



1 **Quantifying spatiotemporal variability in zooplankton dynamics in the Gulf of Mexico with**
2 **a physical-biogeochemical model**

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16 **Abstract**

17 Zooplankton play an important role in global biogeochemistry and their secondary production
18 supports valuable fisheries of the world's oceans. Currently, zooplankton abundances cannot be
19 estimated using remote sensing techniques. Hence, coupled physical-biogeochemical models
20 (PBMs) provide an important tool for studying zooplankton on regional and global scales.
21 However, evaluating the accuracy of zooplankton abundance estimates from PBMs has been a
22 major challenge as a result of sparse observations. In this study, we configure a PBM for the Gulf
23 of Mexico (GoM) from 1993-2012 and validate the model against an extensive combination of in
24 situ biomass and rate measurements including total mesozooplankton biomass, size-fractionated
25 mesozooplankton biomass and grazing rates, microzooplankton specific grazing rates, surface
26 chlorophyll, deep chlorophyll maximum depth, phytoplankton specific growth rates, and net
27 primary production. Spatial variability in mesozooplankton biomass climatology observed in a
28 multi-decadal database for the northern GoM is well resolved by the model with a statistically
29 significant ($p < 0.01$) correlation of 0.90. Mesozooplankton secondary production for the region
30 averaged $66 \pm 8 \text{ mt C yr}^{-1}$ equivalent to approximately 10% of NPP and ranged from 51 to 82 mt
31 C yr^{-1} . In terms of diet, model results from the shelf regions suggest that herbivory is the dominant
32 feeding mode for small mesozooplankton (<1-mm) whereas larger mesozooplankton are primarily
33 carnivorous. However, in open-ocean, oligotrophic regions, both groups of mesozooplankton have
34 proportionally greater reliance on heterotrophic protists as a food source. This highlights the
35 important role of microbial and protistan food webs in sustaining mesozooplankton biomass in the
36 GoM which serves as the primary food source for early life stages of many commercially-
37 important fish species, including tuna.



38 **1. Introduction**

39 Within marine pelagic ecosystems zooplankton function as an important energy pathway between
40 the base of the food chain and higher trophic levels such as fish, birds, and mammals (Landry et
41 al., 2019; Mitra et al., 2014). Zooplankton also have a well-documented impact on chemical
42 cycling in the ocean (Buitenhuis et al., 2006; Steinberg and Landry, 2017; Turner, 2015). The
43 ecological roles of zooplankton, however, are varied and taxon-dependent. Globally, protistan
44 grazing is the largest source of phytoplankton mortality, accounting for 67% of daily
45 phytoplankton growth (Landry and Calbet, 2004). Protistan zooplankton function primarily within
46 the microbial loop leading to efficient nutrient regeneration in the surface ocean (Sherr and Sherr,
47 2002; Strom et al., 1997). By contrast, mesozooplankton contribute significantly less to
48 phytoplankton grazing pressure consuming an estimated 12% of primary production (PP) globally
49 (Calbet, 2001) yet strongly impact the biological carbon pump. In addition to top-down grazing
50 pressure on phytoplankton, mesozooplankton impact the biological carbon pump through
51 production of sinking fecal pellets, consumption of sinking particles and active carbon transport
52 during diel vertical migration (Steinberg and Landry, 2017; Turner, 2015). While contributing
53 notably less to phytoplankton grazing pressure than protists, herbivorous mesozooplankton are
54 important to study as they are often associated with shorter food chains that enable efficient energy
55 transfer from primary producers to higher trophic levels of particular societal interest such as
56 economically valuable fish species and/or their planktonic larvae.

57 Zooplankton populations have been identified as being vulnerable to impacts of a warming ocean
58 (Caron and Hutchins, 2013; Pörtner and Farrell, 2008; Straile, 1997), through both impacts of
59 temperature on metabolic rates (Ikeda et al., 2001; Kjellerup et al., 2012) and thermal stratification-
60 driven alterations in food web structure (Landry et al., 2019; Richardson, 2008). Studies aimed at
61 monitoring and predicting zooplankton populations are therefore critical to understanding the first-
62 order effects of a warming ocean on marine ecosystems given the importance of secondary
63 production and the impact zooplankton have on biogeochemical cycling. Despite their importance,
64 historically zooplankton have been sampled with limited temporal and spatial resolution. While
65 remote sensing has provided an enormous advancement in observing ocean hydrodynamics and
66 phytoplankton variability, zooplankton abundance cannot currently be estimated from space. Thus
67 numerical models provide a unique oceanographic research tool for studying zooplankton on basin
68 and global scales (Buitenhuis et al., 2006; Sailley et al., 2013; Werner et al., 2007). Evaluating the



69 accuracy of zooplankton abundance estimates from numerical models, such as three-dimensional
70 physical-biogeochemical ocean models (PBMs), has been a major challenge in previous modeling
71 studies as a result of sparse ship-based observations in most regions (Everett et al., 2017).
72 Consequently, zooplankton dynamics have been under studied and under validated in PBMs.
73 Instead, PBMs are typically validated predominately against surface chlorophyll (Chl) from
74 remote sensing (Doney et al., 2009; Gregg et al., 2003; Xue et al., 2013).

75 In most marine environments, phytoplankton net growth rates and hence biomass are determined
76 primarily by the imbalance between phytoplankton growth and zooplankton grazing (Landry et
77 al., 2009). PBMs can accurately predict phytoplankton standing stock (i.e. compare well with
78 satellite Chl observations) despite being driven by the wrong underlying dynamics leading to major
79 errors in model estimates of secondary production and nutrient cycling (Anderson, 2005; Franks,
80 2009). For instance, parameter tuning using only surface Chl as a validation metric can allow broad
81 patterns in phytoplankton biomass to be reproduced even with gross over- or underestimation of
82 phytoplankton turnover times. Similarly, even a model that is validated against satellite Chl and
83 net primary production might completely misrepresent the proportion of phytoplankton mortality
84 mediated by zooplankton groups, leading to inaccurate estimates of secondary production. Hence,
85 validating PBMs against zooplankton dynamics is key to increasing confidence in model solutions.
86 The importance of this validation is further witnessed when considering the impact zooplankton
87 have on the behavior of biogeochemical models (Everett et al., 2017). Differences in simulated
88 zooplankton communities expressed through the number of functional types, various mathematical
89 grazing functional responses, and the arrangement of transfer linkages have been shown to have
90 substantial impacts on simple and complex biogeochemical model solutions (Gentleman et al.,
91 2003; Gentleman and Neuheimer, 2008; Mitra et al., 2014; Murray and Parslow, 1999; Saille et
92 al., 2013).

93 The Gulf of Mexico (GoM) is a particularly suitable study region for examining zooplankton
94 dynamics with PBMs. In the northern and central Gulf, zooplankton abundance has been
95 extensively measured for over three decades (1982-present) by the Southeast Area Monitoring and
96 Assessment Program (SEAMAP). Within the SEAMAP dataset, measured zooplankton abundance
97 exhibits strong spatiotemporal variability, due to complex physical circulation features within the
98 GoM. The circulation in regions off the shelf is characterized by substantial upper layer mesoscale



99 activity driven primarily by the energetic Loop Current (Forristall et al., 1992; Maul and Vukovich,
100 1993; Oey et al., 2005). In contrast, coastal and shelf circulation patterns are predominantly wind-
101 driven (Morey et al., 2003a, 2013). Freshwater discharged by the Mississippi River and other
102 smaller rivers is frequently entrained offshore by shelf break interaction with mesoscale features
103 (e.g., anti-cyclonic loop current eddies), leading to strong horizontal and vertical gradients in
104 physical and biogeochemical quantities (Morey et al., 2003b). These gradients overlap with the
105 SEAMAP study region resulting in zooplankton biomass sample collection across
106 biogeochemically heterogeneous and “patchy” environments which provides a powerful model
107 constraint. For instance, Chl can range across approximately three orders-of-magnitude ($\sim 0.01 -$
108 10 mg Chl m^{-3}) from oligotrophic to eutrophic waters. Similarly, mesozooplankton ($\geq 202 \mu\text{m}$)
109 biomass is highly variable ranging from $0.1 - 160 \text{ mg C m}^{-3}$ in the SEAMAP dataset.

110 Several PBM studies have been conducted in the GoM, all primarily examining nutrient and
111 phytoplankton dynamics. Early work by Fennel et al. (2011) examined phytoplankton dynamics
112 on the Louisiana and Texas continental shelf, concluding that loss terms (e.g., grazing) rather than
113 growth rates dictated accumulation rates of phytoplankton biomass. With the same biogeochemical
114 model, Xue et al. (2013) conducted the first gulf-wide PBM study to investigate broad seasonal
115 biogeochemical variability and used the model to constrain a nitrogen budget for the shelf. More
116 recently, Gomez et al. (2018) implemented a biogeochemical model with multiple phytoplankton
117 and zooplankton functional types to gain a more detailed understanding of nutrient limitation and
118 phytoplankton dynamics in the GoM. To examine phytoplankton seasonality and biogeography in
119 the oligotrophic Gulf, Damien et al. (2018) validated a PBM based on a unique subsurface
120 autonomous glider dataset. Together, these studies have demonstrated the utility of PBMs for
121 investigating the GoM lower trophic level and have also highlighted the key role zooplankton play
122 in the ecosystem. Specifically, both Fennel et al. (2011) and Gomez et al. (2018) identified the
123 importance of zooplankton in modulating the simulated seasonal patterns of phytoplankton
124 biomass, emphasizing the importance of top-down control on the shelf. Although results on the
125 simulated zooplankton community were not presented, Damien et al. (2018) noted that biotic
126 processes such as grazing pressure, are “essential to fully understanding the functioning of the
127 GoM ecosystem.” However, in these studies zooplankton validation is largely absent.



128 In this study, we configured a PBM for the GoM to estimate zooplankton abundance and analyze
129 zooplankton community dynamics. The PBM is forced by three-dimensional hydrodynamic fields
130 from a data assimilative Hybrid Coordinate Ocean Model (HYCOM) hindcast of the GoM
131 (<http://www.hycom.org>). The PBM is based on the biogeochemical model NEMURO (North
132 Pacific Ecosystem Model for Understanding Regional Oceanography; Kishi et al., 2007), which is
133 substantially modified here for application to the GoM. The model is integrated over 20-years
134 (1993-2012) and validated extensively against a combination of remote and in situ measurements
135 including total mesozooplankton biomass, size-fractionated mesozooplankton biomass and
136 grazing rates, microzooplankton specific grazing rates, surface Chl, deep Chl maximum depth,
137 phytoplankton specific growth rates, and net primary production. The goals of this study were to:
138 1) develop and validate a PBM to estimate mesozooplankton abundance in the GoM, 2)
139 characterize the spatiotemporal variability in mesozooplankton dietary composition, and 3)
140 quantify regional mesozooplankton secondary production. We focus primarily on the oligotrophic,
141 open ocean GoM where prey (i.e. zooplankton) availability may be limiting for fish, their larvae,
142 and other higher trophic levels.

143 **2 Methods and data**

144 **2.1 Ocean model framework**

145 **2.1.1 Biogeochemical model description**

146 The biogeochemical model for this study is based on NEMURO (Kishi et al., 2007) but has been
147 modified and parameterized to more accurately reflect the ecology of the GoM. NEMURO is a
148 concentration-based lower trophic level ecosystem model originally developed and parameterized
149 for the North Pacific. Like most marine biogeochemical models, it is structured around simplified
150 representations of the lower food web originating from earlier nutrient-phytoplankton-zooplankton
151 models (Fasham et al., 1990; Franks, 2002; Riley, 1946; Steele and Frost, 1977). Complexity is
152 added through additional state variables and transfer functions with the specific goal of resolving
153 dynamics within the nutrient, phytoplankton, and zooplankton pools. In total, NEMURO has
154 eleven state variables: six non-living state variables – nitrate (NO_3), ammonium (NH_4), dissolved
155 organic nitrogen (DON), particulate organic nitrogen (PON), silicic acid ($\text{Si}(\text{OH})_4$), and particulate
156 silica (Opal); two phytoplankton state variables – small (SP) and large phytoplankton (LP); and
157 three zooplankton state variables – small (SZ), large (LZ) and predatory zooplankton (PZ).



158 Each biological state variable in NEMURO is an aggregated representation of taxonomically
159 diverse plankton groups that function similarly in the ecosystem. The phytoplankton community
160 in NEMURO is modeled as two functional types of obligate autotrophs: small phytoplankton (SP,
161 predominantly cyanobacteria and picoeukaryotes in the GoM) and large phytoplankton (LP,
162 diatoms). Small zooplankton (SZ) represent heterotrophic protists. Metazoan zooplankton are
163 divided into suspension-feeding mesozooplankton (LZ) and predatory zooplankton (PZ), which
164 also feed on LP and SZ. Here we assume that LZ and PZ are non-migratory. Heterotrophic bacteria
165 are implicitly represented in NEMURO by temperature-dependent decomposition rates, which
166 represent nitrification and remineralization. Sinking in NEMURO is restricted to PON and Opal
167 pools, and benthic processes are not included. Here, because of the large shelf area in the GoM,
168 we implemented a simple diagenesis of PON/OP to NO_3/SiO_4 and removal of PON/OP through
169 sedimentation, where 1% of the flux sinking out of bottom cell was removed and 10% converted
170 back into NO_3/SiO_4 . However, we found that this had no significant impact on the model.
171 NEMURO uses nitrogen as a model “currency” since it is the major limiting macronutrient in
172 much of the ocean. Silica is also included as a potentially co-limiting nutrient for diatoms. For
173 more details on the specific processes represented and the interactions between state variables in
174 NEMURO, we direct readers to Kishi et al. (2007). All model equations are provided in the
175 Supplement to this manuscript.

176 NEMURO was chosen for the present study because it distinguishes SZ, LZ, and PZ, permitting a
177 detailed analysis of dynamics within the GoM zooplankton community and allowing for
178 investigation of multiple zooplankton functional types. In initial GoM simulations, we found that
179 default NEMURO parameterizations for the North Pacific (Kishi et al., 2007) substantially
180 overestimated both surface Chl and mesozooplankton biomass relative to observations. To a first
181 order, we attribute these differences to: 1) substantially higher temperatures in the GoM compared
182 with the North Pacific, which significantly increase decomposition and growth rates in the model
183 resulting in higher nutrient recycling and sustained elevated standing stocks of phytoplankton and
184 zooplankton near the surface, and 2) distinct differences in taxonomic composition of the
185 phytoplankton and zooplankton communities between the GoM and North Pacific with significant
186 differences in key parameter values associated with growth and grazing. Justification for each
187 parameter modification and steps of the model tuning process are outlined in Supplement S2, with



188 a summary of parameter values in **Table S2**. Biogeochemical model forcing, initial, and open
189 boundary conditions are also outlined in Supplement **S1**.

190 **2.1.2 Modifications to the original biogeochemical model**

191 To improve realism for application to the GoM, a total of five structural changes were made to the
192 original NEMURO transfer functions. First, we removed the SP to LZ grazing pathway. The
193 original SP state variable for the North Pacific represents nanophytoplankton (e.g.
194 coccolithophores), which can be important prey of copepods and other mesozooplankton. In the
195 GoM, however, cyanobacteria and picoeukaryotes (too small for direct feeding by most
196 mesozooplankton) comprise much of the phytoplankton biomass and hence are represented as SP
197 in our model. In addition to adding realism, this change in direct trophic connection between SP
198 and LZ allowed the model to produce a more realistic LP dominated phytoplankton community on
199 the shelf (see Discussion).

200 Next, quadratic mortality was replaced with linear mortality for all biological state variables with
201 the exception of predatory zooplankton (PZ). In biogeochemical models, quadratic mortality is
202 often used for numerical stability and/or to represent implicit loss terms to an un-modeled parasite
203 or predator that may covary in abundance with its prey (e.g. viral lysis of phytoplankton or
204 predation by un-modeled higher predators). However, grazing mortality is explicitly modeled in
205 NEMURO and viral mortality is generally not a substantial loss term for bulk phytoplankton
206 (Brum et al., 2014; Staniewski and Short, 2018). Quadratic mortality was retained for PZ, to
207 account for predation pressure of un-modeled planktivorous fish. We found that removal of
208 quadratic mortality for all other biological state variables led to more realistic mesozooplankton
209 biomass in the oligotrophic region (see Discussion).

210 The default ammonium inhibition term and light limitation functional form was replaced with a
211 more widely adopted parameterization. The exponential ammonium inhibition term in the nitrate
212 limitation function was replaced with the term described by Parker (1993), as has been done in
213 previous PBM studies (Fennel et al., 2006) due to the non-monotonic behavior of the default
214 NEMURO ammonium inhibition term. The default light limitation functional form was replaced
215 with the Platt et al. (1980) functional form that explicitly parameterizes photoinhibition. This
216 formulation is implemented in newer versions of NEMURO, such as the code used in the Regional



217 Ocean Modeling System (ROMS) NEMURO biogeochemical package. Finally, to account for
218 photoacclimation and more accurately simulate Deep Chlorophyll Maximum (DCM) dynamics,
219 we replaced the constant C:Chl parameter with a variable C:Chl module where ratios for SP and
220 LP were allowed to vary based on the formulation described by Li et al. (2010), which considers
221 both light and nutrient limitation (see Supplemental). Herein, “default” NEMURO includes the
222 modified ammonium inhibition, light formulation and variable C:Chl model.

223 In total NEMURO has 75 parameters, 25 of which were modified in the present study. To tune
224 these parameters, we evaluated the model based on three observational benchmarks: surface Chl
225 estimated from seaWIFS, depth averaged mesozooplankton biomass from the SEAMAP dataset,
226 and DCM depth from the SEAMAP dataset. Chl and mesozooplankton biomass were chosen to
227 evaluate basin scale variability in plankton biomass while the DCM depth was chosen to evaluate
228 the vertical structure of the simulated ecosystem. We also considered expected patterns of size
229 structured phytoplankton community composition (i.e. SP:LP ratio), relative magnitudes of total
230 zooplankton grazing contributions, and the magnitude of loss terms for phytoplankton (grazing,
231 mortality, respiration, and excretion). Initial model tuning was carried out in an idealized one-
232 dimensional model before being implemented into the PBM. We outline each parameter change,
233 justification, and the resulting impact on the ecosystem benchmarks simulated by the one-
234 dimensional model in Supplement **Table S1**. Where possible, we modified parameters in groups
235 so that relative changes were consistent throughout the model (e.g. doubling all zooplankton
236 mortality terms). We also conducted a parameter sensitivity analysis to identify impacts of
237 parameter changes on the final three-dimensional PBM solution (herein referred to as NEMURO-
238 GoM) (Section 2.6).

239 **2.1.3 Description of the offline numerical environment**

240 To run large numbers of three-dimensional simulations efficiently for basin scale tuning, the
241 NEMURO-GoM was run offline using the MITgcm offline tracer advection package, which was
242 selected for this study as it has convenient packages for running offline simulations (McKinley et
243 al., 2004). That is, the dynamical equations of motion are not computed during the NEMURO-
244 GoM integration, but rather the physical prognostic variables (i.e., temperature, salinity, and three-
245 dimensional velocity fields) are prescribed from daily-averaged flow fields saved from a previous
246 hydrodynamic model integration. This allows the recycled use of flow fields leaving only the tracer



247 equations to be computed. In the offline MITgcm package, the prognostic variables provide input
248 to an advection scheme and mixing routine that conservatively handles offline advection and
249 diffusion of the biogeochemical tracer fields. MITgcm has many options for linear and non-linear
250 advection schemes. Here we use a 3rd order direct space time flux limiting scheme. Sub grid-scale
251 mixing of the biogeochemical fields is handled offline through the nonlocal K-Profile
252 Parameterization (KPP) package based on mixing schemes developed by Large et al. (1994). For
253 more information about the MITgcm packages, we direct readers to the MITgcm manual
254 (<http://mitgcm.org/>).

255 Advantages of running PBMs in an offline environment include: 1) the physical time step in an
256 offline environment is no longer bound by the dynamical Courant–Friedrichs–Lewy numerical
257 stability criterion, allowing for longer time steps and fewer iterations; and 2) momentum equations
258 are not computed during the integration. Instead, the stability of the tracer advection scheme and
259 time scales needed to resolve biological/physical processes of interest set the limits on the time
260 steps and prescription frequencies of flow fields. When the physical time step is shorter than the
261 flow field prescription frequency, a simple linear interpolation of the flow fields is performed
262 inside the PBM between time steps. It is important to note that offline simulations of tracer
263 advection have been found to closely resemble online runs (that is, computed together with the
264 integration of the hydrodynamic model’s prognostic equations) when the three-dimensional flow
265 fields are prescribed at a frequency that is at or below the inertial period for a region (Hill et al.,
266 2005).

267 In the present study, the NEMURO-GoM time step (30 minutes) is an order of magnitude greater
268 than the hydrodynamic model’s (H-GoM, described in Section 2.1.4) baroclinic time step (120
269 seconds). For reference, the 20-year H-GoM simulation that supplied flow fields for the offline
270 NEMURO-GoM took a total of ~76 days to run to completion on 64 parallel cores. These time
271 requirements would increase considerably with the 11 additional biogeochemical tracers used in
272 NEMURO. In contrast, NEMURO-GoM including the 11 added tracers, ran significantly faster,
273 taking a total of ~50 h on 80 parallel cores. While computationally advantageous, it is important
274 to note that offline simulations inherently have greater input and output (I/O) demands that can
275 become bottlenecks in some applications.



276 **2.1.4 Description of the ocean dynamical fields**

277 The NEMURO-GoM is “forced” by daily averaged three-dimensional velocity, temperature, and
278 salinity fields from a preexisting 20-year (1993-2012) HYCOM (HYbrid Coordinate Ocean
279 Model) (Chassignet et al., 2003) regional GoM hindcast (H-GoM). H-GoM is based on version
280 2.2.99B of the HYCOM code, originally provided by the Naval Oceanographic Office
281 (NAVOCEANO) Major Shared Resource Center. H-GoM was run at 1/25th (~4 km) degree
282 horizontal resolution with 36 vertical hybrid coordinate layers and assimilated historic, in situ, and
283 satellite observations. The domain encompasses the entire GoM and extends south of the Mexican-
284 Cuba Yucatan channel to 18 °N and as far east as 77 °W (**Fig. 1**). Further details on H-GoM
285 (experiment ID: GOMu0.04/expt_50.1) including details on model forcing and the main model
286 configuration file (i.e. blkdat.input_501) can be found at <https://www.hycom.org>.

287 The H-GoM flow fields were mapped from the HYCOM native vertical coordinate to z-levels used
288 by the MITgcm. The NEMURO-GoM was configured for 29 vertical z-levels in MITgcm (10-m
289 intervals from 0-150 m, 25-m intervals from 150-300 m, 50-m intervals from 300-500m, and 1000
290 m, 2000 m, ~4000 m). Mapping is performed by computing total zonal and meridional transports
291 across the lateral boundaries of each MITgcm grid cell (e.g., 0-10 m bin; which may include
292 multiple HYCOM layers) and then dividing by the area of the respective cell face. This vertical
293 mapping approach is consistent as both HYCOM and MITgcm use an Arakawa C-grid orientation
294 for model variables. The H-GoM bathymetry was adjusted such that no partial cells existed in the
295 domain to avoid thin cells. The continuity equation was subsequently used to calculate vertical
296 velocities. The use of transports in this approach ensures conservation and approximately identical
297 profiles of vertical velocity to those in H-GoM fields. For mapping of temperature and salinity
298 fields (used in the KPP mixing routine and for scaling biological temperature dependent rates) a
299 simple linear interpolation was performed.

300

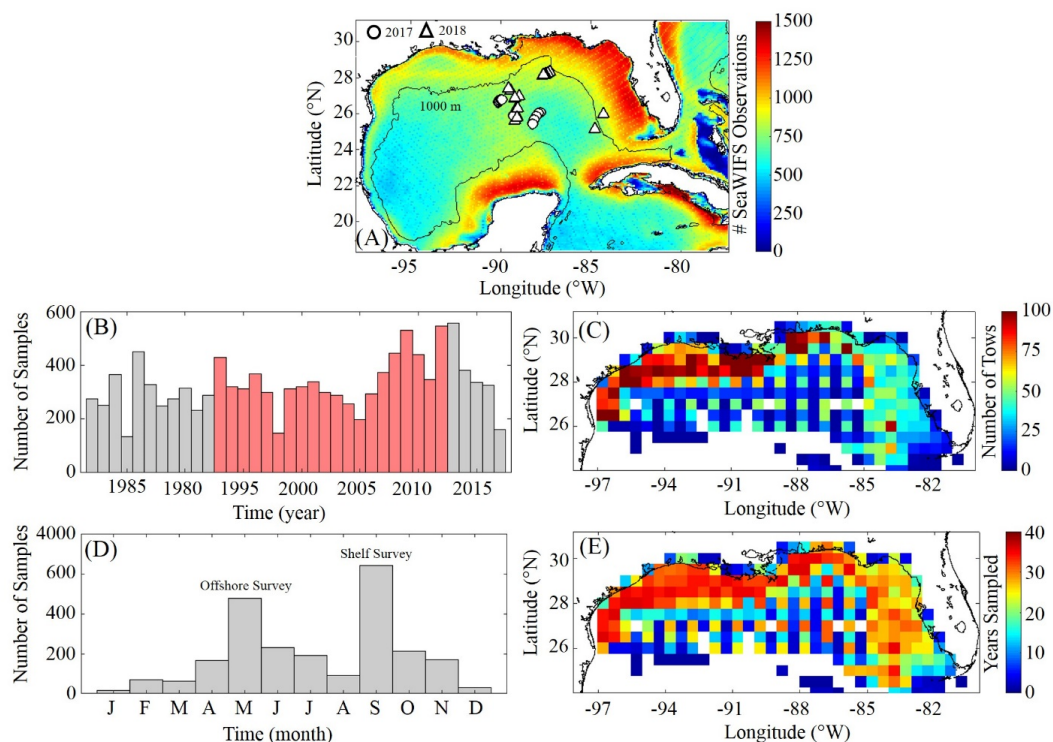
301 **2.2 Model validation**

302 **2.2.1 SeaWIFS observations used for model validation**

303 A benchmark for surface Chl was determined using the Sea-Viewing Wide Field-of-View Sensor
304 (SeaWIFS) product from the Ocean Biology Processing Group (OBPG) of the National
305 Aeronautics and Space Administration (NASA). The product used here is the mapped, level-3,
306 daily, 9-km resolution product from 4 September 1997 to 10 December 2010 processed according



307 to the algorithm of Hu et al. (2012). To compute model-data point-to-point comparisons, we take
308 the corresponding daily averaged simulated surface Chl field and interpolate to the SeaWiFS grid
309 before applying the daily cloud coverage mask corresponding to the matching SeaWiFS image. In
310 total 4,291 daily images consisting of 22,244,513 non-zero Chl cell values (herein referred to
311 seaWiFS measurements) were used to validate the PBM. Approximately 500-1200 daily model-
312 data point-to-point comparisons were made for each SeaWiFS grid cell.



313

314 **Figure 1 (A-E):** Spatial and temporal coverage of all observational data sets used for model
315 validation. Total number of non-zero SeaWiFS values from the level 3 product from 4 September
316 1997 to 10 December, 2010 along with cruise sample locations collected during May, 2017
317 (circles) and 2018 (triangles) (A). Total annual sampling of the SEAMAP surveys from 1983-2017
318 (B) with samples overlapping with the PBM simulation period denoted in red. Total sample density
319 within each $0.5^\circ \times 0.5^\circ$ box (C). Total seasonal sampling (D). Number of years with at least one
320 sample (E). 1000 m isobaths and coastline are denoted by black continuous lines.



321 2.2.2 SEAMAP observations used model validation

322 To evaluate model mesozooplankton biomass estimates, we used zooplankton biomass data
323 collected during SEAMAP surveys in the northern and central GoM. In total, 11,781 zooplankton
324 tows were collected from 1983-2017 with two main annual surveys consisting of a spring offshore
325 and fall shelf sampling grid (**Fig. 1**). These samples were used to generate a climatology which
326 was used to compare with simulated mesozooplankton climatology. On average, SEAMAP
327 surveys collected approximately 300 samples per year with a specific sampling array in the
328 offshore surveys and more general spatial sampling coverage on the shelf. Of these samples, 6,835
329 were used for direct point-to-point model-data comparisons. Zooplankton biomass samples were
330 collected using standard gear consisting of a 61 cm diameter bongo frame fitted with two 333 μm
331 mesh nets. This gear is fished in a double-oblique tow pattern from the surface down to 200 m or
332 5 m off the bottom and back to the surface. During 82 tows in nearshore and oligotrophic regions,
333 additional samples were collected using a 202 μm mesh net concurrently with the standard 333 μm
334 mesh net. Of these samples roughly half were collected in the oligotrophic GoM. The average ratio
335 between 333 and 202 samples (0.5093 ± 0.12) was used to convert biomass measurements from
336 the 333 μm mesh samples so that direct comparisons could be made with simulated
337 mesozooplankton biomass estimates. In this study we consider SZ size to be $< 200 \mu\text{m}$, LZ size to
338 be 0.2-1 mm, and PZ size to be 1-5 mm. Zooplankton biomasses from SEAMAP surveys were
339 originally quantified as displacement volumes (DV). Carbon mass (CM) equivalents were
340 subsequently calculated as $\log_{10}(\text{CM}) = (\log_{10}(\text{DV}) + 1.434)/0.820$ (Wiebe, 1988; Moriarty and
341 O'Brien, 2013). CM estimates were converted to model units (mmol N m^{-3}) assuming Redfield
342 C:N ratio. Simulated mesozooplankton model fields were similarly depth integrated to the bottom
343 or 200 m to generate the model mesozooplankton biomass climatology or to the sample depth
344 when performing point-to-point comparisons.

345 Vertical depth profiles of Chl were also approximated at standard stations during SEAMAP
346 surveys using a SeaBird WETStar pumped fluorometer attached to a CTD. These profiles were
347 used to determine the depths of the fluorescence maxima, which were then compared directly to
348 simulated DCM depths at corresponding times and locations. In total, 2,435 profiles were taken
349 from 2003-2012, with 1,052 profiles overlying bottom depths >1000 m. Profiles were available
350 for earlier SEAMAP surveys; however, no standard QA/QC protocol for fluorometer data was in



351 place prior to 2003. Model-data agreement for DCM magnitude could not be investigated as the
352 fluorometer was not calibrated before each cruise.

353 **2.2.3 Process rate measurements used for model validation**

354 Although in situ rate measurements are made much less frequently than biological standing stock
355 measurements, they offer very powerful constraints for validating the internal dynamics of a
356 biogeochemical model (Franks, 2009). Consequently, we made phytoplankton and zooplankton
357 rate measurements on two cruises in the open ocean GoM in May 2017 and 2018 and used these
358 measurements to validate the model (**Fig. 1A**). Since the cruise sampling does not overlap with
359 our NEMURO-GoM simulation period, we sampled the model at corresponding locations and
360 times of the year for all 20 years of the simulation to investigate model-data comparisons. On these
361 cruises, we utilized a quasi-Lagrangian sampling scheme to investigate plankton dynamics in the
362 oligotrophic GoM. Two drifting arrays (one sediment trap array and one in situ incubation array)
363 were then deployed to serve as a moving frame of reference during ~4-day studies (“cycles”)
364 characterizing the water parcel (Landry et al., 2009; Stukel et al., 2015). During these cycles, we
365 measured daily profiles of Chl, photosynthetically active radiation, phytoplankton growth rates
366 and productivity, protistan grazing rates, and size-fractionated mesozooplankton biomass and
367 grazing rates.

368 Protistan grazing rates were measured using the two-point, “mini-dilution” variant of the
369 microzooplankton grazing dilution method (Landry et al., 1984, 2008; Landry and Hassett, 1982).
370 Briefly, one 2.8-L polycarbonate bottle was gently filled with whole seawater taken from six
371 depths (from the surface to the depth of the mixed layer). A second 2.8-L bottle was then filled
372 with 33% whole seawater and 67% 0.2- μm filtered seawater. Both bottles were then placed in
373 mesh bags and incubated in situ at natural depths for 24 h. These experiments were conducted on
374 each day of the ~4-day cycle. After 24 h, the bottles were retrieved, filtered onto glass fiber filters,
375 and Chl concentrations were determined using the acidification method (Strickland and Parsons.,
376 1972). Net growth rates ($k = \ln(\text{Chl}_{\text{final}}/\text{Chl}_{\text{init}})$) in each bottle were then determined relative to initial
377 Chl samples. Phytoplankton specific mortality rates resulting from the grazing pressure of protists
378 were calculated as $m = (k_d - k_0)/(1-0.33)$, where k_d is the growth rate in the dilute bottle and k_0 is
379 the growth rate in the control bottle. Phytoplankton specific growth rates were calculated as $\mu = k_0$
380 + m . For additional details, see Landry et al. (2016) and Selph et al. (2016). Phytoplankton net



381 primary production was quantified at the same depths by $\text{H}^{13}\text{CO}_3^-$ uptake experiments. Triplicate
382 2.8-L polycarbonate bottles and a fourth “dark” bottle were spiked with $\text{H}^{13}\text{CO}_3^-$ and incubated in
383 situ for 24 h at the same sampling depths as for the dilution experiments. Samples were then
384 filtered, and the $^{13}\text{C}:^{12}\text{C}$ ratios of particulate matter were determined by isotope ratio mass
385 spectrometry.

386 Size-fractionated mesozooplankton biomass and grazing rates were determined from daily day-
387 night paired oblique ring-net tows (1-m diameter, 202- μm mesh) to a depth of 110 m. Upon
388 recovery, the sample was anesthetized using carbonated water, split using a Folsom splitter,
389 filtered through a series of nested sieves (5, 2, 1, 0.5, and 0.2 mm), filtered onto preweighed 200-
390 μm Nitex filters, rinsed with isotonic ammonium formate to remove sea salt, and flash frozen in
391 liquid nitrogen. In the lab, defrosted samples were weighed for total wet weight, and subsampled
392 in duplicate (wet weight removed) for gut fluorescence analyses. The remaining wet sample was
393 dried and subsequently reweighed and combusted for CHN analyses to determine total dry weight
394 and C and N biomasses. Gut fluorescence subsamples were homogenized using a sonicating tip,
395 extracted in acetone, and measured for Chl and phaeopigments using the acidification method.
396 The phaeopigment concentrations in the zooplankton guts were the basis for calculated grazing
397 rates using gut turnover times based on temperature relationships for mixed zooplankton
398 assemblages. For additional details, see Décima et al. (2011) and Decima et al. (2016).

399 **2.3 Description of the parameter sensitivity experiments**

400 After validating the PBM, a parameter sensitivity analysis consisting of 18 numerical experiments
401 was conducted to evaluate how robust the final model solution was to parameter changes. For
402 each experiment, the PBM was configured to simulate four years starting in January 2002. This
403 time period was concurrent with SeaWIFS and SEAMAP sample coverage. Parameter sensitivity
404 experiments were initialized from our standard NEMURO-GoM run at 1 January 2002. The PBM
405 with each parameter change(s) was then allowed to spin up for one year. The last three years (i.e.
406 2003-2005) were subsequently used for the parameter sensitivity analysis. Direct point-to-point
407 comparisons were made between model estimates and observations at corresponding sample times
408 and locations during the model integration. In total, 4,646,459 SeaWIFS Chl measurements, 741
409 SEAMAP mesozooplankton tows, and 481 SEAMAP fluorescence profiles were used to evaluate
410 model sensitivity. To better capture relative differences between model and observations across



411 coastal and oligotrophic GoM regions, a \log_{10} transformation was applied to Chl and
412 mesozooplankton biomass model-data comparisons before calculating Taylor and Target diagram
413 statistics. Point-to-point model-data comparisons were also made using the 20-year PBM output,
414 which included all available data (i.e. 22,244,513 SeaWIFS Chl measurements, 6,835 SEAMAP
415 mesozooplankton tows, and 2,435 SEAMAP fluorescence profiles). Configurations for each
416 parameter sensitivity experiment are outlined in **Table S3**.

417 **3.0 Results**

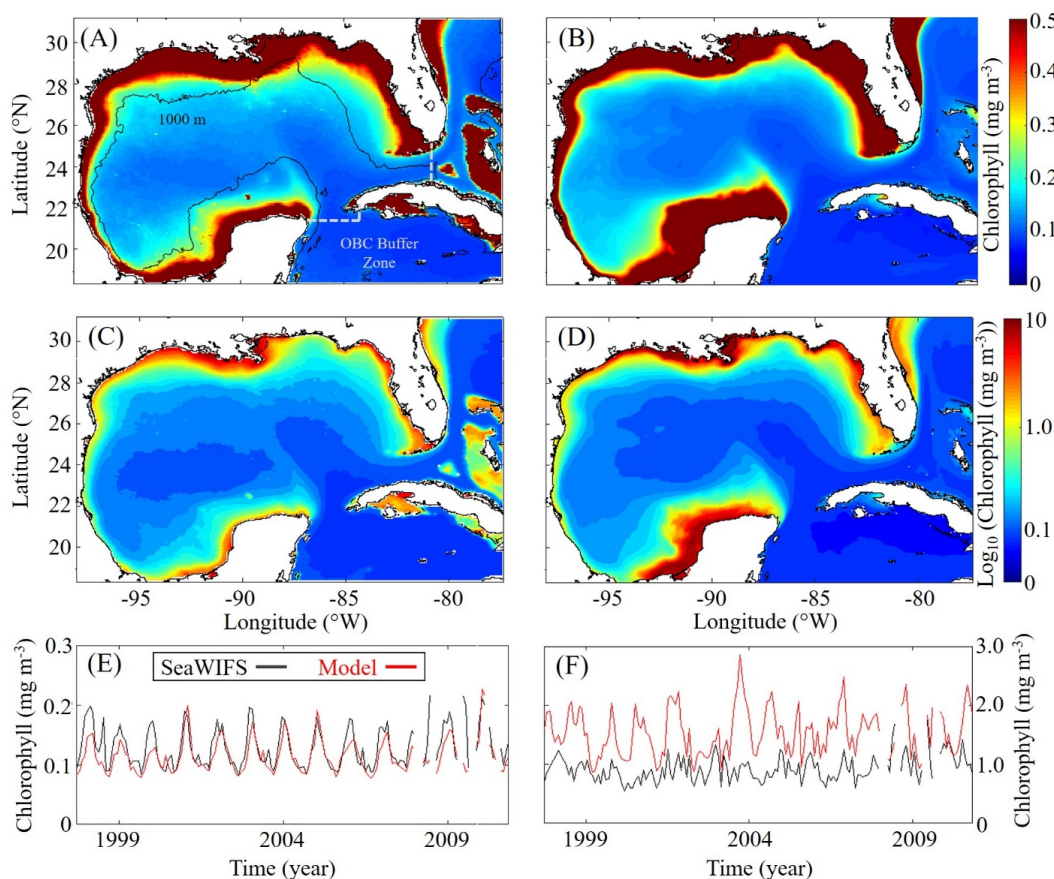
418 **3.1 Regional phytoplankton biomass model-data comparisons**

419 Model surface Chl estimates demonstrate strong agreement with satellite observations (**Fig. 2**).
420 Spatial covariance between SeaWIFS climatology and model surface Chl climatology (calculated
421 with daily cloud cover mask applied) is found to be statistically significant ($p < 0.01$) with a
422 correlation (ρ) of 0.72. When model estimates are compared to all 22,244,513 SeaWIFS
423 measurements at corresponding times and locations (i.e. daily grid cell pairs), we find a ρ value of
424 0.50 ($p < 0.01$). To facilitate more detailed model-data comparisons, the GoM domain was divided
425 into an oligotrophic region (≥ 1000 m bottom depth) and a shelf region (< 1000 m bottom depth).
426 In the oligotrophic region, the correlation between model-data daily grid cell pairs is significant
427 but weak ($\rho = 0.17$, $p < 0.01$) as a result of relatively low large-scale spatial variability, and hence
428 dominance at the mesoscale. However, bias is quite low (-0.014 mg Chl m^{-3}) equivalent to 10%
429 of the observed mean. In the shelf region, the correlation is higher ($\rho = 0.47$, $p < 0.01$) yet the bias
430 is greater ($+0.90$ mg Chl m^{-3}) equivalent to 92% of the mean. Previous GoM studies have
431 determined ρ values based on monthly averages and for reference we calculate them here. Based
432 on 30-day averages we find a ρ value of 0.70 ($p < 0.01$) for the oligotrophic region and 0.26 ($p <$
433 0.01) for the shelf region.

434 In addition to resolving the dominant spatiotemporal variability, the model also captures the
435 amplitude of the seasonal surface Chl signal reasonably well. In the oligotrophic region, the model
436 accurately estimates the observed annual surface Chl minimum (Model: 0.065 ± 0.005 vs.
437 SeaWIFS: 0.065 ± 0.007 mg Chl m^{-3}) while slightly underestimating the observed annual
438 maximum (Model: 0.47 ± 0.15 vs. SeaWIFS: 0.75 ± 0.55 mg Chl m^{-3}). When model estimates for
439 the entire oligotrophic region are taken into account (i.e. not restricted to satellite measurement
440 locations and times), we find the annual minimum develops in early September while the annual



441 maximum develops in late January (**Table 1**). In the shelf region, greater model-data mismatch
442 exists for surface Chl where the model overestimates the observed annual minimum by 15%
443 (Model: 0.23 ± 0.09 vs. SeaWIFS: 0.20 ± 0.07 mg Chl m^{-3}) and the observed annual maximum by
444 102% (Model: 8.09 ± 1.31 vs. SeaWIFS: 4.01 ± 1.23 mg Chl m^{-3}). Here, we find the annual surface
445 Chl seasonal cycle is almost completely out of phase with the oligotrophic region with the annual
446 minimum developing during early February and the annual maximum developing at the end of
447 July (**Table 1**).



448

449 **Figure 2 (A-F):** Comparison of surface chlorophyll (mg m^{-3}) between SeaWIFS observations and
450 model from 4 September 1997 to 10 December 2010. Average SeaWIFS chlorophyll (A). Average
451 model estimated surface chlorophyll (B). Log_{10} of the average SeaWIFS chlorophyll (C). Log_{10} of
452 the average model estimated surface chlorophyll (D). Time series of simulated 30-day average



453 surface chlorophyll (red) and SeaWiFS observations (black) for bottom depths ≥ 1000 m (E) and
 454 bottom depths < 1000 m (F). The 1000 m isobaths and coastline are denoted by black lines.

455 **Table:** Average seasonal minimum and maximum values in the model (1993-2012) and the day
 456 of year in which they occur for surface chlorophyll (mg m^{-3}), depth integrated phytoplankton
 457 biomass (mg C m^{-2}), depth integrated net primary production ($\text{mg C m}^{-2} \text{ d}^{-1}$), depth integrated
 458 mesozooplankton biomass (mg C m^{-2}), and depth integrated mesozooplankton secondary
 459 production ($\text{mg C m}^{-2} \text{ d}^{-1}$) calculated by spatially averaging daily fields over the oligotrophic
 460 region (upper half of table) and shelf region (lower half of table). Day of year values are in the
 461 format “day/month \pm days.”

	Daily Field Value		Day of Year	
	Annual Min.	Annual Max.	Day of Min.	Day of Max.
Diagnostic (Oligotrophic)				
Surface Chlorophyll	0.09 ± 0.005	0.27 ± 0.06	$9/9 \pm 23$	$1/29 \pm 13$
Phytoplankton Biomass	2300 ± 130	3600 ± 140	$12/26 \pm 7$	$4/29 \pm 17$
Net Primary Production	290 ± 70	1000 ± 120	$12/31 \pm 12$	$7/6 \pm 27$
Mesozooplankton Biomass	1000 ± 40	1400 ± 90	$1/1 \pm 4$	$5/19 \pm 18$
Secondary Production	18 ± 4	68 ± 10	$12/31 \pm 10$	$6/4 \pm 15$
Diagnostic (Shelf)				
Surface Chlorophyll	1.96 ± 0.15	3.00 ± 0.30	$2/8 \pm 37$	$7/31 \pm 58$
Phytoplankton Biomass	3200 ± 290	5200 ± 440	$1/1 \pm 9$	$7/18 \pm 11$
Net Primary Production	750 ± 120	2000 ± 220	$12/31 \pm 8$	$7/21 \pm 14$
Mesozooplankton Biomass	670 ± 70	1100 ± 90	$12/29 \pm 7$	$5/23 \pm 25$
Secondary Production	94 ± 17	270 ± 28	$12/31 \pm 6$	$7/20 \pm 16$

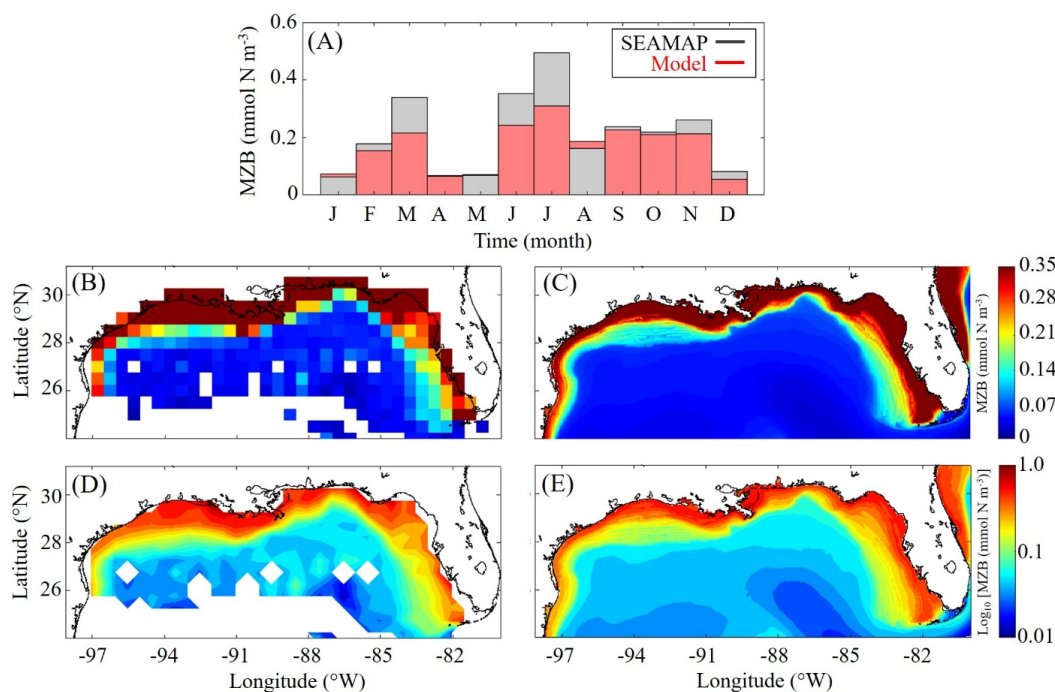
462

463 The model also captures the vertical variability in phytoplankton biomass reasonably well, falling
 464 within one standard deviation of the observed data. When model estimates of DCM depth are
 465 compared to all 2,435 SEAMAP CTD casts at corresponding sample times and locations, we find
 466 a statistically significant correlation ($\rho = 0.59$, $p < 0.01$) with the observed maximum fluorescence
 467 depth. The observed DCM depth ranged from the surface to 143 m while model values show a
 468 similar variability ranging from the surface to 163 m. In the oligotrophic region, we find the model
 469 overestimates the DCM (Model: 95 ± 20 m vs. SEAMAP: 80 ± 25 m) and has a ρ value of 0.38 (p
 470 < 0.01) with a bias of 15 m equivalent to 19% of the observed mean. In the shelf region, the model



471 also overestimates DCM depth (Model: 63 ± 26 m vs. SEAMAP: 53 ± 23 m) and has a ρ value of
472 0.49 ($p < 0.01$) with a bias of 10 m equivalent to 19% of the observed mean.

473 3.2 Regional zooplankton biomass model-data comparisons



474

475 **Figure 3 (A-E):** Comparison of climatological depth-averaged mesozooplankton biomass (MZB,
476 mmol N m⁻³) between SEAMAP observations (left) and model output (right). Monthly average
477 MZB samples organized by month (A). Monthly variability is not representative of seasonality as
478 sampling locations change between months. MZB from all SEAMAP tows (B). MZB 20-year
479 model average (C). Log₁₀ of SEAMAP MZB (D). Log₁₀ of model MZB (E).

480 Model mesozooplankton biomass (i.e. LZ + PZ) fields compare well with observations in both the
481 oligotrophic and shelf region (**Fig. 3**). Spatial covariance between SEAMAP climatology and
482 model climatology of depth-averaged mesozooplankton biomass is statistically significant ($p <$
483 0.01) with a ρ value of 0.90. When model estimates were compared to SEAMAP tows at
484 corresponding sample times and locations for the 6,835 measurements overlapping with the
485 simulation period, the ρ value is 0.55 ($p < 0.01$). In the oligotrophic region, the model slightly



486 overestimates mesozooplankton biomass (Model: $4.09 \pm 1.82 \text{ mg C m}^{-3}$ vs. SEAMAP: 3.52 ± 3.44
487 mg C m^{-3}) with p value of 0.23 ($p < 0.01$) and bias of 0.57 mg C m^{-3} equivalent to 16% of the
488 observed mean. Conversely, in the shelf region the model underestimates mesozooplankton
489 biomass (Model: $17.40 \pm 13.58 \text{ mg C m}^{-3}$ vs. SEAMAP: $20.91 \pm 24.62 \text{ mg C m}^{-3}$), with a p value
490 of 0.49 ($p < 0.01$) and a bias of -3.5 mg C m^{-3} equivalent to 17% of the observed mean. We note
491 that model estimates and SEAMAP measurements also compare well with mesozooplankton
492 biomass measurements (0.2-5 mm) obtained in the oligotrophic region from independent May,
493 2017 and 2018 cruises (Model: $5.55 \pm 2.87 \text{ mg C m}^{-3}$ vs. Cruise: $4.33 \pm 2.28 \text{ mg C m}^{-3}$).

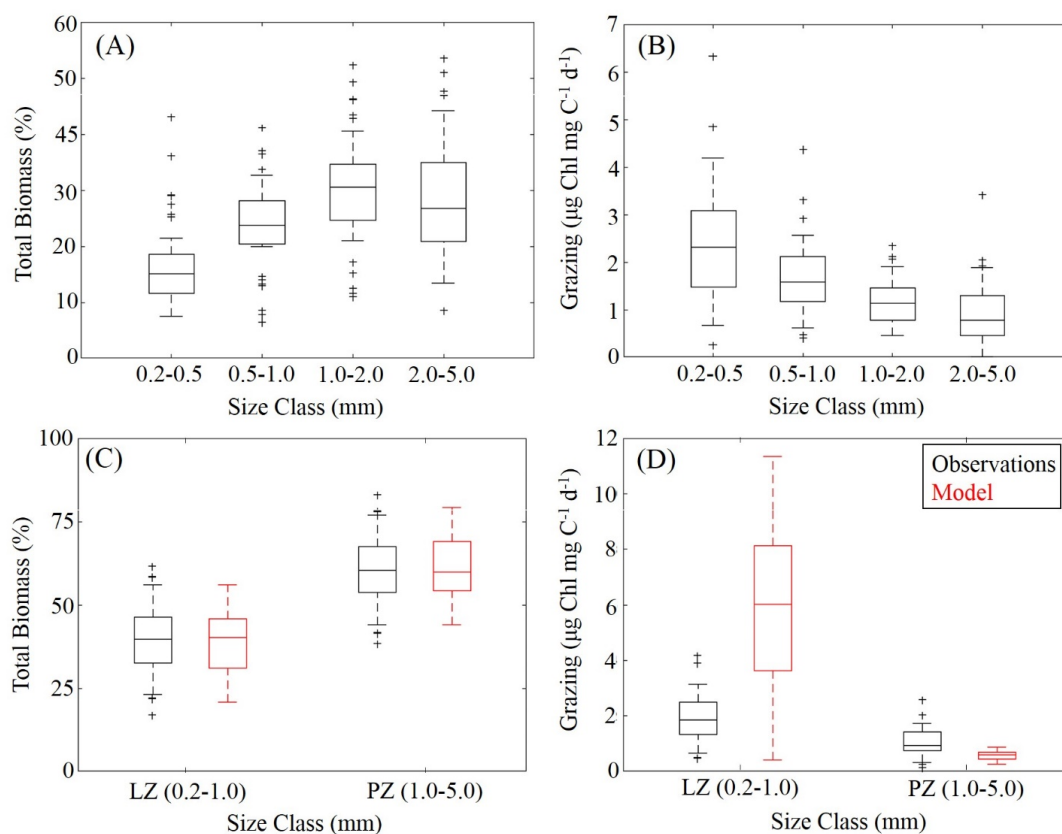
494 Although seasonal cycles in the oligotrophic and shelf regions could not be derived from the
495 SEAMAP dataset given the significant differences in sampling locations over the course of a year,
496 we investigated model-data mismatches for each month. We find the model closely matches or
497 slightly underestimates depth-averaged mesozooplankton biomass throughout most of the year,
498 with the exception of January, May, and August (**Fig. 3A**). The greatest model-data mismatch
499 occurs during the months of March, June, July, and December, where the model underestimates
500 depth-averaged mesozooplankton biomass by approximately 35%. Unlike phytoplankton biomass,
501 the total mesozooplankton biomass (i.e. depth-integrated) seasonality is similar in both regions of
502 the GoM. In the oligotrophic region, the annual mesozooplankton biomass minimum (maximum)
503 develops at the beginning of January (middle of May) while in the shelf region, the annual
504 minimum (maximum) develops in late December (near the end of May) (**Table 1**).

505 **3.3 Phytoplankton growth and zooplankton grazing model-data comparisons**

506 To further constrain the phytoplankton and zooplankton community simulated by the PBM, we
507 utilized in situ measurements of the planktonic community during Lagrangian process studies
508 conducted on two cruises in the oligotrophic GoM during May 2017 and 2018. First, we compared
509 the relative proportions of LZ and PZ biomass to four discrete size classes measured at sea (**Fig.**
510 **4A, C**). In total, 40 oblique bongo net tows (16 in 2017 and 24 in 2018) sampled the oligotrophic
511 GoM mesozooplankton community from near surface to a depth ranging from 100 - 135 m. When
512 the model is sampled yearly corresponding to cruise measurement locations and day of the year,
513 we find nearly identical size distributions when assuming that LZ approximates the smallest two
514 size classes of mesozooplankton sampled (“small mesozooplankton”, 0.2-1.0-mm) and PZ
515 approximates the largest two size classes (“large mesozooplankton”, 1.0-5.0 mm). In both



516 observations and model estimates approximately 40% and 60% of the mesozooplankton
517 community is composed of LZ and PZ, respectively. In the field data, small mesozooplankton
518 biomass varied from 33 to 46 % (median = 40%, at 95% C.I.), while model estimates of LZ
519 biomass vary from 31 to 46% (median = 40%). Large mesozooplankton biomass in the field data
520 varied from 54 to 67% (median = 60%), while model estimates of PZ biomass vary from 54 to
521 69% (median = 60%).



522

523 **Figure 4 (A-D):** A summary of field (black) and model (red) estimates of mesozooplankton size-
524 fractionated biomass and grazing rates. Mesozooplankton size-fractionated biomass as a percent of
525 total biomass for each of the four size classes measured at sea in May, 2017 and 2018 (A).
526 Corresponding mesozooplankton specific grazing rates for each of the four size classes (B). Field
527 data aggregated into two size classes for direct comparison with model biomass estimates for large
528 (LZ) and predatory (PZ) mesozooplankton (C). Similarly, model data comparison of specific



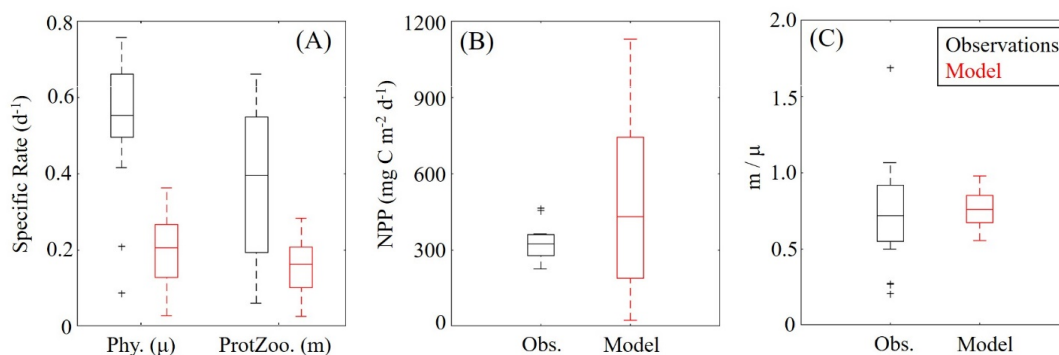
529 grazing rates by large and predatory zooplankton to aggregated field estimates (D). Whiskers
530 extend to 95% confidence interval. Outliers for model estimates are not shown.

531 We also measured the specific grazing rates of each size class using the gut pigment approach.
532 Field measurements showed that specific grazing rates consistently decreased with increasing
533 mesozooplankton size-class (**Fig. 4B**). To compare specific grazing rates in the model to field
534 measurements ($\mu\text{g Chl mg C}^{-1} \text{d}^{-1}$), we computed grazing on LP by LZ and PZ at each depth.
535 Grazing terms were converted into units of Chl using the model estimated C:Chl ratio for LP before
536 being depth-integrated to the corresponding net tow depth and normalized to simulated depth-
537 integrated LZ and PZ biomasses. We find that model mesozooplankton grazing estimates capture
538 the general trend of decreased specific grazing rates with increasing mesozooplankton size (**Fig.**
539 **4D**). However, the model overestimates grazing by small mesozooplankton while underestimating
540 grazing by large mesozooplankton. In the field data, small mesozooplankton grazing varied from
541 1.34 to 2.51 $\mu\text{g Chl mg C}^{-1} \text{d}^{-1}$ (median = 1.85) while model estimates of LZ grazing rates vary
542 from 3.64 to 8.14 $\mu\text{g Chl mg C}^{-1} \text{d}^{-1}$ (median = 6.01). Field measurements of large
543 mesozooplankton grazing varied from 0.76 to 1.44 $\mu\text{g Chl mg C}^{-1} \text{d}^{-1}$ (median = 0.94), while model
544 estimates of PZ grazing vary from 0.44 to 0.70 $\mu\text{g Chl mg C}^{-1} \text{d}^{-1}$ (median = 0.58). In terms of total
545 mesozooplankton grazing, average grazing in the field was found to be $1.38 \pm 0.59 \mu\text{g Chl mg C}^{-1}$
546 d^{-1} , while the model average is $2.99 \pm 2.20 \mu\text{g Chl mg C}^{-1} \text{d}^{-1}$. This model-data mismatch likely
547 results from the fact that, as formulated in NEMURO, LZ and PZ do not necessarily reflect size
548 classes of mesozooplankton, but rather functional types. In reality, there is substantial overlap
549 between taxonomic groups with different functional roles and sizes (see Discussion).

550 In addition to measuring the mesozooplankton community, specific phytoplankton growth rates
551 and specific phytoplankton mortality due to microzooplankton grazing were measured at sea using
552 the microzooplankton grazing dilution method, and net primary production (NPP) was measured
553 with $\text{H}^{13}\text{CO}_3^-$ uptake experiments. We find the model underestimates phytoplankton growth and
554 microzooplankton grazing while overestimating NPP (**Fig. 5A, B**). This model-data mismatch may
555 be driven in part by model errors in simulated vertical patterns of phytoplankton growth rates. We
556 note that model results consistently predict enhanced growth rates at the DCM, while the field
557 measurements showed surface enhancement of growth rates or relatively constant growth rates
558 with depth. We believe the collocation of high growth rates at the DCM estimated by the model



559 may reveal a fundamental issue with how biogeochemical models simulated DCM dynamics. This
560 collocation could explain the lower specific growth rates despite higher NPP we find in the model
561 (see Discussion).



562

563 **Figure 5 (A-C):** Specific phytoplankton growth (μ , d⁻¹) and microzooplankton grazing (m, d⁻¹)
564 between model (red) and field data (black) (A). Depth-integrated net primary production (mg C
565 m⁻² d⁻¹) (B). The fraction of phytoplankton growth that is grazed by protists in the model and field
566 data (C). Whiskers extend to the 95% confidence intervals. Outliers for model estimates are not
567 shown.

568 Phytoplankton specific growth rates in dilution experiments varied from 0.50 to 0.66 d⁻¹ (median
569 = 0.55 d⁻¹) while model estimates of phytoplankton (SP+LP) specific growth rates are lower and
570 vary from 0.13 to 0.27 d⁻¹ (median = 0.21 d⁻¹). In terms of microzooplankton grazing, field data
571 varied from 0.19 to 0.55 d⁻¹ (median = 0.39 d⁻¹) while model estimates of SZ grazing are also lower
572 and vary from 0.10 to 0.21 d⁻¹ (median = 0.16 d⁻¹). NPP estimates between model and data show
573 better agreement where field data varied from 275.61 to 360.09 mg C m⁻² d⁻¹ (median = 321.44 mg
574 C m⁻² d⁻¹) while model estimates vary from 189.75 to 741.04 mg C m⁻² d⁻¹ (median = 430.96 mg C
575 m⁻² d⁻¹). Although we find the model underestimates specific phytoplankton growth and
576 microzooplankton grazing rates, the relative proportion of NPP being consumed by protists
577 compares reasonably well to field measurements (**Fig. 5C**). The proportion of NPP grazed in field
578 data varied from 55% to 92% (median = 72%), while model estimates vary from 67% to 85%
579 (median = 76%). Notably, the model average proportion of phytoplankton production consumed
580 by protists closely matches the mean for all tropical waters reported by Calbet & Landry (2004).



581 When specific phytoplankton mortality due to mesozooplankton grazing was calculated at cruise
582 sample locations, we find that mesozooplankton grazing accounts for $13 \pm 8 \%$ which also closely
583 agrees with the global average (Calbet et al., 2001).

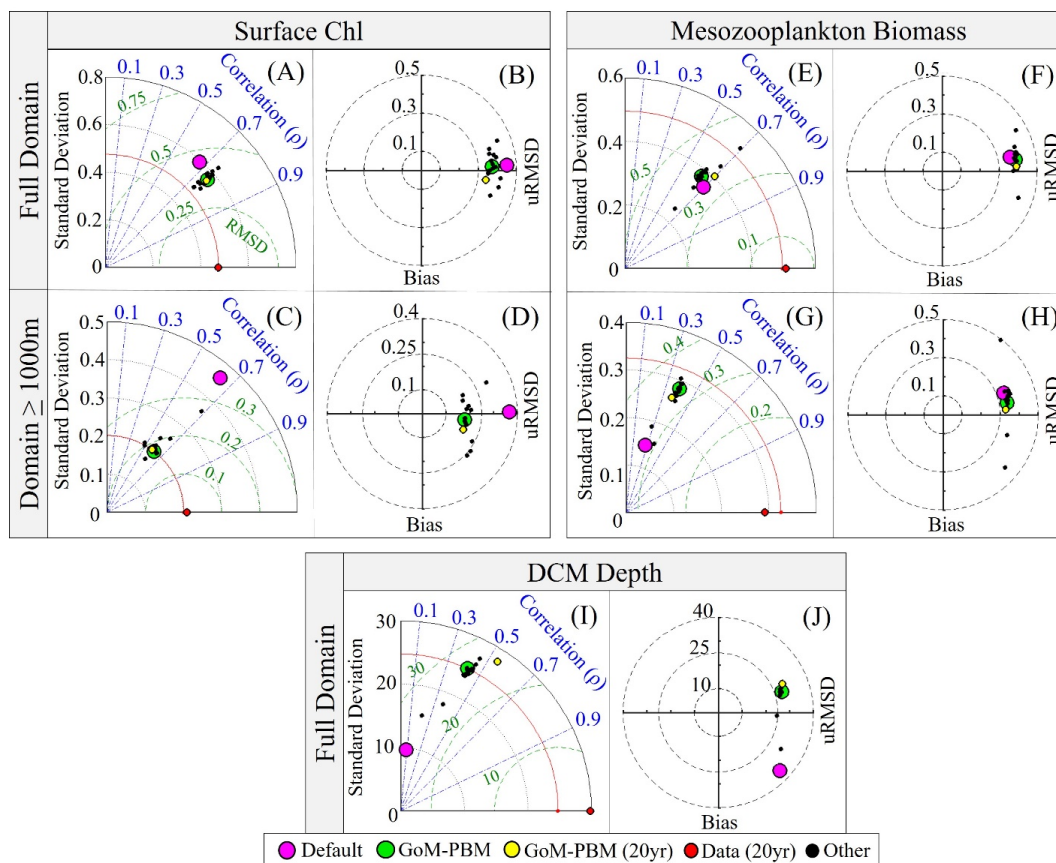
584 **3.4 Parameter sensitivity analysis**

585 To evaluate model sensitivity, we investigated the impact of parameter changes on model estimates
586 over the entire GoM domain and the oligotrophic region, specifically. The separate analysis of the
587 oligotrophic region was undertaken for two reasons: 1) this region is an area where low
588 mesozooplankton biomass likely leads to particularly strong prey limitation for fish, their larvae,
589 and other higher trophic levels and 2) the substantially higher biomass and variability on the shelf
590 dominates region-wide mean estimates. In comparison to default NEMURO, the NEMURO-GoM
591 produces estimates of surface Chl, depth averaged mesozooplankton biomass, and DCM depth that
592 more closely agree with observations (**Fig. 6**). During the parameter sensitivity experiments
593 SEAMAP observations in the oligotrophic region were almost always located near the Loop
594 Current which is strongly influenced by the southern open boundary condition. Hence, differences
595 between simulations were difficult to quantify. Additionally, since mesozooplankton biomass
596 observations is a depth averaged metric differences between simulations can appear small despite
597 extreme differences in the vertical distribution of biomass.

598 All parameter sensitivity experiment configurations are outlined in Supplement **Table S3**. Of the
599 18 sensitivity experiments, the greatest model overestimation of surface Chl occurs when default
600 α values (slope of the photosynthesis-irradiance curve) are included in NEMURO-GoM (**Fig. 6A-**
601 **D**). In default NEMURO, SP and LP α values are an order of magnitude lower (0.01). When default
602 α values are included in the NEMURO-GoM, they restrict the depth range where phytoplankton
603 can grow, resulting in substantially shallower DCM depths than observed. Subsequently, the
604 nitracline becomes unrealistically shallow (~ 25 m in the oligotrophic region), allowing nutrients
605 to mix readily into surface water and support higher phytoplankton biomass. The greatest model
606 underestimation of surface Chl occurs when default quadratic mortality is implemented in the
607 NEMURO-GoM. Although quadratic mortality tends to increase the lower limit of phytoplankton
608 biomass, it also increases zooplankton standing stocks which, in this case, allows zooplankton to
609 graze phytoplankton to unrealistically low levels. We find the exact opposite is true for
610 mesozooplankton biomass. The greatest overestimation of depth-averaged mesozooplankton



611 biomass occurs when default quadratic mortality is included in the NEMURO-GoM. Conversely,
 612 when default α values are included we find the largest underestimation of mesozooplankton
 613 biomass as a result of low phytoplankton biomass at depth (**Fig. 6E-H**).



614

615 **Figure 6 (A-J):** Taylor and Target diagrams comparing 18 parameter sensitivity experiments
 616 (black dots) against observations of surface Chl (top left, A-D) depth-averaged mesozooplankton
 617 biomass (top right, E-H) and deep chlorophyll maximum depth (bottom center, I & J). Each panel
 618 contains Taylor diagrams (left) and Target diagrams (right). The top two panels are further divided
 619 based on analysis of all data (top) and with bottom depths ≥ 1000 m (bottom). The red arc in Taylor
 620 diagrams signifies the standard deviation of all observations in the last three years of the four-year
 621 parameter sensitivity experiments (2002-2006). A \log_{10} transform is applied to surface chlorophyll
 622 and depth-averaged mesozooplankton before computing model-data statistics.



623 We also investigated the influence of parameter changes on simulated DCM depth (**Fig. 6I, J**). For
624 this analysis, we did not isolate the oligotrophic region because average DCM depth does not vary
625 as substantially as biomass between the shelf and oligotrophic regions (i.e., the shelf does not
626 dominate the region-wide signal). In contrast to surface Chl and mesozooplankton biomass, default
627 mortality does not strongly influence DCM depth. However, when default α values are included,
628 the model substantially underestimates the actual DCM depth and the standard deviation of DCM
629 depth as expected. In the NEMURO-GoM, tuned values lead to substantial improvement in DCM
630 depth, with a standard deviation quite close to observations and a substantially improved ρ value
631 (**Fig. 6I**). However, the tuned parameter set results in a small positive bias in DCM depth (i.e.,
632 deeper than measured DCM by ~ 10 m), although this was less significant than the negative bias in
633 DCM depth of default NEMURO (i.e., shallower DCM than observations by ~ 25 m).

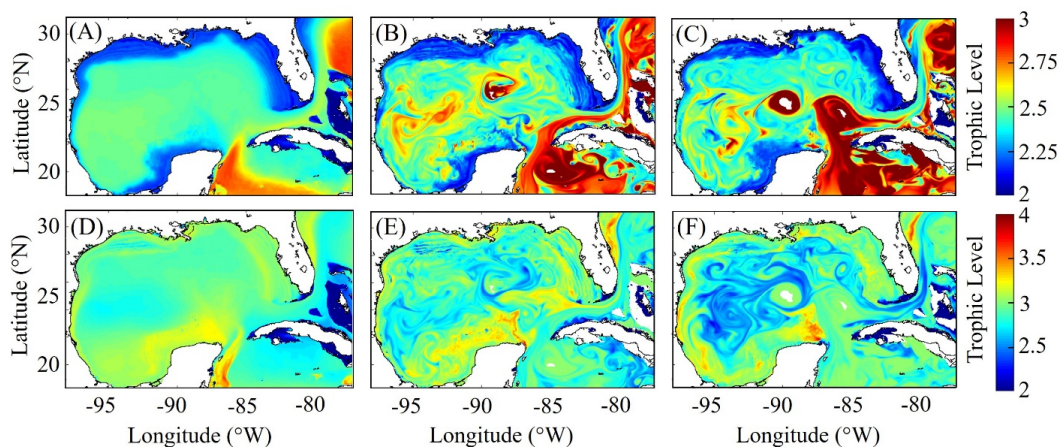
634 **3.5 Simulated mesozooplankton diet and secondary production**

635 Trophic level estimates provide a measure of the cumulative diet for mesozooplankton. We
636 estimated mesozooplankton trophic level in the model by computing the dietary contributions of
637 each prey in LZ (i.e. LP and SZ) and PZ diets (i.e. LP, SZ, and LZ) while assuming that the trophic
638 level of LP = 1 and SZ = 2. In the oligotrophic region, both LP and SZ contribute approximately
639 50% to LZ diet, as indicated by average LZ trophic level near 2.5 (2.54 ± 0.02) (**Fig. 7A**). In the
640 same region, PZ have a trophic level of 2.78 ± 0.04 indicating a higher contribution of zooplankton
641 to their diet (i.e. SZ and/or LZ) (**Fig. 7B**). In the shelf region, LZ are more herbivorous, as indicated
642 by a decrease in trophic level to 2.31 ± 0.01 , while PZ are more carnivorous, as indicated by an
643 increase in trophic level to 2.90 ± 0.04 .

644 Although there is little evidence in the annual average for LZ diets dominated by zooplankton
645 (trophic level ~ 3 as commonly found in PZ diets), we commonly find regions in instantaneous
646 fields during both winter and summer where SZ are the dominant prey source for LZ (**Fig. 7C, E**).
647 These regions, typically in the Loop Current or Loop Current Eddies (LCEs), highlight the episodic
648 importance of heterotrophic protists as prey sources for small mesozooplankton in the GoM. High
649 proportions of SZ in LZ diets can be attributed to the competitive advantage of SP over LP in
650 extremely low nutrient environments such as in the Loop Current. Instantaneous fields also reveal
651 that phytoplankton can be an important prey source for PZ as well. This is particularly the case



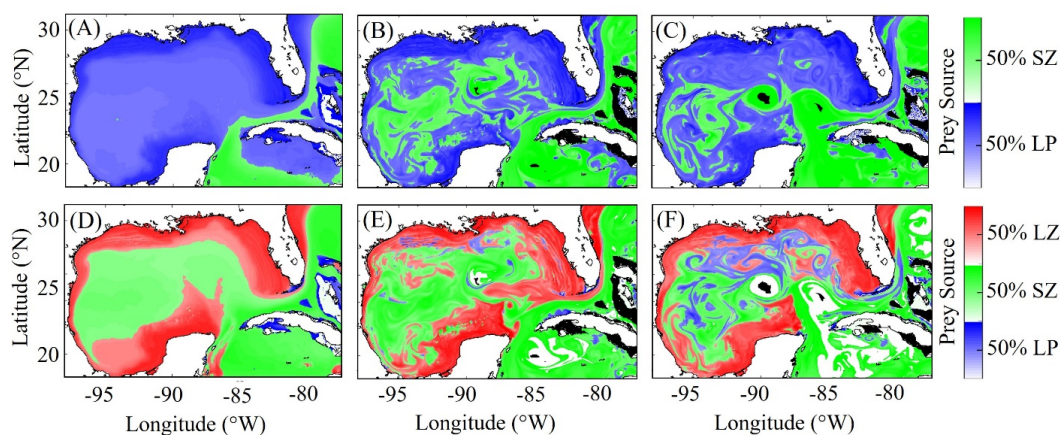
652 during summer, as indicated by trophic levels of around 2.5 in the western oligotrophic GoM (**Fig.**
653 **7F**).



654

655 **Figure 7 (A-F):** Trophic levels of simulated large zooplankton (LZ, top) and predatory
656 zooplankton (PZ, bottom). Annual-average trophic positions of LZ (A) and PZ (D). Instantaneous
657 trophic positions of LZ (B) and PZ (E) for winter conditions on 4 February 2012. Instantaneous
658 trophic positions of LZ (C) and PZ (F) for summer conditions on 5 August 2011.

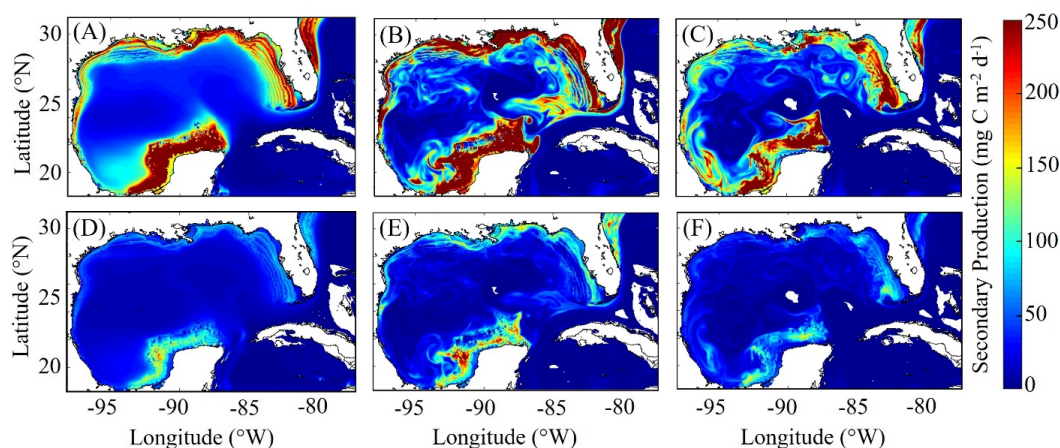
659 In addition to strong variability in trophic positions, there are also regions in the oligotrophic GoM,
660 most clearly in the centers of LCEs during summer, where the model predicts no feeding by
661 mesozooplankton (**Fig. 8E**). The convergent anti-cyclonic circulation of LCEs is typically
662 associated with low phytoplankton biomass, which at times may fall near or below feeding
663 thresholds in the NEMURO grazing formulation. This formulation is designed to simulate
664 suppression of feeding activity for zooplankton at mean prey densities that cannot support the
665 energy expended while searching for prey.



666

667 **Figure 8 (A-F):** Dominant prey source for simulated large zooplankton (LZ, top) and predatory
668 zooplankton (PZ, bottom). Colors indicate which prey are dominant. Brightness indicates percent
669 of the dominant prey in the zooplankton diet. Annual averaged field for LZ (A) and PZ (D).
670 Instantaneous winter condition for LZ (B) and PZ (E) on simulated day 4 February 2012.
671 Instantaneous summer conditions for LZ (C) and PZ (F) on 4 August 2011.

672 To investigate which prey source contribute the most to LZ and PZ diets, we computed each prey
673 source term for both LZ and PZ at each grid cell (**Fig. 8**). As we would expect, the dominant prey
674 source for LZ and PZ closely aligns with the spatial variability in their respective trophic positions.
675 For LZ diet, herbivory dominates throughout the GoM, except for the Loop Current (**Fig. 8A**). The
676 LP contribution to LZ diet is highest on the shelf, where LP biomass is also high due to the
677 competitive advantage LP have over SP in high nutrient conditions. In contrast, PZ diet varies with
678 the relative availability of SZ and LZ prey. In the oligotrophic region, PZ feed mainly on SZ
679 (heterotrophic protists), because LZ biomass is relatively low. On the shelf, they consume
680 primarily LZ (**Fig. 8D**). Despite the significant change in dominant prey between the shelf and
681 oligotrophic regions, PZ trophic positions remain fairly consistent (**Fig. 7D**) because SZ in the
682 oligotrophic region and LZ in the shelf region both feed predominantly on phytoplankton. In the
683 instantaneous fields for winter (**Fig. 8B, E**) and summer (**Fig. 8C, F**), the dominant prey for both
684 LZ and PZ show substantial mesoscale variability indicating that oceanographic features such as
685 fronts and eddies influence not only zooplankton biomass but also their ecological roles.



686

687 **Figure 9 (A-F):** Vertically integrated secondary production ($\text{mg C m}^{-2} \text{d}^{-1}$) by simulated large
688 zooplankton (LZ, top) and predatory zooplankton (PZ, bottom). Annual average of secondary
689 production for LZ (A) and PZ (D). Instantaneous model output of secondary production in winter
690 for LZ (B) and PZ (E) on simulated day 4 February 2012. Instantaneous model output for
691 secondary production in summer for LZ (C) and PZ (F) on 2 August 2011.

692 To our knowledge prior to the current study the regional secondary production for the GoM has
693 yet to be quantified. In terms of the entire GoM, we find that secondary production averaged $66 \pm$
694 8 mt C yr^{-1} and ranged from a minimum of 51 mt C (in 1999) to a maximum of 82 mt C (in 2011).
695 In the oligotrophic region, LZ secondary production averages $35 \pm 5 \text{ mg C m}^{-2} \text{d}^{-1}$ while PZ
696 secondary production is $11 \pm 2 \text{ mg C m}^{-2} \text{d}^{-1}$ (**Fig. 9**). The annual secondary production minimum
697 develops at the end of December while the annual maximum develops in the beginning of June
698 (**Table 1**). In this region, mesozooplankton are responsible for $14 \pm 2 \text{ mt C yr}^{-1}$, equivalent to 6%
699 of NPP. In the shelf region, secondary production is about 4-fold higher, with LZ production of
700 $146 \pm 17 \text{ mg C m}^{-2} \text{d}^{-1}$ and PZ production of $42 \pm 5 \text{ mg C m}^{-2} \text{d}^{-1}$. Here, the annual minimum also
701 develops at the end of December while the seasonal maximum occurs near the end of July (**Table**
702 **1**). Secondary production in the shelf region averages $51 \pm 6 \text{ mt C yr}^{-1}$ and is equivalent to 13% of
703 NPP.

704 **4 Discussion**



705 Many parameters in biogeochemical models are poorly constrained by observations and laboratory
706 studies and/or highly variable in the environment. The numbers and uncertainties around these
707 parameters allow PBMs with varying degrees of tuning to reproduce a single ecosystem attribute
708 (e.g., surface Chl) even if multiple processes are inaccurately represented (Anderson, 2005;
709 Franks, 2009). Once validated, one of the main values of coupling physical and biogeochemical
710 models (i.e. PBMs) is their utility in making inferences about portions of the lower trophic level
711 that are under sampled and/or difficult to measure in the field. If PBMs are to be utilized for
712 explaining variability rather than just fitting an observational dataset, multiple ecosystem attributes
713 must be validated and the underlying model structure and assumptions critically evaluated. In the
714 section below, we further justify changes to model structure by evaluating the underlying
715 assumptions in default NEMRUO and discuss model-data mismatch before drawing conclusions
716 on the GoM zooplankton community and the implications of its dynamics on higher trophic levels.
717

718 **4.1 Justification for NEMURO modifications**

719 The phytoplankton community in the North Pacific (NP) domain where NEMURO was originally
720 designed is largely composed of nanoplankton (i.e. original SP) and microplankton (i.e. original
721 LP). By default, SP are assumed to represent coccolithophores and autotrophic nanoflagellates,
722 which can be important prey of copepods and other mesozooplankton in temperate and subpolar
723 regions (Kishi et al., 2007). However, in tropical regions such as the GoM, smaller
724 picophytoplankton taxa typically dominate particularly in highly oligotrophic regions. Common
725 picophytoplankton found in the GoM include cyanobacteria and picoeukaryotes which are too
726 small for most mesozooplankton to feed on. Consequently, the SP to LZ grazing pathway was
727 removed in the model. We found that removal of this grazing pathway allowed the model to
728 simulate a more realistic phytoplankton community in the shelf region. Despite intuition, SP
729 largely dominated the shelf region in the model when LZ were allowed to graze on SP. After closer
730 inspection we found that grazing of SP sustained LZ biomass on the shelf to levels where top-
731 down pressure constrained LP standing stocks. This prevented large blooms of LP leading to a
732 competitive advantage for SP even in highly eutrophic conditions (e.g. near the Mississippi river
733 delta). We found this was true under a wide range of LP maximum growth rates, LP half saturation
734 constants, and LZ/PZ grazing rates. Thus, removal of SP to LZ grazing pathway added ecological
735 realism and improved the model solution.



736 During the model tuning process, we also found that despite a wide range of tested parameter sets
737 the model (with default quadratic mortality formulation) was unable to simulate mesozooplankton
738 biomass low enough to match SEAMAP observations in the oligotrophic region. Even with
739 unrealistically low phytoplankton biomass, equivalent to approximately 50% of surface Chl
740 observed in SeaWIFS images, the model overestimated mesozooplankton biomass. We found that
741 to achieve realistic levels of mesozooplankton biomass in the oligotrophic region, default LZ and
742 PZ mortality parameter values needed to be increased by an order of magnitude. However, this
743 produced unrealistically high loss rates in the shelf region leading to mesozooplankton biomass
744 estimates that were substantially lower than SEAMAP shelf observations. Implementation of
745 linear mortality on all biological state variables (except PZ) resolved this issue by providing the
746 model with greater dynamic range. In NEMURO, and other biogeochemical models, quadratic
747 mortality is often used to increase model stability and/or is mechanistically justified as representing
748 the impact of unmodeled predators that co-vary in abundance with prey (Gentleman and
749 Neuheimer, 2008; Steele and Henderson, 1992). However, grazing losses of all state variables
750 (except PZ), are already explicitly modeled in NEMURO by default. Hence, removal of quadratic
751 mortality also added ecological realism and improved the model solution. Quadratic mortality was
752 retained for PZ, to account for the implicit predation pressure of un-modeled planktivorous fish.

753 **4.2 Model-data mismatch**

754 The PBM in this study captures a wide range of key regional ecosystem attributes across multiple
755 trophic levels. Surface Chl estimates were found to agree closely with satellite measurements,
756 reproducing patterns in both the oligotrophic and shelf region. The latter of which, apart from the
757 northern shelf, has not been well resolved by previous PBMs (e.g., Gomez et al., 2018; Xue et al.,
758 2013). The lack of a shelf Chl signature in previous studies may, in some cases, be overly attributed
759 to bias in satellite measurement due to high concentrations of colored dissolved organic matter on
760 the shelf. While a clear shelf signature is resolved in the NEMURO-GoM, we find greater model-
761 data mismatch on the shelf compared to oligotrophic regions. This is an expected finding when
762 considering the model incorporates climatological river forcing while actual variability is in reality
763 much more complex. Benthic processes that are not included in the NEMURO-GoM, such as
764 denitrification (Fennel et al., 2006), may also contribute to model-data discrepancies in the shelf
765 region.



766 The most noticeable surface Chl model-data mismatch occurs in the southern GoM on the
767 Campeche Bank (CB) where the model consistently overestimates surface Chl. This
768 overestimation was also notably present in the PBM implemented by Damien et al. (2018) for the
769 GoM, particularly in winter. We believe this discrepancy is driven by a combination of error in
770 the hydrodynamic model associated with overestimation of shelf mixing and simulated nitraclines
771 that are too shallow, which allows for unrealistic mixing of nitrate into surface waters. Nitrate
772 profiles from the oligotrophic GoM during May 2017 and 2018 cruises (A. Knapp, pers. comm.)
773 revealed concentrations are typically below detection limits at depths shallower than 100 m.
774 However, nitracline depths estimated by the model were shallower than observed with an upper
775 limit of approximately 80 m (DCM depth was ~100 m) in summer months. While this discrepancy
776 has minimal impact on average surface Chl over most of the domain, significant model-data
777 mismatch arises in persistent upwelling areas such as north of the Yucatan Peninsula. In this
778 region, strong upwelling produces a thin filament of high Chl water that extends northward as
779 frequently observed in satellite images. To the west, circulation on the CB is characterized by a
780 westward flow. Together with the shallower simulated nitracline depths, we believe the regional
781 circulation supplies the CB with excessive nutrient-rich water leading to an overestimation of Chl
782 by the PBM.

783 We found the model-data mismatch on the CB was reduced in parameter sets that produced
784 nitracline depths down to 100 m. However, these parameter sets were less realistic in other ways
785 (e.g. improbably deep DCMs). Given the strong thermal stratification and depth of the nitracline
786 found in the GoM, we believe nitrogen fixing cyanobacteria may be another important source of
787 new nitrogen (other than upwelling and mixing) supporting the surface phytoplankton community
788 in the GoM. In the process of model tuning, we noticed that increasing the DON pool by increasing
789 the PON to DON decomposition rate was necessary to maintain both relatively deep nitraclines
790 and realistic surface Chl by providing a slow leeching of ammonium near the surface through
791 bacterial communities. The need for this slow production of ammonium in surface layers may
792 reflect the importance of nitrogen fixation, which is not included in NEMURO (Holl et al., 2007;
793 Mulholland et al., 2006). In future studies including diazotrophs as a separate phytoplankton
794 functional type would be valuable to investigate the importance of nitrogen fixation in the GoM.



795 Novel to this study, model estimates of mesozooplankton biomass were shown to agree closely
796 with observations on the shelf and in the oligotrophic GoM. To our knowledge, this study provides
797 the first quasi regional zooplankton biomass model-data comparisons in the GoM along with the
798 first model-data comparisons of size-specific zooplankton biomass and grazing rates. Such
799 comparisons provide the first insights into the potential biases of traditional biogeochemical
800 models pertaining to zooplankton dynamics (Everett et al., 2017). While the PBM shows broad
801 agreement with zooplankton observations, some model-data mismatch occurs, particularly for LZ
802 grazing rates. Some of this discrepancy may arise from temporal sampling issues (rate
803 measurements were only available for May 2017 and May 2018) or from inaccuracies in the field
804 grazing measurements. Due to phytodetrital aggregates and *Trichodesmium* colonies in the
805 zooplankton net tows, our in situ gut pigment measurements were based solely on phaeopigment
806 content. True grazing rates were likely underestimated because undegraded Chl can be abundant
807 in the foreguts of zooplankton. An additional source of model-data discrepancy arises from the
808 fact that the NEMURO model formulation of LZ and PZ does not necessarily reflect a size class
809 of mesozooplankton, but rather reflects a functional type of mesozooplankton. In reality, there is
810 overlap between taxonomic groups with different functional roles and different sizes.

811 Since most PBMs focus on validating against satellite-observed surface chlorophyll, the dynamics
812 of the DCM is often insufficiently investigated. Consequently, many models predict DCM depths
813 that are far too shallow. Identifying this issue in the literature proved to be difficult seeing that
814 most studies don't provide profiles of simulated Chl. We note that DCM depths in the DIAZO
815 model (Stukel et al., 2014) were often quite shallow or completely nonexistent in the portion of
816 the domain that included the oligotrophic GoM region. Underestimates of DCM depth in the
817 unmodified COBALT biogeochemical model has also been identified (Moeller et al., 2019). In our
818 investigation of (Gomez et al., 2018) we found that DCMs in the oligotrophic region were
819 commonly shallow and weak. In the default NEMURO simulation, DCM depths in the
820 oligotrophic region were typically at a depth of 25 m, which is much shallower than SEAMAP
821 observations in the region (80 ± 25 m). While this issue may seem insignificant, particularly if a
822 study is focused on mixed-layer dynamics, accurate placement of the DCM can have profound
823 impacts on PBM behaviors, because the DCM is typically collocated with the nitracline.
824 Unrealistically shallow DCMs and nitraclines permit unrealistically high nitrate fluxes into the
825 surface layer following mixing events. Indeed, we believe that a slight underestimation in



826 nitracline depth near the Yucatan Peninsula in our model contributed significantly to the model
827 overestimation of surface Chl on the Campeche Bank.

828 For these reasons, we devoted substantial effort to tuning phytoplankton dynamics at the DCM.
829 Modifications to α (the slope of the photosynthesis-irradiance curve) and attenuation coefficients
830 allowed us to move the DCM down to realistic depths. However, an additional issue was present
831 in the default NEMURO simulations, the NEMURO-GoM, and every simulation that we
832 attempted. In all simulations that formed DCMs, the location of the DCM was always collocated
833 with a maximum in phytoplankton specific growth rate. However, our field measurements of
834 phytoplankton growth rates and NPP were either relatively constant with depth or declined in the
835 DCM. This is not surprising, given the low photon flux at the base of the euphotic zone and the
836 energetic demands required to upregulate cellular density of light harvesting pigments. However,
837 in traditional PBMs high biomass DCM cannot form with a low growth rate, because specific
838 mortality rates tend to co-vary with biomass even if (as in our model) quadratic mortality is not
839 included.

840 Phytoplankton mortality (in the model and in the observations) is dominated by zooplankton
841 (particularly protists). Since zooplankton abundance covaries with phytoplankton abundance and
842 zooplankton specific grazing rates increase with increasing phytoplankton abundance, specific
843 mortality must co-vary with abundance. This means that phytoplankton mortality rates must be
844 higher at the DCM biomass peak than in the surface layer and thus a DCM can only be maintained
845 if growth rates are high. We tested multiple options to try to maintain a DCM with low growth
846 rates, including using light-dependent grazing formulations (Moeller et al., 2019), but found no
847 parameterizations that could match the observations. We believe this DCM issue was responsible,
848 in part, for the overestimates of LZ grazing rates (**Fig. 4D**). The collocation of the biomass and
849 growth rate maxima also lead to substantial overestimates of production (particularly by LP) at the
850 DCM, which was then grazed by LZ. Future modeling studies should focus more effort on
851 dynamics of the DCM.

852 **4.3 Mesozooplankton dynamics in the open-ocean oligotrophic Gulf of Mexico**

853 Despite its nutrient-poor conditions, the open-ocean GoM ecosystem is a key region for spawning
854 and larval development of many commercially important fishes, including Atlantic bluefin tuna,



855 yellowfin tuna, skipjack tuna, sailfish, and mahi mahi (Cornic and Rooker, 2018; Kitchens and
856 Rooker, 2014; Lindo-Atichati et al., 2012; Muhling et al., 2017; Rooker et al., 2012, 2013). Why
857 so many species choose such oligotrophic waters as habitat for their larval stages is unknown, but
858 may be due to reduced predation risk (Bakun, 2013; Bakun and Broad, 2003). Regardless, rapid
859 growth and survival through the larval period depends on mesozooplankton prey that are suitably
860 abundant and appropriately sized for these larval fishes. These prey taxa may be especially
861 sensitive to increased stratification and oligotrophication associated with climate change, making
862 investigation of their dynamics and production an important topic of research.

863 Mesozooplankton biomass in the oligotrophic GoM was found to be strikingly low in both
864 observations and PBM estimates with approximately an order of magnitude less biomass in
865 comparison to the shelf. PBM results clearly show that this low biomass condition arises from
866 bottom-up resource limitation. Our results suggest that low phytoplankton biomass in oligotrophic
867 regions, and particularly within Loop Current Eddies, may even lead to localized and episodic
868 regions where mean concentrations approach thresholds for triggering collapse of
869 mesozooplankton grazing. Prey limiting conditions for mesozooplankton and their predators
870 would be expected to occur more frequently in the GoM during warmer ocean conditions. Higher
871 sea surface temperatures and increased thermal stratification could suppress vertical mixing,
872 resulting in lower phytoplankton biomass. Indeed, while NEMURO-GoM exhibits severe nutrient
873 limitation in surface waters, the nitracline in the model is actually weaker and shallower than in
874 situ measurements during our cruises (A. Knapp, pers. comm.). This suggests potentially greater
875 nutrient scarcity in surface waters than the model predicts.

876 Despite extreme oligotrophy and dominance of picophytoplankton, our model shows that both PZ
877 and LZ populations can be sustained at modest abundances in the oligotrophic GoM. Indeed, the
878 substantial abundances of large (>1-mm) mesozooplankton equivalent to 60% of total
879 mesozooplankton, as determined by both observations and model results (Fig. 4A, C) is an
880 important result that helps explain the success of larval fish in the region. Our results show that
881 large mesozooplankton (PZ) occupy a trophic position of approximately 3.0 in the open ocean
882 GoM, which is marginally lower than on the shelf where they feed primarily on small
883 mesozooplankton (LZ). This change in trophic position is associated with a switch from carnivory
884 to feeding predominantly on heterotrophic protists in the oligotrophic region. This result highlights



885 the importance of intermediate protistan trophic levels in sustaining mesozooplankton
886 communities in oligotrophic regions. Indeed, both LZ and PZ are found to ingest proportionally
887 more SZ in the open ocean than on the shelf. Notably, these protistan trophic steps cannot be
888 quantified by routine field techniques because they have no pigment signature to make them visible
889 in gut pigment measurements and may not enrich in bulk ^{15}N leading to isotopic invisibility from
890 a trophic perspective (Gutiérrez-Rodríguez et al., 2014). Despite their importance, they are also
891 often missing from GoM ecosystem models (e.g., Fennel et al., 2011) and severely
892 underrepresented or even absent in complex mass-balance constrained models (Arreguin-Sanchez
893 et al., 2004; Geers et al., 2016). (Arreguin-Sanchez et al., 2004; Geers et al., 2016). New insights
894 may arise from focused investigation of phytoplankton→protist→crustacean linkages in
895 oligotrophic regions in both model and experimental studies. This will likely require the use of
896 next-generation technologies such as compound specific isotopic analyses of specific amino acids
897 that have been shown to enrich in protists (Décima et al., 2017) or DNA metabarcoding to assess
898 zooplankton gut contents (Cleary et al., 2016).

899 Another robust result of our model is the dynamic mesoscale variability in zooplankton abundance,
900 diet, and trophic position. These results highlight the impact of Loop Current Eddies and
901 mesoscale fronts and other features in modifying the biogeochemistry and food web of the GoM.
902 The existence of hot spots of productivity in the GoM has been seen in observational studies (Biggs
903 and Ressler, 2001), and the importance of GoM mesoscale features to fish larvae has been
904 hypothesized (Domingues et al., 2016; Lindo-Atichati et al., 2012; Rooker et al., 2012). Our
905 results suggest that these mesoscale structures may not only modify zooplankton abundances, but
906 also their trophic roles in the ecosystem, with implications for the transfer efficiencies of carbon
907 and nitrogen in the pelagic food web.

908 **5.0 Conclusions**

909 In this study, we used an extensive suite of in situ measurements to validate zooplankton dynamics
910 simulated by a PBM of the GoM. The model was able to capture broad patterns in phytoplankton
911 and mesozooplankton abundances, depth of the deep chlorophyll max, and growth and grazing
912 patterns. However, a distinct discrepancy was found between vertical profiles of measured and
913 modeled growth rates of phytoplankton. Despite testing multiple parameterizations for
914 phytoplankton growth and zooplankton grazing, no model solution was found that could simulate



915 a DCM with high biomass, but low growth rates. Future research is needed to diagnose these
916 dynamical issues for the DCM. Once validated, the PBM was used to investigate important
917 characteristics of the GoM mesozooplankton community. Our results suggest that small
918 mesozooplankton are largely herbivorous and large mesozooplankton largely carnivorous on the
919 GoM shelf. However, distinct changes in diet were noted in the oligotrophic GoM, where both
920 groups rely more on protistan prey. Changes in diet and secondary production highlighted in this
921 study have the potential to impact food availability to higher trophic levels, such as pelagic larval
922 fishes. In future work, we plan to couple our model to an individual-based model of larval fish to
923 evaluate the extent to which food resources limit larval fish feeding and growth along their
924 transport pathways in the GoM. Insights from this ecosystem-based approach may help to better
925 resolve stock-recruitment relationship that are needed for sustainable fisheries management and
926 improved stock-assessment models.



927 *Code and data availability.*

928 The model code and model validation data used in this study can be downloaded from GitHub at
929 <https://github.com/tashrops/NEMURO-GoM>. An idealized one-dimensional version of
930 NEMURO-GoM written in Matlab is also provided. The three-dimensional NEMURO-GoM
931 model outputs used in the study are available on the FSU-COAPS server in a Network Common
932 Data Form (NetCDF format).

933 *Author Contribution.*

934 TAS conducted all numerical simulations and model analysis. EPC, SLM, and AB provided
935 expertise on the hydrodynamic modeling. MRS and VJC provided expertise on the biogeochemical
936 model coding and tuning. RS, MRL, and GZ processed and provided data that was central to
937 NEMURO-GoM's validation. TAS wrote the manuscript with contributions from all authors.

938 *Competing interest.*

939 The authors declare that they have no conflict of interest

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