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# Linking climate stressors to ecological processes in ecosystem models, with a case study from the Gulf of Alaska

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## Abstract

As climate stressors are impacting marine ecosystems and fisheries across the world, ecosystem models that incorporate environmental variables are increasingly used to inform ecosystem-based fisheries management. The assumptions around the mechanistic links between climate stressors and the biological processes in these models are important, but the implications for model outcomes of which stressors are captured and how they affect modeled biological processes are seldom explored. Using a whole-ecosystem model (Atlantis) for the Gulf of Alaska, we explore the effects of capturing physical (increased temperature) and biogeochemical (decreased low trophic level productivity) climate stressors, and disentangle the effects of each stressor on the productivity of forage fish, groundfish, and fish-eating seabirds. We then test the effects of alternative model specifications of temperature-driven habitat determination and bioenergetics. Increased temperature resulted in increased weight-at-age and higher natural mortality, while decreased productivity resulted in decreased weight-at-age and higher natural mortality. Model specification of temperature dependence of movement and spawning influenced model outcomes, and decoupling these processes from temperature led to overly optimistic biomass predictions. As the use of ecosystem models to inform fisheries management becomes more operational, we illustrate that the assumptions around the links between climate stressors and ecological processes influence model outcomes.

**Keywords:** climate stressors; temperature; productivity; end-to-end models; Atlantis; Gulf of Alaska; EBFM; ecosystem-based fisheries management

## Introduction

Climate stressors are impacting marine ecosystems and fisheries globally (Hollowed et al. 2013, Cooley et al. 2022). Increased temperature and low trophic level (LTL) productivity shifts are among the key impacts anticipated in marine ecosystems under climate change (Heneghan et al. 2021). Global models of climate projections such as Earth System Models (ESM) generally agree in predicting that future warming will correspond to a decrease in primary

productivity at a global scale (Bopp et al. 2013), although climate models developed as part of the latest Climate Model Intercomparison Project (CMIP6) show larger inter-model variability than previous iterations in CMIP5 (Lehner et al. 2020). In Alaska, large marine ecosystems, including the Bering Sea and the Gulf of Alaska (GOA), that support valuable fisheries are experiencing the effects of climate variability across multiple time scales. Past climate events, including a regime shift (Anderson and Piatt 1999) and the 2013–2016

marine heatwave (Di Lorenzo and Mantua 2016), altered ecosystem productivity and ultimately resulted in negative effects on Alaska fisheries, including the closure of the federal Pacific cod (*Gadus macrocephalus*) fishery in the GOA in 2020 (Barbeaux et al. 2020). Alaska's marine ecosystems are projected to experience altered biophysical conditions, including increased temperatures and more severe heatwaves, in upcoming decades (Hicke et al. 2022).

Multispecies and ecosystem models are increasingly used as tools to inform ecosystem-based fisheries management (EBFM) (Craig and Link 2023, Karp et al. 2023). In the Bering Sea, the Alaska Climate Integrated Modeling (ACLIM) project (Hollowed et al. 2020) has advanced our understanding of climate effects and has illustrated that EBFM can mitigate species declines (Holsman et al. 2020). In the GOA, climate-enhanced multi-species and single-species statistical models have been applied to evaluate the effects of the 2013–2016 heatwave on Pacific cod (Barbeaux et al. 2020) and of variability in bottom temperature on commercially important groundfish stocks (Adams et al. 2022). In addition, foundational ecosystem and multi-species modeling have been undertaken in the region (Aydin et al. 2007, Gaichas et al. 2015). However, efforts to integrate climate information into ecological models for the GOA remain limited compared to the Bering Sea, and this can hinder the uptake of climate considerations in the fisheries management process (Holsman et al. 2019).

Integrating mechanistic links between climate stressors and biological processes into ecological models is an important step in model building, and it is critical when using these models to investigate climate scenarios in an EBFM context (Koenigstein et al. 2016, Checkley et al. 2017). For global and regional ecosystem models, assumptions about the linkages between climate stressors, such as increased temperature and decreased LTL productivity, and ecophysiology are particularly important, but our understanding of such linkages is often limited (Heneghan et al. 2021). Atlantis is a deterministic, end-to-end regional ecosystem simulation model that dynamically couples physics, biology, and fisheries modules over time and in three-dimensional space (Fulton et al. 2011). Atlantis simulates trophic interactions between species, and therefore offers the opportunity to test how links between climate stressors and biological processes propagate upward through food webs to affect predators and fisheries across space.

To date, the effects of different assumptions when integrating temperature and shifts in LTL productivity into complex ecosystem models have rarely been characterized. Here, we apply an Atlantis model for the GOA, a marine ecosystem susceptible to climate-driven productivity changes and projected to experience continued warming, to explore the effects of capturing physical (increased temperature) and biogeochemical (decreased LTL productivity) stressors, isolated and combined, to disentangle the effects of each stressor on species productivity and model outcomes. We then test alternative model specifications of (i) thermal tolerance windows that restrict movement and spawning of key species and (ii) the shape of the bioenergetic response to increased temperature. We focus on these two biological processes because they are the most common ways to link temperature to biology in Atlantis (Audzijonyte et al. 2019), and because the impact on metabolic responses to bioenergetics is also of broad interest for other ecosystem models. We evaluate the effects of different parameterizations of these biological processes on model predictions of winners and losers under warm regimes

by evaluating species biomass, weight-at-age and numbers-at-age, and spatial patterns in abundance of selected species. We show that assumptions about the mechanistic links between climate stressors and ecological processes can greatly influence model outcomes.

## Methods

### Study area

The GOA is a temperate marine ecosystem with complex bathymetry and topography. High ecosystem productivity along the GOA shelf is supported by the confluence of iron in coastal runoff with nitrate from the deep basin, transported both vertically and horizontally across the shelf by topographic stirring, wind stress curl, tides, and eddies (Stabeno et al. 2004, Hermann et al. 2009, Coyle et al. 2013, 2019). This productivity of the GOA supports high species diversity and valuable fisheries managed under state (0–3 nm from shore) and federal (3–200 nm) jurisdictions in the United States, and federally (0–200 nm) in Canada (Ferriss and Zador 2022). Oceanographic data from throughout the GOA have shown that temperature has a strong seasonal signal with minima in March and maxima in August, and that freshwater input and stratification can cause cooler temperatures near the surface in inshore waters during winter months (Stabeno et al. 2004).

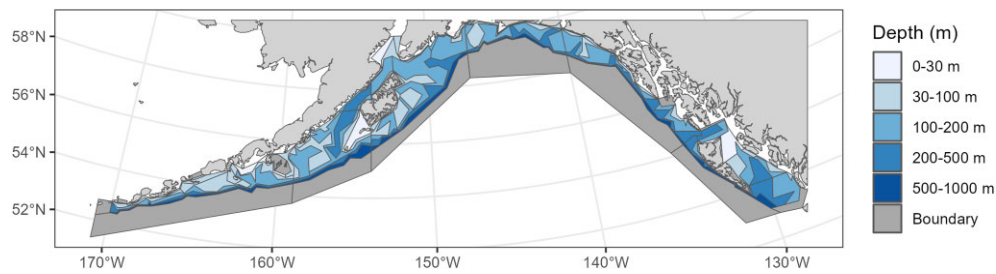
### Atlantis modeling framework

Atlantis is a whole-ecosystem, deterministic, spatially explicit simulation modeling framework that couples physical, biological, and socioeconomic (fisheries) submodels dynamically (Fulton et al. 2004, 2011, Audzijonyte et al. 2019). A detailed description of the development, data sources, assumptions, calibration, and skill assessment of Atlantis GOA can be found in the [Supplementary Material S1](#). Here, we briefly describe the main features of the model. We refer to it hereafter as the “Base model” to distinguish it from alternative model specifications presented in the scenarios section below.

### Model domain

The spatial domain of the model (Fig. 1) extends from 170°W [the western border of National Marine Fisheries Service (NMFS) area 610, off the eastern Aleutian Islands of Alaska, USA] to the northern tip of Vancouver Island in British Columbia, Canada (corresponding to the northern edge of the California Current Atlantis model domain; Kaplan et al. 2014). It is apportioned into 109 spatial polygons that approximate the bathymetry, oceanography, ecography, and management area subdivisions of the region. Dynamic model polygons (i.e. where biological and socioeconomic processes are modeled) extend from the shoreline (excluding embayments) to the 1000-m isobath along the continental slope. The model domain is separated from the surrounding ocean by boundary polygons (shown in dark gray in Fig. 1), where water circulates but dynamic biological and socioeconomic processes are not resolved (Audzijonyte et al. 2019).

The model was parameterized to resemble GOA biological conditions in the early 1990s. This period was chosen because these are the earliest years with adequate data availability required to parameterize the model, and because of the relative ecological stability of the GOA following a regime



**Figure 1.** Spatial domain of the Atlantis GOA model. Boundary boxes where no biological processes or fisheries are evaluated are represented in dark gray.

shift event in the late 1970s (Anderson and Piatt 1999; see [Supplementary Material S1](#) for details).

### Model physics

To force the physical submodel, we mapped the output of a Regional Ocean Modeling System (ROMS) hindcast of the northeast Pacific at 10-km resolution (Hinckley et al. 2009, Coyle et al. 2019) to the Atlantis GOA geometry. ROMS variables used to force Atlantis were temperature, salinity, and water transport. We calibrated the Base model with physical forcings from 1999 in a loop (*sensu* Marshall et al. 2017) to eliminate the interannual variability of environmental variables and thus minimize one source of uncertainty on model outcomes. Doing so allowed us to better evaluate the effects on model outcomes of forcing different climate stressors (increased temperature and decreased LTL productivity) and of using different model specifications of temperature responses. ROMS forcings for the period 1996–2020 were available and the year 1999 was chosen because 1997–1998 were El Niño years characterized by warm temperatures in the GOA (Stabeno et al. 2004), and ROMS output for the first year of simulation run (1996) may have incorporated artifacts stemming from model initialization. Because we did not aim to reproduce accurate historical patterns in this study, which year was used to force model physics was deemed less important, so long as it was prior to the onset of the heatwave in the GOA in 2013.

### Model biology

We categorized the GOA food web into 78 functional groups of varying functional and taxonomic aggregation, with species of commercial and/or conservation interest represented as single-species groups. Vertebrates were modeled as age-structured populations (maximum 10 multi-year age classes), while invertebrates were represented as biomass pools (Audzijonyte et al. 2019). We parameterized initial model conditions with species biomasses from 1990, or the closest year thereafter if information on 1990 was not available. We obtained biological parameters from GOA stock assessments, or from studies from the region for non-assessed species ([Supplementary Material S1](#)). Trophic interactions were defined based on stomach content analyses of fish collected in NOAA's Alaska Fisheries Science Center bottom trawl (Livingston et al. 2017) and surface trawl surveys, or from the literature when survey data were not available ([Supplementary Material S1](#)). Notably, although 1999 was a La Niña year characterized by cool temperatures across the water column (Stabeno et al. 2004), conditions were on average slightly cooler in 1990 than in 1999. When ROMS output for the early

1990s will become available, temporal mismatches between initial model biology and physics will be alleviated.

In this study, we link temperature to biological processes of all 78 functional groups, but we focus on the effects of climate stressors on 17 groups: 6 plankton groups (diatoms and picophytoplankton, microzooplankton, copepods, large zooplankton, and euphausiids); 5 forage fish groups that feed on plankton and have been shown to respond negatively to warm conditions (Baker et al. 2019, von Biela et al. 2019, Arimitsu et al. 2021) (capelin *Mallotus catervarius*, Pacific sand lance *Ammodytes personatus*, Pacific herring *Clupea pallasii*, eulachon *Thaleichthys pacificus*, and slope forage fish comprising Myctophidae and Bathylagidae); 4 commercially and ecologically important groundfish species that, combined, constitute most of the annual groundfish catch in the GOA (NPFMC 2019) (walleye pollock, pollock hereafter, *G. chalcogrammus*; Pacific cod *G. macrocephalus*; arrowtooth flounder *Atheresthes stomias*; and Pacific halibut *Hippoglossus stenolepis*); and 2 groups of fish-eating seabirds (diving and surface-feeding) that have shown negative responses to warm and food-limited conditions (Piatt et al. 2020, Arimitsu et al. 2021).

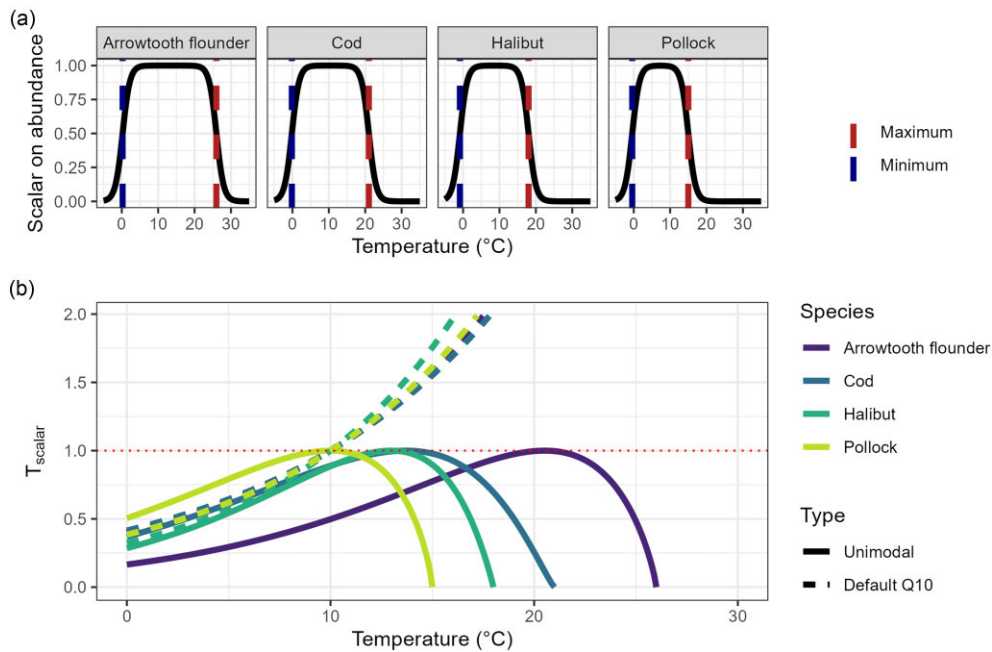
### Spatial distributions

For functional groups sampled by bottom trawl survey gear, we specified time-invariant spatial distributions across the Atlantis model domain with geostatistical modeling (sdmTMB; Anderson et al. 2022) of bottom trawl data from Alaska and from British Columbia ([Supplementary Material S1](#)). Species distributions derived from spatial modeling of these data are representative of summer conditions because these are summer/early fall surveys. For species not sampled by bottom trawl gear (e.g. seabirds, marine mammals, and pelagic species), we used other spatially annotated data sources or the literature ([Supplementary Material S1](#)).

### Fishing mortality

We represented fishing mortality as a fully selected  $F$  of  $\frac{1}{4} F_{MSY}$  for Tier 3 GOA stocks, and of  $\frac{1}{4} M$  for Tier 4+ (data moderate) species. Tier 3 stocks are defined as having reliable point estimates of biomass and  $F_{MSY}$  proxies (e.g.  $B_{35\%}$  and  $F_{35\%}$ ), while Tier 4+ stocks are defined as having reliable point estimates of biomass and natural mortality (NPFMC 2019). Values of  $F_{MSY}$  and  $M$  were collated from recent stock assessment models (Martin Dorn, UW, unpublished data), and are thus single-species estimates. This  $F$  represented light background fishing that had been used to calibrate the model ([Supplementary Material S1](#)). This  $F$  was compatible with the purpose of this study (i.e. evaluating modeled ecological responses to climate stressors) because the focus of the current





**Figure 2.** (a) Thermal niches for four key groundfish species in Atlantis GOA. Vertical dashed lines indicate minimum (blue) and maximum (red) tolerated temperatures; solid black lines indicate the scalar applied to abundance as a function of local temperature. (b) Bioenergetic response to temperature with unimodal formulation (solid lines) and default Atlantis  $Q_{10}$  method (dashed lines). Red horizontal dotted line represents the maximum scalar applied to consumption for the unimodal response.

analysis was not an accurate recreation of historical fishing patterns, nor the evaluation of any particular fishing regime. However, some of the modeled species in the GOA were fished at higher intensity than  $\frac{1}{4} F_{MSY}$  in 1990 (model initial conditions). Future analyses should consider the effects of fishing at different intensities.

### Integrating temperature in the Base model

Temperature influences several processes in Atlantis, and many options exist to regulate how biogeochemistry and biology are linked to temperature (Audzijonyte et al. 2019). Here, we present the options that were chosen for the Base model.

### Constraints on movement and spawning

For all vertebrates (except seabirds, which forage in the water but do not live in it), and for king crabs, other crabs, and pandalid shrimps, we applied temperature-dependent abundance scalars that were a function of species-specific thermal tolerance windows (Fig. 2a). To this end, we set species-specific minimum and maximum tolerated temperatures based on water temperature at location and depth of occurrence obtained from AquaMaps ([www.aquamaps.org](http://www.aquamaps.org), Kaschner et al. 2019). We used bottom temperatures for demersal and benthic species, and surface temperatures for pelagic species, marine mammals, and seabirds. These ranges are meant to represent the maximum spatial footprint attainable by a species based on its temperature preferences, and therefore the full temperature ranges provided by Kaschner et al. (2019) were used. For consistency with parameterization of bioenergetic responses to temperature (see below), maxima from AquaMaps were replaced with values of maximum tolerated temperature from Adams et al. (2022) for pollock, Pacific cod, arrowtooth flounder, and Pacific halibut, which were estimated based on published or fit bioenergetic models for each species and validated

with diet data from the groundfish summer survey (Ciannelli et al. 1998, Holsman and Aydin 2015, Holsman et al. 2022).

Temperature also influences reproductive success of commercially important groundfish species in the GOA, with temperatures exceeding species-specific thresholds resulting in reduced hatching success or egg and larval survival. To capture the thermal sensitivity of reproductive processes in key groundfish species, we defined thermal windows for spawning of pollock (0–13°C, Koenker et al. 2018, Laurel et al. 2018, Kim et al. 2022), Pacific cod (3–7°C, Laurel and Rogers 2020), and Pacific halibut (3–10°C, Liu et al. 1994). The effects of temperature on arrowtooth flounder spawning and early life history are unclear (Doyle et al. 2018), and thus were not modeled here. When temperature in a spatial model cell exceeds these species-specific bounds at the time of spawning, no reproduction occurs in that cell for that species (Audzijonyte et al. 2019). The combination of temperature-based movement and reproduction constraints also means that any spawners are excluded from spawning grounds that sit outside the species thermal window. If no suitable cells are found, complete reproductive failure occurs (Audzijonyte et al. 2019).

### Bioenergetics

In Atlantis, temperature directly influences metabolic rates of consumers, the growth of primary producers, and basal biogeochemical processes like denitrification and detrital decay (Fulton et al. 2011). By default, a  $Q_{10}$  coefficient approach is used, with vital rates multiplied by a monotonically increasing temperature-dependent scalar  $T_{scalar}$

$$T_{scalar} = Q_{10}^{\frac{(T - T_{base})}{10^{\circ C}}},$$

where  $T$  is the current temperature,  $T_{base}$  is a baseline temperature of 10°C, and  $Q_{10}$  defines the slope of the relationship

and can be species-specific but is often set to 2.0 by default (Audzijonyte et al. 2019). This scalar is applied by default to a range of processes, including producer growth rate and, for consumers, rates of consumption, growth, and non-predation natural mortality. One limitation of this approach is that it implies that a complex, interacting suite of metabolic processes ramp up with temperature.

In the bioenergetic literature, it is more typical that the consumption of ectotherms under increased temperature increase until an optimum temperature before declining (Kitchell et al. 1977, Thornton & Lessem 1978). Previous multi-species models in the North Pacific have included bioenergetic response to temperature in the form of a unimodal scalar on consumption and other metabolic processes of key groundfish species (CEATTLE: Holsman et al. 2016, Adams et al. 2022). For consistency with other models in Alaska, we implemented a new temperature response in Atlantis to reproduce the CEATTLE formulation (Holsman and Aydin 2015):

$$T_{corr} = V^X e^{X(1-V)},$$

where:

$$V = \frac{(T_{CM} - T)}{(T_{CM} - T_{C0})},$$

$$X = \left[ Z^2 \left( 1 + \left( 1 + \frac{40}{Y} \right)^{0.5} \right)^2 \right] / 400,$$

$$Z = \log(Q_{10}) (T_{CM} - T_{C0}),$$

$$Y = \log(Q_{10}) (T_{CM} - T_{C0} + 2),$$

where  $T_{C0}$  is the temperature of highest consumption, and  $T_{CM}$  is the temperature above which no consumption occurs. In Atlantis GOA, we applied this unimodal response to walleye pollock, Pacific cod, arrowtooth flounder, and Pacific halibut, and parameterized the curve after Adams et al. (2022) and references therein (Supplementary Table S2.1, Fig. 2b). To capture important bioenergetic effects of warming on key GOA forage fish species (Arimitsu et al. 2021), we used the bioenergetic parameter values for walleye pollock (Supplementary Table S2.1) to parameterize the unimodal response of Pacific capelin, Pacific sand lance, Pacific herring, slope forage fish, and eulachon. We chose pollock because, of the four species for which we had empirically derived bioenergetic parameters, it has the most similar life history to forage fish, especially during the juvenile stage. Capelin occurrence in Alaska declines steeply for temperatures higher than 10.5°C (McGowan et al. 2019), and mean water temperatures recorded from North Pacific herring stocks vary between 7.5°C and 12.75°C (dos Santos Schmidt et al. 2021), suggesting that parameters for pollock constitute an acceptable approximation. We applied the default response described above to the rest of the groups in the model.

### Model calibration and skill evaluation

After the initial parameterization, input parameters of the Base model were tuned to meet a set of criteria: functional group persistence (i.e. no groups going extinct); model equilibrium (i.e. temporal stability of age and size structures); and the ability of the model to reproduce species biomass within the bounds of historical values (Kaplan and Marshall 2016). To address the persistence criterion, we aimed for no functional groups to go extinct (<1% initial biomass). To evaluate model skill with respect to the equilibrium criterion, we calculated the ratio of terminal biomass to initial biomass. Finally,

we evaluated whether terminal biomass was within historical values (for groups where these were available). We evaluated the model against these criteria after a 30-year run, which was selected as the length of the spin-up period for the simulations in the present study (see below). Details on model calibration and skill assessment can be found in [Supplementary Material S1](#), Section 6.

### Scenarios of climate stressors

We evaluated the effects of climate stressors on model outcomes by applying four scenarios with increased temperature and decreased LTL productivity in isolation and in combination. We simulated all scenarios for 50 years, which included 30 years of model spin-up (1999 conditions) and 20 years of simulation with climate forcings. The spin-up period was necessary to allow the model to cycle through initial instabilities (Pethybridge et al. 2019) and was applied to all scenarios.

**Scenario 1: Base model.** This is the Atlantis GOA model, calibrated ([Supplementary Material S1](#)) and with the mechanistic integration of temperature as described above, forced with physics (temperature, salinity, and hydrodynamics) from 1999.

**Scenario 2: Increased temperature.** This scenario is the Base model forced with physics from 2014, chosen as a year of warm conditions in the GOA (Di Lorenzo and Mantua 2016). The 2014 forcing was applied for 20 years after allowing for the 30-year spin-up period with 1999 conditions (Base model). Differences in temperature between the 1999 and 2014 forcings were up to 4°C in some model cells during the summer months ([Supplementary Fig. S2.1](#)).

**Scenario 3: Decreased LTL productivity.** Growth rates of diatoms, mesozooplankton (which represents copepods in Atlantis GOA; see [Supplementary Material S1](#)), and euphausiids were halved compared to the Base model for 20 years, after a 30-year spin-up. Halving growth rates for 20 years resulted in a terminal biomass for these plankton groups of 40–60% the biomass in the Base model ([Supplementary Fig. S2.2](#)).

**Scenario 4: Increased temperature and decreased LTL productivity** (Scenarios 2 and 3 combined).

Scenarios 2, 3, and 4 were compared to the Base model in terms of terminal (average of the last 5 years) biomass for each functional group, and weight-at-age and numbers-at-age for vertebrates.

### Sensitivity tests: realism of thermal niches and bioenergetics

To test the importance of different assumptions when mechanistically integrating temperature in Atlantis GOA, we ran Scenarios 1 and 2 (i.e. Base model and increased temperature) under five sets of assumptions about the effects of temperature on biology. These five model specifications aimed to represent higher and lower realism compared to the Base model. These sensitivity tests seek to identify aspects of structural uncertainty in the simulations that influence model projections and therefore potential future fisheries management advice, or that point to key data gaps (Geary et al. 2020). We computed terminal biomass of the nine species for which we apply unimodal bioenergetic responses in the Base model (i.e. pollock, Pacific cod, arrowtooth flounder, Pacific halibut, Pacific capelin, Pacific sand lance, Pacific herring, slope forage fish, and eulachon) and compared the following simulations:

- (i) Higher realism: Winter spatial distributions. The Base model used fixed ontogenetic spatial distributions representative of summer conditions for groundfish ([Supplementary Material S1](#)). However, several groundfish species in the GOA form spawning aggregations during the winter months in areas that differ from those used in the summer for foraging (Dunn & Matarese 1987, Ciannelli et al. 2007, Doyle et al. 2018). As a result, spawning adults are expected to experience different local conditions during the spawning season. We developed winter distributions for pollock, Pacific cod, arrowtooth flounder, and Pacific halibut with catch data from the Alaska Groundfish Observer Program (AFSC and AKRO 2022) for October–March and a geostatistical modeling framework that accounts for preferential sampling in fishery-dependent data (Alglave et al. 2022). No environmental variables were used in these models, which only incorporated spatiotemporal autocorrelation in fish catch per unit effort (CPUE) index. Unlike the “summer” distribution models used in the Base Atlantis GOA, these models did not account for ontogenetic stages.
- (ii) Higher realism: All species used a unimodal bioenergetic response with the formulation from Holsman and Aydin (2015). As in the Base model, the unimodal responses of pollock, Pacific cod, arrowtooth flounder, and Pacific halibut were derived from CEATTLE. Curves for all other fish species employed a default  $Q_{10} = 2.36$  (Clarke 2004), a  $T_{CM}$  equal to the maximum temperature from Kaschner et al. (2019), and  $T_{C0} = 0.7T_{CM}$ , based on an average  $T_{C0}/T_{CM} = 0.7$  for the four CEATTLE species ([Supplementary Fig. S2.3](#)).
- (iii) Lower realism: No thermal niches constraining movement and spawning (but bioenergetic responses being applied like in the Base model).
- (iv) Lower realism: All species used the default monotonic increasing  $Q_{10}$  bioenergetic response to temperature (see above). This response assumes that consumption, growth, and natural mortality increase as a power function of temperature.
- (v) Lower realism: No temperature sensitivities. None of the limitations to movement and spawning, nor the bioenergetic effects of temperature, were applied.

## Results

### Model calibration

Atlantis GOA was calibrated to 1990 conditions by tuning input parameters so that model outputs were as close as possible to the initial conditions after 30 years of model spin-up (*sensu* Kaplan & Marshall 2016). After a 30-year simulation run, all model functional groups persisted in the Base model. Terminal biomass (5-year average) was between 0.5 and 2 times the initial values for 57 model groups (73%), between 0.25 and 4 times the initial values for 12 groups (15%), and it was outside these bounds for 9 groups (10%), which included all 3 detritus groups, detritivorous meiobenthos, diatoms, small phytoplankton, Pacific halibut, and coho salmon. The size and age structures of vertebrates were calibrated to be realistic and as similar as possible to the input conditions. Biomass estimates for Pacific cod and flathead sole were 3.1 and 2.3 times the historical maximum values observed for these species, respectively, and for Pacific halibut, the demersal

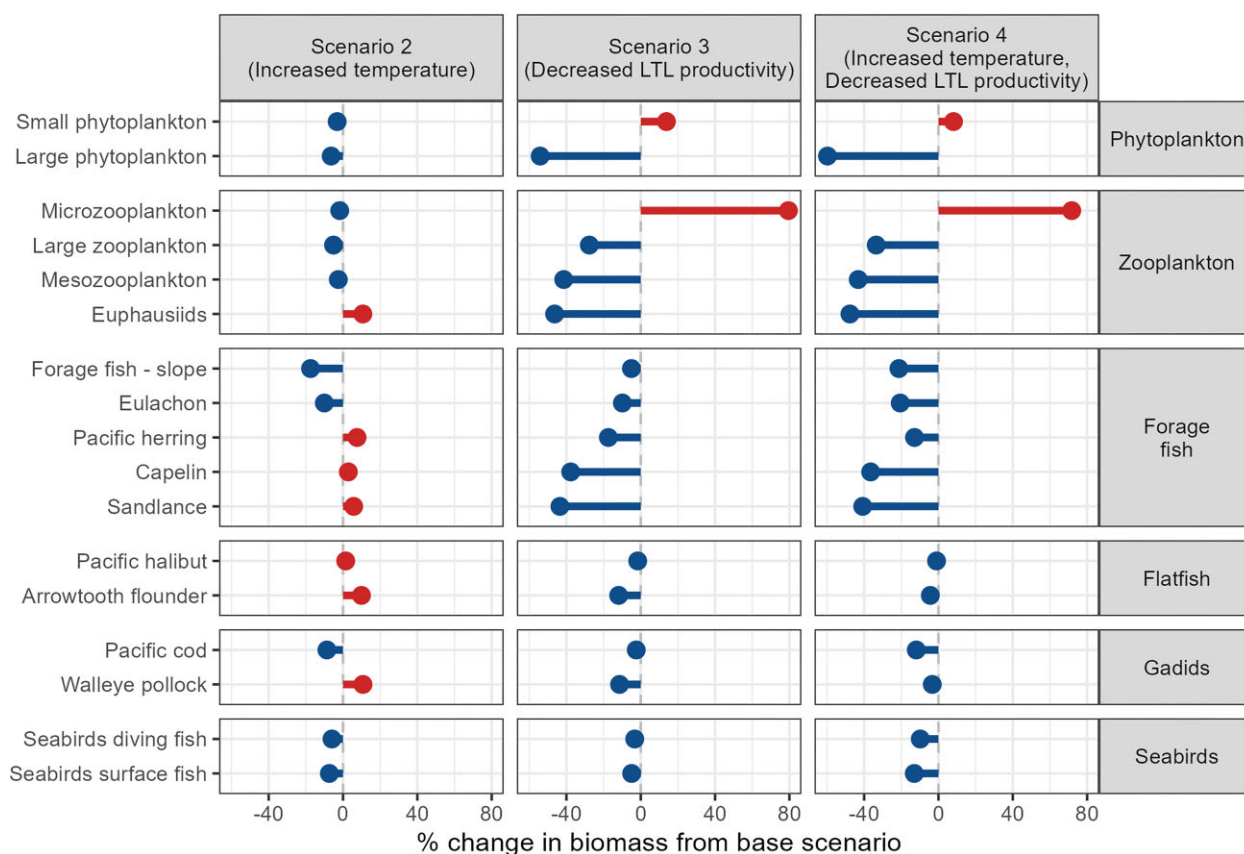
shelf rockfish complex, shallow- and deep-water flatfish, and sculpins, between 1.2 and 1.6 times the historical maxima. For all other groundfish groups, terminal biomass was within the bounds of historical values in the model domain. However, accurate historical estimates were not available for all species. See [Supplementary Material S1](#) (Section 6) for details.

### Scenarios of climate stressors

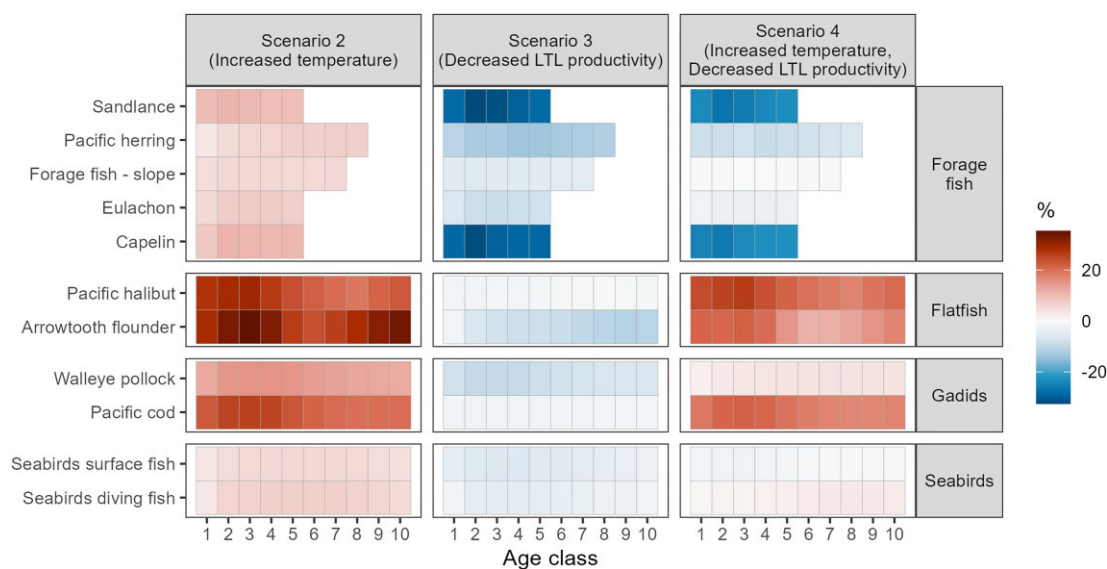
The effects of the different scenarios on model terminal biomass are reported in [Fig. 3](#) for the 17 selected functional groups (see [Supplementary Fig. S2.4](#) for results for all species). Responses to increased temperature in Scenario 2 were species-specific, with some fish groups experiencing increased terminal biomass in warm conditions (e.g. up to +10–11% for arrowtooth flounder and pollock, respectively) and other groups decreased biomass (e.g. –17% for slope forage fish, –10% for eulachon, and –9% for Pacific cod). Conversely, decreased LTL productivity in Scenario 3 led to lower terminal biomass of diatoms (–54%), mesozooplankton (–41%), euphausiids (–46%), sand lance (–43%), capelin (–38%), herring (–17%), and eulachon (–10%), although declines became smaller for flatfish, gadids, and seabirds. Increased temperature and decreased productivity had cumulative effects on terminal biomass in Scenario 4.

Increased temperature in Scenario 2 resulted in higher weight-at-age of all selected vertebrate groups after applying the warm forcings for 20 years ([Supplementary Fig. S2.5](#)), with notable increases for arrowtooth flounder, Pacific halibut, Pacific cod, and walleye pollock (+30%, +24%, +22%, and +13%, respectively, mean across age classes, [Fig. 4](#)). Forage fish weight-at-age also responded positively to increased temperature, but to a lesser extent (all changes  $\leq 10\%$ ). Decreased LTL productivity in Scenario 3 corresponded to significantly lower weight-at-age of forage fish (–30%, –30%, –8%, –12%, and –5% for capelin, sand lance, eulachon, herring, and slope forage fish, respectively). Groundfish weight-at-age was less affected by declines in LTL productivity (all declines  $\leq 10\%$ ). In Scenario 4, opposite effects on weight-at-age from increased temperature and decreased LTL productivity partially counteracted each other, with net weight-at-age decreases in capelin, sand lance, and herring weight-at-age (–24%, –25%, and –8%, respectively), increases in arrowtooth flounder, Pacific cod, and Pacific halibut weight-at-age (+16%, +19%, and +21%, respectively), and small effects on pollock, eulachon, and seabirds.

Increased temperature in Scenario 2 resulted in overall lower numbers-at-age for most species when averaging across age classes ([Fig. 5](#), [Supplementary Fig. S2.6](#)). However, for most fish groups, the number of individuals in the first age class increased in Scenario 2 (except for Pacific cod). Pacific cod experienced the largest declines, with average declines in numbers-at-age of –24% under increased temperature, followed by slope forage fish, Pacific halibut, arrowtooth flounder, eulachon, and fish-eating seabirds (–19%, –17%, –14%, –13%, and –10%, respectively). Decreased LTL productivity in Scenario 3 resulted in reduced numbers-at-age for sand lance and capelin (–22% and –11%, respectively), with smaller negative changes for other species and close to no effect on higher trophic levels, including fish-eating seabirds. Scenario 4 had cumulative effects from the other two scenarios and resulted in the largest decreases in numbers-at-age for all species.

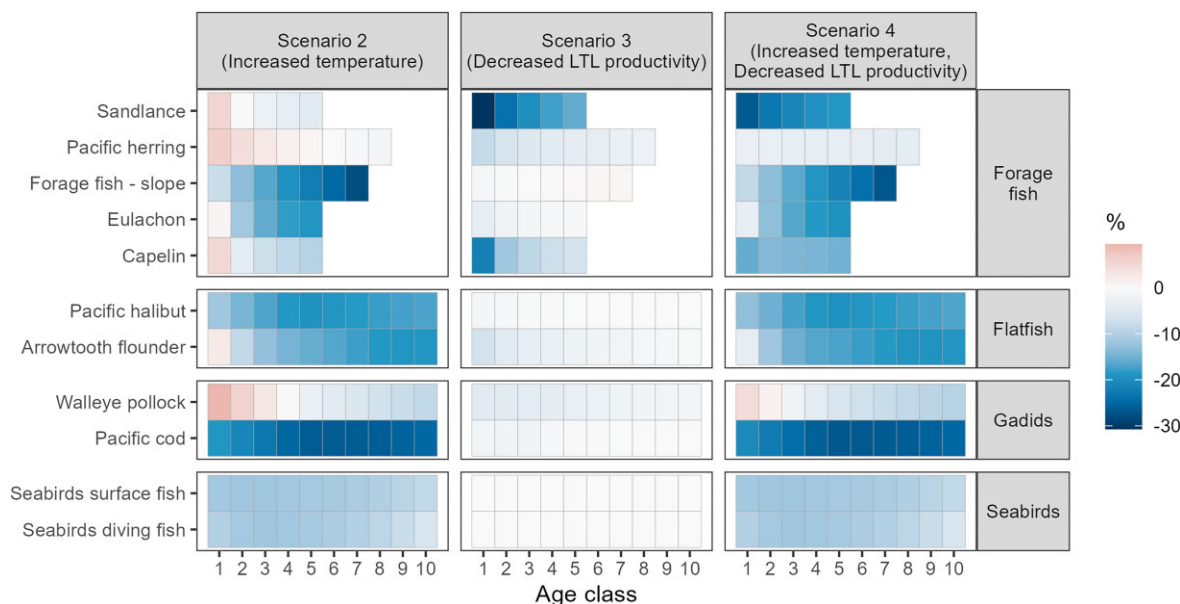


**Figure 3.** Relative changes in terminal biomass (average over the last 5 years) of 17 selected Atlantis GOA functional groups for (left to right): Scenario 2 (increased temperatures), Scenario 3 (50% reduction in low-trophic-level productivity), and Scenario 4 (Scenarios 2 and 3 combined) compared to the Base model (no climate stressors). Gray-dashed vertical lines represent values in the Base model, and red and blue horizontal segments and points represent positive and negative changes, respectively.



**Figure 4.** Relative changes in weight-at-age (average over the last 5 years) of selected Atlantis GOA functional groups for (left to right): Scenario 2 (increased temperatures), Scenario 3 (50% reduction in low-trophic-level productivity), and Scenario 4 (Scenarios 2 and 3 combined) compared to the Base model (no climate stressors). Changes are shown by age class. Duration of age classes varies depending on life history.





**Figure 5.** Relative changes in numbers-at-age (average over the last 5 years) of selected Atlantis GOA functional groups for (left to right): Scenario 2 (increased temperatures), Scenario 3 (50% reduction in low-trophic-level productivity), and Scenario 4 (Scenarios 2 and 3 combined) compared to the Base model (no climate stressors). Changes are shown by age class. Duration of age classes varies depending on life history.

### Sensitivity test results: realism of thermal niches and bioenergetics

For the sensitivity runs with higher realism (1 and 2), capturing winter distributions for pollock, Pacific cod, arrowtooth flounder, and Pacific caused higher terminal biomass for arrowtooth flounder, lower terminal biomass for Pacific cod, and negligible differences for pollock (Fig. 6; also see [Supplementary Fig. S2.7](#) for changes relative to the Base model instead of absolute values); and unimodal bioenergetic responses had negligible effects on terminal biomass for all selected species, but appreciable differences for some other groups, such as thornyheads, skates, Pacific hake, and coho salmon ([Supplementary Fig. S2.8](#)). For the simulations with lower realism (3–5), decoupling thermal tolerance niches from movement and spawning resulted in the model predicting higher terminal biomass for all groundfish except pollock (likely because of the increase in its predators), but particularly so for Pacific cod; applying a monotonic increasing  $Q_{10}$  relationship between vital rates and temperature had positive effects on arrowtooth flounder and Pacific halibut, negative effects on pollock, and negligible effects on Pacific cod; and applying no temperature sensitivity resulted in model outputs being decoupled from temperature forcings and very similar biomasses under cold and warm temperatures. Effects on forage fish species were small compared to the four groundfish species.

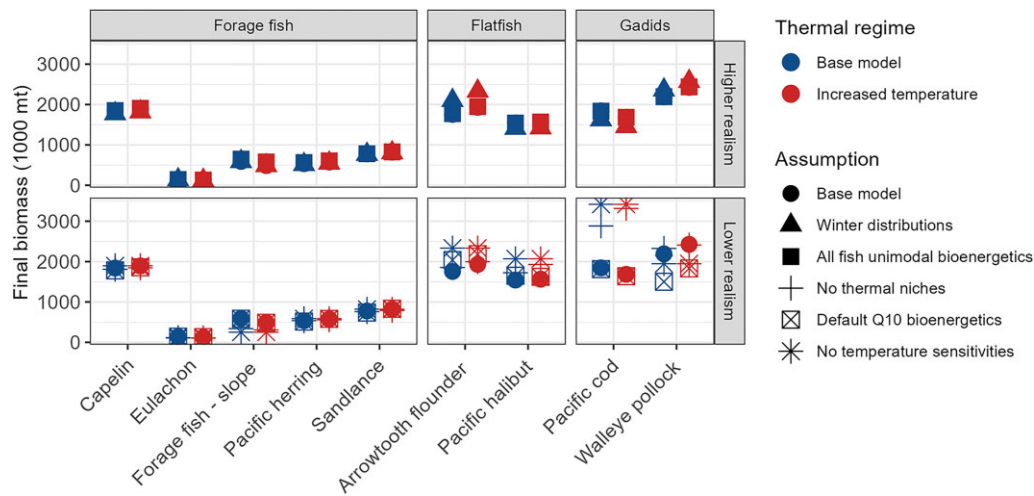
### Discussion

We developed a deterministic end-to-end Atlantis simulation model of the Gulf of Alaska (GOA), and we applied it to explore the effects of increased temperature and decreased low trophic level (LTL) productivity on population-level outcomes for ecologically and commercially important taxa. We found that increased temperature resulted in increased weight-at-age and natural mortality for most species, decreased LTL productivity resulted in decreased weight-at-age and increased mor-

talidity, and the two combined had cumulative effects. We also found that not accounting for thermal limitations to movement and spawning leads to overly optimistic predictions of groundfish biomass in the presence of climate stressors, and that neglecting links between temperature and ecophysiology limits our ability to explore climate scenarios using ecosystem models.

### Simulating climate forcing scenarios

In the increased temperature scenario (Scenario 2), terminal stock biomass across most fish species showed a moderate increase relative to the Base model. This increase was mediated by a positive change in weight-at-age under warmer temperatures and under no food limitation. Bioenergetic theory, largely based on empirical studies, postulates that global warming is driving fish populations towards smaller terminal body sizes (reviewed in Lefevre et al. 2021). However, observations of fish body growth in wild populations showed that 45% of species were larger in warmer water (Audzijonyte et al. 2020). In the Bering Sea, weight-at-age of juvenile pollock increases with temperature (Oke et al. 2022). The higher weight-at-age under warm conditions predicted by our simulations is in agreement with results from size spectrum models where including temperature-dependent physiological processes led to increased consumption and growth and consequently higher size-at-age for some species (Reum et al. 2020), as well as laboratory evaluations for Alaska groundfish (Laurel et al. 2016). In the increased temperature scenario, the increase in weight-at-age was driven by increased consumption resulting from the bioenergetic response to temperature. For species with the unimodal bioenergetic response, this increase continued until the temperature of optimum consumption ( $T_{CO}$ ) was reached, while it was monotonic for species with the default  $Q_{10}$  response. We found that the improvement in weight-at-age under increased temperature and no food limitation was highest for arrowtooth flounder, which



**Figure 6.** Terminal biomass (average over the last 5 years) under different model specifications and assumptions (shapes) for the effects of temperature on biology under higher model realism (winter distributions and unimodal bioenergetic responses) and lower model realism (no thermal constraints to movement and reproduction, default monotonic bioenergetic responses, and no temperature sensitivities). Simulations under base conditions are in blue, increased temperature in red.

was the species with the highest  $T_{C0}$  and  $T_{CM}$  and thus had the most to gain from warmer temperatures.

Decreased LTL productivity had the largest effects on forage fish weight-at-age and numbers-at-age, in particular sand lance and capelin, and some effects on the younger age classes of groundfish like pollock, which are also planktivorous. However, bottom-up effects due to food limitation on both weight-at-age and numbers-at-age of the upper trophic levels were small compared to observations in the GOA (Arimitsu et al. 2021), indicating attenuation of bottom-up effects with increasing trophic level. These results contrast with findings of simulation studies with global ecosystem models, which have reported that climate-driven decreases in biomass can be amplified at higher trophic levels (Lotze et al. 2019). In empirical data from the GOA, prolonged warm conditions and altered plankton productivity were observed to have severe cascading effects on the upper trophic levels (Suryan et al. 2021), causing deteriorated condition in forage fish (Baker et al. 2019, von Biela et al. 2019), recruitment failures in groundfish (Barbeaux et al. 2020), reproductive failures and mass mortalities of seabirds (Piatt et al. 2020). These effects were diminished in Atlantis GOA, likely for two main reasons. First, prey energy density is not modeled dynamically in Atlantis for plankton (Audzijonyte et al. 2019). During recent heatwave events in the GOA, zooplankton community composition shifted towards smaller species (Batten et al. 2018), which is hypothesized to have resulted in lower energy content for the upper trophic levels (von Biela et al. 2019, Piatt et al. 2020, Arimitsu et al. 2021). Though forcing lower zooplankton biomass may approximate the trophic effects of decreased plankton energy content, detrimental effects on upper trophic levels may have been less extreme in our model. Second, while the present analysis did not emphasize fishing, more realistic fishing mortality rates than the light background  $F$  used here may amplify negative effects of bottom-up processes on overall ecosystem productivity (Essington et al. 2015). Future applications of this model should consider fishing alongside climate drivers to better match expected ecosystem dynamics (Gaichas et al. 2010).

When decreased LTL productivity was forced together with increased temperature, the beneficial effects of temperature on weight-at-age were curbed. While metabolic rates are generally predicted to increase as temperature rises (Pörtner and Farrell 2008), increased metabolic demand may not be met by increased food availability if LTL productivity declines (Lotze et al. 2019). Scenario 4 corresponded to warmer water, which consequently boosted metabolic rates, but combined with lowered food availability. Heneghan et al. (2021) showed that warming and decreased LTL productivity had additive effects in explaining biomass declines in future projections. This was true in our study when we evaluated effects of increased temperature and decreased plankton productivity on numbers-at-age, but the two scenarios had opposite effects on weight-at-age. In the GOA, the combination of increased metabolic demand and the co-occurring food limitation during the 2013–2016 heatwave likely had detrimental effects on several species (von Biela et al. 2019, Barbeaux et al. 2020, Arimitsu et al. 2021, Suryan et al. 2021).

Reduced numbers-at-age of adults under warmer temperatures were due to increased consumption from predators, but likely in part also to the amplifying effect of increased temperature on background mortality. This agrees with simulation studies that have shown that climate-driven mortality in marine stocks is caused by increased metabolic rates and lower food availability under warm, low productivity conditions (Carozza et al. 2019, Koenigstein et al. 2022). The negative effects on numbers-at-age under increased temperature were greatest on Pacific cod. This was likely due to the model inclusion of a narrow temperature range for egg hatch success of 3–7°C (Laurel and Rogers 2020), which, in nature, likely caused a loss of spawning habitat for this species in the GOA during the 2013–2016 heatwave. Notably, in the model, the first age class of several fish groups was more abundant in Scenario 2 (increased temperature). This was likely because the reproductive output of age-structured populations in Atlantis scales dynamically with the reserve nitrogen component of weight-at-age, with heavier fish producing more eggs and, as a result, more recruits (Audzijonyte et al. 2019).

## Model specification: realism of thermal niches and bioenergetics

Increasing the realism of the modeled thermal niches and bioenergetics had stronger effects on functional groups that were parameterized to be more sensitive to temperature. For example, lower Pacific cod terminal biomass in the model that captured winter distributions suggested that temperature in the model cells where cod was distributed during the winter increased enough to disrupt the stenothermic spawning. Bioenergetic winter stress is thought to have been one important cause of population decline of Pacific cod in the GOA during the 2013–2016 heatwave (Barbeaux et al. 2020). However, summer and winter distributions for pollock were also different, with pollock aggregating around Kodiak Island in the winter, but pollock terminal biomass was almost the same, highlighting the more eurythermic reproduction compared to Pacific cod. Similarly, the significant increase in Pacific cod terminal biomass when thermal limitations to spawning and movement were removed highlights that the stenothermic hatching success is an important control of cod population size and dynamics.

In general, this illustrates that, though it is difficult to provide *a priori* guidelines for which particular model specification (e.g. bioenergetic formulation, thermal tolerance niches, etc.) should be adopted in an ecosystem model application, effort should be made to capture the best available information on species responses to climate stressors, especially for species of interest. We highlight the value of testing competing specifications of thermal sensitivities, in particular for model applications that address climate-related questions. While our empirical knowledge of thermal sensitivities of many fish species is still limited, modelers should explore different parameterizations of these processes to be aware of their effects on model results.

## Conclusions

Marine ecosystems are expected to respond in complex ways to future conditions of warmer water and shifts in low trophic level (LTL) productivity. In general, population biomass is expected to decline in a warmer future (Lotze et al. 2019). The results from this study highlight that, when selecting which stressors should be forced on an ecosystem model, it is important to capture the key ecological processes that drive the system. For example, simply imposing increased temperature forcings may not be sufficient if the system is also driven by other stressors, like shifts in primary productivity. Furthermore, while it is important to evaluate alternative formulations when linking environmental stressors to the modeled biological processes, using at least some form of temperature dependence is preferable to decoupling such processes from temperature entirely. In our study, neglecting biological properties like thermal restrictions to habitat and bioenergetic responses to temperature led to overly optimistic model outcomes, and also to lower variability of model-derived quantities as temperature increased.

The model was able to reproduce key patterns of biomass, weight-at-age, and numbers-at-age for most functional groups. For the present study, we aimed for species persistence and general model reasonability at equilibrium. However, for complex ecosystem models to be used as projection tools, a more thorough skill assessment is necessary,

particularly if the model aims to inform resource management (Kaplan and Marshall 2016). Future model skill assessment efforts may include, for example, matching observations in hindcast, reproducing spatial and temporal variability at many time scales, and matching expected productivity from stock assessments or life history theory (Kaplan and Marshall 2016).

Effects of increased temperature and food limitation in our model were less pronounced than expected in the real world, possibly because Atlantis does not capture the observed decline in plankton energy content and because of the low background fishing mortality applied in our simulations. Furthermore, climate stressors other than temperature and shifts in LTL productivity will likely impact marine ecosystems with climate variability, including ocean acidification and hypoxia, which may both contribute to altered fish condition under climate change (Lefevre et al. 2021). Our simulations did not explore these or other stressors, but Atlantis provides users with the option of activating sensitivity to pH (Marshall et al. 2017) and oxygen (Audzijonyte et al. 2019), so the impact of these variables could be explored in the future. In addition, the effects of climate stressors on the model should be evaluated in the context of varying levels of fishing to explore the relative importance of anthropogenic climate change and harvesting stressors (Lotze et al. 2019, Woodworth-Jefcoats et al. 2019).

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## Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

*Conflict of interest:* The authors declare no competing interests.

## Data availability

Model input files for the Base model presented here are available on GitHub at [https://github.com/somros/AtlantisGOA\\_Base](https://github.com/somros/AtlantisGOA_Base).

## Author contributions

Conceptualization: A.R., A.E.P., I.C.K., M.W.D., K.A., M.D.B. Methodology: A.R., I.C.K., A.J.H., E.A.F., H.M.L. Data curation: A.R., M.W.D., I.C.K., A.J.H., M.T.W., J.M., K.A., B.E.F., S.S. Formal analysis: A.R., I.C.K., P-Y.H., O.R.L., G.C., B.A.,



A.L.H. Funding acquisition: M.W.D., A.E.P., I.C.K. Writing – original draft: All authors. Writing – review & editing: All authors.

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