

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

3

4 Taylor A Shropshire^{1,2}, Steven L Morey³, Eric P Chassignet^{1,2}, Alexandra Bozec^{1,2}, Victoria J
5 Coles⁴, Michael R Landry⁵, Rasmus Swalethorp⁵, Glenn Zapfe⁶, Michael R Stukel^{1,2}

6

7 ¹Department of Earth Ocean and Atmospheric Sciences, Florida State University, Tallahassee, FL 32303

8 ²Center for Ocean-Atmospheric Prediction Studies, Florida State University, Tallahassee, FL

9 ³School of the Environment, Florida A&M University, Tallahassee, FL

10 ⁴University of Maryland Center for Environmental Science, PO Box 775 Cambridge MD 21613

11 ⁵Integrative Oceanography Division, Scripps Institution of Oceanography, 8622 Kennel Way, La Jolla, CA 92037

12 ⁶University of Southern Mississippi, Division of Coastal Sciences, Hattiesburg, MS, 39406

13

14 Correspondence: Taylor A. Shropshire (tshropshire@fsu.edu)

15 In preparation for: Biogeosciences

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 standing stocks cannot
19 be 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 biomass estimates from PBMs has been a major
22 challenge due to sparse observations. In this study, we configure a PBM for the Gulf of Mexico
23 (GoM) from 1993-2012 and validate the model against an extensive combination of biomass and
24 rate measurements. Spatial variability in a multi-decadal database of mesozooplankton biomass
25 for the northern GoM is well resolved by the model with a statistically significant ($p < 0.01$)
26 correlation of 0.90. Mesozooplankton secondary production for the region averaged $66 \pm 8 \times 10^6$
27 kg C yr^{-1} , equivalent to $\sim 10\%$ of net primary production (NPP), and ranged from 51 to 82×10^6 kg
28 C yr^{-1} , with higher secondary production inside cyclonic eddies and substantially reduced
29 secondary production in anticyclonic eddies. Model results from the shelf regions suggest that
30 herbivory is the dominant feeding mode for small mesozooplankton ($<1\text{-mm}$) whereas larger
31 mesozooplankton are primarily carnivorous. In open-ocean oligotrophic waters, however, both
32 mesozooplankton groups show proportionally greater reliance on heterotrophic protists as a food
33 source. This highlights an important role of microbial and protistan food webs in sustaining
34 mesozooplankton biomass in the GoM, which serves as the primary food source for early life
35 stages of many commercially important fish species, including tuna.

36 **1. Introduction**

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

55 Zooplankton populations have been identified as being vulnerable to impacts of a warming ocean
56 (Caron and Hutchins, 2013; Pörtner and Farrell, 2008; Straile, 1997), through direct temperature
57 effects on metabolic rates (Ikeda et al., 2001; Kjellerup et al., 2012) and thermal stratification-
58 driven alterations in food web structure and productivity (Landry et al., 2019; Richardson, 2008).
59 Studies aimed at monitoring and predicting zooplankton populations are therefore critical for
60 understanding the first-order effects of a warming ocean on marine ecosystems given the
61 importance of secondary production and the impact zooplankton have on biogeochemical cycling.
62 Despite their importance, zooplankton have been historically sampled with limited temporal and
63 spatial resolution. Unlike ocean hydrodynamics and phytoplankton variability, zooplankton
64 abundance cannot currently be estimated remotely from space. Thus, numerical models provide a
65 useful tool for synoptic assessments of zooplankton stocks on basin and global scales (Buitenhuis
66 et al., 2006; Sailley et al., 2013; Werner et al., 2007). Nonetheless, evaluating the accuracy of

67 zooplankton abundance estimates in numerical experiments, such as three-dimensional physical-
68 biogeochemical ocean models (PBMs), is a major challenge due to the sparse ship-based
69 observations in most regions (Everett et al., 2017). Consequently, PBMs are typically
70 predominately validated against surface chlorophyll (Chl) from remote sensing products (Doney
71 et al., 2009; Gregg et al., 2003; Xue et al., 2013).

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

90 The Gulf of Mexico (GoM) is a particularly suitable region for examining zooplankton dynamics
91 with PBMs. In the northern and central Gulf, zooplankton abundances have been extensively
92 measured for over three decades (1982-present) by the Southeast Area Monitoring and Assessment
93 Program (SEAMAP). Within the SEAMAP dataset, zooplankton biomass exhibits strong
94 spatiotemporal variability, reflecting complex physical circulation in the GoM. Circulation off the
95 shelf is characterized by substantial upper layer mesoscale activity driven primarily by the
96 energetic Loop Current (Forristall et al., 1992; Maul and Vukovich, 1993; Oey et al., 2005). In

97 contrast, coastal and shelf circulation patterns are predominantly wind-driven (Morey et al., 2003a,
98 2013). Freshwater discharged by the Mississippi River and other smaller rivers is frequently
99 entrained offshore by shelf break interaction with mesoscale features (e.g., anti-cyclonic loop
100 current eddies), leading to strong horizontal and vertical gradients in physical and biogeochemical
101 quantities (Morey et al., 2003b). Overlap of these gradients with the SEAMAP study region result
102 in zooplankton collections across biogeochemically heterogeneous environments, providing a
103 powerful model constraint. For instance, Chl ranges across three orders-of-magnitude ($\sim 0.01 - 10$
104 mg Chl m^{-3}) from oligotrophic to eutrophic waters.

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

123 In this study, we configured a PBM for the GoM to estimate zooplankton abundance and analyze
124 zooplankton community dynamics. The PBM is forced by three-dimensional hydrodynamic fields
125 from a data assimilative Hybrid Coordinate Ocean Model (HYCOM) hindcast of the GoM
126 (<http://www.hycom.org>) and is based on the biogeochemical model NEMURO (North Pacific

127 Ecosystem Model for Understanding Regional Oceanography; Kishi et al., 2007), which is
128 substantially modified here for application to the GoM. The model is integrated over 20-years
129 (1993-2012) and validated against an extensive combination of remote and in situ measurements
130 including total and size-fractionated mesozooplankton biomass and grazing rates, microzooplankton
131 grazing rates, phytoplankton growth rates and net primary production as well as validation of
132 surface chlorophyll and vertical profiles of chlorophyll and nitrate. Our goals were: 1) to develop
133 and validate a PBM to estimate mesozooplankton abundance, 2) to characterize the spatiotemporal
134 variability in mesozooplankton dietary composition, and 3) to quantify regional mesozooplankton
135 secondary production. We focus primarily on the oligotrophic open-ocean GoM, where prey (i.e.
136 zooplankton) availability may be limiting for fish, their larvae and other higher trophic levels.

137 **2 Methods and data**

138 **2.1 Biogeochemical model configuration**

139 **2.1.1 NEMURO model description**

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

153 Each biological state variable in NEMURO is an aggregated representation of taxonomically
154 diverse plankton groups that function similarly in the ecosystem. The phytoplankton community
155 is modeled as two functional types of obligate autotrophs: small phytoplankton (SP, predominantly
156 cyanobacteria and picoeukaryotes in the GoM) and large phytoplankton (LP, diatoms). Small

157 zooplankton (SZ) represent heterotrophic protists, and metazoan zooplankton are divided into
158 suspension-feeding mesozooplankton (LZ) and predatory zooplankton (PZ). Here, we assume that
159 LZ and PZ are non-migratory. Heterotrophic bacteria are implicitly represented by temperature-
160 dependent decomposition rates, which represent nitrification and remineralization processes.
161 NEMURO uses nitrogen as a model “currency” since it is the major limiting macronutrient in
162 much of the ocean. Silica is also included as a potentially co-limiting nutrient for diatoms (i.e. LP).

163 By default, sinking in NEMURO is restricted to PON and Opal, and benthic processes are not
164 included. Here, because of the large shelf area in the GoM, we implemented a simple diagenesis
165 of PON/Opal to NO_3/SiO_4 and removal of PON/Opal through sedimentation, where 1% of the flux
166 sinking out of bottom cell was removed and 10% converted back into NO_3/SiO_4 . However, we
167 found that this had no significant impact on the simulated surface Chl or mesozooplankton biomass
168 on the shelf. The inclusion of a more complex sediment diagenesis model (including
169 denitrification) would have added further realism (Fennel et al., 2011). However, our main focus
170 was to evaluate zooplankton dynamics in the oligotrophic region where higher trophic levels that
171 depend on mesozooplankton secondary production may experience food limitation and where
172 benthic processes are negligible.

173 NEMURO was chosen for the present study because it distinguishes SZ, LZ and PZ, permitting a
174 detailed analysis of dynamics for multiple functional types in the GoM zooplankton community.
175 During initial GoM simulations, default NEMURO parameterizations, configured for the North
176 Pacific (Kishi et al., 2007), substantially overestimated surface nitrate, surface Chl, and
177 mesozooplankton biomass relative to observations. We attribute these differences to: 1)
178 substantially higher temperatures in the GoM compared with the North Pacific, which significantly
179 increase decomposition and growth rates in the model resulting in higher nutrient recycling and
180 elevated near-surface stocks of phytoplankton and zooplankton, and 2) distinct differences in
181 taxonomic composition of phytoplankton and zooplankton communities in the GoM and North
182 Pacific, with significant differences in key parameter values associated with growth and grazing.

183 For more details on the specific processes represented and the interactions between state variables
184 in NEMURO, we direct readers to Kishi et al. (2007). All model equations are provided in the
185 supplement to this manuscript. Biogeochemical model forcing, initial and open boundary

186 conditions are also outlined in Supplement **S1**. Briefly, daily average shortwave radiation fields
187 obtained from Climate Forecast System Reanalysis (CFSR) were used to force light limitation of
188 phytoplankton. Once a final parameter set was determined (see section 2.1.3), initial and open
189 boundary conditions for all state variables were prescribed from a spun up idealized one-
190 dimensional version of NEMURO-GoM. After initializing, the three-dimensional model was spun
191 up over four years before conducting the full 20-year experiment. River nutrient input from the
192 Mississippi was prescribed using nitrate samples collected by United States Geological Survey
193 (USGS) and due to a lack of observations for other rivers was prescribed for all 37 rivers
194 represented in the model.

195 **2.1.2 Modifications to default NEMURO model**

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

204 Next, quadratic mortality was replaced with linear mortality for all biological state variables with
205 the exception of predatory zooplankton (PZ). In biogeochemical models, quadratic mortality is
206 often used for numerical stability and/or to represent implicit loss terms to an un-modeled parasite
207 or predator that covaries in abundance with its prey (e.g. viral lysis of phytoplankton or predation
208 by un-modeled higher predators) (Anderson et al., 2015). However, grazing mortality is explicitly
209 modeled in NEMURO and viral mortality is generally not a substantial loss term for bulk
210 phytoplankton (Staniewski and Short, 2018). Quadratic mortality was retained for PZ, to account
211 for predation pressure of un-modeled predators (e.g. planktivorous fish). During the model tuning
212 process, we found that removal of quadratic mortality from the four other plankton functional
213 groups was an important parameterization change that allowed the model to simulate more realistic
214 mesozooplankton biomass in the oligotrophic GoM (see Discussion).

215 The default ammonium inhibition term and light limitation functional form in NEMURO were
216 replaced in NEMURO-GoM with more widely adopted parameterizations. The exponential
217 ammonium inhibition term in the nitrate limitation function was replaced with the term described
218 by Parker (1993), as has been done in previous PBM studies (Fennel et al., 2006) due to the non-
219 monotonic behavior of the default NEMURO ammonium inhibition term. At high NO_3
220 concentrations, the default term is known to generate unrealistic phytoplankton nutrient uptake
221 patterns in which total nutrient uptake (i.e. uptake of NO_3 + uptake of NH_4) can actually decrease
222 despite increases in NH_4 (and constant NO_3).

223 Light limitation in NEMURO is based on an optimal light parameterization that implicitly includes
224 photoinhibition. This formulation was replaced with the Platt et al. (1980) functional form that
225 allows one to explicitly control the amount of photoinhibition, which can be important in the GoM
226 where surface irradiances are high. Additionally, the Platt functional form is commonly used and
227 thus parameter values are easier to find for comparison (e.g. initial slope of the PI curve (α)). This
228 formulation is also implemented in newer versions of NEMURO, such as the code used in the
229 Regional Ocean Modeling System (ROMS) NEMURO biogeochemical package.

230 Finally, to account for photoacclimation and more accurately simulate Deep Chlorophyll
231 Maximum (DCM) dynamics, we replaced the constant C:Chl parameter with a variable C:Chl
232 model where ratios for SP and LP were allowed to vary based on the formulation described by Li
233 et al. (2010), which considers both light and nutrient limitation (see Supplemental). The Li et al.
234 (2010) equations build on a previously constructed dynamic regulatory model of phytoplankton
235 physiology which describes C:Chl variability under balanced growth and nutrient saturated
236 conditions at constant temperature (see Geider et al., 1998)). Herein, “default” NEMURO includes
237 the modified ammonium inhibition, light formulation, and variable C:Chl model.

238 **2.1.3 NEMURO-GoM model tuning procedure**

239 In total, NEMURO includes 71 parameters, 23 of which were modified in the present study. For
240 initial model tuning, we used an idealized one-dimensional model designed to mimic the
241 oligotrophic GoM. To guide our tuning procedure, we relied on a semi-quantitative approach
242 where the one-dimensional model solution was evaluated based on five ecosystem benchmarks.
243 Target values for benchmarks and other ecosystem attributes were determined from observations

244 or a theoretical basis. Ecosystem benchmarks included: surface Chl, mesozooplankton biomass,
245 DCM depth, DCM magnitude, and SP:LP ratio. Surface Chl and mesozooplankton biomass were
246 chosen as benchmarks to evaluate the realism of plankton biomass in the model. The DCM depth
247 and magnitude were chosen to evaluate the vertical structure of the simulated ecosystem, and
248 SP:LP ratio was used to gauge the realism of the plankton community composition (i.e. high SP:LP
249 is expected in the oligotrophic GoM). The model was also tuned by considering the relative
250 magnitudes of loss terms for phytoplankton (grazing, mortality, respiration, and excretion), total
251 protistan zooplankton grazing relative to mesozooplankton grazing, as well as surface and deep
252 nitrate concentrations. We outline each parameter change, justification and the resulting impact on
253 the ecosystem benchmarks simulated by the idealized one-dimensional model in Supplement **S3**.
254 Where possible, we modified parameters in groups so that relative changes were consistent
255 throughout the model (e.g. doubling all zooplankton mortality terms). After tuning in the one-
256 dimensional model, parameter sets were implemented into the full three-dimensional model where
257 additional tuning was performed. Once a final parameter set was determined we conducted a
258 parameter sensitivity analysis over 18 individual experiments to identify impacts of parameter
259 changes from default NEMURO values (**S4**).

260 **2.2 Physical model configuration**

261 **2.2.1 Description of the offline numerical environment**

262 To run large numbers of three-dimensional simulations efficiently for basin-scale tuning,
263 NEMURO-GoM was run offline using the MITgcm offline tracer advection package. MITgcm
264 was selected as it contains convenient packages for running offline simulations (McKinley et al.,
265 2004). That is, the dynamical equations of motion are not computed during the NEMURO-GoM
266 integration, but rather the physical prognostic variables (i.e., temperature, salinity and three-
267 dimensional velocity fields) are prescribed from daily-averaged flow fields saved from a previous
268 hydrodynamic model integration. This allows the recycled use of flow fields leaving only the tracer
269 equations to be computed. In the offline MITgcm package, the prognostic variables provide input
270 to an advection scheme and mixing routine that conservatively handles offline advection and
271 diffusion of the biogeochemical tracer fields. MITgcm has many options for linear and non-linear
272 advection schemes. Here we use a 3rd order direct space time flux limiting scheme. Sub grid-scale
273 mixing of the biogeochemical fields is handled offline through the nonlocal K-Profile
274 Parameterization (KPP) package based on mixing schemes developed by Large et al. (1994). For

275 more information about the MITgcm packages, we direct readers to the MITgcm manual
276 (<http://mitgcm.org/>).

277 There are two main advantages to running PBMs in an offline environment: 1) the momentum
278 equations are not integrated during the model run; and 2) the physical time step is no longer bound
279 by the dynamical Courant–Friedrichs–Lewy (CFL) numerical stability criterion, which together
280 significantly reduces the computational cost. Instead, the stability of the tracer advection scheme
281 and time scales needed to resolve biological/physical processes of interest set the limits on the time
282 steps and prescription frequencies of flow fields. When the physical time step is shorter than the
283 flow field prescription frequency, a simple linear interpolation of the flow fields is performed
284 between time steps. Offline simulations of tracer advection have been found to closely resemble
285 online runs (that is, computed together with the integration of the hydrodynamic model’s
286 prognostic equations) when the three-dimensional flow fields are prescribed at a frequency that is
287 at or below the inertial period ($T = 2\pi/f$, $T_{GoM} > 24 \text{ hr}$) for a region (Hill et al., 2005).

288 In the present study, the offline time step (30 minutes) is an order of magnitude greater than the
289 hydrodynamic model’s (HYCOM-GoM, described in Section 2.2.2) baroclinic time step (120
290 seconds). For reference, HYCOM-GoM required ~76 days to run to completion on 64 parallel
291 cores. These time requirements would increase considerably with the 11 additional
292 biogeochemical tracers used in NEMURO. In contrast, NEMURO-GoM ran significantly faster,
293 taking a total of ~50 hours on 80 parallel cores. Offline models offer a valuable tool for integrating
294 PBMs particularly as spatial resolution and complexity in these models continues to increase (e.g.,
295 DARWIN (Follows et al., 2007), GENOME (Coles et al., 2017)). While computationally
296 advantageous, however, offline simulations have inherently greater input and output (I/O)
297 demands that can become bottlenecks in some applications. Issues with conservation can also arise
298 as three-dimensional advection schemes are only approximately positive definite.

299 **2.2.2 Description of the offline dynamical fields**

300 The NEMURO-GoM model is “forced” by daily averaged three-dimensional velocity, temperature
301 and salinity fields from a pre-existing 20-year (1993-2012) HYCOM (HYbrid Coordinate Ocean
302 Model) (Chassignet et al., 2003) regional GoM hindcast (H-GoM). H-GoM is based on version
303 2.2.99B of the HYCOM code, originally provided by the Naval Oceanographic Office

304 (NAVOCEANO) Major Shared Resource Center. H-GoM was run at 1/25th degree (~4 km)
305 horizontal resolution with 36 vertical hybrid coordinate layers and assimilated historic, in situ and
306 satellite observations. The domain encompasses the entire GoM and extends south of the Mexican-
307 Cuba Yucatan channel to 18 °N and as far east as 77 °W (**Fig. 1**). Further details on H-GoM
308 (experiment ID: GOMu0.04/expt_50.1), including model forcing and the main model
309 configuration file (i.e. blkdat.input_501), can be found at <https://www.hycom.org>.

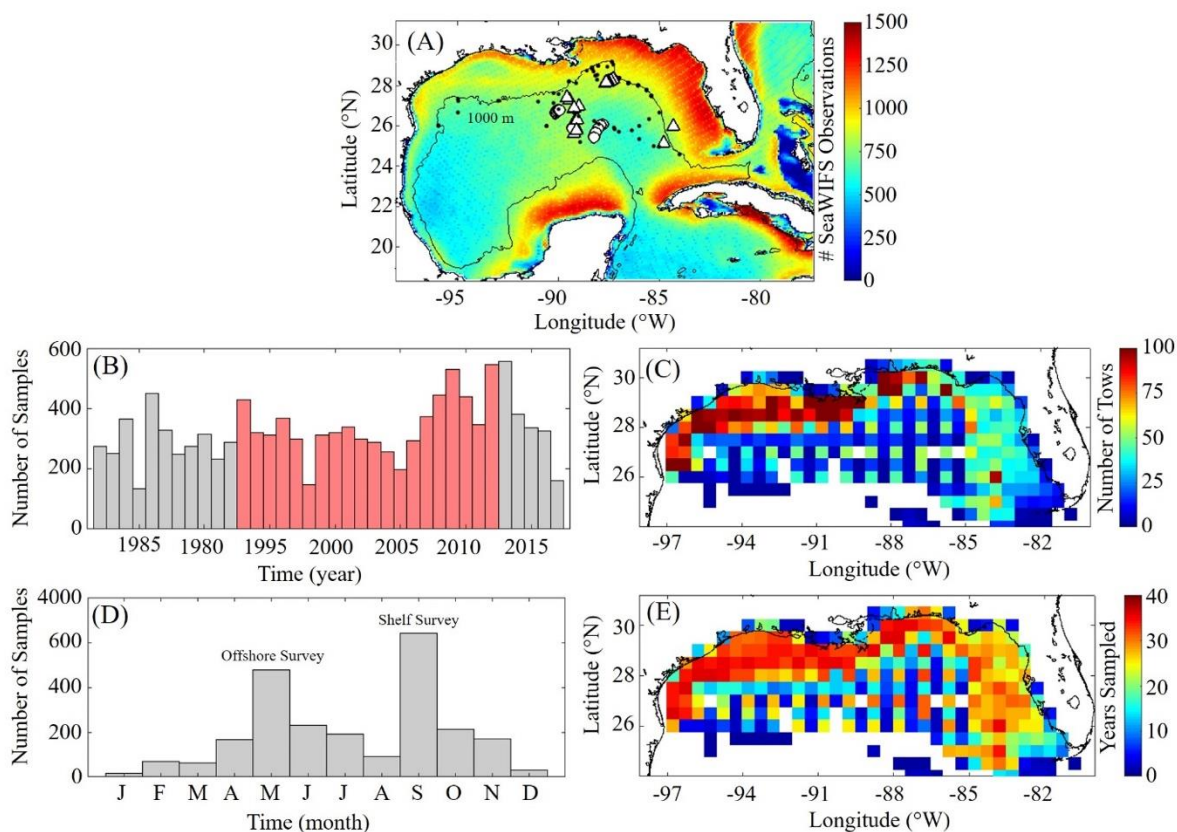
310 The H-GoM flow fields were mapped from the HYCOM native hybrid vertical coordinate to z-
311 levels used by the MITgcm. NEMURO-GoM was configured for 29 vertical z-levels (10-m
312 intervals from 0-150 m, 25-m intervals from 150-300 m, 50-m intervals from 300-500m, and 1000
313 m, 2000 m, ~4000 m).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

323 **2.3 Model validation**

324 **2.3.1 Surface chlorophyll observations**

325 A benchmark for surface Chl was determined using the Sea-Viewing Wide Field-of-View Sensor
326 (SeaWiFS) product from the Ocean Biology Processing Group (OBPG) of the National
327 Aeronautics and Space Administration (NASA). The product used here is the mapped, level-3,
328 daily, 9-km resolution images from 4 September 1997 to 10 December 2010 processed according
329 to the algorithm of Hu et al. (2012). To compute model-data point-to-point comparisons, we take
330 the corresponding daily-averaged simulated surface Chl field and interpolate to the SeaWiFS grid
331 before applying the daily cloud coverage mask corresponding to the matching SeaWiFS image. In
332 total 4,291 daily images consisting of 22,244,513 non-zero cell values (herein referred to SeaWiFS

333 measurements) were used to validate NEMURO-GoM. Approximately 500-1200 daily model-data
 334 point-to-point comparisons were made for each SeaWIFS grid cell (**Fig 1**).



335
 336 **Figure 1 (A-E):** Spatial and temporal coverage of observational data sets used for model
 337 validation. Total number of non-zero values available in daily SeaWIFS images from September
 338 1997 to 10 December, 2010 along with nitrate profiles from the World Ocean Database (black
 339 dots) and the location of in situ measurements collected during May 2017 (circles) and May 2018
 340 (triangles) process study cruises (A). Total annual sampling of the SEAMAP surveys from 1983-
 341 2017 with samples overlapping with the PBM simulation period denoted in red (B). Samples
 342 organized by month (D). Total sample density within each $0.5^\circ \times 0.5^\circ$ box (C) along with the
 343 number of years with at least one sample (E). 1000 m isobaths and coastline are denoted by black
 344 continuous lines.

345 2.3.2 Mesozooplankton biomass observations

346 To evaluate model mesozooplankton biomass estimates, we used plankton tows collected during
 347 Southeast Area Monitoring and Assessment Program (SEAMAP) surveys in the northern and

348 central GoM. In total, 11,781 plankton tows were collected from 1983-2017, with two main annual
349 surveys in the spring (offshore) and fall (shelf) (**Fig. 1**). On average, SEAMAP collected
350 approximately 300 samples per year with a specific sampling array offshore and more general
351 sampling coverage on the shelf. In total, 6,835 samples were used for direct point-to-point model-
352 data comparisons. Samples were collected using standard gear consisting of a 61-cm diameter
353 bongo frame fitted with two 333- μm mesh nets. The nets were fished in a double-oblique tow
354 pattern from the surface down to 200 m or 5 m off the bottom and back to the surface. Simultaneous
355 samples were also collected using a 202- μm mesh net during 82 tows. Of these samples, roughly
356 half were collected in the oligotrophic GoM. The average ratio between biomass measured in the
357 333- and 202- μm bongo tows (0.5093 ± 0.12) was used to convert 333- μm samples so that direct
358 comparisons could be made with model mesozooplankton (LZ+PZ) biomass fields. Zooplankton
359 biomass was originally quantified as displacement volumes (DV). Carbon mass (CM) equivalents
360 were subsequently calculated as $\log_{10}(\text{CM}) = (\log_{10}(\text{DV}) + 1.434)/0.820$ (Wiebe, 1988; Moriarty
361 and O'Brien, 2013).

362 For comparison to in situ biomass measurements size ranges were assumed for zooplankton state
363 variables (see section 2.3.4). In NEMURO-GoM, SZ represent heterotrophic protists (e.g. ciliates)
364 and early stages of mesozooplankton, which are typically $< 200 \mu\text{m}$ in the ocean. Hence, SZ are
365 assumed to range in size from 2-200 μm . LZ are considered to represent small mesozooplankton
366 ranging in size from 0.2 to 1.0 mm while PZ represent large mesozooplankton ranging in size from
367 1.0 to 5.0 mm. For comparison to the SEAMAP climatology the model LZ and PZ fields were first
368 converted to units of carbon assuming Redfield C:N ratio and summed over the entire simulation
369 before being depth averaged to the bottom or 200 m. For point-to-point model-data comparisons,
370 total mesozooplankton biomass fields were interpolated to SEAMAP sample locations/times and
371 then depth averaged to the corresponding sample tow depth.

372 **2.3.3 Observed vertical profiles of chlorophyll and nitrate**

373 Depth profiles of Chl were also collected during SEAMAP surveys using a SeaBird WETStar
374 fluorometer attached to a CTD. Calibration of the fluorimeter was infrequent, and thus profiles
375 were used to determine the depth of the fluorescence maxima for comparisons to DCM depths in
376 the model. In total, 2,435 profiles were collected from 2003 to 2012, with 1,052 profiles overlying

377 bottom depths >1000 m. Profiles were available for earlier SEAMAP surveys; however, no
378 standard QA/QC protocol for fluorometer data was in place prior to 2003.

379 To evaluate DCM magnitudes in the model, we used 145 fluorescence profiles collected during
380 May 2017 and 2018 process study cruises (see section 2.3.4). The fluorometer was attached to a
381 CTD and calibrated using 126 in situ Chl samples. Chl concentrations were determined from
382 filtered samples collected at depths ranging from 5 to 115 m using High Performance Liquid
383 Chromatography (HPLC). Since the cruise sampling does not overlap with our NEMURO-GoM
384 simulation period, model-data comparisons were made for all 20 years of the model run using
385 sample locations and time of the year. This was also done with other field measurements from the
386 process cruises (see section 2.3.4).

387 For model-data comparisons of nitrate, we utilized profiles from the World Ocean Database
388 (WOD). In total, 96 profiles were available during our simulation period and located in the
389 oligotrophic GoM (>1000 m isobath). Profiles were collected during all months except March and
390 December with the majority of samples collected during May, July and August (**Fig. 1A**).

391 **2.3.4 Biomass and rate measurements from process study cruises**

392 Although in situ rate measurements are made much less frequently than biological standing stock
393 measurements, they offer very powerful constraints for validating the internal dynamics of a
394 biogeochemical model (Franks, 2009). Consequently, we made phytoplankton and zooplankton
395 rate measurements on two cruises in the open ocean GoM in May 2017 and 2018 and used these
396 measurements to validate the model (**Fig. 1A**). On the process study cruises, we utilized a quasi-
397 Lagrangian sampling scheme to investigate plankton dynamics in the oligotrophic GoM. Two
398 drifting arrays (one sediment trap array and one in situ incubation array) were deployed to serve
399 as a moving frame of reference during ~4-day studies (“cycles”) characterizing the water parcel
400 (Landry et al., 2009; Stukel et al., 2015). During these cycles, we measured daily profiles of Chl,
401 photosynthetically active radiation, phytoplankton growth rates and productivity, protistan grazing
402 rates, and size-fractionated mesozooplankton biomass and grazing rates.

403 Size-fractionated mesozooplankton biomass and grazing rates were determined from daily day-
404 night paired oblique ring-net tows (1-m diameter, 202- μ m mesh). In total, 40 oblique bongo net
405 tows (16 in 2017 and 24 in 2018) sampled the oligotrophic GoM mesozooplankton community

406 from near surface to a depth ranging from 100-135 m. Upon recovery, the sample was anesthetized
407 using carbonated water, split using a Folsom splitter, filtered through a series of nested sieves (5,
408 2, 1, 0.5, and 0.2 mm), filtered onto pre-weighed 200- μ m Nitex filters, rinsed with isotonic
409 ammonium formate to remove sea salt, and flash frozen in liquid nitrogen. In the lab, defrosted
410 samples were weighed for total wet weight, and subsampled in duplicate (wet weight removed)
411 for gut fluorescence analyses. The remaining wet sample was dried and subsequently reweighed
412 and combusted for CHN analyses to determine total dry weight and C and N biomasses. Gut
413 fluorescence subsamples were homogenized using a sonicating tip, extracted in acetone, and
414 measured for Chl and phaeopigments using the acidification method. The phaeopigment
415 concentrations in the zooplankton guts were the basis for calculated grazing rates using gut
416 turnover times based on temperature relationships for mixed zooplankton assemblages. For
417 additional details, see Décima et al. (2011) and Décima et al. (2016).

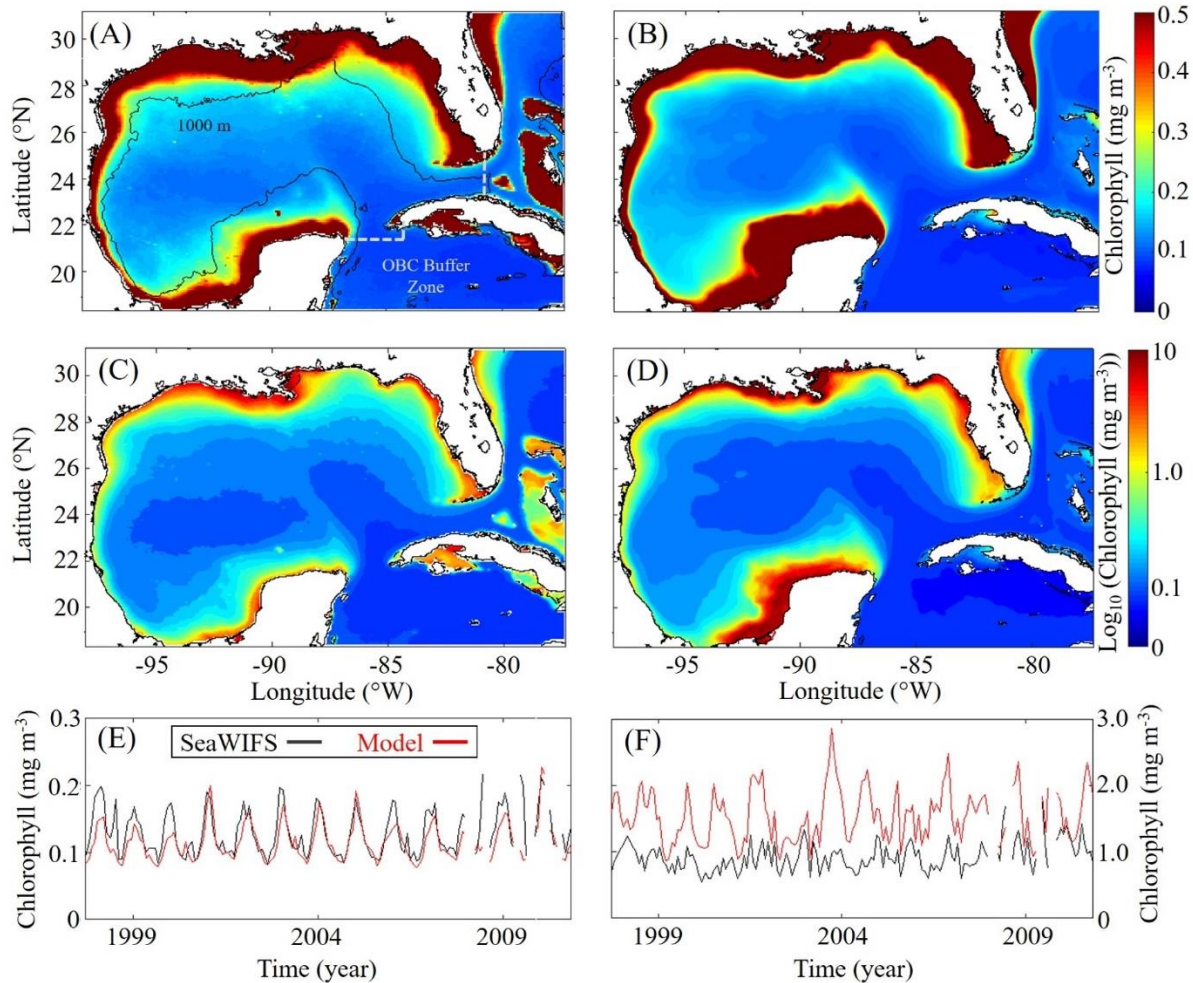
418 Protistan grazing rates were measured using the two-point, “mini-dilution” variant of the
419 microzooplankton grazing dilution method (Landry et al., 1984, 2008; Landry and Hassett, 1982).
420 Briefly, one 2.8-L polycarbonate bottle was gently filled with whole seawater taken from six
421 depths (from the surface to the depth of the mixed layer). A second 2.8-L bottle was then filled
422 with 33% whole seawater and 67% 0.2- μ m filtered seawater. Both bottles were then placed in
423 mesh bags and incubated in situ at natural depths for 24 h. These experiments were conducted on
424 each day of the ~4-day cycle. After 24 h, the bottles were retrieved, filtered onto glass fiber filters,
425 and Chl concentrations were determined using the acidification method (Strickland and Parsons.,
426 1972). Net growth rates ($k = \ln(\text{Chl}_{\text{final}}/\text{Chl}_{\text{init}})$) in each bottle were determined relative to initial Chl
427 samples. Phytoplankton specific mortality rates resulting from the grazing pressure of protists were
428 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 the
429 growth rate in the control bottle. Phytoplankton specific growth rates were calculated as $\mu = k_0 +$
430 m . For additional details, see Landry et al. (2016) and Selph et al. (2016). Phytoplankton net
431 primary production was quantified at the same depths by $\text{H}^{13}\text{CO}_3^-$ uptake experiments. Triplicate
432 2.8-L polycarbonate bottles and a fourth “dark” bottle were spiked with $\text{H}^{13}\text{CO}_3^-$ and incubated in
433 situ for 24 h at the same sampling depths as for the dilution experiments. Samples were then filtered
434 and the $^{13}\text{C}:^{12}\text{C}$ ratios of particulate matter determined by isotope ratio mass spectrometry.

435 **3.0 Results**

436 3.1 Surface chlorophyll model-data comparisons

437 Model surface Chl estimates were found to agree closely with satellite observations reproducing
438 patterns in both the oligotrophic and shelf region (**Fig. 2**). Spatial covariance between SeaWIFS
439 climatology and model surface Chl climatology (calculated with daily cloud cover mask applied)
440 is statistically significant ($p < 0.01$) with a correlation (ρ) of 0.72. When model estimates are
441 compared to all 22,244,513 SeaWIFS measurements at corresponding times and locations (i.e.
442 daily grid cell pairs), we find a ρ value of 0.50 ($p < 0.01$). To facilitate more detailed model-data
443 comparisons, the GoM domain was divided into an oligotrophic region (≥ 1000 m bottom depth)
444 and a shelf region (< 1000 m bottom depth). In the oligotrophic region, the correlation between
445 model-data daily grid cell pairs is significant but weak ($\rho = 0.17$, $p < 0.01$) as a result of relatively
446 low large-scale spatial variability, and hence dominance at the mesoscale. However, bias is quite
447 low (-0.014 mg Chl m^{-3}), equivalent to 10% of the observed mean. In the shelf region, the
448 correlation is higher ($\rho = 0.47$, $p < 0.01$) yet the bias is greater ($+0.90$ mg Chl m^{-3}), equivalent to
449 92% of the mean. Previous GoM studies have determined ρ values for monthly averages, which
450 we calculate here for comparison. Based on 30-day averages, the ρ values are 0.70 ($p < 0.01$) for
451 the oligotrophic region and 0.26 ($p < 0.01$) for the shelf region.

452 In addition to resolving the dominant spatiotemporal variability, the model also captures the
453 amplitude of the seasonal surface Chl signal reasonably well. In the oligotrophic region, the model
454 accurately estimates the observed annual surface Chl minimum (Model: 0.065 ± 0.005 vs.
455 SeaWIFS: 0.065 ± 0.007 mg Chl m^{-3}) while slightly underestimating the observed annual
456 maximum (Model: 0.47 ± 0.15 vs. SeaWIFS: 0.75 ± 0.55 mg Chl m^{-3}). When model estimates for
457 the entire oligotrophic region are taken into account (i.e. not restricted to satellite measurement
458 locations and times), the annual minimum develops in early September, and the maximum
459 develops in late January (**Table 1**). In the shelf region, greater model-data mismatch exists for
460 surface Chl, with the model overestimating the observed annual minimum by 15% (Model: $0.23 \pm$
461 0.09 vs. SeaWIFS: 0.20 ± 0.07 mg Chl m^{-3}) and the observed annual maximum by 102% (Model:
462 8.09 ± 1.31 vs. SeaWIFS: 4.01 ± 1.23 mg Chl m^{-3}). Here, we find the annual surface Chl seasonal
463 cycle almost completely out of phase with the oligotrophic region, with the annual minimum
464 developing in early February and the annual maximum developing at the end of July (**Table 1**).



465

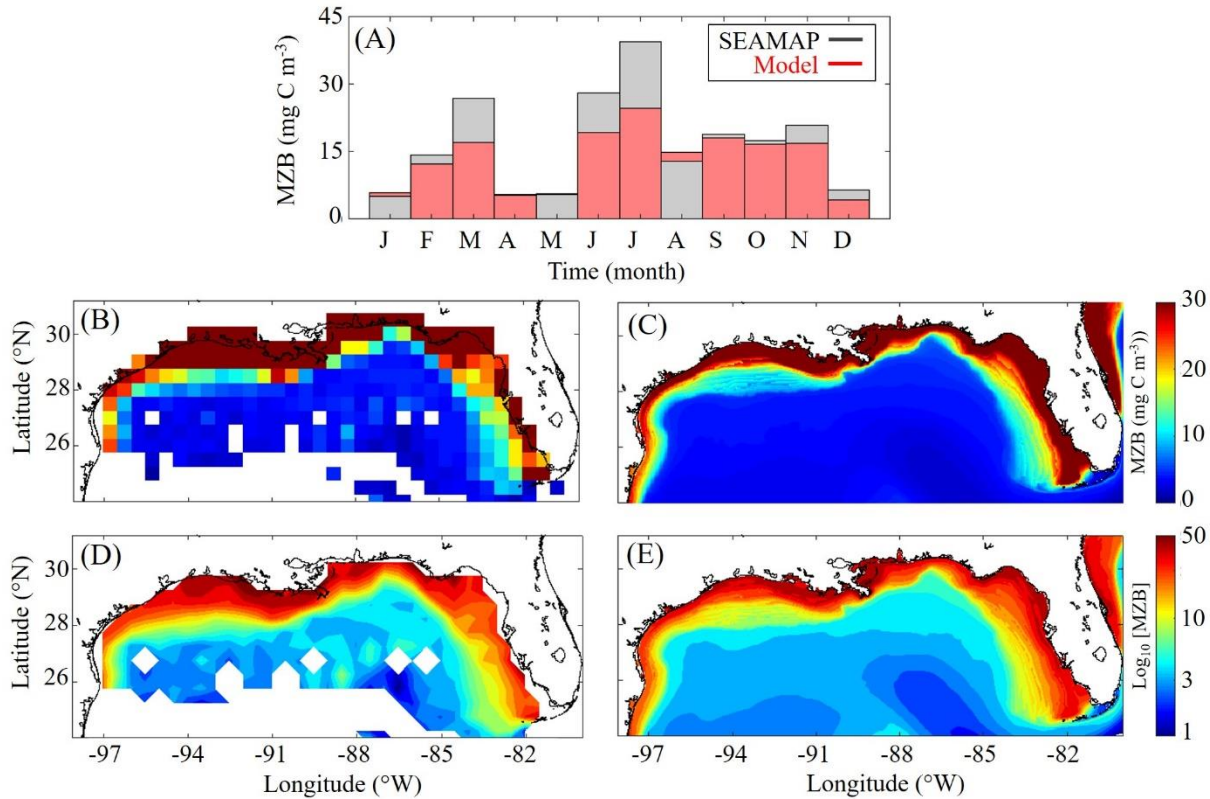
466 **Figure 2 (A-F):** Comparison of surface chlorophyll (mg m^{-3}) between SeaWIFS observations (left
 467 column) and model (right column) from 4 September 1997 to 10 December 2010. Surface
 468 chlorophyll climatology computed from daily SeaWIFS images (A) and the corresponding \log_{10}
 469 field (C). Surface chlorophyll climatology computed from daily averages over the entire model
 470 simulation (1993-2012) (C) and the corresponding \log_{10} field (D). Time series of simulated 30-
 471 day average surface chlorophyll based on SeaWIFS observations (black) and model (red) for the
 472 oligotrophic region (grid cells with bottom depths ≥ 1000 m) (E) and shelf region (grid cells with
 473 bottom depths < 1000 m) (F).

474 3.2 Regional mesozooplankton biomass model-data comparisons

475 Model mesozooplankton biomass (i.e. LZ + PZ) fields also agree closely with observations in both
 476 the oligotrophic and shelf region (**Fig. 3**). Spatial covariance between SEAMAP climatology and

477 model is statistically significant ($p < 0.01$) with a ρ value of 0.90. When model estimates are
478 compared to SEAMAP tows at corresponding sample times and locations for the 6,835
479 measurements in the simulation period, the ρ value is 0.55 ($p < 0.01$). In the oligotrophic region,
480 the model slightly overestimates mesozooplankton biomass (Model: $4.09 \pm 1.82 \text{ mg C m}^{-3}$ vs.
481 SEAMAP: $3.52 \pm 3.44 \text{ mg C m}^{-3}$) with ρ value of 0.23 ($p < 0.01$) with a bias of 0.57 mg C m^{-3} ,
482 equivalent to 16% of the observed mean. Conversely, in the shelf region the model underestimates
483 mesozooplankton biomass (Model: $17.40 \pm 13.58 \text{ mg C m}^{-3}$ vs. SEAMAP: $20.91 \pm 24.62 \text{ mg C m}^{-3}$),
484 with a ρ value of 0.49 ($p < 0.01$) and a bias of -3.5 mg C m^{-3} , equivalent to 17% of the observed
485 mean. Model estimates and SEAMAP measurements also compare well with total
486 mesozooplankton biomass measurements (0.2-5 mm) collected in the oligotrophic region during
487 the process study cruises (Model: $5.55 \pm 2.87 \text{ mg C m}^{-3}$ vs. Cruise: $4.33 \pm 2.28 \text{ mg C m}^{-3}$).

488 Although seasonal cycles in the oligotrophic and shelf regions could not be derived from the
489 SEAMAP dataset given the significant differences in sampling locations over the course of a year,
490 we investigated model-data mismatches for each month. The model closely matches or slightly
491 underestimates mesozooplankton biomass for most of the year, with the exception of January, May
492 and August (**Fig. 3A**). The largest model-data mismatch occurs during March, June, July and
493 December, when the model underestimates mesozooplankton biomass by approximately 35%.
494 Unlike surface Chl, the total mesozooplankton biomass (i.e. depth-integrated) seasonality is
495 similar in both regions of the GoM. In the oligotrophic region, the annual biomass minimum
496 (maximum) occurs at the beginning of January (middle of May), while in the shelf region, the
497 annual minimum (maximum) occurs in late December (end of May) (**Table 1**).



498

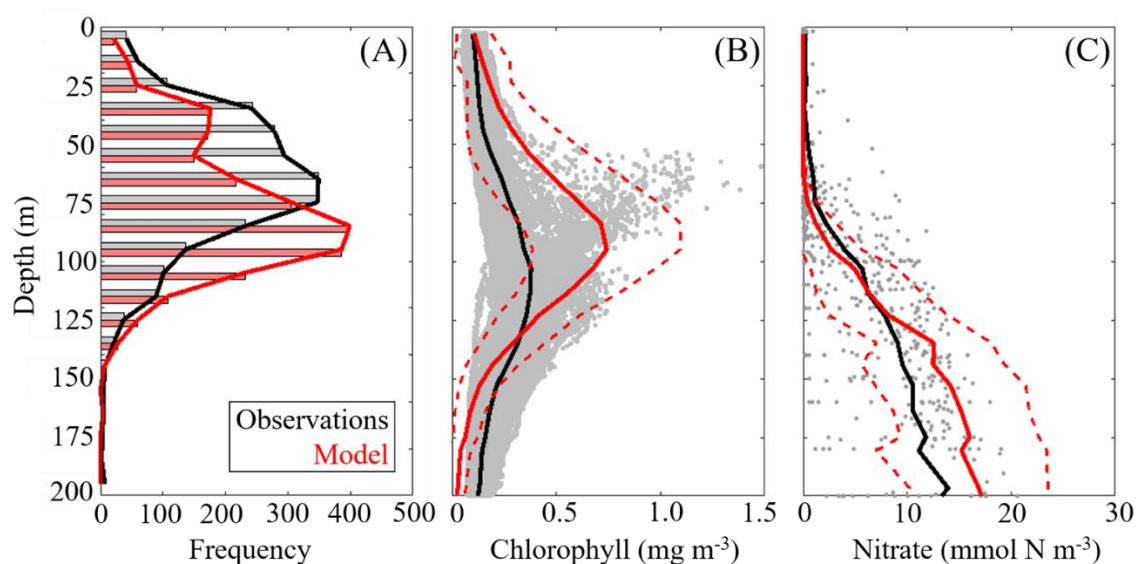
499 **Figure 3 (A-E):** Comparison of climatological depth-averaged (0–200 m) mesozooplankton
 500 biomass (MZB, mg C m^{-3}) between SEAMAP observations (B&D) and model (C&E). Monthly
 501 average MZB in SEAMAP observations (black) and model (red) (A) (monthly variability is not
 502 representative of MZB seasonality because sampling locations change between months). MZB
 503 climatology computed from SEAMAP plankton tows (B) and the corresponding \log_{10} field (D).
 504 MZB climatology computed from daily averages over the entire model simulation (1993–2012)
 505 (C) and the corresponding \log_{10} field (E).

506 3.3 Chlorophyll and nitrate profile model-data comparisons

507 To validate the vertical structure of the simulated ecosystem, we utilized observed profiles of
 508 fluorescence, Chl, and nitrate. When simulated DCM depths were compared to all 2,435
 509 SEAMAP fluorescence profiles, we find a statistically significant correlation ($\rho = 0.59$, $p < 0.01$)
 510 with the observed maximum fluorescence depth. The maximum fluorescence depth ranged from
 511 the surface to 143 m while model values show a similar variability ranging from the surface to 163
 512 m (**Fig. 4A**). In the oligotrophic region, the model overestimates the DCM depth (Model: 95 ± 20
 513 m vs. SEAMAP: 80 ± 25 m) and has a ρ value of 0.38 ($p < 0.01$) with a bias of 15 m, equivalent

514 to 19% of the observed mean. In the shelf region, the model also overestimates DCM depth
 515 (Model: 63 ± 26 m vs. SEAMAP: 53 ± 23 m) and has a p value of 0.49 ($p < 0.01$) with a bias of
 516 10 m, equivalent to 19% of the observed mean.

517 In contrast, the model slightly underestimated the DCM depth when compared to calibrated
 518 fluorescence profiles collected during the process cruises (Model: 100 ± 18 m vs. Observed: $107 \pm$
 519 21 m) (**Fig. 4B**). In terms of magnitude, the model overestimates DCM Chl (Model: 0.74 ± 0.35
 520 mg Chl m^{-3} vs. Observed: $0.38 \pm 0.13 \text{ mg Chl m}^{-3}$), although most of the observations fall within
 521 one standard deviation of the model average. Despite this model-data mismatch, simulated nitrate
 522 profiles closely match profiles from the World Ocean Database (WOD). In both model and
 523 observations, the mean nitracline occurred at approximately 75 m (**Fig. 4C**). On average, model
 524 nitrate tended to be lower at the surface and higher at depth relative to observations. Above the
 525 nitracline, model nitrate was $0.071 \pm 0.39 \text{ mmol N m}^{-3}$ while observed nitrate was 0.55 ± 1.29
 526 mmol N m^{-3} . Below 200 m, model and data show better agreement, with deep nitrate in the model
 527 of $24.92 \pm 3.28 \text{ mmol N m}^{-3}$ compared to $23.55 \pm 5.21 \text{ mmol N m}^{-3}$ in WOD profiles.



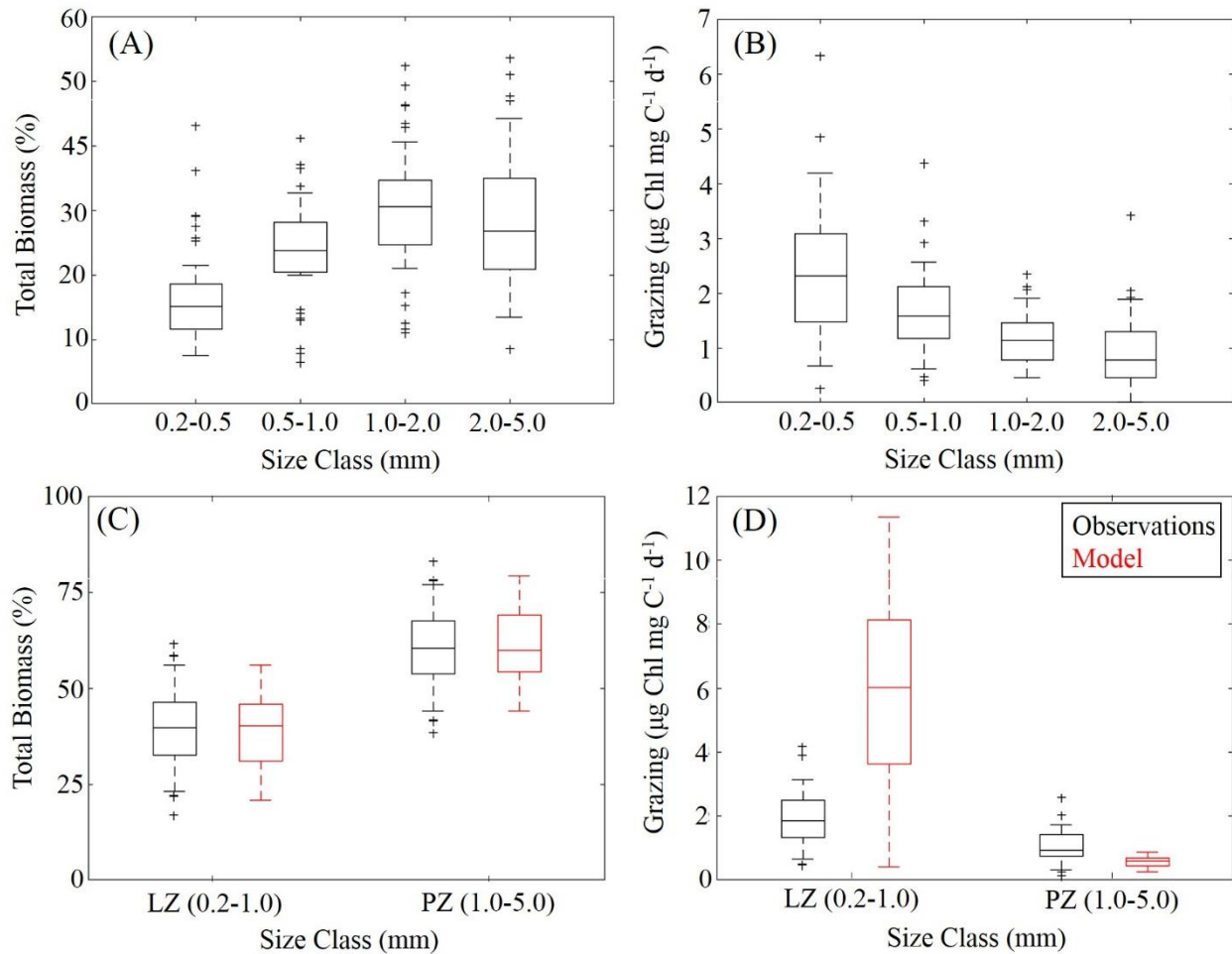
528
 529 **Figure 4 (A-C):** Model-data comparisons in the vertical distribution of chlorophyll (A&B) and
 530 nitrate (C). Comparison between maximum fluorescence depths observed in SEAMAP profiles
 531 and simulated maximum chlorophyll depths (m) (A). Comparison between in situ chlorophyll
 532 samples collected during May, 2017 and 2018 process study cruises and simulated chlorophyll
 533 concentrations (mg m^{-3}) (B). Grey dots represent cruise sample values and red dashed line denotes

534 1 standard deviation away from the model average. Comparison between nitrate profiles obtained
535 from World Ocean Database (WOD) and simulated nitrate (mmol N m^{-3}) (C). Gey dots represent
536 WOD sample values and red dashed line denotes 1 standard deviation away from the model
537 average.

538 DCM depth was evaluated using un-calibrated fluorescence profiles obtained during SEAMAP
539 cruises. Chlorophyll profiles were collected during the May 2017 and 2018 Lagrangian process
540 cruises. For comparisons, the model and data were sampled at corresponding locations and time
541 of the year for all simulated years. Nitrate values from World Ocean Database that overlapped with
542 the simulation period and were located in the oligotrophic GoM (>1000 m) were used for model-
543 data comparisons.

544 **3.4 Size fractionated mesozooplankton biomass and grazing model-data comparisons**

545 To further constrain the phytoplankton and zooplankton community simulated by NEMURO-
546 GoM, we utilized in situ measurements collected during the process study cruises. First, we
547 compared the relative proportions of LZ and PZ biomass to four discrete size classes measured at
548 sea (**Fig. 5A, C**). In both model and observations, we find nearly identical size distributions
549 assuming that LZ approximates the smallest two size classes of mesozooplankton sampled (“small
550 mesozooplankton”, 0.2-1.0-mm) and PZ approximates the largest two size classes (“large
551 mesozooplankton”, 1.0-5.0 mm). In the field data, small mesozooplankton biomass varied from
552 33 to 46 % (median = 40%, at 95% C.I.), while model estimates of LZ biomass vary from 31 to
553 46% (median = 40%). Large mesozooplankton biomass in the field data varied from 54 to 67%
554 (median = 60%), while model estimates of PZ biomass vary from 54 to 69% (median = 60%).



555

556 **Figure 4 (A-D):** Mesozooplankton size-fractionated biomass (A&C) and grazing rates (C&D) in
 557 field measurements (black) and model estimates (red). Mesozooplankton size-fractionated biomass
 558 measured during May 2017 and May 2018 process study cruises (A) along with corresponding
 559 measured grazing rates (B). Comparisons of model estimated mesozooplankton biomass to
 560 aggregated (size class 1-2, 3-4) field measurements (C). Comparisons of model estimated specific
 561 mesozooplankton grazing rates to aggregated (size class 1-2, 3-4) field measurements (D).
 562 Whiskers extend to 95% confidence interval. Outliers for model estimates are not shown.

563 Mesozooplankton specific grazing rates measured during the process study cruises were also used
 564 to validate the simulated mesozooplankton community. Field measurements showed that specific
 565 grazing rates ($\mu\text{g Chl mg C}^{-1} \text{d}^{-1}$), decreased consistently with increasing mesozooplankton size-
 566 class (**Fig. 5B**). For model-data comparisons, we computed grazing on LP by LZ and PZ at each
 567 depth. Grazing terms were converted into units of Chl using the model estimated C:Chl ratio for

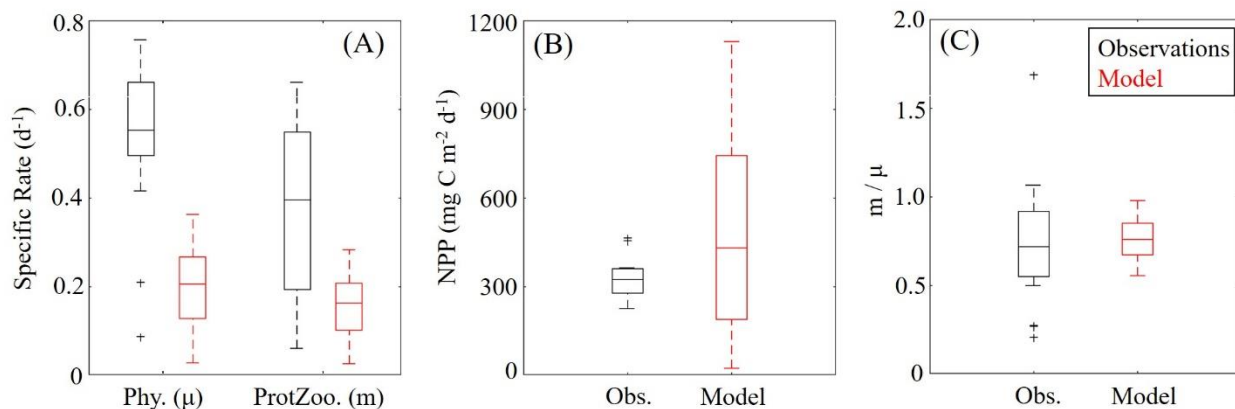
568 LP before being depth-integrated to the corresponding net tow depth and normalized to simulated
569 depth-integrated LZ and PZ biomasses. We find that model mesozooplankton grazing estimates
570 capture the general trend of decreased specific grazing rates with increasing mesozooplankton size
571 (**Fig. 5D**). However, the model overestimates grazing by small mesozooplankton while
572 underestimating grazing by large mesozooplankton. In the field data, small mesozooplankton
573 grazing ranges from 1.34 to 2.51 $\mu\text{g Chl mg C}^{-1} \text{d}^{-1}$ (median = 1.85) while model estimates of LZ
574 grazing rates vary from 3.64 to 8.14 $\mu\text{g Chl mg C}^{-1} \text{d}^{-1}$ (median = 6.01). Field measurements of
575 large mesozooplankton grazing range from 0.76 to 1.44 $\mu\text{g Chl mg C}^{-1} \text{d}^{-1}$ (median = 0.94), while
576 model 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
577 of total grazing, the model average is also considerably higher ($2.99 \pm 2.20 \mu\text{g Chl mg C}^{-1} \text{d}^{-1}$)
578 relative to field measurements ($1.38 \pm 0.59 \mu\text{g Chl mg C}^{-1} \text{d}^{-1}$) (see Discussion).

579 **3.5 Phytoplankton growth and microzooplankton grazing model-data comparisons**

580 Measurements of specific phytoplankton growth rates, phytoplankton mortality due to
581 microzooplankton grazing, and net primary production (NPP) were used to evaluate protistan
582 dynamics in the model. We find the model underestimates phytoplankton growth and
583 microzooplankton grazing while overestimating NPP (**Fig. 6A, B**). Phytoplankton specific growth
584 rates from dilution experiments range from 0.50 to 0.66 d^{-1} (median = 0.55 d^{-1}) while model
585 estimates of phytoplankton (SP+LP) specific growth rates vary from 0.13 to 0.27 d^{-1} (median =
586 0.21 d^{-1}). In terms of microzooplankton grazing rates, field data range from 0.19 to 0.55 d^{-1} (median
587 = 0.39 d^{-1}) while model estimates of SZ vary from 0.10 to 0.21 d^{-1} (median = 0.16 d^{-1}). NPP
588 estimates show better agreement with observations with rates from 276 to 360 $\text{mg C m}^{-2} \text{d}^{-1}$
589 (median = 321 $\text{mg C m}^{-2} \text{d}^{-1}$) in field data while model estimates vary from 190 to 741 mg C m^{-2}
590 d^{-1} (median = 431 $\text{mg C m}^{-2} \text{d}^{-1}$).

591 Although the model underestimates phytoplankton growth and microzooplankton grazing rates,
592 the relative proportion of NPP consumed by protists in the model (67 - 85%; median = 76%)
593 compares reasonably well to field measurements (55 - 92%; median = 72%) (**Fig. 6C**). Notably,
594 the model average proportion of phytoplankton production consumed by protists closely matches
595 the mean for all tropical waters reported by Calbet & Landry (2004). When phytoplankton
596 mortality due to mesozooplankton grazing was evaluated in the model at cruise sample locations

597 we find mesozooplankton grazing accounts for $13 \pm 8 \%$, which also closely agrees with the global
 598 average (Calbet et al., 2001).



599
 600 **Figure 5 (A-C):** Specific phytoplankton growth (μ , d^{-1}) and microzooplankton grazing (m , d^{-1})
 601 between model (red) and field data (black) (A). Depth-integrated net primary production ($mg\ C$
 602 $m^{-2}\ d^{-1}$) (B). The fraction of phytoplankton growth that is grazed by protists in the model and field
 603 data (C). Whiskers extend to the 95% confidence intervals. Outliers for model estimates are not
 604 shown.

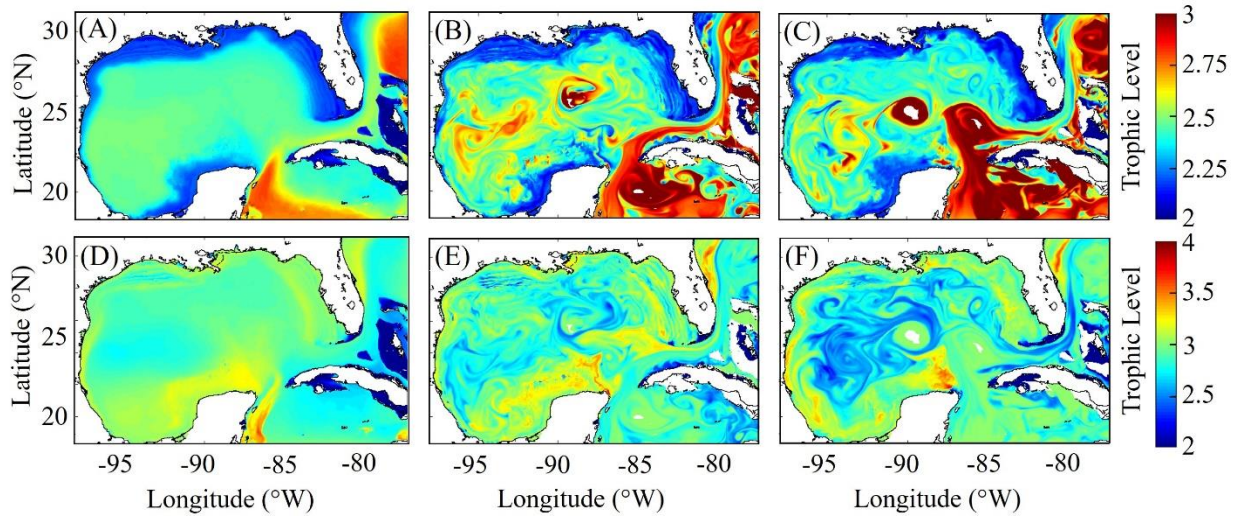
605 3.6 Simulated mesozooplankton diet

606 After model tuning and validation, we utilized NEMURO-GoM to investigate spatiotemporal
 607 variability in diet and secondary production of the GoM mesozooplankton community. First, we
 608 examined the trophic level of LZ and PZ in the model, which provides a measure of their
 609 cumulative diet. Trophic level is calculated by computing the dietary contributions of each prey in
 610 LZ (i.e. LP and SZ) and PZ diets (i.e. LP, SZ, and LZ), assuming that the trophic level of LP = 1
 611 and SZ = 2. In the oligotrophic region, both LP and SZ contribute approximately 50% to LZ diet,
 612 as indicated by a mean trophic level near 2.5 (2.54 ± 0.02) for LZ (**Fig. 7A**). In the same region,
 613 PZ have a trophic level of 2.78 ± 0.04 indicating a higher contribution of zooplankton to their diet
 614 (i.e. SZ and/or LZ) (**Fig. 7B**). In the shelf region, LZ are more herbivorous, as indicated by a
 615 decrease in trophic level to 2.31 ± 0.01 , while PZ are more carnivorous, as indicated by an increase
 616 in trophic level to 2.90 ± 0.04 .

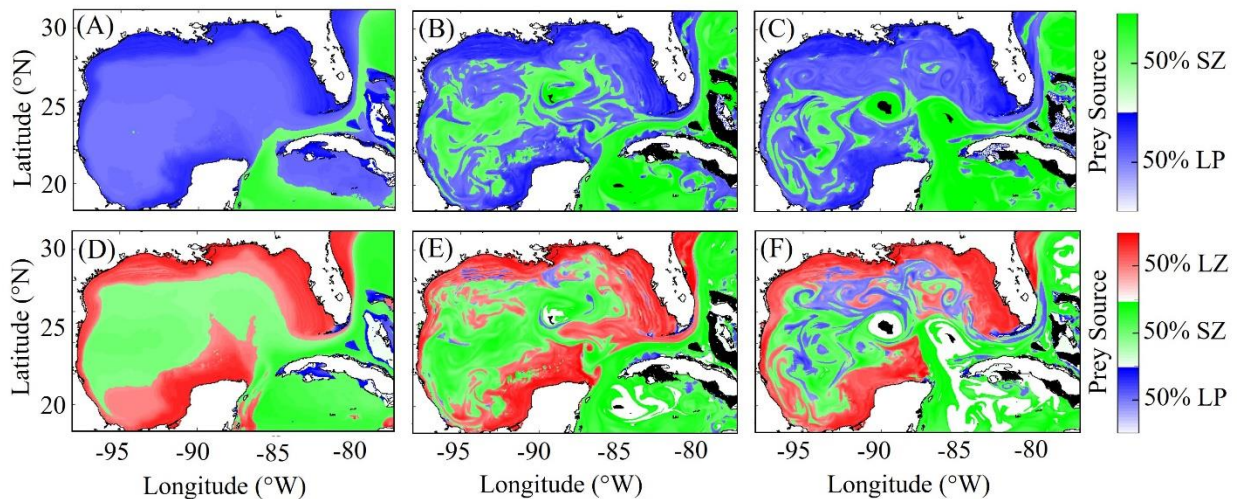
617 Despite little evidence for LZ diets dominated by zooplankton in the annual average (in contrast
 618 to PZ, which often have a trophic level ~ 3), we commonly find regions in instantaneous fields

619 during both winter and summer conditions where SZ are the dominant prey source for LZ (**Fig.**
620 **7C, E**). These regions, typically in the Loop Current or Loop Current Eddies (LCEs), highlight the
621 episodic importance of heterotrophic protists as prey sources for small mesozooplankton in the
622 GoM. High proportions of SZ in LZ diets can be attributed to the competitive advantage of SP
623 over LP in extremely low nutrient environments such as in the Loop Current, resulting in high
624 abundances of SP and their predators (SZ) relative to LP. Instantaneous fields also reveal that
625 phytoplankton can be important prey for PZ as well, particularly during summer, as indicated by
626 trophic levels of around 2.5 in the western GoM (**Fig. 7F**). In addition to strong variability in
627 trophic positions, there are also regions in the oligotrophic GoM, most clearly in the centers of
628 LCEs during summer, where the model predicts no feeding by mesozooplankton (**Fig. 8E**). The
629 convergent anti-cyclonic circulation of LCEs is typically associated with low phytoplankton
630 biomass, which at times may fall near or below feeding thresholds in the NEMURO grazing
631 formulation. This formulation is intended to simulate suppression of feeding activity for
632 zooplankton at mean prey densities that cannot support the energy expended while searching for
633 prey.

634 To investigate which prey contributes most to LZ and PZ diets, we computed each prey source
635 term for both LZ and PZ at each grid cell (**Fig. 8**). As one would expect, the dominant prey for LZ
636 and PZ align closely with spatial variability in their respective trophic positions. For LZ diet,
637 herbivory dominates throughout the GoM, except for the Loop Current (**Fig. 8A**). LP contribution
638 to LZ diet is highest on the shelf, where LP biomass is also high due to the competitive advantage
639 of LP over SP in high nutrient conditions. In contrast, PZ diet varies with the relative availability
640 of SZ and LZ prey. In the oligotrophic region, PZ feed mainly on SZ (heterotrophic protists)
641 because LZ biomass is relatively low. On the shelf, they consume primarily LZ (**Fig. 8D**). Despite
642 the significant change in diet between the shelf and oligotrophic regions, PZ trophic positions
643 remain fairly consistent (**Fig. 7D**). This is due to the fact that SZ in the oligotrophic region and LZ
644 in the shelf region both feed predominantly on phytoplankton and hence occupy similar trophic
645 levels. In the instantaneous fields for winter (**Fig. 8B, E**) and summer (**Fig. 8C, F**), the dominant
646 prey for both LZ and PZ show substantial mesoscale variability, indicating that oceanographic
647 features such as fronts and eddies influence not only biomass but also zooplankton ecological roles
648 (see Discussion).



649
 650 **Figure 7 (A-F):** Trophic levels of simulated large zooplankton (LZ, top) and predatory
 651 zooplankton (PZ, bottom). Annual-averaged trophic positions of LZ (A) and PZ (D). Instantaneous
 652 model field of trophic positions during winter conditions for LZ (B) and PZ (E) on 4 February
 653 2012. Instantaneous model field of trophic positions during summer conditions for LZ (C) and PZ
 654 (F) on 2 August 2011.



655
 656 **Figure 8 (A-F):** Dominant prey source for simulated large zooplankton (LZ, top) and predatory
 657 zooplankton (PZ, bottom). Annual-averaged diet contributions for LZ (A) and PZ (D).
 658 Instantaneous model field of zooplankton diet during winter conditions for LZ (B) and PZ (E) on
 659 4 February 2012. Instantaneous model field of zooplankton diet during summer conditions for LZ
 660 (C) and PZ (F) on 2 August 2011.

661 3.7 Simulated mesozooplankton secondary production

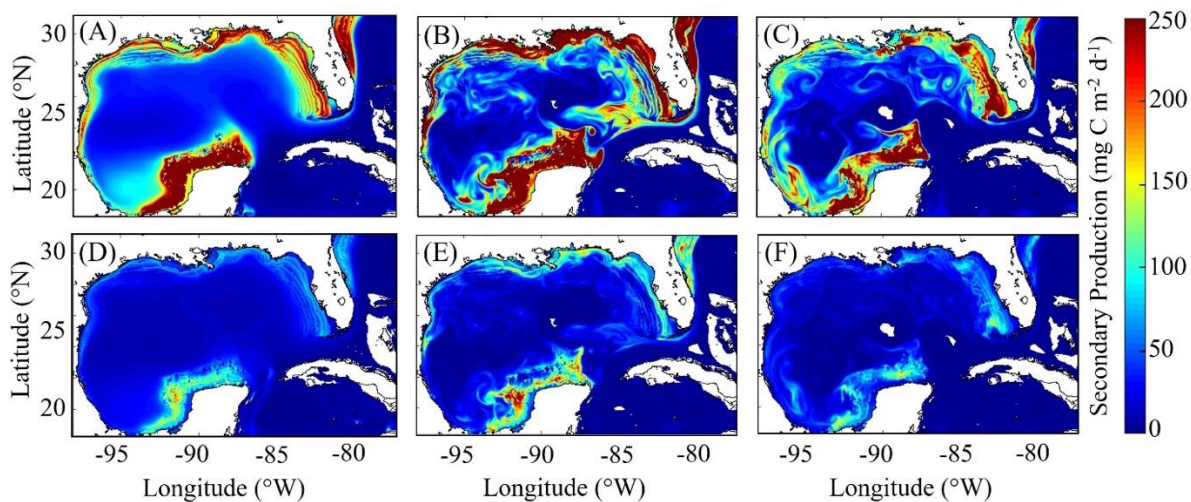
662 To our knowledge, regional secondary production for the GoM has not been quantified previously.
663 Based on our model, secondary production due to mesozooplankton averages $66 \pm 8 \times 10^6$ kg C yr⁻¹,
664 and ranged from a minimum of 51×10^6 kg C (in 1999) to a maximum of 82×10^6 kg C (in
665 2011). In the oligotrophic region, LZ secondary production averages 35 ± 5 mg C m⁻² d⁻¹ while
666 PZ secondary production is 11 ± 2 mg C m⁻² d⁻¹ (**Fig. 9**). The annual secondary production
667 minimum develops at the end of December while the annual maximum occurs at the beginning of
668 June (**Table 1**). In this region, mesozooplankton secondary production is $14 \pm 2 \times 10^6$ kg C yr⁻¹,
669 equivalent to 6% of NPP. On the shelf, secondary production is about 4-fold higher, with LZ
670 production of 146 ± 17 mg C m⁻² d⁻¹ and PZ production of 42 ± 5 mg C m⁻² d⁻¹. Here, the annual
671 minimum also occurs at the end of December while the maximum occurs later at the end of July
672 (**Table 1**). On the shelf, secondary production constitutes a higher proportion of NPP (13%) and
673 averages $51 \pm 6 \times 10^6$ kg C yr⁻¹.

674 In addition to differences in total secondary production, significant differences were found in the
675 mesozooplankton community response to changes in total phytoplankton biomass on the shelf and
676 in the oligotrophic region. On the shelf, the average ratio between LZ and PZ secondary production
677 is 3.51 and remains almost constant with increasing phytoplankton biomass ($\rho = 0.13$, $p < 0.01$).
678 Although we find a similar average value in the oligotrophic region (3.14), ratios are more variable
679 and strongly dependent on phytoplankton biomass ($\rho = 0.52$, $p < 0.01$). Ratios of LZ to PZ
680 secondary production reached values of ~ 2.5 in the lowest phytoplankton biomass regions of the
681 open ocean GoM and increased to ~ 4.0 during times and places where local phytoplankton biomass
682 was high. These differences likely stem from the longer turnover times of PZ, which make them
683 less sensitive to variability in bottom-up drivers and allows them to have a proportionally greater
684 role in oligotrophic settings.

685 As witnessed in the instantaneous fields of diet and secondary production, mesoscale eddies are
686 common features in the GoM and hence important to quantify for regional zooplankton dynamics.
687 To investigate secondary production inside cyclonic and anticyclonic eddies we
688 implement the TOEddies eddy detection algorithm (Laxenaire et al., 2018) which uses surface
689 velocities along closed contours of sea surface height (SSH) for detection of mesoscale eddies
690 (Chaigneau et al., 2011; Laxenaire et al., 2019; Pegliasco et al., 2015). Grid cells located inside

691 each eddy are defined within the SSH contour associated with the maximum mean surface velocity
 692 (interior grid cells). Grid cells located between the outer most closed contour and within 1.5 radius
 693 of the eddy center and not within another eddy were used to define background conditions outside
 694 of eddies (exterior grid cells). Only eddies with areas larger than an equivalent circular diameter
 695 of 100 km and not within the Loop Current were considered in the analysis. On average, 3.78
 696 cyclonic and 3.33 anticyclonic eddies were identified in each daily velocity field.

697
 698 In the model cyclonic eddies were associated with 10% higher secondary production relative to
 699 exterior grid cells and the ratio of secondary production in interior cells to exterior cells ranged
 700 from 0.4 to 3.37 (95% CI). In contrast, secondary production was substantially lower inside
 701 anticyclonic eddies accounting for only 46% of the average secondary production in exterior cells
 702 (0.03 - 1.87 (95% CI)). In addition to their convergent nature that dampens nutrient input, lower
 703 rates of secondary production in anticyclonic eddies can likely be attributed to the presence of
 704 highly oligotrophic Loop Current water trapped within large anticyclonic LCEs.



705
 706 **Figure 9 (A-F):** Vertically integrated secondary production ($\text{mg C m}^{-2} \text{d}^{-1}$) of simulated large
 707 zooplankton (LZ, top) and predatory zooplankton (PZ, bottom). Annual-averaged secondary
 708 production for LZ (A) and PZ (D). Instantaneous model field of secondary production during
 709 winter conditions for LZ (B) and PZ (E) on 4 February 2012. Instantaneous model field of
 710 secondary production during summer conditions for LZ (C) and PZ (F) on 2 August 2011.

711 **Table1:** Average seasonal minimum and maximum values in the model (1993-2012) and the day
712 of year in which they occur for surface chlorophyll (mg m^{-3}), depth-integrated estimates of
713 phytoplankton biomass (mg C m^{-2}), net primary production ($\text{mg C m}^{-2} \text{ d}^{-1}$), mesozooplankton
714 biomass (mg C m^{-2}), and mesozooplankton secondary production ($\text{mg C m}^{-2} \text{ d}^{-1}$) calculated by
715 spatially averaging daily fields over the oligotrophic region (grid cells with bottom depths
716 $\geq 1000\text{m}$) and shelf region (grid cells with bottom depths $< 1000 \text{ m}$). Day of year values are in the
717 format “day/month \pm days.”

	Daily Field Value		Day of Year	
Diagnostic (Oligotrophic)	Annual Min.	Annual Max.	Day of Min.	Day of Max.
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)	Annual Min.	Annual Max.	Day of Min.	Day of Max.
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	$12/31 \pm 6$	$7/20 \pm 16$

718

719 4.0 Discussion

720 Many parameters in biogeochemical models are poorly constrained by observations and laboratory
721 studies and/or highly variable in the environment. The numbers and uncertainties around these
722 parameters allow PBMs with varying degrees of tuning to reproduce a single ecosystem attribute
723 (e.g., surface Chl) even if multiple processes are inaccurately represented (Anderson, 2005;
724 Franks, 2009). Once validated, one of the main values of coupling physical and biogeochemical
725 models (i.e. PBMs) is their utility for making inferences about portions of the lower trophic level
726 that are under sampled and/or difficult to measure in the field. If PBMs are to be utilized to explain
727 variability rather than simply fit an observational dataset, multiple ecosystem attributes, must be
728 validated and the underlying model structure and assumptions critically evaluated. In the section

729 below, we further justify changes to model structure by evaluating the underlying assumptions in
730 default NEMURO and discuss model-data mismatch before drawing conclusions about the GoM
731 zooplankton community and the implications of its dynamics for higher trophic levels.

732 **4.1 Justification for NEMURO modifications**

733 The phytoplankton community in the North Pacific (NP) domain where NEMURO was originally
734 designed is largely composed of nanoplankton (original SP) and microplankton (original LP). By
735 default, SP is assumed to represent coccolithophores and autotrophic nanoflagellates, which can
736 be important prey of copepods and other mesozooplankton in temperate and subpolar regions
737 (Kishi et al., 2007). However, in tropical regions such as the GoM, smaller picophytoplankton taxa
738 typically dominate, particularly in highly oligotrophic regions. Common picophytoplankton of the
739 GoM include cyanobacteria and picoeukaryotes, which are too small for most mesozooplankton
740 to feed on. Hence, the SP to LZ grazing pathway was removed in our model. We found that
741 removal of this grazing pathway allowed the model to simulate a more realistic phytoplankton
742 community on the shelf region. Despite intuition, SP largely dominated the shelf region in the
743 model when LZ were allowed to graze on SP. After closer inspection, we found that grazing of SP
744 sustained LZ biomass on the shelf to levels where top-down pressure constrained LP standing
745 stocks. This prevented large blooms of LP, leading to a competitive advantage for SP even in
746 highly eutrophic conditions (the Mississippi river delta), which was observed for a wide range of
747 LP maximum growth rates, LP half-saturation constants, and LZ/PZ grazing rates. Thus, removal
748 of the SP to LZ grazing pathway added ecological realism and improved the model solution.

749 During the model tuning process (outlined in the supplemental), we also found that, despite a wide
750 range of tested parameter sets, the model was unable to simulate mesozooplankton biomass low
751 enough to match SEAMAP observations in the oligotrophic region. Even with unrealistically low
752 phytoplankton biomass, equivalent to approximately 50% of surface Chl observed in SeaWiFS
753 images, the model overestimated mesozooplankton biomass. To achieve realistic levels of
754 mesozooplankton biomass in the oligotrophic region, default LZ and PZ mortality parameter
755 values needed to be increased by an order of magnitude. However, this produced unrealistically
756 high loss rates on the shelf region, leading to mesozooplankton biomass estimates that were
757 substantially lower than SEAMAP shelf observations. Implementation of linear mortality on all
758 biological state variables (except PZ) resolved this issue by providing the model with a greater

759 dynamic range. In NEMURO, and other biogeochemical models, quadratic mortality is often used
760 to increase model stability and/or is mechanistically justified as representing the impact of
761 unmodeled predators that co-vary in abundance with prey (Gentleman and Neuheimer, 2008;
762 Steele and Henderson, 1992). However, grazing losses of all state variables (except PZ), are
763 already explicitly modeled in NEMURO by default. Hence, removal of quadratic mortality also
764 added ecological realism and improved the model solution. Quadratic mortality was retained for
765 PZ to account for the implicit predation pressure of un-modeled predators (e.g. planktivorous fish).

766 **4.2 Model-data mismatch**

767 **4.2.1 Surface chlorophyll discrepancies**

768 Within our model-data comparisons of surface Chl we find that NEMURO-GoM reproduces
769 important patterns in both the oligotrophic and shelf region. The latter of which, apart from the
770 northern shelf, has not been well resolved by previous PBMs (e.g., Gomez et al., 2018; Xue et al.,
771 2013). The absence of a shelf Chl signature may, in some cases, be overly attributed to bias in
772 satellite measurement due to high concentrations of colored dissolved organic matter (CDOM).
773 While a clear shelf signature is well resolved in NEMURO-GoM, the model-data mismatch is
774 greater on the shelf compared to oligotrophic regions. This is an expected result considering that
775 the model incorporates climatological river forcing while actual variability is much more complex.
776 Furthermore, the absence of CDOM in the model likely contributes to the overestimation of
777 phytoplankton biomass on the shelf.

778 In future studies, the inclusion of daily nutrient data like that produced for the Mississippi River
779 by USGS starting in 2011 is needed for PBMs to better resolve variability on the shelf. Including
780 benthic processes, such as denitrification (Fennel et al., 2006), may also reduce model-data
781 mismatch in shelf regions. Implementing more realistic light attenuation (e.g. wavelength-specific
782 light attenuation or inclusion of CDOM) could further improve estimates of phytoplankton
783 biomass on the shelf as primary production can be sensitive to different light attenuation
784 formulations (Anderson et al., 2015). In our model, it was difficult to simulate deep DCMs in the
785 oligotrophic GoM while also simulating DCMs on the shelf that were shallow enough to maintain
786 high nitrate. This may reflect the need for more realistic light attenuation in the model.

787 Quantifying uncertainty in C:Chl ratios is also an important task moving forward as future PBMs
788 will likely continue to depend heavily on satellite Chl for the bulk of model validation. To correctly
789 parameterize C:Chl ratios more in situ samples are needed that resolve changes in phytoplankton
790 light harvesting pigments along gradients from coastal to oligotrophic regions and from the surface
791 to the DCM. Without these observations, it is difficult to gauge mismatches between model and
792 satellite ocean color products (e.g. discrepancies on the Campeche Bank in our model) or in situ
793 profiles of Chl. In addition to validation, these measurements are needed to avoid erroneous model
794 tuning. For instance, a model that exhibits significant mismatch with respect to surface Chl may
795 in fact accurately estimate carbon based phytoplankton biomass while using unrealistic C:Chl
796 ratios. One could arrive at incorrect conclusions about regional ecosystem dynamics as a result of
797 modifying model parameters or structure in an effort to better fit Chl observations. Given the
798 importance of C:Chl ratios in PBMs, future studies should quantify uncertainty in modeled Chl
799 through sensitivity experiments focused on C:Chl model parameters and formulation, with explicit
800 comparison to direct field measurements of phytoplankton C:Chl.

801 In our model, the most noticeable surface Chl model-data mismatch occurs on the southern GoM
802 shelf (Campeche Bank), where the model consistently overestimates surface Chl. This bias was
803 also notable in the GoM PBM implemented by Damien et al. (2018), particularly in winter. We
804 believe this discrepancy is driven by a combination of errors involving overestimation of shelf
805 mixing by the hydrodynamic model, entrainment of high Chl water (given the overestimated DCM
806 magnitude in the model), or errors in the open boundary conditions which result in an
807 overestimation of upwelled nutrients/biomass near the Yucatan Peninsula that are transported
808 westward by shelf currents. We found that the Campeche Bank model-data mismatch was reduced
809 when open boundary conditions included nitracline depths of greater than 100 m. This may reflect
810 realistic in situ conditions considering that Caribbean water entering the GoM is highly
811 oligotrophic. During our process cruises, nitrate was often undetectable above 100 m in samples
812 collected near the Loop Current (A. Knapp, pers. comm.).

813 Although modifying the boundary conditions may be justified, deepening the nitracline at the
814 boundaries made it increasingly difficult to sustain realistic surface phytoplankton biomass in the
815 oligotrophic GoM. This may point to the importance of nitrogen fixing cyanobacteria, which
816 provide an alternative source of new nitrogen (other than upwelling and mixing) that could be

817 supporting phytoplankton at the surface given the strong stratification and deep nitraclines in the
818 GoM. In the process of model tuning, we noticed that increasing the DON pool by increasing the
819 PON to DON decomposition rate was necessary to maintain both relatively deep nitraclines and
820 realistic surface Chl by providing a slow leeching of ammonium near the surface through bacterial
821 communities. The need for this slow production of ammonium in surface layers may compensate
822 for nitrogen fixation, which is not included in NEMURO (Holl et al., 2007; Mulholland et al.,
823 2006). In future studies, including diazotrophs as a separate phytoplankton functional type would
824 be essential for evaluating the importance of nitrogen fixation in the GoM.

825 Despite the model-data mismatch on the Campeche Bank, this discrepancy appears to have little
826 impact on the rest of the GoM. However, the model overestimates surface Chl in the southwestern
827 GoM, which can likely be attributed to entrainment of high Chl water originating from the
828 Campeche Bank. Locally, the ecological impact is likely more significant. Higher phytoplankton
829 biomass would be expected to support higher mesozooplankton grazing rates and secondary
830 production. Indeed, some of the highest model rates of secondary production occur on the
831 Campeche Bank. Hence, the surface Chl model-data mismatch may lead to an overestimation of
832 secondary production for this region.

833 **4.2.2 Deep chlorophyll maximum discrepancies**

834 Since most PBMs focus on validating against satellite derived surface chlorophyll, the dynamics
835 of the DCM is often insufficiently investigated. Consequently, many models predict DCM depths
836 that are far too shallow. Identifying this issue in the literature proved to be difficult because most
837 studies do not provide profiles of simulated Chl (an exception is the recent GoM PBM by Damien
838 et al. (2018)). We note that DCM depths in the DIAZO model (Stukel et al., 2014) were often quite
839 shallow or completely nonexistent in the portion of the domain that included the oligotrophic GoM
840 region. Underestimates of DCM depth in the unmodified COBALT biogeochemical model has
841 also been identified (Moeller et al., 2019). In our investigation of the GoM PBM implemented by
842 Gomez et al. (2018), we found that DCMs in the oligotrophic region were commonly shallow and
843 weak. In the default NEMURO simulation, DCM depths in the oligotrophic region were typically
844 at a depth of 25 m, which is much shallower than observed (SEAMAP: 80 ± 25 m, Process cruises:
845 107 ± 21 m). While this issue may seem insignificant, particularly if a study is focused on mixed-
846 layer dynamics, accurate placement of the DCM can have profound impacts on PBM behaviors,

847 because the DCM is typically co-located with the nitracline. Unrealistically shallow DCMs and
848 nitraclines permit unrealistically high nitrate fluxes into the surface layer following mixing events;
849 thus, validating the DCM in PBMs is critical.

850 For these reasons, we devoted substantial effort to tuning phytoplankton dynamics in the DCM.
851 Modifications to α (the slope of the photosynthesis-irradiance curve) and attenuation coefficients
852 allowed the model to estimate deeper more realistic DCM depths. Inclusion of a variable C:Chl
853 module was also implemented to better resolve the DCM. However, an additional issue was
854 present in the default NEMURO simulations, the NEMURO-GoM, and every simulation that we
855 attempted. In all simulations that formed DCMs, the location of the DCM was always co-located
856 with a maximum in phytoplankton specific growth rate, even though field measurements indicate
857 that phytoplankton growth rates and NPP are either relatively constant with depth or decline in the
858 DCM. This is not surprising, given the low photon flux at the base of the euphotic zone and the
859 energetic demands required to up-regulate cellular density of light harvesting pigments.
860 Additionally, our field measurements show that the DCM was not associated with a biomass
861 maximum (biomass was fairly constant with depth), suggesting that DCM formation in the GoM
862 is physiologically driven.

863 We believe this DCM dynamical issue was responsible, in part, for the underestimation of specific
864 phytoplankton growth and microzooplankton grazing rates by the model despite estimating higher
865 NPP (**Fig. 4D**). An underestimation of C:Chl ratios or overestimation of phytoplankton biomass
866 may also contribute to the model-data mismatch at the DCM. The ecological impact of this
867 mismatch is likely to be greatest in the model during the summer months when the mixed layer
868 depth is shallow and the DCM reaches its maximum depth. Elevated growth rates or biomass at
869 the DCM during this period could significantly decrease nitrate flux into the mixed layer causing
870 the model to underestimate near surface primary and secondary production.

871 Future PBM studies need to focus more effort on resolving ecological dynamics responsible for
872 the formation of the DCM. Errors originating from the hydrodynamic model or use of temporally
873 averaged velocity fields used in offline models may also contribute to model-data mismatch at the
874 DCM. Vertical mixing is particularly important to PBMs, but is often poorly validated in
875 hydrodynamic models. Greater coordination between physical modelers and biologists to constrain

876 vertical fluxes should be considered an important avenue for improving PBM simulations moving
877 forward.

878 **4.2.3 Mesozooplankton grazing discrepancies**

879 Novel to this study, model estimates of mesozooplankton biomass are shown to agree closely with
880 observations on the shelf and in the oligotrophic GoM. To our knowledge, this study includes the
881 first quasi-regional zooplankton biomass model validation in a PBM. Our model also provides the
882 first model-data comparisons of size-specific zooplankton biomass and grazing rates for the GoM.
883 Such comparisons provide valuable insights into the potential biases of traditional functional group
884 biogeochemical models pertaining to zooplankton dynamics (Everett et al., 2017). While
885 NEMURO-GoM shows broad agreement with zooplankton observations, some model-data
886 mismatch occurs, particularly for mesozooplankton grazing rates.

887 We identify three factors that may explain the model-data mismatch for mesozooplankton grazing
888 rates. The first and most obvious factor is the temporal sampling discrepancy as measurements
889 were collected outside our model simulation period. Model-data mismatch may also arise from
890 inaccuracies in the field measurements. During our process cruises, the zooplankton gut pigment
891 measurements were based solely on phaeopigment content due to phytodetrital aggregates and
892 *Trichodesmium* colonies found in our zooplankton net tows, which can lead to substantial
893 contamination. Thus, true mesozooplankton grazing rates were likely underestimated because
894 undegraded Chl can be abundant in the foreguts of mesozooplankton. Furthermore, the gut pigment
895 approach assumes that any group of mesozooplankton has a constant gut throughput time (as a
896 function of temperature), which is an oversimplification.

897 Uncertainties in model grazing formulations could also contribute to model-data mismatch
898 (Gentleman et al., 2003a; Sailley et al., 2015). Future in situ grazing measurements are needed to
899 enable an objective selection of grazing formulations and parameter values. In particular, field
900 studies that shed light on prey selectivity would be useful for parameterizing PBMs with multiple
901 mesozooplankton functional groups, such as NEMURO-GoM. Such studies are challenging,
902 however, because the difficulty of making in situ grazing measurements on mesozooplankton,
903 combined with the inherent uncertainty of these measurements can make it challenging to
904 differentiate between, for instance Ivlev and Holling's disk grazing formulations (e.g., Fig. 4 in

905 Morrow et al. (2018)). Nevertheless, differences in parameterizing grazing can lead to
906 substantially different model behavior (Anderson et al., 2010; Sailley et al., 2015; Wainwright et
907 al., 2007). In NEMURO-GoM, secondary production and dietary preferences of the
908 mesozooplankton community are both strongly influenced by model grazing formulation. While
909 we carefully chose parameterizations that gave reasonable fits to extensive field datasets of
910 zooplankton biomass and grazing rates, this does not preclude the possibility that other functional
911 forms would have more accurately simulated zooplankton dynamics. Hence, future PBMs should
912 investigate how different grazing formulations impact zooplankton dynamics in the region. We
913 especially recommend collaborations between experimentalists (potentially using new techniques
914 such as DNA metabarcoding of gut contents) and modelers to develop synthetic approaches with
915 the potential to quantitatively assess the realism of different grazing formulations.

916 Clear model-data mismatch is also evident in the proportion of grazing mediated by PZ and LZ.
917 This may be due to the fact that PZ is by default explicitly defined and parameterized as a higher
918 trophic level mesozooplankton that can feed on LZ. In reality, while there is a correlation between
919 size and trophic level in the ocean, many predatory zooplankton are <1 mm, and many suspension-
920 feeding zooplankton are >1 mm; hence, the overlap of taxonomic groups with different functional
921 roles and sizes makes it difficult to directly compare model categories to field data. For example,
922 shelf suspension-feeding zooplankton are likely larger than their counterparts in the oligotrophic
923 GoM although their functional role in the ecosystem does not change between environments.

924 The ecological impact of the model's potential overestimation of LZ grazing rates is most likely
925 to manifest through an increase in the ratio of secondary production to mesozooplankton biomass.
926 Since both LZ and PZ biomasses are accurately modeled by NEMURO-GoM, the overestimation
927 of grazing rates suggests that LZ turnover times may be too high, thus leading to higher estimates
928 of secondary production. However, this interpretation may oversimplify the complex interactions
929 within pelagic protistan communities. In the oligotrophic region where our model overestimates
930 LZ grazing rates, the model indicates that heterotrophic protists comprise approximately half of
931 the LZ diet. Thus, overestimates of grazing on LP do not necessarily lead to overestimates in total
932 consumption if <1-mm zooplankton derive substantial nutrition from non-phototrophic sources in
933 the field. Furthermore, the model's construction (i.e., LZ and PZ are functional groups, while the
934 field data are size classes) suggests that part of the model-data mismatch in Fig. 5d may result

935 from the presence of some suspension-feeders (i.e., LZ) in the >1-mm zooplankton size class and
936 some carnivorous zooplankton (i.e., PZ) in the <1-mm zooplankton size class. In this case, the
937 model may simply attribute too high of a LP:SZ prey ratio to LZ. If this is the issue, the model's
938 estimate of LZ secondary production may be accurate, but its trophic level too low (or, conversely,
939 the trophic level of PZ too high). Direct assessments of zooplankton trophic position (e.g., by
940 compound specific isotopic analysis of amino acids,(Chikaraishi et al., 2009; Décima et al., 2017)
941 may help resolve these issues.

942 **4.3 Mesozooplankton dynamics in the open-ocean oligotrophic Gulf of Mexico**

943 Despite its nutrient-poor conditions, the open-ocean GoM ecosystem is a key region for spawning
944 and larval development of many commercially important fishes, including Atlantic bluefin tuna,
945 yellowfin tuna, skipjack tuna, sailfish and mahi mahi (Cornic and Rooker, 2018; Kitchens and
946 Rooker, 2014; Lindo-Atichati et al., 2012; Muhling et al., 2017; Rooker et al., 2012, 2013). Why
947 so many species choose such oligotrophic waters as habitat for their larval stages is unknown, but
948 may be due to reduced predation risk (Bakun, 2013; Bakun and Broad, 2003). Regardless, rapid
949 growth and survival through the larval period depends on mesozooplankton prey that are suitably
950 abundant and appropriately sized for these larval fishes. These prey taxa may be especially
951 sensitive to increased stratification and oligotrophication associated with climate change, making
952 investigation of their dynamics and production an important topic of research.

953 Mesozooplankton biomass in the oligotrophic GoM was found to be strikingly low in both
954 observations and model estimates, approximately an order of magnitude less than on the shelf.
955 Model results clearly show that this low biomass condition arises from bottom-up resource
956 limitation. Our results suggest that low phytoplankton biomass in oligotrophic regions, and
957 particularly within Loop Current Eddies, may even lead to localized and episodic regions where
958 phytoplankton concentrations approach thresholds low enough that trigger collapse of
959 mesozooplankton grazing. Prey limiting conditions for mesozooplankton and their predators
960 would be expected more frequently in the GoM during warmer ocean conditions. Higher sea
961 surface temperatures and increased thermal stratification could suppress vertical mixing, resulting
962 in lower phytoplankton biomass.

963 Despite extreme oligotrophy and dominance of picophytoplankton, our model shows that both PZ
964 and LZ can be sustained at modest abundances in the oligotrophic GoM. Indeed, the substantial
965 abundances of large (>1 mm) mesozooplankton, equivalent to 60% of total mesozooplankton in
966 both observations and model results (**Fig. 4A, C**), is an important result that helps explain the
967 success of larval fish in the region. Our results show that large mesozooplankton (PZ) occupy a
968 trophic position of approximately 3.0 in the open ocean GoM, which is marginally lower than on
969 the shelf where they feed primarily on small mesozooplankton (LZ). The change in trophic position
970 is associated with a switch from carnivory to feeding predominantly on heterotrophic protists in
971 the oligotrophic region. This result highlights the importance of intermediate protistan trophic
972 levels in sustaining mesozooplankton communities in oligotrophic regions. Indeed, both LZ and
973 PZ ingest proportionally more SZ in the open ocean than on the shelf. Notably, these protistan
974 trophic steps cannot be quantified by routine field techniques because they have no pigment
975 signature to make them visible in gut pigment measurements and may not enrich in bulk ¹⁵N
976 leading to isotopic invisibility from a trophic perspective (Gutiérrez-Rodríguez et al., 2014).
977 Despite their importance to phytoplankton grazing, they are sometimes missing from GoM
978 ecosystem models (e.g., Fennel et al., 2011) and severely underrepresented or even absent in
979 complex mass-balance constrained models (Arreguin-Sanchez et al., 2004; Geers et al., 2016).
980 New insights may arise from focused investigations of phytoplankton→protist→crustacean
981 linkages in oligotrophic regions in both model and experimental studies. This will likely require
982 the use of next-generation technologies such as compound specific isotopic analyses of specific
983 amino acids that have been shown to enrich in protists (Décima et al., 2017) or DNA
984 metabarcoding to assess zooplankton gut contents (Cleary et al., 2016).

985 Another robust finding from this study is the dynamic mesoscale variability in zooplankton
986 abundance, diet, and trophic position. These model results highlight the impact of Loop Current
987 Eddies and mesoscale fronts and other features in modifying the biogeochemistry and food web of
988 the GoM. The existence of hot spots of productivity in the GoM has been noted in observational
989 studies (Biggs and Ressler, 2001), and the importance of GoM mesoscale features to fish larvae
990 has been hypothesized (Domingues et al., 2016; Lindo-Atichati et al., 2012; Rooker et al., 2012).
991 Indeed, cyclonic eddies were found to have enhanced secondary production in our model, while
992 secondary production was depressed within anticyclonic eddies. Our results further suggest that
993 these mesoscale structures may not only modify zooplankton abundances, but also their trophic

994 roles in the ecosystem, with implications for the transfer efficiencies of carbon and nitrogen in the
995 pelagic food web.

996 **5.0 Conclusions**

997 In this study we developed a PBM for the GoM and after extensive validation used the model to
998 investigate zooplankton community dynamics. The model was able to capture broad ecosystem
999 attributes including phytoplankton and mesozooplankton abundances, depth of the DCM and
1000 nutricline, as well as growth and grazing patterns. Based on model estimates of trophic position
1001 and diet our results suggest that on the shelf small mesozooplankton are strongly herbivorous while
1002 large mesozooplankton are strongly carnivorous. However, distinct changes in diet were noted in
1003 the oligotrophic GoM, where both groups rely more on protistan prey. Changes in diet and
1004 secondary production highlighted in this study have the potential to impact food availability to
1005 higher trophic levels, such as pelagic larval fishes. In future work, we plan to couple NEMURO-
1006 GoM to an individual-based model to evaluate the extent to which mesozooplankton abundance
1007 limits larval fish feeding, growth, and survival along transport pathways in the GoM. Insights from
1008 this ecosystem-based approach may help to better resolve stock-recruitment relationships that are
1009 needed for sustainable fisheries management and improved stock-assessment models.

1010

1011 *Code and data availability.*

1012 The model code and model validation data used in this study can be downloaded from GitHub at
1013 <https://github.com/tashrops/NEMURO-GoM>. An idealized one-dimensional version of
1014 NEMURO-GoM written in Matlab is also provided. The three-dimensional NEMURO-GoM
1015 model outputs used in the study are available on the FSU-COAPS server in a Network Common
1016 Data Form (NetCDF format).

1017 *Author Contribution.*

1018 TAS conducted all numerical simulations and model analysis. EPC, SLM, and AB provided
1019 expertise on the hydrodynamic modeling. MRS and VJC provided expertise on the biogeochemical
1020 model coding and tuning. RS, MRS, MRL, and GZ processed and provided data that was central
1021 to NEMURO-GoM's validation. TAS wrote the manuscript with contributions from all authors.

1022 *Competing interest.*

1023 The authors declare that they have no conflict of interest

1024 *Acknowledgements.*

1025 We thank the captains and crew of the NOAA ship Nancy Foster and many of our colleagues from
1026 NOAA SEFSC and the NASA-funded Zooplankton from Space project. We thank Oliver Jahn for
1027 providing valuable direction in configuring the offline MITgcm package. We also thank Mandy
1028 Karnauskas, Sang-Ki Lee, and Fabian Gomez for their input during model development. This
1029 paper is a result of research supported by The Gulf of Mexico Research Initiative under the
1030 CSOMIO project, the NOAA RESTORE Science Program under federal funding opportunity
1031 NOAA-NOS-NCCOS-2017-2004875, the NOAA Center for Coastal and Marine Ecosystems
1032 (NOAA Office of Education/Educational Partnership Program award NA16SEC48100009), the
1033 NOAA NMFS Fisheries and the Environment program, the Northern Gulf Institute (projects 18-
1034 NGI3-41 and 18-NGI3-52) under NOAA award NA06OAR4320264 06111039, and by NASA
1035 IDS grant #80NSSC17K0560. Data are publicly available through the Gulf of Mexico Research
1036 Initiative Information and Data Cooperative 9GRIIDC) at <https://data.gulfresearchinitiative.org>
1037 (doi: XXXXX).

1038 **References**

1039

1040 Anderson, T. R.: Plankton functional type modelling: Running before we can walk?, *J. Plankton*
1041 *Res.*, 27(11), 1073–1081, doi:10.1093/plankt/fbi076, 2005.

1042 Anderson, T. R., Gentleman, W. C. and Sinha, B.: Influence of grazing formulations on the
1043 emergent properties of a complex ecosystem model in a global ocean general circulation model,
1044 *Prog. Oceanogr.*, 87(1–4), 201–213, doi:10.1016/j.pocean.2010.06.003, 2010.

1045 Anderson, T. R., Gentleman, W. C. and Yool, A.: EMPOWER-1.0: An Efficient Model of
1046 Planktonic ecOsystems WrittEn in R, *Geosci. Model Dev.*, 8(7), 2231–2262, doi:10.5194/gmd-8-
1047 2231-2015, 2015.

1048 Arreguin-Sanchez, F., Zetina-Rejón, M., Manickchand-Heileman, S., Ramírez-Rodríguez, M.
1049 and Vidal, L.: Simulated response to harvesting strategies in an exploited ecosystem in the
1050 southwestern Gulf of Mexico, *Ecol. Modell.*, 172(2–4), 421–432,
1051 doi:10.1016/j.ecolmodel.2003.09.016, 2004.

1052 Bakun, A.: Ocean eddies, predator pits and bluefin tuna: Implications of an inferred “low risk-
1053 limited payoff” reproductive scheme of a (former) archetypical top predator, *Fish Fish.*, 14(3),
1054 424–438, doi:10.1111/faf.12002, 2013.

1055 Bakun, A. and Broad, K.: Environmental “loopholes” and fish population dynamics:
1056 Comparative pattern recognition with focus on El Niño effects in the Pacific, *Fish. Oceanogr.*,
1057 12(4–5), 458–473, doi:10.1046/j.1365-2419.2003.00258.x, 2003.

1058 Biggs, D. C. and Ressler, P. H.: Distribution and abundance of phytoplankton, zooplankton,
1059 ichthyoplankton, and micronekton in the deepwater Gulf of Mexico, *Gulf Mex. Sci.*, 2001(1), 7–
1060 29, doi:10.18785/goms.1901.02, 2001.

1061 Buitenhuis, E., Le Quere, C., Aumont, O., Beaugrand, G., Bunker, A., Hirst, A., Ikeda, T., T. O.
1062 B., Piontkovski, S. and Straile, D.: Biogeochemical fluxes through mesozooplankton - art. no.
1063 GB2003, *Global Biogeochem. Cycles*, 20 (2), NIL_1-NIL_18, doi:10.1029/2005GB002511,
1064 2006.

1065 Calbet, A.: Mesozooplankton grazing effect on primary production: A global comparative
1066 analysis in marine ecosystems, *Limnol. Oceanogr.*, 46(7), 1824–1830,
1067 doi:10.4319/lo.2001.46.7.1824, 2001.

1068 Caron, D. A. and Hutchins, D. A.: The effects of changing climate on microzooplankton grazing
1069 and community structure: Drivers, predictions and knowledge gaps, *J. Plankton Res.*, 35(2), 235–
1070 252, doi:10.1093/plankt/fbs091, 2013.

1071 Chaigneau, A., Le Texier, M., Eldin, G., Grados, C. and Pizarro, O.: Vertical structure of
1072 mesoscale eddies in the eastern South Pacific Ocean: A composite analysis from altimetry and
1073 Argo profiling floats, *J. Geophys. Res. Ocean.*, 116(11), 1–16, doi:10.1029/2011JC007134,
1074 2011.

1075 Chassignet, E. P., Smith, L. T., Halliwell, G. R. and Bleck, R.: North Atlantic simulations with
1076 the Hybrid Coordinate Ocean Model (HYCOM): Impact of the vertical coordinate choice,
1077 reference pressure, and thermobaricity, *J. Phys. Oceanogr.*, 33(12), 2504–2526,
1078 doi:10.1175/1520-0485(2003)033<2504:NASWTH>2.0.CO;2, 2003.

1079 Chikaraishi, Y., Ogawa, N. O., Kashiya, Y., Takano, Y., Suga, H., Tomitani, A., Miyashita,
1080 H., Kitazato, H. and Ohkouchi, N.: Chikaraishi_et_al-2009-
1081 Limnology_and_Oceanography%3A_Methods, (2003), 740–750, 2009.

1082 Cleary, A. C., Durbin, E. G., Rynearson, T. A. and Bailey, J.: Feeding by Pseudocalanus
1083 copepods in the Bering Sea: Trophic linkages and a potential mechanism of niche partitioning,
1084 Deep. Res. Part II Top. Stud. Oceanogr., 134, 181–189, doi:10.1016/j.dsr2.2015.04.001, 2016.

1085 Coles, V. J., Stukel, M. R., Brooks, M. T., Burd, A., Crump, B. C., Moran, M. A., Paul, J. H.,
1086 Satinsky, B. M., Yager, P. L., Zielinski, B. L. and Hood, R. R.: Ocean biogeochemistry modeled
1087 with emergent trait-based genomics, Science (80-.), 358(6367), 1149–1154,
1088 doi:10.1126/science.aan5712, 2017.

1089 Cornic, M. and Rooker, J. R.: Influence of oceanographic conditions on the distribution and
1090 abundance of blackfin tuna (*Thunnus atlanticus*) larvae in the Gulf of Mexico, Fish. Res.,
1091 201(July 2017), 1–10, doi:10.1016/j.fishres.2017.12.015, 2018.

1092 Damien, P., Pasqueron de Fommervault, O., Sheinbaum, J., Jouanno, J., Camacho-Ibar, V. F. and
1093 Duteil, O.: Partitioning of the Open Waters of the Gulf of Mexico Based on the Seasonal and
1094 Interannual Variability of Chlorophyll Concentration, J. Geophys. Res. Ocean., 123(4), 2592–
1095 2614, doi:10.1002/2017JC013456, 2018.

1096 Decima, M., Landry, M. R., Stukel, M. R., Lopez-Lopez, L. and Krause, J. W.:
1097 Mesozooplankton biomass and grazing in the Costa Rica Dome: Amplifying variability through
1098 the plankton food web, J. Plankton Res., 38(2), 317–330, doi:10.1093/plankt/fbv091, 2016.

1099 Décima, M., Landry, M. R. and Rykaczewski, R. R.: Broad scale patterns in mesozooplankton
1100 biomass and grazing in the eastern equatorial Pacific, Deep. Res. Part II Top. Stud. Oceanogr.,
1101 58(3–4), 387–399, doi:10.1016/j.dsr2.2010.08.006, 2011.

1102 Décima, M., Landry, M. R., Bradley, C. J. and Fogel, M. L.: Alanine $\delta^{15}\text{N}$ trophic fractionation
1103 in heterotrophic protists, Limnol. Oceanogr., 62(5), 2308–2322, doi:10.1002/lno.10567, 2017.

1104 Domingues, R., Goni, G., Bringas, F., Muhling, B., Lindo-Atichati, D. and Walter, J.: Variability
1105 of preferred environmental conditions for Atlantic bluefin tuna (*Thunnus thynnus*) larvae in the
1106 Gulf of Mexico during 1993–2011, Fish. Oceanogr., 25(3), 320–336, doi:10.1111/fog.12152,
1107 2016.

1108 Doney, S. C., Lima, I., Moore, J. K., Lindsay, K., Behrenfeld, M. J., Westberry, T. K.,
1109 Mahowald, N., Glover, D. M. and Takahashi, T.: Skill metrics for confronting global upper
1110 ocean ecosystem-biogeochemistry models against field and remote sensing data, J. Mar. Syst.,
1111 76(1–2), 95–112, doi:10.1016/j.jmarsys.2008.05.015, 2009.

1112 Everett, J. D., Baird, M. E., Buchanan, P., Bulman, C., Davies, C., Downie, R., Griffiths, C.,
1113 Heneghan, R., Kloser, R. J., Laiolo, L., Lara-Lopez, A., Lozano-Montes, H., Matear, R. J.,
1114 McEnulty, F., Robson, B., Rochester, W., Skerratt, J., Smith, J. A., Strzelecki, J., Suthers, I. M.,
1115 Swadling, K. M., van Ruth, P. and Richardson, A. J.: Modeling what we sample and sampling
1116 what we model: Challenges for zooplankton model assessment, Front. Mar. Sci., 4(MAR), 1–19,
1117 doi:10.3389/fmars.2017.00077, 2017.

1118 Fasham, M. J. R., Ducklow, H. W. and McKelvie, S. M.: A nitrogen-based model of plankton
1119 dynamics in the ocean mixed layer, J. Mar. Res., 48(3), 591–639, 1990.

- 1120 Fennel, K., Wilkin, J., Levin, J., Moisan, J., O'Reilly, J. and Haidvogel, D.: Nitrogen cycling in
 1121 the Middle Atlantic Bight: Results from a three-dimensional model and implications for the
 1122 North Atlantic nitrogen budget, *Global Biogeochem. Cycles*, 20(3), 1–14,
 1123 doi:10.1029/2005GB002456, 2006.
- 1124 Fennel, K., Hetland, R., Feng, Y. and Dimarco, S.: A coupled physical-biological model of the
 1125 Northern Gulf of Mexico shelf: Model description, validation and analysis of phytoplankton
 1126 variability, *Biogeosciences*, 8(7), 1881–1899, doi:10.5194/bg-8-1881-2011, 2011.
- 1127 Follows, M. J., Dutkiewicz, S., Grant, S. and Chisholm, S. W.: Emergent biogeography of
 1128 microbial communities in a model ocean., *Science*, 315(5820), 1843–1846,
 1129 doi:10.1126/science.1138544, 2007.
- 1130 Forristall, G. Z., Schaudt, K. J. and Cooper, C. K.: Evolution and kinematics of a loop current
 1131 eddy in the Gulf of Mexico during 1985, *J. Geophys. Res.*, 97(C2), 2173,
 1132 doi:10.1029/91jc02905, 1992.
- 1133 Franks, P. J. S.: NPZ models of plankton dynamics: Their construction, coupling to physics, and
 1134 application, *J. Oceanogr.*, 58(2), 379–387, doi:10.1023/A:1015874028196, 2002.
- 1135 Franks, P. J. S.: Planktonic ecosystem models: Perplexing parameterizations and a failure to fail,
 1136 *J. Plankton Res.*, 31(11), 1299–1306, doi:10.1093/plankt/fbp069, 2009.
- 1137 Geers, T. M., Pikitch, E. K. and Frisk, M. G.: An original model of the northern Gulf of Mexico
 1138 using Ecopath with Ecosim and its implications for the effects of fishing on ecosystem structure
 1139 and maturity, *Deep. Res. Part II Top. Stud. Oceanogr.*, 129, 319–331,
 1140 doi:10.1016/j.dsr2.2014.01.009, 2016.
- 1141 Geiderl, R. J., MacIntyre, H. L. and Kana, T. M.: A dynamic regulatory model of
 1142 phytoplanktonic acclimation to light, nutrients, and temperature, *Limnol. Ocean.*, 43(4), 679–
 1143 694, doi:10.4319/lo.1998.43.4.0679, 1998.
- 1144 Gentleman, W., Leising, A., Frost, B., Strom, S. and Murray, J.: Functional responses for
 1145 zooplankton feeding on multiple resources : a review of assumptions and biological dynamics, ,
 1146 50, 2847–2875, doi:10.1016/j.dsr2.2003.07.001, 2003a.
- 1147 Gentleman, W., Leising, A., Frost, B., Strom, S. and Murray, J.: Functional responses for
 1148 zooplankton feeding on multiple resources: A review of assumptions and biological dynamics,
 1149 *Deep. Res. Part II Top. Stud. Oceanogr.*, 50(22–26), 2847–2875, doi:10.1016/j.dsr2.2003.07.001,
 1150 2003b.
- 1151 Gentleman, W. C. and Neuheimer, A. B.: Functional responses and ecosystem dynamics: How
 1152 clearance rates explain the influence of satiation, food-limitation and acclimation, *J. Plankton*
 1153 *Res.*, 30(11), 1215–1231, doi:10.1093/plankt/fbn078, 2008.
- 1154 Gomez, F. A., Lee, S. K., Liu, Y., Hernandez, F. J., Muller-Karger, F. E. and Lamkin, J. T.:
 1155 Seasonal patterns in phytoplankton biomass across the northern and deep Gulf of Mexico: A
 1156 numerical model study, *Biogeosciences*, 15(11), 3561–3576, doi:10.5194/bg-15-3561-2018,
 1157 2018.
- 1158 Gregg, W. W., Ginoux, P., Schopf, P. S. and Casey, N. W.: Phytoplankton and iron: Validation
 1159 of a global three-dimensional ocean biogeochemical model, *Deep. Res. Part II Top. Stud.*
 1160 *Oceanogr.*, 50(22–26), 3143–3169, doi:10.1016/j.dsr2.2003.07.013, 2003.

- 1161 Gutiérrez-Rodríguez, A., Décima, M., Popp, B. N. and Landry, M. R.: Isotopic invisibility of
 1162 protozoan trophic steps in marine food webs, *Limnol. Oceanogr.*, 59(5), 1590–1598,
 1163 doi:10.4319/lo.2014.59.5.1590, 2014.
- 1164 Holl, C. M., Waite, A. M., Pesant, S., Thompson, P. A. and Montoya, J. P.: Unicellular
 1165 diazotrophy as a source of nitrogen to Leeuwin Current coastal eddies, *Deep. Res. Part II Top.*
 1166 *Stud. Oceanogr.*, 54(8–10), 1045–1054, doi:10.1016/j.dsr2.2007.02.002, 2007.
- 1167 Hu, C., Lee, Z. and Franz, B.: Chlorophyll a algorithms for oligotrophic oceans: A novel
 1168 approach based on three-band reflectance difference, *J. Geophys. Res. Ocean.*, 117(1), 1–25,
 1169 doi:10.1029/2011JC007395, 2012.
- 1170 Ikeda, T., Kanno, Y., Ozaki, K. and Shinada, A.: Metabolic rates of epipelagic marine copepods
 1171 as a function of body mass and temperature, *Mar. Biol.*, 139(3), 587–596,
 1172 doi:10.1007/s002270100608, 2001.
- 1173 Kishi, M. J., Kashiwai, M., Ware, D. M., Megrey, B. a., Eslinger, D. L., Werner, F. E., Noguchi-
 1174 Aita, M., Azumaya, T., Fujii, M., Hashimoto, S., Huang, D., Iizumi, H., Ishida, Y., Kang, S.,
 1175 Kantakov, G. a., Kim, H. C., Komatsu, K., Navrotsky, V. V., Smith, S. L., Tadokoro, K., Tsuda,
 1176 A., Yamamura, O., Yamanaka, Y., Yokouchi, K., Yoshie, N., Zhang, J., Zuenko, Y. I. and
 1177 Zvalinsky, V. I.: NEMURO-a lower trophic level model for the North Pacific marine ecosystem,
 1178 *Ecol. Modell.*, 202(1–2), 12–25, doi:10.1016/j.ecolmodel.2006.08.021, 2007.
- 1179 Kitchens, L. L. and Rooker, J. R.: Habitat associations of dolphinfish larvae in the Gulf of
 1180 Mexico, *Fish. Oceanogr.*, 23(6), 460–471, doi:10.1111/fog.12081, 2014.
- 1181 Kjellerup, S., Dünweber, M., Swalethorp, R., Nielsen, T. G., Møller, E. F., Markager, S. and
 1182 Hansen, B. W.: Effects of a future warmer ocean on the coexisting copepods *Calanus*
 1183 *finmarchicus* and *C. glacialis* in Disko Bay, western Greenland, *Mar. Ecol. Prog. Ser.*, 447, 87–
 1184 108, doi:10.3354/meps09551, 2012.
- 1185 Landry, M., Haas, L. and Fagerness, V.: Dynamics of microbial plankton communities:
 1186 experiments in Kaneohe Bay, Hawaii, *Mar. Ecol. Prog. Ser.*, 16, 127–133,
 1187 doi:10.3354/meps016127, 1984.
- 1188 Landry, M. R. and Calbet, A.: Microzooplankton production in the oceans, *ICES J. Mar. Sci.*,
 1189 61(4), 501–507, doi:10.1016/j.icesjms.2004.03.011, 2004.
- 1190 Landry, M. R. and Hassett, R. P.: Estimating the grazing impact of marine micro-zooplankton,
 1191 *Mar. Biol.*, 67(3), 283–288, doi:10.1007/BF00397668, 1982.
- 1192 Landry, M. R., Decima, M., Simmons, M. P., Hannides, C. C. S. and Daniels, E.:
 1193 Mesozooplankton biomass and grazing responses to Cyclone Opal, a subtropical mesoscale
 1194 eddy, *Deep. Res. Part II Top. Stud. Oceanogr.*, 55(10–13), 1378–1388,
 1195 doi:10.1016/j.dsr2.2008.01.005, 2008.
- 1196 Landry, M. R., Ohman, M. D., Goericke, R., Stukel, M. R. and Tsyrklevich, K.: Lagrangian
 1197 studies of phytoplankton growth and grazing relationships in a coastal upwelling ecosystem off
 1198 Southern California, *Prog. Oceanogr.*, 83(1–4), 208–216, doi:10.1016/j.pocean.2009.07.026,
 1199 2009.
- 1200 Landry, M. R., Selph, K. E., Decima, M., Gutierrez-Rodríguez, A., Stukel, M. R., Taylor, A. G.
 1201 and Pasulka, A. L.: Phytoplankton production and grazing balances in the Costa Rica Dome, J.

- 1202 Plankton Res., 38(2), 366–379, doi:10.1093/plankt/fbv089, 2016.
- 1203 Landry, M. R., Beckley, L. E. and Muhling, B. A.: Climate sensitivities and uncertainties in
1204 food-web pathways supporting larval bluefin tuna in subtropical oligotrophic oceans, ICES J.
1205 Mar. Sci., 76(2), 359–369, doi:10.1093/icesjms/fsy184, 2019.
- 1206 Large, W. G., McWilliams, J. C. and Doney, S. C.: Oceanic vertical mixing: A review and a
1207 model with a nonlocal boundary layer parameterization, Rev. Geophys., 32(4), 363–403,
1208 doi:10.1029/94RG01872, 1994.
- 1209 Laxenaire, R., Speich, S., Blanke, B., Chaigneau, A., Pegliasco, C. and Stegner, A.: Anticyclonic
1210 Eddies Connecting the Western Boundaries of Indian and Atlantic Oceans, J. Geophys. Res.
1211 Ocean., 123(11), 7651–7677, doi:10.1029/2018JC014270, 2018.
- 1212 Laxenaire, R., Speich, S. and Stegner, A.: Evolution of the Thermohaline Structure of One
1213 Agulhas Ring Reconstructed from Satellite Altimetry and Argo Floats, J. Geophys. Res. Ocean.,
1214 124(12), 8969–9003, doi:10.1029/2018JC014426, 2019.
- 1215 Li, Q. P., Franks, P. J. S., Landry, M. R., Goericke, R. and Taylor, A. G.: Modeling
1216 phytoplankton growth rates and chlorophyll to carbon ratios in California coastal and pelagic
1217 ecosystems, J. Geophys. Res. Biogeosciences, 115(4), 1–12, doi:10.1029/2009JG001111, 2010.
- 1218 Lindo-Atichati, D., Bringas, F., Goni, G., Muhling, B., Muller-Karger, F. E. and Habtes, S.:
1219 Varying mesoscale structures influence larval fish distribution in the northern Gulf of Mexico,
1220 Mar. Ecol. Prog. Ser., 463, 245–257, doi:10.3354/meps09860, 2012.
- 1221 Maul, G. A. and Vukovich, F. M.: The Relationship between Variations in the Gulf of Mexico
1222 Loop Current and Straits of Florida Volume Transport, , 785–796, 1993.
- 1223 McKinley, G. A., Follows, M. J. and Marshall, J.: Mechanisms of air-sea CO₂ flux variability in
1224 the equatorial Pacific and the North Atlantic, Global Biogeochem. Cycles, 18(2), 1–14,
1225 doi:10.1029/2003GB002179, 2004.
- 1226 Mitra, A., Flynn, K. J., Burkholder, J. M., Berge, T., Calbet, A., Raven, J. A., Granéli, E.,
1227 Glibert, P. M., Hansen, P. J., Stoecker, D. K., Thingstad, F., Tillmann, U., Väge, S., Wilken, S.
1228 and Zubkov, M. V.: The role of mixotrophic protists in the biological carbon pump,
1229 Biogeosciences, 11(4), 995–1005, doi:10.5194/bg-11-995-2014, 2014.
- 1230 Moeller, H. V., Laufkötter, C., Sweeney, E. M. and Johnson, M. D.: Light-dependent grazing can
1231 drive formation and deepening of deep chlorophyll maxima, Nat. Commun., 10(1),
1232 doi:10.1038/s41467-019-09591-2, 2019.
- 1233 Morey, S. L., Martin, P. J., O’Brien, J. J., Wallcraft, A. A. and Zavala-Hidalgo, J.: Export
1234 pathways for river discharged fresh water in the northern Gulf of Mexico, J. Geophys. Res. C
1235 Ocean., 108(10), 1–1, doi:10.1029/2002jc001674, 2003a.
- 1236 Morey, S. L., Schroeder, W. W., O’Brien, J. J. and Zavala-Hidalgo, J.: The annual cycle of
1237 riverine influence in the eastern Gulf of Mexico basin, Geophys. Res. Lett., 30(16),
1238 doi:10.1029/2003GL017348, 2003b.
- 1239 Morey, S. L., Zavala-Hidalgo, J. and O’Brien, J. J.: The Seasonal Variability of Continental
1240 Shelf Circulation in the Northern and Western Gulf of Mexico from a High-Resolution
1241 Numerical Model, in Circulation in the Gulf of Mexico: Observations and Models, vol. 161, pp.
1242 203–218., 2013.

- 1243 Morrow, R. M., Ohman, M. D., Goericke, R., Kelly, T. B., Stephens, B. M. and Stukel, M. R.:
1244 CCE V: Primary production, mesozooplankton grazing, and the biological pump in the
1245 California Current Ecosystem: Variability and response to El Niño, *Deep. Res. Part I Oceanogr.*
1246 *Res. Pap.*, 140(June), 52–62, doi:10.1016/j.dsr.2018.07.012, 2018.
- 1247 Muhling, B. A., Lamkin, J. T., Alemany, F., García, A., Farley, J., Ingram, G. W., Berastegui, D.
1248 A., Reglero, P. and Carrion, R. L.: Reproduction and larval biology in tunas, and the importance
1249 of restricted area spawning grounds., 2017.
- 1250 Mulholland, M. R., Bernhardt, P. W., Heil, C. A., Bronk, D. A. and O’Neil, J. M.: Nitrogen
1251 fixation and release of fixed nitrogen by *Trichodesmium* spp. in the Gulf of Mexico, *Limnol.*
1252 *Oceanogr.*, 51(5), 2484, doi:10.4319/lo.2006.51.5.2484, 2006.
- 1253 Murray, A. G. and Parslow, J. S.: The analysis of alternative formulations in a simple model of a
1254 coastal ecosystem, *Ecol. Modell.*, 119(2–3), 149–166, doi:10.1016/S0304-3800(99)00046-0,
1255 1999.
- 1256 Oey, L., Ezer, T. and Lee, H.: Loop Current, rings and related circulation in the Gulf of Mexico:
1257 A review of numerical ..., *Geophys. Monogr. ...*, 161, 31–56 [online] Available from:
1258 <http://scholar.google.com/scholar?cites=642048877832323420&hl=en#46>, 2005.
- 1259 Parker, R. A.: Dynamic models for ammonium inhibition of nitrate uptake by phytoplankton,
1260 *Ecol. Modell.*, doi:10.1016/0304-3800(93)90042-Q, 1993.
- 1261 Pegliasco, C., Chaigneau, A. and Morrow, R.: Main eddy vertical structures observed in the four
1262 major Eastern Boundary Upwelling Systems, *J. Geophys. Res. Ocean.*, 120(9), 6008–6033,
1263 doi:10.1002/2015JC010950, 2015.
- 1264 Pörtner, H. O. and Farrell, A. P.: Physiology and Climate Change Hans, *Science* (80-.),
1265 322(October), 690–692 [online] Available from:
1266 <http://epic.awi.de/epic/Main?puid=32305&lang=en>, 2008.
- 1267 Richardson, A. J.: In hot water: Zooplankton and climate change, *ICES J. Mar. Sci.*, 65(3), 279–
1268 295, doi:10.1093/icesjms/fsn028, 2008.
- 1269 Riley, G. A.: Factors controlling phytoplankton populations on Georges Bank, *J. Mar. Res.*, 6(1),
1270 54–73, 1946.
- 1271 Rooker, J. R., Simms, J. R., David Wells, R. J., Holt, S. A., Holt, G. J., Graves, J. E. and Furey,
1272 N. B.: Distribution and habitat associations of billfish and swordfish larvae across mesoscale
1273 features in the gulf of Mexico, *PLoS One*, 7(4), doi:10.1371/journal.pone.0034180, 2012.
- 1274 Rooker, J. R., Kitchens, L. L., Dance, M. A., Wells, R. J. D., Falterman, B. and Cornic, M.:
1275 Spatial, Temporal, and Habitat-Related Variation in Abundance of Pelagic Fishes in the Gulf of
1276 Mexico: Potential Implications of the Deepwater Horizon Oil Spill, *PLoS One*, 8(10),
1277 doi:10.1371/journal.pone.0076080, 2013.
- 1278 Sailley, S. F., Vogt, M., Doney, S. C., Aita, M. N., Bopp, L., Buitenhuis, E. T., Hashioka, T.,
1279 Lima, I., Le Quéré, C. and Yamanaka, Y.: Comparing food web structures and dynamics across a
1280 suite of global marine ecosystem models, *Ecol. Modell.*, 261–262, 43–57,
1281 doi:10.1016/j.ecolmodel.2013.04.006, 2013.
- 1282 Sailley, S. F., Polimene, L., Mitra, A., Atkinson, A. and Allen, J. I.: Impact of zooplankton food
1283 selectivity on plankton dynamics and nutrient cycling, *J. Plankton Res.*, 37(3), 519–529,

1284 doi:10.1093/plankt/fbv020, 2015.

1285 Selph, K. E., Landry, M. R., Taylor, A. G., Gutierrez-Rodríguez, A., Stukel, M. R., Wokuluk, J.
1286 and Pasulka, A.: Phytoplankton production and taxon-specific growth rates in the Costa Rica
1287 Dome, *J. Plankton Res.*, 38(2), 199–215, doi:10.1093/plankt/fbv063, 2016.

1288 Sherr, E. B. and Sherr, B. F.: Significance of predation by protists in aquatic microbial food
1289 webs, *Antonie van Leeuwenhoek, Int. J. Gen. Mol. Microbiol.*, 81(1–4), 293–308,
1290 doi:10.1023/A:1020591307260, 2002.

1291 Staniewski, M. A. and Short, S. M.: Methodological review and meta-analysis of dilution assays
1292 for estimates of virus- and grazer-mediated phytoplankton mortality, *Limnol. Oceanogr.*
1293 *Methods*, 16(10), 649–668, doi:10.1002/lom3.10273, 2018.

1294 Steele, J. H. and Henderson, E. W.: The role of predation in plankton models, *J. Plankton Res.*,
1295 doi:10.1093/plankt/14.1.157, 1992.

1296 Steinberg, D. K. and Landry, M. R.: Zooplankton and the Ocean Carbon Cycle, *Ann. Rev. Mar.*
1297 *Sci.*, 9(1), 413–444, doi:10.1146/annurev-marine-010814-015924, 2017.

1298 Straile, D.: and metazoan efficiencies of protozoan Gross growth on food concentration , and
1299 their dependence zooplankton group ratio , and taxonomic, *Limnol. Oceanogr.*, 42(6), 1375–
1300 1385, 1997.

1301 Strickland, J. D. H. and Parsons., T. R.: A practical handbook for seawater analysis. Second
1302 Edition. [online] Available from: <http://www.dfo-mpo.gc.ca/Library/1507.pdf>, 1972.

1303 Strom, S. L., Benner, R., Ziegler, S. and Dagg, M. J.: Planktonic grazers are a potentially
1304 important source of marine dissolved organic carbon, *Limnol. Oceanogr.*, 42(6), 1364–1374,
1305 doi:10.4319/lo.1997.42.6.1364, 1997.

1306 Stukel, M. R., Coles, V. J., Brooks, M. T. and Hood, R. R.: Top-down, bottom-up and physical
1307 controls on diatom-diazotroph assemblage growth in the Amazon River plume, *Biogeosciences*,
1308 11(12), 3259–3278, doi:10.5194/bg-11-3259-2014, 2014.

1309 Stukel, M. R., Kahru, M., Benitez-Nelson, C. R., Décima, M., Goericke, R., Landry, M. R. and
1310 Ohman, M. D.: Using Lagrangian-based process studies to test satellite algorithms of vertical
1311 carbon flux in the eastern North Pacific Ocean, *J. Geophys. Res. Ocean.*, 120(11), 7208–7222,
1312 doi:10.1002/2015JC011264, 2015.

1313 Turner, J. T.: Zooplankton fecal pellets, marine snow, phytodetritus and the ocean’s biological
1314 pump, *Prog. Oceanogr.*, 130, 205–248, doi:10.1016/j.pocean.2014.08.005, 2015.

1315 Werner, F. E., Ito, S. I., Megrey, B. A. and Kishi, M. J.: Synthesis of the NEMURO model
1316 studies and future directions of marine ecosystem modeling, *Ecol. Modell.*, 202(1–2), 211–223,
1317 doi:10.1016/j.ecolmodel.2006.08.019, 2007.

1318 Xue, Z., He, R., Fennel, K., Cai, W. J., Lohrenz, S. and Hopkinson, C.: Modeling ocean
1319 circulation and biogeochemical variability in the Gulf of Mexico, *Biogeosciences*, 10(11), 7219–
1320 7234, doi:10.5194/bg-10-7219-2013, 2013.

1321