far fewer collapses (although an increasing trend remains), and fisheries in some regions are projected to recover (Worm et al. 2009). Examination of trends in catch and biomass time series for the same populations (e.g., Fig. 3) suggests that catch is only rarely a reasonable proxy for biomass.

Catch data have also been used to calculate mean trophic levels in catches, to infer that fisheries first depleted high-value predatory fish, before sequentially depleting fish lower and lower in marine food webs (Pauly et al. 1998). However, in most regions where mean trophic levels declined, they did so because low trophic level fisheries expanded, not because predator catches declined; other than the Northwest Atlantic, catches of predators remained high or increased (Essington et al. 2006). Additionally, patterns of fishery development were related more closely to prices, ease of access (shallow before deep), and the size of the potential fishery, than to trophic levels (Sethi et al. 2010). Just as for the 2048 prediction, when ecosystem biomass is examined directly from ecosystem models, scientific trawl surveys and stock assessments, trends in mean trophic levels frequently diverge from patterns observed in catches (Branch et al. 2010).

To correct for the inadequacies of catch data alone, catches are commonly divided by fishing effort, e.g. the equation in Schaefer (1954), $C = qEN$ or $C/E = qN$. In other words catch (C) divided by effort (E), or CPUE, is directly related to abundance (N) by the catchability coefficient (q). The implied proportionality between CPUE and N turns out to be relatively rare. A meta-analysis of 297 CPUE time series for which independent time series of abundance were available showed that CPUE tends to be hyperstable—it declines less rapidly than abundance (Harley et al. 2001). This was true for all of the taxonomic groups examined in the analysis (cod, other gadiformes, and flatfishes). Conversely, there is evidence of hyperdepletion in catch rates for large open ocean pelagic species (sharks, billfishes, and tunas), where CPUE declined 80% within 15 years of fishery development (Myers and Worm 2003), even though early catches were too small to have produced a biomass decline of that magnitude (Sibert et al. 2006; Hampton et al. 2005). Thus, while CPUE is correlated with abundance, it needs to be standardized (Maunder and Punt 2004), and even after standardization CPUE should be treated with caution when trying to infer fishery impacts on ecosystems.

Conclusions: insights from large-scale unplanned manipulations

Insights into ecological theory have often come from small-scale, carefully controlled and replicated experi-

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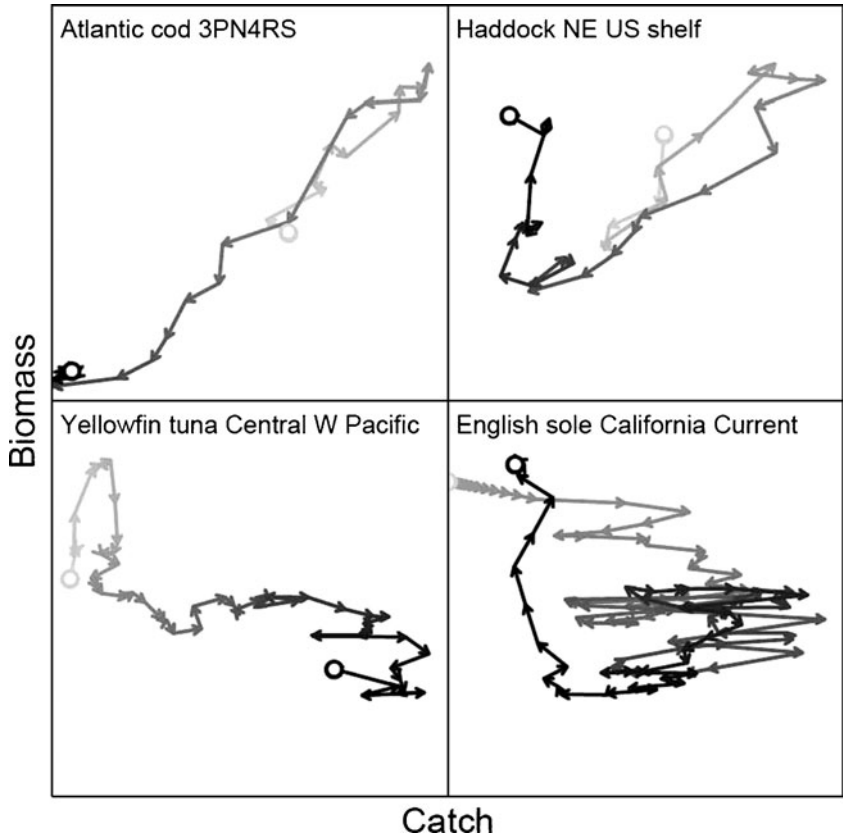

Fig. 3 Total biomass versus catch for four example fish populations: Atlantic cod in region 3PN4RS, haddock on the Northeastern US continental shelf, yellowfin tuna in the central-western Pacific Ocean, and English sole in the California Current. Time series start in *light gray* and end in *black*. Data from the RAM Legacy stock assessment database (Ricard et al. 2012)

ments that conform to the ideals of experimental design (e.g., Paine 1966; Dayton 1971). However, such experiments frequently fail to scale up to ecosystem-level effects, because they cannot mimic major processes, must exclude rare but important species, and leave out potentially important interactions among species (Carpenter et al. 1995). By simplifying the system being studied, they omit many of the most interesting effects (Mitsch and Day 2004), and limit the opportunities to observe the kind of surprising outcomes (Pine et al. 2009), incompatible with accepted theory, that lead to wholesale changes in thinking (Kuhn 1962).

Instead, fishing effects should be treated like whole-ecosystem experiments, which have gained wide favor in studies of lakes (Schindler 1998; Carpenter et al. 2001), lake–watershed interactions (Likens et al. 1970), and terrestrial systems (Krebs et al. 1995). Purposeful experiments at such scales are usually expensive, difficult to implement and cannot always be exactly replicated (Schindler 1998). However, there are many instances where whole-ecosystem experiments have been conducted inadvertently (e.g., acid rain) or to "enhance" ecosystems (e.g., introducing nonnative species), and much can be learned from the results (Schindler 1998; Bakun and Weeks 2006). Fisheries fall into this latter category of inadvertent whole-ecosystem experiments. They possess many of the interesting aspects of controlled ecosystem experiments, while also offering the advantages of replicability and low cost (at least to the scientist). Provided results can be shoehorned into conforming to aspects of experimental design, fisheries may offer many insights that are broadly applicable at the ecosystem level.

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