

1 **Interactions between temperature and nutrients determine the population
2 dynamics of primary producers**

3
4 Carling Bieg^{1*} and David Vasseur¹
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6 1. Department of Ecology and Evolutionary Biology, Yale University

7 carling.bieg@gmail.com *

8 david.vasseur@yale.edu

9 * corresponding author
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12 **Abstract**

13 Global change is rapidly and fundamentally altering many of the processes regulating the flux of
14 energy throughout ecosystems and although researchers now understand the effect of
15 temperature on key rates (such as aquatic primary productivity), the theoretical foundation
16 needed to generate forecasts of biomass dynamics and extinction risk remains
17 underdeveloped. We develop new theory that describes the interconnected effects of nutrients
18 and temperature on phytoplankton populations and show that the thermal response of
19 equilibrium biomass (i.e., carrying capacity) always peaks at a lower temperature than for
20 productivity (i.e., growth rate). This difference results from trade-offs between the thermal
21 responses of growth, death, and per-capita impact on the nutrient pool, making this thermal
22 mismatch highly general and applicable to widely used population models. We further show
23 that non-equilibrium dynamics depend on the pace of environmental change relative to
24 underlying vital rates, and that populations respond to variable environments differently at
25 high vs. low temperatures due to thermal asymmetries.

26
27
28 **Keywords**

29 *Thermal performance, carrying capacity, population dynamics, phytoplankton, Droop model,*
30 *nutrient limitation, theoretical ecology*

31

32 **Introduction**

33

34 Global change is rapidly altering the abiotic environment in multiple ways, including changes in
35 the mean and variability of temperatures and suites of other anthropogenic impacts like
36 eutrophication (Doney *et al.* 2012; Steffen *et al.* 2015). Within the ecological hierarchy,
37 populations lie at the interface between abiotic environmental changes and biotic community
38 or ecosystem dynamics, integrating and coupling various responses to environmental change.
39 Despite this, we lack a mechanistic understanding of how population dynamics and resilience
40 respond to multiple axes of global change (i.e., changes in the environment across multiple
41 niche axes) and especially to combinations of abiotic and biotic stressors. The multitude of
42 rapidly changing environmental conditions is effectively altering multiple niche axes at once,
43 creating novel environments and highlighting the importance of understanding the interaction
44 between multiple “stressors.” Critically, our current theory is not equipped to understand
45 population structure and persistence under multiple simultaneous environmental changes,
46 making it difficult to forecast population dynamics in today’s changing, and increasingly
47 variable, world. For example, while the thermal dependence of vital rates has long been
48 acknowledged as important in regulating population performance or fitness (i.e., growth), and
49 researchers have begun understanding the interactive nature of multiple stressors for some
50 population-level processes, it remains to be seen how populations will dynamically respond to
51 suites of anthropogenic impacts associated with global change. Similarly, it remains to be seen
52 how environmental variability along these niche axes will alter population responses. Indeed,
53 environmental variability can have drastically different effects on population performance than
54 what would be predicted in static environments (Vasseur *et al.* 2014; Bernhardt *et al.* 2018b;
55 Slein *et al.* 2023).

56

57 Researchers are beginning to come to the consensus that there is an interactive effect of
58 temperature and resource limitation on population performance. Specifically, a species’
59 optimal temperature for growth, as well as the critical limits of its thermal niche, are functions
60 of resource availability such that populations are more sensitive to increasing temperature
61 when resources are limited (Thomas *et al.* 2017; Bestion *et al.* 2018; Huey & Kingsolver 2019;
62 Vinton & Vasseur 2022). While clearly important for intrinsic rates of population growth, it is
63 less clear how this interaction translates to population-dynamic processes such as the thermal
64 response of biomass and long-term population persistence. That is, while thermal performance
65 curves relate directly to population rates of change under idealized (i.e., density-independent)
66 conditions, additional information on density- or resource- dependent population growth is
67 needed to determine the size, dynamics, and extinction risk of populations. Importantly,
68 understanding trends in population biomass is central to population forecasting and necessary
69 for management at various scales. For example, population decline is the key element used to

70 determine a species' extinction risk (e.g., IUCN status), and biomass is central to dictating the
71 flow of energy throughout food webs and whole ecosystems (i.e., energy flux and carbon or
72 nutrient cycling via numerical responses). Developing theory to understand populations'
73 thermal and multi-stressor responses at the scale of management is critical for forecasting –
74 and mitigating – the effects of global change.

75
76 Empirically, the thermal dependence of population equilibrium biomass (i.e., carrying capacity)
77 is somewhat ambiguous, with evidence ranging from invariant (Jarvis *et al.* 2016) to negative
78 (Fussmann *et al.* 2014; Bernhardt *et al.* 2018a) relationships, while theoretically a variety of
79 nonlinear relationships have been suggested (Savage *et al.* 2004; Amarasekare 2015; Uszko *et*
80 *al.* 2017; Lemoine 2019; Vasseur 2020). Vasseur (2020) set the logical context for why carrying
81 capacity ought to follow a unimodal relationship with temperature given density- and
82 temperature-dependent birth and death rates, but empirical evidence for this is still lacking as
83 few researchers aim to measure carrying capacity near thermal extremes (and with high
84 enough resolution to capture the thermal limits) – perhaps in large part because of the inherent
85 experimental challenges in doing so – as well as variability in how carrying capacity is measured
86 empirically. More recently, (Vinton & Vasseur 2022) described the thermal dependence of long-
87 term (equilibrium) behaviour of populations under limiting resources, confirming this unimodal
88 relationship and showing that carrying capacity is dependent on both temperature and
89 resource availability. Despite this new understanding of how long-term behaviour ought to
90 respond to multiple stressors, population dynamics involve nonlinearities that make
91 equilibrium behaviour just the starting point for forecasting responses to variable environments
92 (Hastings *et al.* 2018).

93
94 Fundamentally, population patterns depend on a dynamic integration of both past and current
95 population densities, abiotic conditions, and trade-offs between costs (metabolism, death) and
96 benefits (somatic and reproductive growth) of functioning within a given environment. These
97 interacting factors regulate population rates of change (i.e., the speed and direction of changes
98 in biomass) and generate inherently lagged responses to changing environments. Under the
99 rapid pace of global change, populations may or may not be able to “keep up” with changing
100 environmental conditions, while also responding to the underlying variability that characterizes
101 natural environments (i.e., the various frequencies of environmental noise; Dillon *et al.* 2016).
102 Some organisms may be able to adapt or acclimate to different environments, while others are
103 less equipped to do so. The importance of environmental acclimation in regulating populations'
104 performance has received more attention recently (e.g., (Fey *et al.* 2021; Layden *et al.* 2022)),
105 however mechanistic yet generalizable insight into how this impacts population dynamics
106 remains to be seen. Ultimately, acclimation potential dictates an organism or population's
107 ability to persist in changing environments, but physiological trade-offs determine long-term

108 implications for persistence. Recently, Anderson et al. (unpublished) showed that thermal
109 acclimation of phytoplankton growth can be explained as a dynamic interplay between
110 temperature, nutrient availability and nutrient storage, giving important mechanistic insight
111 into how populations may respond to changing environments. It remains to be seen how these
112 interacting dynamics and environmental legacy effects translate to longer-term population
113 dynamics – that is, population rates of change as well as biomass trajectories and extinction
114 risk. Effective population forecasting in a time of global change requires an integration of
115 mechanistic organismal research and efficient generalizable population dynamics theory.
116

117 In this paper, we begin to do so by integrating recent empirical insights on the thermal
118 dependence of various vital rates within a generalizable framework for population dynamics of
119 phytoplankton populations under limiting nutrients. As the base of all aquatic food webs and a
120 vital element of global carbon cycles, phytoplankton have critical functional importance and
121 have become the hallmark for studying both metabolic/thermal ecology and for experimentally
122 testing theoretical predictions, making them an excellent starting point for developing a
123 mechanistically-informed general theory. Here we use a nutrient- and temperature-dependent
124 Droop model (Droop 1974, 1977; Sauterey & Ward 2022), recently amended and empirically-
125 validated by Anderson et al. (unpublished), to explore how temperature and nutrient limitation
126 collectively impact populations in both constant and variable thermal environments. This model
127 is useful because it is well equipped to understand limiting factors for population growth and
128 biomass accrual, as it separates the rates of nutrient uptake and assimilation via a dynamic
129 cellular nutrient quota – both rates that are now known to be differentially-regulated by
130 temperature. Anderson et al. (unpublished) showed that by differentiating uptake and
131 assimilation processes, temperature limitation can occur at different steps creating thermally-
132 dependent bottlenecks for population growth and suggesting the potential for complex
133 population dynamics.
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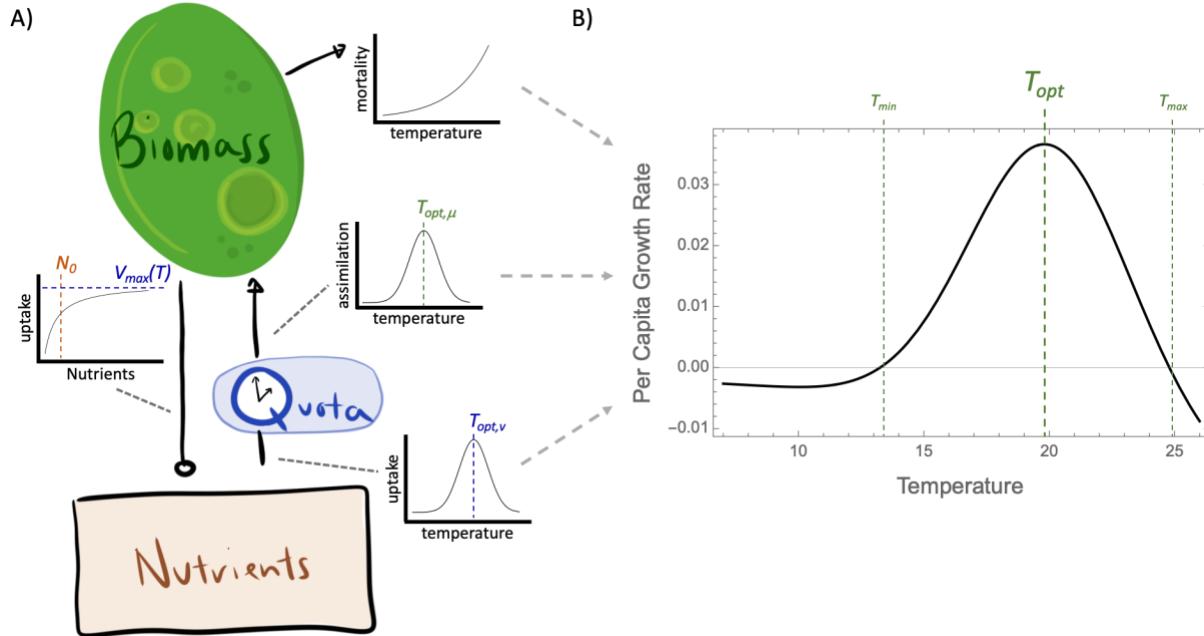
135 Importantly, our work relates to understanding nonequilibrium (e.g., transient, seasonal)
136 dynamics, in lakes and marine systems where primary productivity is important for the food
137 web, for carbon storage and carbon sequestration, as well as better understanding harmful
138 algal blooms (HABs), which are becoming increasingly prevalent and seemingly connected to
139 nutrients and temperature. This research provides mechanistic insight into phytoplankton
140 population dynamics under global change, with implications for whole ecosystem functioning.
141 Simultaneously, we use a combination of analytical and numerical approaches, allowing us to
142 make generalizable conclusions consistent with phenomenological modeling approaches. As
143 such, our insights also motivate the inclusion of more realistic environmental context into our
144 general population models.
145

146

147 **The Model**

148

149 To explore the interaction between nutrient availability and temperature on population
150 growth, biomass and dynamics, we use a 3-dimensional system of ordinary differential
151 equations to describe the coupled dynamics of nutrient (N) availability, intracellular nutrient
152 flux modeled using a dynamic quota (Q) and population biomass of phytoplankton (B). We build
153 off the framework first described by Droop (1974; 1977), which was recently amended by
154 Anderson et al. (unpublished) to incorporate the role of temperature (T) (Figure 1). The
155 dynamic nutrient quota component in this model separates nutrient uptake and assimilation
156 into two separate, temperature-dependent processes (Figure 1). This is useful because it more
157 accurately accounts for nutrient-phytoplankton interactions when not at a steady state (Droop
158 1977), allowing us to explore non-equilibrium dynamics while retaining the analytical
159 tractability of equilibrium solutions of more simple models (Cunningham & Nisbet 1980; Grover
160 1992; Smith & Waltman 1994). In this model, nutrient drawdown and biomass accrual is largely
161 regulated by nutrient accessibility – that is, the availability and uptake rate of nutrients.
162 Nutrient assimilation, which determines the rate at which stored nutrients (via Q) are
163 converted into biomass, regulates the magnitude of quota build-up, and together uptake and
164 assimilation rates (both of which are temperature dependent) create a trade-off determining
165 the accumulation (rate and magnitude) of an internal nutrient pool via the quota. More
166 broadly, the quota regulates the total flux from resource (nutrients) to biomass and is
167 determined by the balance between density- (and temperature-) dependent uptake and
168 assimilation rates, as well as the available external nutrient pool. While the dynamic nutrient
169 quota has no explicit loss term included here, growth is now scaled by an internal nutrient pool
170 relative to some minimum level required for positive assimilation, and in turn this term can
171 create a lag in population biomass responses to changing environmental conditions.
172



173
174

175 **Figure 1.** A) Schematic showing model state variables and temperature dependence of various rates. Here,
176 the inclusion of the nutrient quota splits uptake and assimilation into two separate temperature- (and
177 density-) dependent processes, and therefore acts to create a lag in the conversion of nutrients into biomass.
178 The upward arrow indicates conversion of nutrients into biomass (via the intracellular nutrient quota), and
179 the maximum rate of nutrient uptake (negative interaction, open circle) follows a saturating function of
180 nutrient concentration. B) Collectively, these temperature-dependent rates define a population's thermal
181 performance curve (TPC), which is defined as the per-capita rate of growth at near-zero densities (i.e., non-
182 limiting nutrients).

183

184 **Model Equations**

185 Here, nutrient availability (N) is modeled as a chemostat, with nutrient uptake by
186 phytoplankton (B) following a type-II functional response (Monod function), thus allowing for
187 saturation in per-capita uptake:

$$\frac{dN}{dt} = D(N_{in} - N) - B \frac{V_{max}(T)N}{N + N_0} \quad (1)$$

188 where, N_0 is the half-saturation constant for nutrient uptake, D is the dilution rate, and N_{in} is
189 the concentration of nutrients entering the system. $V_{max}(T)$ is the temperature-dependent
190 maximum rate of nutrient uptake (moles of nutrient per unit of algal biomass per unit of time).
191 Previous work has shown that V_{max} (or, more broadly, consumption when not distinguished
192 from assimilation) is a unimodal function of temperature (see (Englund *et al.* 2011) for meta-
193 analysis) and following the work of (Amarasekare & Savage 2012; Thomas *et al.* 2017; Huey &
194 Kingsolver 2019; Vinton & Vasseur 2022), we define V_{max} as a normally-distributed function of
195 temperature around some optimal temperature for nutrient uptake, $T_{opt,v}$:

$$V_{max}(T) = v_0 + v_1 e^{-\left(\frac{(T-T_{opt,v})^2}{\beta_v}\right)} \quad (2)$$

196 where β_v defines the breadth of the temperature-response for uptake.

197

198 Within the cell, the nutrient quota, Q , determines the flux of nutrients based on differences
199 between temperature-dependent uptake and assimilation rates:

$$\frac{dQ}{dt} = \frac{V_{max}(T)N}{N + N_0} - \mu_\infty(T)(Q - Q_{min}) \quad (3)$$

200 where Q_{min} is the minimum nutrient quota (moles cell⁻¹) needed to maintain a positive
201 assimilation rate and $\mu_\infty(T)$ is the temperature-dependent maximum rate of nutrient
202 assimilation (time⁻¹), defined again as a normally-distributed function of temperature around
203 some optimal temperature for assimilation ($T_{opt,\mu}$):

$$\mu_\infty(T) = \mu_0 + \mu_1 e^{-\left(\frac{(T-T_{opt,\mu})^2}{\beta_\mu}\right)} \quad (4)$$

204 β_μ defines the breadth of the temperature-response for assimilation. μ_∞ is so-named because it
205 represents the rate of per-capita biomass growth that is achieved when the nutrient quota is
206 infinitely large. Biomass dynamics are thus described as:

$$\frac{dB}{dt} = B(\mu_\infty(T))(1 - \frac{Q_{min}}{Q}) - d(T) \quad (5)$$

207 where B is population biomass density (volume⁻¹; interchangeable with cell density since cell
208 size is not considered in this model), and $d(T)$ is the temperature-dependent mortality rate
209 (time⁻¹). Previous work has shown that mortality rates scale as Boltzmann-Arrhenius
210 relationships (Gillooly *et al.* 2001; Brown *et al.* 2004; McCoy & Gillooly 2008); however, similar
211 to other theoretical work (Amarasekare 2015; Vinton & Vasseur 2022) we represent mortality
212 as an exponential function of temperature to increase model tractability without losing much
213 accuracy over biologically relevant temperature ranges:

$$d(T) = d_0 + d_1 e^{d_2 T} \quad (6)$$

214 Together, these temperature-dependent rates define the population's thermal performance.

215

216 Although we represent the temperature-dependent functions $V_{max}(T)$ and $\mu_\infty(T)$ as symmetric
217 unimodal functions, others have assumed that these are monotonically increasing functions of
218 temperature (e.g. Boltzmann-Arrhenius functions; (Thomas *et al.* 2017)). We show in the
219 Appendix that either choice of function leads to a similarly shaped thermal performance curve

220 for phytoplankton growth and that the qualitative patterns demonstrated by our model are not
221 affected by our choice of a unimodal function (Figure A3).

222

223 ***Numerical & Analytical Analyses***

224 Importantly, our analysis and conclusions are generalizable, particularly due to the analytical
225 approaches we use. That is, while the parameters used in our analysis are loosely based on
226 empirical measurements of important rates, the qualitative relationships between variables
227 gives us insight into phytoplankton growth and population dynamics in general.

228

229 When not explicitly stated (e.g., if individually varied for analytical/simulation purposes) the
230 following parameter set was used: $T_{opt,v} = 20$, $T_{opt,\mu} = 20$, $\sigma_v = 3.25$, $\sigma_\mu = 3.25$, $v_0 = 0.0005$, $v_1 =$
231 0.005 , $\mu_0 = 0.1$, $\mu_1 = 0.5$, $d_0 = 0.005$, $d_1 = 0.0012$, $d_2 = 0.1$, $Q_{min} = 0.1$, $r_0 = 0.5$, $N_{in} = 1$ and $D = 1$.
232 By setting D and N_{in} to 1, we normalize the inputs of the chemostat model and reduce its
233 dimensionality. We then explore the role of nutrient limitation by varying the half-saturation
234 constant, N_0 (uptake saturation), relative to the normalized parameters (as N_0 increases for a
235 given nutrient concentration, N, growth is more limited by nutrients). Although uptake
236 saturation and V_{max} often vary in concert (Aksnes & Egge 1991), we keep these terms separate
237 to better isolate the effects of temperature-dependent uptake and uptake efficiency ($1/N_0$) as a
238 tractable way of imposing nutrient limitation. Note that in certain applications of the chemostat
239 model, D is often incorporated into the population's mortality or loss term to reflect individuals
240 being washed out; however, consistent with other theory studying biomass dynamics (León &
241 Tumpson 1975; Sauterey & Ward 2022; Vinton & Vasseur 2022) and so that we can better
242 isolate the effects of temperature on dynamics, we assume that phytoplankton mortality is
243 independent of the flow rate D . The inclusion of additional mortality to reflect wash-out would
244 not alter general patterns on population responses (i.e., qualitative responses to changing
245 environments) so long as we also include an additive temperature-dependent effect on
246 mortality. The chosen parameter set allows for population persistence (positive growth; stable
247 interior equilibrium) across a reasonable thermal breadth, as shown in Figure 1B, and allows us
248 to qualitatively explore the effects of varying multiple parameters on population persistence
249 and dynamics relative to this baseline.

250

251 While the individual rates used in this model are scaled by temperature and/or nutrient
252 availability, we note that this format has not qualitatively changed the set of possible outcomes
253 of the model (i.e., possibility of and qualitative stability properties of stable interior
254 equilibrium). That is, since the model structure has not changed, the possible outcomes of our
255 model are restricted to a set of well-understood phenomena (Droop 1977; Smith & Waltman
256 1994); Anderson et al. unpublished). Equilibrium solutions for all state variables are described in
257 the Appendix (Equations A1-3), along with the isolines depicting how temperature changes the

258 general equilibrium structure (Figure A1). This model has two possible stable equilibrium states,
259 depending on the availability of and ability to take up nutrients, one with algae absent ($B=0$)
260 and one with a positive biomass ($B>0$) (Figure 2) (Droop 1977; Cunningham & Nisbet 1980;
261 Nisbet & Gurney 1982). In the case where $B>0$ the population always approaches the
262 equilibrium monotonically and the model does not produce any complex (i.e., cyclic) dynamics.
263 This equilibrium structure therefore reflects the asymptotic behaviour of all simulations under
264 static environmental conditions, and simultaneously serves as a reference for simulation results
265 when environmental variability is incorporated. That is, we refer to all simulation results
266 relative to underlying analytical solutions (i.e., the deterministic skeleton; (Higgins *et al.* 1997))
267 to further emphasize the generality of our approach and results. Here, rather than focusing on
268 the effects of specific parameterizations (e.g., using an empirically parameterized model or
269 conducting a full parameter sensitivity analysis) we instead focus on the general nature of
270 temperature and nutrient interactions.

271
272 All analyses were done in Wolfram Mathematica v13.1. Numerical simulations were performed
273 using Mathematica's NDSolve function with automatic integration method. Simulations were
274 run for sufficient time to account for any transient dynamics before evaluating asymptotic
275 behaviour. This duration depended on the analysis being done (e.g., constant versus variable
276 temperature and the time scale of temperature variation, if any).

277
278 To explore the effect of temperature variation we modelled temperature using a sinusoidal
279 function as follows:

$$T(t) = T_{mean} + A * \sin(p2\pi t) \quad (7)$$

280 Where T_{mean} is the average temperature, A represents the amplitude of temperature variation,
281 and p is the period of forcing.

282
283

284 Equilibrium behaviour along a temperature gradient

285
286 We begin by deriving the thermal performance curve (TPC) for algae (B), given by the per-capita
287 growth rate (dB/Bdt) when nutrients are non-limiting. In this case, $N/(N + N_0) \rightarrow 1$ and the
288 maximum equilibrium nutrient quota, Q , value, hereafter referred to as Q_{max} , is reached. This
289 maximum equilibrium value is obtained by simplifying Equation (3) and solving:

$$\frac{dQ}{dt} = 0 = V_{max}(T) - \mu_{\infty}(T)(Q - Q_{min}) \quad (8)$$

290

$$Q_{max} = \frac{V_{max}(T)}{\mu_{\infty}(T)} + Q_{min} \quad (9)$$

291

292 Substituting this value into Equation 5 yields the population's fundamental TPC:

$$\frac{dB}{Bdt} = \frac{V_{max}(T) \mu_{\infty}(T)}{V_{max}(T) + \mu_{\infty}(T)Q_{min}} - d(T) \quad (10)$$

293

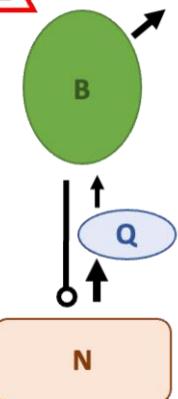
294 This curve represents a typical left-skewed unimodal function of temperature, which peaks at
295 the temperature that maximizes growth (T_{opt}), and positive growth rates are bounded by the
296 lower and upper thermal limits, T_{min} and T_{max} , that define the fundamental thermal niche
297 (Figure 1 and 2). The shape of this curve results from the fact that the first term of Equation 10
298 is unimodal with respect to T , reflecting the product of the two gaussian functions $V_{max}(T)$ and
299 $\mu_{\infty}(T)$ (and therefore a symmetric, nearly gaussian function when $T_{opt,\mu} = T_{opt,v}$). Subsequently,
300 subtracting $d(T)$ from this curve creates the classic-shaped TPC (see (Amarasekare & Savage
301 2012; Vinton & Vasseur 2022), and results in $T_{opt} < T_{opt,v} & T_{opt,\mu}$ because of this differential.
302

303 Previous work has established that the optimum for thermal performance (here measured by
304 the per-capita growth rate dB/Bdt , decreases under nutrient limitation due to the non-linearity
305 of the two terms in Equation 10 (Thomas *et al.* 2017; Vinton & Vasseur 2022). Under limiting
306 nutrients, N cannot be factored out of Equation 10 (though it retains the same general shape)
307 and nutrient limitation therefore scales this curve. We demonstrate this result in Figure 2B by
308 solving dB/Bdt (from Equation 5) for different levels of nutrient uptake half-saturation constant
309 (N_0 ; indicating the efficiency of nutrient uptake, or de-facto nutrient limitation) where N is held
310 at the supply concentration ($N_{in}=1$) (i.e., the realized TPC). Eventually, nutrients become so
311 limiting that the upper and lower limiting values of the thermal niche converge upon a single
312 temperature; further nutrient limitation beyond this does not support population growth at any
313 temperature.
314

315 With the addition of a dynamic nutrient pool (N, equation 1), we can solve for the equilibrium
316 algal biomass at different temperatures. This equilibrium is similar to the concept of the
317 carrying capacity in the logistic growth model, only here it is an emergent property of the
318 dynamics of our model (whereas in the logistic equation it is a parameter or input function; see
319 (Vasseur 2020). We find that temperature and nutrients have an interactive effect on
320 equilibrium biomass that does not match the thermal performance curve (Figure 2). Although
321 equilibrium biomass is a unimodal function of temperature with lower and upper critical points
322 matching those of the TPC, it is maximized at temperatures less than T_{opt} . That is, the
323 temperature response of equilibrium biomass, hereafter referred to as $K(T)$ or the **thermal**

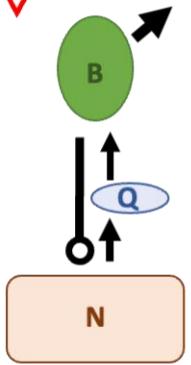
324 **biomass curve** (TBC), is skewed opposite to that of the TPC. The difference between these two
325 temperature optima, which we will denote T_r and T_K for optimal temperatures for growth and
326 biomass, respectively, is affected by the accessibility of nutrients. Increasing the efficiency of
327 nutrient uptake (i.e., decreasing N_0) effectively decreases nutrient limitation and enhances the
328 differences between the shape and optima of the thermal performance and thermal biomass
329 curves (Figure 2). Here, we see that increasing uptake efficiency alters both curves such that
330 they become more dissimilar when nutrients are non-limiting (i.e., saturated). On the other
331 hand, when nutrients are highly limiting, the thermal performance and biomass curves
332 ultimately converge to the same at the very point where T_{min} and T_{max} intersect; T_r and T_K
333 necessarily converge. That is, when nutrients become so limiting that the TPC has only a single
334 critical point (where $dB/Bdt=0$) the two curves have the same optimal temperature.
335 Importantly, this result suggests that population productivity (i.e., growth rate, r) and biomass
336 (i.e., carrying capacity, K) have different temperature-dependencies, and that these differential
337 responses are mediated (specifically, decreased) by nutrient limitation (Figure 2). Importantly,
338 equilibrium biomass is always optimized at seemingly sub-optimal temperatures, relative to the
339 TPC. We will hereafter refer to this as ***r*-K mismatch**, or simply mismatch for our purposes.
340

A) 1 Saturated nutrient uptake

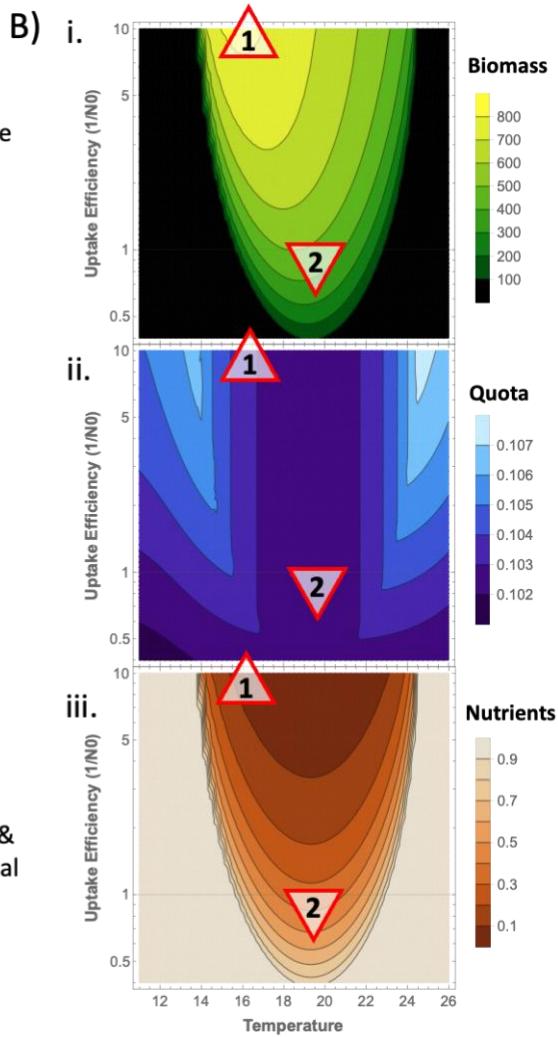


- Efficient @ low temperatures to utilize available nutrients
- Lower mortality @ T_K
- Maximizes nutrient storage & Biomass accrual
- Larger lag & slower dynamics

2 Limited nutrient uptake

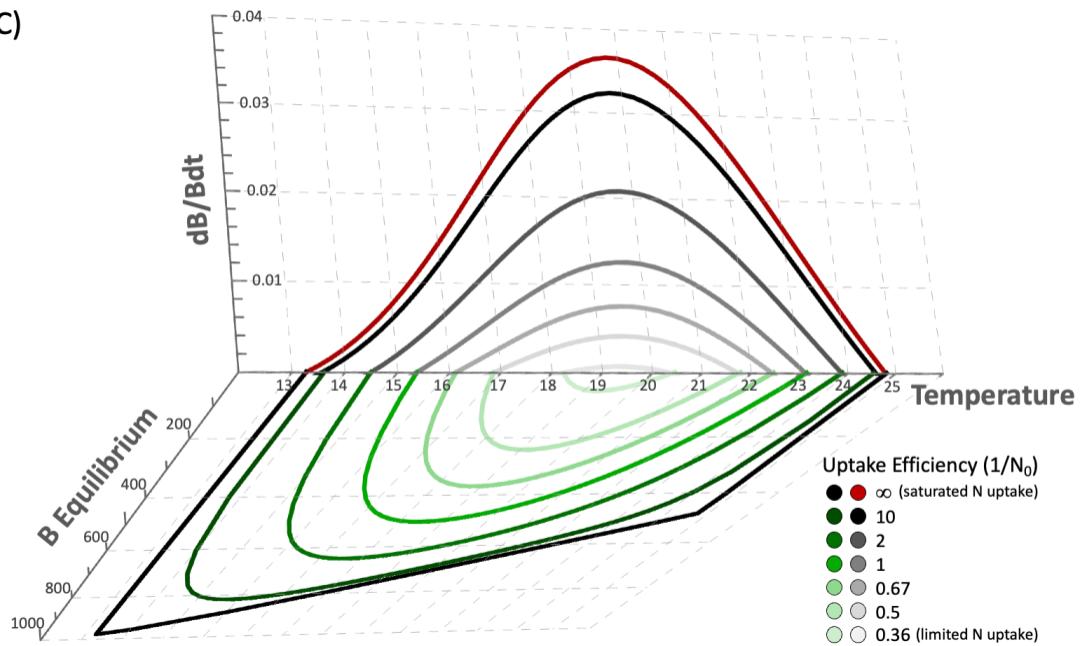


- Requires optimal temperatures for sufficient nutrient utilization
- Higher mortality @ T_r
- Less nutrient storage & loses Biomass potential
- Smaller lag & faster dynamics



341

C)



342

343 **Figure 2.** A) Schematic showing the combined influence of nutrient uptake efficiency (defined as $1/N_0$,
344 therefore describing the saturation of uptake) and temperature and their interactive effect in regulating the
345 various rates defining our system; and B) corresponding Nutrient, Quota and Biomass equilibria. C)
346 Temperature responses of productivity (i.e., the TPC; red line representing the fundamental TPC – i.e., infinite
347 nutrients – and black-grey lines representing productivity (i.e., the realized TPC) under changing uptake
348 efficiencies when $N=N_{in}=1$) and equilibrium biomass (green lines), at different levels of nutrient uptake
349 efficiency, defined as $1/N_0$. Specifically notice the temperature mismatch between the two temperature
350 optima, T_r and T_k , for the TPC and equilibrium biomass (i.e., carrying capacity; K), respectively. Here, N_0 is
351 varied with line/point opacity reflecting limitation of nutrient uptake (higher uptake efficiency, $1/N_0$,
352 effectively equates to saturating nutrients). From light to dark colouring: $N_0 = 0.1, 0.5, 1.0, 1.5, 2.0$.

353

354

355 Although our modified Droop model is specific to phytoplankton growth, it is interesting to
356 note that the mismatch between the thermal performance and thermal biomass curves has
357 been shown to occur in similar models where nutrient quotas were not included as a dynamic
358 component (Vinton and Vasseur 2022), suggesting that it is a general phenomenon generated
359 by the interaction between temperature and nutrient (or, more broadly, resource)
360 consumption and supply. In **Box 1**, we demonstrate the conditions under which our model can
361 be simplified into a more general 2-equation system (analogous to Vinton and Vasseur's
362 consumer-resource model) and show that biomass is always maximized at lower temperatures
363 than productivity (i.e., $T_k < T_r$) in this simpler model because of trade-offs between resource
364 availability, (over-) consumption (i.e., density-dependence), and temperature-dependent death
365 rates, which together regulate the "efficiency" of the system for turning resources into
366 biomass. Specifically, at colder temperatures, a single unit of resources can support more
367 population biomass because less is lost to death (or respiration) since $d(T)$ is small. However at
368 warmer temperatures, a single unit of resources supports less population biomass because $d(T)$
369 is large. This observation combines with the fact that resource (nutrient) equilibrium densities
370 follow a flat-bottomed U-shaped function of temperature; that is, resource equilibrium changes
371 very little over much of the thermal niche, but the amount of consumers supported by it
372 changes quite drastically (Figure B1). Therefore, the relationships identified in Box 1 ought to be
373 generally true in consumer-resource models that fit our two simplifying assumptions (e.g., the
374 model used in Vinton and Vasseur 2022).

375

Box 1: What drives the thermal mismatch between production and biomass?

Figure 2 shows that equilibrium biomass consistently peaks at a lower temperature than thermal performance (per-capita population growth). The difference between the two peaks grows when individuals are more efficient at accessing their resources (nutrients in our case; decreasing N_0 of the uptake function). Vinton and Vasseur (2022) showed the same pattern when investigating the interactive nature of temperature- and resource- dependence in heterotrophic consumer populations, suggesting our inferences here are relevant for general consumer-resource systems. Here we investigate the origin of this mismatch. We find that

the population's equilibrium response to temperature is dependent on trade-offs between nutrient uptake/assimilation and turnover – both temperature-dependent processes – such that biomass optimization becomes less dependent on optimal growth conditions as nutrients become saturated.

In both models (ours and Vinton and Vasseur's), equilibrium biomass is an asymmetric unimodal function of temperature that is skewed opposite to that of the TPC, such that equilibrium densities peak at values closer to T_{min} than T_{max} (i.e., the optimal temperature for biomass, T_K , is less than the optimal temperature for the TPC, hereafter referred to as T_r) (Figures 2, B1).

The analytical derivation of the (consumer) population's equilibrium biomass depends directly on the temperature dependent rate $V_{max}(T)$ (uptake or consumption), and on the equilibrium nutrient (resource) density which also changes as a function of temperature. From Equation 1, this expression is given by:

$$B_{eq}(T) = \frac{D(N_{in} - N_{eq}(T))(N_{eq}(T) + N_0)}{V_{max}(T) N_{eq}(T)} \quad (B1)$$

Where $N_{eq}(T)$ is the temperature dependent nutrient equilibrium. Direct inference from this expression is challenging due to the incorporation of both direct and indirect impacts of temperature. Instead, we employ two simplifications to understand the r-K mismatch.

First, given that the simpler 2-equation model of Vinton and Vasseur admits the same behavior as our more complex 3-equation model, we can recover the simpler 2-equation model of Vinton and Vasseur by assuming that the nutrient quota remains at equilibrium ($Q = Q_{eq}$) and that Q_{eq} is constant across temperature. This effectively removes the dynamic effects of the nutrient Quota from our model and treats it as a constant. Therefore, from Equation 3:

$$\frac{V_{max}(T)N}{N + N_0} = \mu_{\infty}(T)Q_{eq} \left(1 - \frac{Q_{min}}{Q_{eq}}\right) \quad (B2)$$

Substituting this relationship into Equation 5 gives:

$$\frac{dB}{dt} = B \left(\frac{V_{max}(T) N}{Q_{eq} (N + N_0)} - d(T) \right) \quad (B3)$$

where $1/Q_{eq}$, when treated as a constant, is equivalent to the energy conversion efficiency in classical consumer-resource models. This assumption makes our approach analogous to classical consumer-resource models without a dynamic nutrient quota. In reality, different environmental or physiological conditions make this assumption more or less accurate – such as, for example, the availability of or efficiency of consuming nutrients (Figure 2).

Solving Equation B3 = 0, with some rearranging, yields:

$$\frac{V_{max}(T) N_{eq}}{(N_{eq} + N_0)} = Q_{eq} d(T) \quad (B4)$$

which can be substituted into expression B1 to give a simplified expression for the biomass equilibrium:

$$B_{eq}(T) = \frac{D(N_{in} - N_{eq}(T))}{d(T) Q_{eq}} \quad (B5)$$

Notably, this is a simpler form than expression B1, but still retains both direct and indirect impacts of temperature change.

Our second simplifying assumption relies on the fact that the nutrient equilibrium is a nearly symmetric U-shaped function of temperature across the domain of the population's fundamental niche. This means that we can identify two temperatures within this domain (T_{cold} and T_{hot}) that have equal nutrient equilibria ($N_{eq}(T_{cold}) = N_{eq}(T_{hot})$), but different population biomass equilibria ($B_{eq}(T_{cold}) \neq B_{eq}(T_{hot})$) (Figure B1). At these two temperatures we can therefore remove the indirect effect of temperature via N_{eq} from equations B1 and B5.

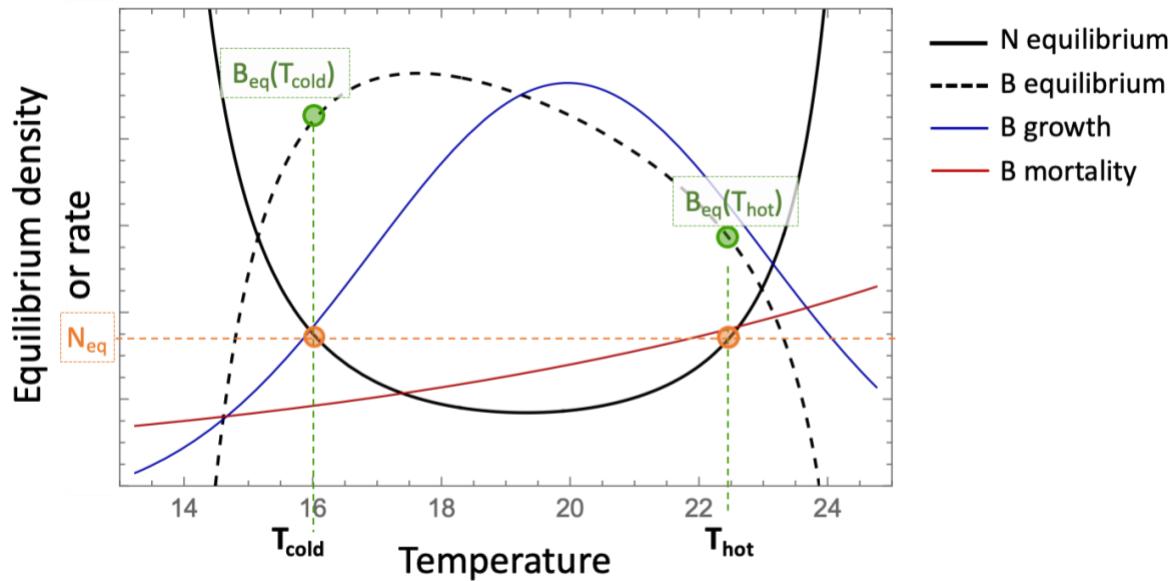


Figure B1: Summary of differential temperature responses of model equilibrium and vital rates.

Therefore, from these symbolic solutions (B1 and B5), differences between $B_{eq,hot}$ and $B_{eq,cold}$ are inversely proportional to the differences in uptake ($V_{max}(T)$) and mortality ($d(T)$) rates at

the two temperatures. That is, where $N_{eq,cold} = N_{eq,hot}$ and $B_{eq,cold} > B_{eq,hot}$, $V_{max}(T_{cold}) < V_{max}(T_{hot})$ and $d(T_{cold}) < d(T_{hot})$ (Figure B1). Specifically,

$$\frac{B_{eq}(T_{cold})}{B_{eq}(T_{hot})} = \frac{V_{max}(T_{hot})}{V_{max}(T_{cold})} = \frac{d(T_{hot})}{d(T_{cold})} \quad (B6)$$

Despite the rate of nutrient uptake (V_{max}) being lower at T_{cold} , this is counteracted by the similarly lower mortality (i.e., turnover) rates and allows for larger biomass accrual. At T_{hot} , nutrients are taken up at a faster rate, but more biomass is lost to turnover. Stronger temperature-responses of $V_{max}(T)$ and $d(T)$ will cause larger differences between $B_{eq,hot}$ and $B_{eq,cold}$, and therefore stronger asymmetry in the equilibrium solution and increased mismatch between the optimal temperatures for biomass (equilibrium) and productivity (growth). Since N_0 scales the resource uptake rate, V_{max} is maximized and it becomes intuitive why resource saturation (decreased N_0) increases mismatch.

To summarize, for a given nutrient density (N_{eq}), more population biomass can accumulate at lower temperatures, even though the nutrient uptake rate is lower. In other words, for a population that can achieve a particular N_{eq} ($R^* \text{ à la } (Tilman 1982)$ for resources in general) but has a large V_{max} , it will necessarily have fewer individuals because each of those individuals has a large impact on the nutrient levels. That is, the per capita impact of each B is higher for a higher V_{max} , so there can be fewer consumptive individuals for a given N_{eq}^* . If a population can achieve the same N_{eq} but with a smaller V_{max} , then each individual B will have a smaller effect on nutrients, allowing for more of them. Ultimately, the nutrient equilibrium is set by the ratio of $V_{max}(T)/d(T)$, but the biomass equilibrium is set by the magnitude of $V_{max}(T)$ and $d(T)$.

376

377 Our full 3-dimensional model that incorporates a dynamic, temperature-dependent nutrient
378 Quota adds complexity, yet retains the same general rules as identified in Box 1. From equation
379 B5 (Box 1) we can see that the Quota is indeed important in determining equilibrium biomass,
380 and therefore scales the ratios identified in solution B6 with temperature, providing important
381 mechanistic nuance for understanding growth and biomass accumulation specific to
382 phytoplankton populations. From Figures 1 and 2, temperature and nutrient limitation have an
383 interactive effect on population biomass that is mediated by trade-offs between uptake and
384 mortality (Box 1) and regulated via the nutrient Quota. When nutrients are saturated, growth
385 occurs as soon as temperatures allow. This means that population biomass can be optimized at
386 lower temperatures – where the equilibrium quota is larger (see Figure 2B for equilibria), and
387 nutrients are efficiently turned into biomass without the large loss of biomass due to turnover
388 at higher temperatures. Here, despite the surplus of resources fueling ample biomass, the rates
389 of uptake and assimilation at these temperatures are lower, creating a greater lag through the
390 Quota and overall slower growth and dynamics. Alternatively, when nutrients are limited T_r and
391 T_K begin to converge. The fundamental niche shrinks ($T_{max} - T_{min}$) and low-temperature rates of

392 uptake and assimilation are not sufficient to maximize population growth, so biomass is
393 optimized at temperatures closer to where growth is optimized (i.e., T_r) – reducing mismatch.
394 However, biomass can not reach the same maximum as under nutrient-saturated conditions
395 because of the corresponding increased turnover at these temperatures. Here, biomass is
396 maximized under high flux (i.e., fast) conditions, with nutrients rapidly converted into
397 population biomass – with less lag through the Quota (and less stored nutrients) – and then
398 much of it lost to mortality.

399

400 It is worth noting that here we are assuming uptake and assimilation rates have symmetrical
401 and equal thermal responses. Given the importance of trade-offs between uptake and
402 assimilation rates in regulating the flux through the Quota, it is possible that asymmetry in
403 these rates' temperature responses may alter our results. However, while asymmetry between
404 these temperature responses affects the magnitude of the biomass response, it does not affect
405 mismatch because it simultaneously shifts the entire thermal niche to follow the temperature-
406 dependence of nutrient uptake (see Appendix Figures A4-5). This is because uptake and
407 assimilation are sequential processes, so do not have equal weighting in terms of regulating the
408 thermal dependence of population growth and dynamics. That said, asymmetry in these
409 temperature-responses (particularly when the thermal optimum for uptake is less than that for
410 assimilation) allows for greater and earlier quota peaks, resulting in more efficient conversion
411 to biomass before the quota is over-depleted by less efficient consumption at higher
412 temperatures (Figure A5).

413

414 Importantly, the Quota represents the *potential* for biomass growth of a population, and
415 therefore ought to be an important component regulating non-equilibrium responses to
416 variable environments. The differential rates of biomass growth, and ability for nutrients to
417 accumulate within the cell, across the thermal niche will become important under varying
418 environments, such that both the nutrient storage ability (when assimilation rates are low) and
419 implicit lag caused by the Quota ought to act as a buffering mechanism for populations during
420 stressful or harsh times. Collectively, the nutrient quota – or more accurately the lag associated
421 with the quota – ought to drive differential dynamic responses to environmental variability at
422 high and low temperatures.

423

424

425 ***r-K* mismatch and implications for transient dynamics**

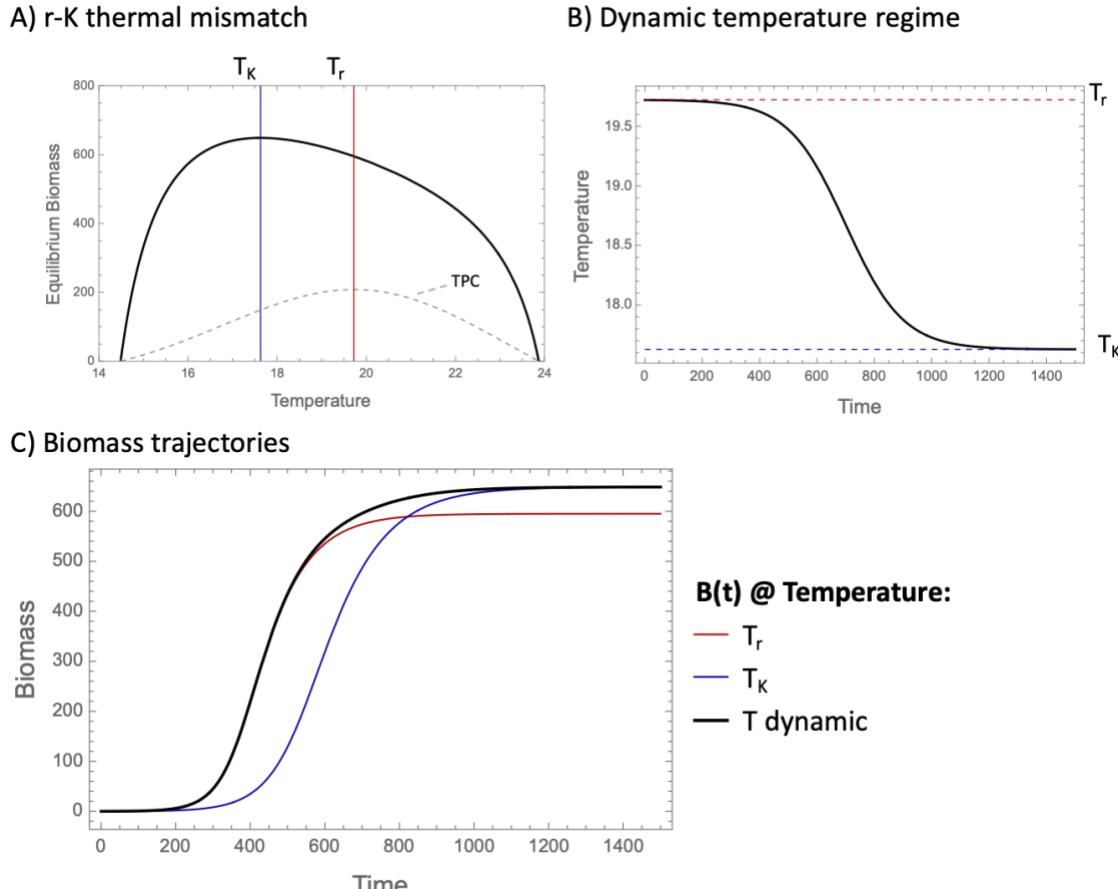
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427 We can now build off this insight on the equilibrium response to temperature, to understand
428 transient population dynamics. Here, the temperature-dependence of vital rates and
429 equilibrium biomass play important roles in determining the eventual state of a population (i.e.,

430 the equilibrium) and how long it takes to get there (i.e., transient length or return time). For
431 example, while temperatures that optimize rates of population growth will result in short
432 transients and therefore the fastest approach to equilibrium, this equilibrium is not optimized.
433 Alternatively (and as suggested in Figure 2), temperatures that maximize equilibrium biomass
434 (i.e., K) will lead to the highest population levels but take much longer to get there due to the
435 lower rates at these temperatures. As described above, and eloquently shown by Anderson et
436 al. (unpublished), despite the nutrient quota not being a strong determinant of equilibrium
437 biomass, it can have a strong impact on the non-equilibrium dynamics of the system.
438 Furthermore, the fact that temperature cannot optimize both performance (growth) and
439 biomass (production) has implications for population trajectories under climate change and for
440 effective management strategies.

441
442 This suggests the intriguing possibility that certain forms of temperature variation between
443 these two optima may be able to facilitate both optimal growth and optimal biomass. In
444 classical population models (e.g., the logistic), r and K have an interesting relationship during
445 dynamic population growth where the impact of r on dynamics is large when biomass is low,
446 but weak when near K . This suggests that temperature could change dynamically to favour fast
447 growth when biomass is low, and then favour large K when biomass has increased. Our model
448 elucidates growth and biomass dynamics for phytoplankton populations more mechanistically
449 than the logistic model, but follows the same principles. T_r maximizes population growth at
450 near-0 biomass densities, but as biomass grows and resources become more depleted, this
451 temperature may no longer be the “optimal” environment for a population collectively to be in.
452 At higher densities, it becomes more beneficial for temperatures to be lower (near T_K) where
453 the efficiency of conversion from nutrients to biomass is maximized, turnover is low, and
454 therefore biomass can be maximized. Indeed, we can see that T_r and T_K result in both different
455 equilibria and transient lengths, but when properly timed, a transition between the two
456 temperatures can maximize both the rate of population increase and ultimate biomass
457 obtained (Figure 3). These differential responses of population growth and size at different
458 temperatures also imply potentially interesting dynamic effects of continuously varying
459 temperatures (e.g., seasonality).

460



461
462 **Figure 3.** Thermal optima for maximizing biomass (K) or growth rate (r) and corresponding transient dynamics
463 (approach to equilibrium). When temperature is varied such that temperature starts at T_r (maximum growth
464 rates when biomass densities are low), then gradually decreases to T_K (maximum equilibrium biomass), the
465 population is able to reach equilibrium faster. In this sense, temperature is optimized to facilitate rapid
466 growth from low densities and keep this pace as it then approaches maximum biomass.
467

468 Non-equilibrium dynamics and population responses

469
470 Figures 1-3 collectively show that population growth rate and quota-induced lags, transient
471 lengths, and equilibrium biomass have different and interacting temperature-dependencies.
472 This means that the time scales that population dynamics operate on are temperature
473 dependent and suggests that the time scale of environmental variation ought to be important
474 in determining long-term population dynamics. Effective population forecasting requires us to
475 identify time scales at which variation in temperature is going to have important effects beyond
476 those predicted by equilibrium dynamics or average temperatures.
477

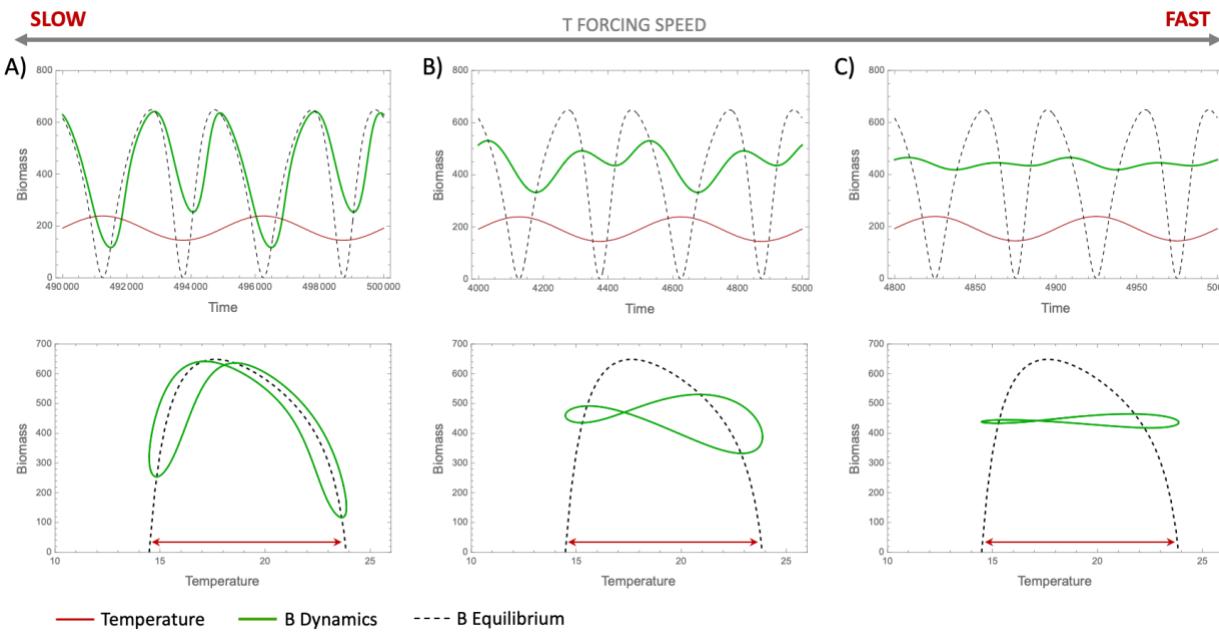
478 When temperature is varied sinusoidally between the boundaries of a population's thermal
479 niche (T_{min} and T_{max}), the equilibrium approaches (but does not pass) 0 at both of these extreme
480 temperatures – therefore doubling the period of expected biomass dynamics over one period

481 of temperature forcing. Figure 4 shows the biomass dynamics over time under this form of
482 temperature variation, relative to the (changing) equilibrium (also see Figure A7 in the
483 Appendix for additional temporal scales and Figures A8-9 for dynamics of N and Q). Note that
484 when the forcing period is *very* long (e.g., with this parameterization, >500 000 time steps),
485 biomass almost perfectly tracks the equilibrium curve (Figure A7) and population dynamics can
486 therefore be accurately predicted using the thermal biomass curve at all temperatures. At the
487 other extreme, when forcing is *very* fast, biomass dynamics effectively cannot respond to the
488 rapidly changing temperature and biomass becomes nearly invariant – approaching the mean
489 equilibrium biomass over the thermal range (Figure 4C and Figure A7). These responses reflect
490 two extremes of dynamical responses along a gradient of environmental forcing speed, relative
491 to the underlying vital rates of the model (i.e., the population’s rate of change, or ability to
492 respond to environmental changes). At intermediate speeds of temperature variation, the
493 dynamics become less predictable (Figure 4). Here, there is a dynamic interplay between a
494 changing attractor (equilibrium), local stability, and thermally asymmetric population rates of
495 change (e.g., growth rates and the Quota-induced lag), together causing the dynamics to lag
496 unevenly behind the changing deterministic equilibrium; we thus see the amplitude of biomass
497 variation decreasing with increasing forcing speeds (Figure 4).

498

499 Under still relatively slow forcing (e.g., Figure 4A), population dynamics can nearly track the
500 equilibrium but fail near the temperature extremes – that is, where population rates of change
501 slow and local stability approaches zero (Figure A6). This is also where thermal asymmetry in
502 the Quota-induced lag becomes apparent: the lag is higher at low versus high temperatures,
503 even where population growth rates (dB/Bdt) are equally low (i.e., near T_{min} and T_{max}), meaning
504 the time scale that population dynamics operate on is different at high and low temperatures,
505 and biomass dynamics are less responsive to changing temperature when they are low. What
506 this means is that populations track the equilibrium better at high temperatures than at low
507 temperatures, and are therefore more likely to collapse when temperatures approach T_{max}
508 (most apparent in Figure 4A) or even surpass the temperature extremes (e.g., see Figure A10).
509 On the other hand, the more pronounced lag at lower temperatures means that the population
510 will retain higher biomass for longer as temperatures approach T_{min} (Figure 4, as well as Figure
511 A10 for temperature varying beyond the thermal niche). This suggests that as long as forcing is
512 fast enough, the population effectively does not have enough time to crash at these low
513 temperatures before temperature rises again (Figure 4A,B). Next, as temperature forcing
514 becomes faster (Figure 4B,C), this same dynamic thermal asymmetry remains, and the
515 temperature-dependent rates of change drive a form of perpetual “overshoot” at high
516 temperatures, reinforcing this high-temperature-variability (relative to low temperatures) even
517 though the dynamics can no longer closely follow the equilibrium. The magnitude of this
518 variability is again dependent on the time scale of temperature variation, relative to the

519 population, eventually approaching invariant population dynamics as forcing speeds further
520 increase.
521



522
523 **Figure 4.** Population dynamics, relative to the temperature-dependent equilibrium, in response to
524 sinusoidally varying temperatures between T_{\min} and T_{\max} . Here, dynamics have differential abilities to “track”
525 the changing equilibrium depending on the speed of forcing and temperature-dependent rates of population
526 growth. Forcing periods shown here: A) 5000, B) 500, and C) 100 time units. Temperature in top row is scaled
527 for visualization purposes (multiplied by 10).

528
529 Finally, the mechanisms behind these dynamics are qualitatively general despite a modest
530 interactive effect with nutrient limitation (saturation of nutrient uptake, or “efficiency”) on the
531 realized dynamics under variable temperature. When nutrient uptake is less efficient (i.e., N_0 is
532 higher), both the TPC and the equilibrium response are altered (Figure 2), and together these
533 changes reduce the asymmetric dynamics between high and low temperatures (i.e., via the
534 quota) while also lowering the overall “pace” of population growth. Under these circumstances,
535 r - K mismatch is decreased, the buffering effect of low temperatures seen above is lessened,
536 and the population dynamics become more invariant than when nutrients are less limited
537 (Figure A11). Note, however, that this is in large part a result of *relative* time scales of
538 population dynamics and temporal forcing, since a given frequency of forcing will “seem” faster
539 to a population with slower growth rates.

540

541 Discussion

542

543 Here we demonstrate that under the assumption of a constant supply of resources (a
544 chemostat supplying nutrients), the thermal performance of a phytoplankton population (i.e.,

545 the temperature dependence of per-capita growth rate under density-independent conditions)
546 is different than the thermal performance of equilibrium biomass, with biomass always peaking
547 at cooler temperatures than performance. The thermal biomass curve outlined here describes
548 how carrying capacity (K) varies with temperature for a population consuming finite resources
549 (with a constant supply); hence, we refer to this thermal differential as r - K mismatch.
550 Furthermore, we demonstrate that these thermal relationships have differential responses to
551 changes in resource availability; the optimal temperatures for the two attributes converge as
552 resources become more limiting, ultimately intersecting at the point where resources are so
553 scarce that they can no longer support a viable population (Figure 2). Our mechanistic insight
554 into the drivers of r - K mismatch for phytoplankton populations show that this pattern is a result
555 of trade-offs between nutrient uptake and death, and that inclusion of a dynamic nutrient
556 quota allows us to determine how both equilibrium and non-equilibrium dynamics depend on a
557 combination of nutrients, temperature, and variability (speed of fluctuations) in the
558 environment. Furthermore, these results – and the trade-offs generating them – ought to be
559 common phenomenon for more general consumer-resource interactions (i.e., thermal
560 mismatch between r and K in a population with density dependent growth; Box 1). Specifically,
561 these patterns ought to always hold so long as mortality increases with temperature and
562 differences between the thermal responses of growth and mortality define an organism's
563 thermal niche – together driving r - K mismatch. Indeed, although our model and analytical
564 results here rely on a unimodal function of temperature for population growth (nutrient uptake
565 and assimilation rates), we note that the model behaves similarly when we shift to
566 monotonically increasing (i.e., exponential) functions (see Appendix, Figure A3). This is in line
567 with common “double exponential” approaches to modelling population performance (e.g.,
568 (Thomas *et al.* 2017)), and importantly highlights that our results reveal a general
569 representation of the thermal response of growth, turnover and density-dependence.
570
571 One of the major challenges associated with predicting the dynamic response of populations to
572 changes in temperature and other environmental attributes is the role of indirect effects;
573 temperature-dependent changes in the productivity of resources or density of competitors, for
574 example, make it difficult to anticipate how a focal species will respond. At the population level,
575 a variety of indirect effects manifest as changes in the strength of density dependence.
576 Understanding these changes will inform improved general models of population responses.
577 Our demonstration of differences in the optimal temperatures for performance and biomass is
578 generated by a strengthening of density-dependence as temperature increases, such that at
579 warmer temperatures fewer individuals are supported per unit of resource (Box 1). When
580 framed in terms of classic Logistic population dynamics, the increase in the strength of density-
581 dependence leads to an r - K mismatch, where r is optimized at a warmer temperature than that
582 which optimizes K . Importantly, the thermal dependence of both rates of change (productivity)

583 and equilibrium (biomass) will dictate population trajectories and dynamics under global
584 change, and understanding the potential for thermal mismatches is necessary to predict or
585 forecast dynamics into the future.

586

587 Predictive population forecasts are often based on organisms' physiological thermal
588 performance (i.e., their TPCs extrapolated to match changing environments), but our results
589 suggest that the effect of global change on population densities may not match these forecasts:
590 when there is an r - K mismatch, projections cannot be informed by the TPC of fitness ($r(T)$)
591 alone. Clearly TPCs are necessary for understanding rates of productivity for populations,
592 energy flux within food webs and nutrient cycling within ecosystems, but without a mechanistic
593 understanding of biomass responses we cannot accurately predict extinction risk of populations
594 nor numerical responses of important processes (e.g., interactions, energy flux). Certainly,
595 increasing temperatures towards T_{max} – when r and K are both declining – will have strong
596 effects on the extinction risk of a population, relative to any estimates that ignore any effect on
597 K . However, we also show that there is a range of temperatures over which the TPC increases,
598 but K decreases, where the risk of warming could be much harder to evaluate – for example
599 due to increasing resilience (local stability or rates of “attraction”) toward a smaller equilibrium
600 population size. Furthermore, the nonlinear effects of nutrient uptake saturation (i.e., effective
601 nutrient limitation) on both the magnitude and shape of the thermal biomass curve highlights
602 another layer of complexity important for accurate population forecasting under global change,
603 and similarly suggests interesting implications for temporal patterns in population dynamics
604 under variable temperature and nutrient regimes.

605

606 Elucidating the thermal biomass curve for populations is a necessary first step towards
607 understanding population dynamics – and therefore extinction risk – under global change.
608 These results provide a baseline for understanding the patterns we see in non-equilibrium
609 dynamics under variable environments, even when the dynamics do not perfectly “track” the
610 equilibrium. As shown here, the temporal dynamics exhibited by a species in a thermally
611 varying environment indeed get interesting when variation in r and K occur simultaneously. In
612 ‘classic’ models where only r responds to the environment, the effect of the environment
613 quickly wanes as a population approaches its carrying capacity. However, in the case where
614 both r and K continually change in response to the environment, there is an interplay among
615 the two parameters: K sets the target to which the population is attracted, and the strength of
616 that attraction is determined by r . In this case, it is important to understand where natural
617 thermal variation lies relative to both the thermal biomass and performance curves. For
618 example, in scenarios where thermal variability exists only below T_r (the thermal optimum for
619 growth) one might predict that populations will directly follow this environmental signature
620 (e.g., (Smith 1997), despite the true period of population fluctuations being doubled if the

621 variation actually spans either side of T_K (that is, the actual attractor), leading to fundamentally
622 different predicted population dynamics over time. As an example of this, phytoplankton are
623 known to have spring and fall peaks in biomass, a phenomenon generally thought to be driven
624 by a combination of nutrient cycling and predation (Cebrian & Valiela 1999; Martinez *et al.*
625 2011; Sigler *et al.* 2014), but which could in fact be enhanced by temperature in a case such as
626 this.

627

628 Under varying thermal conditions, our results also highlight important thermal asymmetries in
629 population rates of change and how populations respond to changing environments – a result
630 that can be explained mechanistically by the implicit lag associated with our dynamic nutrient
631 quota. While others have incorporated explicit lags into nutrient quota dynamics (e.g.,
632 (Cunningham & Nisbet 1980), thermal asymmetries within our purely monotonic model clearly
633 have implications for population dynamics. In Figure 4, we showed that the time scale of
634 environmental variation is important for determining population dynamics as the relative
635 influence of the thermally asymmetric lag wanes with increasing forcing period. This in turn
636 changes the potential for collapse when temperatures approach an organism's thermal limits.
637 Notably, these results suggest that 1) lagged population dynamics mean that populations can
638 likely withstand brief periods with temperatures outside the fundamental niche; and 2) brief
639 periods with temperatures below T_{min} ought to be substantially less catastrophic for population
640 persistence than brief periods above T_{max} (Figures 4, A7 and A10). Furthermore, a population's
641 response to or recovery from perturbations (i.e., mass mortality events or environmental
642 stochasticity) based on its rates of change and lagged responses has important implications for
643 its dynamics in variable environments and the potential to detect warning signs of collapse.
644 These results indicate that classical approaches to detecting early warning signals of critical
645 transitions (e.g., critical slowing down) may be impeded by the interacting thermal asymmetries
646 of growth rates, equilibria, and lagged dynamics. Finally, the non-equilibrium dynamics here
647 highlight an important relationship between temperature and population variability resulting
648 from these thermal asymmetries (Figure 4). These results suggest that periodic environments
649 (e.g., seasonal) could lead to increased variability in warmer (average) climates, and similarly
650 that we may see more variability during warm (summer) versus cool (winter) times. This also
651 suggests implications for population dynamics – and primary productivity for whole ecosystems
652 – when seasons become less predictable (i.e., variability in the environment is amplified by
653 higher vital rates).

654

655 Importantly, linking physiological processes at the individual level to higher order processes and
656 dynamics at the population-level allows us to more intentionally build generalizable population
657 models that are better grounded in first principles. There is often a need to simplify to more
658 general models and contexts when making predictions and forecasting, and for developing

659 fundamental ecological theory. One such example is the Logistic model, which continues to be
660 central to the study of population dynamics, despite the reliance of parameters on
661 environmental attributes (e.g., resource limitation and temperature) remaining open to
662 interpretation. Investigating more specific models allows us to have a more reasonable
663 understanding of the temperature-dependence of important rates and processes. Here, we
664 have developed important mechanistic understanding of the dynamics of phytoplankton
665 populations – the keystone to energy supply in all aquatic food webs, central to global carbon
666 cycling, and a common study taxon for linking theoretical and empirical approaches in ecology.
667 Simultaneously, our analytical insights apply to more generalizable model contexts with the
668 goal of constructing fundamental theory in an intentional, informed way. Specifically, our r - K
669 mismatch provides a framework for the nutrient- and temperature-dependence of population
670 dynamics, and the next step ought to be developing a generalizable analytical form consistent
671 with both our model and that used by Vinton and Vasseur (2022). Gaining a better
672 understanding of the “true” shape of the thermal biomass curve, $K(T)$, will be important for
673 understanding the thermal response of primary production for whole food webs and therefore
674 general ecological functioning in changing environments.

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