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11 **Title:** Risks of ocean acidification in the California Current food web and fisheries:

12 ecosystem model projections

13 **Running head:** Ocean acidification in the California Current

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Abstract

35   The benefits and ecosystem services that humans derive from the oceans are threatened

36   by numerous global change stressors, one of which is ocean acidification. Here, we

37   describe the effects of ocean acidification on an upwelling system that already

38   experiences inherently low pH conditions, the California Current. We used an end-to-end

39   ecosystem model (Atlantis), forced by downscaled global climate models and informed

40   by a meta-analysis of the pH sensitivities of local taxa, to investigate the direct and

41   indirect effects of future pH on biomass and fisheries revenues. Our model projects a 0.2

42   unit drop in pH during the summer upwelling season from 2013 to 2063, which results in

43   wide-ranging magnitudes of effects across guilds and functional groups. The most

44   dramatic direct effects of future pH may be expected on epibenthic invertebrates (crabs,

45   shrimps, benthic grazers, benthic detritivores, bivalves), and strong indirect effects

46   expected on some demersal fish, sharks, and epibenthic invertebrates (Dungeness crab)

47   because they consume species known to be sensitive to changing pH. The model's

48   pelagic community, including marine mammals and seabirds, was much less influenced

49   by future pH. Some functional groups were less affected to changing pH in the model

50   than might be expected from experimental studies in the empirical literature due to high

51 population productivity (e.g. copepods, pteropods). Model results suggest strong effects

52 of reduced pH on nearshore state-managed invertebrate fisheries, but modest effects on

53 the groundfish fishery because individual groundfish species exhibited diverse responses

54 to changing pH. Our results provide a set of projections that generally support and build

55 upon previous findings and set the stage for hypotheses to guide future modeling and

56 experimental analysis on the effects of OA on marine ecosystems and fisheries.

57 **Introduction**

58 Humans rely on healthy ocean ecosystems for the benefits and services they provide.

59 However, global climate changes caused by continued fossil fuel emissions are subjecting

60 the oceans to multiple stressors, including increasing temperature and changes in water

61 chemistry (Harley *et al.*, 2006; Crain *et al.*, 2008; Solomon *et al.*, 2009). As oceans cover

62 a majority of the Earth's surface and provide critical resources for human communities,

63 understanding how future climate conditions will affect factors such as food security and

64 coastal economies is a central question in climate change research (Crain *et al.*, 2008).

65 This question must be addressed at a global scale, but also for downscaled bio-physical

66 interactions within individual ecosystems (Barange *et al.*, 2014), expressed in terms of

67 regional and national ecosystem services such as fisheries, recreation, and coastal

68 protection (Gattuso *et al.*, 2015).

69 Global change manifests in the ocean in multiple ways, one of which is ocean

70 acidification (OA), the process by which oceans absorb anthropogenic CO_2 from the

71 atmosphere and experience decreased pH and carbonate ion concentrations (Orr *et al.*,

72 2005; Doney *et al.*, 2009). Dissolution of CO_2 in water creates free hydrogen ions,

73 lowering the pH and thus altering a defining trait of the seawater to which marine

74 organisms are adapted. The oceans absorb about one-third of the anthropogenic CO_2

75 released into the atmosphere. Since the mid-1700s, this CO_2 uptake has decreased mean

76 pH in surface ocean waters by 0.1 units; by the end of this century, surface ocean pH may

77 decline by an additional 0.3 units (Caldeira & Wickett, 2003), with changes likely to vary

78 spatially (McElhany & Busch, 2013).

79 Upwelling systems may be particularly vulnerable to OA because they already

80 experience seasonal drops in pH compared to other ocean ecosystems (Feely *et al.*, 2008).

81   The upwelling process brings deep, cold, nutrient-rich waters up onto the continental

82   shelf, fueling highly productive coastal ecosystems. However, these upwelled waters also

83   have relatively low pH and low oxygen concentrations, and thus introduce potentially

84   stressful conditions into coastal areas. Alternatively, regular exposure to low pH could

85   lead to higher rates of adaptation to changing ocean chemistry (Reum *et al.*, 2014).

86   Regardless, changes to ocean chemistry have the potential to affect susceptible marine

87   organisms, particularly those that lay down a calcium carbonate shell (Kroeker *et al.*,

88   2013; Wittmann & Pörtner, 2013). Calcifiers include species such as bivalves,

89   crustaceans, and echinoderms that are commercially and ecologically important; as such,

90   the direct and indirect effects of OA may be widespread throughout a food web (Kaplan

91   *et al.*, 2010; Busch *et al.*, 2013). We define *direct effects* as changes caused by exposure

92   to corrosive waters, while *indirect effects* are changes caused by interactions with species

93   that are directly affected (e.g., predators or prey of calcifiers).

94   Here, we focus on the California Current, an Eastern Boundary Current ecosystem where

95   the physical processes that combine upwelling with changing ocean chemistry have been

96   studied extensively (Feely *et al.*, 2008; Gruber *et al.*, 2012). Understanding cumulative

97   impacts of OA at the scale of an ecosystem like the California Current requires models

98   that can project direct and indirect effects. For example, end-to-end models (Plagányi,

99   2007; Travers *et al.*, 2007; Rose *et al.*, 2010) that incorporate processes like physics,

100   multi-species trophic effects, and fisheries can be used to simulate future projections of

101   ecosystem dynamics and to evaluate trade-offs among alternative fishery management

102   strategies (Fulton *et al.*, 2014), while evaluating consequences of global change (Lehodey

103   *et al.*, 2010), and coupling between oceanography and species dynamics (Fiechter *et al.*,

104   2014). Atlantis (Fulton, 2004; Fulton *et al.*, 2011) is a spatially explicit end-to-end model

105   that includes physical oceanography, biogeochemistry, food web dynamics, and human

106   uses and impacts such as fishing and nutrient loading. The Atlantis framework has been

107   applied in simple ways to test impacts of ocean acidification in Australia (Griffith *et al.*,

108   2011, 2012) and Guam (Weijerman *et al.*, 2015). Atlantis models have been developed

109   for the California Current (Brand *et al.*, 2007; Horne *et al.*, 2010) and applied to test

110   impacts of new and existing fisheries (Kaplan *et al.*, 2013; Marshall *et al.*, 2014) and

111   alternative management strategies (Kaplan *et al.*, 2012; Pacific Fishery Management

112   Council & NMFS, 2014), as well as coarse scale effects of ocean acidification (Kaplan *et*

113   *al.*, 2010).

114   Building on these earlier Atlantis modeling efforts, we projected the cumulative effects of

115   future ocean acidification on the California Current ecosystem. First, we projected pH in

116   the California Current 50 years in the future (2063), using global earth systems models to

117   force a regional ocean-climate model (dynamical downscaling). This regional model

118   provided the physical conditions that underpinned Atlantis simulations of marine food

119   web interactions and US West Coast fisheries dynamics. We lowered survival of

120   functional groups sensitive to changing pH, based on a meta-analysis of experimental

121   studies. We then ran Atlantis scenarios that simulated: 1) the direct effects of a 0.2 unit

122   change in pH by 2063 on biomass of organisms sensitive to acidification; 2) the indirect

123   effects of changing pH on the rest of the food web; and 3) the resulting effects on

124   fisheries landings and revenues.

125   **Materials and Methods**

126   Atlantis is a spatially explicit modeling platform (Fulton, 2004) that couples three sub-

127   models: 1) an oceanographic sub-model, 2) an ecology sub-model, and 3) a human sub-

128   model (Fig. 1). We focused on the first two components for this application and used a

129   simple representation of fishing for the third component. Below we summarize the three

130   sub-models, how we parameterized pH sensitivity, and the scenarios we developed to

131   investigate the effects of changing pH on the California Current ecosystem. Our current

132   application of the California Current Atlantis model builds on and updates earlier

133   versions (Brand *et al.*, 2007; Horne *et al.*, 2010; Kaplan *et al.*, 2012). Additional details

134   are available in the online Supporting Information (S1).

135   *Model domain*

136   Our model domain covers 1.475 million km^2, with 92,000 km^2 on the continental shelf

137   (0-200 m), 127,500 km^2 on the continental slope (200-1200 m), and 1.12 million km^2 in

138   pelagic waters offshore of the 1200-m isobath. The model domain covers the extent of

139   the California Current, from its origin where the North Pacific Current meets the coast of

140   North America at the north end of Vancouver Island (Checkley & Barth, 2009) south to

141 Punta Eugenia, Baja California, Mexico (Fig. 2). The domain is divided into 2-

142 dimensional polygons. Polygon boundaries parallel to the coast (running North-South,

143 approximately) follow the bathymetry of the 50-m, 100-m, 200-m, 550-m, and 1200-m

144 isobaths, and the 200-nautical mile (370-km) limit of the Exclusive Economic Zone

145 (EEZ). Polygon boundaries perpendicular to the coast (running East-West, approximately

146 were based on a compromise between biogeography, fishery management and catch

147 reporting areas, and areas utilized by particular fleets and fisheries. Three-dimensional

148 model cells are created by adding depth layers in vertical dimension, which were set

149 using the same interval as isobaths listed above. The offshore pelagic polygons, which

150 extend from the 1200-m isobath to the EEZ limit, are assumed to be 2400 m deep (with

151 an open boundary representing deeper waters lying underneath and along the western

152 boundary of this upper ocean slab). We refer readers to the online Supporting Information

153 (S1) for further description and justification of the model domain.

154

155

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

157 To capture the local effects of global change between years 2011-2020 and 2061-2070,

158 we coupled a high resolution Regional Ocean Modeling System (ROMS, version 3.7,

159 (Moore *et al.*, 2011)) to global circulation models and Intergovernmental Panel on

160 Climate Change (IPCC) CO_2 scenarios. The results capture effects of global change on

161 pH, temperature, nutrients, and oxygen on an ecologically relevant spatial scale. We

162 discuss this briefly below, and in detail in the Supporting Information (S1, Figs. S1.2-

163 S1.5).

164 To represent global climate, we used output from the GFDL ESM2M earth system model

165 (Dunne *et al.*, 2012, 2013) driven under IPCC climate scenario RCP8.5, which assumes

166 continuation of present emissions trajectories (Moss *et al.*, 2010). ESM2M includes an

167 embedded global biogeochemical/NPZ model (TOPAZ, Stock *et al.*, 2014). We used

168 ESM2M results to generate the initial and boundary conditions for ROMS. ROMS is

169 well-suited to resolve small-scale coastal phenomena, and has been successfully applied

170 in a wide range of regional studies worldwide (Haidvogel *et al.*, 2008). The ROMS

171   spatial domain was chosen to encompass the domain of the Atlantis model with ~10-km

172   grid spacing. We included tidal forcing, and applied atmospheric forcing from the

173   ESM2M projections using bulk formulae (Fairall *et al.*, 1996, 2003). We used a regional

174   nutrient-phytoplankton-zooplankton (NPZ) model coupled within the ROMS code, which

175   is based on that of Fennel et al. (Fennel *et al.*, 2006, 2008) and includes carbonate

176   dynamics. Initial and boundary conditions for the NPZ variables were supplied from the

177   global TOPAZ output. The primary output of this coupled ESM2M-ROMS system is a 3-

178   dimensional gridded field of time series of temperature, salinity, water flux (currents),

179   and pH (derived from the carbonate output) in the California Current. We interpolated

180   these four variables onto the Atlantis spatial domain, and forced their values within the

181   Atlantis simulations described below (see S1 for detailed description). We note that

182   future climate scenarios did not include changes to primary productivity due to increased

183   atmospheric carbon dioxide.

184   *Ecology Sub-model*

185   Our ecology sub-model represents the food web of the California Current, simulating

186   population dynamics, movement, and ecological interactions of 75 different functional

187   groups. The functional groups, data sources, and core biological and ecological

188   parameters and functional forms are detailed in the Supporting Information (S1, Part II).

189   Generally, functional groups are aggregates of species with similar life histories, habitats,

190   and diets, with finer taxonomic resolution for harvested fish or species of conservation

191   concern, and coarser aggregation of many invertebrate groups. This model updates and

192   improves on data sources used in an earlier version of the California Current Atlantis

193   model (Horne *et al.*, 2010), and functional groups were added to allow for better

194   representation of processes related to ocean acidification. In particular, groups added or

195   given finer taxonomic resolution in the present model were three coral taxa (stony corals,

196   soft corals, and black corals), Dungeness crab (*Metacarcinus magister*), pteropods,

197   coccolithophores, and market squid (*Doryteuthis opalescens*). In total the model includes

198   25 benthic and planktonic invertebrate groups, five primary producer groups, 36 fish

199   groups, 10 marine mammal groups, two bird groups, and two detritus groups.

200   Invertebrates and primary producers are represented as simple dynamic biomass pools

201   per 3-dimensional model cell, while vertebrate age and size structure are modeled

202 explicitly and vary through time. Results below are presented both as functional groups

203 and also in simplified, aggregated guilds such as 'Sharks' or 'Demersal Fish'.

204 Recruitment of vertebrates (the production of juveniles) is based on the total abundance

205 of adults, and recruits in the model are distributed spatially proportional to adult

206 abundance. Recruitment of fish follows Beverton-Holt stock-recruitment dynamics

207 (Beverton & Holt, 2012). When stock assessments were available, initial parameter

208 estimates for Beverton-Holt parameters were calculated based on estimates of steepness

209 (slope of the stock-recruit curve at the origin), unfished recruitment, and unfished

210 spawning biomass. Recruitment of marine mammals, sharks, and birds were based on

211 estimates of a fixed number of offspring per adult per year.

212 We parameterized diets by drawing from multiple sources. We largely drew from the

213 database compiled by Dufault et al. (2009), but updated these estimates to reflect the new

214 functional group structure of the model and also to incorporate new literature sources,

215 including many contributed by Szoboszlai et al. (2015). Those additions are noted in the

216 Supporting Information (S1, Part II).

217 *Human sub-model: Fishing mortality*

218 As noted above, the representation of human activities (other than anthropogenically-

219 driven climate change) in these simulations is restricted to fishing, and this

220 representation is quite simple. We assembled catch information for all Atlantis functional

221 groups, summing total catches across US, Canada, and Mexico (Figs. S1.8 and S1.9). We

222 did not model specific fleets, but instead implemented a fixed fishing mortality rate (yr^{-1}).

223 This fishing mortality gives a catch for the initial year of the simulation (2013) equal to

224 summed 2013 US, Canadian, and Mexican catches. Fishing mortality rates were

225 distributed evenly in space and we did not include marine protected areas or other forms

226 of spatial management. Because fishing removes a fixed proportion of a species in each

227 year, catches are proportional to biomass throughout these simple simulations.

228 *Parameterizing pH sensitivity and response to changing pH*

229 Our scenarios for pH impacts on invertebrate survival derive from a study by Busch and

230 McElhany (2016), which synthesized 393 papers reporting temperate species sensitivity

231   to changes in seawater carbon chemistry. In that manuscript, summary understanding of

232   the relative sensitivity of functional groups in the California Current ecosystem was

233   based on how well published studies related to functional groups in and pH conditions of

234   the California Current ecosystem, experimental design and quality, and the type of

235   variables measured to characterize sensitivity. Busch and McElhany (2016) provided

236   "relative survival scalars", which were derived from qualitative scoring of three factors:

237   direction of pH effect recorded in each study, total amount of evidence available for the

238   functional group, and the level of agreement among the studies with respect to the

239   functional group's response. These qualitative scores were scaled relative to the most

240   sensitive functional group's score to arrive at a relative survival scalar that describes the

241   relationship between survival and pH (Table 1). In this study, we focused on functional

242   groups that showed the strongest direct negative effects of pH on survival (primarily

243   calcifiers).   This is consistent with previous global efforts to synthesize effects of

244   acidification, namely strong negative impacts on calcifiers such as corals and mollusks,

245   but a broader range of detectable impacts on other invertebrates (Kroeker et al., 2013,

246   2010; Wittmann and Pörtner, 2013).

247

248   The relative survival scalars in Busch and McElhany (2016) represent our best

249   understanding of acidification impacts in the California Current. We translated these

250   relative values into quantitative effects on mortality that we implemented in the Atlantis

251   model. Specifically, we defined mortality due to pH effects for each functional group *f* in

252   Atlantis polygon *p* at time-step *t* as:

253   *(1)* $M_{fpt}^{pH} = (8.0 - pH_{pt}) \times -0.1 * S_f$

254   where M_{fpt}^{pH} is in units of yr $^{-1}$, pH is specified by Atlantis spatial polygon and time-step,

255   and S_f is the relative survival scalar for each functional group (Table 1). A pH of 8.0 was

256   chosen because average pH in the top 200 m of the water column for ROMS year 2013

257   was ~7.95. If pH_{pt} was greater than 8.0, M_{fpt}^{pH} was set to zero. As an example, this

258   parameterization implies that for the most sensitive functional group (Benthic

259   Herbivorous Grazers, containing species such as non-nearshore sea urchins), a decrease

260   in pH from 8.0 to 7.0 increased their mortality rate by 0.1 yr^{-1}. This induced mortality rate

261   is twice the maximum predation mortality rate on Benthic Herbivorous grazers during the

262   100 year baseline simulation, without ocean acidification impacts (0.047). We scaled S_f

263   by 0.1 after testing a range of values from 0.1 to 1 (described below).

264

265   *Ocean Acidification Scenarios*

266   We simulated direct effects of acidification on the ten functional groups with the

267   strongest negative ocean acidification responses, based on Busch and McElhany (2016).

268   We grouped these ten functional groups into four scenarios: Benthic Calcifiers, Non-

269   Calcifying Benthos, Copepods and Pteropods, and Crabs and Shrimps (Table 1). Note

270   that scenario names are capitalized to differentiate them from functional group names.

271   For each scenario, we tested the effects of 2063 pH and oceanographic conditions and pH

272   sensitivity on the functional groups within that scenario. We also tested an additional

273   scenario where all groups in Table 1 were simultaneously sensitive to pH (referred to as

274   the "Cumulative" scenario below).

275   All scenarios ran for 100 simulated years, with initial biological conditions set to year

276   2013, and constant fishing mortality at 2013 rates (units of yr^{-1}), but with the ROMS

277   oceanography (including pH) for a single year looped 100 times. We ran two baseline

278   simulations with no OA sensitivity, one using 2013 ROMS oceanography and one using

279   2063 ROMS oceanography. Runs with OA sensitivity used 2063 ROMS oceanography.

280   We used a single year of ROMS oceanography for two reasons: 1) creating a 50 year

281   downscaled hydrodynamic model was too computationally intensive, and 2) using a

282   single year of ROMS oceanography controlled for interannual variability in ocean

283   conditions and allowed us to isolate the effects of ocean acidification from other potential

284   drivers of change. We note that 2063 ROMS oceanography included increases in

285   temperature as well as decreased pH, and we isolated the effects of changing pH using

286   the baseline runs (see *Metrics of pH effects* below).

287   To test model sensitivity to our quantitative interpretation of the rankings from Busch and

288   McElhany (2016), we repeated all 5 scenarios but with 2.5, 5, and 10x stronger increases

289   in mortality per 1 unit decline in pH. The most extreme case (10x) would increase

290   mortality rates for Benthic Herbivorous Grazers by 1.0 yr^{-1} if pH fell from 8.0 to 7.0, and

291   proportionally smaller mortality increases among the other groups, based on the relative

292   survival scalars (Table 1).

293

294   *Metric of pH effect*

295   Recognizing that multiple factors in the physical environment change when projecting

296   future oceanography, we wanted to isolate the effects of changing pH. We developed a

297   metric that standardizes the pH sensitivity of functional groups within a scenario (Table

298   1) while accounting for changes in circulation and other food web effects. We define the

299   relative effect (E) of changing pH on biomass (B) for each functional group as:

300   (2) $$E = \frac{B_{test} - B_{2063Baseline}}{B_{2013Baseline}}$$

301   where B_{test} is the biomass of a group in a given scenario, $B_{2063Baseline}$ is the biomass for

302   the group in the baseline model with future circulation, and $B_{2013Baseline}$ is the biomass for

303   the group in the baseline model with present circulation. For each simulation, we used the

304   mean biomass of the final 10 years of a 100-year run for B. This metric represents the

305   marginal effect of ocean acidification over 50 years, subtracting out any effect of a

306   change in temperature, and translates that change into the context of the ecosystem that

307   most closely matches current data (2013). We calculated a second metric that

308   standardizes by 2063 rather than 2013 baseline biomass, which represents the percent

309   change in biomass due to changes in pH. Those results were qualitatively similar and we

310   refer readers to the Supporting Information (S4) for comparison.

311   While it is difficult to determine what constitutes a non-zero effect, we follow the

312   conventions of similar ecosystem modeling exercises (Smith *et al.*, 2011; Kaplan *et al.*,

313   2013; Marshall *et al.*, 2014), focusing on $|E| > 0.20$. The intended use of this model is to

314   inform strategic (e.g., big picture, contextual, goal-setting, risk assessment), rather than

315   tactical (e.g., specific actions over short time scales) management questions (FAO 2008).

316   Therefore, we focus on large magnitude effects that are likely to be readily detectable

317   should they occur in real world observational data. Below, we present pH effects in two

318   ways: 1) at the scale of the ecosystem, grouping functional groups into guilds, and 2) by

319   functional group. Guild-level pH effects were calculated as biomass-weighted means of
320   the pH effects of the functional groups within the guild. Guild membership is defined in
321   Table S1.2 in the Supporting Information.

322   *pH effects on fishery revenue*
323   We translated the effects of pH on biomass (*E in Eq. 2*) to revenue using 2013 landings
324   and revenue data (PacFIN 2013). Because fishing mortality was fixed at 2013 rates in our
325   simulations, the effect of pH on fisheries catches is equivalent to the pH effect on
326   biomass. Within the US fishery management system, individual species (and therefore
327   Atlantis functional groups) fall within distinct management units, governed by one of
328   several federal Fishery Management Plans (FMPs) or by state plans (deReynier,
329   2014).We grouped functional groups into management units and projected the effects of
330   changing pH on revenue at that scale. We show results for the following units: State
331   (including all crabs and shrimps, nearshore urchins, bivalves), Groundfish (all
332   commercially landed groundfish except Pacific Hake), Pacific Hake, and Coastal Pelagic
333   Fish (sardine, anchovy, mackerels). We calculated the pH effect on revenue (*U*) for each
334   management unit *k* as a weighted average of its component functional group effects (*E_i*)
335   such that:

$$U_k = \frac{\sum E_j * R_{j\ 2013}}{\sum R_{j\ 2013}}$$

336   Where the weight R_j is the 2013 revenue for functional group *j*, and revenue was
337   calculated as the product of U.S. price per metric ton and expected 2013 catch for each
338   functional group. Additional details on reconstructing 2013 catch are provided in the
339   Supporting Information (S1, Part II).

340   *Calibrating the ecology sub-model*
341   Following guidelines developed for an earlier version of the California Current Atlantis
342   model (Horne *et al.*, 2010), we calibrated the model in two phases: initial simulations
343   with no fishing; and secondary calibrations testing constant fishing pressure. Atlantis
344   explicitly models numbers-at-age (or number-per-cohort), and dynamic weight-at-age,
345   and we evaluated these model outputs following a Pattern Oriented Modeling approach

346 (Grimm *et al.*, 2005). Specifically, we evaluated Atlantis outputs of biomass, spatial

347 distributions, age structure, and weight-at-age that resulted from the simulations without

348 fishing and those with constant fishing pressure. The POM approach and iterative

349 calibration leads to refinement of both model processes and parameterization, as these

350 outputs are compared to observations at multiple spatial and temporal scales. Secondary

351 calibration tested a range of fixed levels of fishing mortality applied simultaneously to all

352 groups. As a rule of thumb we expected that F_{MSY} might fall within 0.5-0.8 of natural

353 mortality rates (Patterson, 1992; Patterson *et al.*, 2001; Walters & Martell, 2002).

354

355 **Results**

356 *ROMS forced with ESM2M*

357 Our ROMS projection of future ocean conditions (year 2063) suggests marked declines in

358 pH relative to present day simulations (year 2013). In the top 100 m of the water column,

359 mean August pH in the ROMS model declines from 7.96 in the present day to 7.77 in the

360 future (Fig. 3); this is equal to the ~0.2 unit drop in pH predicted by the coarser ESM2M

361 model (S1, Fig. S1.2), and represents a 55% increase in acidity (e.g., 55% change in

362 $[H^+]$). As expected, the late summer period depicted in Fig. 3 has the lowest pH of the

363 year, in response to the preceding spring-summer upwelling period that characterizes the

364 California Current. ROMS effectively represents the present day spatial pattern we expect

365 for the system as well, with summertime reductions in pH along the coast, and a shoaling

366 of pH clines near shore (S1, Fig. S1.4). Compared to ESM2M, the spatially downscaled

367 ROMS yields much finer predictions of spatial patchiness of future acidification; for

368 example, some of the lowest pH values are predicted to occur very close to shore at depth

369 (Fig. 3d), and the northern continental shelf is predicted to experience slightly greater pH

370 than in regions south of 40°N latitude (Fig. 3c, d). This spatial resolution is critical for

371 driving the future pH responses of biological groups within each Atlantis polygon. In

372 addition, ROMS predicts warmer conditions in 2063 relative to 2013; the annual mean

373 temperature increase in the upper 100 m of the water column is 0.9°C.

374

375 *Calibrating the ecology sub-model*

376   Initial simulations with no fishing resulted in 86% of functional groups persisting for

377   more than 50 years (S1, Tables S1.1 and S1.2), with quasi-stable population dynamics for

378   most groups after approximately year 50. Similar to other simulation modeling efforts

379   (Gaichas *et al.*, 2012; Thorpe *et al.*, 2015), we found that ensuring persistence of all

380   functional groups was not trivial, and we were forced to accept a parameterization that

381   allowed 11 functional groups to decline to low levels in base case simulations (without

382   ocean acidification). This is largely a reflection of the fact that Atlantis's feedback

383   structure complicates optimization and finding ecologically feasible parameter

384   combinations is difficult given the need for a human step in the process (to check for

385   nonsensical outcomes). This iterative, manually intensive, searching of a large parameter

386   space is particularly difficult when combined with the relatively long run times for this

387   model. To provide some context, in a similar food web model, Gaichas et al. (2012)

388   found that randomly drawn predator-prey interaction terms led to persistence of all

389   species in less than 1 in 400 cases. As a suitable parameter combination could not be

390   found at this time, these functional groups were excluded from the analysis: arrowtooth

391   flounder, pelagic sharks, sea stars and brittle stars, pandalid shrimp, grenadiers, large

392   phytoplankton, market squid, Pacific Ocean perch, large pelagic predators, Chinook

393   salmon, and large demersal predators.   The excluded species comprise <2% of vertebrate

394   biomass and ~1% of heterotroph (consumer) biomass. While the excluded species

395   represent 28% of the revenue generated in 2013, they do not include the top two fished

396   species by 2013 landings (Pacific sardine and Pacific Hake). For persisting species, we

397   obtained sensible age structures and weight-at-age within tolerance; e.g., within ±50% of

398   initial values and ideally within ±20% (Horne *et al.*, 2010).

399   Secondary calibration suggested fishing rates at maximum sustainable yields (F_{MSY}) near

400   0.05-0.1 for most groundfish stocks, with higher values (>0.2) for most pelagic species

401   (Fig. S2). This was consistent with expectations that demersal stocks have lower

402   productivity, as evidenced by lower estimates of natural mortality (Fig. S2). We also

403   found that most groups targeted by commercial fishing were able to sustain fishing

404   mortality held at 2013 levels. Two functional groups, petrale sole and shallow small

405   rockfish, persisted in unfished simulations and were included in our analyses of outputs,

406   but showed strong biomass declines under relatively moderate fishing (see Fig. S2).

407   Therefore, interpretation of results regarding these groups should be cautious.

408   *Effects of future pH on biomass*

409   Applying 2063 pH projections within 100-year Atlantis simulations caused a wide range

410   of effects across the ecosystem, and most of these effects were negative (Fig. 4). In

411   general, there were few strong guild-level responses to decreasing pH (Fig. 4a). Only one

412   guild-level pH effect was stronger than the $|E| > 0.2$ threshold (Epibenthos in the

413   Calcifying Benthos scenario). Overall, the functional groups in the Demersal Fish and

414   Epibenthos guilds exhibited the highest variability, with some groups experiencing a

415   strong pH effect and others little to no effect (Fig. 4b). Several guilds (Mammals,

416   Seabirds, Pelagic Fish, Squid, and Primary Producers) were insensitive ($|E| < 0.2$ for all

417   functional groups) across all the scenarios.

418   In contrast to the few guild-level effects of changing pH, many individual functional

419   groups responded strongly in each scenario (Fig. 5). The scenarios directed at Calcifying

420   Benthos, Non-Calcifying Benthos, and Crabs and Shrimps each had five functional

421   groups with $|E| > 0.2$. In contrast, only one functional group (microzooplankton)

422   responded strongly to the scenario directed at Copepods and Pteropods. The Cumulative

423   scenario, which applied future conditions and pH sensitivity to all 10 functional groups in

424   Table 1, led to strong responses in 16 functional groups (Fig. 5).

425   Sensitivity to pH in the Calcifying Benthos scenario led to strong direct effects of future

426   pH on benthic grazers and bivalves, but no direct effects on shallow benthic filter feeders

427   (Fig. 5). Declines in benthic grazers and bivalves led to declines for three of their

428   predators: cowcod, deep large rockfish, and Dungeness crab. All negative effects

429   observed in Calcifying Benthos scenario were retained when pH sensitivity was added to

430   other groups in the Cumulative scenario.

431   Applying pH sensitivity and future climate conditions in the Crabs and Shrimps scenario

432   resulted in strong direct effects on the general crab group and crangon shrimp, but not

433   Dungeness crab (Fig. 5). Strongly negative indirect effects occurred on petrale sole,

434   shallow small rockfish, and skates and rays, all of which depend heavily on crangon

435   shrimp in their model diets. All of the negative effects observed in the Crabs and Shrimp

436   scenario were also present in the Cumulative scenario, and strong negative effects on

437   Dungeness crab emerged in the Cumulative scenario.

438   The Non-Calcifying Benthos scenario resulted in strong direct negative effects in both

439   sensitive functional groups: benthic detritivores and benthic carnivores (Fig. 5). Petrale

440   sole, small demersal sharks, and Dover sole experienced strong indirect negative effects

441   in this scenario even though none of these species preys directly on the pH-sensitive

442   groups. It is likely these indirect effects were modulated through a shared prey group

443   (e.g., crangon shrimp) that was weakly affected by declines in benthic detritivores and

444   benthic carnivores. All negative effects in the Non-Calcifying Benthos scenario were also

445   present in the Cumulative scenario, except benthic carnivores were only weakly affected

446   ($E < |0.2|$) when all species were sensitive to pH.

447   The Copepods and Pteropods scenario resulted in no strong responses by either of the

448   directly affected groups: copepods and pteropods declined by 2 and 5 %, respectively.

449   However, copepods are a very abundant group (estimated at nearly 20 million metric tons

450   for our large model domain, approximately 28 percent of the total biomass of

451   zooplankton; S1, Table S1.1), and this is a substantial shift in absolute terms.

452   Microzooplankton, a prey group for both copepods and pteropods, responded strongly in

453   the positive direction to the negative effects on its predators (Fig. 5). This indirect effect

454   was also seen in the Cumulative scenario.

455   The Cumulative scenario produced more strong responses than the preceding scenarios,

456   primarily negative responses by Demersal Fishes and Epibenthos (Fig. 4). It also resulted

457   in two strong indirect effects not observed in any of the other scenarios (Fig. 5). Deep

458   small rockfish, which prey upon many of the pH-sensitive groups, responded negatively

459   ($E = -0.40$) when all of the sensitive groups declined with pH. The other new indirect

460   response was by nearshore urchins, which had a strong positive response ($E = 0.68$).

461   Nearshore urchins are fed upon by many of the fish groups that experienced indirect

462   negative effects. Moreover, nearshore urchins were assumed not to be directly sensitive

463   to ocean acidification in our model; the meta-analysis of Busch and McElhany (2016)

464 suggests that these commercially harvested nearshore urchins are less susceptible to

465 acidification than our benthic herbivorous grazers group, which includes deeper-dwelling

466 urchin species, although fewer experimental studies have targeted the nearshore urchin

467 species (Busch and McElhany 2016).

468 *Effects of future pH on catch and revenue in the Cumulative scenario*

469 Our simplistic representation of fishing and revenue projected that most fishery

470 management units we explored were negatively affected by future pH in the Cumulative

471 scenario (Table 2). Proportional effects of pH on catch and biomass at the functional

472 group level are equal because we parameterized fishing using fixed fishing mortality rates

473 for each functional group. The State-managed unit had the largest projected pH effect on

474 revenue (U = -0.29), driven by the strong negative indirect effect of pH on Dungeness

475 crab, which supports a valuable fishery (200 million USD in 2013). Other crabs and

476 bivalves were negatively affected by future pH, but the 2013 revenue from those fisheries

477 is an order of magnitude lower than the Dungeness crab fishery. The urchin fishery

478 targets the nearshore urchin group, which was the only harvested functional group that

479 was projected to increase under future pH conditions.

480

481 The Groundfish management unit (excluding Pacific hake) did not experience a

482 substantial pH effect on revenue (U=-0.18). This group of species generated $88 million

483 in revenue in 2013. While this decline was not dramatic ($|U| < 0.20$) for the total revenue

484 from species managed under the groundfish FMP, our model projects more substantial

485 declines for particular commercially important groundfish such as petrale sole, Dover

486 sole, and deep large rockfish (mostly shortspine thornyhead, *Sebastolobus alascanus*).

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

488 The model projected a very small pH effect (U= -0.038) on Hake fishery revenue, in a

489 fishery generating 76 million USD of revenue in 2013. For species managed collectively

490 under the Coastal Pelagic Species FMP, the pH effect was less than 0.01. We do not

491 show results for Salmon or Highly Migratory Species FMPs due to the poor performance

492   of those species in the model (Chinook and large pelagic predators were removed due to

493   low biomass in baseline runs).

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

495   As would be expected *a priori*, the effects of future pH at the guild-level were sensitive

496   to the magnitude of the mortality scalar. The magnitude of positive and negative effects

497   increased as the scalar increased to 2.5x to 10x our base case values (Fig. S3). However,

498   the directions of pH effects at the guild and functional group levels were consistent

499   regardless of the mortality scalar, as was the set of functional groups and guilds identified

500   as likely impacted by pH effects.

501   **Discussion**

502   *Interpretation of Atlantis results*

503   Global change is projected to have pronounced impacts on marine ecosystems and

504   resources in temperate zones. The climate change scenario applied here, IPCC scenario

505   RCP 8.5, will have high impacts on mid-latitude bivalve fisheries and aquaculture, and

506   high to moderate impacts on mid-latitude finfish fisheries, according to a growing body

507   of research (Barange *et al.*, 2014; Gattuso *et al.*, 2015). In fact, many symptoms of global

508   change are already being observed in the California Current ecosystem, including

509   warming, shifts in community structure and phenology (Thorson *et al.*, 2016), and major

510   hypoxic events (reviewed in Doney *et al.*, 2012). There is already evidence of ocean

511   acidification impacts: episodic year-class failures of Pacific oysters (*Crassostrea gigas*)

512   along the US West Coast have been attributed to OA (Barton *et al.*, 2012), and Bednaršek

513   and Ohman (2015) have documented OA-driven shell dissolution in the pteropod

514   *Limacina helicina* in the southern California Current.

515   Our modeling effort, which synthesized downscaled climate models, experimental and

516   empirical studies, and a well-established end-to-end marine ecosystem modeling

517   framework, provides a broad overview of potential ecosystem-scale effects of OA in the

518   California Current. We saw wide-ranging effects across multiple guilds and functional

519   groups, but more losers than winners in terms of biomass and lost fishery revenue. Model

520   predictions suggest the most dramatic effects of future pH decreases will be felt by

521 demersal fish, sharks, and epibenthic invertebrates, and less so by pelagic species, marine

522 mammals and seabirds. This was likely driven by the stronger responses of sensitive

523 benthic organisms to changing pH, compared to relatively weak responses of sensitive

524 zooplankton groups. Our approach demonstrated that combining multiple scenarios into a

525 single, cumulative scenario can lead to unanticipated, indirect responses by groups that

526 were relatively insensitive in simpler scenarios.

527 The value of taking both a population and systems approach is further evident when

528 comparing our preliminary ranking of direct pH responses (Table 1) to the cumulative

529 impacts projected by the Atlantis model (Fig. 4 and 5). Although experimental and

530 empirical literature suggests that copepods, shallow benthic filter feeders, and Dungeness

531 crabs may be sensitive to OA (Busch and McElhany, 2016), none of them responded

532 strongly in scenarios where they were directly affected by pH. All three functional groups

533 exhibited relatively high productivity, which prevented substantial declines in their

534 biomass due to direct effects. Indirect effects were responsible for declines in Dungeness

535 crab, a major fishery target. We only observed a strong pH effect on Dungeness crab

536 when their prey declined due to OA (Calcifying Benthos scenario), but not due to direct

537 pH-driven mortality (Crabs and Shrimp scenario). This insight highlights the utility of

538 end-to-end models for comparing multiple scenarios (Busch *et al.*, 2013), as well as the

539 ability of the Atlantis model to integrate over direct effects, indirect trophic effects, and

540 population-level productivity.

541 From a fishery management perspective, economic impacts in the California Current may

542 stem from indirect ocean acidification effects on high-value target species such as

543 Dungeness crab and groundfish. Aggregating pH effects on revenue to units relevant to

544 management bodies allows us to identify particular management bodies, and teams within

545 those bodies, that may benefit from monitoring of OA effects (e.g., nearshore state-

546 managed fisheries, or the groundfish management team with the Pacific Council). This

547 kind of strategic targeting of advice may help prioritize efforts, rather than making a

548 blanket statement that managers should be concerned about OA, for example. Previous

549 research has focused on global economic and nutritional losses due to projected direct

550 ocean acidification effects on shellfish (Cooley *et al.*, 2012), but our work suggests

551 careful consideration must also be given to the supporting role that shellfish and other

552 species play in the food web. At a minimum, economic impact assessments should

553 include fisheries that target species dependent on calcifying prey (e.g., Cooley & Doney,

554 2009). However, our model results do not take into account potential shifts in effort

555 across fisheries that may occur as a result of reduced catches of one species/management

556 unit (e.g, potential tradeoffs between crab and groundfish).

557

558 Other investigations of future change in the California Current provide more context for

559 interpreting our results. Using an earlier version of the California Current Atlantis model,

560 Kaplan et al. (2010) forced moderate, acidification-driven declines on benthic

561 invertebrates, which caused declines in flatfish, small demersal sharks, and skates and

562 rays. These projected declines were consistent with ours, even though the meta-analysis

563 of Busch and McElhany (2016) that informed the current analysis suggested that seastars

564 and brittlestars are less sensitive to acidification than was assumed by Kaplan et al.

565 (2010). Kaplan et al. (2010) also found indirect effects leading to increased canary

566 rockfish and the shallow miscellaneous fish group. These increases were not supported

567 by our analysis because we changed the functional group composition to better represent

568 groups susceptible to OA, which resulted in changes to the diet parameterization in these

569 groups. In a food web model with much simpler spatial structure and no oceanographic

570 forcing, Ainsworth et al. (2011) found very limited system-level effects of changing pH

571 on the northern portion of the California Current. In contrast to our results, cumulative

572 impacts of multiple stressors in their study were greater for the pelagic than demersal

573 components of the food web; this is likely because Ainsworth et al. (2011) assumed that

574 euphausiids were also sensitive to OA, which was not robustly supported by Busch and

575 McElhany (2016).

576 Ocean acidification is not the only global change stressor affecting this ecosystem. King

577 et al. (2011) used conceptual models to forecast the effects of climate change on the

578 California Current, and focused primarily on changes in temperature, dissolved oxygen

579 and precipitation. They predicted that many demersal fish (such as Dover sole, sablefish,

580 and rockfish) may be buffered against ocean warming because they can move north or

581 into deeper water temperature refuges. They did not consider ocean acidification,

582 however, and our results suggest that OA may create vulnerability for demersal fish, even

583 relatively mobile ones, through erosion of their prey base. King et al. (2011) also

584 forecasted that warmer waters may support larger sardine populations, and since our

585 Atlantis results did not indicate indirect sensitivities to OA in the pelagic fish guild, this

586 may be an opportunity for a global change "winner" when combining the effects of

587 temperature and OA. Overall, further consideration of the joint effects of temperature,

588 ocean acidification and hypoxia are warranted within the California Current. King et al.

589 (2011) noted that some demersal fishes, such as Dover sole, may be able to take

590 advantage of expanding hypoxic zones on the continental shelf. Global modeling by

591 Barange et al. (2014) that includes temperature effects but omits acidification suggests

592 that some mid to high-latitude fisheries may benefit in the future, and that primary

593 production may increase in the northern portion of the California Current. Stressors like

594 OA, warming temperatures and low dissolved oxygen will likely co-occur and interact

595 (Reum *et al.*, 2014), and future Atlantis scenarios that attempt to address these combined

596 stressors will have to rely on experimental studies that examine their cumulative effects

597 on key species.

598 *Uncertainty, caveats, and gaps*

599 Projections of living marine resources under global change contain uncertainty stemming

600 from three sources: internal variability, model uncertainty (including parameter and

601 structural uncertainty), and scenario uncertainty (Cheung *et al.*, 2016). We controlled for

602 some of the effects of internal variability (e.g. interannual climate variation, interdecadal

603 climate regime shifts) by forcing Atlantis with a single representative year of

604 oceanography and biogeochemistry (2013 or 2063), and accounted for interannual effects

605 of ecological dynamics by averaging over the final 10 years of each model run.

606 Model parameter uncertainty is harder to address: large numbers of input parameters

607 within models such as Atlantis preclude some formal quantification methods such as

608 Bayesian or Monte Carlo approaches (Cheung et al. 2016). The computational expense

609 and long run-times of Atlantis model simulations present an additional challenge. In the

610 future, parameter uncertainty may be addressed by bounded parameterizations (Fulton *et

611 al.*, 2011) that bracket stock productivities, i.e. conducting simulations with a base model

612   but also testing at least two alternate, realistic parameter sets that result in higher or lower

613   productivity for the ecosystem or species of interest. This approach that has been applied

614   for an earlier version of the California Current Atlantis model (Pacific Fishery

615   Management Council & NMFS, 2014). Uncertainties stemming from model structure can

616   be understood via model inter-comparisons and skill assessment (Payne *et al.*, 2015).

617   Scenario uncertainty is likely to be the most important factor for long term projections

618   (Hawkins & Sutton, 2009) beyond the 2060s; we agree with Cheung et al. (2016) that this

619   is best captured using scenarios for not only emissions and climate but also fishery

620   development and management. Though our scenarios here assume simple fixed fishing

621   mortalities, global efforts (Merino *et al.*, 2010; Msangi *et al.*, 2013) and nascent local

622   efforts (Kaplan *et al.*, 2012) to develop meaningful social-economic scenarios offer

623   promise in this respect.

624   Ecosystem model outcomes are fundamentally affected by modelers' assumptions and

625   decisions about input data, parameter development, and model structure (Link *et al.*,

626   2012). An assumption that is central to the present study is our parameterization of

627   sensitivity to pH. Despite a large body of experimental work (e.g., Busch and McElhany,

628   2016), the sensitivities to pH for functional groups in our model are known with very

629   little precision. We expect the ranking of pH sensitivity to be generally robust, but the

630   scale of that sensitivity is hard to quantify in part because we are translating effects on

631   individuals under controlled experimental conditions to functional group-level effects in

632   the model. Further, we modeled pH sensitivity as reduced survival because that is the

633   most straightforward to implement and an approach similar to others' (Kaplan *et al.*,

634   2010; Griffith *et al.*, 2011; Weijerman *et al.*, 2015). However, meta-analyses suggest the

635   physiological effects of changing pH may also involve reproduction, growth, or

636   behavioral changes (Kroeker *et al.*, 2010; Wittmann & Pörtner, 2013). Modifying

637   mortality rates as we have done here may be an appropriate proxy in some cases but may

638   over or under-represent the effect of changing pH on some organisms. Using mortality

639   rates to capture pH sensitivity has another limitation in our Atlantis model; we are unable

640   to project direct effects of OA that are positive (e.g., for seagrasses), which limits the

641   scope of our forecasts. However, we can, and did, project some positive indirect effects

642   of future pH. Lastly, our results reflect the way we chose to model the process of ocean

643 acidification—by projecting pH, not aragonite or some other calcium carbonate

644 saturation state. Alternate ways of modeling OA may lead to different conclusions about

645 ecosystem and fishery effects.

646 Our California Current Atlantis model does not capture the dynamics of all functional

647 groups in the ecosystem—for example pandalid shrimp, market squid, and tuna

648 functional groups do not persist in our baseline 100-year model simulation. Therefore,

649 we cannot infer potential effects of OA on these components of the food web (or the

650 fisheries that target these groups). Two of the modeled fish groups (Petrale sole and

651 shallow small rockfish) persist in the baseline simulation and demonstrate strong indirect

652 sensitivity to pH, but these simulated groups may be less productive in the model than

653 they are in reality, and we may therefore overestimate their sensitivity to OA. This low

654 productivity is evident from calibration tests for some groups that suggest lower

655 sustainable yields than what has been estimated by stock assessments (Fig. S2).

656 The caveats associated with ecosystem model projections are a good reminder of how

657 these results should be interpreted and used. Our findings about winners and losers in the

658 ecosystem, functional groups that are more or less sensitive to changing pH in the

659 California Current, and potential impacts to fisheries revenues provide a set of forecasts

660 that build upon previous findings and pave the way for hypotheses to guide future

661 modeling and experimental analysis. For example, in this study we summarized the

662 effects of changing pH at a coast-wide scale. We found limited effects at the coarse guild-

663 level but stronger effects when we looked at individual functional groups. Similarly,

664 aggregating across space likely had a smoothing effect that obscured more dramatic and

665 meaningful changes in particular locations. Spatial scale is particularly important when

666 considering the way that fishing communities interact with ocean ecosystems - typically

667 with local knowledge and long histories of particular fishing grounds within reach of

668 home ports (St. Martin & Hall-Arber, 2008). Therefore, a key next step for this model is

669 to investigate how the effects of changing pH vary across space, and what that means for

670 place-based human communities, similar to a recent risk assessments for Alaskan fishing

671 regions (Mathis *et al.*, 2015) and larger US regions (Ekstrom *et al.*, 2015).

672 *Implications for management*

673 We can begin to understand cumulative impacts on large marine ecosystems by using

674 models that combine experimental studies, physical models, and food web models such

675 as the one presented here for the California Current. Describing and understanding effects

676 of global change on large marine ecosystems, including human communities, requires

677 integration of diverse methodologies and interdisciplinary teams (Hollowed *et al.*,

678 2013a). While this type of end-to-end model is not intended to make precise, tactical

679 forecasts for fisheries management, it can be used to identify risks to marine ecosystem

680 structure and function (Hollowed *et al.*, 2013b). Combined with information about the

681 adaptive capacity of human communities (Morzaria-Luna *et al.*, 2014; Mathis *et al.*,

682 2015), end-to-end models can inform risk assessments of human communities to global

683 change. Ocean acidification is occurring in the California Current, and our model

684 suggests the risks of changing pH are greatest for epibenthic invertebrates and demersal

685 fish, and the fisheries that target these groups. Models such as Atlantis can be used to

686 present broad alternatives for how ecosystems and populations may evolve under global

687 change, and highlight which resources are likely to be affected by these changes. Our

688 results provide strategic guidance to state and federal fisheries managers on the West

689 Coast of the U.S. that can be followed up with tactical simulation tests to identify robust

690 management strategies (Punt *et al.*, 2013).

691 **Acknowledgments**

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698

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915 **Supporting Information**

916 S1. Atlantis model documentation.

917 S2. Model sensitivity to fishing mortality rates.

918 S3. Sensitivity of the pH effect of Benthic herbivorous grazers to the survival scalar.

919 S4. Ecosystem responses to changing pH using alternative pH effect metric.

920

921

922 **Table 1**. Scenario descriptions for projections of the effects of ocean acidification on the

923 California Current ecosystem. Affected functional groups listed by Scenario with their

924 relative survival scalar that indicates that group's sensitivity to declines in pH (as per

925 Busch and McElhany (2016)).

Scenario	Affected functional groups	Relative survival scalar	Example species

Calcifying Benthos	benthic herbivorous grazers	-1	sea urchins (*Allocentrotus fragilis*), snails
	bivalves	-0.89	bivalves
	shallow benthic filter feeders	-0.55	tunicates, sponges
Copepods & Pteropods	mesozooplankton	-0.99	copepods
	pteropods	-0.81	thecosome pteropods
Crabs & Shrimp	crabs	-0.7	crabs (excluding Dungeness crab)
	crangon shrimp	-0.45	shrimps (excluding pandalids)
	Dungeness crab	-0.41	Dungeness crab
Non-calcifying Benthos	carnivorous infauna	-0.39	polychaetes, nematodes
	deposit feeders	-0.37	amphipods, isopods

926

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

931

Management Unit	Most Affected Functional Groups	pH Effect Biomass and Catch	pH Effect Revenue	Baseline Revenue (millions USD)
State			-0.29	260
	Dungeness crab	-0.30		220
	crabs	-0.61		9.5
	bivalves	-0.29		17
	urchins	0.61		6.8
Groundfish			-0.18	88

	petrale sole	-1.1		7.5
	Dover sole	-0.39		9.0
	deep large rockfish	-0.35		5.0
Hake	hake	-0.038	-0.038	76
Coastal Pelagics			-0.0080	110
	sardine	-0.030		27
	jack mackerel	-0.050		1.5
	anchovy	-0.026		1.3

932

933

934 **Figure captions:**

935

936 **Figure 1.** Conceptual diagram of modeling approach for the California Current Atlantis

937 Model. The general diagram of the Atlantis platform and the three coupled sub-models

938 are shown on the right, with the key modifications and points of entry for information

939 related to this application for projecting ocean acidification shown on the left.

940

941 **Figure 2.** Map of California Current Atlantis model domain

942

943 **Figure 3.** ROMS projections of pH in August 2013 (a and b) and August 2063 (c and d),

944 at the surface (a and c) and bottom (b and d). ROMS runs are initialized Jan 1, 2010 or

945 Jan 1, 2060, and are forced by GFDL ESM2M under IPCC RCP 8.5. pH within ROMS is

946 calculated from carbonate variables simulated using the model of Fennel et al. (2006,

947 2008).

948 **Figure 4.** Ecosystem responses to forecasted pH for guilds in the California Current

949 Atlantis model. We ran five OA scenarios, varying the sensitivity of Non-calcifying

950 benthos (light blue), Copepods and Pteropods (green), Crabs and Shrimp (yellow),

951 Calcifying Benthos (dark blue), and a Cumulative scenario with all of the previous

952 scenarios combined (black). Biomass-weighted mean pH effect (E) for each guild shown

953   as the heights of the bars in (A). In (B), functional group responses for each group within

954   the guild are shown as open circles, with the transparently shaded area highlighting the

955   range of functional group responses within the guild (colors as in B). For comparison, the

956   mean guild-level effect shown in A is shown as a filled circle in B. Horizontal dotted

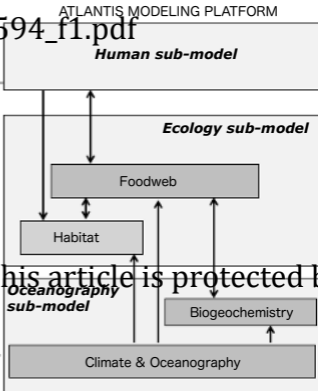957   lines at $E=\pm0.2$ indicate the threshold that we considered a strong effect.

958

959   **Figure 5.** Projected effects of future pH on functional group biomass for those groups

960   with a strong effect (|E| > 0.2). Bars are shaded by scenario (with the same colors as in

961   Fig. 4 in the online version): Non-calcifying benthos (light blue), Copepods and

962   Pteropods (green), Crab and Shrimp (yellow), Calcifying benthos (dark blue), and

963   Cumulative (black).

ATLANTIS MODELING PLATFORM

Human sub-model

Ecology sub-model

Foodweb

pH sensitivities from Busch et al. (2016)

Habitat

This article is protected b

Oceanography sub-model

Biogeochemistry

ROMS forced by global climate model (2013 and 2063)

Climate & Oceanography

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(a) Legend:
- Non-Calcifying Benthos
- Copepods/Pteropods
- Crab/Shrimp
- Calcifying Benthos
- Cumulative

Y-axis: pH Effect

(b) Y-axis: pH Effect

X-axis categories: Mammal, Seabird, Shark, Demersal Fish, Pelagic Fish, Squid, Filter Feeder, Epibenthos, Zooplankton, Primary Producer, Infauna

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Legend (top right):
- Non−calcifying Benthos
- Copepods/Pteropods
- Crab/Shrimp
- Calcifying Benthos
- Cumulative

Y-axis categories (top to bottom):
- Petrale sole
- Cowcod
- Small demersal sharks
- Crabs
- Benthic grazers (urchins)
- Deep small rockfish
- Dover sole
- Deep large rockfish
- Crangon Shrimp
- Dungeness crab
- Bivalves
- Shallow small rockfish
- Benthic detritivores
- Skates and rays
- Benthic Carnivores
- Microzooplankton
- Nearshore urchins

X-axis: pH Effect (−1.0, −0.5, 0.0, 0.5, 1.0)

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