

From nutrients to fish: Impacts of mesoscale processes in a global CESM-FEISTY eddying ocean model framework

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Abstract

The ocean sustains ecosystems that are essential for human livelihood and habitability of the planet. The ocean holds an enormous amount of carbon, and serves as a critical source of nutrition for human societies worldwide. Climate variability and change impacts marine biogeochemistry and ecosystems. Thus, having state-of-the-art simulations of the ocean, which include marine biogeochemistry and ecosystems, is critical for understanding the role of climate variability and change on the ocean biosphere. Here we present a novel global eddy-resolving (0.1° horizontal resolution) simulation of the ocean and sea ice, including ocean biogeochemistry, performed with the Community Earth System Model (CESM). The simulation is forced by the atmospheric dataset based on the Japanese Reanalysis (JRA-55) product over the 1958 – 2021 period. We present a novel configuration of the CESM marine ecosystem model in this simulation which includes two zooplankton classes: microzooplankton and mesozooplankton. This novel planktonic food web structure facilitates “offline” coupling with the Fisheries Size and Functional Type (FEISTY) model. FEISTY is a size- and trait-based model of fish functional types contributing to fisheries. We present an evaluation of the ocean biogeochemistry, marine ecosystem (including fish types), and sea ice in this high-resolution simulation compared to available observations and a corresponding low resolution (nominal 1°) simulation. Our analysis offers insights into environmental controls on trophodynamics within the ocean. We find that this high resolution simulation provides a realistic reconstruction of nutrients, oxygen, sea ice, plankton and fish distributions over the global ocean. On global and large regional scales the high-resolution simulation is comparable to the standard 1° simulation, but on smaller scales, explicitly resolving the mesoscale dynamics is shown to be important for accurately capturing trophodynamic structuring, especially in coastal ecosystems. We show that fine scale ocean features leave imprints on ocean ecosystems, from plankton to fish, from the tropics to polar regions. This simulation also offers insights on ocean acidification over the past 64 years, as well as how large scale climate variations may impact upper trophic levels. The data generated by the simulations are publicly available and will be a fruitful community resource for a large variety of oceanographic science questions.

1 Introduction

The ocean plays a prominent role in our Earth system, holds tremendous biodiversity, and provides nutrition and culture to human societies. The ocean is the dominant active reservoir of carbon –

storing roughly 38,000 Pg C of natural carbon – and it is a major sink for atmospheric CO₂, absorbing approximately one-quarter of human-generated CO₂ emissions annually (Friedlingstein et al., 2022). Ocean ecosystems are critical to food security: fish, crustaceans, and molluscs are an essential source of nutrition for much of the world’s population, with fish accounting for roughly 17% of animal protein consumed (FAO, 2018). Fisheries are both culturally important and economically vital—contributing, for instance, over \$200 billion in economic activity and more than 1.7 million jobs in the U.S. annually (NMFS, 2018). The ocean also contains 90% of the habitable space on Earth and is home to species from all clades of life too numerous to count (COML, 2010). Preserving this biodiversity in the face of human impact is essential for the continued habitability of our planet (Worm et al., 2006).

An ability to understand, predict, and proactively manage human use and impacts on marine ecosystems is a critical societal need – one that is particularly urgent in the context of climate change and the increasing footprint of human activities. The ocean has absorbed ~90% of the anomalous heat trapped due to rising atmospheric CO₂ concentrations (Cheng et al., 2017) and ocean circulation strongly determines regional climate. Warming, acidification, and loss of dissolved oxygen from the ocean constitute ecosystem stressors (e.g., Gruber et al., 2011) that are unprecedented in the history of life and pose significant risk of large-scale extinctions (Penn & Deutsch, 2022).

Comprehensive models of the ocean ecosystem are an essential element for understanding the impacts of global change on the ocean biosphere. Earth system models (ESMs), while originally developed for the purpose of simulating carbon-climate feedbacks (Friedlingstein et al., 2006), have relevance to questions related to ocean ecosystems (Bopp et al., 2013; Stock et al., 2011; Tommasi et al., 2017). Notably, ESMs represent mechanistic linkages between the physical climate system and marine ecosystems. Three-dimensional ocean general circulation models are coupled with ocean biogeochemical models (OBMs) that represent the lower trophic levels of marine ecosystems (i.e., plankton) that play a key role in mediating carbon fluxes and elemental cycles of nutrients, such as nitrogen and phosphorus. Primary productivity converts inorganic nutrients and carbon in the sunlit surface ocean to organic matter; the sinking and remineralization of this material constitute “the biological pump”: a mechanism sequestering carbon at depth, as well as providing benthic organisms with a food resource, especially in coastal shelf regions. Net primary productivity (NPP) by phytoplankton supports nearly all marine life and is tightly controlled by physical processes which control nutrient and light availability. Marine phytoplankton account for roughly half of the globally-integrated annual NPP, but with only ~1% of the photosynthetic biomass of that on land (Field et al., 1998). Lacking biomass-derived inertia typical of terrestrial systems, marine ecosystems are sensitive to perturbation by short-timescale variations in physical forcing.

As the ultimate supply of energy to higher trophic levels, NPP places an upper limit on ecosystem production; however, relationships between, for instance, fisheries yields and NPP are not straightforward (Stock et al., 2017; Straile, 1997). In particular, a variety of ecological mechanisms modulate trophodynamics contributing to variable higher trophic levels yields. OBMs are capable of simulating the large-scale distribution of NPP associated biogeography (e.g., Follows et al., 2007), and the dynamic response of lower-trophic levels to climate variability and change (Stock et al., 2014a; Stock et al., 2014b). Simulated ocean biogeochemical dynamics are driven by bottom-up forcing: physical processes regulate temperature distributions and nutrient supply to the euphotic zone, mixed layer depths control light availability and biomass concentrations; these processes together affect phytoplankton growth directly by modulating resource availability and influence which types of phytoplankton thrive. Simultaneously, zooplankton respond in the context of environmentally-dependent rate processes, changes in prey concentrations, and community composition. State-of-the-art OBMs represent zooplankton grazing explicitly, which is a fundamental control on phytoplankton bloom dynamics (e.g., Behrenfeld & Boss, 2014; Friedland et al., 2016) and export of organic matter from the surface ocean (Turner, 2015). However, OBMs, including the one we present in this study, do not typically have an explicit representation of higher-trophic-level predation on zooplankton, relying instead on a nonlinear density-dependent loss term that implicitly represents predation (i.e., “closure” term; e.g., Edwards & Yool, 2000; Fasham, 1995; Ohman & Hirche, 2001; Steele & Henderson, 1992).

Physical regimes structure the upper-ocean habitat, but ecosystem processes further modulate trophic energy transfers and the trophic efficiency of marine ecosystems is regionally variable (Ryther, 1969). In the oligotrophic systems characteristic of subtropical gyres, for instance, nutrient supply is limited by strong stratification; algal assemblages are dominated by small-celled organisms with high nutrient-uptake efficiencies. Planktonic food webs in these systems are tightly coupled, dominated by

microzooplankton grazers, high rates of upper-ocean recycling, and little material available for export or consumption by higher trophic levels. High latitude systems, by contrast, tend to be nutrient replete, but light-limited and strongly seasonal; these systems are dominated by larger phytoplankton and tend to export greater fractions of primary production - either as sinking organic matter or up the food chain. Further, continental shelves tend to have a large benthic component, fueled by particulate organic carbon (POC) falling to the seafloor, where it is consumed by benthic organisms. While OBMs simulate zooplankton and POC dynamics, additional model efforts need to be made to understand, e.g., the impacts of climate change and variability on fisheries.

Predicting fish biomass and productivity globally is one of the current challenges in fisheries ecology. This is typically done by using size- and/or trait-based representations of fish (K. Andersen, 2019; Kiørboe et al., 2018). Projections of fish biomass and productivity are made by forcing fish models with ESM output, allowing an assessment of the implications of climate change on higher trophic levels in marine environments (Heneghan et al., 2021; Maury, 2010; Petrik et al., 2020; Tittensor et al., 2018). In these models, fish are subject to bottom-up drivers, i.e., prey biomass and temperature. Previous work has acknowledged the effect of climate change on fish biomass: for example, Lotze et al. (2019) showed that declines in NPP are amplified in ocean animal biomass (i.e., trophic amplification). Further, ESM-forced fish models have showed that large pelagic fishes may be most sensitive to climate change (Heneghan et al., 2021; Petrik et al., 2020).

Notably, however, most ESMs are typically integrated at a horizontal resolution of about 1° or 100 km. This coarse grid-spacing precludes resolving the ocean mesoscale (10-100 km)—which is the dominant energetic scale in the ocean (Stammer, 1997) - and limits the model fidelity in coastal regions that are important areas of human activity, accounting for >80% of global fish catch (K. Sherman et al., 2009). Moreover, mesoscale features can be hotspots of biological activity, for example, by concentrating nutrients along fronts or eddies which can shift planktonic communities and lead to more efficient ecosystem transfer efficiency (Godø et al., 2012; Woodson & Litvin, 2015). Thus, simulating the ocean at resolutions that permit coastal and mesoscale dynamics is desirable for many applications.

In this study, we introduce a new global high-resolution (nominal 0.1° horizontal resolution) ocean and sea ice simulation using the Community Earth System Model (CESM; Danabasoglu et al., 2020). The model is forced by the JRA55-do atmospheric state and runoff dataset over the period 1958 to 2021 (Kobayashi et al., 2015; Tsujino et al., 2020). The simulation employs the Marine Biogeochemical Library (MARBL; Long et al., 2021) with a novel planktonic ecosystem that includes an explicit mesozooplankton group, thereby providing a food resource to higher trophic levels. In addition to presenting results from CESM, another major goal of this simulation was to enable offline simulation of fish. We used the Fisheries Size and Functional Type (FEISTY) model to simulate higher trophic levels (Petrik et al., 2019). The FEISTY model is a size- and trait-based model that resolves the structure of fish communities from environmental forcing, i.e., mesozooplankton biomass, temperature, and detritus flux to the seafloor. In the present configuration, FEISTY is run offline, forced by the high-resolution CESM model output; in the future, it will be an online component of CESM.

In addition to documenting the offline coupling of FEISTY to CESM, we also evaluate this high-resolution simulation with respect to available observations, focusing in particular on elements of the solution pertinent to ocean biogeochemistry and marine ecosystems. We present analyses that highlight the influence of model resolution, ocean acidification over the 64-year reconstruction, the factors governing biogeography of trophic energy transfer, oxygen distributions, and fish biomass estimates from FEISTY. The overarching objectives of this integration are to 1) provide a reconstruction of the ocean’s physical and biogeochemical state over the last several decades; 2) create initial conditions for high-resolution, retrospective multi-annual forecast integrations with the full ESM (Chang et al., 2020; Yeager et al., 2023), enabling assessment of predictability characteristics of various elements of the Earth system, inclusive of an active ocean biogeochemistry model; and 3) serve as a baseline for comparison to a two-way, online coupled FEISTY-CESM simulation.

This paper is organized as follows. In section 2 we present the configuration details of our numerical experiments and describe the novel planktonic ecosystem in MARBL; section 3 focuses on model evaluation, providing comparisons to observations to evaluate the model skill of CESM and FEISTY in simulating global biogeochemistry and marine ecosystems, including a comparison of FEISTY fish catch to observed fish catches. Section 4 provides an overview of the model solution, offering preliminary analysis of large-scale to mesoscale ecosystem processes, from plankton to fish. Lastly, in Section 5 we

summarize our findings and identify areas for future work.

2 Methods

2.1 CESM-MARBL configuration

We use the ocean and sea-ice components of CESM version 2.2 (Danabasoglu et al., 2020). The ocean component is the Parallel Ocean Program version 2 (POP2; Danabasoglu et al., 2012; Smith et al., 2010) and the sea-ice component is the CICE version 5.1.2 (CICE5; Hunke et al., 2015). We perform two forced ocean – sea-ice (FOSI) simulations integrated over the 1958–2021 period using the JRA55-do atmospheric state and runoff dataset (JRA55-do; Tsujino et al., 2018). The primary difference between the two simulations is the change in model horizontal resolution: the high-resolution simulation (here after FOSI-HR) uses a nominal 0.1° horizontal resolution (the same grid as in Chang et al. (2020) and Harrison et al. (2018)), while the low-resolution simulation relies on the standard nominal 1° horizontal resolution (here after FOSI-LR). Additional details about the implementation and parameter settings used for FOSI-HR and FOSI-LR can be found in Chassignet et al. (2020). The main distinctions between the simulations presented in this manuscript and the ones discussed in Chassignet et al. (2020) are: (1) MARBL is enabled, and (2) additional tuning of the sea-ice were implemented to improve the realism of simulations. The default CICE5 parameter set, which are tuned for a 1° simulation, did not provide realistic ice coverage at 0.1° so some changes were made. All non-default parameters are listed in Table S1.

The FOSI-HR has $\sim 70\times$ the number of grid cells as the FOSI-LR, and the time step is $1/38$ the size, so the expectation is that the FOSI-HR requires roughly $2700\times$ the computer resources as the FOSI-LR. CESM does not scale optimally, and different choices in how to balance model cost and model throughput for the two runs resulted in the FOSI-HR only using $1000\times$ the computer resources of the FOSI-LR but taking almost $30\times$ the time to complete the simulation.

To initialize these simulations, we performed multiple repeating 61-year cycles (1958 - 2018) of JRA55-do forcings. For FOSI-HR a combined 244-year ocean sea-ice spin up simulation (four cycle) at the nominal 0.1° resolution is used. For FOSI-LR the ocean-sea ice with MARBL turned on spinup was forced by five repeating 61-year cycles of JRA55-do (305-year) of simulation at the nominal 1° resolution). The January 1st restart at the end of the respective spin up simulations are used to initialize FOSI-HR and FOSI-LR. MARBL was not enabled in the high-resolution spin up due to the prohibitive cost associated with running a prognostic ocean biogeochemistry model at this resolution. The MARBL initial condition for FOSI-HR was obtained by interpolating the restart at the end of the low resolution spin up onto the 0.1° POP grid.

In addition to the heat, freshwater, and momentum fluxes obtained from JRA-do, MARBL requires additional forcings in these FOSI simulations. We used historical atmospheric CO_2 ramping over the period 1958 to 2021, but also enable “ALT-CO2” parallel carbonate chemistry system, which functions as if atmospheric CO_2 remains at preindustrial levels. This allows a clean disentanglement of anthropogenic and natural carbon in the ocean, as well as a clear ocean acidification signal resulting from anthropogenic carbon. Transient atmospheric nitrogen deposition, from a previous fully coupled CESM2 simulation, was prescribed (Danabasoglu et al., 2020). Riverine inputs of dissolved inorganic carbon, dissolved organic matter, alkalinity, and nutrients (N, P, Si, and Fe) were held constant at year 1900 values from the GlobalNews dataset (Mayorga et al., 2010).

While most variables in the FOSI-HR were written out at a monthly time step, we created higher frequency time averages for certain variables. For example, the variables needed to force FEISTY (see section 2.2) were output at a daily time step since 1980. Additional 5 day output for some variables starts at 2006.

MARBL (marbl-ecosys.github.io) is the ocean biogeochemistry/planktonic ecosystem component in CESM2 (Long et al., 2021). In the following section, we describe the new configuration of the CESM-MARBL planktonic ecosystem, which has four phytoplankton functional types (PFTs) and two zooplankton functional types (MARBL-4p2z; Fig. 1, left side). Parameters in this ecosystem configuration were tuned in the 1° resolution and then applied for both the FOSI-LR and FOSI-HR simulations described here.

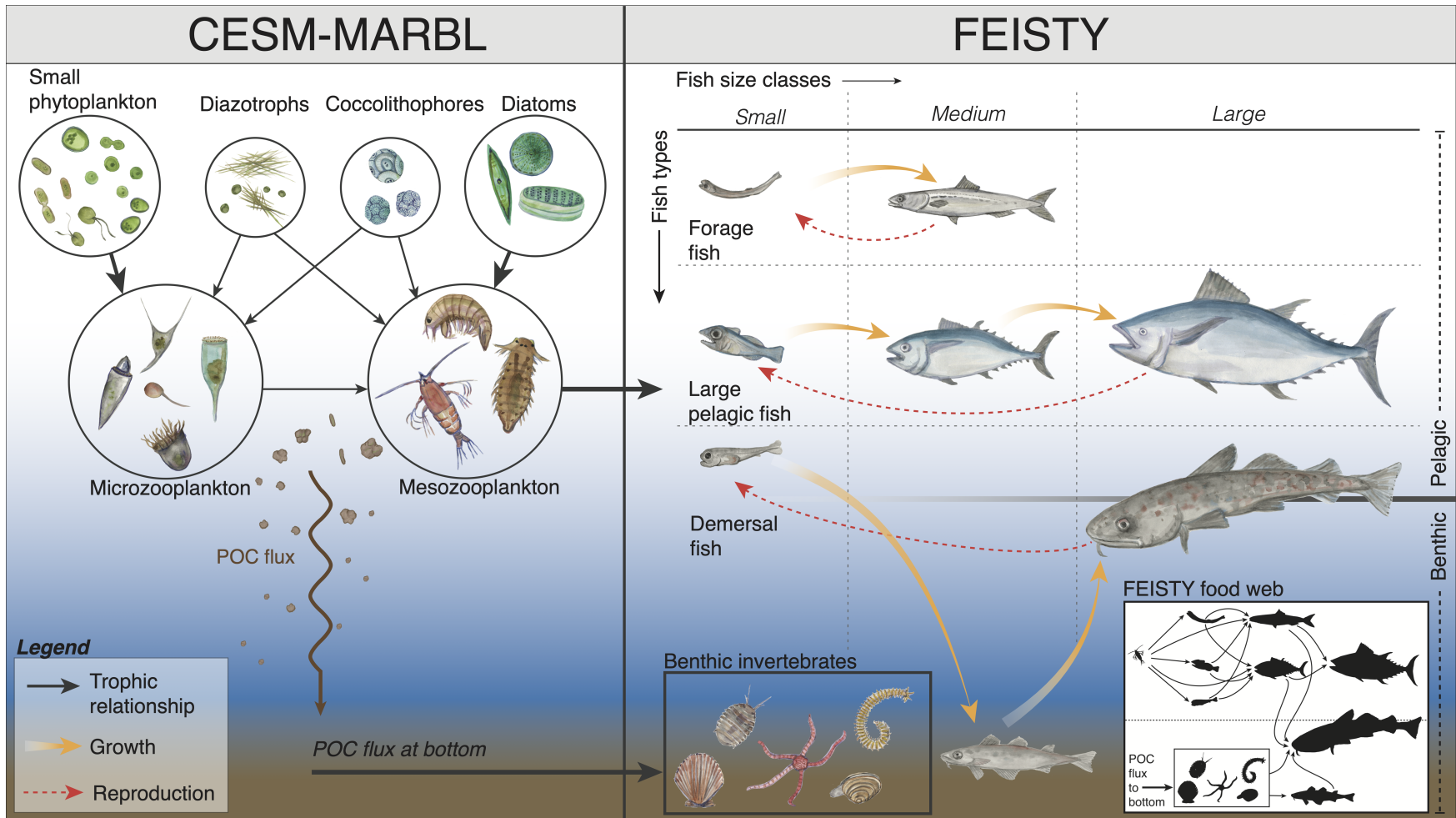


Figure 1: Connecting the CESM MARBL-4p2z planktonic ecosystem with the FEISTY fish model. The MARBL planktonic ecosystem configuration in CESM2 is shown on the left side, with illustrations of example organisms falling into each functional group. Grazing relationships implemented in the model are indicated by black arrows, with thicker arrows for small phytoplankton and diatom grazing because these comprise the bulk of global marine primary production in the model. A schematic of the FEISTY model (Petrik et al., 2019) is shown on the right side with yellow arrows indicating growth from one size class to the next and red dashed arrows indicating reproduction. FEISTY food web relationships are shown in the lower right corner. Abbreviations: particulate organic carbon (POC).

Table 1: List of relevant phytoplankton parameterizations used in MARBL-4p2z ecosystem. Abbreviations: Small phytoplankton (SP), diatoms (Diat), diazotrophs (Diaz), coccolithophores (Cocco), dissolved organic phosphorus (DOP).

Parameter	Unit	Definition	Cocco	Diat	SP	Diaz
μ_{ref}	d^{-1}	Max. C-specific growth rate	4.7	5.3	4.8	1.6
α	$\frac{mmolCm^2}{mgChlWs}$	Initial slope of photosynthesis-irradiance curve	0.31	0.39	0.35	0.31
Θ_{max}	$\frac{mgChl}{mmolN}$	Maximum Chl:N ratio	3.8	4.0	2.5	2.5
K_{Fe}	$\mu mol m^{-3}$	Fe half saturation constant	0.032	0.05	0.03	0.045
K_{PO_4}	$mmol m^{-3}$	PO ₄ half saturation constant	0.006	0.05	0.01	0.015
K_{DOP}	$mmol m^{-3}$	DOP half saturation constant	0.25	0.5	0.3	0.075
K_{NO_3}	$mmol m^{-3}$	NO ₃ half saturation constant	0.41	0.4	0.2	2
K_{NH_4}	$mmol m^{-3}$	NH ₄ half saturation constant	0.01	0.05	0.01	0.2
K_{SiO_3}	$mmol m^{-3}$	SiO ₃ half saturation constant	n/a	1.6	n/a	n/a
K_{CO_2}	$mmol m^{-3}$	CO ₂ half saturation constant	1	n/a	n/a	n/a
$mort$	d^{-1}	Linear mortality rate	0.1	0.1	0.1	0.1
$mort2$	d^{-1}	Non-linear aggregation rate	0.01	0.01	0.01	0.01

2.1.1 Phytoplankton in MARBL

Phytoplankton types are similar to previous versions of MARBL documented in Krumhardt et al. (2019) and Krumhardt et al. (2020): small phytoplankton (SP), diatoms, diazotrophs, and coccolithophores. Briefly, SP and diatom PFTs comprise the bulk of phytoplankton productivity, with diatoms dominating in nutrient-rich, light-limited regimes and SP thriving in nutrient-limited regions. The diazotroph PFT represents nitrogen-fixing phytoplankton, limited to areas warmer than 15°C. The coccolithophore PFT forms summertime blooms in high latitude, temperate regions, with a low level presence in low latitude regions. Its calcification is dependent on aqueous CO₂ concentration, nutrient limitation, and temperature (Krumhardt et al., 2019, 2020).

All phytoplankton growth equations in MARBL are described in Long et al. (2021). Here, we briefly report the phytoplankton growth parameters associated with the planktonic ecosystem in this new, slightly more complex version (see Table 1). Phytoplankton growth rates (μ) are parameterized as the product of the resource-unlimited growth rate (μ_{ref}) at a reference temperature (30°C) and fractional limitation terms. Diatoms have the fastest μ_{ref} , while diazotrophs have the slowest μ_{ref} (Table 1). μ_{ref} is scaled by temperature, nutrient, and irradiance limitation terms. Diatoms, SP, and diazotrophs have the same temperature limitation function (T_f), parameterized as a Q10 temperature limitation function:

$$T_f = 1.7^{\left(\frac{T-30^{\circ}C}{10^{\circ}C}\right)}, \quad (1)$$

the parameters of which are based on results from E. Sherman et al. (2016). The coccolithophore PFT temperature limitation curve is a power function (Fielding, 2013; Krumhardt et al., 2017) and is less sensitive than the Q10 function to increases in temperatures higher than ~15° C. Light limitation (I_{lim}) of phytoplankton follows Geider et al. (1997), using the values for the initial slope of the photosynthesis-irradiance curve (α) and the maximum chlorophyll to nitrogen ratio (Θ_{max}) reported in Table 1. Nutrient limitation is represented via Michaelis-Menten uptake kinetics, with nutrient half saturation constants reported in Table 1; aqueous CO₂ concentration may also limit coccolithophore growth via a half saturation constant for CO₂ (K_{CO_2}), as described in Krumhardt et al. (2019) and Krumhardt et al. (2017).

Phytoplankton losses include a linear mortality rate, a non-linear aggregation rate, and grazing. Mortality and aggregation rates and formulas are shown in Long et al. (2021) (rates listed in Table 1), while zooplankton grazing is described in the following paragraphs.

Table 2: List of relevant zooplankton parameters used in MARBL-4p2z ecosystem. Abbreviations: reference temperature (T_{ref} , 30°C), and maximum grazing rate (g_{max}).

Parameter	Unit	Definition	Microzooplankton	Mesozooplankton
Maximum grazing rate	d ⁻¹	sum of g_{max} of all prey at T_{ref}	6.8	1.615
GGE	fraction	Gross growth efficiency	0.25 – 0.35	0.25
K_P	mmol/m ³	Range of half saturation constants for prey	1.2 – 1.5	1 – 1.4
<i>mort</i>	d ⁻¹	Linear mortality rate at T_{ref}	0.1	0.035
<i>mort2</i>	d ⁻¹ / (mmol/m ³)	Non-linear, density dependent mortality rate at T_{ref}	0.0028	0.020

2.1.2 Zooplankton in MARBL

Two broad zooplankton functional groups, nominally “microzooplankton” and “mesozooplankton”, graze on the PFTs. The zooplankton groups are divided according to their size (though size - and parameters based on size - are not explicitly represented in MARBL-4p2z), mortality rate (i.e., lifespan or turnover time), and feeding preferences. While we provide some examples of what species these groups could represent (e.g., see Figure 1, left side), these are not meant to be specifically describing any particular zooplankton species in great detail. Because this is a global model, what species each zooplankton group represents would depend on geographic location; for instance, the mesozooplankton group could represent both Antarctic krill and copepods in the Southern Ocean.

General zooplankton parameters are shown in Table 2. Gross growth efficiency (GGE), the ratio of growth over ingestion (Welch, 1968), is highest at 0.35 for microzooplankton grazing on SP or diazotrophs. GGE is 0.25 for microzooplankton grazing on coccolithophores, reflecting reduced nutrition from a calcium carbonate-protected cell (Haunost et al., 2021). Mesozooplankton have a GGE of 0.25 for all prey. These GGE values are all within the range of observations (Straile, 1997). The maximum grazing rate (Tables 2 and 3) is higher for microzooplankton than mesozooplankton, and therefore decreases as zooplankton size increases, in line with observations (Hansen et al., 1997). Linear mortality rates (*mort*) reflect metabolic losses, as well as zooplankton longevity, with faster mortality rates for shorter-lived (smaller) zooplankton groups. A non-linear, density dependent mortality term (*mort2*) represents predation by organisms not explicitly simulated in the model; therefore, the mesozooplankton group has a higher *mort2* than microzooplankton because it is not preyed upon by the other (larger) zooplankton in CESM (Table 2). Zooplankton grazing and mortality rates are scaled by the same Q10 function as for phytoplankton above (Equation 1).

2.1.3 Planktonic grazing relationships in MARBL

Grazing relationships are indicated in Figure 1, as well as in Table 3. The microzooplankton group has a diverse diet consisting of SP (e.g., *Prochlorococcus* and *Synechococcus*; Bernal and Anil (2019)), diazotrophs (e.g., small, unicellular diazotrophs; Wang et al. (2019)), and coccolithophores (small coccolithophores, such as *E. huxleyi*). Grazing of small phytoplankton by microzooplankton follows a Holling Type III relationship following findings of Bernal and Anil (2019) who showed that grazing on picophytoplankton follows this type of relationship:

$$G = g_{max} \cdot T_{lim} \cdot Z \cdot \left(\frac{P^2}{P^2 + K_P^2} \right), \quad (2)$$

where g_{max} is the maximum grazing rate of microzooplankton (Table 3), T_{lim} is the same Q10 function as described above for phytoplankton temperature limitation (Equation 1), Z is the microzooplankton concentration, P is the small phytoplankton concentration, and K_P is the half-saturation constant for grazing for this relationship (see Table 3). All the other grazing relationships in this MARBL configuration are Holling type II, as shown in Long et al. (2021).

The mesozooplankton diet in the model consists primarily of diatoms, reflecting observations that diatoms serve as the dominant food source for copepods (Irigoien et al., 2002). The mesozooplankton group also grazes on coccolithophores (e.g., larger coccolithophores such as *Coccolithus pelagicus*),

Table 3: Maximum grazing rates (g_{\max} ; d^{-1}) and half saturation constants for grazing (K_P ; mmol m^{-3}) for each grazer-prey relationship in the MARBL-4p2z. Abbreviations: Small phytoplankton (SP), diatoms (Diat), diazotrophs (Diaz), coccolithophores (Cocco), microzooplankton (Microzoo), mesozooplankton (Mesozoo)

	Prey items									
	SP		Diaz		Cocco		Diat		Microzoo	
Grazers ↓	K_P	g_{\max}	K_P	g_{\max}	K_P	g_{\max}	K_P	g_{\max}	K_P	g_{\max}
microzoo	1.4	4.1	1.2	1	1.5	1.7	–	–	–	–
mesozoo	–	–	1.2	0.5	1.4	0.015	1.0	0.9	1.3	0.2

diazotrophs (e.g., larger N-fixing phytoplankton such as *Trichodesmium*), and microzooplankton. Diatoms have lower overall grazing rates than other phytoplankton in the model due to opal shell/spines protection from grazing, e.g., see Smetacek et al. (2002). Coccolithophores and diazotrophs are grazed by both microzooplankton and mesozooplankton, reflecting the wide size range of both of these groups (Balch, 2018; Nejstgaard et al., 1997).

2.2 Offline coupling of CESM to FEISTY

The FEISTY model was run in an “offline” fashion using output from the FOSI-HR and FOSI-LR simulations; results from the FEISTY simulations are referred hereinafter to as “FEISTY-HR” and “FEISTY-LR” for the FOSI-HR and FOSI-LR, respectively. In this context, “offline” means that CESM and FEISTY are only coupled in one direction (from CESM to FEISTY), and there is no feedback from fish on zooplankton or biogeochemistry in CESM. The CESM variables used to force FEISTY are pelagic temperature (top 150 m mean), mesozooplankton biomass and mesozooplankton loss rate (top 150 m depth integral), particulate organic carbon flux at the ocean floor, and temperature at the ocean floor (Petrik et al., 2019). Though the mesozooplankton loss rate ideally should just include the quadratic losses (*mort2*) (Petrik et al., 2019), here we included all losses (*mort* and *mort2*) because the separate loss terms were not output by CESM. These FEISTY forcing variables are output at a daily frequency from 1980 to 2021 and were used to force FEISTY at a daily time resolution; we note that this represents an improvement from previous FEISTY studies, where the forcing was monthly ESM output (Petrik et al., 2019, 2020). We spun up the FEISTY model by repeating FOSI-HR and FOSI-LR year 1980 forcing one hundred times. In order to run FEISTY with daily forcings on the FOSI-HR grid, we have rewritten the MATLAB code used in Petrik et al. (2019) in Python (see section 6). The Python version allows parallel computations for FEISTY integration, thanks to thriving scientific Python ecosystem, and more specifically to the Xarray and Dask python libraries.

Here, we summarize the FEISTY model from Petrik et al. (2019). FEISTY simulates three fish functional types subdivided into several size classes (Figure 1, right side). The fish functional groups differ by their feeding and size niches. Forage fish are small pelagic fishes with small (larval) and medium (adult) size classes in FEISTY. Forage fish serve as prey for many marine animals and feed exclusively on zooplankton; examples include sardines, herring, and anchovies. Large pelagic fish coexist with forage fish in the upper water column and are characterized by a large adult size. FEISTY resolves three size classes of large pelagic fish: small (larval), medium (juvenile), and large (adult). Examples include tuna and mackerel. Lastly, demersal fish are generalist feeders that can feed on benthic resources, as well as pelagic resources in shallow shelf environments. Particulate organic carbon flux to the seafloor serves as a food resource for benthic invertebrates (Figure 1), which are consumed by juvenile and adult demersal fish. Larval demersal fish begin life in the pelagic realm and migrate to the seafloor as juveniles. Adult demersal fish can feed in both pelagic and benthic oceanic habitats in continental shelf regions <200 m. Examples of demersal fish include cod and flounder. The size structure, i.e., that individuals grow from the offspring size to the adult size, is a key aspect of the FEISTY model, as it determines most physiological processes, such as predation, mortality, and allocation of energy to growth and reproduction (K. H. Andersen et al., 2009; K. Andersen, 2019; Olsson & Gislason, 2016).

2.3 Evaluation datasets

Sea ice is an important control on biological productivity in Arctic and Antarctic regions (Arrigo et al., 2008). Therefore, we use sea ice index from the National Snow and Ice Data Center NSIDC; Fetterer et al., 2017 to evaluate modeled sea ice concentrations in FOSI-HR and FOSI-LR.

We use a variety of global biogeochemical metrics to evaluate the large scale biogeochemistry in FOSI-HR and FOSI-LR model solutions. These include globally-integrated NPP (Behrenfeld & Falkowski, 1997; Behrenfeld et al., 2005; Carr et al., 2006), particulate organic carbon (POC) export at 100 m (DeVries & Weber, 2017), diatom production and silicification (Holzer et al., 2014; Nelson et al., 1995), nitrogen fixation (Wang et al., 2019), and calcification (Liang et al., 2023; Ziveri et al., 2023, and references therein). For global scale zooplankton biomass and productivity, we use estimates of global microzooplankton and mesozooplankton biomass reported in Moriarty and O’Brien (2013) and Buitenhuis et al. (2010).

We use several spatially-resolved observation-based datasets to evaluate CESM model performance on a global scale. Modeled global macronutrient distributions, averaged over the period 1997 to 2017, are compared to World Ocean Atlas version 2 (Garcia et al., 2018), interpolated vertically and horizontally onto the model grids. We compare surface nutrients (top 10 m) and nutrients roughly below the thermocline (defined as 461.8 m to 503.7 m). We use the gridded monthly GOBAl-O2 product (2004–2021; Sharp et al., 2022) to validate oxygen distributions in both FOSI-LR and FOSI-HR. Modeled chlorophyll concentrations are compared to the GlobColour merged chlorophyll product, which incorporates NASA remote sensing observations from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS), MODIS Aqua, and VIIRS satellite remote sensing platforms (Garnesson et al., 2019). The Coastal and Oceanic Plankton Ecology, Production, and Observation Database (COPEPOD) is used to evaluate the mesozooplankton biomass field in our simulations (Moriarty & O’Brien, 2013); we compare the 200-m mean mesozooplankton biomass estimates from COPEPOD to 150-m mean mesozooplankton biomass estimates from the model.

We employ the Sea Around Us (SAU) fish catch dataset to tune and validate the fish catch estimates in Large Marine Ecosystems (LMEs; Pauly et al., 2020), following Petrik et al. (2019) and Stock et al. (2017). Simulated “catches” in FEISTY are calculated by multiplying each fish functional group biomass by the fishing mortality rate. For simplicity, the fishing mortality rate is held constant at 0.3 yr^{-1} at all grid points, assuming constant fishing effort. The fished biomass is removed from the fish population at each timestep. We classify the fish functional groups from the SAU dataset into the three fish functional types in FEISTY following Petrik et al. (2019) and calculate area-weighted average catches for each LME. We only use 45 out of the 66 total LMEs, eliminating outliers that had low fishing effort and low catch, as in Stock et al. (2017) and Petrik et al. (2019). Further, we use the mean of the top 10 fish SAU catches for each LME in order to best represent potential fish catches, as discussed in Stock et al. (2017). We compare this processed SAU catch data to the mean of the FEISTY catch data over the 1980-2010 period. This time period was chosen because the SAU catch data that we used here spans from 1950-2010 while the FEISTY catch data spans from 1980-2021, so 1980-2010 is the overlap between the two datasets. We used the same SAU data that was used in the FEISTY description paper (Petrik et al., 2019). We compute correlation coefficients that characterize the mean spatial fidelity of the modeled fish catches (mean modeled catch versus mean observed SAU catch in each LME), as well as correlations in fish catch over time for certain highly fished LMEs (e.g., the California Current) to evaluate temporal variability in fish catch.

3 Evaluation of ecosystem-related fields

From a global perspective, ecosystem and biogeochemistry metrics calculated for FOSI-HR and FOSI-LR are similar to observation-based metrics (Table 4). Globally-integrated marine NPP in both FOSI-HR and FOSI-LR falls within the range of observation-based estimates at $\sim 52 \text{ Pg C yr}^{-1}$, with about 38% (40%) of that production coming from diatoms for FOSI-HR (FOSI-LR). Approximately 12% (13%) of NPP, $6.39 \text{ Pg C yr}^{-1}$ (6.73), is exported below 100m (POC export 100m; Table 4) in the FOSI-HR (FOSI-LR). Net globally-integrated silicification within the top 100m is on the low end of observation-based estimates at just above $100 \text{ Tmol of Si yr}^{-1}$ for both simulations. The diazotroph phytoplankton type in the model fixes approximately 176 Tg N yr^{-1} in FOSI-HR, which falls into the plausible range estimated using an inverse model by Wang et al. (2019). Observation-

Table 4: Global biogeochemical metrics from the FOSI-HR, FOSI-LR, and observationally-derived estimates. Modeled metrics are averaged over the period 1986 to 2005. Abbreviations: net primary productivity (NPP), particulate organic matter flux at 100m (POC export 100m)

Metric	Unit	FOSI-HR	FOSI-LR	Observations	Reference
Globally-integrated NPP	Pg C y ⁻¹	52.26	52.95	43.5 to 67	Behrenfeld and Falkowski (1997), Behrenfeld et al. (2005), and Carr et al. (2006)
POC export 100m	Pg C y ⁻¹	6.39	6.73	4 to 12	DeVries and Weber (2017)
% NPP by diatoms	%	38.17	39.66	40%	Nelson et al. (1995)
Net globally-integrated silicification within top 100 m	Tmol Si y ⁻¹	101.73	104.91	100 to 140	Holzer et al. (2014) and Nelson et al. (1995)
Globally-integrated nitrogen fixation	Tg N y ⁻¹	176.34	169.83	125.6 to 222.9	Wang et al. (2019)
Globally-integrated calcification	Pg C y ⁻¹	0.87	0.90	0.7 to 4.7	Liang et al. (2023) and Ziveri et al. (2023) and refs therein
Microzooplankton biomass	Pg C	0.24	0.23	0.14 to 0.33	Buitenhuis et al. (2010)
Mesozooplankton biomass	Pg C	0.38	0.40	0.19	Moriarty and O'Brien (2013)
Zooplankton production % of NPP	%	25.35%	25.20	at least 21%	Landry and Calbet (2004)

based estimates of globally-integrated calcification vary greatly, between 0.7 and 4.7 Pg C yr⁻¹, with much of the discrepancy likely due to uncertainty regarding the potentially large portion of biogenic CaCO₃ remineralized in the photic zone (Ziveri et al., 2023). In the FOSI-HR, the coccolithophore PFT produces 0.87 Pg C yr⁻¹ (net calcification) in the top 100 m; FOSI-LR calcification is just slightly higher at 0.90 Pg C yr⁻¹.

While there are large uncertainties associated with global inventories of zooplankton biomass, we do provide a comparison to previously published estimates for microzooplankton and mesozooplankton, the two zooplankton groups in FOSI-HR. Buitenhuis et al. (2010) estimated a global microzooplankton biomass inventory of between 0.14 to 0.33 Pg C and the FOSI-HR microzooplankton falls within this range at 0.24 Pg C. While observation-based estimates of mesozooplankton biomass are similar to microzooplankton at 0.19 Pg C, FOSI-HR has a substantially higher mean global inventory of 0.38 Pg C of mesozooplankton biomass. Though an uncertainty range was not provided in Moriarty and O'Brien (2013), the median biomass concentration on which the estimate is based is bounded by a large standard deviation (2.7 µg C L⁻¹ ±10.6). Furthermore, the absence of an explicit macrozooplankton representation in MARBL could mean the mesozooplankton group may also represent macrozooplankton biomass. For example, the mesozooplankton group in MARBL consumes both diatoms and microzooplankton (Figure 1) and thus could also be representative of Antarctic krill which also consume these two groups (Haberman et al., 2003), but are not included in the observationally-based mesozooplankton biomass estimate (rather krill are classified as macrozooplankton). This could explain why FOSI-HR (and FOSI-LR) has more mesozooplankton biomass than the observation-based estimate from Moriarty and O'Brien (2013). Lastly, total zooplankton production (microzooplankton + mesozooplankton groups) should be at least 21% of globally integrated NPP (Landry & Calbet, 2004); in FOSI-HR it is ~25%. All of the metrics listed in Table 4 are very similar between the low- and high-resolution integrations, demonstrating consistency in large scale CESM marine ecosystem characteristics regardless of resolution.

3.1 Sea ice

Sea ice impacts ecosystems both directly (e.g., as substrate for resting, hunting, breeding, protection from predators; and by limiting light availability for phytoplankton) and indirectly (e.g., sea ice and

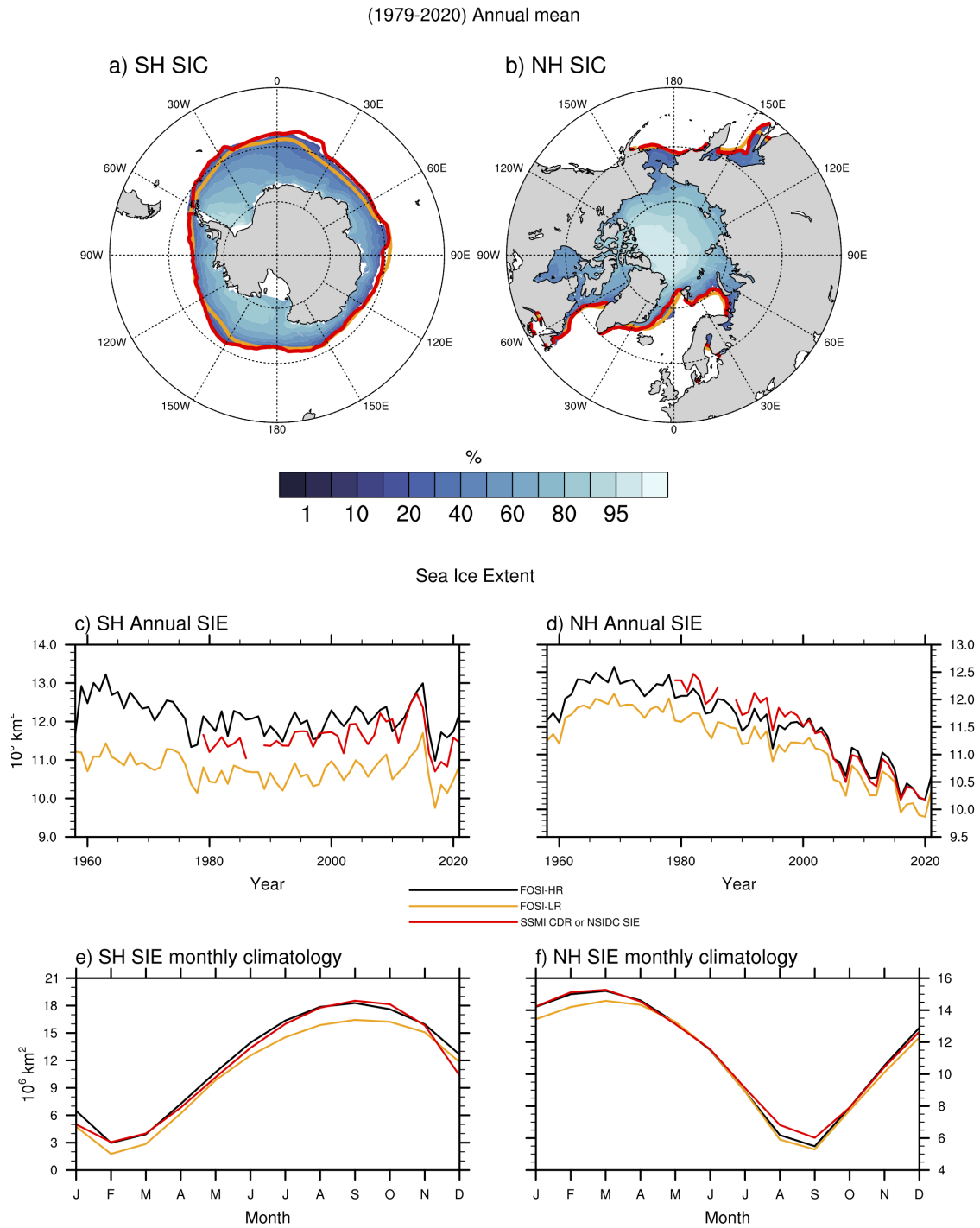


Figure 2: Annual mean sea ice concentrations (top), sea ice extent (SIE; middle) and climatological SIE seasonal cycle for Southern Hemisphere (left) and Northern Hemisphere (right) sea ice. Filled contours shown on maps in panels a and b are from FOSI-HR, with 15% sea ice concentration (SIC) for FOSI-LR (orange line) and SSMI-Climate Data Record (red line) overlain. Time-series and climatological cycle plots (panels c-f) show values for FOSI-HR (black), FOSI-LR (orange) and NSIDC SIE (red). Climatologies are calculated from 1979-2020. Observed SIE are from the National Snow and Ice Data Center (NSIDC) Sea Ice Index version 3.0 (Fetterer et al., 2017).

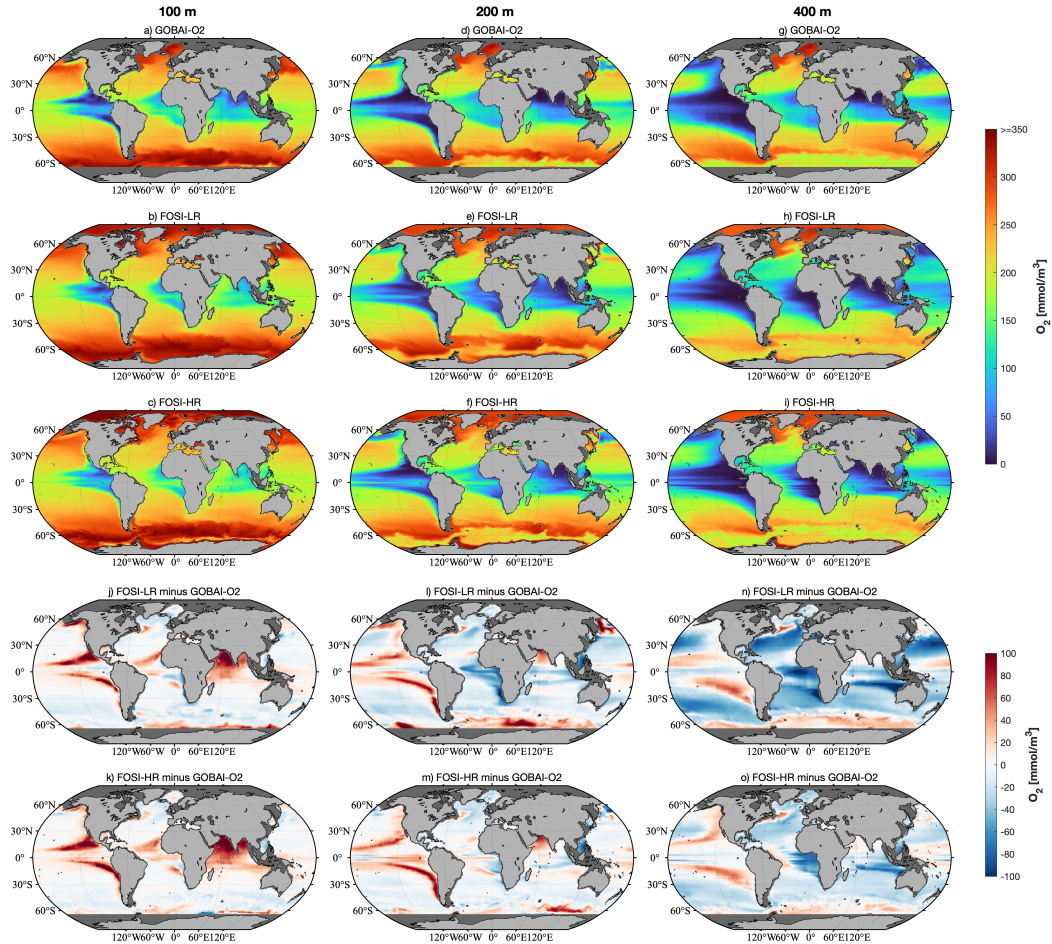


Figure 3: Time-mean (2004-2021) oxygen concentrations at depths of 100, 200, and 400 m for the gridded monthly observation-based GOBAI-O2 (Sharp et al., 2022) product (top row), the FOSI-LR (second row), and the FOSI-HR (middle row). Difference maps are shown between the GOBAI-O2 product and the FOSI-LR and FOSI-HR (bottom two rows) for each depth level.

its seasonal cycle can impact ocean circulation, water column physics and chemistry, weather patterns, coastal erosion rates, etc.) in both Arctic and Antarctic marine environments (e.g., Deppeler & Davidson, 2017; Macias-Fauria & Post, 2018, and references therein). Adequate simulations of sea ice including seasonality, distributions, regionalities and trends - are critical for modeling of high latitude marine ecosystems and sea ice-related changes in marine ecosystems (e.g., Flores et al., 2023).

Sea ice concentrations (SICs) in FOSI-LR and FOSI-HR compare well with National Snow and Ice Data Center (NSIDC) Climate Data Record (CDR; Meier et al., 2021) for both Arctic and Antarctic (Figure 2). Trends, interannual variability and climatological seasonal cycle for sea ice extent (SIE; defined as the area covered by sea ice concentrations of 15% or higher) are particularly well captured by FOSI-HR, as compared to the NSIDC Sea Ice Index (Fetterer et al., 2017) and the FOSI-LR. In general, FOSI-LR tends to underestimate Antarctic and Arctic SIEs throughout the year. FOSI-HR SIE, on the other hand, closely follows the observed SIE climatology for both hemispheres, except it is somewhat too low during the summer months in the Arctic. Nevertheless, we see a marked improvement in the high resolution simulation of sea ice in CESM. In turn, polar ecosystems, in which sea ice plays a substantial role, are likely to be better simulated in FOSI-HR as compared to the lower resolution version of CESM.

3.2 Oxygen distributions in the ocean

Oxygen concentrations are important for characterizing habitable parts of the ocean. Ocean oxygen distributions at various depths in the upper ocean in the FOSI-HR and FOSI-LR are compared to an observation-based gridded oxygen product (GOBAI-O2; Sharp et al., 2022) in Figure 3. At 100 m depth, oxygen concentrations in both high and low resolution CESM simulations match well with the geographic patterns of time-mean oxygen concentrations in the GOBAI-O2 product, except for some positive biases in low latitude regions. However, there are small regions where we observe a notable improvement in the FOSI-HR, as compared to the FOSI-LR. Spatial oxygen variability in coastal regions, such as the Gulf of Alaska, for example, in FOSI-HR match the GOBAI-O2 product better than the FOSI-LR. However, the low oxygen concentrations at 100 m depth in the northern Indian Ocean shown in the observation-based product are not fully captured in either CESM simulation. At 200 m depth, oxygen concentrations decline in equatorial regions and the North Pacific (Figure 3, middle column). The spatial patterns of this decline in oxygen are somewhat better captured in the FOSI-HR than the FOSI-LR, compared to the GOBAI-O2 product. Notably, oxygen at 200 m depth in the equatorial Atlantic declines too much in the FOSI-LR, while FOSI-HR better matches observations. FOSI-HR appears to resolve deep eastward equatorial jets that help oxygenate this region. Mesoscale eddies may also help ventilate equatorial regions, as shown by Eddebbbar et al. (2021) using a similar high resolution CESM simulation. This is also evident at 400 m depth, where thin zonal strips of the equatorial regions have slightly higher oxygen than the FOSI-LR. Overall, however, FOSI-HR captures the expansive oxygen minimum zones at 400m seen the GOBAI-O2 product. Though the GOBAI-O2 product only extends down to 64.5°S, we also infer a notable improvement in oxygen concentrations in the FOSI-HR Southern Ocean at 200 m and 400 m as compared to the FOSI-LR, which has larger positive biases.

The widespread negative biases in oxygen at 400m seen in the FOSI-LR are not as prominent in the FOSI-HR (Figure 3n,o.) This suggests that some of the oxygen ventilation issues discussed in Long et al. (2021) may be improved using high resolution. Note that the expected improvement in equatorial ventilation from the higher resolution in FOSI-HR is not fully realized because the FOSI-HR simulation was initialized from a lower resolution spin up simulation where the ventilation biases had established overly extensive low oxygen zones at ~400 m (see Methods).

3.3 Global distribution of nutrients

Global surface nutrient concentration distributions in the FOSI-HR match the World Ocean Atlas (WOA) well in most regions (Figure 4a–i; see Figure S1 for a FOSI-LR version of the figure). Surface nitrate (NO_3) and phosphate (PO_4) concentrations are low in low to mid-latitude regions and elevated in regions polewards of $\sim 45^\circ$. The FOSI-HR captures these overall patterns, except for some negative biases in the North Pacific, North Atlantic and equatorial Pacific. Surface silicate (SiO_3) matches well in low to midlatitudes and in the North Atlantic (Figure 4g–i). SiO_3 concentrations, however, are too low in FOSI-HR in the North Pacific where diatom growth (and hence SiO_3 drawdown) is perhaps too vigorous. We note that these negative nutrient biases in the North Pacific were also present in previous versions of CESM (Long et al., 2021; Moore et al., 2013). In the Southern Ocean there are large swaths of too much surface SiO_3 , as well as NO_3 and PO_4 , where diatom growth may not be vigorous enough, perhaps overly limited by iron availability. Curiously, FOSI-LR has the opposite problem in the Southern Ocean – not enough SiO_3 at the surface relative to observations (Figure S1i).

Deeper in the water column, around the thermocline at 483 m, nutrient biases in FOSI-HR change relative to the surface (Figure 4j–r; Figure S1 for the FOSI-LR version of the figure). While the overall geographical patterns match, there are some notable mismatches. NO_3 concentration biases are largely negative at this depth, especially in the Pacific Ocean. Some of this negative bias could be due too much detritification in the model within the oxygen minimum zones (section 3.2). PO_4 is also somewhat negatively biased globally around the thermocline, suggesting that more PO_4 should be remineralized higher in the water column. The bias patterns for NO_3 and PO_4 are substantially different for the FOSI-LR, where positive biases in the model manifest in mid-latitude regions (Figure S1, panels l and o). Lastly, SiO_3 concentrations are somewhat too high for much of the global ocean at 400 m in the FOSI-HR, except for the North Pacific and the Southern Ocean. In the North Pacific too much SiO_3 from overactive diatoms at the surface is being exported below 500 m causing a negative bias in the model. In the Southern Ocean, the positive SiO_3 bias at the surface (Figure 4i) switches to being

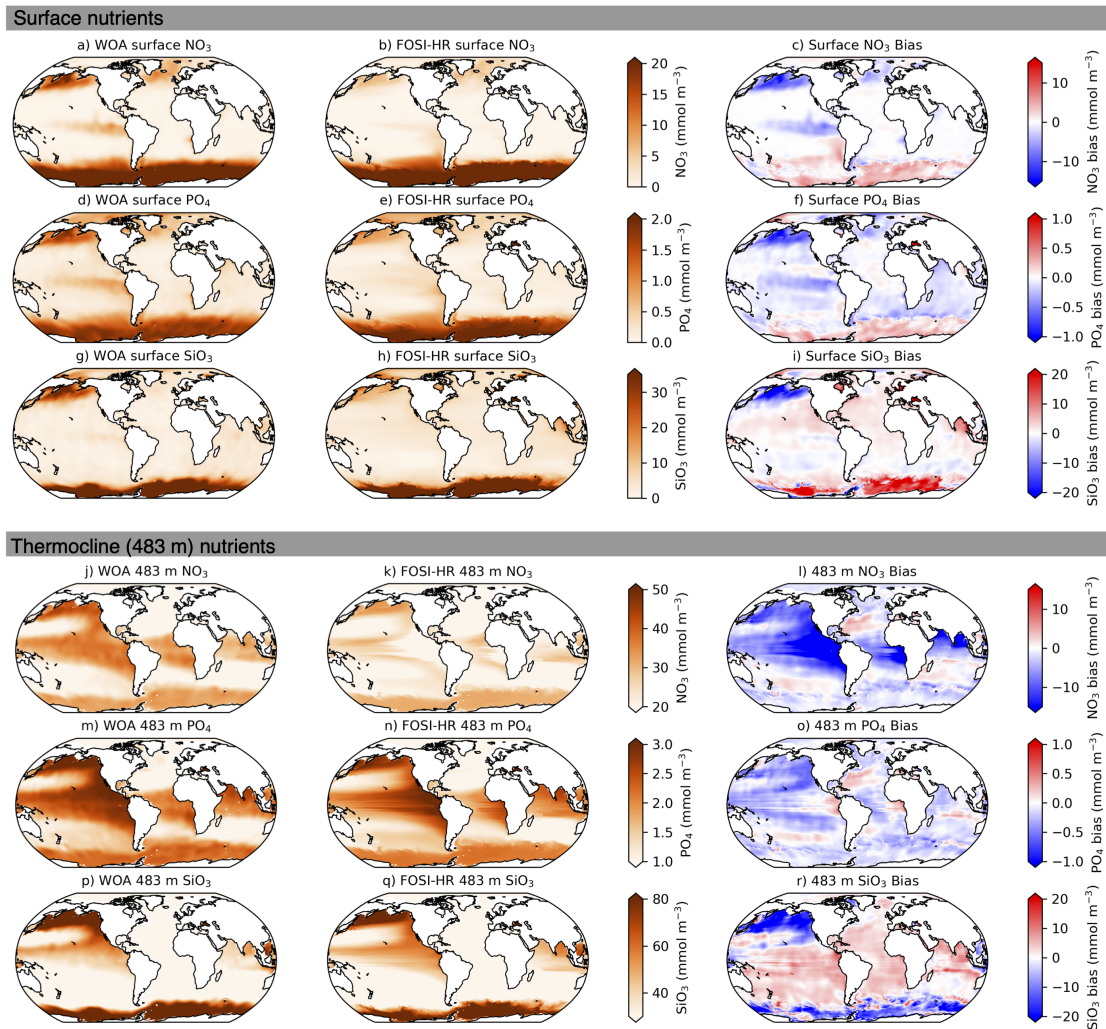


Figure 4: Comparison of FOSI-HR surface and thermocline (depth range between 461.8 m and 503.7 m) nutrients to World Ocean Atlas, v2 (WOA) (Garcia et al., 2018).

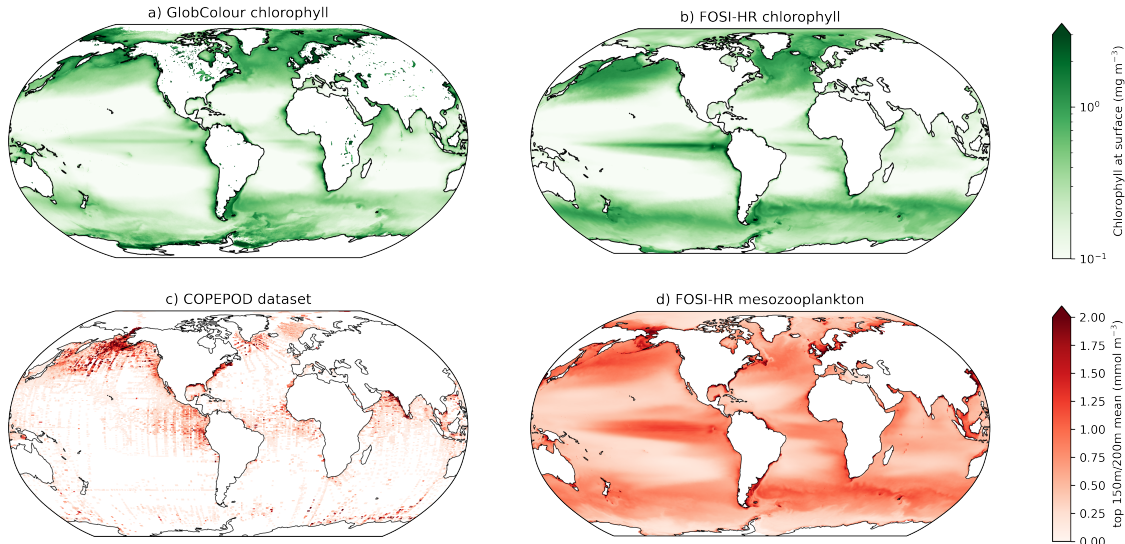


Figure 5: FOSI-HR chlorophyll comparison to GlobColour merged product (SeaWiFS, MODIS, VIIRS) and mesozooplankton/COPEPOD comparison (Garnesson et al., 2019). The chlorophyll observations and FOSI-HR chlorophyll are a mean over 1997 to 2021. We compare mesozooplankton biomass from FOSI-HR averaged over the same time period to the COPEPOD database.

negatively biased by 500 m, indicating that while there may not be enough diatom silicification at the surface, what is being produced is being exported too deep; these same biases are present in the thermocline for FOSI-LR (Figure S1).

3.4 Global distribution of plankton

Global spatial patterns of surface chlorophyll match well between satellite observations and FOSI-HR simulation (Figure 5a,b; see Figure S2 for a FOSI-LR version of the figure). The chlorophyll maps presented in Figure 5a and b show elevated chlorophyll in the high latitudes ($>45^\circ$), with lower concentrations in the subtropical gyres, for both FOSI-HR and the NASA satellite merged product (Garnesson et al., 2019). Chlorophyll is too elevated, however, for the equatorial Pacific and subantarctic Southern Ocean in FOSI-HR. By contrast, chlorophyll concentrations in the Arctic and Antarctic sea ice zones is generally underestimated in FOSI-HR according to this comparison. However, the satellite observations of chlorophyll in high latitude regions are only averaged over polar day, when expansive phytoplankton blooms are underway, and enough light and low sea ice allow ocean color retrieval. Therefore, we expect “annual average” chlorophyll observations in polar regions to be higher than the annual averages in the model, which averages over all months of the year.

The COPEPOD database (Moriarty & O’Brien, 2013) provides mean top 200 m concentration of mesozooplankton biomass, particularly copepods, which we compare to top 150 m mean biomass of the mesozooplankton functional type (see Figure 1) from the FOSI-HR (only the top 150 m of ecosystem variables are written out by the model). Like chlorophyll, the global spatial patterns of mesozooplankton biomass are similar between the observations and the model (Figure 5c,d; Figure S2c,d). Though the COPEPOD database is lacking coverage in the subantarctic part of the Southern Ocean, the data points that are present suggest an overestimation of mesozooplankton biomass in this region in the model. The extremely high mesozooplankton biomass seen in the COPEPOD dataset in the North Pacific is only partially captured by FOSI-HR.

3.5 Spatial and temporal variability in NPP

To evaluate FOSI-HR representation of mean state and temporal variability of marine ecosystems, we compare 150 m depth-integrated NPP from the model to satellite-derived NPP (Figure 6; see also Figure S3 for a FOSI-LR version of the figure). As different algorithms for estimating NPP from ocean color data can vary substantially with respect to spatial patterns and magnitudes (Saba et al., 2011),

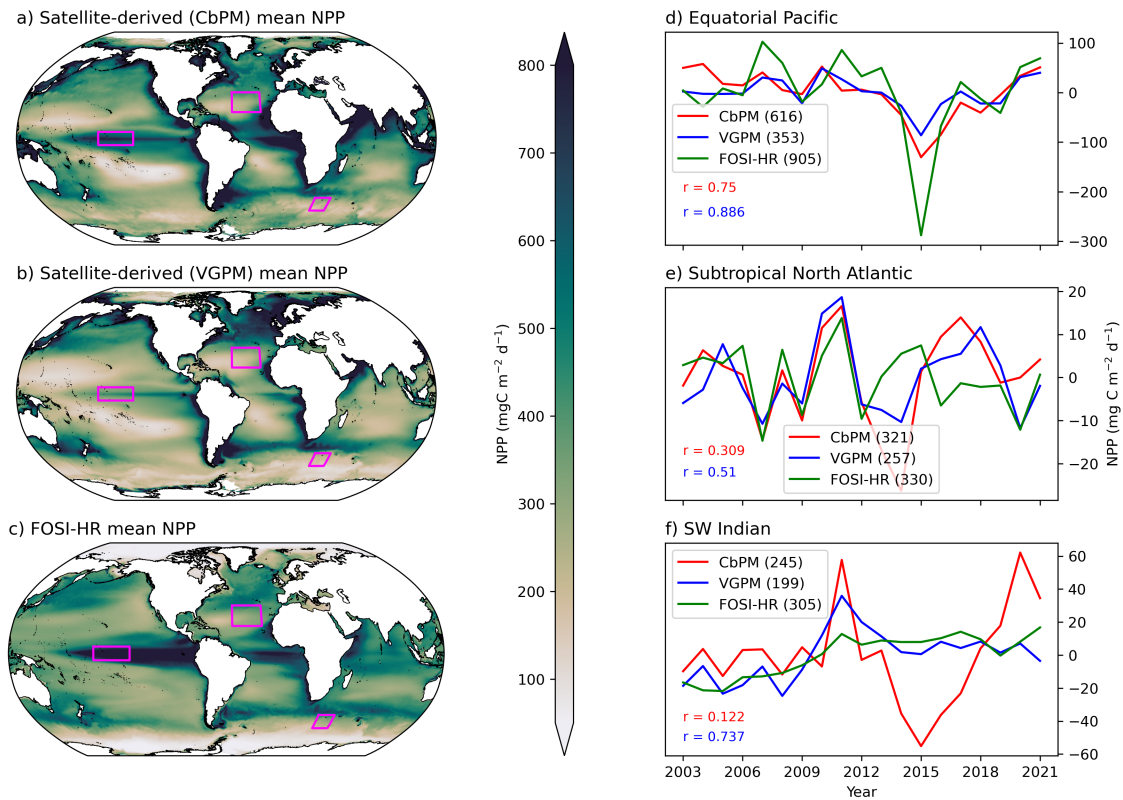


Figure 6: Mean net primary productivity (NPP) over the period 2003 to 2021 as estimated via the Vertically Generalized Production Model VGPM; Behrenfeld and Falkowski, 1997, the Carbon-based Productivity model CbPM; Behrenfeld et al., 2005; Westberry et al., 2008 and the FOSI-HR (panels a, b, and c, respectively). Time-series anomalies of NPP from the VGPM, CbPM, and the FOSI-HR plotted along the right-hand side are area-weighted means in the three boxes indicated on the maps (panels d–f). Correlation coefficients between FOSI-HR NPP and each observation-based estimate are indicated in each panel (CbPM in red and VGPM in blue). We use anomalies to compare variability, but the average magnitude of NPP varies for each region; we report the magnitudes of NPP for each boxed region in the legend (in $\text{mg C m}^{-2} \text{d}^{-1}$) for each region.

we compare NPP from FOSI-HR to two different algorithms: the Vertically Generalized Production Model (VGPM; Behrenfeld & Falkowski, 1997) and the Carbon-based Productivity model (CbPM; Behrenfeld et al., 2005; Westberry et al., 2008). Both algorithms tend to have more concentrated NPP along coastal regions, as compared to the FOSI-HR. However, the VGPM has very low NPP in the oligotrophic gyres (Figure 6a), while the CbPM algorithm captures higher NPP in open ocean regions and productivity is spread out further from the coast (Figure 6b). Mean FOSI-HR NPP matches better to the CbPM oligotrophic gyres, even though the modeled NPP is slightly higher than CbPM. FOSI-HR is substantially higher than both NPP algorithms in the equatorial Pacific (Figure 6c) This is also true for FOSI-LR (Figure S3c). On the other hand, NPP in FOSI-HR is somewhat too low in polar regions, as compared to both observation-based estimates. For some regions, such as the northern Indian Ocean, FOSI-HR NPP falls between VGPM and CbPM. Overall large scale geographic patterns in ocean NPP match well between FOSI-HR and satellite-based estimates (Figure 6a–c).

In order to examine how well NPP variability is captured in the FOSI-HR, we consider regional averages of ocean NPP in three regions representing a variety of oceanographic environments: the equatorial Pacific, subtropical Atlantic, and the Indian sector of the subantarctic Southern Ocean (Figure 6d–f). We created anomalies to compare the interannual variability in NPP in each region. Overall FOSI-HR matches the VGPM better in terms of NPP variability than the CbPM, as all correlation coefficients are above 0.5 and statistically significant ($p < 0.05$); this is also the case for FOSI-LR (Figure S3). CESM NPP is substantially higher than both satellite-derived estimates for the equatorial Pacific ($905 \text{ mg C m}^{-2} \text{ d}^{-1}$, compared to 616 and 353 from CbPM and VGPM, respectively); equatorial Pacific NPP in the FOSI-LR is $733 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Figure S3d). However, the variability in NPP matches well in this region with both NPP algorithms, both showing significant correlations with FOSI-HR NPP, likely driven by a strong response to El Niño-Southern Oscillation (ENSO). For the subtropical North Atlantic, all three NPP anomaly time-series match well during the first half of the time-series, but post-2012 the time-series diverge. However, the overall magnitude of NPP for the subtropical North Atlantic matches well for all the estimates (ranging from 257 to $330 \text{ mg C m}^{-2} \text{ d}^{-1}$). The southwest Indian Ocean NPP is more uncertain and the CbPM NPP appears to be the outlier with respect to interannual variability (Figure 6f). Overall, FOSI-HR NPP features low variability in the southwest Indian Ocean as compared to CbPM- and VGPM-based estimates.

3.6 Evaluating fish catch in Large Marine Ecosystems

We use SAU observations of fish catches (Pauly et al., 2020) in a subset of Large Marine Ecosystems (LMEs; see Methods section 2.3; see Figure S4 for the FOSI-LR version of this figure) to evaluate the simulation of fish in FEISTY subject to outputs from FOSI-HR. The top half of Figure 7 shows a mean state evaluation of fish catches in the FEISTY-HR, where each dot represents one of 45 LMEs included in the comparison (see Methods); see Figure S4 for a FOSI-LR version of the figure. In general, we observe a moderate match between the FEISTY and SAU datasets, which is in most cases slightly better for FOSI-HR than for FOSI-LR. We note a particularly positive correlation for demersal fish ($r = 0.66$), while forage fish are not correlated ($r = -0.01$), with SAU data showing a greater spread than FEISTY data. We note that Petrik et al. (2019) also report a lower correlation for forage fish with the SAU data than the other two fish functional types in FEISTY. Large pelagic fish match the SAU data moderately well ($r = 0.35$).

While it is challenging to pinpoint why one fish type would match the SAU data better than another, we speculate here on reasons for the mismatch but also refer readers to Petrik et al. (2019) for more details. For forage fish, it could be that there is substantial variation across LMEs in fishing effort of forage fish, which is not reflected in the constant fishing mortality applied in the simulations. It could also be that the forage fish functional type is representing a portion of mesopelagic fish biomass, which is not targeted by fisheries. Furthermore, the forage fish biomass is heavily influenced by predation by - and competition with - the large pelagic fish type in FEISTY, so biases in large pelagic fish will be propagated to forage fish. Possible reasons for biases in large pelagic fish include competition with marine mammals and sea birds in cooler oceanic environments, as well as lack of simulated fish movement, neither of which are represented in FEISTY. Not simulating movement for feeding or spawning by large pelagic fish could lead to an underestimate of biomass in the tropics and subtropics. Further analysis on biases in fish biomass with regard to the SAU data is beyond the scope of this manuscript, and could be a focus area for future research effort.

The bottom half of Figure 7 shows annual mean time-series for two LMEs: the California Current

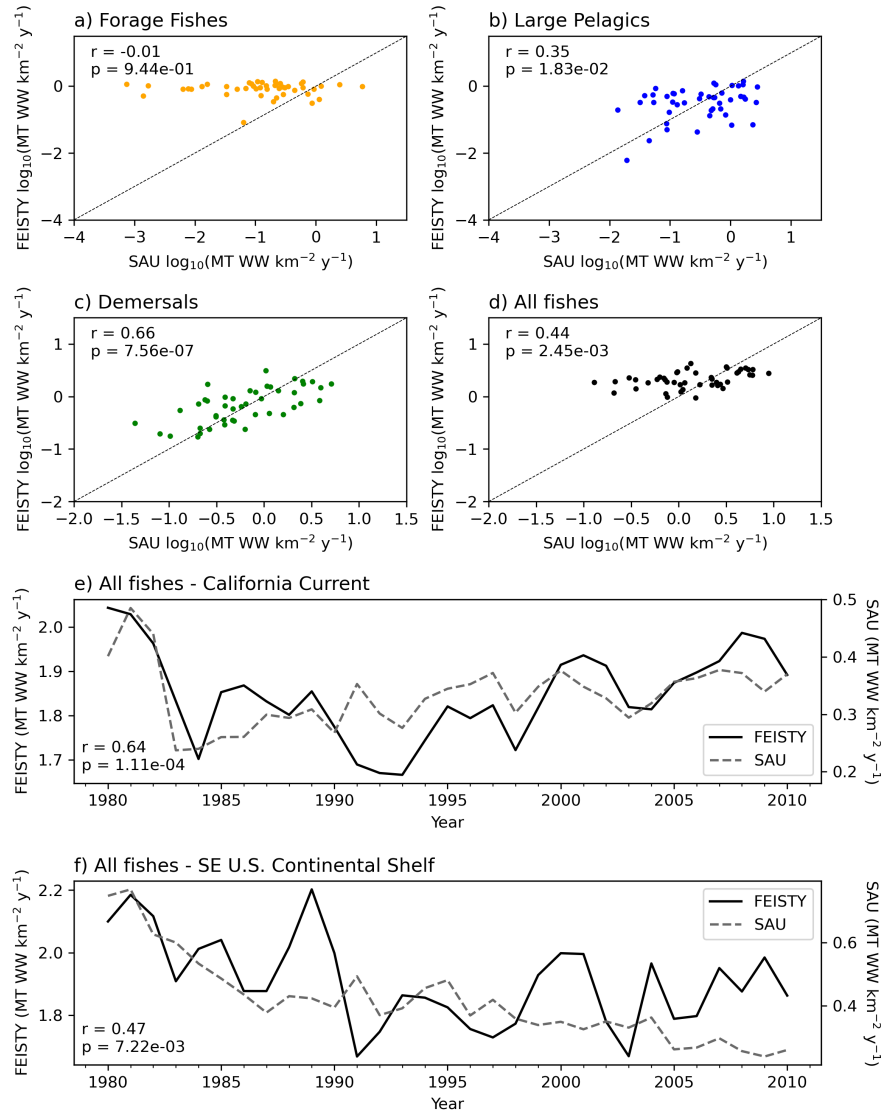


Figure 7: Fish catch yields from FEISTY-HR forced by the FOSI-HR simulation compared to the Sea Around Us (SAU) dataset for 45 Large Marine Ecosystems (LMEs), a subset of the total 66 LMEs where outliers that had low fishing effort and low catch were eliminated. The top four panels (a–d) show scatter plots of SAU versus FEISTY-HR fish catches - each dot represents the “mean” fish catch in an LME. For SAU data, we take the mean of the top 10 fish SAU catches for each LME. For FEISTY data, we take the mean of the catch data over the 1980-2010 period; this time period was chosen because the SAU catch data spans from 1950-2010 while the FEISTY catch data spans from 1980-2021, so 1980-2010 is the overlap between the two datasets. See Methods section 2.3 for further details. Panels e and f show time-series of fish catches from SAU and FEISTY-HR for the California Current and Southeast U.S. Continental Shelf LMEs. Correlation coefficients (r values) of the log₁₀ catches for FEISTY-HR and SAU catches are indicated in panels a –d, while correlations between the SAU and FEISTY-HR timeseries are indicated in panels e and f. Note the different y-axis scales for SAU and FEISTY in panels e and f.

and the Southeast U.S. Continental Shelf. For the California Current LME, interannual variability is well-correlated between the two datasets, while the relationship is less pronounced for the Southeast U.S. Continental Shelf. Note the different axes used for FEISTY and SAU data; for both of these LMEs, FEISTY catch magnitudes are consistently higher than SAU catches. This disparity could be expected given that in FEISTY, fish catch is represented as a simple fraction of total fish biomass, while the SAU data is affected by many other factors like variability in fishing effort, which is influenced by human factors distinct from climate forcing alone. Nevertheless, the comparison in variability between these datasets is still meaningful despite the difference in magnitude.

4 Results

4.1 Large scale biogeography of plankton to fish

The high resolution simulations, FOSI-HR and FEISTY-HR, aim to link nutrients to fish on a global scale. While the fine scale details in this high-resolution global simulation are what make it truly unique, it is important to contextualize these details in a global overview. In Figure 8 we present global biomass distributions of the four phytoplankton and two zooplankton functional types FOSI-HR (panels a–f) and fish types from FEISTY-HR (panels g–i). Also, please refer to Figure S5 for a FOSI-LR version of this figure, which looks similar.

The small phytoplankton (SP) functional type represents a wide variety of algal species, from *Prochlorococcus* and *Synechococcus* in central ocean gyres to cryptophytes or *Phaeocystis* in polar ecosystems. Thus, the SP functional type has very broad spatial coverage in FOSI-HR. Concentrations of SP range from ~ 0.4 to 0.6 g C m^{-2} for all oceanic regions outside of areas that are covered by sea ice for part of the year (Figure 8a). In sea ice zones, SP concentrations drop to roughly 0.2 g C m^{-2} , likely due to the strong seasonal light limitation imparted by sea ice and the solar zenith angle cycle. SP fare well under nutrient limitation and thus make up the majority of phytoplankton biomass in the nutrient-limited ocean gyres (Figure 8k). In contrast, the diatom functional type thrives in nutrient-rich high latitude environments; the highest concentrations of diatoms are in the subantarctic Southern Ocean, as well as the North Pacific and North Atlantic (Figure 8b). Diatoms are favored in light-limited environments due to their greater potential to increase their chlorophyll to carbon ratio than SP (Table 1). Indeed they are the dominant phytoplankton type in regions polewards of $\sim 45^\circ$ latitude (Figure 8k). Like SP, diatoms are also in low abundance in the Arctic and Antarctic sea ice zones, compared to other regions of the ocean, despite being the dominant functional type in these light-limited regions.

While coccolithophore and diazotroph PFTs account for smaller portions of phytoplankton biomass than SP or diatoms, they have important functional roles in global biogeochemistry. Coccolithophores synthesize a calcium carbonate shell around their single cell and thus are a critical component of the carbon cycle, influencing air-sea CO_2 exchange, as well as ballasting organic matter to the deep sea (Krumhardt et al., 2020). Diazotrophs, on the other hand, can fix dissolved N_2 gas, and thus are not limited in their production by nitrogen availability; diazotrophs comprise a critical part of the nitrogen cycle and are an important source of “new” nitrogen into the upper ocean (Dugdale & Goering, 1967). The parameterization of coccolithophores in CESM is largely based on *E. huxleyi* (Krumhardt et al., 2017), the most well-studied coccolithophore. As such, the coccolithophore distribution (Figure 8c) follows that of *E. huxleyi* (see Balch et al., 2005), with blooms in temperate oceanic environments with plentiful iron availability, such as the Patagonian shelf, the North Atlantic and the North Pacific. Coccolithophore biomass is generally $< 0.1 \text{ g m}^{-2}$ in low latitude regions and polar waters, where nutrient availability and temperature limits their production, respectively. Diazotrophs also have a strong thermal component to their biogeography, as they are confined to water temperatures $> 15^\circ\text{C}$ in MARBL (Long et al., 2021). The geographic distribution of the diazotroph functional type shows that they are mainly in warm, nitrogen-limited regions, matching well with maps produced using an inverse modeling approach (Wang et al., 2019). Coccolithophores and diazotrophs do not dominate the phytoplankton communities anywhere in the global ocean in an annual mean sense (Figure 8k), though coccolithophores do show some summertime blooms that may lead them to be the dominant phytoplankton type on a seasonal basis in some regions (not shown).

Zooplankton distributions largely follow the source of their primary phytoplankton food source (Figure 8e and f). Microzooplankton mainly rely on SP for grazing and thus they show a broad global

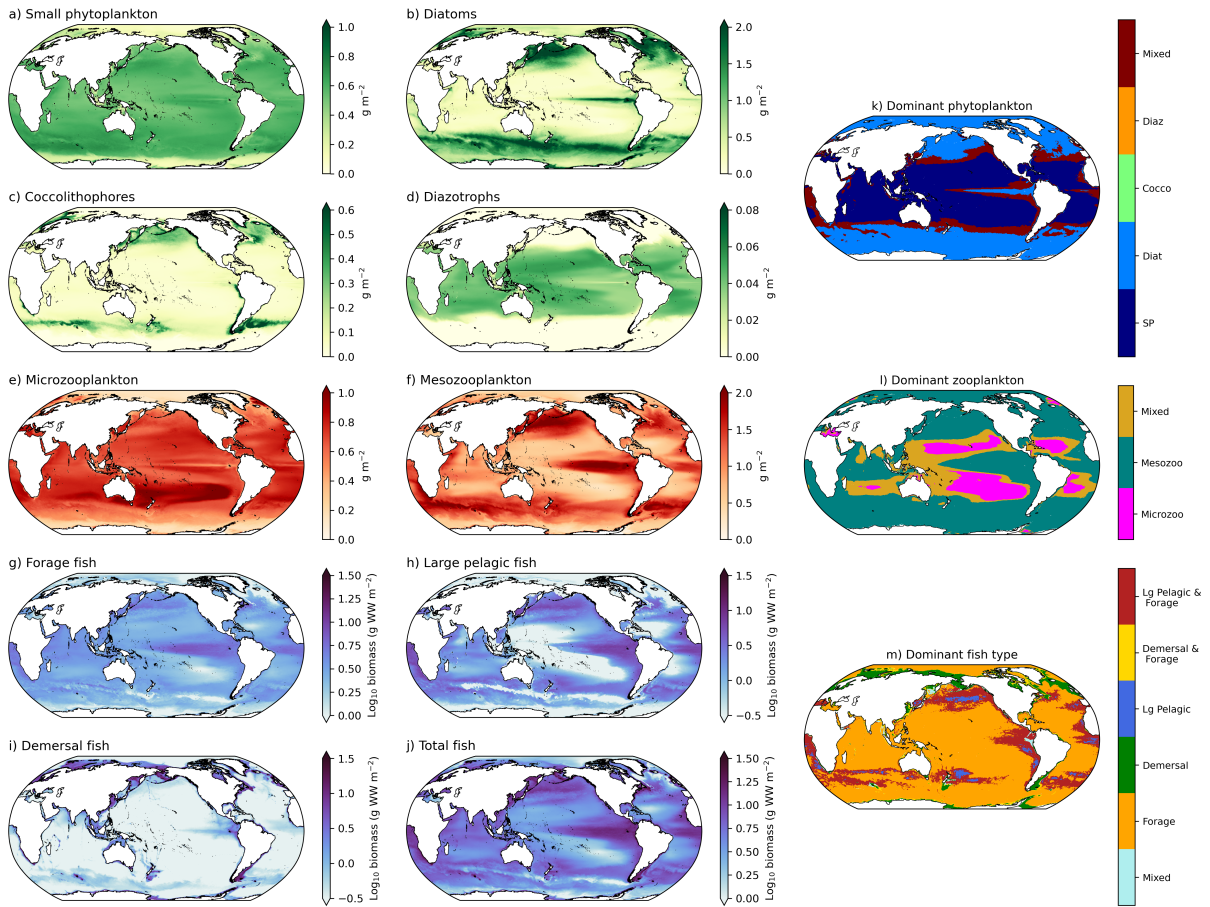


Figure 8: Depth-integrated mean biomass (averaged over years 1980–2005) for phytoplankton (a–d), zooplankton (e–f), and fish (g–j) from FOSI-HR and FEISTY-HR simulations. Note the varying color bar scales for each map. Dominant types for each group are shown along the right side of the figure (panels k–m). For phytoplankton and zooplankton, dominant type was determined as the type that comprised >50% of biomass. For fish, dominant type was determined as follows: areas where a single functional type comprised >50% of all fish biomass were classified as dominated by that type. Areas where no single type comprised >50% of biomass, but two types combined comprised >80%, were classified as co-dominated by two types. Areas where no single type comprised >50% of biomass and two types were not co-dominated were classified as mixed dominance.

distribution, as with SP. Microzooplankton are only the dominant zooplankton in the central ocean gyres, with particularly high biomass in the South Pacific (Figure 8e,l). Mesozooplankton, in contrast, mainly graze on diatoms (Table 3) and thus their geographic distribution pattern mainly follows that of diatoms. Mesozooplankton can also be part of a longer food chain, however, from SP to microzooplankton to mesozooplankton, for example (Figure 1, left side). Therefore mesozooplankton dominate in most ocean regions in the FOSI-HR, outside of the central gyres (Figure 8f and l). Mesozooplankton act as a food resource for forage and large pelagic fish in FEISTY (Figure 1).

Mean fish distributions of each fish functional type are shown in Figure 8g-i, with total fish biomass shown in Figure 8j. Forage fish show a cosmopolitan distribution, with particularly high biomass in equatorial regions, the North Pacific and the northwest Atlantic. Forage fish tend to dominate the fish biomass in most open ocean regions (see orange areas on Figure 8m). Large pelagic fish biomass has more spatial variability, with high biomass in the same regions mentioned above for forage fish, but with particularly low biomass in the western low latitude Pacific and Atlantic Ocean basins. While large pelagic fish do not dominate much of the ocean in terms of biomass, they do co-dominate with forage fish in some subpolar regions and in the equatorial Pacific. However, there is also a strip of very low large pelagic fish biomass in the Indian and Pacific sectors of the subantarctic Southern Ocean. Demersal fish are concentrated on the continental shelves (where they are the dominant fish type; green regions in Figure 8m) with low biomass in open ocean regions, as we would expect for this fish type that relies mainly on benthic organisms for nourishment. Demersal fish biomass is also slightly elevated on the ocean ridges in the Southern Ocean. In general, these large-scale fish biomass distributions are remarkably similar to those shown in Petrik et al. (2019), despite being forced by a different ESM at a lower resolution.

To summarize, large scale biogeography features described above are consistent between FOSI-HR and FOSI-LR (Table 4 and Figure S5). However, taking a closer look at regional trophodynamics allows us to examine the unique features of the FOSI-HR simulation.

4.2 High resolution regional scale trophodynamics

Resolving mesoscale dynamics is important for capturing influential physical features in various ocean regions, especially coastal areas. Resolving details of topography and ocean physics to 0.1° (~ 10 km horizontal resolution) allows for a more accurate representation of coastal currents, upwelling, and other characteristic circulation features relevant for regional scales (Chang et al., 2023). Monthly snapshots from the FOSI-HR show how marine NPP responds to these physical dynamics, compared to the standard 1° version of CESM (Figure 9). We chose snapshots of NPP for months of peak productivity in each region; California Current and Southeast U.S. Shelf NPP peaks in March, while Antarctic productivity peaks in December in FOSI-HR.

Marine phytoplankton have short life cycles and respond to short-term, fine-scale perturbations in their environment. In the California Current LME, upwelling of nutrient-rich waters is more confined to the near shore regions with filaments and eddies moving west. Snapshots from March 1999 of FOSI-HR and FOSI-LR show that NPP responds to this high-nutrient upwelled water (Figure 9a and b); however, the response is much more widespread in the low resolution version when these fine scale dynamics are not resolved. This indicates that broader upwelling in FOSI-LR results in a saturation of phytoplankton growth over a larger area, whereas in FOSI-HR, high productivity is confined to a more narrow strip of coastal upwelling. Generally, NPP in the California Current is higher in FOSI-LR than FOSI-HR throughout the simulations, but the area-averaged interannual variability is similar in both simulations (Figure 9c). While we do not delve into more rigorous analysis here, we speculate that two processes could be contributing to lower overall productivity in the high-resolution simulation. First, resolving mesoscale features may act to reduce biological production via eddy-induced lateral transport and subduction of nutrients (Gruber et al., 2011). Secondly, as nutrients are likely more concentrated in mesoscale features and along the coast in FOSI-HR than in FOSI-LR, this may act to shift the phytoplankton composition to more diatoms (as opposed to small phytoplankton), thus increasing export of carbon and nutrients and leading to less recycled NPP in the 0.1° simulation.

Maps of the southeast U.S. shelf LME also show the importance of resolving fine scale coastal processes (Figure 9d-f). Resolving the Gulf Stream and the fine scale topography in the Caribbean basin lead to completely different spatial distributions of NPP around the southeast U.S. coast. For instance, the loop current (and spawning eddies) appear in FOSI-HR (Figure 9d) but are absent in FOSI-LR (Figure 9e). Similarly, a well resolved Gulf Stream results in depressed NPP right along the

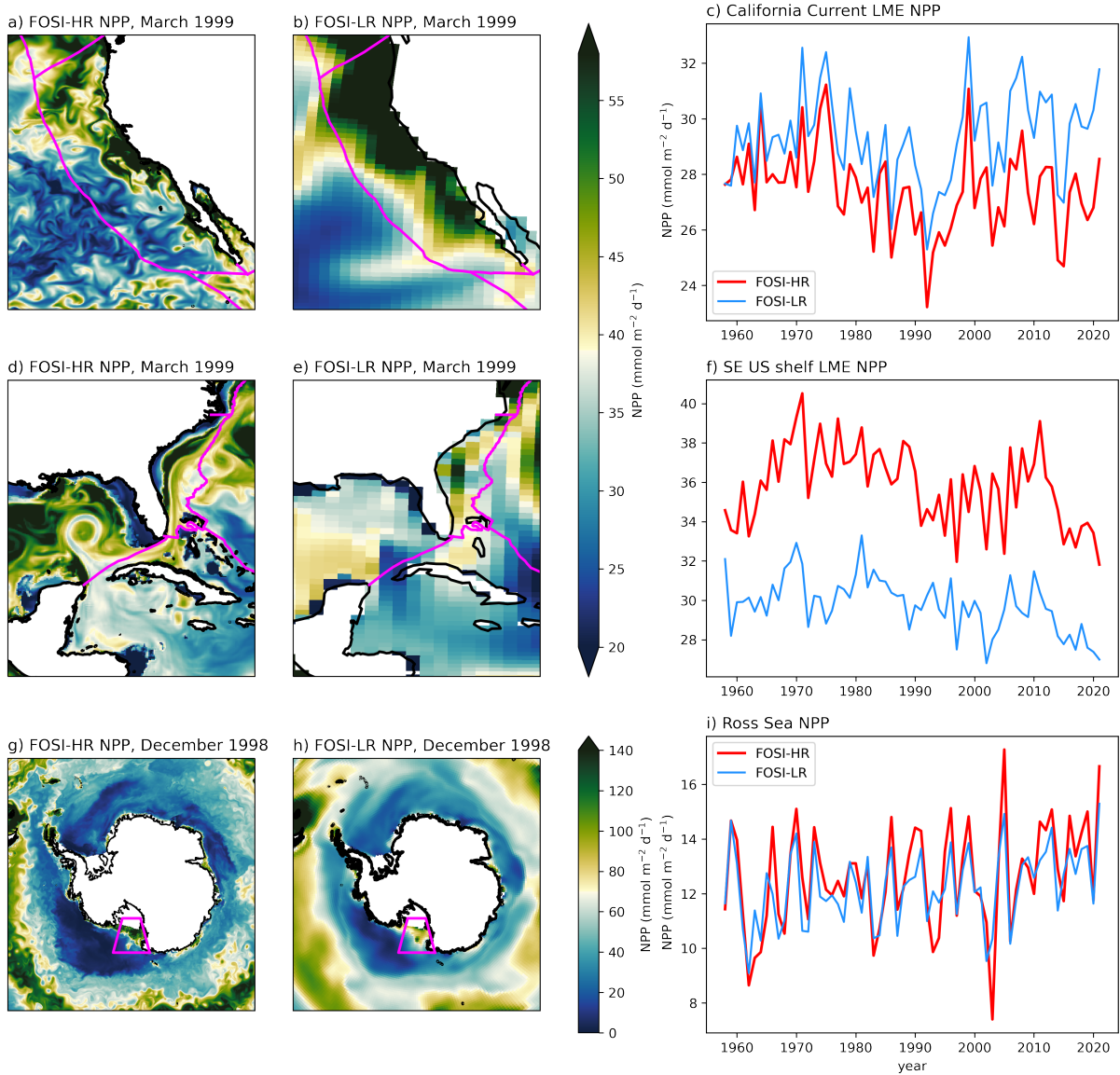


Figure 9: The influence of resolution on simulating NPP in coastal ecosystems: California Current (panels a – c), southeast U.S. (panels d – f), and Antarctic coastal region, Ross Sea timeseries (panels g – i). The top two rows use Large Marine Ecosystem (LME) masks for the California Current and Southeast U.S. Shelf to create time-series (outlines for LMEs shown on maps), while the bottom row timeseries is for the Ross Sea region (see box on maps g and h).

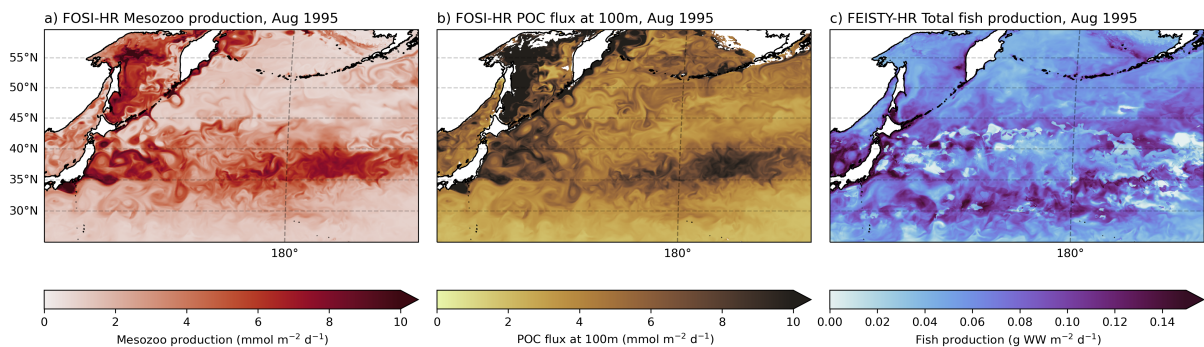


Figure 10: Kuroshio Current region mesozooplankton production and particulate organic carbon (POC) flux for August 1995 of FOSI-HR, and total fish biomass from August 1995 of FEISTY-HR.

eastern coast of the U.S. and elevated NPP just off the shelf; these features are not resolved in FOSI-LR (Figure 9e). Thus the FOSI-HR simulation has roughly 20% more productivity than FOSI-LR with somewhat different phasing of interannual variability.

Antarctic productivity also shows some small scale differences between the FOSI-HR and FOSI-LR. NPP during December of 1998 (Figure 9g and h) is higher along the coastal regions, including the Ross Sea, in FOSI-HR, as compared to FOSI-LR. This likely concerns sea ice dynamics; specifically coastal polynyas are opening up earlier in the season in the high-resolution simulation. Further, NPP is more concentrated in FOSI-HR around $\sim 60^{\circ}\text{S}$ (on the outer edges of Figure 9g and h), likely from eddy-induced mixing in the Antarctic circumpolar current. The time-series shown in Figure 9i is for the Ross Sea region (see boxed region on map). While the simulations match well in overall NPP magnitude, the magnitude of variability in FOSI-HR is greater (standard deviation is $1.88 \text{ mmol m}^{-2} \text{ d}^{-1}$ for the FOSI-HR and 1.37 for the FOSI-LR; Figure 9f). Furthermore, it appears that the Ross Sea polynya has opened up earlier in the season in FOSI-HR, as NPP is greater (darker green on the maps). Further work is needed to understand how model resolution affects the sea ice retreat-advance and how this may affect Antarctic productivity and potentially food resources for higher trophic levels.

Additional snapshots of the marine ecosystem in FOSI-HR show that important components of the marine ecosystem respond to mesoscale variability in ocean physics. As an example, we show snapshots from August 1995 of mesozooplankton production, POC flux, and fish production in the North Pacific Kuroshio current region (Figures 10 and S6). Mesozooplankton production is elevated in energetic Kuroshio current eddies propagating eastward over the dateline. This is likely due to mixing and eastward transport of high nutrient water from depth, which fuels phytoplankton growth and subsequent mesozooplankton grazing and production. POC flux is also elevated and shows the imprint of mesoscale features. Since POC flux in CESM is simulated implicitly following Armstrong et al. (2001), i.e., sinking POC is distributed instantaneously across the water column, it retains the mesoscale imprints from the upper ocean. We also show total fish production from FEISTY-HR in Figure 10c for the same month and year as the upper two panels. While fish production does appear to have imprints from mesoscale variability, it does not follow the same regional patterns as mesozooplankton biomass and POC flux. Rather, fish production is quite low in the 35°N to 40°N band where mesozooplankton and POC flux are elevated, and higher to the north and south of that band. Including fish movement in FEISTY could potentially lead to smoother fish biomass and production at monthly timescales. Interestingly, the 1° CESM version of this figure shows a different spatial distribution of fish production during August 1995 (Figure S6). This leads to questions about the controls on spatial and temporal variability in fish production and biomass on regional scales.

The FOSI-HR simulation can also be used to examine the impacts of extreme climate events on the marine food chain. As an example for the North Pacific region, we created maps from May 2015 of FOSI-HR to illustrate how a marine heatwave may influence the ocean ecosystem (Figure 11). During 2014-2015, the Northeast Pacific experienced a strong marine heatwave (Di Lorenzo & Mantua, 2016), commonly referred to as “the blob.” While some of the biogeochemical imprints of this marine heatwave have been explored (Mogen et al., 2022), analysis of the impacts on nutrients to fish at 0.1° could also offer insights into this extreme event. In Figure 11 we show anomalies of sea surface temperature (SST), NPP, and mesozooplankton biomass during May of 2015. In general the subpolar

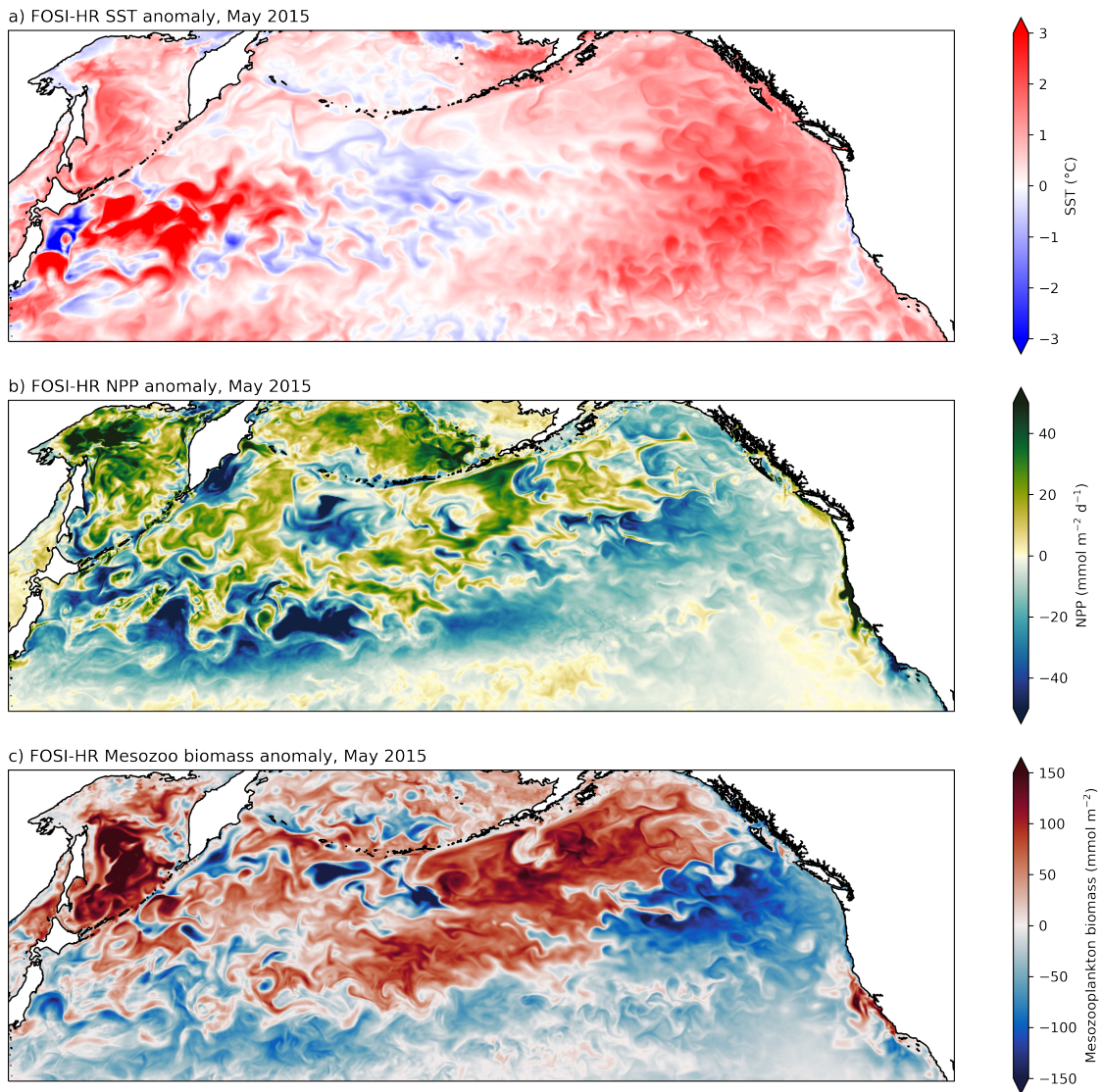


Figure 11: Biogeochemical effects from the 2014/2015 marine heatwave in the North Pacific in the FOSI-HR. These maps show anomalies in sea surface temperature (SST), net primary productivity (NPP), and mesozooplankton biomass during May of 2015 relative to a baseline May average (mean over Mays, 1980-2000) in FOSI-HR.

part of the North Pacific shows increases in NPP and mesozooplankton in response to the warm SSTs, while the southern part of the domain showed decreases in these fields. The California Current region also shows NPP increases to the north and decreases to the south during this heatwave in FOSI-HR, though mesozooplankton biomass does not mirror these changes as it does in open ocean regions. Instead, mesozooplankton increases are constrained to the coastal region between Mendocino and Point Conception. Further analysis, e.g., impact on fish distributions, could help illuminate how heatwaves influence upper trophic levels.

Indeed, fish biomass fields from FEISTY forced by the FOSI-HR also show interesting interannual variability. In order to illustrate this variability, we show annual mean time-series plots from different oceanic regimes with maps of dominant fish type for several years in Figure 12 (see also Figure S8 for a FOSI-LR version of this figure). Climate forcing can cause variations in fish biomass, as the dominant fish type in a geographical location may vary over the course of the 1980 to 2021 FEISTY-HR simulation, hence the variable dominant fish type maps shown in Figure 12g–j. While we have not investigated long term trends in fish biomass associated with, e.g., oceanic warming, we note that large pelagic fish in the southwest Pacific and Canary Current appear to decrease over time (Figure 12a and e).

One particularly interesting region is the equatorial Pacific, which is dominated by both forage and large pelagic fish types (Figure 12b). During the 1982-1983, 1997-1998, and 2014-2016 El Niños, both forage and large pelagic fish drop in biomass. The year after an El Niño event, forage fish rebound faster and become dominant over the large pelagic fish. Large pelagic fish, however, recover ~ 2 years after an El Niño event. Note that in the FEISTY model, fish cannot move laterally between grid cells, meaning that they cannot avoid unfavorable climatic conditions. This is in contrast to real life, where fish populations can migrate in response to, for example, the elevated temperatures caused by El Niño (e.g. Lehodey et al., 2006). This may make the ecosystem response observed in FEISTY-HR less realistic, especially at high-resolution where lack of modeling fish movement may be a bigger issue than when the grid cells in the model are bigger, as in FOSI-LR.

In general, forage fish show more interannual variability than the other FEISTY fish types in the regions we examine. For example, in the North Atlantic, demersal fish (e.g., North Atlantic cod) are the dominant type, but forage fish show much larger fluctuations than demersal fish. Forage fish could show heightened sensitivity to climate variations given their smaller size and shorter time to reach maturity.

4.3 Ocean acidification over the past 64 years

One important feature of FOSI-HR is the implementation of historical atmospheric CO_2 forcing, thereby creating a reconstruction of ocean acidification from anthropogenic carbon emissions over the period 1958 to 2021. A complication of analyzing the anthropogenic increase is CO_2 drift in the natural carbon system. It is not feasible to spin up the FOSI-HR configuration due to computational costs. We mitigate this in our analysis by using two parallel carbonate systems: one where the ocean is exposed to anthropogenic atmospheric CO_2 concentrations and one with preindustrial ($285 \mu\text{atm}$) CO_2 concentrations. Anthropogenic CO_2 can be computed by differencing these two systems, accounting for drift in the natural carbon system. Applying this differencing to the pH field, we determined that global mean pH of the ocean in 2021 was lower by 0.089 since the preindustrial era due to the absorption of anthropogenic carbon into the ocean in FOSI-HR.

The coccolithophore phytoplankton functional type in the MARBL ecosystem configuration is sensitive in its growth and calcification to aqueous CO_2 in the water, as well as temperature and nutrient limitation (Krumhardt et al., 2019, 2020). We focus our attention on the North Atlantic to assess the effects of environmental changes on coccolithophores over the past 64 years (Figures 13 and S9). Here, coccolithophores form regional blooms in the summertime that show in the imprints of mesoscale ocean dynamics (see Figure 13a for a snapshot from July 2005, when coccolithophores blooms are underway). This region has accumulated $\sim 70 \text{ mmol m}^{-3}$ anthropogenic dissolved inorganic carbon (DIC) in the surface ocean (upper 10 m) since industrialization, dropping pH by roughly 0.1 units (Figure 13b and c). Though pH has dropped across the entire North Atlantic domain shown in Figure 13 the eastern part shows less of a drop, while the coastal region along North America has the steepest declines in pH. SST has also warmed over most of the North Atlantic in FOSI-HR, except for an area of cooling just south of Greenland and some small patches along the Gulf Stream.

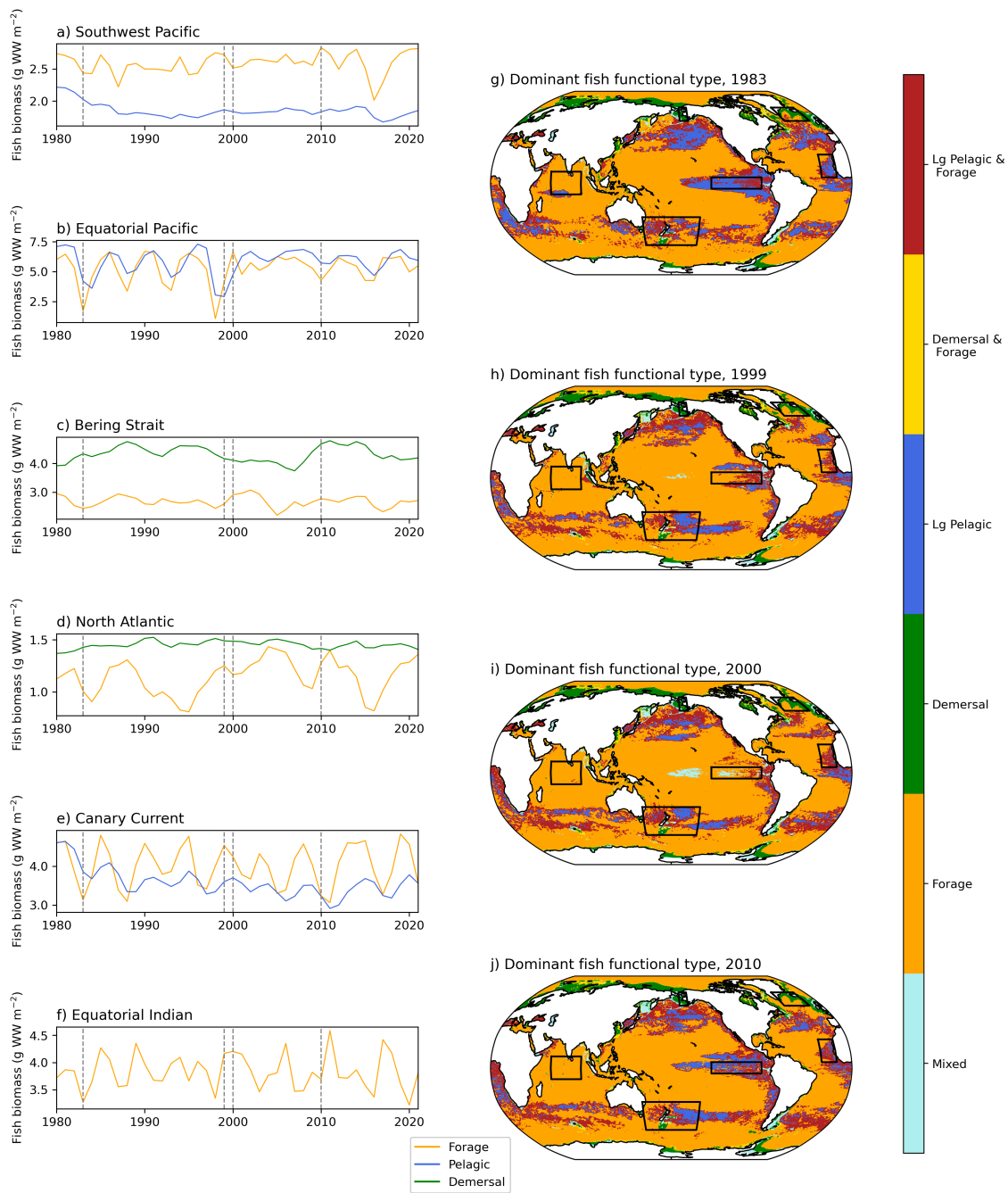


Figure 12: Interannual variability in fish biomass in various oceanic regions from the FEISTY-HR simulation. Timeseries for 6 regions and maps showing how dominant fish types may vary from year to year. See Figure 8 caption for details about dominant fish type classification.

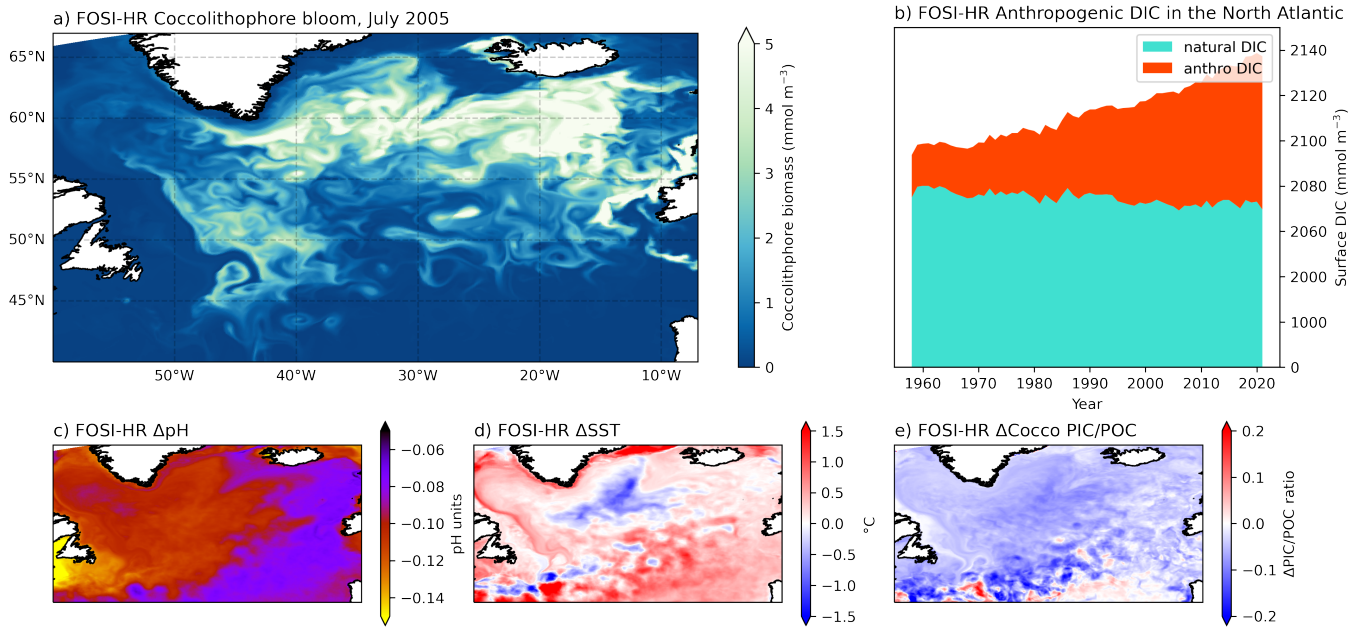


Figure 13: Ocean acidification and warming influences North Atlantic coccolithophores. Panel a shows an example of a modeled coccolithophore bloom in the North Atlantic region during July, 2005 of the FOSI-HR simulation. Panel b shows a time series of surface (top 10 m) dissolved inorganic carbon (DIC) concentration in this region (60°W to 7.6°E, 38.8°N to 67.6°N) over the course of the simulation; note that the y-axis ticks on panel b are not evenly spaced. Panels c, d and e show changes over the period 1958 to 2021 (last 5 years-mean minus first 5 years-mean) in pH, sea surface temperature (SST), and the coccolithophore particulate inorganic carbon to particulate organic carbon (PIC/POC) ratio, respectively.

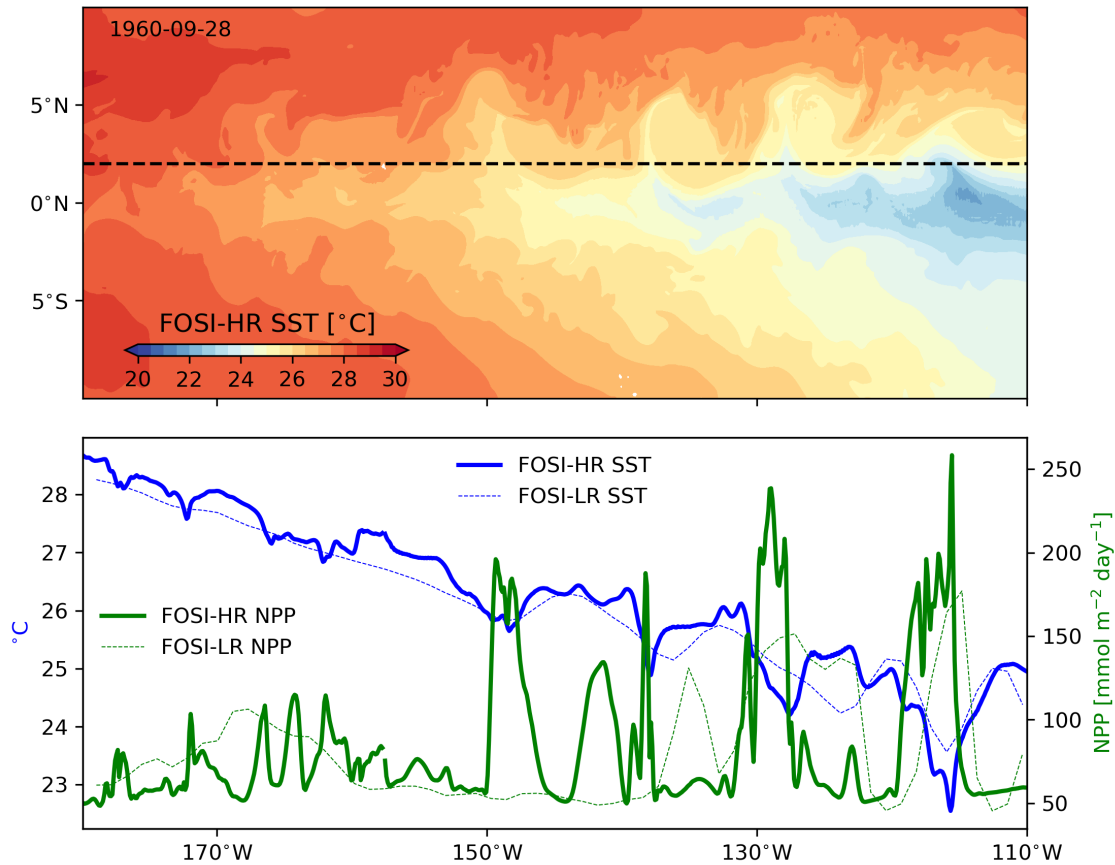


Figure 14: Spatial variability in sea surface temperature (SST) in the equatorial Pacific and its influence on NPP. A snapshot of SST on September 28, 1960 from the FOSI-HR is shown in panel a. SST and NPP along 2°N transect (shown by a black dashed line in panel a) are plotted in panel b with FOSI-HR data in bolder solid lines and FOSI-LR data in thin dashed lines.

These environmental changes have resulted in changes to the coccolithophore calcification. The particulate inorganic carbon to particulate organic carbon ratio (PIC/POC) of coccolithophores is an indication of how calcified they are. The negative effect of ocean acidification on PIC/POC is most prominent, as large areas of the North Atlantic show decreases in coccolithophore PIC/POC ratios over the past 64 years in this CESM simulation (Figure 13e). However, the subtropical parts of the North Atlantic in the southern part of the domain shown in Figure 13 show slightly increased PIC/POC ratios, likely due to increases in temperature (for more details on the coccolithophore parameterization see Krumhardt et al., 2019, 2020; Krumhardt et al., 2017). Ocean stratification and subsequent increases in nutrient limitation could also work to increase PIC/POC; indeed coccolithophores tend to calcify more when nutrient limited (van Bleijswijk et al., 1994). Thus, increased PIC/POC in the southern part of the domain shown in Figure 13 could also stem from warming-induced ocean stratification and decreased nutrient availability.

4.4 Fine scale environmental modulation of the marine ecosystem

Mesoscale features modulate light, nutrients, and temperature, and thereby have the capacity to affect ecosystem dynamics. Resolving ocean processes on the scales of 10 km improves the mean state representation in areas of vigorous mesoscale activity, such as coastal and upwelling regions, and it also allows for resolving the larger baroclinic eddies in most regions of the ocean (Chang et al., 2020; Kirtman et al., 2012).

As well as being a strong upwelling area, the equatorial Pacific is also an area of strong eddy activity in the form of tropical instability waves (TIWs), westward propagating features with wave

lengths on the order of 1000 km and periods of 13-40 days (Halpern et al., 1988; Legeckis, 1977; Miller et al., 1985; Qiao & Weisberg, 1995). The passage of a TIW not only modifies temperature gradients and currents, but also biogeochemistry. Eddebbbar et al. (2021) demonstrate that TIWs modify the availability of dissolved oxygen using the same ocean model as used in FOSI-HR. Eddebbbar et al. (2021) also demonstrate that the equatorial undercurrent and the oxygen minimum zone are better represented in FOSI-HR than in FOSI-LR (see also Section 3.2). While there is some indication of TIW activity in FOSI-LR, the fronts are much more distinct in the FOSI-HR (Fig. 14). The 5-day average SST shows well defined wave structures emanating from the eastern tropical Pacific and extending from the equator into the Northern Hemisphere. A longitudinal transect along 2°N shows the clearly-defined frontal features in SST and their relationship with NPP: strong temperature gradients coincide with strong NPP peaks on the cold sides of the fronts, likely due to increased nutrient availability in colder (upwelled) waters. This relationship is more pronounced in FOSI-HR than in FOSI-LR, allowing for detailed investigation of the impact of these mesoscale features in an already highly productive area of the ocean.

Fish distributions also respond to features only resolved by FOSI-HR, in contrast to FOSI-LR. An example of this is the Antarctic coastal current (e.g., see Schubert et al., 2021) in the Amundsen Sea and Bellinghousen Sea region in Western Antarctica (Figure 15). Here, coastal polynyas in the sea ice zone open up in the springtime allowing early light access to the water column and fueling primary production. This coastal springtime bloom is captured by FOSI-HR, but not by FOSI-LR (Figure 15a,b). While some of the NPP is recycled or passed up the pelagic food web, much of the organic carbon produced by the bloom is exported to the seafloor in this shallow coastal shelf. This supplies benthic invertebrates in FEISTY with a food source, which, in turn, are consumed by demersal fish. An example of a demersal fish in this geographic location would be the Antarctic toothfish, an important species to fisheries (Hanchet et al., 2015). Having fine scale features, such as the Antarctic coastal current, resolved could allow more accurate representation of trophodynamics that are important for fisheries and understanding food resources for endangered Antarctic marine predators, such as Emperor Penguins (Jenouvrier et al., 2021).

The subantarctic Southern Ocean is a region of vigorous mesoscale eddy activity. The eddies and fronts in this region of the ocean modulate several environmental processes that influence phytoplankton growth (see, e.g., Song et al., 2018), with cascading effects for the rest of the marine ecosystem. In Figure 16, we show snapshots from early December 2020 of various fields from FOSI-HR. Sea surface height (SSH) anomalies are shown by contour lines, demonstrating how eddies may modify trophodynamics. The subantarctic Southern Ocean is characterized by moderately high trophic transfer efficiency, shown here by the z-ratio, the ratio of mesozooplankton production to NPP, an indication of how much energy is transferred up the food web (Figure 16h; Stock et al., 2014a). Eddies modify these mean state dynamics by modulating environmental characteristics that influence phytoplankton growth.

We labeled four eddies in Figure 16: eddies A and B are cyclonic (negative SSH anomalies) and eddies C and D are anticyclonic (positive SSH anomalies). These two types of eddies alter the ocean environment in contrasting ways. Mixed layer depths are deep in the anticyclonic eddies C and D (Figure 16a), resulting in more iron availability (Figure 16b), but also more light limitation for phytoplankton. Indeed productivity of both diatoms and coccolithophores, two important primary producers in this region, is suppressed in anticyclonic eddies C and D, likely due to light limitation. The shallower mixed layer depths in cyclonic eddies A and B result in more light availability but iron becomes more limiting, especially in eddy B. As coccolithophores fare better under iron limitation than diatoms (i.e., they have a lower Fe half saturation constant; Table 1) coccolithophores outcompete diatoms in eddy B (Figure 16d), while diatoms dominate in the eddy A, which has relatively more iron. This demonstrates how eddies can modulate phytoplankton community composition.

Nevertheless, light availability, controlled by the depth of the mixed layer, appears to be the primary factor regulating trophodynamics in this region during this time of the year. Mesozooplankton biomass is especially enriched in eddy A with a shallow mixed layer, while it is starkly suppressed in eddies C and D. These dynamics transfer up the food chain. Forage fish biomass is also suppressed near eddies C and D, but the imprints of these eddies are slightly offset to the northeast, implying a slower response time for forage fish than for phytoplankton and zooplankton. Further, large pelagic fish biomass barely retains the imprints of mesoscale activity, showing a small patch of low biomass near eddy D, with higher biomass towards the eastern side of the box. This is likely to do the longer lifespan

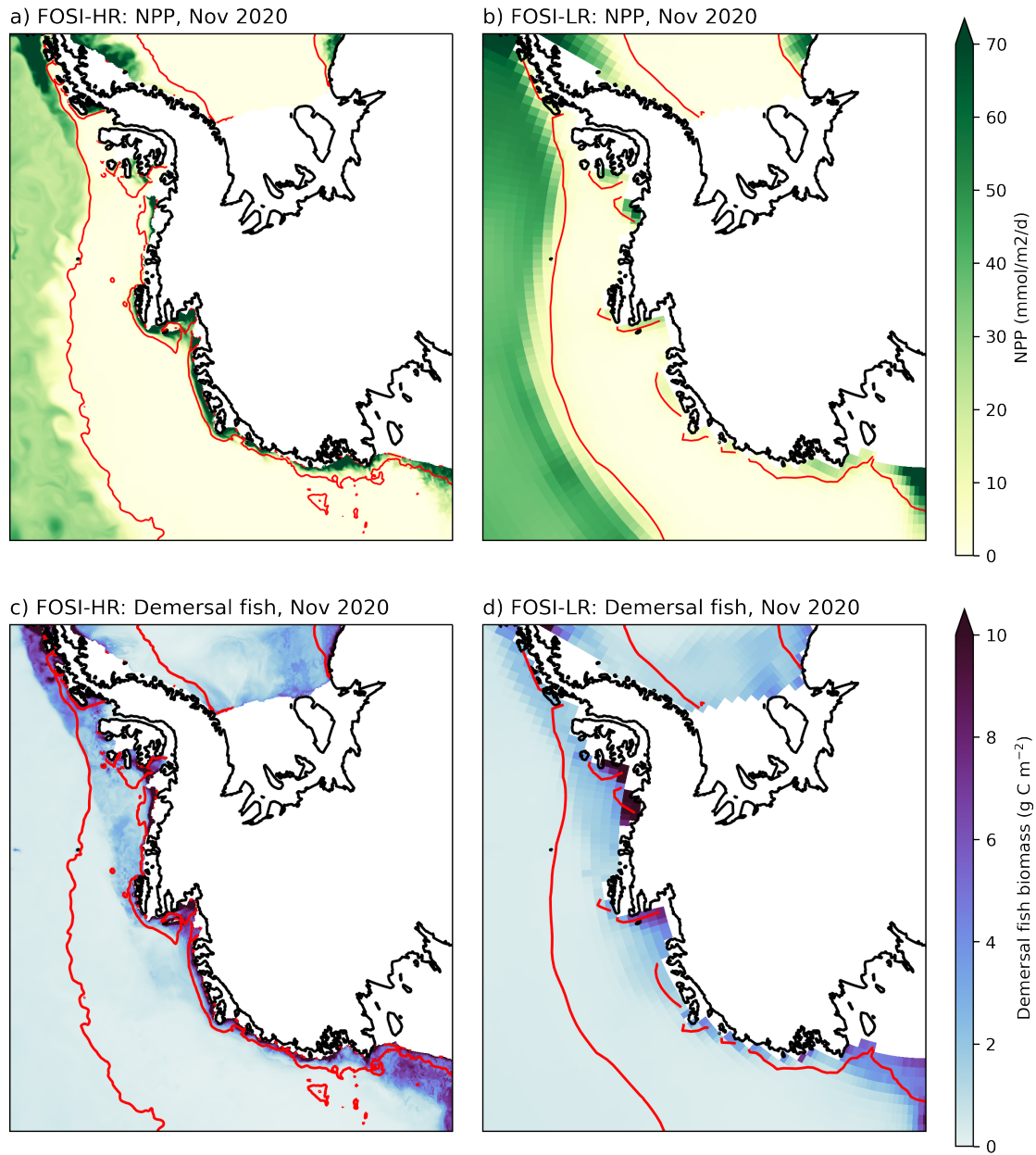


Figure 15: NPP (panels a and b) and Demersal fish biomass (panels c and d) during November 2020 for the Amundsen-Bellinghousen Sea region of the Antarctic coast for FOSI-HR (left) and FOSI-LR (right). Red contours represent 85% sea ice concentration.

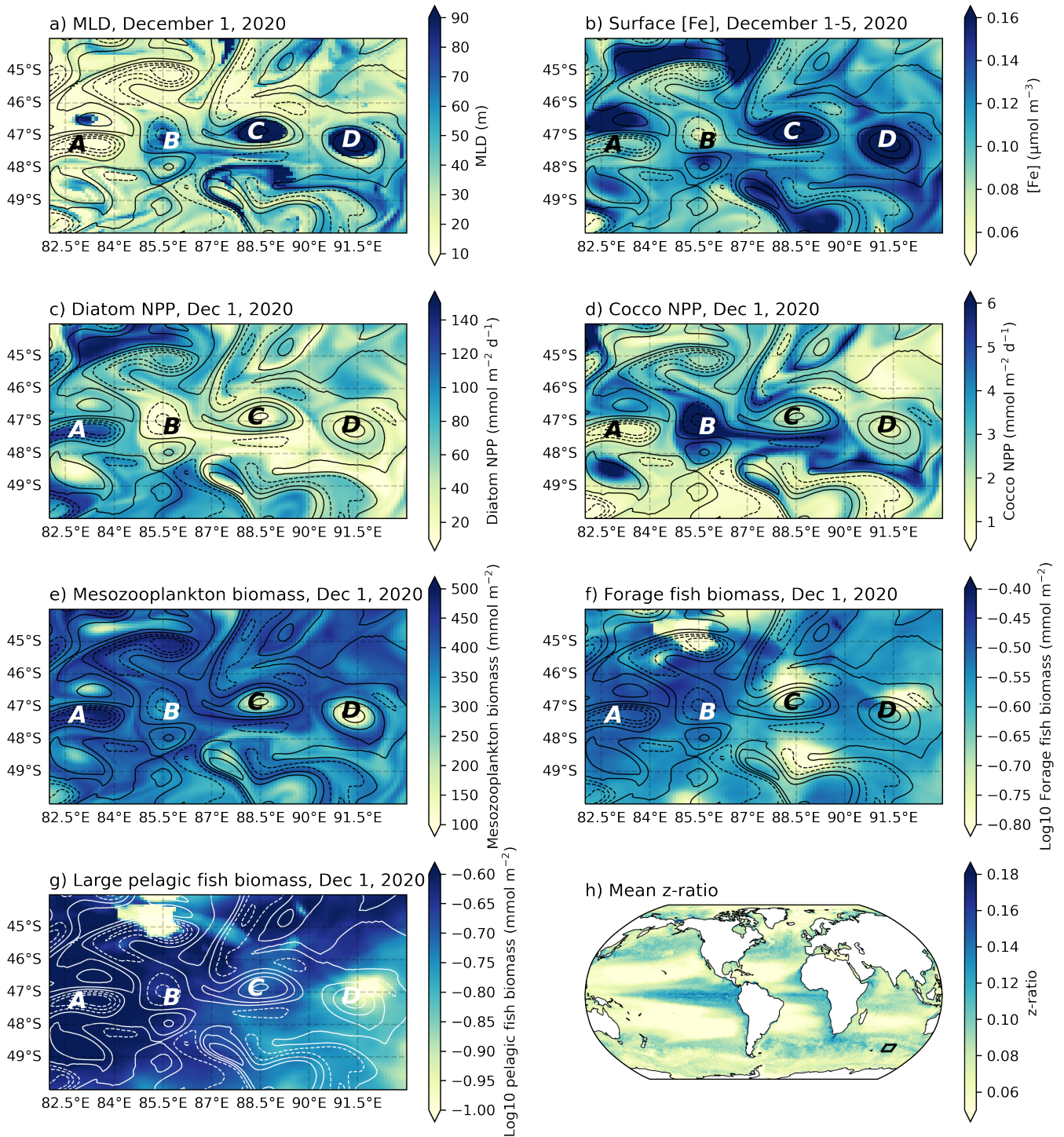


Figure 16: Trophodynamics across scales. Panels a–g show snapshots of daily data for December 1, 2020 for various fields from FOSI-HR, except panel b, which shows the 5-day average for surface iron (Fe) concentration from December 1-5, 2020. Panel h shows the mean z-ratio over the course of the FOSI-HR simulation and the box indicated in the subantarctic Indian section of the Southern Ocean is the region that is shown in panels a–g. Sea surface height (SSH) anomalies are indicated by black contours (except for panel g, they are white) every 3 cm with dashed lines indicating negative SSH anomalies. Four eddies are labeled A–D in order to facilitate discussion of the dynamics in the text. Abbreviations: mixed layer depth (MLD), iron (Fe), net primary productivity (NPP), coccolithophores (cocco), and z-ratio (mesozooplankton production/NPP).

and slower response time of these large fish. In short, eddies project environmental variations on to a mean background state and have the capacity to influence how energy/carbon is transformed in the ocean.

5 Conclusions and future directions

In this study we document novel CESM and FEISTY simulations that could be immensely useful for many biogeochemical and oceanographic questions, from studying mesoscale dynamics and their effects on ecosystems to understanding large-scale ocean processes. Applying the FEISTY model to FOSI-HR furthers its applicability for marine food web questions and provides a benchmark for advancing ecological modeling using an Earth System Model. FOSI-HR and FEISTY-HR together effectively provide a reconstruction of the ocean physical state and ecosystem over 64 years. These simulations can be used to investigate recent ocean change and variability, as well as providing initial conditions for high-resolution climate prediction studies.

We evaluate a variety of model fields in FOSI-HR, focusing on metrics relevant for marine ecosystems and biogeochemistry. We show that the FOSI-HR and FEISTY-HR simulations exhibit a reasonable correspondence to available observational datasets and, in many cases, improve upon the lower resolution version of CESM. Sea ice, for example, shows a clear improvement in FOSI-HR, as compared to FOSI-LR, as the FOSI-HR sea ice extents in both hemispheres are closer to those observed (Figure 2). Oxygen and nutrient concentration patterns in the FOSI-HR generally match observations, but there are still some notable biases, showing that some model infidelities cannot be improved with increasing resolution (Figures 3 and 4). Phytoplankton chlorophyll patterns also match available observations in most regions (Figure 5a,b). FOSI-HR NPP correlates well with two observation-based NPP algorithms (Figure 6). Further, while zooplankton observations are sparse, the mesozooplankton observations available correspond well to mesozooplankton biomass in FOSI-HR (Figure 5c,d). Lastly, by comparing FEISTY-HR fish catches to historical fish catch records, we show that FEISTY-HR captures mean fish distributions in LMEs reasonably well, as well as capturing interannual variability in fish catches in certain highly-fished regions.

The FOSI-HR and FEISTY-HR simulations offer a consistent framework within which to analyze how upper trophic levels respond to climate forcing. For example, we show that both forage and large pelagic fish drop in biomass in the equatorial Pacific during an El Niño event, but that forage fish populations recover faster (Figure 12). In future studies one could analyze these dynamics, from El Niño impacts on nutrients to plankton to fish, using the FOSI-HR and FEISTY-HR simulations documented here.

Additionally, we show how the eddies captured in FOSI-HR may potentially impact ecosystem dynamics, from better resolved tropical instability waves in the equatorial Pacific (Figure 14) to eddies in the subantarctic Southern Ocean (Figure 16). Indeed, mesoscale activity leaves imprints on physical fields, such as mixed layer depth and temperature. This leads to bottom up forces on the biogeochemistry and ecosystem. Mesozooplankton biomass, for example, still retains a strong imprint of eddies (Figures 10 and 16), but for fish the imprint is more muted.

Here we provide a variety of short analyses in order to showcase the multiple utilities of this simulation data set. While there is still more work to do to advance global marine ecosystem modeling, such as including FEISTY as an online component within CESM, the CESM-FEISTY framework documented here provides an important benchmark. We hope that this high-resolution simulation of the ocean and marine ecosystem, including fish, will be a useful community resource in the coming years.

6 Data and code availability

The full datasets from FOSI-HR, FOSI-LR, FEISTY-HR and FEISTY-LR simulations will be made available on a Globus Guest Collection upon publication of this manuscript. Model data and scripts for making the figures in this manuscript will be made available via a DASH repository upon publication: <https://data.ucar.edu/>. All observational datasets used for model validation are publicly available.

Further details on the model setup can be found at https://github.com/mnlevy1981/frontera_highres/tree/main. The Python-based FEISTY code used in this study can be found here: https://github.com/mnlevy1981/frontera_highres/tree/main.

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8 Declaration of competing interest

The authors declare no competing interests.

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Supplementary Information to:

From nutrients to fish: Impacts of mesoscale
processes in a global CESM-FEISTY eddy ocean
model framework

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1 Supplementary Table and Figures

Table S1: List of non-default POP2 (above the horizontal line) and CICE5 (below the horizontal line) parameters

Parameter name	Value
lcvmix	.false.
h_upper	20.0
ltidal_mixing	.true.
shf_strong_restore	79.1
shf_strong_restore_ms	79.1
sfwf_strong_restore	0.56
sfwf_strong_restore_ms	0.56
dt_count	816
time_mix_freq	17
ndtd	2
dt_mlt	0.5
r_snw	1.60
rsnw_mlt	1000.
f_blkmask	.true.

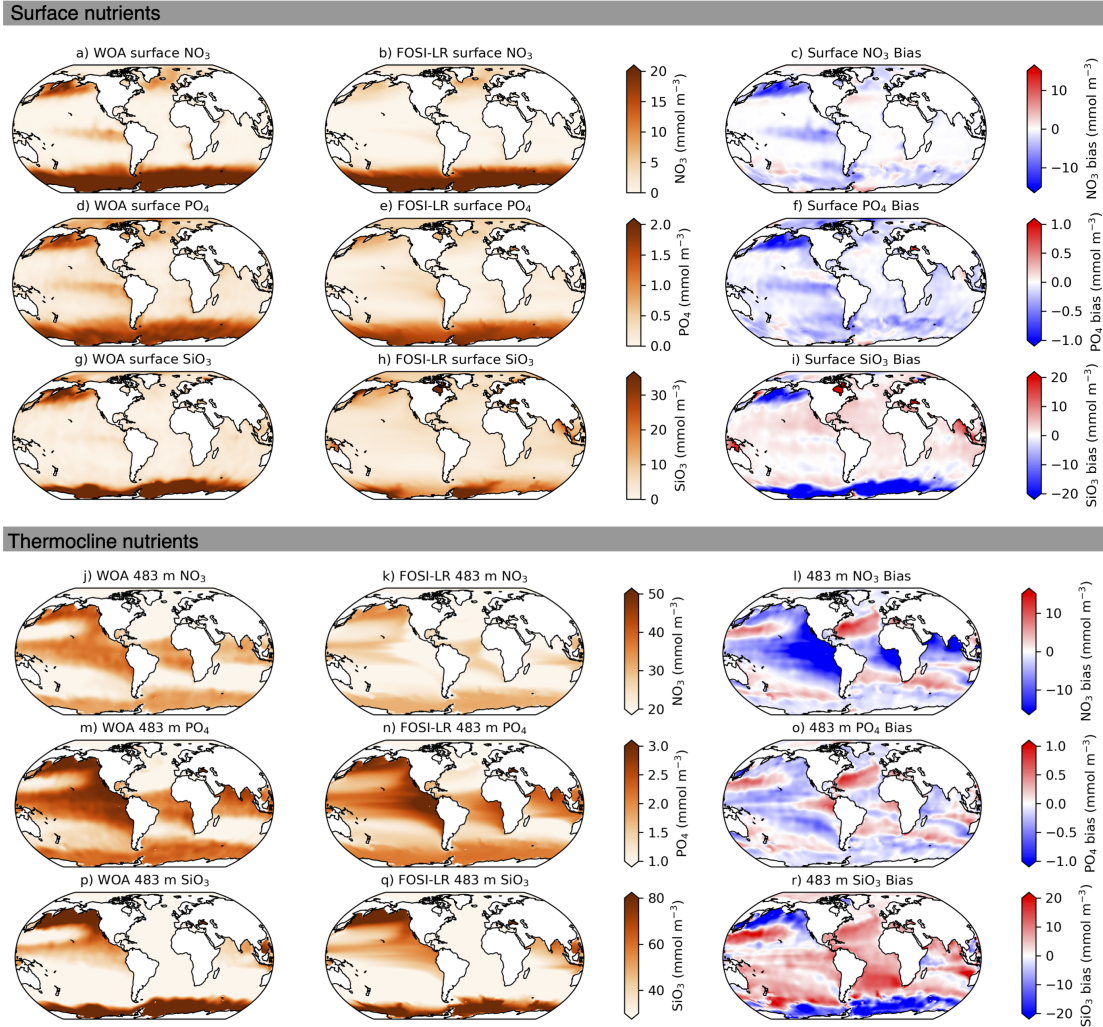


Figure S1: Comparison of FOSI-LR surface and thermocline (depth range between 461.8 m and 503.7 m) nutrients to World Ocean Atlas, v2 (WOA) (Garcia et al., 2018). Figure 4 in the main text is the same, but for the FOSI-HR simulation.

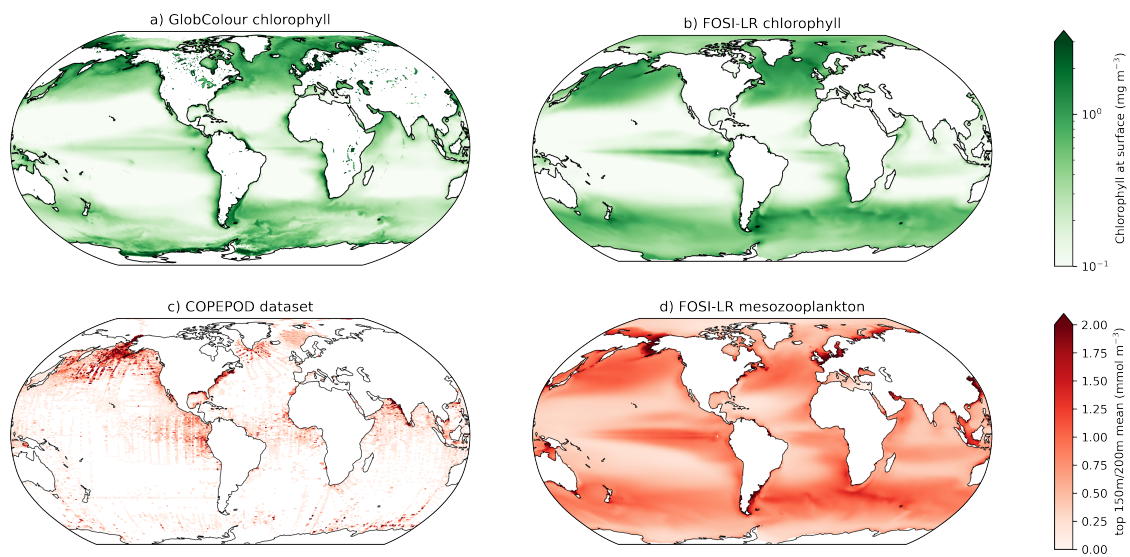


Figure S2: FOSI-LR chlorophyll comparison to GlobColour merged product (SeaWiFS, MODIS, VIIRS) and mesozooplankton/COPEPOD comparison (Garnesson et al., 2019). Figure 5 in the main text is the same, but for the FOSI-HR.

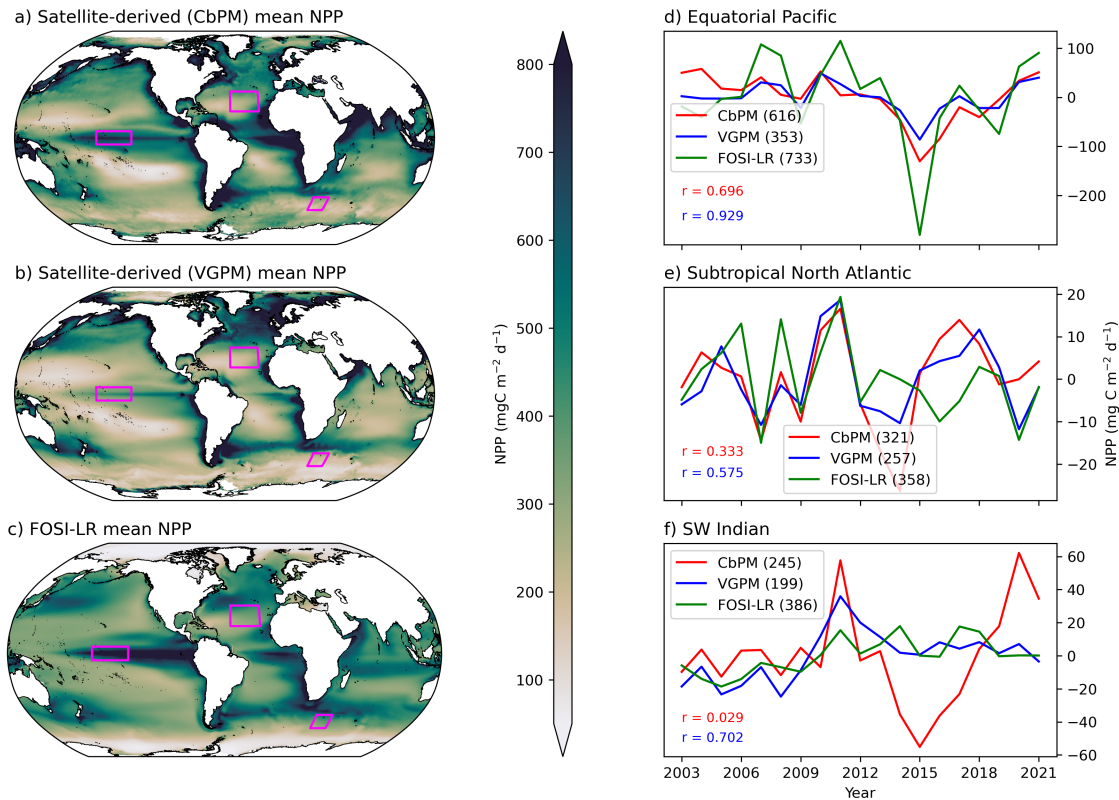


Figure S3: Mean net primary productivity (NPP) over the period 2003 to 2021 as estimated via the Vertically Generalized Production Model (VGPM; Behrenfeld & Falkowski, 1997), the Carbon-based Productivity model (CbPM; Behrenfeld et al., 2005; Westberry et al., 2008) and the FOSI-LR (panels a, b, and c, respectively). Time-series anomalies of NPP from the VGPM, CbPM, and the CESM-FOSI-HR plotted along the right-hand side are area-weighted means in the three boxes indicated on the maps (panels d–f). Correlation coefficients between FOSI-LR NPP and each observation-based estimate are indicated in each panel (CbPM in red and VGPM in blue). We created anomalies to compare variability, but the average magnitude of NPP varies for each region; we report the magnitudes of NPP for each boxed region in the legend (in $\text{mg C m}^{-2} \text{d}^{-1}$) for each region. Figure 6 in the main text is the same, but for FOSI-HR.

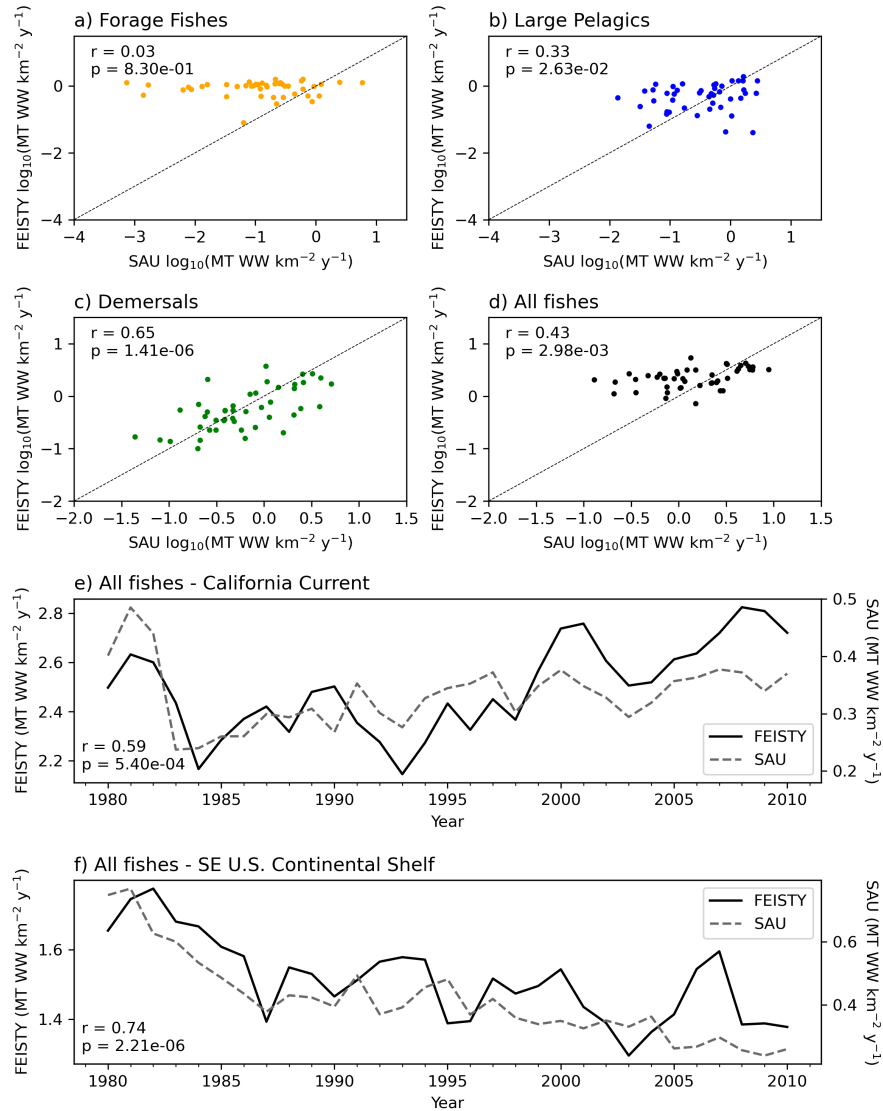


Figure S4: Fish catch yields from FEISTY-LR compared to the Sea Around Us (SAU) dataset for 45 Large Marine Ecosystems (LMEs). The top four panels (a–d) show scatter plots of SAU versus FEISTY fish catches - each dot represents the “mean” fish catch in an LME (see Methods for further details). Panels e and f show time-series of fish catches from SAU and FEISTY for the California Current and Southeast U.S. Continental Shelf LMEs. Figure 7 in the main text is the same, but for the FOSI-HR.

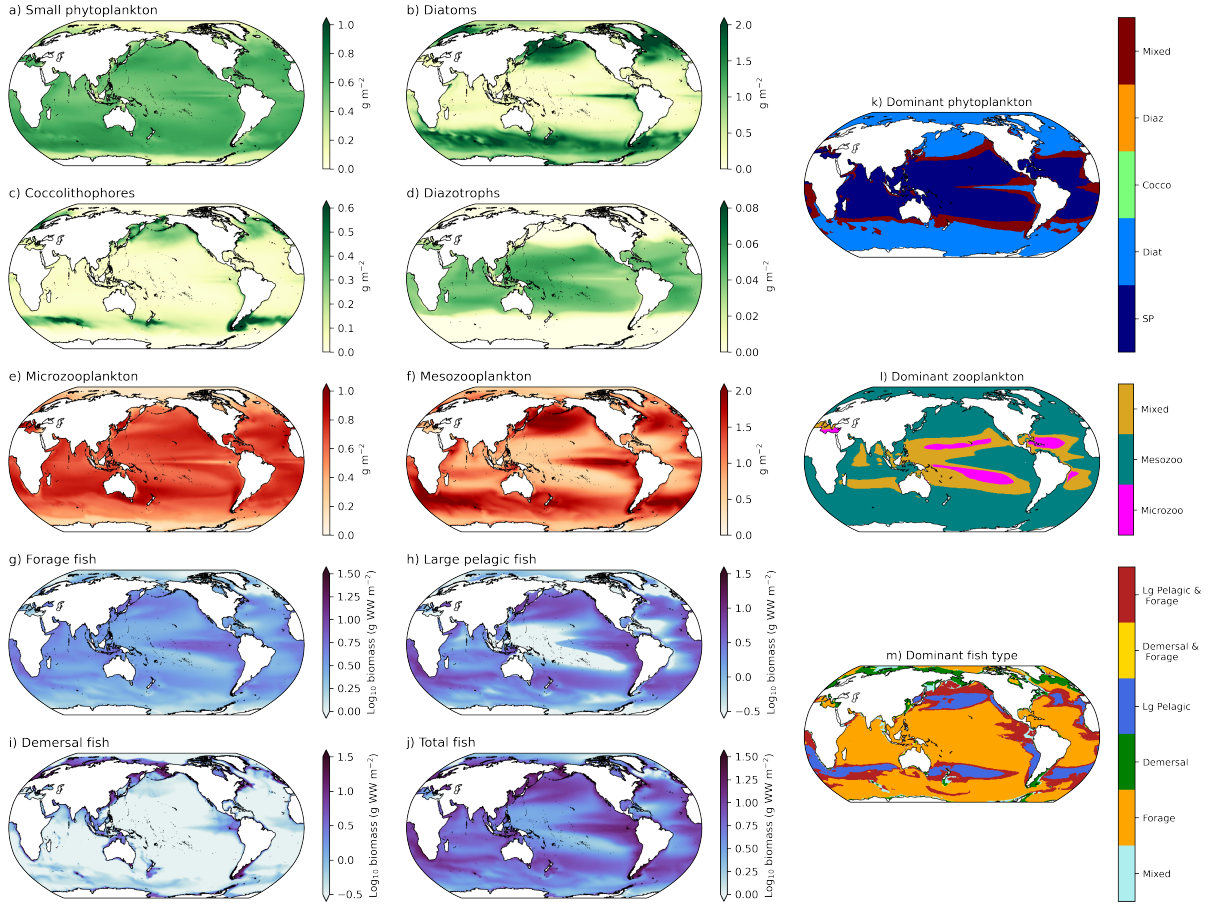


Figure S5: Depth-integrated mean biomass (averaged over years 1980–2005) for phytoplankton (a–d), zooplankton (e–f), and fish (g–j) from the FOSI-LR simulation. Dominant types (>50% of biomass) for each group are shown along the right side of the figure (panels k–m). Note the varying color bar scales for each map. Figure 8 in the main text is the same, but for the FOSI-HR.

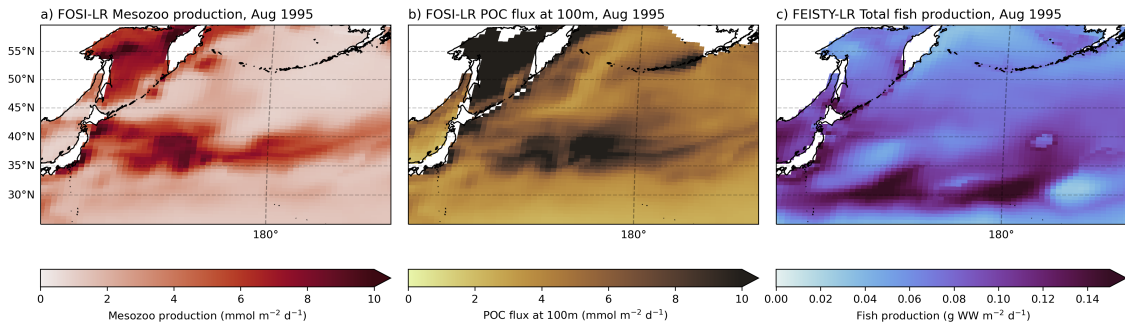


Figure S6: Kuroshio Current region mesozooplankton production, particulate organic carbon (POC) flux, and total fish biomass from FEISTY for August 1995 of the FOSI-LR. Figure 10 in the main text is the same, but for the FOSI-HR.

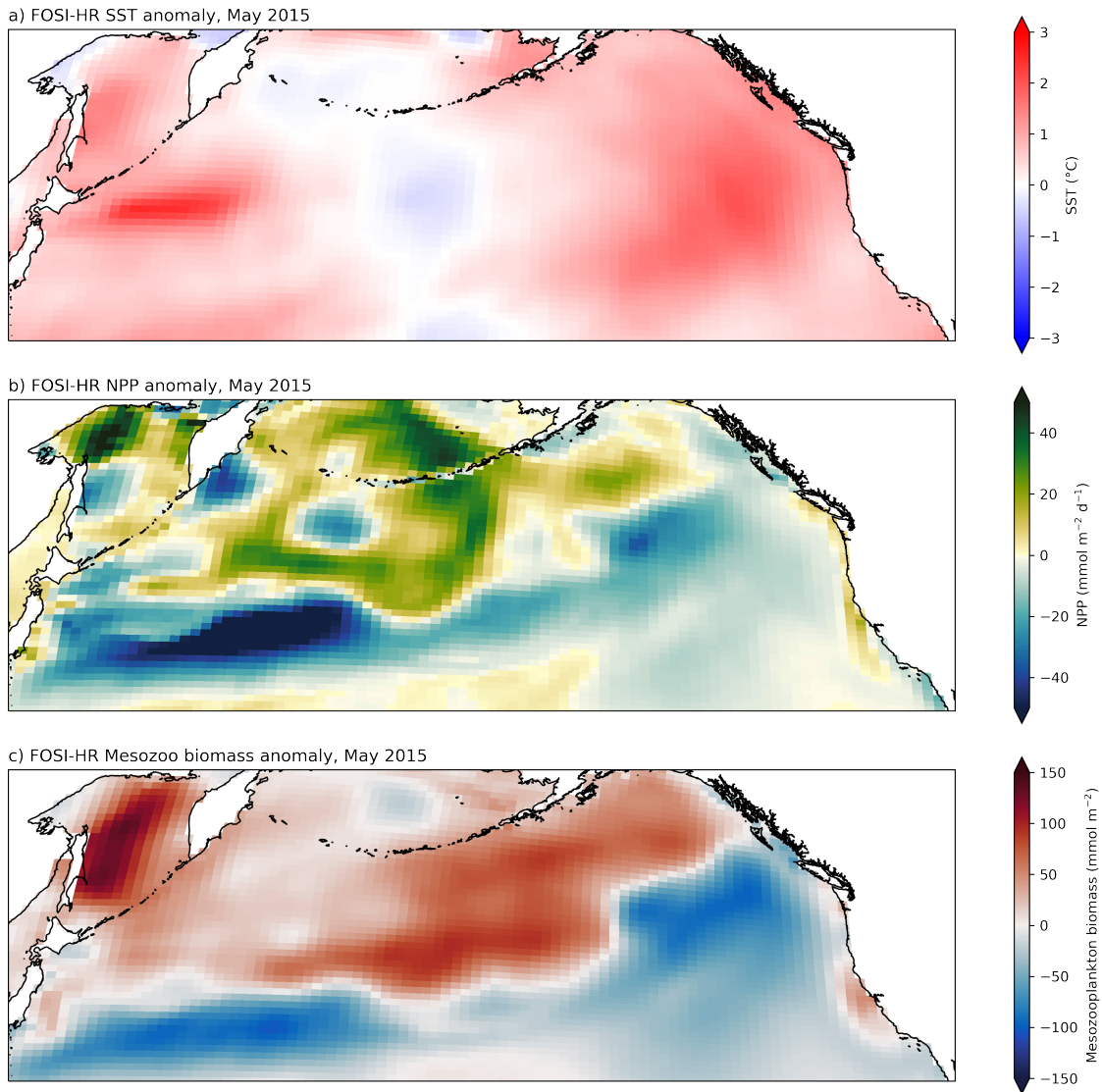


Figure S7: Biogeochemical effects from the 2014/2015 marine heatwave in the North Pacific in the FOSI-LR. These maps show anomalies in sea surface temperature (SST), net primary productivity (NPP), and mesozooplankton biomass during May of 2015 relative to a baseline May average (mean over Mays, 1980-2000) in FOSI-LR. Figure 11 in the main text is the same, but for the FOSI-HR.

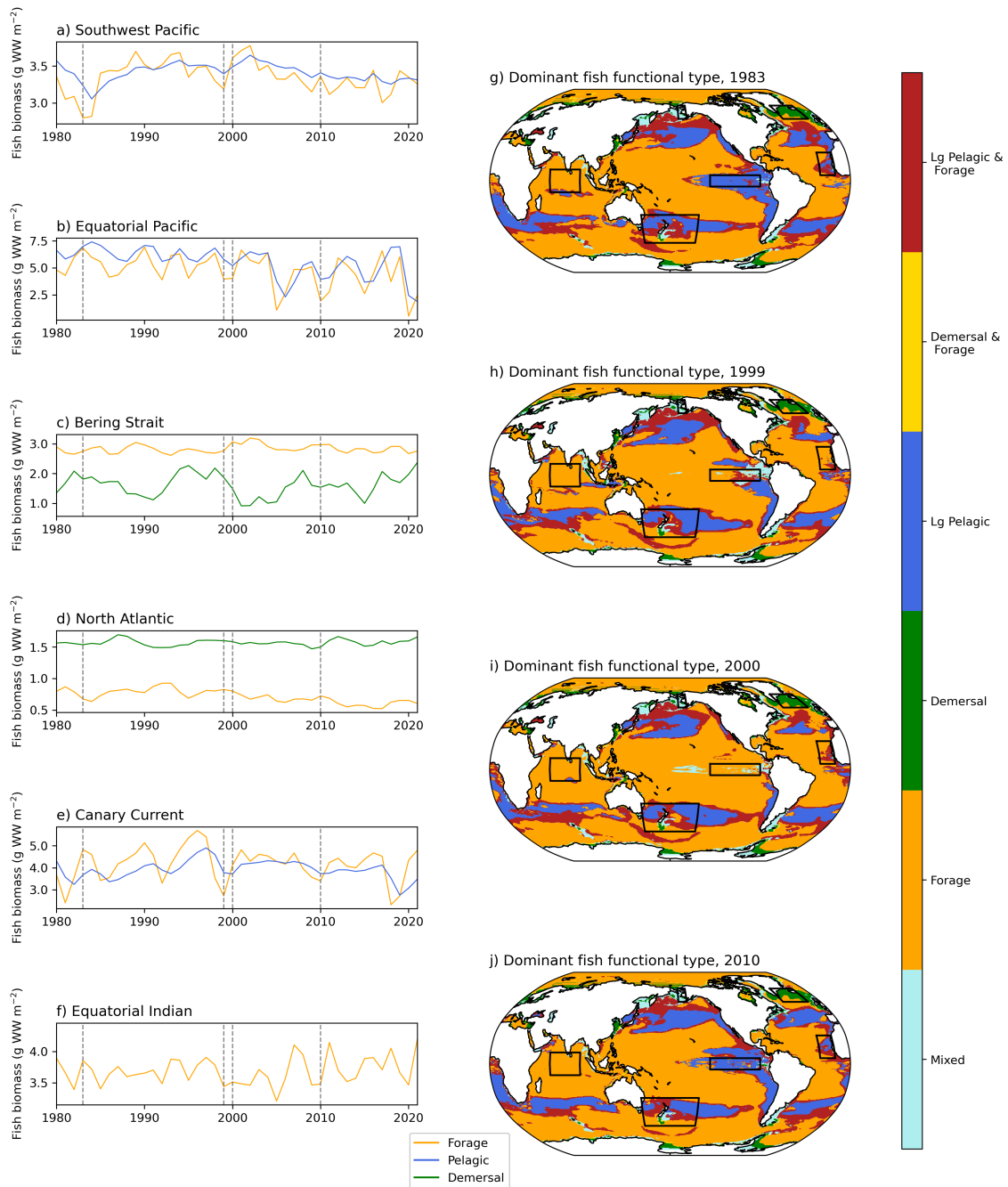


Figure S8: Interannual variability in fish biomass in various oceanic regions from the FEISTY-LR simulation. Timeseries for 6 regions and maps showing how dominant fish types may vary from year to year. Figure 12 in the main text is the same, but for FEISTY-HR.

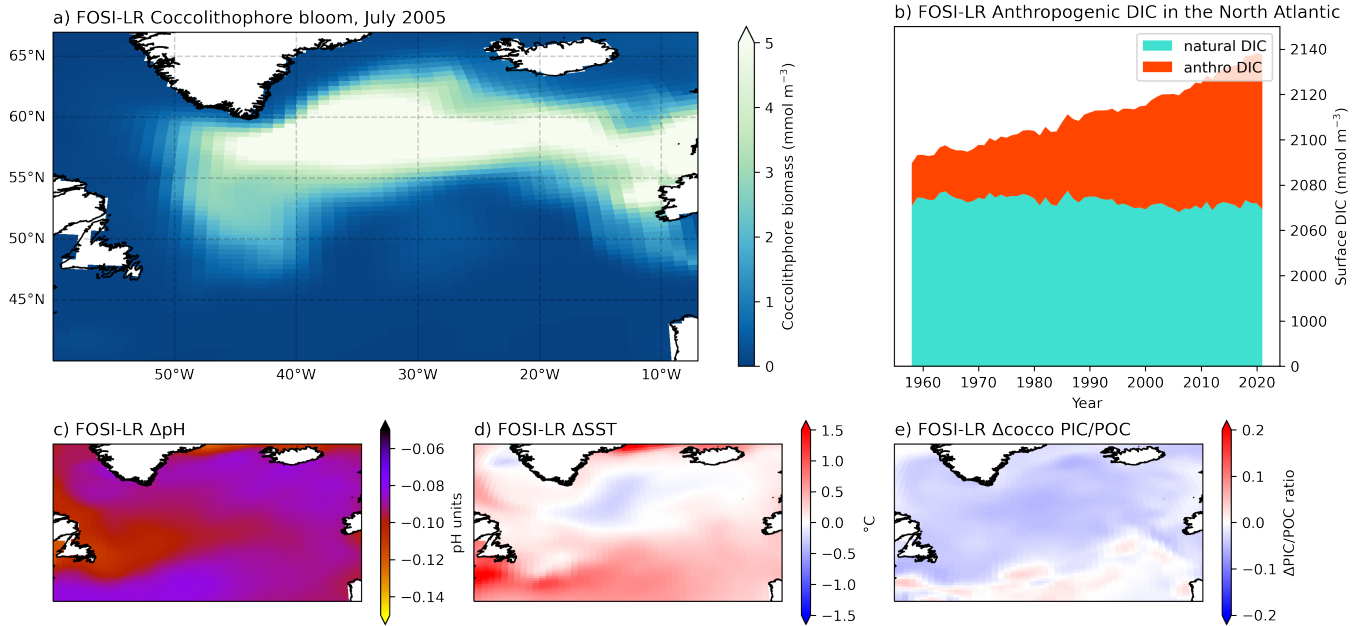


Figure S9: Ocean acidification and warming influences North Atlantic coccolithophores in FOSI-LR. Panel a shows an example of a modeled coccolithophore bloom in the North Atlantic region during July, 2005 of the FOSI-LR. Panel b shows a time series of surface (top 10 m) dissolved inorganic carbon (DIC) concentration in this region (60°W to 7.6°E , 38.8°N to 67.6°N) over the course of the simulation; note that the y-axis ticks on panel b are not evenly spaced. Panels c, d and e show changes over the period 1958 to 2021 (last 5 years-mean minus first 5 years-mean) in pH, sea surface temperature (SST), and the coccolithophore particulate inorganic carbon to particulate organic carbon (PIC/POC) ratio, respectively. Figure 13 in the main text is the same, but for the FOSI-HR.

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