Fishing catch shares in the face of global change: a framework for integrating cumulative impacts and single species management

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Abstract: Any fishery management scheme, such as individual fishing quotas (IFQs) or marine protected areas, should be designed to be robust to potential shifts in the biophysical system. Here we couple possible catch scenarios under an IFQ scheme with ocean acidification impacts on shelled benthos and plankton, using an Atlantis ecosystem model for the US West Coast. IFQ harvest scenarios alone, in most cases, did not have strong impacts on the food web, beyond the direct effects on harvested species. However, when we added the impacts of ocean acidification, the abundance of commercially important groundfish such as English sole (*Pleuronectes vetulus*), arrowtooth flounder (*Atheresthes stomias*), and yellowtail rockfish (*Sebastes flavidus*) declined up to 20%–80%, owing to the loss of shelled prey items from their diet. English sole exhibited a 10-fold decline in potential catch and economic yield when confronted with strong acidification impacts on shelled benthos. Therefore, it seems prudent to complement IFQs with careful consideration of potential global change effects such as acidification. Our analysis provides an example of how new ecosystem modeling tools that evaluate cumulative impacts can be integrated with established management reference points and decision mechanisms.

Résumé : Tous les schémas d'aménagement de la pêche, tels que les quotas individuels de pêche (IFQ) et les zones de protection marine, devraient être planifiés de manière à demeurer robustes face à des variations potentielles dans le système biophysique. Nous associons ici des scénarios de capture possibles dans un projet d'IFQ à des impacts de l'acidification de l'océan sur le benthos à coquilles et le plancton, à l'aide d'un modèle d'écosystème Atlantis pour la côte ouest des É.-U. Dans la plupart des cas, les scénarios de récolte IFQ par eux-mêmes n'ont pas d'impact important sur le réseau alimentaire, au-delà des effets directs sur les espèces récoltées. Cependant, lorsqu'on ajoute les impacts de l'acidification de l'océan, l'abondance de poissons de fond d'importance commerciale, tels que la sole anglaise (*Pleuronectes vetulus*), la plie à grande bouche (*Atherestes stomias*) et le sébaste à queue jaune (*Sebastes flavidus*), décroît de jusqu'à 20–80 % à cause de la perte des proies à coquilles dans leur régime alimentaire. La sole anglaise connaît une réduction de dix fois dans la capture potentielle et le rendement économique en présence de forts impacts de l'acidification sur le benthos à coquilles. C'est pourquoi, il paraît prudent améliorer les IFQ en portant une attention particulière aux effets potentiels du changement climatique, tels que l'acidification. Notre analyse est un exemple illustrant comment les nouveaux outils de modélisation des écosystèmes qui évaluent les impacts cumulatifs peuvent être intégrés aux points de référence de gestion établis et aux mécanismes décisionnels.

[Traduit par la Rédaction]

Introduction

The social, economic, and political context for fisheries management and conservation is daunting, involving overcapacity of fishing fleets, perverse economic incentives, lack of international governance, and rising seafood demand (Hilborn et al. 2004; Pauly et al. 2005; Branch et al. 2006*a*). In many ways, these problems have been more vexing than the complicated underlying biological processes such as recruitment (i.e., the production of juveniles), dispersal of larvae, and annual or decadal shifts in ocean condition (Chavez et al. 1999; Hare and Mantua 2000; Kinlan and Gaines 2003). Fishery management tools that seek to address these problems include marine protected areas (Halpern and Warner 2002), payments to fishers in exchange for exiting the fishery (Holland et al. 1999), international fishery treaties (Levesque 2008), and seafood eco-labeling (Potts and Haward 2007), in addition to more traditional approaches such as caps on catch, landings, and effort. Catch shares, or individual fishing quotas (IFQs), have been implemented in

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some jurisdictions as a promising method to address many of the core problems related to fisher behavior, incentives, and governance (US Commission on Ocean Policy 2004; Costello et al. 2008; Heal and Schlenker 2008). IFQs allocate individual fishers a set portion or share of the total catch. Frequently these catch shares can be traded between vessels, similar to cap and trade systems for atmospheric pollution. Increased flexibility and certainty under catch shares should improve profitability and reduce overcapitalization (Branch et al. 2006*a*). A guaranteed long-term stake in the resource can also align fisher incentives towards more sustainable fishing practices and conservation-oriented management decision, such as lower quotas (Branch 2009).

While catch share schemes show promise as management tools, they still must effectively account for the realities of the biophysical system. Cumulative impacts such as climate change, ocean acidification, and habitat degradation threaten the productivity of marine systems beyond the fishing impacts mitigated by catch shares. Climate change and ocean acidification are separate but related phenomena, both driven by anthropogenic release of CO_2, and are among the most pressing concerns. Scenarios for fossil fuel emissions suggest an increase in CO_2 levels from the current 385 ppmv (718 mg/m^3 at 14.5 °C) to at least 750 ppmv (1398 mg/m^3 at 14.5 °C) (IPCC 2001) and possibly higher than 1000 ppmv (1865 mg/m^3 at 14.5 °C) by the year 2100 (Royal Society 2005). In the oceans this is likely to lead to 1.8–4 °C increases in sea surface temperature and declines in pH of 0.14–0.35 (IPCC 2007) or as extreme as 0.3–0.5 (Caldeira and Wickett 2005), from a current level of ~ pH 8.1. Reductions in pH of this magnitude could lead to mortality of shell-forming corals, benthos, and plankton groups, owing to reduced calcification rates in an acidic ocean (Fabry et al. 2008; Hall-Spencer et al. 2008). Shifts in temperature and subsequent alterations to climate may lead to shifts in the distribution and foraging of vertebrates and reduced reproductive success (Bograd et al. 2009). Thus we suggest that any fisheries policy, including IFQs, should be considered in light of scenarios for global change. In a departure from what is familiar to fisheries managers, the biological implications of ocean acidification or rising temperatures could in the future become more important than social and economic effects.

Here we present a case study of the US West Coast, where the Pacific Fishery Management Council recently began the implementation of an IFQ program for the groundfish trawl fleet. For this particular fishery, a combination of IFQs and expansion of on-board observer coverage is expected to increase individual accountability and to reduce bycatch and discard rates, but IFQs will not radically change the fishing mortality rates on most target species. Beginning in 1983, the Fishery Management Council imposed increasingly strict per-vessel landings limits, and in 1994 the Council dramatically reduced open-access entry to the fishery. In 2000, the Secretary of Commerce declared the West Coast a federal fishery disaster, and since then, mandatory rebuilding plans have severely limited catches on over nine species (Field 2004). Thus, compared with cases where IFQs are imposed on previously unregulated fisheries, we expect the impacts of IFQs on West Coast groundfish to be more subtle, and more focused on bycatch species or previously lightly-exploited target species.

This US West Coast trawl fishery primarily targets benthic species that derive a substantial portion of their diet from shelled organisms, which may show the greatest declines under future ocean acidification. The fleet targets species such as Dover sole (*Microstomus pacificus*), English sole (*Pleuronectes vetulus*), sablefish (*Anopoploma fimbria*), rockfish (*Sebastes* spp.), and thornyhead (*Sebastolobus* spp.). Shelled organisms such as bivalves, snails, sea urchins, sea stars, brittle stars, and euphausiids compose up to 35% of the diets of some flatfish and rockfish groups (Buckley et al. 1999). Loss of these diet items may cause declines in biomass and landings of target species, separate from what would be expected under simple assumptions about harvest under IFQs.

In this exploration, we couple possible catch scenarios under an IFQ fishery with ocean acidification impacts, using an Atlantis ecosystem model for the US West Coast (Brand et al. 2007; Kaplan and Levin 2009). The ecosystem model includes the full food web, oceanography, and fisheries. Our intent is to evaluate the impact of IFQs and acidification on the ecosystem, but also to illustrate an overall approach that links tools like Atlantis to the established system of single-species reference points that underlie current management and conservation decisions. Specifically, we evaluate (*i*) the direct effects of fishing under IFQs, (*ii*) whether the performance of IFQ scenarios varies in the face of ocean acidification and subsequent declines in benthic and planktonic prey species, and (*iii*) the indirect effects, primarily through predator–prey linkages, that result from fishing under IFQs and from ocean acidification.

We present the results using biological reference points and decision tables (Hilborn and Walters 1992) that are familiar to fisheries managers, but which are informed by a full consideration of the cumulative impacts of fishing, trophic effects, and ocean acidification. Our analyses demonstrate the importance of building global change projections into natural resource management plans, and the pitfalls that face policy makers who focus only on the direct human impact (fishing) rather than cumulative anthropogenic impacts.

Materials and methods

Harvest scenarios and rationale

We developed four scenarios for future catch (landings + discards) that reflect likely fisher behavior under the new incentives and flexibility expected with IFQs for the US West Coast groundfish trawl fleet. The catch scenarios and the analyses supporting them (see supplementary data,[3] Appendix S1) derive from an accepted model used by fishery decision makers on the US West Coast (PFMC 2003). The scenarios reflect the possibility that the incentives created through IFQs may lead fishermen to improve their ability to avoid overfished rockfish species that have very low quotas, thereby allowing the vessels to catch higher amounts of target species. Overfished species include canary rockfish (*Sebastes pinniger*), yelloweye rockfish (*S. ruberrimus*),

[3] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca)

darkblotched rockfish (*S. crameri*), Pacific ocean perch (*S. alutus*), bocaccio rockfish (*S. paucispinis*), and cowcod (*S. levis*). Target species with the potential for higher catches include arrowtooth flounder (*Atheresthes stomias*), Dover sole (*Microstomus pacificus*), shortspine (*Sebastolobus alascanus*) and longspine thornyheads (*S. altivelis*), slope rockfish, chilipepper rockfish (*Sebastes goodei*), yellowtail rockfish (*S. flavidus*), lingcod (*Ophiodon elongatus*), and various flatfish species that make up the "other flatfish" complex.

We consider four catch scenarios. In the Status Quo scenario, catches per species and area occur based on the assumption that regulations in the future are the same as those set between 2003 and 2006. Catches of target and bycatch species under this scenario are roughly the same as those that occurred from 2003 to 2006. In Scenario 1 (Low Catch scenario), fishermen have only minimal success at avoiding overfished species, and therefore can only minimally increase catches of target species compared with the Status Quo scenario. Bycatch rates (kilograms overfished rockfish bycatch/kilograms target species) are assumed to be 55% of Status Quo. In Scenario 2 (Medium Catch scenario), fishermen have moderate success at avoiding catch of overfished species, and therefore can increase catch of some target species. Bycatch rates are assumed to be 30% of Status Quo. In Scenario 3 (High Catch scenario), fishermen are highly successful at avoiding overfished species, and therefore can substantially increase catch of target species. Bycatch rates are assumed to be 15% of Status Quo.

Note that in all scenarios, total catches of overfished species (e.g., canary rockfish) remain constant or increase slightly even though the bycatch rate may decline; the catch of target species is the main driver that we explore here. Catch of several flatfish species varies more than other stocks because their catches are currently well below allowable levels, and therefore can be harvested in much higher quantities than are harvested currently. Catches of many other stocks, such as sablefish and spiny dogfish (*Squalus acanthias*), are already near allowable levels specified by the Pacific Fishery Management Council, are constrained to a greater degree by encounters of overfished stocks, or have limited markets and are therefore not actively pursued.

We do not simulate the full management response to changes in fish abundance; instead we use simple constant catch scenarios. Simulating the full management response would involve modeling a harvest control rule, and the appropriate lags in implementation and monitoring. The Pacific Fishery Management Council's current threshold control rule specifies a fixed fishing mortality rate when biomass is above 40% of unfished levels, and proportional decreases in this rate as biomass falls from 40% to 10% of unfished levels (PFMC and NMFS 2009). Most species are assessed every 2–4 years, with lags of approximately one year for monitoring and policy implementation. Although we do not simulate the management process, Fulton et al. (2007) have used Atlantis to do so in Australia, and ultimately our approach here could be extended to include this in a management strategy evaluation framework (MSE; Sainsbury et al. 2000).

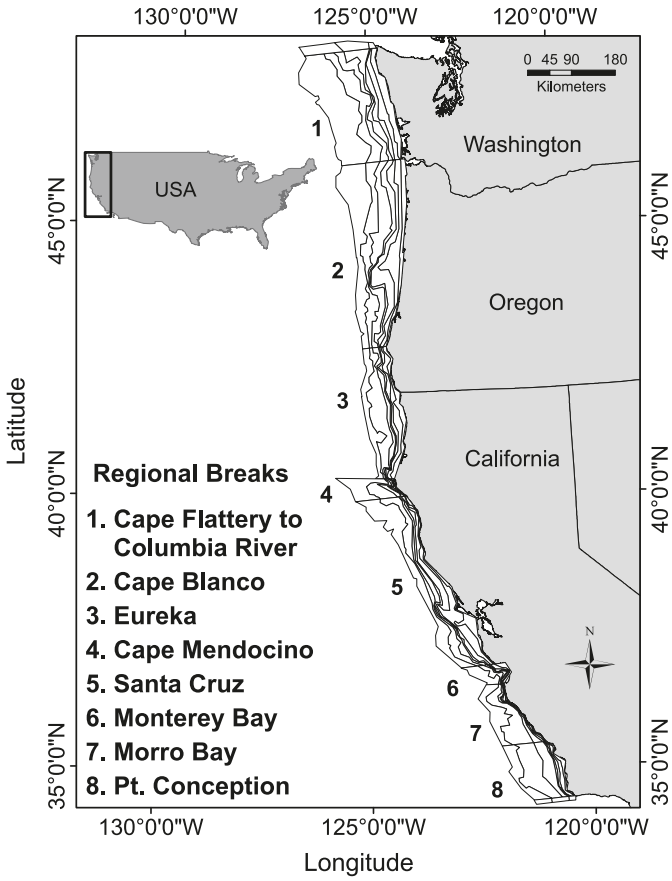
The Atlantis ecosystem model for the California Current

The Atlantis ecosystem model for the California Current (Brand et al. 2007; Kaplan and Levin 2009) is built to address the impacts of climate, oceanography, nutrient dynamics, and spatially explicit fishing effort on a dynamic food web. The generic Atlantis code is well developed at this time, and Fulton (2001; 2004) and Fulton et al. (2005; 2007) have parameterized it for several systems in Australia. Most recently, Fulton et al. (2007) have used the southeastern Australia model to rank alternative policy scenarios, quantitatively evaluating alternative management packages of quotas, protected areas, closed seasons, and other policy options.

Atlantis is a flexible modeling framework that includes many options for modeling ecology, oceanography, fisheries, and management. Key ecological options and assumptions in the present application and in most other Atlantis models built to date include density dependent movement, with predators moving toward areas with higher food availability; forced migrations into and out of the model domain (e.g., for highly migratory species such as whales); reproduction based on standard Beverton Holt stock recruitment relationships (for fish) and fixed offspring/adult (for mammals and birds); predation governed by a modified Holling Type II functional response with gape limitation, allowing predator diets to vary in relation to prey availability and prey length relative to the predator's length; and dynamic weight-at-age, meaning that realized consumption rates throughout the modeled time period translate into variable weight-at-age of each cohort. Primary production is influenced by temperature, light, and nutrient availability, with nutrients and plankton advected by current fields. Though many options for these ecological processes are available within the Atlantis code base, analyses by Fulton (2001; 2004) and Fulton et al. (2003; 2004) have supported the appropriateness of these particular representations, in particular for the functional response, physiological detail, and typical levels of aggregation for functional groups and spatial cells.

Our California Current Atlantis model extends from the US–Canada border to Point Conception, California, and out to the 1200 m isobath (Fig. 1). The trophic dynamics are represented by 55 functional groups in the food web (see supplementary data,[3] Appendix S2, Tables S2.1–S2.2). Functional groups are typically composed of pools of 1–10 species with similar ecological roles. General classes of functional groups include habitat-forming species like kelp, corals, and sponges, as well as vertebrate consumers, benthic invertebrates, zooplankton, phytoplankton, and detritus. Vertebrate populations have age structure, and Atlantis explicitly tracks weight-at-age. The model is divided into 62 spatial zones, each with up to seven depth layers. Although we do not address these questions here, the spatial structure of the model allows us to explicitly test hypotheses regarding fish migrations and movement behavior, fleet dynamics, and spatial management. The model is forced with daily hydrodynamic flows, salinity, and temperature outputs from a high-resolution three-dimensional Regional Ocean Modeling System (www.myroms.org), implemented by E. Curchitser and K. Hedstrom (Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, New Jersey, USA, personal communication, 2009), and recently

Fig. 1. Spatial extent of the Atlantis ecosystem model for the California Current Atlantis. The region includes 62 spatial boxes ranging from the coastline to 2400 m.



applied by Hermann et al. (2009). A separate sub-module simulates simplified effort dynamics for fisheries. The full parameterization for the California Current is available in Brand et al. (2007).

Initial conditions for the model (e.g., biomass or numbers-at-age, and spatial distributions) represent approximately 1995–2005, and are taken from sources detailed in Brand et al. (2007). Briefly, for biological groups these sources include a 1998–2003 continental shelf and slope trawl survey for most fish species (e.g., Keller et al. 2006), published stock assessments for commercially harvested fish species, population assessments of mammals and birds, and in the absence of other information, mass-balance estimates of biomass (Field 2004). Initial nutrient and phytoplankton concentrations are taken primarily from 1997–2004 GLOBEC and 2000–2004 CALCOFI research cruises (Brand et al. 2007). Zooplankton initial abundance varies with depth and distance from shore, and was derived from a variety of research cruises from 1967–2003 off Newport and Brookings, Oregon. Benthic invertebrate abundances primarily derive from grab samples taken from 0–850 m off the coast of Washington and Oregon. Fish and mammal growth and consumption rates are dynamic, but under initial conditions these were set such that predicted growth rates (e.g., von Bertalanffy) matched observed growth rates reported in stock assessments. Stock–recruit parameters (and thus stock productivity) were informed by values in published stock assessments. These initial conditions defined model year 2009, the initiation of our simulations. The model has been calibrated in three phases: a first phase that tests the model's ability to reproduce unfished biomasses, which can be compared to estimates from stock assessments (Brand et al. 2007); a second phase that tests stock productivities under constant fishing rates, and a final phase that tests the model's ability to fit historical time series. A further description of the calibration methodology and the main parameters adjusted in each phase are found in Horne et al. (2010).

Modifications since the publication of Brand et al. (2007) primarily involve addition of canary rockfish and English sole groups (see supplementary data,[3] Appendix S2, Table S2.1), minor updates to stock abundance as reported in the 2007 stock assessments (PFMC 2008), and inclusion of updated diet data (Dufault et al. 2009). The new diet data are particularly important, since they dictate the links in the food web, and thus predator/prey interactions.

Incorporating catch scenarios and ocean acidification into the Atlantis ecosystem model

All model runs presented here begin with the same base parameterization and model behavior. The annual catch projections (see supplementary data,[3] Appendix S1, Table S1.1) were applied beginning in model year 2009, with these catches imposed for 20 years (through 2028).

We converted the catch scenarios (see supplementary data,[3] Appendix S1, Table S1.1) to annual catch estimates per functional group, and applied these catches beginning in model year 2009. This required matching regions defined in the catch projections with Atlantis regions (see supplementary data,[3] Appendix S3, Table S3.1), as well as matching the species from the catch projection to functional groups within Atlantis (online Supplemental Appendix S3, Table S3.2). For functional groups not listed in the catch scenarios (i.e., not contained in online Supplemental Appendix S1, Table S1.1[3]), we applied the final year of data we had from the PacFIN landings database (2004) to all projection years. These functional groups included five pelagic fish groups, four invertebrate groups, and only three demersal fish groups (skates and rays, shallow small rockfish, and deep miscellaneous fish). Annual catches were applied in each model year as long as they did not exceed the standing stock. We did not decrease harvests if biomass declined (i.e., we did not simulate a management response).

We represented ocean acidification as additional mortality on benthic shelled organisms, specifically the three benthic filter feeder groups (e.g., bivalves and corals), benthic herbivorous grazers (e.g., sea urchins), and deep macrozoobenthos (e.g., sea stars). We also considered possible effects on two plankton functional groups, large zooplankton (which include thecosome pteropods) and "small phytoplankton" (primary producers that are generally smaller than diatoms, including coccolithophores and foraminifera with photosynthetic endosymbionts) (see supplementary data,[3] Appendix S2, Table S2.2). Although in nature the effect of acidification likely differs between species within a functional group, here we simply model the aggregate effect on the total functional group.

Our simulations involving declines in benthos are informed by Hall-Spencer et al. (2008), who were the first to

publish in-situ observations of declines in benthos under pH levels likely to occur in the next 100 years. Studying the area near underwater volcanic CO_2 vents, the authors found significantly depressed levels of limpets and near-zero abundance of sea urchins at sites with pH around 7.83. They also observed decreases in limpet and snail shell thickness with reduced pH. Laboratory studies on benthic invertebrates support these in situ observations (brittle stars: Dupont et al. 2008; sea urchins: Kurihara and Shirayama 2004; mussels and oysters: Gazeau et al. 2007; Kurihara et al. 2007; 2009). However, the laboratory studies frequently use unrealistically low pH levels, focus on juvenile stages only, and cannot usually be translated directly onto the population level. Many of these studies of benthic invertebrates (excluding corals) have been reviewed in Fabry et al. (2008). For corals, laboratory studies on a limited number of species suggest that acidification can cause declines in calcification of 4.5%–40% when standardized to a pCO_2 of $\sim$420 ppmv (Kleypas and Langdon 2006, their Table 3). Guinotte et al. (2003) extended the modeling work of Kleypas et al. (1999) and predicted that even conservative projections of atmospheric CO_2 level rise by the year 2069 will reduce the whole Pacific Ocean to be marginal habitat for coral reefs.

Our simulations involving acidification impacts on plankton stem from laboratory experiments on large zooplankton (pteropods) and small phytoplankton (foraminifera and coccolithophores). Our modeling of large zooplankton response to acidification is informed by experiments with the pteropod *Clio pyramidata* that demonstrated shell dissolution within 48 h of being exposed to ocean chemistry similar to that predicted for 2100 (Feely et al. 2004; Orr et al. 2005; Fabry et al. 2008). The effects of acidification on coccolithophores have been demonstrated by Riebesell et al. (2000), who found 16%–45% decreases in calcification rates at CO_2 levels of 750 ppmv. Other authors have pointed out that the responses of coccolithophores may also be species specific (Langer et al. 2006), and there is evidence for slight increases in carbon fixation rates under higher CO_2 concentrations (Riebesell et al. 2000). Evidence for negative impacts of 4%–14% on foraminifera under pH expected in 2100 is summarized in Fabry et al. (2008), but laboratory experiments have only been conducted on two of $\sim$54 species.

Owing to the lack of quantitative laboratory experiments that translate realistic future pH into mortality rates, we used the studies above primarily to point to the functional groups that are most likely to suffer under ocean acidification. There is a strong need for further laboratory studies that identify the effects of acidification on more species, throughout the entire life cycle, and under realistic environmental conditions. Lacking these further studies, we considered four regimes that bracket the range of possible acidification effects: no effects, strong impacts on benthic invertebrates, moderate impacts on benthic invertebrates, and moderate impacts on benthic invertebrates and plankton. The regime with strong impacts on benthic invertebrates assumed an increased mortality rate of 1% per day for these groups. This drove shallow benthic filter feeders and sea urchins to decline by 83%–90%, respectively, over 20 years relative to their abundance without acidification. The three other benthic shelled groups were driven to extinction. The regimes with moderate impacts on benthic invertebrates assumed an increased mortality rate of less than 0.4%per day, leading these groups to decline by 20%–70%. The regime with moderate effects of acidification for large zooplankton (additional mortality of 1% per day) and small phytoplankton (additional mortality of 30% per day) caused decreases of 75% and 20% in those groups, respectively.

Results

Individual fishing quota catch scenarios

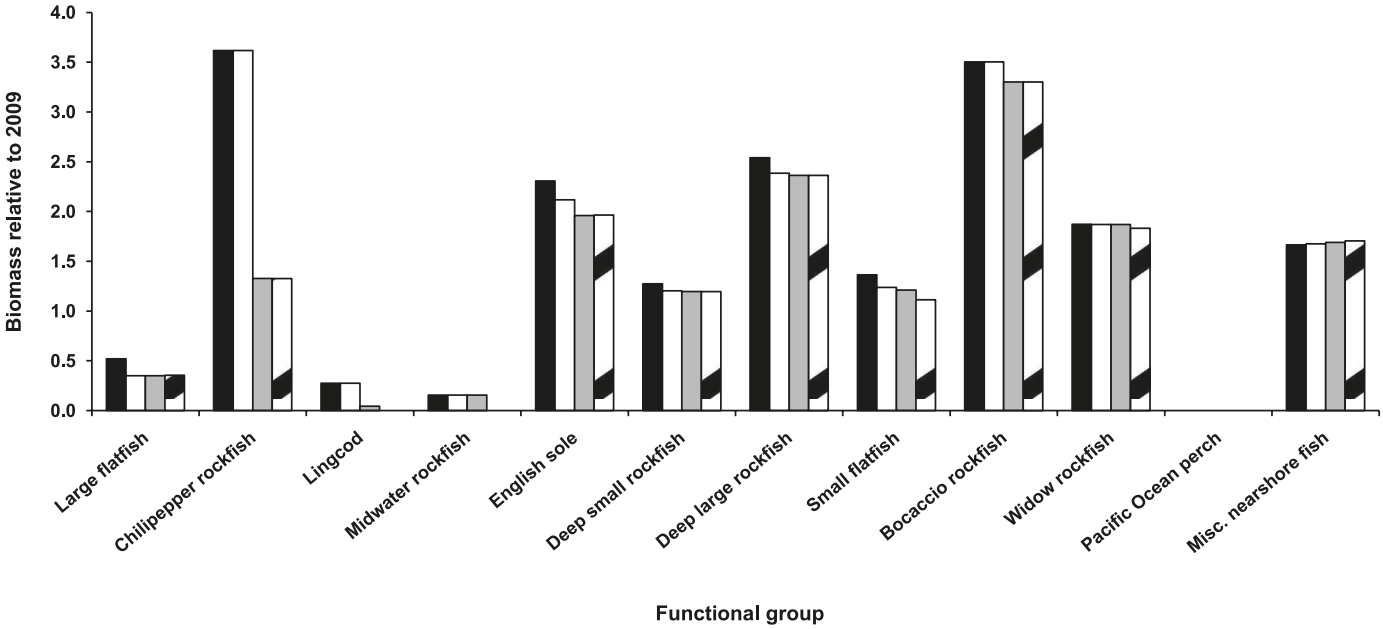
As expected, the scenarios with higher catch of target species led to lower abundances of these species over the course of the simulations (Fig. 2; Table 1). The target species with increased catch included large flatfish (e.g., arrowtooth flounder), chilipepper rockfish, lingcod, midwater rockfish, English sole, deep small rockfish (e.g., longspine thornyhead), deep large rockfish (e.g., shortspine thornyhead), and small flatfish (e.g., Dover sole). Bycatch groups with increased catch included bocaccio, widow rockfish (*S. entomelas*), and Pacific ocean perch.

Over the course of all the 20-year simulations, the abundance of most rockfish and flatfish groups increased (Fig. 2), since the initial conditions of the model are primarily based on biomass estimates from 2000–2007, a period when many of the stocks were beginning to recover from historic overfishing. Several of the species with increased catches also followed this trend, since fishing mortality rates were relatively low. Even in the scenario with the highest total mortality (Scenario 3), the fishing mortality rates are approximately 5% per year for large flatfish (arrowtooth flounder) and 1%–3% for the other target species. For most of these species, the fishing rates considered here accounted for less than a 30% difference in final abundance between scenarios. Exceptions to this were chilipepper rockfish, lingcod, and midwater rockfish, which declined steeply in the scenarios with higher fishing. Chilipepper, lingcod, and midwater rockfish are "underutilized" species that managers aim to target under the IFQ system; IFQs would not change the total allowable catch for these 'underutilized' species, but reduced bycatch rates (e.g., of bocaccio) under IFQs may increase the likelihood that fishers reach the total allowable catch for the underutilized species, rather than being limited by bycatch caps (see supplementary data,[3] Appendix S1). For example, Scenario 3 assumed a chilipepper rockfish catch of 2000 metric tons (mt) compared with 17.8 mt under Status Quo. The additional catch led to final biomasses equal to 37% of their projected biomass under the Status Quo. Midwater rockfish and lingcod both were extirpated in Scenario 3, owing to quota increases of 20-fold and 3-fold, respectively.

The direct effects of fishing presented above are straightforward, and would be captured by single species models that are much simpler than the Atlantis ecosystem model. The motivation for using Atlantis here is that it captures indirect effects related to shifts in predation, which are not represented in single species assessment models. Therefore, we focus more on indirect effects as we present further results from the IFQs and ocean acidification below.

Under the IFQ scenarios, higher levels of fishing led to reduced predation by these target species on their prey. The miscellaneous nearshore fish showed minor increases due to

Fig. 2. Relative abundance (biomass in 2028 / biomass in 2009) for select functional groups. From left to right, for each group, the bars represent the status quo scenario, Scenario 1, Scenario 2, and Scenario 3. The eight target species on the left experience increasing fishing pressure as we shift from the Status Quo scenario towards Scenario 3. Catches of bycatch species (bocaccio and widow rockfish and Pacific ocean perch) also increase from left to right. For miscellaneous nearshore fish, fishing pressure does not vary between scenarios, but differences in predation mortality cause differences in abundance.



this decline in predation (Fig. 2; Table 1). This group, which includes sculpin (Cottidae) and white croaker (*Genyonemus lineatus*), increased by approximately 2%, owing to the reduction in abundance of lingcod. Twenty percent of lingcod diet is composed of these nearshore fish species (Dufault et al. 2009).

We did not see strong indirect effects (>5%) on target or forage species in these particular fishing scenarios. This may be a function of the inherent structure of the food web and ecosystem, but also may be due to the fact that the management scenarios considered here involve low total fishing mortality rates of <5% per year. The small differences in fishing mortality rates between the scenarios translate into small differences in target species biomass, and a limited impact on the other components of the food web.

Scenarios with ocean acidification impacts on benthos

Combining the IFQ catch scenarios with ocean acidification confronted the benthic fish species with a food web that was depleted in shelled benthos, such as bivalves, snails, corals, sea urchins, sea stars, and brittle stars. Our scenarios with strong impacts on shelled benthos resulted in 80%–100% declines in these benthic groups within 20 years, relative to what would be expected without additional mortality due to acidification. Our scenarios with moderate impacts resulted in declines of 20%–70% for these groups (Table 1). We illustrate the impacts of this in two ways: the results for the status quo harvest scenario under each acidification regime are shown (Fig. 3), in terms of stock increase or stock decline relative to initial (~2009) biomasses. Complete results for all simulations are provided (Table 1), but for ease of comparison we have standardized all biomasses relative to the Status Quo scenario without acidification.

The loss of shelled benthic prey groups led to declines primarily in English sole and, to a lesser extent, in small demersal sharks (e.g., spiny dogfish) (Fig. 3; Table 1). Observations from Washington and Oregon suggest that both functional groups derive about 10% of their diets from shelled benthos (Dufault et al. 2009). Rather than doubling in biomass as they did without ocean acidification, with strong acidification and the Status Quo scenario, English sole fell to 40% of initial levels (Fig. 3), and to as low as 6% of initial levels in the more heavily fished scenarios. With moderate acidification, ending biomass was 160%–190% of initial levels, which is approximately 16% lower than would be expected without acidification (Fig. 3, Table 1). The effect of acidification on small demersal sharks was more constrained: without acidification or with only moderate acidification they increased in abundance to about 2.0× initial levels, and with extreme acidification this fell to ~1.9× (Fig. 3).

Three additional impacts of the benthic acidification scenarios were a decline in skates and rays, a slight increase in canary rockfish, and a slight increase in miscellaneous nearshore fish (croakers and sculpins) (Fig. 3; Table 1). Skates and rays declined under acidification, owing to decreases in the abundance of benthic grazers (sea urchins), which are a minor component of skate diet. Strong acidification caused a 30% decline in skates and rays, and moderate acidification caused a 10% decline, relative to the scenario with no acidification (Table 1). Under strong acidification impacts, the biomass of miscellaneous nearshore fish and canary rockfish increased toward the end of the simulations by ~13% and 6%, respectively (relative to the no acidification scenario) owing to the decline in their predator, small demersal sharks (Table 1). These interactions are driven by small (<5%) diet

Table 1. Biomass of functional groups at year 20, for each harvest scenario and acidification regime.

	No ocean acidification				Strong acidification impacts on benthos				Moderate acidification impacts on benthos				Moderate acidification impacts on benthos and plankton			
Functional group	Stat. Quo	Scen1	Scen2	Scen3	Stat. Quo	Scen1	Scen2	Scen3	Stat. Quo	Scen1	Scen2	Scen3	Stat. Quo	Scen1	Scen2	Scen3
Large planktivores(mackerel)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Canary rockfish	1.00	1.00	1.01	1.01	1.06	1.06	1.07	1.08	1.00	1.01	1.01	1.02	1.80	1.83	1.86	1.89
Small planktivores (sardine, anchovy)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	0.97	0.97	0.97
Large flatfish (arrowtooth)	1.00	**0.67**	**0.67**	**0.68**	0.99	**0.66**	**0.66**	**0.67**	1.00	**0.67**	**0.67**	**0.68**	**0.66**	**0.38**	**0.39**	**0.40**
Chilipepper rockfish	1.00	1.00	**0.37**	**0.37**	1.00	1.00	**0.37**	**0.37**	1.00	1.00	**0.37**	**0.37**	1.00	1.00	**0.37**	**0.37**
Lingcod	1.00	1.00	**0.16**	**0.00**	0.98	0.98	**0.14**	**0.00**	1.00	1.00	**0.16**	**0.00**	**0.78**	**0.78**	**0.00**	**0.00**
Salmon	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Large pelagic predators (tuna)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Shearwaters	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.99	0.99	0.99
Hake	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	0.98	0.98	0.98
Sablefish	1.00	1.00	1.00	1.00	1.03	1.03	1.03	1.03	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Deep vert.migrators (myctophids)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.99	0.99	0.99
Deep misc. fish (slickhead, eelpout)	1.00	1.00	1.00	1.00	0.98	0.98	0.98	0.98	1.00	1.00	1.00	1.00	0.98	0.98	0.98	0.98
Misc. nearshore fish (croaker, sculpin)	1.00	1.01	1.02	1.02	1.13	1.14	1.16	1.17	1.01	1.02	1.02	1.03	2.75	2.81	2.87	2.93
Midwater rockfish	1.00	1.00	1.00	**0.00**	1.01	1.01	1.01	**0.00**	1.00	1.00	1.00	**0.00**	**0.79**	**0.79**	**0.79**	**0.00**
Bocaccio rockfish	1.00	1.00	**0.94**	**0.94**	1.00	1.00	**0.94**	**0.94**	1.00	1.00	**0.94**	**0.94**	1.00	1.00	**0.94**	**0.94**
English sole	1.00	**0.92**	**0.85**	**0.85**	**0.17**	**0.09**	**0.02**	**0.02**	**0.84**	**0.76**	**0.69**	**0.69**	0.96	**0.88**	**0.80**	**0.80**
Shallow small rockfish	1.00	1.00	1.00	1.00	1.02	1.02	1.02	1.02	1.01	1.01	1.01	1.01	0.99	0.99	0.99	0.99
Deep small rockfish (longspine)	1.00	**0.94**	**0.94**	**0.94**	1.00	**0.94**	**0.94**	**0.94**	1.00	**0.94**	**0.94**	**0.94**	1.01	0.95	**0.95**	**0.95**
Deep large rockfish (shortspine)	1.00	**0.94**	**0.93**	**0.93**	1.00	**0.94**	**0.93**	**0.93**	1.00	**0.94**	**0.93**	**0.93**	0.95	**0.89**	**0.88**	**0.88**
Small flatfish (petrale, dover, etc.)	1.00	**0.91**	**0.89**	**0.82**	1.00	**0.91**	**0.89**	**0.81**	1.00	**0.91**	**0.89**	**0.82**	1.03	**0.94**	**0.92**	**0.85**
Small demersal sharks (dogfish)	1.00	1.00	1.00	1.00	0.96	0.96	0.96	0.96	0.99	0.99	0.99	0.99	0.95	0.95	0.95	0.95
Large demersal sharks (sixgill, etc.)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.02	1.02	1.02	1.02
Pacific Ocean perch	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pelagic sharks	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	**0.93**	**0.93**	**0.93**	**0.93**
Shallow large rockfish	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00	1.00	1.00	1.05	1.05	1.06	1.06
Skates and rays	1.00	1.00	1.00	1.01	**0.68**	**0.69**	**0.69**	**0.69**	**0.90**	**0.91**	**0.91**	**0.91**	1.15	1.16	1.16	1.17
Surface feed birds (gulls)	1.00	0.99	0.98	0.98	1.03	1.02	1.01	1.01	0.99	0.99	0.97	0.97	0.98	0.97	0.96	0.96
Diving birds	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.03	1.04	1.04	1.04
Pinnipeds	1.00	1.00	1.00	1.00	0.98	0.98	0.98	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Transient orcas	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Baleen whales	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Widow rockfish	1.00	1.00	1.00	0.98	1.00	1.00	1.00	0.98	1.00	1.00	1.00	0.98	1.00	1.00	1.00	0.98
Toothed whales	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Otters	1.00	1.00	1.00	1.00	0.98	0.98	0.98	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Squid	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Shallow benthic filter feeders	1.00	1.01	1.02	1.02	**0.17**	**0.17**	**0.17**	**0.17**	**0.82**	**0.82**	**0.83**	**0.83**	1.04	1.05	1.06	1.06
Other benthic filter feeders	1.00	1.01	1.01	1.01	**0.00**	**0.00**	**0.00**	**0.00**	1.86	1.88	1.88	1.88	2.31	2.32	2.32	2.32
Deep benthic filter feeders	1.00	1.00	1.00	1.00	**0.00**	**0.00**	**0.00**	**0.00**	**0.33**	**0.33**	**0.33**	**0.33**	**0.35**	**0.35**	**0.35**	**0.35**
Urchins	1.00	1.00	1.01	1.02	**0.10**	**0.10**	**0.10**	**0.09**	**0.36**	**0.36**	**0.37**	**0.38**	**0.44**	**0.44**	**0.44**	**0.43**

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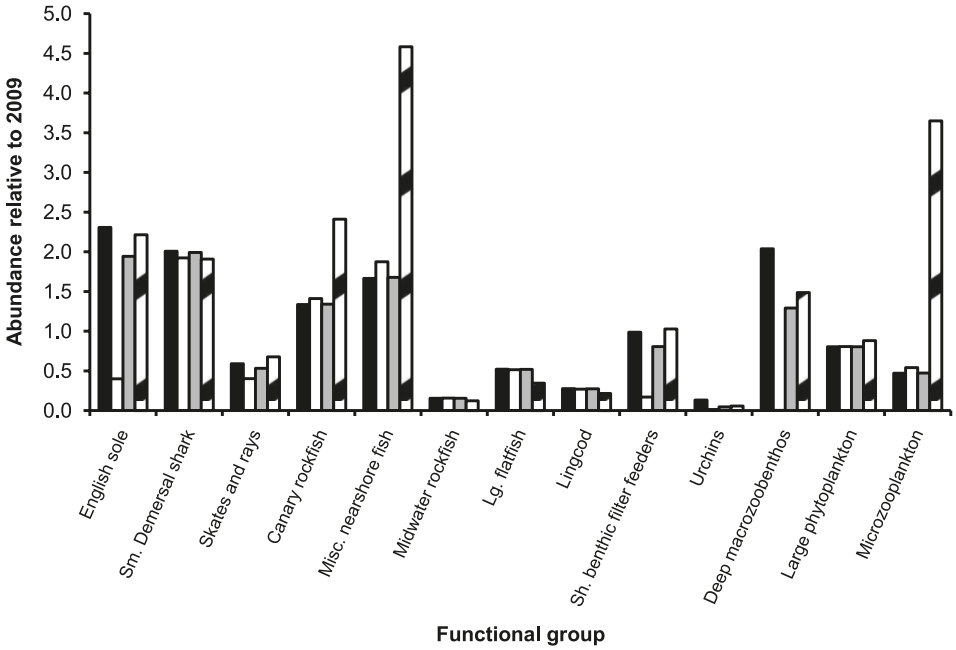
Table 1 (*concluded*).

Functional group	No ocean acidification				Strong acidification impacts on benthos				Moderate acidification impacts on benthos				Moderate acidification impacts on benthos and plankton			
	Stat. Quo	Scen1	Scen2	Scen3	Stat. Quo	Scen1	Scen2	Scen3	Stat. Quo	Scen1	Scen2	Scen3	Stat. Quo	Scen1	Scen2	Scen3
Deep macrozoobenthos	1.00	1.00	1.02	1.01	**0.00**	**0.00**	**0.00**	**0.00**	**0.63**	**0.64**	**0.65**	**0.64**	**0.73**	**0.73**	**0.74**	**0.74**
Large crabs	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Octopus	1.00	1.00	1.00	1.00	**0.93**	**0.93**	**0.93**	**0.93**	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99
Shrimp	1.00	1.00	1.00	1.00	1.00	1.07	1.07	1.07	1.00	1.00	1.00	1.00	1.07	1.07	1.07	1.07
Large zooplankton (euphausid)	1.00	1.00	1.00	1.00	1.04	1.04	1.04	1.04	1.00	1.00	1.01	1.00	**0.24**	**0.24**	**0.24**	**0.24**
Deposit feeders	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Macroalgae (kelp)	1.00	1.00	1.00	1.00	1.55	1.55	1.54	1.54	1.05	1.05	1.05	1.05	0.98	0.98	0.98	0.98
Seagrass	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Carnivorous infauna	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Gelatinous zooplankton	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	2.65	2.65	2.62	2.61
Large phytoplankton	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.10	1.10	1.10
Small phytoplankton	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	**0.81**	**0.81**	**0.81**	**0.81**
Mesozooplankton (copepods)	1.00	1.00	1.00	1.00	1.00	0.99	0.99	0.99	1.00	1.00	1.00	1.00	1.29	1.29	1.28	1.27
Microzooplankton	1.00	1.01	1.01	1.00	1.15	1.18	1.17	1.19	1.01	1.01	1.01	1.01	7.75	7.75	7.73	7.72
Pelagic bacteria	1.00	1.02	1.03	1.03	1.33	1.35	1.38	1.35	1.05	1.07	1.08	1.08	2.40	2.41	2.42	2.42
Benthic bacteria	1.00	1.02	1.08	1.05	1.78	1.81	1.93	1.87	1.11	1.13	1.20	1.17	1.33	1.35	1.41	1.39
Meiobenthos	1.00	1.01	1.06	1.03	1.43	1.44	1.53	1.48	1.06	1.07	1.13	1.09	1.48	1.49	1.58	1.57
Labile detritus	1.00	1.02	1.08	1.05	1.78	1.81	1.94	1.87	1.11	1.13	1.20	1.17	1.33	1.34	1.40	1.39
Refractory detritus	1.00	1.02	1.08	1.03	1.13	1.15	1.22	1.17	1.05	1.07	1.13	1.08	1.15	1.17	1.22	1.18
Carrion	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Dissolved inorganic N	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	**0.00**	1.33	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**

Note: Biomass is relative to biomass at year 20 in the Status Quo harvest + No Ocean acidification simulations. For reference, cells with values less than 0.95 have bold font. Functional groups that went extinct in the Status Quo harvest + No Ocean Acidification are indicated as "—". Stat. Quo, Status Quo scenario; Scen1, scenario 1; Scen2, scenario 2; Scen3, scenario 3.

Fig. 3. Relative abundance (biomass in 2028 / biomass in 2009) for select functional groups. All bars represent scenarios with Status Quo management. From left to right, for each group, the bars represent regimes with no acidification, strong acidification on shelled benthos, moderate acidification on shelled benthos, and moderate acidification on shelled benthos + plankton.



fractions derived from limited field observations, and may be considered more uncertain than the impacts on English sole and small demersal sharks.

Scenarios with ocean acidification impacts on plankton

The scenarios that represented acidification as a decline in plankton affected more groups than did the scenario above that involved a decline in shelled benthic groups. The additional mortality we imposed on large zooplankton and small phytoplankton caused these plankton groups to decline 75% and 20%, respectively, relative to scenarios with no acidification (Table 1). This led to a considerable reorganization of the food web, most easily seen in a comparison of the Status Quo harvest scenarios across all acidification regimes (Fig. 3); other harvest scenarios follow similar patterns (Table 1). The declines in large zooplankton (pteropods) and small phytoplankton (foraminifera and coccolithophores) released large phytoplankton from both grazing and competition, leading to a 10% increase in biomass. The release in grazing pressure by large zooplankton allowed microzooplankton (e.g., ciliates, dinoflagellates, nanoflagellates) to increase to $\sim 8\times$ the abundance that would be expected without acidification. These increases in plankton groups led to strong increases in detritus production and bacterial groups' biomass, subsequently causing increases in shallow benthic filter feeders and benthic detritivores such as sea urchins and deep macrozoobenthos (e.g., brittle stars). Fish groups such as midwater rockfish and large flatfish declined, owing to the loss of large zooplankton (Fig. 3), which comprises 38% and 10% of the diets of these species, respectively (Dufault et al. 2009). One second-order effect was a decline in lingcod, owing to the loss of midwater rockfish as prey. Another second-order effect included increases in canary rockfish and skates and rays, both of which benefited from increased sea urchin abundance and minor increases in shrimp abundance. We observed one third-order effect: miscellaneous nearshore fish increased to $\sim 4.6\times$ initial abundance, owing to declines in their predator, lingcod (Fig. 3).

Evaluating cumulative impacts of fishing strategies and ocean acidification

Resource managers may be interested in two aspects of our results, in relation to sustainable use of target fish species and conservation of bycatch species: (*i*) how robust against acidification is the decision to implement IFQs (the decision regarding the overall management system), and (*ii*) how can we evaluate the impacts of acidification in setting harvests for individual species (the decisions regarding specific management policies)?

To evaluate the decision regarding implementation of IFQs, we calculated the relative economic performance of each of the four IFQ scenarios, across each of the ocean acidification regimes. Regardless of the assumptions about acidification, the ranking of landed value summed over all species (tons × price, PacFIN 2008) was Status Quo < Scenario 1 < Scenario 2 < Scenario 3, following the overall pattern of target species landings. Therefore, in terms of total revenue, the Pacific Fishery Management Council's decision to switch to IFQs (Scenarios 1–3) from Status Quo appears robust to acidification. This sort of scenario screening and ranking is one of the strong suits of Atlantis, and ecosystem models in general (Fulton et al. 2007; Plaganyi 2007).

Evaluation of the cumulative impacts of fishing, acidification, and trophic effects can be accomplished using single-species reference points and decision theory (Hilborn and Walters 1992; Quinn and Deriso 1999) that are standard components of fishery management decisions on the US West Coast (e.g., Stewart 2007). As an example, here we focus on English sole, which suffered the most severely of any commercially important species under strong benthic acidifi-

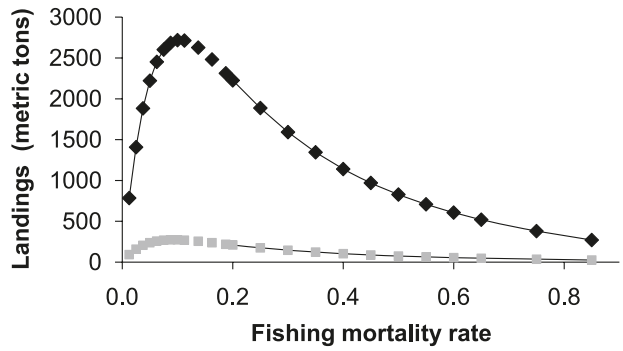
cation impacts. To give some context, on the US West Coast, 1078 mt of English sole were caught in 2006 (Stewart 2007), with a value of approximately US$700 000; this was approximately one third of the allowable catch set by managers.

Selecting management policies for English sole involves setting quotas based on the status of the stock (depletion) and estimates of the maximum sustainable yield (MSY) and the biomass at which this occurs. These reference points trigger legally mandatory actions; for instance, depleting a stock to less than 25% of unfished biomass necessitates large cuts in harvest and the development of a formal "rebuilding plan" (e.g., MacCall 2008). Using Atlantis analogously to a single species stock assessment, we calculated depletion as the ratio of current spawning stock biomass (SB) to unfished SB. Also analogous to single species assessments, we used two methods to identify MSY: a proxy biomass level (SB = 40% of unfished SB), and direct estimation of MSY and SB_{MSY}. We estimated unfished SB by projecting the Atlantis model for 50 years with no fishing, at which point most species including English sole had increased to quasi-equilibrium levels. Direct estimation of MSY involved fixing the harvest rate at a range of levels, and evaluating catches in year 50 of a 50-year simulation (Fig. 4). We considered the simple case without acidification (i.e., just fishing and trophic effects), and the case with the full cumulative impacts of strong acidification on shelled benthic organisms, fishing, and trophic effects.

Our estimated reference points clearly illustrate the dramatic impact of this acidification regime on English sole (Table 2). As current catches are only a third of the quota, there appears to be much scope for a future expansion of catch. However this may not actually be possible, as unfished spawning stock biomass (SB_0) fell by 90% when confronted with strong acidification impacts on benthos. MSY therefore fell 90% as well, regardless of whether we estimated MSY or assumed the $SB_{40\%}$ MSY proxy. The fishing mortality rate corresponding to maximum yield was similar (0.1/year for no acidification and 0.0875/year for strong benthic acidification effects). For comparison, using a single species model, Stewart (2007) estimated single species MSY to be 3452 mt with a fishing mortality rate of 0.13/year, based on a target of 40% of unfished spawning biomass. These results demonstrate that under status quo conditions, our ecosystem model generates similar stock productivity and estimates of fishery reference points as does an "orthodox" single species assessment model for English sole. The main added value of the ecosystem model in this case is that it is able to forecast how the dynamics of the stock change under scenarios with decreased prey abundances due to ocean acidification.

We considered the implications of the four harvest scenarios on the biomass of English sole when the ecosystem involves alternate "states of nature": either no acidification or strong acidification of shelled benthos (Table 3). This approach follows the standard decision table format adopted by US West Coast fishery managers, but adds the full cumulative effects within the Atlantis model. Without acidification, abundance over 20 years under all IFQ scenarios increases relative to initial (2009) abundance; the Status Quo scenario at year 20 even temporarily exceeds the long-term estimate of SB_0. On the other hand, with strong benthic acidification the IFQ catches drive biomass to as low as 7% of initial (2009) abundance; the species appears more depleted even when scaled against the unfished spawning biomass estimated under acidification (SB_{2028}/SB_{0Acid}). This depletion is expected since catch (557–1772 mt) is much greater than our MSY reference points (270 or 260 mt).

Fig. 4. Yield of English sole (*Pleuronectes vetulus*) under various fishing mortality rates (*x*-axis) with current ecological processes (top curve) vs. strong ocean acidification impacts on benthos (bottom curve). Yield is based on catches in year 50 of a 50-year simulation; this is an approximation of an equilibrium sustainable yield.



Discussion

Though complex simulation models like Atlantis have been successfully used to evaluate management strategies and ecological tradeoffs (Fulton et al. 2007) and in adaptive "gaming" exercises with stakeholders (Christensen and Walters 2004), they are notoriously hard to translate into metrics useful to policy makers. Frequently modelers attempt to summarize the state of the ecosystem using multiple indicators that represent particular components or processes of interest (Fulton et al. 2005; Link 2005). Here we have demonstrated that the messages in these models can also be captured in terms of accepted single-species benchmarks. The potential impact of acidification on unfished biomass (SB_0) and sustainable yield (MSY) of English sole is one example. One of the few similar articles in the literature is by Walters et al. (2005), who calculated MSY for each species in 11 simulated ecosystems, and illustrated interdependence and tradeoffs in sustainable yields of species within each food web. Though natural resource managers increasingly accept ecosystem-based management (EBM) in concept, their day-to-day mandates and their training are usually grounded in single species considerations. Therefore, summarizing cumulative "whole ecosystem" impacts in terms of established reference points and decision mechanisms provides one way to integrate new ecosystem modeling tools with existing scientific and legal frameworks.

Resource managers have implemented individual quotas in many fisheries over the last 20–30 years, including Australia (Young 1999), New Zealand (Annala 1996), Iceland (Arnason 1996), and Alaska (Sigler and Lunsford 2001). In many cases, IFQs have proven to be a successful way to increase the economic and biological performance of fishing industries (Grafton et al. 2006; Costello et al. 2008). In the

Table 2. Management reference points for English sole, based on maximum sustainable yield (MSY) and spawning stock biomass.

	MSY estimated iteratively		MSY based on 40% of SB_0	
Reference point	Status quo	Acidification	Status quo	Acidification
SB_0, unfished spawning biomass (mt)	123 000	15 000	123 000	15 000
MSY (mt)	2 700	270	2 700	260
Spawning stock biomass (MSY; mt)	41 500	4 900	49 100	6 000
Fishing mortality rate (MSY)	0.1	0.0875	0.0875	0.075

Note: MSY was estimated by two methods, both iteratively by testing a range of fishing mortalities, and by using a proxy of 40% of unfished biomass; mt, metric tons.

Table 3. Decision table for English sole evaluating the impact of Status Quo harvest or three alternate Individual Fishing Quota (IFQ) scenarios, faced with either no ocean acidification or strong acidification impacts on benthos.

	State of nature					
	No acidification ($SB_{0NoAcid}$ = 123 000)			Strong acidification on benthos (SB_{0Acid} = 15 000)		
Harvest policy (catch, mt)	SB_{2028}	SB_{2028}/SB_{2009}	$SB_{2028}/SB_{0NoAcid}$	SB_{2028}	SB_{2028}/SB_{2009}	SB_{2028}/SB_{0Acid}
SQ (557 mt)	137 000	2.69	1.12	24 500	0.48	1.63
Scenario 1 (1131)	125 000	2.45	1.02	13 000	0.26	0.87
Scenario 2 (1772)	115 000	2.26	0.94	3 500	0.07	0.23
Scenario 3 (1772)	115 500	2.27	0.94	3 500	0.07	0.23

Note: We simulated harvest policies for 20 years. Results are reported as spawning biomass (SB) at the end of the simulation, relative to 2009 biomass or relative to the appropriate estimate of unfished spawning biomass (SB_0) from Table 2. SQ, status quo; mt, metric tons

British Columbia trawl fishery adjacent to the one modeled here, Branch et al. (2006*b*) found that IFQs, when coupled with full observer coverage and accounting of discards, changed fishing behavior and reduced discards. Our modeling illustrates that as the Pacific Fishery Management Council shifts to an IFQ system, we should not expect past performance to guarantee future results, if the future is dominated by global change. The results shown here suggest that in the absence of ocean acidification the primary impact of IFQ strategies will be on species that are targeted for greatly increased catches, such as chilipepper rockfish. The IFQ harvest scenarios alone will, in most cases, not have strong impacts on the food web, beyond the direct effects on harvested species. This is largely due to fact that the fleet's catches and our scenarios are limited by estimates of optimum yield from stock assessments; harvest on the much larger scale of the 1960s to early 1990s could have had much stronger food web impacts (Field 2004). Most predators and prey of target species were not strongly affected by the scenarios considered here. We observed tradeoffs between lingcod and a primary component of their diets, miscellaneous nearshore fish. Similar indirect effects are commonly evident in multispecies models (e.g., Hinke et al. 2004) and have been observed in the field, particularly in heavily fished systems (Daskalov 2002; Lilly et al. 2000). Given the relatively small differences in fishing mortality associated with the proposed scenarios, it is not surprising that the models predict only minor indirect effects on prey species. Our ecosystem modeling of the food web effects of IFQs is a first step to provide quantitative predictions regarding the ecological impact of IFQs (Branch 2009; Griffith 2008).

Global change, and specifically ocean acidification, may have strong impacts on some target species, separate from what would be expected under a world with IFQs and only fishing effects. The ocean acidification regimes that we considered here range in intensity from no acidification to extirpation of benthic and planktonic shelled organisms. These intensities likely bracket the impacts of declining pH in the world's oceans; in reality, the effects of acidification will ultimately be mediated by competition within functional groups, and species-level characteristics related to shell formation. Previous work by Cooley and Doney (2009) similarly translated projected acidification into 10%–25% declines in mollusks, and equated this to economic losses by US mollusk fisheries of $75–187 million, annually. We have used our ecosystem model to trace the damage from acidification up the food web, revealing that commercially important groundfish stocks such as English sole, arrowtooth flounder (i.e., large flatfish), and yellowtail rockfish (midwater rockfish) are also particularly susceptible to the loss of shelled prey items from their diet. One target species, English sole, exhibited a 10-fold decline in potential catch and economic yield when confronted with strong acidification impacts on shelled benthos. Levin et al. (2006) document that status quo management has resulted in the decline of low productivity rockfish and the increase in more productive species such as flatfish. Thus, the modeled effects of ocean acidification are of concern since they disproportionately affect a portion of the fishery that is productive and currently healthy.

Our work here is only a start toward identifying the implications of ocean acidification on the fishery food web, but it does hint at the important role that the predator/prey response can have on the ultimate effects of acidification on commercial fish stocks. In our modeling, both English sole and small demersal sharks were initialized to have 10% of their diets as shelled benthos, and yet declines in shelled

benthos caused much stronger declines in the former than the latter. For English sole, the impact of acidification was increased by a limited supply of alternate prey sources and gape limitation exacerbated by declines in size-at-age. Thus we expect that more modeling and observations of predator diets will be needed to forecast acidification effects, rather than a simple linear response (i.e., a 10% decline if 10% of a predator diet is removed).

The IFQ and acidification simulations presented here are fairly simple. We use projections of total catches, rather than full simulation of fleet dynamics. These projections are meant to capture improvements in targeting with trawl gear, but do not explicitly capture changes in spatial allocation of effort, gear switching, or investment/disinvestment likely to occur to some degree under a trawl IFQ program. The model also lacks management feedback; in reality, fishing mortality rates are not constant, but are adjusted downwards when assessments indicate that the stock has declined below 40% of unfished levels. We ignored discards of species other than groundfish, not only fish but also corals, sponges, and other habitat-forming species. Finally, we should note that the Atlantis modeling framework requires fairly coarse representation of the geography and functional groups. Our fish functional groups typically include 3–4 fish species that in reality are managed separately, while invertebrate functional groups include many genera that may respond differently to acidification.

Our scenarios treated acidification as fixed additional mortality rates on shelled plankton and benthos groups. More detailed modeling of acidification requires coupling global ocean carbon models with empirical studies of calcification rates, as has been done for corals (Kleypas et al. 1999; Guinotte et al. 2003). These authors and others (Fabry et al. 2008) have produced maps predicting decreases in the saturation state of aragonite (a type of calcium carbonate secreted by marine organisms) on a global scale in 50–100 years. The maps suggest decreases in both the area and depths inhabitable by calcifying organisms. Spatially explicit models such as Atlantis can include these projected range contractions, both horizontal and vertical, and can examine the spatial impacts on the food web. For plankton and shelled benthos, a first step might be to assume a fixed effect of acidification only for time periods and areas that have aragonite or calcite saturation states below some generic thresholds (as in Guinotte et al. 2003). A second step, once the necessary empirical studies are available, would relate a gradient of calcite and aragonite saturation states to species' calcification rates and subsequent impacts on population dynamics.

As with any complex simulation model, Atlantis is not intended for making short-term tactical decisions (e.g., annual decisions about total catch limits). Such decisions are best made with single-species stock assessments. For instance, the strong effect of fishing on chilipepper rockfish predicted in our scenarios can be compared to predictions from Field's (2008) stock assessment. In our Scenario 3, sustained catches of 2000 mt/year over 20 years led to biomasses that were 35% of the level expected under negligible fishing (Status Quo). Field (2008) estimated that removing a maximum sustainable yield of 2100 mt would reduce biomass to 46% of unfished levels. Single species models such as Field (2008) are also designed to explicitly estimate parameter uncertainty. The complexity and long run-times of Atlantis prevent the estimation of uncertainty using traditional statistical techniques or sensitivity analyses (e.g., Saltelli et al. 2004); instead, approaches such as bounded parameterization and perturbation analysis can be used to consider both parameter and structural uncertainty (Fulton 2010). Although we would defer to single species models for setting exact quotas or estimating statistical confidence intervals, Atlantis is a useful tool for exercises like the one here, which aim to screen management policies and consider cumulative impacts in addition to fishing. As we have shown, the results can be summarized in terms that have immediate meaning to policy makers.

From the standpoint of balancing local conservation and economic needs, it is perhaps most encouraging that the policy scenarios analyzed here all indicate a fairly low level of fishing mortality on most target species, and a limited impact on predator and prey species. This is indicative of the restrictive total allowable catches implemented over the last ten years, during which time several of the stocks have been managed under rebuilding plans. Arnason (1996) and Branch et al. (2006*a*) emphasize that IFQ programs alone will not reduce overfishing of target stocks or impacts on the ecosystem. Instead these authors argue that IFQs must be matched with conservative total allowable catch limits, monitoring and enforcement, and accounting of discards. We add to these conclusions that the efficacy of any fisheries management system, including IFQs and catch limits, is best evaluated in the context of potential global change. Therefore, it seems prudent to complement IFQs with careful consideration of potential global change effects, active monitoring for such effects, and adaptive policies to adjust catch limits if ocean acidification or other environmental change begin to drive underlying population dynamics.

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