**Micro-scale variability enhances trophic transfer and potentially
sustains biodiversity in plankton ecosystems**

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25 **Abstract:**

26 We develop moment closure approximations to represent micro-scale spatial
27 variability in the concentrations of nutrients (N), phytoplankton (P) and zooplankton (Z) in
28 an NPZ model, which we apply to examine the impact of different levels of micro-scale
29 variability on both ecosystem dynamics and trophic transfer. Accounting explicitly for both
30 the mean-field and fluctuating components of each prognostic variable in the NPZ model
31 yields different dynamics for the mean-field concentrations, as well as lower phytoplankton
32 biomass and greater zooplankton biomass, compared to the conventional NPZ model
33 without micro-scale variability. The biomass of zooplankton consistently increases with
34 increasing total micro-scale variability, and a minimum threshold of such variability is
35 required for the existence of stable steady state solutions in the NPZ closure model.
36 Compared to the conventional NPZ model, the domain of parameter space over which stable
37 solutions exist is larger than for the NPZ closure model, and this stable domain widens with
38 increasing total variability. The latter result suggests that natural systems with greater
39 micro-scale variability may have the potential to sustain greater biodiversity. We find that
40 with the NPZ closure model: 1) the stability domains increases with micro-scale variability,
41 2) increase of the level of total micro-scale variability enhances trophic transfer, i.e.
42 increases the biomass of zooplankton, and 3) the coefficient of variation (CV_P) of
43 phytoplankton increases with micro-scale variability.

44

45 **Keywords:** spatial heterogeneity, intermittency, food chain, coefficient of variation

46

47 **1. Introduction:**

48 Plankton constitute the productive base of aquatic ecosystems and play vital roles in
49 the global cycles of nutrients and carbon. The complex interactions of plankton, other
50 organisms and biogenic particles in turbulent flows drive plankton dynamics and nutrient
51 cycling with influences expected to be accumulative across multiple scales (Franks et al.,
52 1986, 2002; Loreau 2001; Azam et al., 2004). Theoretical explanations are established by
53 means of various models (from simple two-component systems to highly complex multi-
54 component systems) using a set of differential equations (Steel et al., 1981, 1992; Fasham
55 1993; Edward et al., 1996; Huisman et al., 2006). Nearly all such models have been
56 developed based on the mean-field assumption, in which each concentration is treated as
57 uniform (i.e., well mixed) below the spatial resolution of the model, e.g. within a modeled
58 batch incubator, or within each grid cell of a 1-D or 3-D numerical model. However, Dobell
59 et al., (2009, 2014) reported that high micro-scale variance of phytoplankton at mm scale is
60 observed ubiquitously and it plays a major role in determining plankton population
61 dynamics.

62 Although equations for plankton growth rates are typically based on controlled
63 laboratory experiments, in reality plankton population dynamics differ from such idealized
64 laboratory settings, which cannot account for relevant biological and physical factors
65 (Berntnall et al., 2003; Wallhead et al., 2008). For example, spatial heterogeneity in
66 plankton distribution is well known among empirical ecologists due to large-scale turbulent
67 mixing (Okubo and Levin 1980). Berntnall et al., (2003) have shown that using second
68 order moment approximations to account for spatial heterogeneity yields results very
69 different from the typical first order moment (i.e., mean field) approximation. Furthermore,
70 Wallhead et al., (2008) find that at scales larger than 10 m heterogeneously distributed
71 plankton population respond differently compared to well-mixed conditions.

72 To account for the effects of dynamical nonlinearity acting on spatial variability,
73 which may lead to failure of the mean field approximation, moment closure methods have
74 been applied in terrestrial ecology (Bolker et al., 1997; Lewis et al., 2000; Murrell et al.,
75 2004; Barraquand et al., 2013) and terrestrial epidemiology (Ferguson et al., 2001; Filipe et
76 al., 2001, 2003). In spatial predator-prey models (Murdoch and Oaten, 1975; Weisser et al.,
77 1997; Neubert et al., 2002; Murdoch et al., 1992) dispersal can promote stability (Jansen,
78 1995). Several spatial models found that spatial or temporal heterogeneity can lead to a
79 stable equilibrium at the local and hence also global scale (Crowley, 1981; Holt and Hassell,
80 1993; McCann et al., 2000). On the other hand, dispersal enhances the persistence of
81 unstable host-parasitoid dynamics in host-parasitoid spatial models (Briggs & Hoopes
82 2004), and other studies (Allen 1975; Reeve 1988; Rohani et al., 1996) found destabilizing
83 effects of spatial dispersal. These previous studies all considered spatial heterogeneity at
84 scales above 10m.

85 The moment closure model introduced in Mandal et al., (2014) differs from previous
86 closure approaches in several respects. It is based on observed fluctuations in the
87 distribution of micro-scale phytoplankton data (Doubell et al., 2009, 2014). Also, it uses a
88 spatially explicit second order moment approximation to calculate the dynamics of the
89 variance and covariance of each variable. The mean fields are averaged quantities at the m
90 scale, and the fluctuating fields are qualified at the mm scale. Due to explicit equations for
91 the rate of change of means, variances and covariances, the second order moments impact
92 the dynamics of the mean field and vice-versa.

93 Mandal et al., (2014) purposely kept their plankton ecosystem model simple by
94 considering only phytoplankton and nutrient. However, zooplankton grazing strongly affects
95 the biomass and composition of phytoplankton communities (Storm et al., 1991; Carpenter
96 et al., 1984; Sterner 1989). Although nutrient inputs determine the potential biomass of

97 phytoplankton, zooplankton grazing can cause a significant deviation from simple nutrient-
98 phytoplankton dynamics (Carpenter et al., 1988; Yool 1998). Consequently, nutrient-
99 phytoplankton-zooplankton (NPZ) models have become standard tools for studying
100 plankton ecosystems in the ocean. Here we extend the closure modelling approach to an
101 NPZ closure model, and for the first time consider the effects of micro-scale variability on
102 trophic transfer and dynamics of planktonic ecosystems with multiple trophic levels. We
103 define the “micro-scale variability”, β , in a similar manner as in Mandal et al., (2014), as the
104 sum of all variances and covariances of fluctuating components divided by the square of the
105 sum all mean-field concentrations. This study focuses on how micro-scale variability, β ,
106 impacts the modelled ecosystem, and specifically addresses the following questions:

- 107 (a) How does micro-scale variability impact ecosystem stability?
108 (b) How does micro-scale variability affect ecosystem dynamics and trophic transfer?
109 (c) How is the coefficient of variation of phytoplankton (CV_P), which is an observable
110 quantity, related to micro-scale variability?

111 The manuscript has been arranged as follows: the detailed model formulations of the
112 conventional NPZ and the NPZ closure models are described in the section 2, “Model
113 Formulation”. The parameter choice and the discussion of model simulations are described
114 in the Section 3, “Results and discussion”. The interpretation of the results is also discussed
115 throughout the section “Results and Discussion”, and the questions posed in the introduction
116 are answered in the Section 4, “Conclusions”.

117

118 **2. Model Formulation:**

119 **2.1 Conventional NPZ model**

120 Many studies have used controlled laboratory settings to determine species-specific
121 grazing rates (Peter et al., 1984; Bertilsson et al., 2003) and other studies have estimated

122 grazing rates for zooplankton communities on phytoplankton communities (Sprules, 1980;
 123 Cyr et al., 1998). However, zooplankton-grazing functional forms remain a major
 124 uncertainty in ecological modeling. Several explicit grazing functional forms (linear,
 125 Holling type II, Ivetsov, sigmoidal, etc.) have been proposed and studied (Franks et al., 1986,
 126 2002; Fasham 1993, Edwards et al., 1996). For this first study to develop an NPZ closure
 127 model, we assumed a linear grazing rate, because it is the simplest among many options.

128 Taking N , P and Z as the biomass of nutrient, phytoplankton and zooplankton in the
 129 plankton ecosystem, a simple conventional NPZ model (based on Franks et al., 1986, 2002)
 130 can be explicitly described by the following set of differential equations:

$$131 \quad \frac{dP}{dt} = \nu_{\max} \frac{N}{K+N} P - M P - R P Z \quad (1a)$$

$$132 \quad \frac{dZ}{dt} = (1-\gamma) R P Z - G Z \quad (1b)$$

$$133 \quad \frac{dN}{dt} = -\nu_{\max} \frac{N}{K+N} P + M P + \gamma R P Z + G Z \quad (1c)$$

134 In the above (1a-c), the phytoplankton response to light is considered as a constant ($\nu_{\max}$)
 135 and the growth phytoplankton is considered to follow a Monod expression $\frac{N}{K+N}$, where K
 136 denotes the half-saturation constant (MacIsaac et al., 1969; Eppely et al., 1969; Lehman et
 137 al., 1975). At this stage, the model is 0-dimensional, so $\nu_{\max}$ does not depend on the
 138 intensity of light. The specific mortality rates of phytoplankton, M , and zooplankton, G , are
 139 assumed constant, and the zooplankton assimilation $(1-\gamma)$ is a simple linear function of
 140 food ingested. A linear zooplankton grazing function, RP , is considered, in which R is the
 141 specific grazing rate of zooplankton. The total nutrient within the NPZ model (1a-c) is
 142 conserved so that,

$$N + P + Z = \text{constant} = A \quad (2)$$

where A represents total nutrient content in the system.

2.2 NPZ Closure Model

To derive the NPZ closure model from the conventional NPZ model (1a-c), each of its components is considered to be a function of both time (t) and space (s):

$$N(s, t) = N_0(s, t) + N'(s, t), \quad P(s, t) = P_0(s, t) + P'(s, t), \quad Z(s, t) = Z_0(s, t) + Z'(s, t) \quad (3)$$

where N_0, P_0 and Z_0 are spatial mean values of nutrient, phytoplankton and zooplankton respectively, and N', P' and Z' are their fluctuating components with respect to corresponding mean values. According to Foloni-Neto et al., (2015), horizontal and vertical sampling for micro-scale phytoplankton distribution reveal the same statistics at the cm scale. The statistics are also similar at the mm scale except for the extreme values. Therefore, we consider the statistics of the fluctuating components to be isotropic, i.e. independent of the direction of sampling. At any particular time, the spatial average of each fluctuating component is zero ($\langle N'(s) \rangle = \langle P'(s) \rangle = \langle Z'(s) \rangle = 0$), while its temporal average can be nonzero, which also implies that spatial average of each variable equals its mean value $\langle N(s) \rangle = N_0(s), \langle P(s) \rangle = P_0(s)$ and $\langle Z(s) \rangle = Z_0(s)$. Putting (3) in equation (1a-c) and retaining only up to second-order terms in Taylor expansion, yields the following set of equations for the temporal variation of mean, variance and covariance of N, P and Z :

$$\frac{d P_0}{dt} = v_{\max} \left(\frac{N_0}{K + N_0} P_0 - \frac{K P_0}{(K + N_0)^3} \langle N'^2 \rangle + \frac{K}{(K + N_0)^2} \langle N' P' \rangle \right) - M P_0 - R(P_0 Z_0 + \langle P' Z' \rangle) \quad (4a)$$

$$\frac{d Z_0}{dt} = (1 - \gamma) R(P_0 Z_0 + \langle P' Z' \rangle) - G Z_0 \quad (4b)$$

$$164 \quad \frac{d N_0}{dt} = -\nu_{\max} \left(\frac{N_0}{K + N_0} P_0 - \frac{K P_0}{(K + N_0)^3} \langle N'^2 \rangle + \frac{K}{(K + N_0)^2} \langle N' P' \rangle \right) + M P_0 + \gamma R (P_0 Z_0 + \langle P' Z' \rangle) + G Z_0 \quad (4c)$$

$$165 \quad \frac{d \langle N'^2 \rangle}{dt} = -2 \nu_{\max} \left(\frac{N_0}{K + N_0} \langle N' P' \rangle + \frac{K P_0}{(K + N_0)^2} \langle N'^2 \rangle \right) + 2 M \langle N' P' \rangle + 2 \gamma R (Z_0 \langle N' P' \rangle + P_0 \langle N' Z' \rangle) + 2 G \langle N' Z' \rangle \quad (4d)$$

$$166 \quad \frac{d \langle P'^2 \rangle}{dt} = 2 \nu_{\max} \left(\frac{N_0}{K + N_0} \langle P'^2 \rangle + \frac{K P_0}{(K + N_0)^2} \langle N' P' \rangle \right) - 2 M \langle P'^2 \rangle - 2 R (Z_0 \langle P'^2 \rangle + P_0 \langle P' Z' \rangle) \quad (4e)$$

$$167 \quad \frac{d \langle Z'^2 \rangle}{dt} = 2(1 - \gamma) R (Z_0 \langle P' Z' \rangle + P_0 \langle Z'^2 \rangle) - 2 G \langle Z'^2 \rangle \quad (4f)$$

$$168 \quad \frac{d \langle N' P' \rangle}{dt} = \nu_{\max} \left(\frac{N_0}{K + N_0} (\langle N' P' \rangle - \langle P'^2 \rangle) + \frac{K P_0}{(K + N_0)^2} (\langle N'^2 \rangle - \langle N' P' \rangle) \right) - M (\langle N' P' \rangle - \langle P'^2 \rangle) + G \langle P' Z' \rangle + R Z_0 (\gamma \langle P'^2 \rangle - \langle N' P' \rangle) + R P_0 (\gamma \langle P' Z' \rangle - \langle N' Z' \rangle) \quad (4g)$$

$$169 \quad \frac{d \langle P' Z' \rangle}{dt} = \nu_{\max} \left(\frac{N_0}{K + N_0} \langle P' Z' \rangle + \frac{K P_0}{(K + N_0)^2} \langle N' Z' \rangle \right) - (M + G) \langle P' Z' \rangle + R Z_0 ((1 - \gamma) \langle P'^2 \rangle - \langle P' Z' \rangle) + R P_0 ((1 - \gamma) \langle P' Z' \rangle - \langle Z'^2 \rangle) \quad (4h)$$

$$170 \quad \frac{d \langle N' Z' \rangle}{dt} = -\nu_{\max} \left(\frac{N_0}{K + N_0} \langle P' Z' \rangle + \frac{K P_0}{(K + N_0)^2} \langle N' Z' \rangle \right) + M \langle P' Z' \rangle + G (\langle Z'^2 \rangle - \langle N' Z' \rangle) + R Z_0 ((1 - \gamma) \langle N' P' \rangle + \gamma \langle P' Z' \rangle) + R P_0 ((1 - \gamma) \langle N' Z' \rangle + \gamma \langle Z'^2 \rangle) \quad (4i)$$

171 Among the above nine equations of the NPZ closure model, the first three (4a-c) are
 172 the rates of change for the means of nutrient, phytoplankton and zooplankton respectively,
 173 while the next three (4d-f) represent the rates of change for their respective variance. The
 174 last three equations (4g-i) describe the rates of change for the covariances. The following
 175 conservation relationships hold among these nine equations:

176 (i) The total mean content in the system is conserved:

$$177 \quad N_0 + P_0 + Z_0 = \text{constant} = A \quad (5)$$

178 (ii) The total spatial variability in the system is conserved:

179
$$\langle P'^2 \rangle + \langle Z'^2 \rangle + \langle N'^2 \rangle + 2(\langle N'P' \rangle + \langle P'Z' \rangle + \langle N'Z' \rangle) = \text{constant} = B \quad (6)$$

180 We define a new dimensionless quantity called “micro-scale variability” β as:

181
$$\beta = \frac{B}{A^2} = \frac{\langle P'^2 \rangle + \langle Z'^2 \rangle + \langle N'^2 \rangle + 2(\langle N'P' \rangle + \langle P'Z' \rangle + \langle N'Z' \rangle)}{(N_0 + P_0 + Z_0)^2} \quad (7)$$

182 which represents a standardized measure of total variability in the closure model. Mandal et
183 al., (2014), by non-dimensionalizing their NP model, showed that the model dynamics
184 depend critically on β . We have similarly non-dimensionalized our NPZ closure model to
185 derive a set of equations explicitly in terms of β (Supplement S1.2.2).

186 In the NPZ closure model, mean of zooplankton z_0 (dimensionless), Z -variance $\langle z'^2 \rangle$
187 (dimensionless), and micro-scale variability, β , have the following relation (See Supplement
188 S1.2.2):

189
$$(z_0)^2 = \beta \langle z'^2 \rangle \quad (8)$$

190 Where, the Z -variance $\langle z'^2 \rangle$ is always non-negative for the biologically feasible solutions
191 and therefore, zooplankton mean z_0 always increases with micro-scale variability, β . This
192 implies that spatial variability should enhance trophic transfer in plankton food webs.

193 **3. Results and Discussion:**

194 **3.1 Parameter Range for Stability**

195 The numerical simulations are carried out with suitable choices of biologically
196 feasible parameter values (Table 1) based on empirical and theoretical studies (Sprules et
197 al., 1980; Peter et al., 1984; Franks et al., 1986; Storm et al., 1991) to investigate the global
198 behavior of conventional and closure models. We have also present extensive bifurcation
199 analyses (Supplement) to identify the parameter domain in which the stable steady state
200 solutions occur.

201 **Table 1.** Parameter values and ranges for dimensional and dimensionless model

Para Meter	Description	Reported value	Dimen- sionless quantity	Dimen- sionless Values	Inves- tigated Range
A	Sum of mean nitrogen contain	2 $\mu\text{g N l}^{-1}$ (Franks et al., 1986)	-----	-----	-----
$\nu_{\max}$	P -maximum growth rate	2 day^{-1} (Franks et al., 1986; Clark et al., 2000)	-----	-----	0.5-2
K	Half- saturation uptake constant	0.6-1.8 $\mu\text{g N l}^{-1}$ (Eppely et al., 1969; Lehman et al., 1975; Edward 1996)	$k = K/A$	0.3-0.9	0-2.5
M	P -mortality rate	0.07-0.9 day^{-1} (Lehman et al., 1975; Cyr 1992, 1998; Edward 1996)	$m = M/\nu_{\max}$	0.035- 0.45	0-1
R	Z -grazing rate	0.4-1.4 day^{-1} N^{-1} (Sprules et al., 1980; Cyr 1992, 1998; Edward 1996; Bertilsson et al., 2003)	$r = R A/\nu_{\max}$	0.4-1.4	0-2.5
G	Z -mortality rate	0.1-2.0 day^{-1} (Cyr 1998; Edward 1996; Bertilsson et al., 2003)	$g = G/\nu_{\max}$	0.05-1	0-1
γ	Unassimilated grazing fraction	0.3 (Sprules 1980; Franks 2002)	γ	0.3	0.3

202

203 The simulations of dimensionless conventional (S3-S4) and closure NPZ models (S20.1-
204 S20.7) (see the Supplement S2), are carried out with following parametric values:

205
$$r = 0.5, m = 0.3, g = 0.15, k = 0.5, \gamma = 0.3 \quad (9)$$

206 The above parameter set (9) satisfies the analytic conditions (S23) obtained for the existence
207 and stability of the interior steady state solutions of the conventional NPZ model (see the
208 Supplement S2).

209

210 3.2 Impact of “micro-scale variability” in Closure Model

211 3.2.1 Trophic-transfer in food web

212 The effect of varying the Z-grazing rate is shown in Fig. 1a for the conventional NPZ
213 model, and similar results are shown for the NPZ closure model in Fig. 1b and Fig. 1c for
214 two fixed values of $\beta = 2.0$ and 3.0 . In case of $\beta = 2.0$, the stable steady state solution is only
215 obtained for $0 < r < 1.6$ (for $r > 1.6$ only boundary solutions are possible). Zooplankton
216 biomass is consistently higher, and phytoplankton biomass consistently lower, in the NPZ
217 closure model compared to the corresponding conventional NPZ model. The Z-biomass
218 also increases with the level of micro-scale variability in the model.

219

Fig. 1 Impact of β : The proportion of ecosystem nutrient found in compartment is shown on the y-axis in each subfigure (a-c). The effect of varying grazing rate, r , based on the parameter set (9) on N , P and Z in a) the conventional NPZ model, and the NPZ closure model b) with $\beta = 2.0$ diagram is depicted for the range $0 < r < 1.6$, and c) with $\beta = 3.0$ in the range $0 < r < 5.0$.

The results are robust, as confirmed by further investigating the three possible cases. We investigate the dynamics and the standing stocks of biomass for the following three cases:

Case (i) N -dominating over P and Z biomasses

Case (ii) P -dominating over N and Z biomasses

Case (iii) Z -dominating over P and N biomasses

To get these three scenarios, we have chosen the following three sets of parameters:

$$r = 0.8, m = 0.2, g = 0.1, k = 0.5, \gamma = 0.3 \quad (N\text{-dominating}) \quad (10a)$$

$$r = 0.5, m = 0.3, g = 0.15, k = 0.5, \gamma = 0.3 \quad (P\text{-dominating}) \quad (10b)$$

$$r = 0.5, m = 0.2, g = 0.1, k = 0.5, \gamma = 0.3 \quad (Z\text{-dominating}) \quad (10c)$$

In case of N -dominating (10a), the standing stock of planktonic variables for the conventional NPZ model is $p = 0.18$, $z = 0.35$, $n = 0.47$, while for P -dominating case (10b), the standing stock is $p = 0.43$, $z = 0.22$, $n = 0.35$. In case of Z -dominating (10c), the standing stock of planktonic variables for the conventional NPZ model is $p = 0.29$, $z = 0.39$, $n = 0.33$. The standing stocks of planktonic variables for the conventional NPZ model are shown in Fig. 2a-c respectively. For the same three-parameter sets, the time series of planktonic variables for the NPZ closure model at different β values are drawn in Fig. 3. In each of these figures, the standing stocks of N , P and Z for the NPZ closure model are compared with the standing stock of the conventional NPZ model.

In all three cases, the standing stock of zooplankton biomass is higher and that of

246 phytoplankton is lower in the NPZ closure model, than in the corresponding conventional
 247 NPZ model. Increasing micro-scale variability, β , enhances the zooplankton biomass while
 248 it reduces the phytoplankton biomass. Furthermore, in the NP closure model (Mandal et al.,
 249 2014), β enhances the biomass of phytoplankton, which is the highest trophic level in that
 250 model. Thus, increasing micro-scale patchiness in the plankton distributions favours the
 251 highest trophic level present in either closure model. This suggests that natural ecosystems
 252 with high variability may favour trophic transfer upwards within the food chain. These
 253 results were obtained without explicitly accounting for the complicated behavioural
 254 dynamics of zooplankton (e.g., active swimming and optimal foraging strategies), which are
 255 beyond the scope of this study.
 256

257
 258 **Fig. 2 Conventional NPZ model:** The y-axis represents the ‘proportion of ecosystem
 259 nutrient found in compartment’ in each subfigure. Time-series of N , P and Z from the
 260 conventional NPZ model for three cases: a) N -dominance, b) P -dominance, and c) Z -
 261 dominance, obtained using three different parameter sets (10a-c), respectively.

Fig. 3 In each three cases, y-axis represents the proportion of ecosystem nutrient found in compartment. At different values of micro-scale variability, β , the time-series of mean-field concentrations of i) zooplankton, ii) phytoplankton, and iii) nutrient for three possible cases of NPZ closure model: a-c) ***N*-dominating case**, d-f) ***P*-dominating case** and g-i) ***Z*-dominating case**.

3.2.2 Minimum micro-scale variability threshold for stability in closure model

A minimum threshold of variability is required for the stability of the NPZ closure model. The shaded region in the two-parameters bifurcation diagram (Fig. 4) is the parameter domain for stability. For each value of parameter r , there is a minimum threshold of micro-scale variability β required for interior solutions. The same was found for the NP model (Mandal et al., 2014) in which so-called β^* is the minimum threshold variability beyond which interior solutions exist in the closure model. Below β^* only boundary solutions are possible, which are not relevant for analysis as we are mainly interested in interior solutions for which all variables are non-zero.

Fig. 4 NPZ closure model (r, β): Two-parameter (r, β) bifurcation diagram for parameter set (9). The shaded region in the diagram is the parameter domain for which the NPZ closure model has stable steady state solutions and in which all variables coexist. There is a minimum β , below which no stable steady state solutions exist. The values of other parameters are used from parameter set (9).

3.2.3 Variability favours higher probability of coexistence and greater biodiversity

Variability in nature is ubiquitous and plays a vital role in determining ecological patterns and hence traits. The heterogeneity of habitats and landscapes is undoubtedly a key to biodiversity. Many authors have reported that heterogeneity leads to increased species richness. In fact, the overall mean effect of heterogeneity on species richness is positive across taxa and regions. Most have claimed that heterogeneity is in all cases beneficial to biodiversity (Doi et al., 2013; Katayama et al., 2014; Calbet et al., 2015). Biodiversity certainly depends upon the ecological pattern considered (landscape heterogeneity, spatially- or temporally-variable environments, species size range, traits heterogeneity etc). Similar to our finding that variability enhances the biomass of the highest trophic level present, we also find that the potential for species richness increases with variability. This is because the stability domain (r, k) in Fig. 5 widens with increasing level of variability in the

298 closure model. This parameter domain defines the region over which coexistence of species
 299 is possible. A wider stability domain (r , k) is found for the closure model than for the
 300 corresponding conventional model, although some limited regions of parameter space that
 301 are stable for the conventional model may become unstable for the closure model at low
 302 values of β (Supplemental Figure S2). The same ecological pattern (a wider stability domain
 303 at higher variability) is found with all other parameter combinations, and this finding holds
 304 for both the NP and NPZ closure models. The result suggests that natural systems with
 305 greater micro-scale variability may have the potential to sustain greater biodiversity, i.e. that
 306 many different species with a wide range of parameter values may be able to coexist.
 307 Although a wider stability domain does not guarantee greater biodiversity, a narrower
 308 stability domain (as found at lower variability) necessarily reduces the set of viable
 309 combinations of parameter values (corresponding to trait values), and therefore limits
 310 potential biodiversity.

311

312

Fig. 5. Two-parameter (r , k) bifurcation diagram for the conventional NPZ and NPZ closure models for different values of β . The region underneath each curve represents the stable parameter space for each value of β , respectively. For all curves shown, values of other parameters were: $m = 0.4$, $g = 0.3$, $\gamma = 0.3$. The shaded area shows the realistic parameter domain, based on reported values, for r and k (Table 1).

3.2.4 Coefficient of variation (CV_P) of phytoplankton in NPZ closure model

Dobell et. al. (2009, 2014) reported intermittency in micro-scale phytoplankton data which they observed in Tokyo Bay with microstructure profiler TurboMAP-L. This instrument carries a laser fluorescence probe that resolves mm scale spatial variability of phytoplankton distribution, yielding high standard deviation of fluorescence signals. The “coefficient of variation (CV)” is defined as a ratio of standard deviation to the mean of a variable. Since CV_P is a measurable quantity, it is important to investigate how CV_P and micro-scale variability impact the dynamics of plankton ecosystems.

The relationship between CV_P and variability, β , in the NPZ closure model is shown in Fig. 6 using the parameter set (9), with different curves drawn by varying the parameter m , which is directly related to $v_{\max}$ as $m = M/v_{\max}$. Since the phytoplankton growth rate $v_{\max}$ depends on light intensity, it varies with vertical depth in seawater. As the intensity of light decreases with the depth from the sea surface, it is assumed that the maximum growth rate of phytoplankton $v_{\max}$ decreases which affects the coefficient of variation of the phytoplankton CV_P in the seawater. The CV_P is found to be greater than 1 for all stable steady states solutions in the NPZ closure model. Further, CV_P and β are positively correlated in the NPZ closure model.

336

337 **Fig. 6 NPZ Closure model (CV_P and β):** Coefficient of variation of phytoplankton (CV_P) is
 338 shown with respect to micro-scale variability, β , for different values of m .

339

340 In the NP closure model (Mandal et al., 2014) as well, CV_P and β are related in a
 341 similar way, and CV_P is greater than one for all stable solutions (Fig. 7). However, CV_P is
 342 less than one for some β values, at which boundary solutions exist. CV_P and β are positively
 343 correlated for both the NPZ and NP closure models.

344

345 **Fig. 7 NP Closure model case:** Total micro-scale variability, β , versus coefficient of

346 variation (CV_P) for phytoplankton in the absence of Z (Mandal et al., 2014) . In this case, for
347 boundary solutions in the NP closure model, CV_P may be < 1 , while for all stable solutions
348 $CV_P > 1$.

349

350 Mandal et al., (2014) presented observed profiles of chlorophyll (phytoplankton)
351 collected at the mouth of Tokyo Bay, Japan at different observation stations in May 2011,
352 and at one particular station from 2006 to Feb 2008, up to 120-m depth from the ocean
353 surface. The observed coefficient of variation for phytoplankton was less than one in the
354 interior of Tokyo Bay (coastal area), and greater than one far away from the coastal area.
355 Theoretical models (NP and NPZ) predict that CV_P is always greater than 1 for stable steady
356 state solutions. The theoretical results regarding $CV_P > 1$ are consistent with the
357 observations (Mandal et al., 2014) in open water where $CV_P > 1$. In the coastal region
358 (interior of Tokyo bay), a very low scale of heterogeneity may prevent the TubrboMAP-L
359 profiler from detecting high variance against high background phytoplankton mean, which
360 could result in observed values of $CV_P < 1$. In open water, the variability is very high
361 relative to the mean-field phytoplankton biomass. In this case, the phytoplankton aggregates
362 are abundant and a wide range of parameter space allows stable solutions. This suggests that
363 natural systems with greater micro-scale variability may have the potential to support
364 greater biodiversity of plankton.

365

366 **4. Conclusions**

367 We have extended the previously presented closure approach to develop an NPZ
368 closure model and applied it to conduct the first modelling study of how micro-scale
369 variability impacts plankton ecosystem dynamics, focusing specifically on the potential for
370 coexistence of species, trophic transfer between multiple trophic levels, and the persistence

371 of higher trophic levels. Our model predicts a range of values for the coefficient of variation
372 (CV_p) of phytoplankton, in agreement with the range observed for Tokyo Bay (Mandal et al.
373 2014). We also aimed to clarify the role of micro-scale variability, β , in determining the
374 coefficient of variation (CV_p) of phytoplankton. This study has yielded the following
375 answers to the questions posed in the Introduction:

- 376 a) micro-scale variability enhances the domain of ecosystem stability.
- 377 b) micro-scale variability enhances trophic transfer from phytoplankton to zooplankton.
- 378 c) the coefficient of variation (CV_p) of phytoplankton increases with micro-scale variability, β .

379 Thus we have successfully applied a spatial moment closure approach to predator-prey
380 dynamics, in essence like the terrestrial studies reviewed by Barraquand and Murrel (2013),
381 but here specifically for plankton ecosystems. Spatial heterogeneity increases the diversity
382 of resources and hence the available niche space (structural complexity), which ultimately
383 promotes species coexistence (Hutchinson, 1959) and enhances species persistence through
384 increased probability of finding shelter and refuge from adverse environmental conditions
385 (Svenning and Skov, 2007). Spatial heterogeneity is known to result in the diversification of
386 species via evolutionary adaptation to diverse environmental conditions (Hughes and
387 Eastwood, 2006). Similarly, we find that micro-scale variability increases the domain of
388 trait space over which stable solutions are possible with our closure modelling approach,
389 which suggests that the potential variety of coexisting phytoplankton and zooplankton
390 species increases with micro-scale spatial heterogeneity.

391 The fast growth and continual transport of plankton in water make it essential to account
392 explicitly for the dynamics of the spatial moments (variances and co-variances), which some
393 recent terrestrial moment closure studies have not made explicit functions of the ecological
394 dynamics nor of transport (Barraquand and Murrel, 2013). Still, understanding remains

quite limited concerning the effects of realistic levels of micro-scale variability, particularly in combination with physical transport, on plankton ecosystems (Mandal et al., 2016). Further advances will require the testing of theoretical predictions against observations. To this end, we have identified three specific testable predictions based on our results herein:

- 1) Micro-scale variability enhances trophic transfer up the food chain,
- 2) Stability of plankton ecosystems requires a coefficient of variation for phytoplankton biomass, $CV_P > 1$,
- 3) Total micro-scale variability, β , can be predicted based on observed CV_P .

Nevertheless, given that high levels of micro-scale variability are observed ubiquitously in the ocean, our findings herein reinforce the conclusions of previous studies (Mandal et al., 2014; Doubell et al., 2009, 2014), namely that the large-scale impact of micro-scale distributions may not be ignored. Furthermore, the relationship identified herein between the coefficient of variation (CV_P) of phytoplankton and the standardized total variability, β , may help to estimate the latter from observed CV_P . Thus, CV_P may be useful as an index for the potential of aquatic systems to support plankton biodiversity.

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423

424 **References**

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