Potential effects of ocean acidification on the California Current food web and fisheries: ecosystem model projections

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Running title: Potential effects of ocean acidification in the California Current

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Abstract

The benefits and ecosystem services that humans derive from the oceans are threatened by numerous global change stressors, one of which is ocean acidification. Here, we describe the effects of ocean acidification on an upwelling system that already experiences inherently low pH conditions, the California Current. We used an end-to-end ecosystem model (Atlantis), forced by downscaled global climate models and informed by a meta-analysis of the pH sensitivities of local taxa, to investigate the direct and indirect effects of future pH on biomass and fisheries revenues. Our model projects a 0.2 unit drop in pH during the summer upwelling season, which results in wide-ranging magnitudes of effects across guilds and functional groups. The most dramatic direct effects of future pH may be expected on epibenthic invertebrates, and strong indirect effects expected on demersal fish, sharks, and epibenthic invertebrates because they consume species sensitive to changing pH. The model’s pelagic community, including marine mammals and seabirds, was much less influenced by future pH. Some functional groups were less sensitive to changing pH in the model than might be expected from experimental studies in the empirical literature due to high population productivity (e.g. copepods, pteropods, Dungeness crabs). Model results suggest strong effects of reduced pH on nearshore state-managed invertebrate fisheries but modest effects on the groundfish fishery. Our results provide a set of projections that generally support and build upon previous findings and set the stage for hypotheses to guide future modeling and experimental analysis on the effects of OA on marine ecosystems and fisheries.
Introduction

Humans rely on healthy ocean ecosystems for the benefits and services they provide. However, global climate changes caused by continued fossil fuel emissions are subjecting the oceans to multiple stressors (Harley et al., 2006; Crain et al., 2008; Solomon et al., 2009). As oceans cover a majority of the Earth’s surface and provide critical resources for human communities, understanding how future climate conditions will affect factors such as food security and coastal economies is a central question in climate change research (Crain et al., 2008). This question must be addressed at a global scale, but also for downscaled bio-physical interactions within individual ecosystems (Barange et al., 2014), expressed in terms of regional and national ecosystem services such as fisheries, recreation, and coastal protection (Gattuso et al., 2015).

Global change manifests in the ocean in multiple ways, one of which is ocean acidification (OA), the process by which oceans absorb anthropogenic CO\textsubscript{2} from the atmosphere and experience decreased pH and carbonate ion concentrations (Orr et al., 2005; Doney et al., 2009). Dissolution of CO\textsubscript{2} in water creates free hydrogen ions, lowering the pH and thus altering a defining trait of the seawater to which marine organisms are adapted. The oceans absorb about one-third of the anthropogenic CO\textsubscript{2} released into the atmosphere. Since the mid-1700s, this CO\textsubscript{2} uptake has decreased mean pH in surface ocean waters by 0.1 units; by the end of this century, surface ocean pH may decline by an additional 0.3 units (Caldeira & Wickett, 2003), with changes likely to vary spatially (McElhany & Busch, 2013).

Upwelling systems may be particularly vulnerable to OA because they already experience seasonal drops in pH compared to other ocean ecosystems (Feely et al., 2008).
The upwelling process brings deep, cold, nutrient-rich waters up onto the continental shelf, fueling highly productive coastal ecosystems. However, these upwelled waters also have relatively low pH and low oxygen concentrations, and thus introduce potentially stressful conditions into coastal areas. Alternatively, regular exposure to low pH could lead to higher rates of adaptation to changing ocean chemistry (Reum et al., 2014).

Regardless, changes to ocean chemistry have the potential to affect susceptible marine organisms, particularly those that lay down a calcium carbonate shell (Kroeker et al., 2013; Wittmann & Pörtner, 2013). Calcifiers include species such as bivalves, crustaceans, and echinoderms that are commercially and ecologically important; as such, the direct and indirect effects of OA may be widespread throughout a foodweb (Kaplan et al., 2010; Busch et al., 2013).

Here, we focus on the California Current, an Eastern Boundary Current ecosystem where the physical processes that combine upwelling with changing ocean chemistry have been studied extensively (Feely et al., 2008; Gruber et al., 2012). Understanding cumulative impacts of OA at the scale of an ecosystem like the California Current requires models that can project direct and indirect effects. For example, end-to-end models (Plagányi, 2007; Travers et al., 2007; Rose et al., 2010) that incorporate processes like physics, multi-species trophic effects, and fisheries can be used to simulate future projections of ecosystem dynamics and to evaluate trade-offs among alternative fishery management strategies (Fulton et al., 2014), while evaluating consequences of global change (Lehodey et al., 2010), and coupling between oceanography and species dynamics (Fiechter et al., 2014). Atlantis (Fulton, 2004; Fulton et al., 2011) is a spatially explicit end-to-end model that includes physical oceanography, biogeochemistry food web dynamics, and human
uses and impacts such as fishing and nutrient loading. The Atlantis framework has been applied in simple ways to test impacts of ocean acidification in Australia (Griffith et al., 2011, 2012) and Guam (Weijerman et al., 2015). Atlantis models have been developed for the California Current (Brand et al., 2007; Horne et al., 2010) and applied to test impacts of new and existing fisheries (Kaplan et al., 2013; Marshall et al., 2014) and alternative management strategies (Kaplan et al., 2012; Pacific Fishery Management Council & NMFS, 2014), as well as coarse scale effects of ocean acidification (Kaplan et al., 2010).

Building on these earlier Atlantis modeling efforts, we projected the cumulative effects of future ocean acidification on the California Current ecosystem. First, we projected pH in the California Current 50 years in the future (2063), using global earth systems models to force a regional ocean-climate model (dynamical downscaling). This regional model provided the physical conditions that underpinned Atlantis simulations of marine food web interactions and US West Coast fisheries dynamics. We lowered survival of functional groups sensitive to changing pH, based on a meta-analysis of experimental studies. We then ran Atlantis scenarios that simulated: 1) the direct effects of a 0.2 unit change in pH by 2063 on biomass of organisms sensitive to acidification; 2) the indirect effects of changing pH on the rest of the food web; and 3) the resulting effects on fisheries landings and revenues.

Methods

Atlantis is a spatially explicit modeling platform (Fulton, 2004) that couples three sub-models: 1) an oceanographic sub-model, 2) an ecology sub-model, and 3) a human sub-model (Figure 1). We focused on the first two components for this application and used a
simple representation of fishing for the third component. Below we summarize the three sub-models, how we parameterized pH sensitivity, and the scenarios we developed to investigate the effects of changing pH on the California Current ecosystem. Our current application of the California Current Atlantis model builds on and updates earlier versions (Brand et al., 2007; Horne et al., 2010; Kaplan et al., 2012). Additional details are available in the online Supplementary Materials.

**Figure 1.** Conceptual diagram of modeling approach for the California Current Atlantis Model. The general diagram of the Atlantis platform and the three coupled sub-models are shown on the right, with the key modifications and points of entry for information related to this application for projecting ocean acidification shown on the left.

*Model domain*

Our model domain covers 1.475 million km$^2$, with 92,000 km$^2$ on the continental shelf (0-200 m), 127,500 km$^2$ on the continental slope (200-1200 m), and 1.12 million km$^2$ in pelagic waters offshore of the 1200-m isobath. The model domain covers the extent of the California Current, from its origin where the North Pacific Current meets the coast of...
North America at the north end of Vancouver Island (Checkley & Barth, 2009) south to Punta Eugenia, Baja California, Mexico (Figure 2). The domain is divided into 2-dimensional polygons. Longitudinal breaks follow the bathymetry of the 50-m, 100-m, 200-m, 550-m, and 1200-m isobaths, and the 200-nautical mile (370-km) limit of the Exclusive Economic Zone (EEZ). Latitudinal breaks were based on a compromise between biogeography, fishery management and catch reporting areas, and areas utilized by particular fleets and fisheries. Three-dimensional model cells are created by adding depth layers in vertical dimension, which were set using the same interval as isobaths listed above. The offshore pelagic polygons, which extend from the 1200-m isobath to the EEZ limit, are assumed to be 2400 m deep (with an open boundary representing deeper waters lying underneath and along the western boundary of this upper ocean slab). We refer readers to the online Supplementary Materials for further description and justification of the model domain.
Figure 2. Map of California Current Atlantis model domain

Oceanographic Sub-model: Regional Ocean Modeling System (ROMS)

To capture the local effects of global change between years 2011-2020 and 2061-2070, we coupled a high resolution Regional Ocean Modeling System (ROMS, version 3.7, (Moore et al., 2011)) to global circulation models and Intergovernmental Panel on Climate Change (IPCC) CO$_2$ scenarios. The results capture effects of global change on pH, temperature, nutrients, and oxygen on an ecologically relevant spatial scale. We discuss this briefly below, and in detail in the Supplementary Materials (Appendix A).

To represent global climate, we used output from the GFDL ESM2M earth system model (Dunne et al., 2012, 2013) driven under IPCC climate scenario RCP8.5, which assumes continuation of present emissions trajectories (Moss et al., 2010). ESM2M includes an embedded global biogeochemical/NPZ model (TOPAZ, Stock et al., 2014). We used ESM2M results to generate the initial and boundary conditions for ROMS. ROMS is well-suited to resolve small-scale coastal phenomena, and has been successfully applied
in a wide range of regional studies worldwide (Haidvogel et al., 2008). The ROMS
spatial domain was chosen to encompass the domain of the Atlantis model with ~10-km
grid spacing. We included tidal forcing, and applied atmospheric forcing from the
ESM2M projections using bulk formulae (Fairall et al., 1996, 2003). We used a regional
nutrient-phytoplankton-zooplankton (NPZ) model coupled within the ROMS code, which
is based on that of Fennel et al. (Fennel et al., 2006, 2008) and includes carbonate
dynamics. Initial and boundary conditions for the NPZ variables were supplied from the
global TOPAZ output. The primary output of this coupled ESM2M-ROMS system is a 3-
dimensional gridded field of time series of temperature, salinity, water flux (currents),
and pH (derived from the carbonate output) in the California Current. We interpolated
these four variables onto the Atlantis spatial domain, and forced their values within the
Atlantis simulations described below. We note that future climate scenarios did not
include changes to primary productivity due to increased atmospheric carbon dioxide.

Ecology Sub-model

Our ecology sub-model represents the food web of the California Current, simulating
population dynamics, movement, and ecological interactions of 75 different functional
groups. The functional groups, data sources, and core biological and ecological
parameters and functional forms are detailed in Appendix A. Generally, functional
groups are aggregates of species with similar life histories, habitats, and diets, with finer
taxonomic resolution for harvested fish or species of conservation concern, and coarser
aggregation of many invertebrate groups. This model updates and improves on data
sources used in an earlier version of the California Current Atlantis model (Horne et al.,
2010), and functional groups were added to allow for better representation of processes
related to ocean acidification. In particular, groups added or given finer taxonomic resolution in the present model were three coral taxa (stony corals, soft corals, and black corals), Dungeness crab (*Metacarcinus magister*), pteropods, coccolithophores, and market squid (*Doryteuthis opalescens*). In total the model includes 25 benthic and planktonic invertebrate groups, five primary producer groups, 36 fish groups, 10 marine mammal groups, two bird groups, and two detritus groups. Invertebrates and primary producers are represented as simple dynamic biomass pools per 3-dimensional model cell, while vertebrate age and size structure are modeled explicitly and vary through time. Results below are presented both as functional groups and also in simplified, aggregated guilds such as ‘Sharks’ or ‘Demersal Fish’.

Recruitment of vertebrates (the production of juveniles) is based on the total abundance of adults, and recruits in the model are distributed spatially proportional to adult abundance. Recruitment of fish follows Beverton-Holt stock-recruitment dynamics (Beverton & Holt, 2012). When stock assessments were available, initial parameter estimates for Beverton-Holt parameters were calculated based on estimates of steepness (slope of the stock-recruit curve at the origin), unfished recruitment, and unfished spawning biomass. Recruitment of marine mammals, sharks, and birds were based on estimates of a fixed number of offspring per adult per year.

To parameterize diets, we drew from the database compiled by Dufault et al. (2009), which we updated to reflect the new functional group structure of the model and also to incorporate new literature sources, including many contributed by Szoboszlai et al. (2015). Those additions are noted in the Supplementary Materials (Appendix A).
Human sub-model: Fishing mortality

As noted above, the representation of human activities (other than anthropogenic-driven climate change) in these simulations is restricted to fishing, and this representation is quite simple. We assembled catch information for all Atlantis functional groups, summing total catches across US, Canada, and Mexico (Appendix A). We did not model specific fleets, but instead implemented a fixed fishing mortality rate ($\text{yr}^{-1}$). This fishing mortality gives a catch for the initial year of the simulation (2013) equal to summed 2013 US, Canadian, and Mexican catches. Fishing mortality rates were distributed evenly in space and we did not include marine protected areas or other forms of spatial management. Because fishing removes a fixed proportion of a species in each year, catches are proportional to biomass throughout these simple simulations.

Parameterizing pH sensitivity and response to changing pH

Our scenarios for pH impacts on invertebrate survival derive from a study by Busch and McElhany (submitted), which synthesized 393 papers reporting temperate species sensitivity to changes in seawater carbon chemistry. In that manuscript, summary understanding of the relative sensitivity of functional groups in the California Current ecosystem was based on how well published studies related to functional groups in and pH conditions of the California Current ecosystem, experimental design and quality, and the type of variables measured to characterize sensitivity. The results of Busch and McElhany (submitted) focus on a qualitative ranking of the sensitivity of survival of California Current functional groups to declines in pH, and they translate this qualitative ranking into a scalar that describes the relationships between functional group survival and pH (Table 1). We focused on species that showed the strongest direct negative effects
of pH on survival (primarily calcifiers). This is consistent with previous global efforts to
synthesize effects of acidification, namely strong negative impacts on calcifiers such as
corals and mollusks, but a broader range of detectable impacts on other invertebrates
(Kroeker et al., 2013, 2010; Wittmann and Pörtner, 2013).

Table 1. Scenario descriptions for projections of the effects of ocean acidification on the
California Current ecosystem. Affected functional groups are listed by Scenario with
their relative survival scalar that indicates that groups sensitivity to declines in pH (as per
Busch and McElhany (submitted)).

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Affected Functional Groups</th>
<th>Relative Survival Scalar</th>
<th>Example species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calcifying Benthos</td>
<td>benthic herbivorous grazers</td>
<td>-1</td>
<td>sea urchins (<em>Allocentrotus fragilis</em>), snails</td>
</tr>
<tr>
<td></td>
<td>bivalves</td>
<td>-0.89</td>
<td>bivalves</td>
</tr>
<tr>
<td></td>
<td>shallow benthic filter feeders</td>
<td>-0.55</td>
<td>tunicates, sponges</td>
</tr>
<tr>
<td>Copepods &amp; Pteropods</td>
<td>mesozoooplankton pteropods</td>
<td>-0.99</td>
<td>copepods</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-0.81</td>
<td>thecosome pteropods</td>
</tr>
<tr>
<td>Crabs &amp; Shrimp</td>
<td>crabs</td>
<td>-0.7</td>
<td>crabs (excluding Dungeness crab)</td>
</tr>
<tr>
<td></td>
<td>crangon shrimp</td>
<td>-0.45</td>
<td>shrimps (excluding pandalids)</td>
</tr>
<tr>
<td></td>
<td>Dungeness crab</td>
<td>-0.41</td>
<td>Dungeness crab</td>
</tr>
<tr>
<td>Non-calcifying Benthos</td>
<td>carnivorous infauna deposit feeders</td>
<td>-0.39</td>
<td>polychaetes, nematodes</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-0.37</td>
<td>amphipods, isopods</td>
</tr>
</tbody>
</table>

The survival scalars in Busch and McElhany (submitted) represent our best understanding of acidification impacts in the California Current. We translated their values into effects on mortality that we implemented in the Atlantis model. Specifically, we defined mortality due to pH effects for each functional group $f$ in Atlantis polygon $p$ at time-step $t$ as:

\[
M_{fpt}^{PH} = (8.0 - pH_{pt}) \times S_f
\]
where $M_{fpt}^{PH}$ is in units of yr$^{-1}$, pH is specified by Atlantis spatial polygon and time-step, and $S_f$ is -0.1* the relative survival scalar for each functional group (Table 1). A pH of 8.0 was chosen because average pH in the top 200 m of the water column for ROMS year 2013 was ~7.95. If $pH_{pt}$ was greater than 8.0, $M_{fpt}^{PH}$ was set to zero. As an example, this parameterization implies that for the most sensitive functional group (Benthic Herbivorous Grazers, containing species such as non-nearshore sea urchins), a decrease in pH from 8.0 to 7.0 increased their mortality rate by 0.1 yr$^{-1}$. We also tested alternate, stronger assumptions about mortality due to pH, increasing $S_f$ by up to tenfold (described below).

Ocean Acidification Scenarios

We simulated direct effects of acidification on the ten functional groups with the strongest negative ocean acidification responses, based on Busch and McElhany (submitted). We grouped these ten functional groups into four scenarios: Benthic Calcifiers, Non-Calcifying Benthos, Copepods and Pteropods, and Crabs and Shrimps (Table 1). For each scenario, we tested the effects of 2063 pH and oceanographic conditions and pH sensitivity on the functional groups within that scenario. We also tested an additional scenario where all groups in Table 1 were simultaneously sensitive to pH (referred to as the “Cumulative” scenario below).

All scenarios ran for 100 simulated years, with initial biological conditions set to year 2013, and constant fishing mortality at 2013 rates (units of yr$^{-1}$), but with the ROMS oceanography (including pH) for a single year looped 100 times. We ran two baseline simulations with no OA sensitivity, one using 2013 ROMS oceanography and one using
2063 ROMS oceanography. Runs with OA sensitivity used 2063 ROMS oceanography.

We used a single year of ROMS oceanography for two reasons: 1) creating a 50 year downscaled hydrodynamic model was too computationally intensive, and 2) using a single year of ROMS oceanography controlled for interannual variability in ocean conditions and allowed us to isolate the effects of ocean acidification from other potential drivers of change. We note that 2063 ROMS oceanography included increases in temperature as well as decreased pH, and we isolated the effects of changing pH using the baseline runs (see Metrics of pH effects below).

To test model sensitivity to our quantitative interpretation of the rankings from Busch and McElhany (submitted), we repeated all 5 scenarios but with 2.5, 5, and 10x stronger increases in mortality per 1 unit decline in pH. The most extreme case (10x) would increase mortality rates for Benthic Herbivorous Grazers by 1.0 yr\(^{-1}\) if pH fell from 8.0 to 7.0, and proportionally smaller mortality increases among the other groups, based on the Relative Survival Scalars (Table 1).

Metric of pH effect

Recognizing that multiple factors in the physical environment change when projecting future oceanography, we wanted to isolate the effects of changing pH. We developed a metric that standardizes the pH sensitivity of functional groups within a scenario (Table 1) while accounting for changes in circulation and other food web effects. The relative effect \(E\) of changing pH on biomass \(B\) for each functional group is:

\[
(2) \quad E = \frac{B_{\text{test}} - B_{2063\text{Baseline}}}{B_{2013\text{Baseline}}}
\]
where \( B_{test} \) is the biomass of a group in a given scenario, \( B_{2063Baseline} \) is the biomass for the group in the baseline model with future circulation, and \( B_{2013Baseline} \) is the biomass for the group in the baseline model with present circulation. For each simulation, we used the mean biomass of the final 10 years of a 100-year run for \( B \). While it is difficult to determine what constitutes a non-zero effect, we follow the conventions of similar ecosystem modeling exercises (Smith et al., 2011; Kaplan et al., 2013; Marshall et al., 2014), focusing on \(|E| > 0.20\). Focusing on these large effects is consistent with the overall strategic rather than tactical use of this type of end-to-end model (FAO, 2008) and means that attention is on effects of a magnitude likely to be readily detectable should they occur in real world observational data.

**pH effects on fishery revenue**

We translated the effects of pH on biomass (\( E \) in Eq. 2) to revenue using 2013 landings and revenue data (PacFIN 2013). Because fishing mortality was fixed at 2013 rates in our simulations, the effect of pH on fisheries catches is equivalent to the pH effect on biomass. We grouped functional groups into coarser management units and projected the effects of changing pH on revenue at that scale. Within the US fishery management system, individual species (and therefore Atlantis functional groups) fall within distinct management units, governed by one of several federal Fishery Management Plans (FMPs) or by state plans (deReynier, 2014). We show results for the following units: State (including all crabs and shrimps, nearshore urchins, bivalves), Groundfish (all commercially landed groundfish except Pacific Hake), Pacific Hake, and Coastal Pelagic Fish (sardine, anchovy, mackerels). We calculated the pH effect on revenue (\( U \)) for each
management unit $k$ as a weighted average of its component functional group effects ($E_j$) such that:

$$U_k = \frac{\sum E_j \cdot R_{j2013}}{\sum R_{j2013}}$$

Where the weight $R_j$ is the 2013 revenue for functional group $j$, and revenue was calculated as the product of U.S. price per metric ton and expected 2013 catch for each functional group. Additional details on reconstructing 2013 catch are provided in the Supplementary Online Material (Appendix A).

Calibrating the ecology sub-model
Following guidelines developed for an earlier version of the California Current Atlantis model (Horne et al., 2010), we calibrated the model in two phases: initial simulations with no fishing; and secondary calibrations testing constant fishing pressure. Atlantis explicitly models numbers-at-age (or number-per-cohort), and dynamic weight-at-age, and we evaluated these emergent properties following a Pattern Oriented Modeling approach (Grimm et al., 2005). Secondary calibration tested a range of fixed levels of fishing mortality applied simultaneously to all groups. As a rule of thumb we expected that $F_{MSY}$ might fall within 0.5-0.8 of natural mortality rates (Patterson, 1992; Patterson et al., 2001; Walters & Martell, 2002).

Results

ROMS forced with ESM2M
Our ROMS projection of future ocean conditions (year 2063) suggests marked declines in pH relative to present day simulations (year 2013). In the top 100 m of the water column, mean August pH in the ROMS model declines from 7.96 in the present day to 7.77 in the future (Figure 3); this is equal to the ~0.2 unit drop in pH predicted by the coarser ESM2M model (Appendix A, Figure A2), and represents a 55% increase in acidity (e.g., 55% change in \([H^+])\). As expected, the late summer period depicted in Figure 3 has the lowest pH of the year, in response to the preceding spring-summer upwelling period that characterizes the California Current. ROMS effectively represents the present day spatial pattern we expect for the system as well, with summertime reductions in pH along the coast, and a shoaling of pH clines near shore (Appendix A, Figures A3, A4). Compared to ESM2M, the spatially downscaled ROMS yields much finer predictions of spatial patchiness of future acidification; for example, some of the lowest pH values are predicted to occur very close to shore at depth (Figure 3d), and the northern continental shelf is predicted to experience slightly greater pH than in regions south of 40°N latitude (Figure 3c, d). This spatial resolution is critical for driving the future pH responses of biological groups within each Atlantis polygon. In addition, ROMS predicts warmer conditions in 2063 relative to 2013; the annual mean temperature increase in the upper 100 m of the water column is 0.9°C.
Figure 3. ROMS projections of pH in August 2013 (a and b) and August 2063 (c and d), at the surface (a and c) and bottom (b and d). ROMS runs are initialized Jan 1, 2010 or Jan 1, 2060, and are forced by GFDL ESM2M under IPCC RCP 8.5. pH within ROMS is calculated from carbonate variables simulated using the model of Fennel et al. (2006, 2008).

Calibrating and validating the ecology sub-model

Initial simulations with no fishing resulted in 86% of functional groups persisting for more than 50 years (Appendix A, Tables A1 and A2), with quasi-stable population dynamics for most groups after approximately year 50. Similar to other simulation modeling efforts (Gaichas et al., 2012; Thorpe et al., 2015), we found that ensuring persistence of all functional groups was not trivial, and we were forced to accept a parameterization that allowed 11 functional groups to decline to low levels in base case simulations (without ocean acidification). These functional groups were excluded from the analysis: arrowtooth flounder, pelagic sharks, sea stars and brittle stars, pandalid...
shrimp, grenadiers, large phytoplankton, market squid, Pacific Ocean perch, large pelagic predators, Chinook salmon, and large demersal predators. The excluded species comprise <2% of vertebrate biomass and ~1% of heterotroph (consumer) biomass. The excluded species represent 28% of the revenue generated in 2013, and do not include the top two fished species by 2013 landings (Pacific sardine and Pacific Hake). For persisting species, we obtained sensible age structures and weight-at-age within tolerance; e.g., within ±50% of initial values and ideally within ±20% (Horne et al., 2010).

Secondary calibration suggested fishing rates at maximum sustainable yields ($F_{MSY}$) near 0.05-0.1 for most groundfish stocks, with higher values (>0.2) for most pelagic species (Appendix B). This was consistent with expectations that demersal stocks have lower productivity, as evidenced by lower estimates of natural mortality (Appendix B). We also found that most groups targeted by commercial fishing were able to sustain fishing mortality held at 2013 levels. Two functional groups, petrale sole and shallow small rockfish, persisted in unfished simulations and were included in our analyses of outputs, but showed strong biomass declines under relatively moderate fishing (see Appendix B). Therefore, interpretation of results regarding these groups should be cautious.

**Effects of future pH on biomass**

Applying 2063 pH projections within 100-year Atlantis simulations caused a wide range of effects across the ecosystem, and most of these effects were negative (Figure 4). In general, there were few strong guild-level responses to decreasing pH (Figure 4A). Only one guild-level pH effect was stronger than the $|E| > 0.2$ threshold (Epibenthos in the Calcifying Benthos scenario). Overall, the functional groups in the Demersal Fish and Epibenthos guilds exhibited the highest variability, with some groups experiencing a strong pH effect and others little to no effect. Several guilds (Mammals, Seabirds, Pelagic Fish, Squid, and Primary Producers) were insensitive ($|E| < 0.2$ for all functional groups) across all the scenarios.
**Figure 4.** Ecosystem responses to forecasted pH for guilds in the California Current Atlantis model. We ran five OA scenarios, varying the sensitivity of Non-calcifying benthos (light blue), Copepods and Pteropods (green), Crabs and Shrimp (yellow), Calcifying Benthos (dark blue), and a Cumulative scenario with all of the previous scenarios combined (black). Biomass-weighted mean pH effect (E) shown as the heights of the bars in (A) and individual functional group responses in (B). Solid circles in B indicate the mean guild-level effect shown in A for comparability. Horizontal dotted lines at E=±0.2 indicate the threshold that we considered a strong effect.
In contrast to the few guild-level effects of changing pH, many individual functional groups responded strongly in each scenario (Figure 5). The scenarios directed at Calcifying Benthos, Non-Calcifying Benthos, and Crabs and Shrimps each had five functional groups with $|E| > 0.2$. In contrast, only one functional group (microzooplankton) responded strongly to the scenario directed at Copepods and Pteropods. The Cumulative scenario, which applied future conditions and pH sensitivity to all 10 functional groups in Table 1, led to strong responses in 16 functional groups (Figure 5).

**Figure 5.** Projected effects of future pH on functional group biomass for those groups with a strong effect ($|E| > 0.2$). Bars are colored according to scenario, with the same colors as in Figure 4 (Non-calcifying benthos (light blue), Copepods and Pteropods (green), Crab and Shrimp (yellow), Calcifying benthos (dark blue), and Cumulative (black)).
Sensitivity to pH in the Calcifying Benthos scenario led to strong direct effects of future pH on benthic grazers and bivalves, but no direct effects on shallow benthic filter feeders (Figure 5). Declines in benthic grazers and bivalves led to declines for three of their predators: cowcod, deep large rockfish, and Dungeness crab. All negative effects observed in Calcifying Benthos scenario were retained when pH sensitivity was added to other groups in the Cumulative scenario.

Applying pH sensitivity and future climate conditions in the Crabs and Shrimps scenario resulted in strong direct effects on the general crab group and crangon shrimp, but not Dungeness crab (Figure 5). Strongly negative indirect effects occurred on petrale sole, shallow small rockfish, and skates and rays, all of which depend heavily on crangon shrimp in their model diets. All of the negative effects observed in the Crabs and Shrimp scenario were also present in the Cumulative scenario, and strong negative effects on Dungeness crab emerged in the Cumulative scenario.

The Non-Calcifying Benthos scenario resulted in strong direct negative effects in both sensitive functional groups: benthic detritivores and benthic carnivores (Figure 5). Petrale sole, small demersal sharks, and Dover sole experienced strong indirect negative effects in this scenario even though none of these species preys directly on the pH-sensitive groups. It is likely these indirect effects were modulated through a shared prey group (e.g., crangon shrimp) that was weakly affected by declines in benthic detritivores and benthic carnivores. All negative effects in the Non-Calcifying Benthos scenario were also present in the Cumulative scenario, except benthic carnivores were only weakly affected ($E < 0.2$) when all species were sensitive to pH.
The Copepods and Pteropods scenario resulted in no strong responses by either of the
directly affected groups: Copepods and pteropods declined by 2 and 5 %, respectively.
However, copepods are a very abundant group (estimated at nearly 20 million metric tons
for our large model domain; Appendix A, Table A1), and this is a substantial shift in
absolute terms. Microzooplankton, a prey group for both copepods and pteropods,
responded strongly in the positive direction to the negative effects on its predators
(Figure 5). This indirect effect was also seen in the Cumulative scenario.

The Cumulative scenario produced more strong responses than the preceding scenarios,
primarily negative responses by Demersal Fishes and Epibenthos (Figure 4). It also
resulted in two strong indirect effects not observed in any of the other scenarios (Figure
5). Deep small rockfish, which prey upon many of the pH-sensitive groups, responded
negatively (E = -0.40) when all of the sensitive groups declined with pH. The other new
indirect response was by nearshore urchins, which had a strong positive response (E =
0.68). Nearshore urchins are fed upon by many of the fish groups that experienced
indirect negative effects. Moreover, nearshore urchins were assumed not to be directly
sensitive to ocean acidification; the meta-analysis of Busch and McElhany (submitted)
suggests that these commercially harvested nearshore urchins are less susceptible to
acidification than our benthic herbivorous grazers group, which includes deeper-dwelling
urchin species.

Effects of future pH on catch and revenue in Cumulative scenario

Our simplistic representation of fishing and revenue projected that most fishery
management units we explored were negatively affected by future pH in the Cumulative
scenario (Table 2). Proportional effects of pH on catch and biomass at the functional
group level are equal because we parameterized fishing using fixed fishing mortality rates for each functional group. The State-managed unit had the largest projected pH effect on revenue \( (U = -0.29) \), driven by the strong negative effect of pH on Dungeness crab, which supports a valuable fishery (200 million USD in 2013). Other crabs and bivalves were negatively affected by future pH, but the 2013 revenue from those fisheries is an order of magnitude lower than the Dungeness crab fishery. The urchin fishery targets the nearshore urchin group, which was the only harvested functional group that was projected to increase under future pH conditions.

Table 2. Effects of future pH on commercially important management units, from the scenario with all groups in Table 1 sensitive to pH. Management units are listed in order of greatest to least effects of pH on revenue, and the three-four most strongly affected functional groups within those management units are identified.

<table>
<thead>
<tr>
<th>Management Unit</th>
<th>Most Affected Functional Groups</th>
<th>pH Effect Biomass and Catch</th>
<th>pH Effect Revenue</th>
<th>Baseline Revenue (millions USD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>State</td>
<td>Dungeness crab</td>
<td>-0.30</td>
<td>220</td>
<td>260</td>
</tr>
<tr>
<td></td>
<td>crabs</td>
<td>-0.61</td>
<td>9.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>bivalves</td>
<td>-0.29</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td></td>
<td>urchins</td>
<td>0.61</td>
<td>6.8</td>
<td></td>
</tr>
<tr>
<td>Groundfish</td>
<td>petrale sole</td>
<td>-1.1</td>
<td>7.5</td>
<td>88</td>
</tr>
<tr>
<td></td>
<td>Dover sole</td>
<td>-0.39</td>
<td>9.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>deep large rockfish</td>
<td>-0.35</td>
<td>5.0</td>
<td></td>
</tr>
<tr>
<td>Hake</td>
<td>hake</td>
<td>-0.038</td>
<td>-0.038</td>
<td>76</td>
</tr>
<tr>
<td>Coastal Pelagics</td>
<td>sardine</td>
<td>-0.030</td>
<td>27</td>
<td>110</td>
</tr>
<tr>
<td></td>
<td>jack mackerel</td>
<td>-0.050</td>
<td>1.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>anchovy</td>
<td>-0.026</td>
<td>1.3</td>
<td></td>
</tr>
</tbody>
</table>
The Groundfish management unit (excluding Pacific hake) did not experience a substantial pH effect on revenue ($U=-0.18$). This group of species generated $88$ million in revenue in 2013. While this decline was not dramatic ($|U| < 0.20$) for the total revenue from species managed under the groundfish FMP, our model projects more substantial declines for particular commercially important groundfish such as petrale sole, Dover sole, and deep large rockfish (mostly shortspine thornyhead, *Sebastolobus alascanus*).

The remaining management units did not show strong effects of changing pH ($|U| < 0.2$).

The model projected a very small pH effect ($U=-0.038$) on Hake fishery revenue, in a fishery generating 76 million USD of revenue in 2013. For species managed collectively under the Coastal Pelagic Species FMP, the pH effect was less than 0.01. We do not show results for Salmon or Highly Migratory Species FMPs due to the poor performance of those species in the model (Chinook and large pelagic predators were removed due to low biomass in baseline runs).

**Sensitivity of pH effects to strength of the pH response**

As would be expected *a priori*, the effects of future pH at the guild-level were sensitive to the magnitude of the mortality scalar. The magnitude of positive and negative effects increased as the scalar increased to 2.5x to 10x our base case values (Appendix C).

However, the directions of pH effects at the guild and functional group levels were consistent regardless of the mortality scalar, as was the set of functional groups and guilds identified as likely impacted by pH effects.

**Discussion**

*Interpretation of Atlantis results*
Global change is projected to have pronounced impacts on marine ecosystems and resources in temperate zones. The climate change scenario applied here, IPCC scenario RCP 8.5, will have high impacts on mid-latitude bivalve fisheries and aquaculture, and high to moderate impacts on mid-latitude finfish fisheries, according to a growing body of research (Barange et al., 2014; Gattuso et al., 2015). In fact, many symptoms of global change are already being observed in the California Current ecosystem, including warming, shifts in community structure and phenology (Thorson et al., 2016), and major hypoxic events (reviewed in Doney et al., 2012). There is already evidence of ocean acidification impacts: episodic year-class failures of Pacific oysters (Crassostrea gigas) along the US West Coast have been attributed to OA (Barton et al., 2012), and Bednaršek and Ohman (2015) have documented OA-driven shell dissolution in the pteropod Limacina helicina in the southern California Current.

Our modeling effort, which synthesized downscaled climate models, experimental and empirical studies, and a well-established end-to-end marine ecosystem modeling framework, provides a broad overview of potential ecosystem-scale effects of OA in the California Current. We saw wide-ranging effects across multiple guilds and functional groups, but more losers than winners in terms of biomass and lost fishery revenue. Model predictions suggest the most dramatic effects of future pH decreases will be felt by demersal fish, sharks, and epibenthic invertebrates, and less so by pelagic species, marine mammals and seabirds. This was likely driven by the stronger responses of sensitive benthic organisms to changing pH, compared to relatively weak responses of sensitive zooplankton groups. Our approach demonstrated that combining multiple scenarios into a
single, cumulative scenario can lead to unanticipated, indirect responses by groups that were relatively insensitive in simpler scenarios.

The value of taking both a population and systems approach is further evident when comparing our preliminary ranking of direct pH responses (Table 1) to the cumulative impacts projected by the Atlantis model (Figure 4 and 5). Although experimental and empirical literature suggests that copepods, shallow benthic filter feeders, and Dungeness crabs may be susceptible to OA (Busch and McElhany, submitted), none of them responded strongly in scenarios where they were directly affected by pH. All three functional groups exhibited relatively high productivity, which prevented substantial declines in their biomass due to direct effects. Indirect effects were responsible for declines in Dungeness crab, a major fishery target. We only observed a strong pH effect on Dungeness crab when their prey declined due to OA (Calcifying Benthos scenario), but not due to direct pH-driven mortality (Crabs and Shrimp scenario). This insight highlights the utility of end-to-end models for comparing multiple scenarios (Busch et al., 2013), as well as the ability of the Atlantis model to integrate over direct effects, indirect trophic effects, and population-level productivity.

From a fishery management perspective, economic impacts in the California Current may stem from indirect ocean acidification effects on high-value target species such as Dungeness crab and groundfish. Previous research has focused on global economic and nutritional losses due to projected direct ocean acidification effects on shellfish (Cooley et al., 2012), but our work suggests careful consideration must also be given to the supporting role that shellfish and other species play in the food web. At a minimum,
economic impact assessments should include fisheries that target species dependent on calcifying prey (e.g., Cooley & Doney, 2009).

Other investigations of future change in the California Current provide more context for interpreting our results. Using an earlier version of the California Current Atlantis model, Kaplan et al. (2010) forced moderate, acidification-driven declines on benthic invertebrates, which caused declines in flatfish, small demersal sharks, and skates and rays. These projected declines were consistent with ours, even though the meta-analysis of Busch and McElhany (submitted) that informed the current analysis suggested that seastars and brittlestars are less sensitive to acidification than was assumed by Kaplan et al. (2010). Kaplan et al. (2010) also found indirect effects leading to increased canary rockfish and the shallow miscellaneous fish group. These increases were not supported by our analysis because we changed the functional group composition to better represent groups susceptible to OA, which resulted in changes to the diet parameterization in these groups. In a food web model with much simpler spatial structure and no oceanographic forcing, Ainsworth et al. (2011) found very limited system-level effects of changing pH on the northern portion of the California Current. In contrast to our results, cumulative impacts of multiple stressors in their study were greater for the pelagic than demersal components of the food web; this is likely because Ainsworth et al. (2011) assumed that euphausiids were also sensitive to OA, which was not robustly supported by Busch and McElhany (submitted).

Ocean acidification is not the only global change stressor affecting this ecosystem. King et al. (2011) used conceptual models to forecast the effects of climate change on the California Current, and focused primarily on changes in temperature, dissolved oxygen
and precipitation. They predicted that many demersal fish (such as Dover sole, sablefish, and rockfish) may be buffered against ocean warming because they can move north or into deeper water temperature refuges. They did not consider ocean acidification, however, and our results suggest that OA may create vulnerability for demersal fish, even relatively mobile ones, through erosion of their prey base. King et al. (2011) also forecasted that warmer waters may support larger sardine populations, and since our Atlantis results did not indicate indirect sensitivities to OA in the pelagic fish guild, this may be an opportunity for a global change “winner” when combining the effects of temperature and OA. Overall, further consideration of the joint effects of temperature, ocean acidification and hypoxia are warranted within the California Current. King et al. (2011) noted that some demersal fishes, such as Dover sole, may be able to take advantage of expanding hypoxic zones on the continental shelf. Global modeling by Barange et al. (Barange et al., 2014) that includes temperature effects but omits acidification suggests that some mid to high-latitude fisheries may benefit in the future, and that primary production may increase in the northern portion of the California Current. Stressors like OA, warming temperatures and low dissolved oxygen will likely co-occur and interact (Reum et al., 2014), and future Atlantis scenarios that attempt to address these combined stressors will have to rely on experimental studies that examine their cumulative effects on key species.

Uncertainty, caveats, and gaps

Projections of living marine resources under global change contain uncertainty stemming from three sources: internal variability, model uncertainty (including parameter and structural uncertainty), and scenario uncertainty (Cheung et al., 2016). We have reduced
the effects of internal variability (e.g. interannual climate variation, interdecadal climate
regime shifts) by forcing Atlantis with a single representative year of oceanography and
biogeochemistry (2013 or 2063). Model parameter uncertainty is harder to address: large
numbers of input parameters within models such as Atlantis preclude some formal
quantification methods such as Bayesian or Monte Carlo approaches (Cheung et al.
2016). The computational expense and long run-times of Atlantis model simulations
present an additional challenge. In the future, parameter uncertainty may be addressed by
bounded parameterizations (Fulton et al., 2011) that bracket stock productivities, an
approach that has been applied for an earlier version of the California Current Atlantis
model (Pacific Fishery Management Council & NMFS, 2014). Uncertainties stemming
from model structure can be understood via model inter-comparisons and skill
assessment (Payne et al., 2015). Scenario uncertainty is likely to be the most important
factor for long term projections (Hawkins & Sutton, 2009) beyond the 2060s; we agree
with Cheung et al. (2016) that this is best captured using scenarios for not only emissions
and climate but also fishery development and management. Though our scenarios here
assume simple fixed fishing mortalities, global efforts (Merino et al., 2010; Msangi et al.,
2013) and nascent local efforts (Kaplan et al., 2012) to develop meaningful social-
economic scenarios offer promise in this respect.

Ecosystem model outcomes are fundamentally affected by modelers’ assumptions and
decisions about input data, parameter development, and model structure (Link et al.,
2012). An assumption that is central to the present study is our parameterization of
sensitivity to pH. Despite a large body of experimental work (e.g., Busch and McElhany,
submitted), the sensitivities to pH for functional groups in our model are known with
very little precision. We expect the ranking of pH sensitivity to be generally robust, but
the scale of that sensitivity is hard to quantify in part because we are translating effects on
individuals under controlled experimental conditions to functional group-level effects in
the model. Further, we modeled pH sensitivity as reduced survival because that is the
most straightforward to implement and an approach similar to others’ (Kaplan et al.,
2010; Griffith et al., 2011; Weijerman et al., 2015). However, meta-analyses suggest the
physiological effects of changing pH may also involve reproduction or growth (Kroeker
et al., 2010). Modifying mortality rates as we have done here may be an appropriate
proxy in some cases but may over or under-represent the effect of changing pH on some
organisms. Using mortality rates to capture pH sensitivity has another limitation in our
Atlantis model; we are unable to project direct effects of OA that are positive (e.g., for
seagrasses), which limits the scope of our forecasts. However, we can, and did project
some positive indirect effects of future pH. Lastly, our results reflect the way we chose to
model the process of ocean acidification—by projecting pH, not aragonite or some other
calcium carbonate saturation state. Alternate ways of modeling OA may lead to different
conclusions about ecosystem and fishery effects.

Our California Current Atlantis model does not capture the dynamics of all functional
groups in the ecosystem—for example pandalid shrimp, market squid, and tuna
functional groups do not persist in our baseline 100-year model simulation. Therefore,
we cannot infer potential effects of OA on these components of the food web (or the
fisheries that target these groups). Two of the modeled fish groups (Petrale sole and
shallow small rockfish) persist in the baseline simulation and demonstrate strong indirect
sensitivity to pH, but these simulated groups may be less productive in the model than
they are in reality, and we may therefore overestimate their sensitivity to OA. This low productivity is evident from calibration tests for some groups that suggest lower sustainable yields than what has been estimated by stock assessments (see online material Appendix B).

The caveats associated with ecosystem model projections are a good reminder of how these results should be interpreted and used. Our findings about winners and losers in the ecosystem, functional groups that are more or less sensitive to changing pH in the California Current, and potential impacts to fisheries revenues provide a set of forecasts that build upon previous findings and pave the way for hypotheses to guide future modeling and experimental analysis. For example, in this study we summarized the effects of changing pH at a coast-wide scale. We found limited effects at the coarse guild-level but stronger effects when we looked at individual functional groups. Similarly, aggregating across space likely had a smoothing effect that obscured more dramatic and meaningful changes in particular locations. Spatial scale is particularly important when considering the way that fishing communities interact with ocean ecosystems-- typically with local knowledge and long histories of particular fishing grounds within reach of home ports (St. Martin & Hall-Arber, 2008). Therefore, a key next step for this model is to investigate how the effects of changing pH vary across space, and what that means for place-based human communities, similar to a recent risk assessments for Alaskan fishing regions (Mathis et al., 2015) and larger US regions (Ekstrom et al., 2015).

Implications for management

We can begin to understand cumulative impacts on large marine ecosystems by using models that combine experimental studies, physical models, and food web models such
as the one presented here for the California Current. Describing and understanding effects of global change on large marine ecosystems, including human communities, requires integration of diverse methodologies and interdisciplinary teams (Hollowed et al., 2013a). While this type of end-to-end model is not intended to make precise, tactical forecasts for fisheries management, it can be used to identify risks to marine ecosystem structure and function (Hollowed et al., 2013b). Combined with information about the adaptive capacity of human communities (Morzaria-Luna et al., 2014; Mathis et al., 2015), end-to-end models can inform risk assessments of human communities to global change. Ocean acidification is occurring in the California Current, and our model suggests the risks of changing pH are greatest for epibenthic invertebrates and demersal fish, and the fisheries that target these groups. Models such as Atlantis can be used to present broad alternatives for how ecosystems and populations may evolve under global change, and our results provide strategic guidance to managers on the West Coast of the U.S. that can be followed up with tactical simulation tests to identify robust management strategies (Punt et al., 2013).

Acknowledgments

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Supplementary Materials

Appendix A. Atlantis model documentation.
Appendix B. Model sensitivity to fishing mortality rates.

Appendix C. Sensitivity of the pH effect of Benthic herbivorous grazers to the survival scalar.

References


Statement (DEIS) for proposed Harvest Specifications and Management Measures for the Pacific Coast Groundfish Fishery and Amendment 24 to The Pacific Coast Groundfish Fishery Management Plan. PFMC and NMFS, Portland, OR and Seattle, WA.


