SPECIES DIVERSITY AND FOUNDATION SPECIES: POTENTIAL INDICATORS OF FISHERIES YIELDS AND MARINE ECOSYSTEM FUNCTIONING

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ABSTRACT

Recent calls to incorporate ecosystem-based approaches, which consider multiple physical and biological aspects of a system instead of a single stock, into fisheries management have proven challenging to implement. Here, we suggest that managers can use the diversity of species in an area and the presence of foundation species as two indicators of marine ecosystem functioning. We used data from the 2006 sablefish (*Anoplopoma fimbria*) test fishery in the inside waters of southeastern Alaska to evaluate the relationship between the diversity of fish species present in an area and the abundance of both target and total fish caught. We found that areas where more fish species were present were characterized by higher catch levels of both sablefish and total fish, suggesting that diversity may be a reasonable indicator of fishery yields and productivity. Furthermore, because the incidence of deep-water coral was also logged in the surveys, we explored the relationship between coral, which provides habitat for groundfish, and catch levels. We found that abundances were highest where coral was present. Finally, we conducted meta-analyses of the importance of marine foundation species, such as corals, kelps, seagrasses, and oyster reefs, in promoting the diversity and abundance of associated taxa and found that diversity was 1.4-fold higher and abundances were 3.4-fold higher where these habitat-forming species were present. Together, these results suggest that biodiversity and the presence of foundation species can serve as useful indicators of a marine ecosystem's ability to provide the goods, services, and functions that we and other organisms rely on. We therefore suggest that these indicators be incorporated into fisheries management strategies.

INTRODUCTION

Ecosystem-based management has been proposed as an improvement over traditional single-species approaches to resource management. Dramatic failures in single-species management, such as the collapse of the northwest Atlantic cod fishery (Walters and McGuire 1996; Myers et al. 1997), have highlighted the need for alternative approaches. The Sustainable Fisheries Act of 1996 calls for each of the major marine ecosystems in the United States to be managed using an ecosystem-based approach which considers the whole functioning system instead of individual fishery stocks (Ecosystem Principles Advisory Panel 1999). Furthermore, in response to demonstrated declines in fisheries stocks in the United States (Rosenberg et al. 2006), the Pew Oceans Commission (2003) and the U.S. Commission on Ocean Policy (2004) both indicated that ecosystem-based approaches are necessary to curb these declines. Despite this need, scientists and managers still grapple with what ecosystem-based management is and how it can be meaningfully applied.

The difficulties associated with defining and applying ecosystem-based management are compounded because the approaches contrast dramatically with traditional single-species fisheries management strategies (e.g., Ricker 1954; Beverton and Holt 1957; Pella and Tomlinson 1969). Even the more recent complex stochastic models, which use available data from fisheries catches and research surveys along with variability in year-class strength to determine the probability of future stock levels (e.g., Hilborn et al. 1994; Powers 2004), and the F_{35}% or F_{40}% harvest strategies commonly used over the last decade to manage fisheries (Clark 1991, 2002), predict only the future (fishable) abundance of single species or, at best, assemblages of closely associated species. They do not take into consideration the ecological integrity of the systems in which the fished species live (Larkin 1996).

Incorporating ecosystem principles into fisheries management therefore represents a substantial change in perspective and poses equally substantial challenges. Given these challenges, we suggest that the results of recent ecological research into the factors influencing ecosystem processes can provide some insights into indicators, such as biodiversity, of an ecosystem's ability to provide crucial goods, services, and functions. Motivated by global declines in biodiversity (Pimm et al. 1995; Vitousek et al. 1997), ecologists have been collecting an increasingly robust body of evidence regarding the ecosystem-level consequences of changing biodiversity (Loreau et al. 2001; Naeem 2002; Hooper et al. 2005). Because different organisms uniquely mediate biogeochemical

processes (e.g., nutrient cycling, carbon fluxes), it has become clear that the diversity of organisms in an ecosystem has important ramifications for how that system functions (Kinzig et al. 2002).

Whereas most of the research on the relationships between diversity and ecosystem function has been conducted in terrestrial systems (Naeem and Wright 2003; Gessner et al. 2004), recent work indicates that similar relationships can be found in marine systems (Worm et al. 2006). For example, the number and identity of seaweed species in a marine community influence rates of nitrogen uptake and primary productivity (Bruno et al. 2005; Bracken and Stachowicz 2006); the diversity of native fouling organisms inhabiting a subtidal habitat mediates the ability of invasive organisms to successfully recruit (Stachowicz et al. 2002); and the number of predator species in a kelp-forest community influences the strength of trophic cascades (Byrnes et al. 2006). In fact, a recent synthesis of evidence from marine systems supports an overall positive effect of diversity on a variety of ecosystem functions and suggests that fishery yields and resilience are higher in more diverse ecosystems (Worm et al. 2006).

In benthic marine systems, the majority of habitat complexity is provided by foundation species (sensu Dayton 1972). These species, including coral reefs (Idjadi and Edmunds 2006), seagrass beds (Orth and Heck 1980; Reed and Hovel 2006), kelp forests (Carr 1989; Estes and Duggins 1995; Graham 2004), and oyster reefs (Lenihan and Peterson 1998; Grabowski et al. 2005; Kimbro and Grosholz 2006), provide biogenic structure, thereby facilitating the diversity and abundance of associated organisms. Foundation species are often threatened by anthropogenic stressors (e.g., coral bleaching, fishing, eutrophication), and their depletion can have cascading effects throughout an ecosystem. For example, because the physical structure of oyster reefs elevates oysters and associated organisms above the oxygen-depleted bottom layer of the water column, destructive fishing by oyster dredges exposes both oysters and associated fish and invertebrates to lethal hypoxic conditions (Lenihan and Peterson 1998). In benthic marine systems foundation species can therefore serve as indicators of an ecosystem's ability to provide the goods, services, and functions on which we and other organisms rely (Lubchenco et al. 1995; Coleman and Williams 2002).

In this study, we used fishery survey data and meta-analyses to evaluate the potential utility of these concepts—the relationship between biodiversity and ecosystem function and presence/absence of foundation species—in explaining the abundance and diversity of fish and other marine species, and in exploring their contribution to ecosystem-based management. Specifically, we evaluated the relationships between the diversity of groundfish species and the abundance of both target and total fish caught in longline surveys to evaluate whether regions with higher catch diversity were characterized by higher catch abundances. We also used the same data set, which included information on the presence of deep-water corals, to examine whether a foundation species facilitated the abundance of groundfish. Finally, we conducted meta-analyses to quantify the degree to which marine foundation species enhance the abundance and diversity of associated taxa.

MATERIALS AND METHODS

Fisheries benefits of diversity and foundation species

We examined the relationships between diversity, foundation species, and fishery catches using data from the 2006 sablefish (*Anoplopoma fimbria*, Pallas, 1814) test fisheries in the inside waters of southeastern Alaska (Holum, in press; O'Connell and Vaughn, in press). Sablefish is a high-value deep-water species, with adult fish most abundant at depths of between 600 and 800 m (Stocker and Saunders 1997). This species has been commercially harvested in southeastern Alaska since the early 1900s, and catch records indicate that the fishery was well-established by 1907 (Bracken 1983).

In 1988, the Alaska Department of Fish and Game began to conduct annual sablefish stock assessment surveys in two areas of southeastern Alaska's inside waters, Chatham Strait (also known as the Northern Southeast Inside [NSEI] Area) and Clarence Strait and Dixon Entrance (also known as the Southern Southeast Inside [SSEI] Area) (Bracken et al. 1997; fig. 1). Commercial longline gear has been used to survey these populations, and the gear has been standardized to the same specifications used by NOAA Fisheries to survey sablefish in the offshore waters of the Gulf of Alaska (C. Brylinsky, ADF&G, pers. comm.).

Each set of conventional benthic longline gear consisted of 25 skates of 45 #13/0 Mustad circle hooks. The vessel crew attached new hooks to all skates prior to each set as needed to replace missing hooks. The bait consisted of 100–200 g squid (Argentina *Illex* spp.). The head and tentacles were discarded, and the remainder was cut into 4–5 cm pieces and placed on the hooks at a rate of approximately 5.7 kg per 100 hooks. The gear was set on stations previously determined by random selection within the known habitat range of adult sablefish in the survey areas. The gear was deployed by commercial fishing vessels under contract to the Alaska Department of Fish and Game. Multiple vessels were contracted to ensure that all stations within an area could be fished within a seven-day period. Sets were made at 44 stations in the NSEI Area and 38 stations in the SSEI Area.

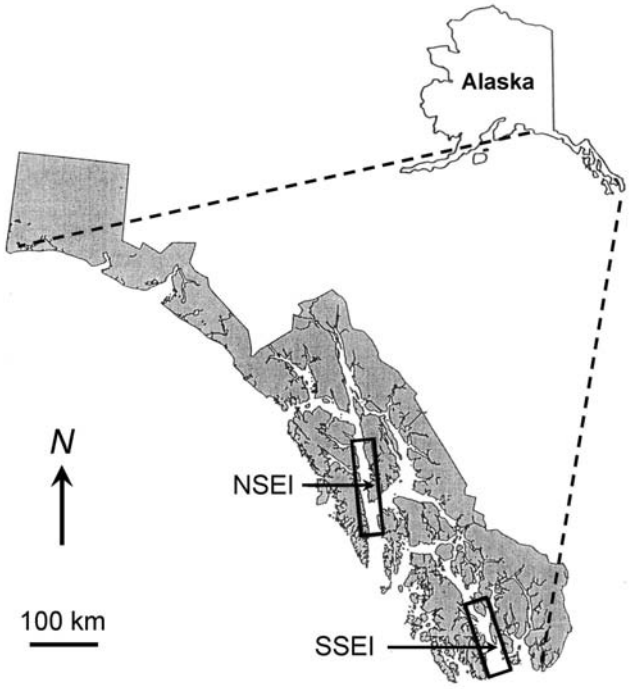

Figure 1. Sablefish (*Anoplopoma fimbria*) test fishery areas in southeastern Alaska. Data are from the 2006 surveys of 44 stations in the Northern Southeast Inside (NSEI) and 38 stations in the Southern Southeast Inside (SSEI) Areas.

For each set, the number of deployed hooks was recorded, and we used this number as a covariate in all analyses. As each set was brought onboard, the number of sablefish and a variety of other groundfish and bycatch species (including Pacific cod, dover sole, flounders, halibut, sharks, skates, and thornyhead rockfish) were recorded. Because these longlines run along the substratum, they occasionally snagged pieces of deep-water corals, which were subsequently brought onboard. In the SSEI survey, researchers logged the occurrence of corals in each set, and we used this as an indicator of biogenic habitat.

Based on these data, we used general linear models to examine the relationships between the number of fish species caught on a particular set and the abundance of both the target species (sablefish) and all fish species together, after accounting for the number of hooks deployed and regional differences (NSEI versus SSEI). We did not include an intercept in our models, because when species richness is zero, catch must, by definition, be zero. However, including the y-intercepts did not change the results, as the intercepts were indistinguishable from zero ($t < 0.13$, $P > 0.898$). Additionally, we compared abundances of both sablefish and total fish caught on sets where coral was present and absent to evaluate the potential role that deep-water corals play as foundation species that provide essential habitat for groundfish species.

In correlative studies like this one, it is difficult to determine whether diversity drives abundance or vice versa. For example, diversity could be positively related to abundance simply because higher catches are characterized by an increased probability of sampling rare species (Sanders 1968). Based on the observed diversity and abundance of species at each sampling station, we calculated diversity-abundance curves based on 1,000 iterations of a rarefaction algorithm (Gotelli and Entsminger 2001). We then used those curves to interpolate the diversity at each station to the minimum catch (15 individuals) recorded in any longline set.

Effects of marine foundation species on diversity and abundance

While many independent studies have demonstrated important effects of individual foundation species on the diversity and abundance of associated taxa in various marine habitats, no studies to date have synthetically and quantitatively evaluated the effects of foundation species across all marine systems. We therefore used meta-analytical techniques to synthesize the existing evidence for foundation species' roles in enhancing the diversity and abundance of other marine organisms.

Studies for this analysis were selected by examining the abstracts of all papers returned from searches on ISI Web of Science and Aquatic Sciences and Fisheries Abstracts databases for terms such as "ecosystem engineer," "foundation species," and "biogenic habitat." We searched those papers and the literature cited therein for observational or experimental comparisons of either diversity or abundance of taxa where habitat-forming species were present (or at high abundances) or absent (or at low abundances). Based on these criteria, we identified 30 separate studies conducted in marine systems (there were often multiple studies within a given paper) which quantified the effect of foundation species on abundances and 41 separate studies which quantified effects on diversity (see Appendix A for a complete list of studies). Where possible, we used species richness as the metric of diversity. Where richness data were not available, we used the Shannon-Wiener diversity index. Our data set allowed us to quantify the collective effects of a variety of marine foundation species, including bivalves, corals, hydroids, kelps, seagrasses, seaweeds, snails, tubeworms, and tunicates.

We used the log response ratio as our effect-size metric. This metric is one of the most widely used effect metrics in ecological meta-analyses (Hedges et al. 1999; Shurin et al. 2002; Borer et al. 2006). Unlike Hedge's "d" (another commonly used metric), the log response ratio does not require a measure of sample variability, which was important because many studies did not report variances. Furthermore, the log ratio is easily

interpretable (it represents the proportional change in the response variable), it shows the least bias of the meta-analysis metrics, and its sampling distribution is approximately normal (Hedges et al. 1999).

We calculated our effect sizes for abundance (E_A) and diversity (E_D) as follows:

$$E_A = \ln\left(\frac{A_1}{A_0}\right) \quad (1)$$

where A_1 was the abundance of organisms where the foundation species was present and A_0 was the abundance where it was absent, and

$$E_D = \ln\left(\frac{D_1}{D_0}\right) \quad (2)$$

where D_1 was the diversity of organisms where the foundation species was present and D_0 was the diversity where it was absent. Thus, effect-size metrics greater than zero indicate positive effects on abundance or diversity and metrics less than zero indicate negative effects. We averaged the effect sizes for each study to calculate the grand mean effects of foundation species (±95% confidence intervals) on abundance and diversity. We also separately analyzed the effects of producers and consumers as foundation species. Note that not all effects of ecosystem engineers are positive. Many habitat-forming species shade out or otherwise negatively affect other species (Bégin et al. 2004; Eriksson et al. 2006; Riesewitz et al. 2006), and our average effects take into consideration both positive and negative effects of foundation species.

RESULTS

Fisheries benefits of diversity and foundation species

When we used catch data from sablefish test fisheries to evaluate relationships between the number of fish species caught on a longline set and the abundances of both sablefish and total fish, and after accounting for regional differences and the number of hooks on a set, we found that the catch of both sablefish ($F_{1,78}$ = 3.9, P = 0.051) and all species together ($F_{1,78}$ = 16.5, P < 0.001) was higher in sets where more groundfish species were caught (fig. 2). Eliminating an obvious outlier, the set in the SSEI survey where only 15 individuals (all sablefish) were caught, did not affect this result. On average, each unit increase in groundfish species richness was associated with an additional 11.5 ± 5.8 (mean ± s.e.) sablefish and 29.5 ± 7.3 total fish caught.

When we used a rarefaction algorithm (Gotelli and Entsminger 2001) to interpolate the number of species caught in each set to the minimum number of individuals (n = 15) caught in any set and after adjusting for differences in catch levels at each location, we found a similar relationship between diversity and both total catch ($F_{1,81}$ = 314.0, P < 0.001) and sablefish catch ($F_{1,81}$ = 204.1, P < 0.001) to the one we describe above, but only when the diversity-catch function was forced through the origin. After including an intercept variable in the model and accounting for regional differences and the number of hooks on a set, there was no relationship between the number of fish species caught and the catch of either sablefish ($F_{1,78}$ = 3.0, P = 0.087) or all species together ($F_{1,78}$ = 1.9, P = 0.169). We were therefore unable to completely rule out the possibility that sites with higher catch rates are likely to have more species, simply due to the increased probability of sampling rare species.

In the SSEI test fishery we used the record of coral pieces caught on the longline sets to assess the potential for deep-water corals to serve as foundation species, enhancing the catch of both sablefish and total fish because corals provide structural complexity on the seafloor. After accounting for the number of hooks, we found that sablefish ($F_{1,35}$= 7.65, P = 0.009) and total fish ($F_{1,35}$ = 5.77, P = 0.022) catches were higher on sets where corals

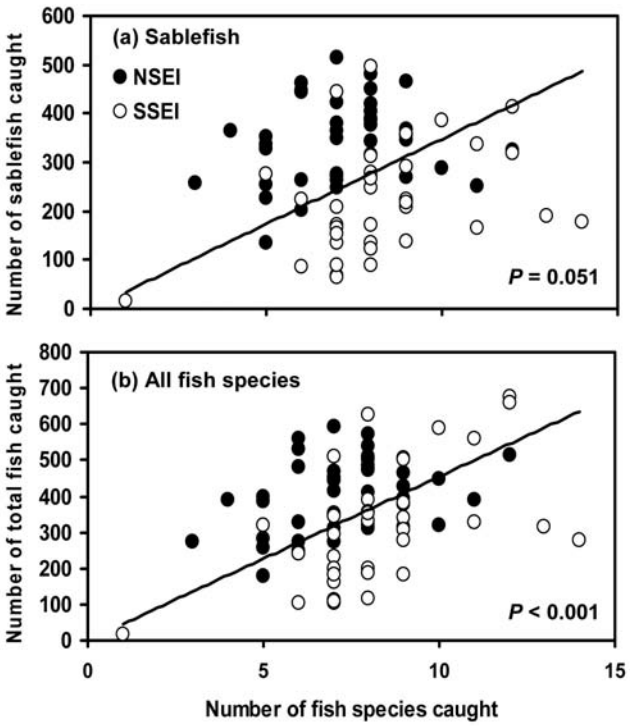

Figure 2. The number of both target and non-target fish caught in a longline set increased with the number of fish species caught. Data are from longline surveys conducted in 2006 in the Northern Southeast Inside (NSEI) and Southern Southeast Inside (SSEI) sablefish (*Anoplopoma fimbria*) test fisheries in Alaska. After accounting for regional differences and the number of hooks on each longline, catch of both (A) sablefish and (B) all species pooled was higher in sets where more fish species were caught ($F_{1,78}$ = 3.9, P = 0.051 and $F_{1,78}$ = 16.5, P < 0.001, respectively).

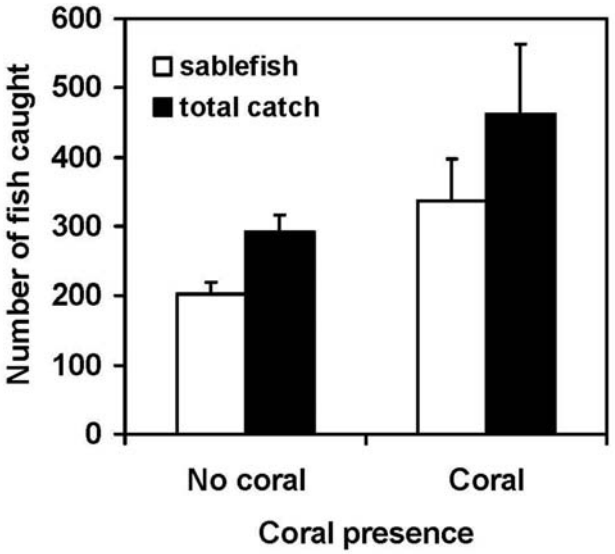

Figure 3. The number of both target and non-target fish caught in a longline set was higher where deep-water corals were present. Data are from longline surveys conducted in 2006 in the Southern Southeast Inside sablefish (*Anoplopoma fimbria*) test fishery in Alaska. Values are means ± standard errors. After accounting for the number of hooks on a given set, catches of both sablefish and total fish were higher ($F_{1,35}$ = 7.65; P = 0.009 and $F_{1,35}$ = 5.77, P = 0.022, respectively, after log-transformation) where coral was present.

were snagged and brought to the surface (fig. 3). The presence of corals was associated with a 67% higher catch of sablefish and a 58% higher total catch.

Effects of marine foundation species on diversity and abundance

When we used meta-analyses to compare diversity and abundance of organisms in marine ecosystem, when the habitat-forming species, including corals, kelps, oysters, and seagrasses, were present (or at relatively high abundances) and when they were absent (or at relatively low abundances), we found that both abundance (t = 4.33, df = 29, P < 0.001) and diversity (t = 2.59, df = 40, P = 0.013) of associated organisms, particularly invertebrates and fishes, were enhanced (fig. 4a). These analyses (i.e., after back-calculating from the log response ratios) indicated that species' abundances were 3.1-fold higher, and their diversity was 1.4-fold higher when foundation species were present compared to when they were not.

When the roles of consumers and producers as foundation species were analyzed separately, we found similar positive effects of consumers (e.g., bivalves, corals, and tubeworms) on the diversity (t = 3.29, df = 12, P = 0.006) and abundance (t = 5.257, df = 16, P < 0.001) of associated taxa. Species abundances were 2.6-fold higher, and diversity was 1.7-fold higher where heterotrophic foundation species were present (fig. 4b). Producers (e.g., seaweeds and seagrasses) were associated

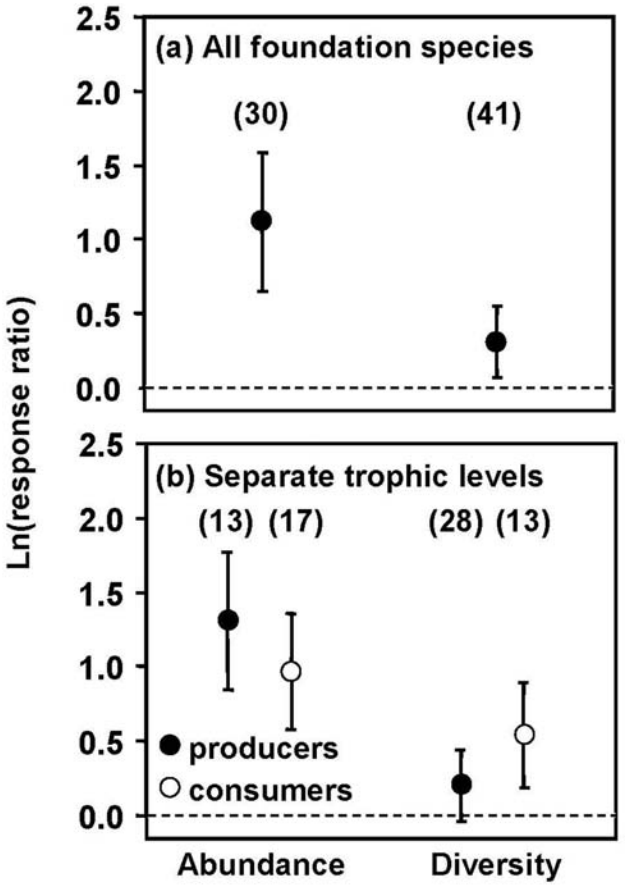

Figure 4. Abundance and diversity of marine organisms are higher in the presence of foundation species. Data are from meta-analyses of studies describing the enhanced abundance and diversity of organisms associated with foundation species. Mean log-response ratios (foundation species present versus absent) ± 95% confidence intervals are shown for (A) all foundation species together and (B) producers and consumers analyzed separately. Sample sizes for each log-response ratio are shown in parentheses. Overall, foundation species were associated with a 3.1-fold increase in species abundance (t = 4.33, df = 29, P < 0.001) and a 1.4-fold increase in diversity (t = 2.59, df = 40, P = 0.013).

with a 3.7-fold increase in the abundance of associated taxa (t = 2.789, df = 12, P = 0.016) but had no consistent effect on diversity (t = 1.308, df = 27, P = 0.202) (fig. 4b). Thus, whereas the effects of producers and consumers on associated taxa were fairly comparable for both abundance (t = 0.749, df = 28, P = 0.460) and diversity (t = 1.319, df = 39, P = 0.195), producers had a slightly greater positive effect on abundance, and consumers had a slightly greater (and statistically significant) effect on diversity.

DISCUSSION

Based on fishery survey data from southeastern Alaska, we found that the abundances of both target and total fish caught at a site were higher at locations where more fish species were present (fig. 2) and where deep-water corals were snagged in the gear (fig. 3). These data

suggest that the diversity of organisms in an ecosystem and the presence of foundation species can have important ramifications for the goods, services, and functions provided by that system. We therefore propose that marine biodiversity and presence of foundation species can serve as potential indicators of fisheries productivity and should be incorporated into fisheries management strategies. Below, we discuss the potential use of biodiversity and foundation species as indicators of marine ecosystem functioning and their consequent usefulness for ecosystem-based management.

Fisheries benefits of marine biodiversity

Our work supports other recent findings on the importance of marine biodiversity to fisheries. Worm et al. (2006) examined fisheries catches at the scale of large marine ecosystems and found that fisheries in species-rich systems (>500 species) collapse less rapidly than those in species-poor systems (<500 species). Furthermore, both catches and rates of recovery after collapse were higher for fisheries in more diverse large marine ecosystems. Together with our data from the southeastern Alaska sablefish test fishery, these results suggest that the link between species diversity and fishery yields may be a general phenomenon.

Many studies have demonstrated mechanistic links between the diversity of organisms and the rates of ecosystem processes in a system (Loreau et al. 2001; Hooper et al. 2005), and it is tempting to suggest that similar mechanisms (e.g., partitioning of resources such as food or available habitat) may be operating here. However, the relationship between diversity and functioning is reciprocal; diversity both influences and is influenced by the rates of key biogeochemical processes (Naeem 2002). Especially given the correlative nature of our data and the fact that we were not able to definitively rule out the potential effect of abundance on diversity using rarefaction, we cannot demonstrate a causal effect of diversity on the number of fish caught, highlighting the need for experiments to evaluate the mechanisms underlying this relationship. Nevertheless, the fact that more fish were caught in areas where more fish species were present suggests that diversity can, at the very least, be used as an indicator of an area's potential for higher fisheries yields. Conversely, a decrease in diversity could be an indicator of ecosystem stress.

Roles of foundation species in marine ecosystems

Both our analysis of the role that foundation species play in mediating the abundance and diversity of marine organisms (fig. 4) and the enhanced groundfish catches we observed in areas where deep-water corals were found, suggest that more attention needs to be paid to the potential fisheries benefits of habitat-providing organisms and other positive species interactions in marine ecosystems (Bertness and Leonard 1997). Whereas our data relating sablefish and total catch to coral presence are correlative, they indicate that where corals were definitively present—we cannot know for sure that corals were absent at locations where they were not brought onboard—catches were higher, indicating that either the presence of corals or the habitat associated with them (i.e., corals only grow on rocky substrata) was more suitable for groundfish. Seagrass beds and kelp forests are known to be crucial nursery habitats for many commercially important species (Orth and Heck 1980; Carr 1989; Graham 2004), and both scientific (fig. 4) and anecdotal (see below) evidence suggests that both the diversity and abundance of fish is higher where foundation species are present.

When we considered the foundation-species effects of producers (e.g., seaweeds and seagrasses) and consumers (e.g., bivalves, tubeworms, and corals) separately, we found no differences in the effects of producers and consumers on either abundance or diversity (fig. 4b). However, producers did not have a consistent positive effect on the diversity of associated taxa, largely due to occasional negative effects of canopy-forming seaweeds on both understory algae and fish. This result highlights the fact that organisms can have both positive and negative effects on associated taxa. Furthermore, the relative importance of positive versus negative interactions is likely to vary with environmental and ecological context (e.g., Bertness et al. 1999).

Furthermore, fishing activities can have direct impacts on the abundances of foundation species. For example, the spine canopy of sea urchins provides physical structure for invertebrates, including juvenile abalone (Rogers-Bennett and Pearse 2001), and this biogenic habitat is lost when urchins are fished. Prior to the collapse of the Pacific Ocean perch (*Sebastes alutus*) stocks in the Gulf of Alaska, commercial fishermen knew that *S. alutus* were more abundant in areas where deep-water corals were present. However, it was difficult to trawl those areas because the gear became fouled on the corals. A heavy cable was therefore connected to two boats and dragged across the bottom, eliminating the corals before the area was trawled to capture the rockfish (anonymous fisherman, pers. comm.). The destruction of foundation species by fishing, especially trawling, has been likened to the clear-cutting of forests (Watling and Norse 1998). Clearly, the absence of foundation species has negative impacts on both marine biodiversity and fishery productivity, suggesting that the importance of foundation species and the essential fish habitat they provide should be incorporated into ecosystem-based management strategies (National Marine Fisheries Service 1997).

Ecosystem-based management

While more work is necessary to evaluate the generality of our findings, we suggest that biodiversity and foundation species can be used as metrics of a system's productivity, functioning, and potential fisheries yields. One of the most difficult aspects of managing functioning ecosystems is the fact that conventional indicators of ecosystem change, such as production rates, cannot be used as indicators of a system's ability to provide goods, services, and functions, because once these processes are altered, the system has often been irreversibly changed (Schindler 1990). Instead, more sensitive indicators, such as species diversity and (especially in marine systems) the presence of foundation species, can serve as useful indicators of a system's functioning.

Diversity data, in particular, are easily obtainable from the test fishery and catch data that serve as the basis for many current marine fisheries management decisions (e.g., Holum, in press; O'Connell and Vaughn, in press). Given that diversity is a metric that can be quantified in space and time, biodiversity can then be managed for, giving fisheries managers and research biologists a tool for implementing ecosystem-based management plans. Fisheries biologists are also beginning to pay more attention to the habitat requirements of species (Mangel et al. 2006), though many of these efforts have focused on the physical structure provided by rocky reefs (e.g., Johnson 2006; Love et al. 2006; O'Connell et al. 2007). Because of the importance of foundation species in promoting the diversity and abundance of associated organisms (fig. 4), including many commercially targeted species (e.g., fig. 3), we suggest that surveys of both living and non-living habitat be used to predict the ability of a system to sustain abundant and diverse fish stocks.

We suggest that these sorts of indicators of ecosystem functioning, with clear ramifications for fisheries productivity, can play a major role in management strategies, such as fisheries ecosystem plans (Field et al. 2001), that consider entire ecosystems instead of separate stocks. Our work and the analysis of large marine ecosystem fisheries data by Worm et al. (2006) suggest that managers need to explicitly consider the diversity and abundance of both fished and unfished species. Furthermore, because foundation species provide essential habitat for fish, the habitat they provide needs to be considered in management plans, as mandated by the Sustainable Fisheries Act (National Marine Fisheries Service 1997).

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APPENDIX A
Studies Used in the Meta-Analyses

Study	Foundation species	Common name	Response taxa	Response (A = abundance, D = diversity)	Citation
1	*Mytilus edulis*	mussel	invertebrates	A	1
2-3	*Lessonia trabeculata, Macrocystis integrifolia*	kelps	fishes	A, D	2
4-7	*Agarum cribrosum, Alaria esculenta, Desmarestia viridis, Ptilota serrata*	kelps and other seaweeds	invertebrates	D	3
8	*Zostera marina*	seagrass	fishes	A	4
9-10	*Macrocystis pyrifera*	kelp	fishes	A, D	5
11-12	*Cladophora columbiana*	seaweed	invertebrates	A, D	6
13-16	*Halecium* spp., *Hydrallmania falcata, Nemertesia* spp., *Sertularella* spp., *Sertularia cupressina*	hydroids	invertebrates	A, D	7
17-18	*Macrocystis pyrifera*	kelp	fishes	A, D	8
19	*Pyura praeputialis*	tunicate	all taxa	D	9
20-21	*Carpophyllum flexuosum*	seaweed	fishes	A, D	10
22-23	*Musculista senhousia*	mussel	invertebrates	A, D	11
24-28	*Fucus vesiculosis*	seaweed	seaweeds	A, D	12
29-30	*Ecklonia radiata*	kelp	invertebrates	D	13
31	*Crassostrea virginica*	oyster	invertebrates	A	14
32	*Macrocystis pyrifera*	kelp	all taxa	D	15
33	*Centrostephanotus coronatus*	urchin	fish	A	16
34-35	*Laminaria hyperborea*	kelp	all taxa	A, D	17
36-37	*Agaricea agaricites, Montastraea annularis, Porites astreoides*	corals	invertebrates	A, D	18
38	*Ostreola conchaphila*	oyster	invertebrates	D	19
39-40	*Austrovenus stuchburyi*	cockle	invertebrates	A, D	20
41-42	*Zostera marina*	seagrass	fishes	A, D	21
43-44	*Zostera marina*	seagrass	invertebrates	A, D	22
45-47	*Agarum cribrosum, Laminaria* spp.	kelps	fish	D	23
48-51	*Chaetopterus variopedatus, Macreoclymene zonalis*	tubeworms	invertebrates	A, D	24
52-55	*Cystophora torulosa, Hormosira banksii*	seaweeds	all taxa	D	25
56	*Mytilus californianus*	mussel	all taxa	D	26
57-58	*Laminaria hyperborea*	kelp	invertebrates	A, D	27
59-62	*Ecklonia radiata*	kelp	fishes	A, D	28
63-66	*Modiolus modiolus*	mussel	infauna	A, D	29
67-69	*Batillaria attramentaria*	snail	various taxa	A	30
70-71	*Lanice conchilega*	tubeworm	invertebrates	A, D	31

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