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2 **Pelagic food-webs in a changing Arctic: A trait-based perspective suggests a mode of resilience**

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23

24 **Abstract**

25 Arctic marine ecosystems support fisheries of significant and increasing economic and nutritional  
26 value. Commercial stocks are sustained by pelagic food webs with relatively few keystone taxa  
27 mediating energy transfer to higher trophic levels, and it remains largely unknown how these taxa will  
28 be affected by changing climate and the influx of boreal taxa. *Calanus* species store large quantities of  
29 lipids, making these zooplankton a critical link in marine food-webs. The Arctic *Calanus* species are  
30 usually larger and, importantly, have been suggested to contain disproportionately larger lipid stores  
31 than their boreal congeners. Continued climate warming and subsequent changes in primary  
32 production regimes have been predicted to lead to a shift from the larger, lipid-rich Arctic species, *C.*  
33 *glacialis* and *C. hyperboreus*, toward the smaller, boreal *C. finmarchicus* in the European Arctic, with  
34 negative consequences for top predators. Our data show that lipid content is closely related to body  
35 size for all three species, i.e. is not a species-specific trait, and that there is considerable overlap in  
36 size between *C. finmarchicus* and *C. glacialis*. A trait-based life-history model was used to examine an  
37 idealized scenario where, in a changed Arctic with a longer period of primary production, *C. glacialis*-  
38 and *C. hyperboreus*-like copepods are indeed replaced by *C. finmarchicus*-like individuals, whether  
39 through competition, plasticity, hybridization, or evolution. However, the model finds that transfer of  
40 energy from primary producers to higher predators may actually be *more* efficient in this future  
41 scenario, because of the changes in generation length and population turnover rate that accompany  
42 the body-size shifts. These findings suggest that Arctic marine food webs may be more resilient to  
43 climate-related shifts in the *Calanus* complex than previously assumed.

## 44 **Introduction**

45 Large-scale re-organization of Arctic marine communities and significant functional changes in the  
46 ecosystem are expected as a result of accelerated climatic warming and sea-ice withdrawal  
47 (Wassmann *et al.*, 2011; Sunday *et al.*, 2012; Fossheim *et al.*, 2015; Kortsch *et al.*, 2015). Empirical  
48 studies have already detected some structural and functional changes (Wassmann *et al.*, 2011;  
49 Fossheim *et al.*, 2015; Wiedmann *et al.*, 2014), but predicting specific compositional changes and the  
50 ecosystem consequences of such changes is challenging. These consequences are not just of academic  
51 interest as seasonal migrations of tens of millions of seabirds, valuable commercial fisheries (Atlantic  
52 cod, Pacific pollock), and recovery of large baleen whales (blue, fin, bowhead, humpback) all depend  
53 on the temporally and spatially concentrated productivity of the Arctic and its marginal seas. A key  
54 link between primary producers and commercial stocks are large copepods of the genus *Calanus*,  
55 which usually dominate zooplankton biomass in temperate and polar seas. *Calanus* spp. can be  
56 thought of as part of the “wasp waist” in the food web (a concept usually applied to forage fish (Hunt  
57 and McKinnell, 2006)), in the sense that they sit at a trophic nexus at which the organism- and  
58 population-level biology of just a few species has ecosystem-level consequences.

59 Large-scale biogeochemical models have predicted widespread changes in response to Arctic warming  
60 and sea-ice loss, particularly at and near the base of the food web. Such changes include a longer  
61 season of pelagic primary productivity, a moderate increase in total primary production (Slagstad *et al.*  
62 *et al.*, 2011; Slagstad *et al.*, 2015), an increase in Atlantic zooplankton species (*Calanus finmarchicus*) and  
63 strong reduction in Arctic zooplankton (*Calanus glacialis*) in the Barents Sea, and spreading of *C.*  
64 *glacialis* along the Eurasian shelves (Slagstad *et al.*, 2011; Feng *et al.*, 2016). *C. finmarchicus* has  
65 expanded northward in the western Atlantic over the last 30 years (Chust *et al.*, 2014), and is  
66 increasing in abundance at the expense of *C. glacialis* in the Barents Sea (Dalpadado *et al.*, 2012). The  
67 fate of the third *Calanus* species in the region, *C. hyperboreus*, has so far not been considered (Slagstad  
68 *et al.*, 2015; Feng *et al.*, 2016; Feng *et al.*, 2017). Although *C. hyperboreus* occurs on the shelf, it is

69 primarily an oceanic species (Conover, 1988; Hirche, 1991; Kosobokova and Hirche, 2009) with  
70 markedly different life history strategies, grows considerably larger than *C. glacialis* and *C.*  
71 *finmarchicus* (Falk-Petersen *et al.*, 2009), and, therefore, is likely subject to different environmental  
72 forcing than the smaller, short-lived *Calanus* species.

73 Any prediction regarding the ecological consequences of a replacement of Arctic *Calanus* by *C.*  
74 *finmarchicus* inevitably hinges on current understanding of *Calanus* physiology and life-history.  
75 Empirical data (Pasternak *et al.*, 2013; Alcaraz *et al.*, 2014) suggest an upper thermal tolerance of  
76 approximately 6° C for *C. glacialis*. Additionally, Arctic species have been suggested to possess  
77 inherently higher species-specific lipid-storage than their boreal congeners: 60-70 mass % in Arctic  
78 *Calanus* species versus up to 30-50% in *C. finmarchicus* (Scott *et al.*, 2000). Despite the limited data  
79 supporting these estimates, this understanding underlies the current paradigm on how warming will  
80 affect Arctic food-webs. The paradigm posits that a shift in species dominance from *C. glacialis* to the  
81 smaller, boreal *C. finmarchicus* will lead to a reduction in lipid production at the population level, and  
82 a loss in nutritional value for iconic predators of *Calanus*, including fish, seabirds, and baleen whales  
83 (Dalpadado *et al.*, 2012; Kwasniewski *et al.*, 2012; Fossheim *et al.*, 2015). Thus, replacing one species  
84 with the other, with all else remaining equal, has been predicted to have major consequences for the  
85 entire Atlantic Arctic food web.

86 It can be misleading, however, to treat species as fixed types, with no plasticity or variation, in  
87 investigations of how ecosystems are likely to respond to unprecedented conditions. In fact, this kind  
88 of fixed-species approach can prevent important questions from being asked in the first place. It is  
89 increasingly clear that *C. glacialis* and *C. finmarchicus* have diverse and plastic strategies for  
90 reproduction, foraging, and dormancy that are in part responses to environmental variation (Falk-  
91 Petersen *et al.*, 2009; Daase *et al.*, 2013; Melle *et al.*, 2014). In addition, morphology-based  
92 identification of these two species has been shown to be unreliable in some areas (Lindeque *et al.*,  
93 2006; Gabrielsen *et al.*, 2012; Choquet *et al.*, 2018), and reports of hybridization between the two

94 species (Parent *et al.*, 2012) complicate the picture further still. In this study, we use a combination of  
95 molecular tools for species identification and a recent, well-validated life-history model (Banas *et al.*,  
96 2016a) to show that a trait-based, as opposed to species-based, approach allows us to formulate and  
97 test hypotheses that cut across the organismal, population, and community scales. We find that intra-  
98 and interspecific variation in key organismal traits (body size, lipid content) may be more congruent  
99 across species than thought, allowing a huge conceptual simplification. The model, by placing  
100 individual life history and population dynamics in a common mathematical frame, lets us scale up to  
101 the expected tradeoff between these organismal traits and population productivity. In this framework,  
102 we can begin to reason systematically about whether the sum of these changes is a net gain or loss  
103 for particular classes of predator.

104

#### 105 **A UNIFIED VIEW OF BODY SIZE AND ENERGY CONTENT**

106 To evaluate overlap in size between *C. finmarchicus* and *C. glacialis*, and whether lipid content is  
107 species or size dependent, we sampled *Calanus* in three fjords in Svalbard (78-81 °N, 10-24 °E,  
108 including Arctic and Atlantic hydrographic domains) using a Hydrobios Multi Plankton Sampler or a  
109 WP2 net (mesh size 200 µm, mouth opening 0.25 m<sup>2</sup>). Samples were taken between mid-September  
110 and early October in 2012 (Billefjorden 180-0 m, Rijpfjorden 265-0 m) and 2014 (Kongsfjorden 320-0  
111 m, Rijpfjorden 265-0 m). This is the start of the overwintering period of *Calanus* spp. when lipid  
112 content is commonly at its highest, thus the variability in lipid content and size reflects natural  
113 variability in the population, but not seasonal variability. We measured the prosome length of more  
114 than 1500 individual copepods (copepodite IV and V, and adult females) and each specimen was  
115 preserved in absolute ethanol and identified to species using molecular techniques as described in  
116 Gabrielsen *et al.* (2012). Prior to being preserved, approximately 650 individual copepods (copepodite  
117 stages IV, V and VI) were photographed while still alive using a Leica MZ 95 stereomicroscope with a  
118 Motec camera. The pictures were used to measure prosome length, prosome area and area of the

119 lipid sac. Total lipid content was calculated based on lipid sac area following Vogedes et al. (2010). To  
120 compare the lipid- size relationship in the *C. finmarchicus* and *C. glacialis* complex with that of the  
121 third *Calanus* congener in the study area, *C. hyperboreus*, we included measurements of prosome  
122 length and lipid sac area of 430 *C. hyperboreus* (CIII–CV and adult females) from Svalbard waters  
123 sampled between August and October (2010, 2012, 2014, max. sampled depth 2000 m). *C.*  
124 *hyperboreus* were not genetically identified as they are substantially larger than the other two *Calanus*  
125 species and can be distinguished morphologically by a spine at the last thoracic segment, which is  
126 present from stage CIV.

127 We found considerable overlap in prosome length of *C. glacialis* and *C. finmarchicus* identified to  
128 species using molecular tools (Figure 1), indicating that size-based classification is inaccurate for the  
129 larger developmental stages included in this study (copepodite IV, V, and females) (Figure 1). The  
130 relationship between size and lipid content was statistically indistinguishable for the two species  
131 (Table 1, Figure 2). The relationship for copepodite stages CIII and CIV of *C. hyperboreus*, a range of  
132 body sizes that better matches *C. finmarchicus* and *C. glacialis* CIII–AF (Table 1, Figure 2), was also  
133 indistinguishable from that of the two smaller species. The relationship for all size classes of *C.*  
134 *hyperboreus* (Figure 2) displayed a significantly lower exponent coefficient ( $a$  in the equation in Table  
135 1). This difference, however, appears to be an effect of scale—the range of body size considered in  
136 relation to intraspecific variability in lipid content—rather than a true species difference. Our results,  
137 therefore, suggest that there is little inherent, species-specific difference in lipid-storage capacity  
138 between the Arctic *C. glacialis* and the boreal *C. finmarchicus* (Figure 1), or indeed the younger stages  
139 of *C. hyperboreus*. The amount of lipid that can be stored, therefore, is dependent largely on body size  
140 (and developmental stage as it relates to size). This is in contrast to previous studies that have reported  
141 or assumed a higher species-specific lipid content in Arctic *C. glacialis* compared with *C. finmarchicus*  
142 (Scott *et al.*, 2000; Falk-Petersen *et al.*, 2009). This misconception has probably been caused by a  
143 general underrepresentation of *C. glacialis* in the community based on morphological identification  
144 (Choquet *et al.*, 2018).

145 The high number of *C. glacialis* individuals not growing as large as previously assumed suggests there  
146 is considerable plasticity in morphology across its geographic range (Gillooly, 2000; Leinaas *et al.*,  
147 2016; Choquet *et al.*, 2018). A reduction in body size has been suggested to be a universal response  
148 to warming (Gillooly, 2000; Daufresne *et al.*, 2009; Gardner *et al.*, 2011). Since body size is viewed as  
149 a 'master trait,' it can have an overarching influence on a large number of physiological processes and  
150 ecological functions (Stamieszkin *et al.*, 2015). *C. glacialis* is known to exhibit large spatial variability  
151 in its phenology and energy allocation to reproduction (Daase *et al.*, 2013). Such a high variation in  
152 body size is consistent with the findings of misidentified individuals when only morphological  
153 taxonomy is used (Parent *et al.*, 2011; Gabrielsen *et al.*, 2012; Choquet *et al.*, 2018) (Figure 3). It may  
154 also result from hybridization between *C. finmarchicus* and *C. glacialis* (Parent *et al.*, 2012), although  
155 no evidence of hybridization has been found in a large scale survey including our study area (Choquet  
156 *et al.*, 2017). In fact, populations of *C. glacialis* overlapping in size with *C. finmarchicus* have been  
157 found all along the coast of Norway (Niehoff and Hirche, 2005; Choquet *et al.*, 2017). Similarly, at the  
158 southern end of its range, *C. finmarchicus* has been found to overlap in size almost completely with *C.*  
159 *helgolandicus* as a function of temperature (Wilson *et al.*, 2015). While there is little overlap in size  
160 with older copepodites and adults of *C. hyperboreus*, there is an overlap in size with the younger  
161 copepodite stages CIII and CIV of that species. Being lipid-rich overwintering stages, they are in a  
162 similar life history stage as older stages of the smaller *Calanus* species, and likely provide similar energy  
163 subsidies for predators. These findings suggest that environmental plasticity, changes in geographic  
164 range, and potentially hybridization all contribute to a continuum in size, and therefore lipid content,  
165 with analogous consequences at the ecosystem level. This suggests the potential utility of a trait-  
166 based, instead of species-based, approach when investigating ecological functions of assemblages.

#### 167 **SCALING UP FROM INDIVIDUAL TRAITS TO POPULATION PRODUCTIVITY**

168 As shown by the review of growth and development studies by Banas and Campbell (2016), body size  
169 in copepods can be thought of as a direct consequence of the combination of individual development  
170 time and the mean rate of energy gain during that time, i.e., life-history strategy and foraging strategy.

171 In highly seasonal environments, these strategies are strongly constrained by external conditions (prey  
172 availability, temperature, predation risk), such that relatively few combinations of ontogenetic  
173 development rate, dormancy strategy, foraging strategy, and reproductive strategy lead to viable  
174 annual energy budgets when the period of prey availability is short (Banas *et al.*, 2016a; Sainmont *et*  
175 *al.*, 2014). As a result, generation length (and thus population turnover rate), body size, and lipid  
176 content are not independent, uncorrelated traits once all possible combinations are passed through  
177 the environmental filter. These emergent associations among traits form testable model predictions  
178 (Banas *et al.*, 2016a), and provide a basis for predicting how linked traits may change in the future.  
179 One simple model experiment along these lines—examining only one mode of environmental  
180 variation out of many that deserve consideration—is described below.

181 The copepod life-history model Coltrane (Copepod Life-history Traits and Adaptation to New  
182 Environments) version 1.0 is described in detail by Banas *et al.* (2016a). Matlab source code is available  
183 at <http://github.com/neilbanas/coltrane>. Coltrane is an individual-based model that represents the  
184 time-evolution of one cohort of a clonal population, all bearing the same traits and spawned on the  
185 same date, with four state variables: relative developmental stage  $D$  (0 at spawning, 1 at adulthood),  
186 survivorship  $N$  (the fraction of initially spawned individuals that remain after some amount of  
187 cumulative predation mortality); structural biomass per individual  $S$ , and individual reserve or storage-  
188 lipid biomass  $R$  (Fig. 4a). Families of cases of the cohort model are then combined to produce  
189 population- and community-level results, as shown in schematic form in (Banas *et al.*, 2016a) for a  
190 complete model description. A population in Coltrane (Fig. 4b) is considered to have identical traits,  
191 and to have a seasonal pattern of spawning dates that maximises fitness (lifetime egg production per  
192 initial egg) while also solving internal life-history mismatch (Varpe *et al.*, 2007). Mathematically, this  
193 optimization involves running the cohort model (Fig. 4a) for a complete spectrum of spawning dates  
194 and also a spectrum of imposed delays between maturation and the start of spawning (Fig. 4b; Banas  
195 *et al.* 2016a). A community—or rather a metacommunity, an estimate of “all possible ways to be a  
196 copepod” in a given environment—is generated in the present version of the model by varying a single



197 life-history trait, the prey-saturated development rate  $u_0$ . This rate was varied from 0.005 – 0.01 d<sup>-1</sup>,  
198 corresponding to a total egg-to-adult development time of 100–200 d at 0°C under prey-saturated  
199 conditions (Banas and Campbell, 2016).

200 An environmental scenario in Coltrane is defined by annual cycles of three variables: total  
201 concentration of phytoplankton/microzooplankton prey, surface temperature, and deep  
202 temperature. The model does not explicitly predict absolute abundance or biomass, but rather  
203 compares the fitness value of competing strategies and predicts trait correlations. For example,  
204 Coltrane is able to predict the relationship among body size, generation length, and income/capital  
205 breeding strategy across the three coexisting *Calanus* spp. in Disko Bay, West Greenland (Banas *et al.*,  
206 2016a). In each scenario, a spectrum of copepod types was generated by varying  $u_0$  and calculating an  
207 optimal population-level solution for each case. Adult size (Figure 5b), generation length (Figure 5c),  
208 and the division of egg production into capital and income fractions (Figure 5d) were calculated as in  
209 Banas *et al.* (2016a: see the Disko Bay experiment in that study). Additional metrics were calculated  
210 by integrating the mortality (survivorship) term over time to produce total energetic yield to predators

$$211 \quad Y = \int m(S+R)N dt$$

212 and the lipid fraction of that yield

$$213 \quad Y^{-1} \int mRN dt.$$

214

215 In this study, the model was run for a pair of idealised scenarios, which differed only in the duration  
216 of prey availability, in order to evaluate the common assumption that a longer ice-free period of  
217 spring-autumn pelagic phytoplankton production will lead to shrinking individual sizes and potential  
218 species shifts, and how such a shift toward smaller, faster-reproducing individuals would affect total  
219 secondary production by *Calanus*. The first of the two scenarios assumes phytoplankton prey occur in  
220 a Gaussian seasonal window equivalent to 3.5 months of saturating prey per year, as opposed to a

221 window equivalent to 4.5 months in the second scenario (Fig. 5a). These can be taken as idealisations  
222 of present-day and reduced-ice conditions in a West Svalbard fjord or a similar Arctic environment  
223 (mathematically, these cases correspond to the “global” experiment of Banas et al. (2016a) with  $\partial t' =$   
224 40, 50 d). In reality, the length of the productive season need not correlate closely with the overall  
225 amount of food, or its nutritional quality, or its timing relative to the annual light cycle: all details that  
226 deserve consideration in a more complex, spatially-resolved model study. Seasonal cycles were  
227 assumed to repeat exactly, such that the model results here describe optimal strategies in two  
228 contrasting but stable environments. For simplicity, both surface and deep temperature were held  
229 constant at 0°C in both scenarios, although Banas et al. (2016a) explored the effect of temperature  
230 variation in relation to prey variation in the same model. Specific mortality  $m$  is assumed to follow the  
231 same allometry as specific ingestion (Banas *et al.*, 2016a): this simplifying assumption has a theoretical  
232 and coarse empirical basis (Hirst and Kiørboe, 2002), but may well be inappropriate in a high-latitude  
233 context where gradients in light availability and thus visual predation may be particularly strong (Varpe  
234 *et al.*, 2015).

235 Across these simple model scenarios at 0°C, lengthening of the primary-productivity season does,  
236 indeed, shift the optimal strategy of modelled mid-size *Calanus* analogs toward smaller adult size  
237 (Figure 5b), from a 2-year to a 1-year life-cycle (solid symbols, Figure 5c), and from a combination of  
238 capital and income breeding to almost pure income breeding (Figure 5d). In the short-season scenario,  
239 a 1-year life cycle is unviable for these mid-size cases because of internal life-history mismatch (Varpe  
240 *et al.*, 2007): the initial generation is able to survive to maturity without starving only if it is spawned  
241 long before the bloom maximum, but is unable to spawn the next generation at the same time of year,  
242 such that no stable cycle is possible. A 2-year life cycle in the short-season scenario solves this internal  
243 mismatch problem, although productivity (LEP) under this strategy is very low (Figure 5e, blue solid  
244 symbols). Under the longer growing season, the mismatch problem observed for a 1-year generation  
245 time is solved, such that either a 1- or 2-year life cycle is possible, and survivorship and lifetime egg  
246 production are much higher for the 1-year cycle (Figure 5e, red solid symbols).

247 Thus, the assumptions and review of laboratory data behind Coltrane (Banas and Campbell, 2016;  
248 Banas *et al.*, 2016a) support the idea that whether by plasticity, hybridization, evolution, or  
249 competitive replacement—the model is agnostic regarding the mechanism—we might indeed expect  
250 a shift in the changing Atlantic Arctic in which mid-sized, long-generation-length *Calanus* are replaced  
251 by smaller, shorter-generation-length organisms. Replacing a two-year reproductive cycle with a one-  
252 year cycle increases survivorship and turnover, such that this shift is accompanied by more than a two-  
253 fold increase in lifetime egg production per adult (Figure 5e). More surprising, it is also accompanied  
254 by a more than two-fold increase in specific energetic yield to predators (Figure 5f). The fraction of  
255 the yield to predators that consists of storage lipid decreases from ~30% to ~20% (Figure 5g; note that  
256 the lipid fraction of yield, summed across all life stages, is not directly comparable to measurements  
257 of the lipid content of late stage individuals). However, the increase in total energetic yield outweighs  
258 the decrease in lipid fraction, so that the total yield of lipid to predators (per initial copepod egg)  
259 actually increases slightly in the longer-productive-season scenario.

260 Translating these trait-based results into species-specific predictions is ambiguous, particularly given  
261 the idealized nature of the model experiment. Body size depends on growth and development rates  
262 via a high exponent, such that 10% uncertainty in each of those rates translates into fourfold  
263 uncertainty in adult size (Banas and Campbell, 2016). Accordingly, body-size/generation-length  
264 combinations are likely to be skewed relative to the real *Calanus* populations (a more realistic  
265 application would address this through systematic parameter tuning). One could interpret the mid-  
266 sized cases that change generation length between scenarios as larger *C. glacialis* analogs, shifting  
267 toward a *C. finmarchicus*-like life history under a longer productive season, or else as small *C.*  
268 *hyperboreus* analogs, replaced by *C. glacialis* and *C. finmarchicus* in a more boreal environment.  
269 Predicting these specific futures is a complex oceanographic and spatial-ecology problem, well beyond  
270 an idealized model (or for that matter any first-principles biological argument). It is likely that currently  
271 observed shifts in size distributions are consequences of internal population-level plasticity, and it is  
272 not clear whether any required genetic shifts (as climatic shifts surpass the range of phenotypic

273 flexibility) could occur fast enough to reach these modeled optima. What we *can* conclude from this  
274 model experiment is that ecological shifts along the body size–lipid content curve in high-latitude  
275 *Calanus* (Figure 2) are likely to be accompanied by shifts in generation time and population turnover  
276 rate that have strong, compensating effects on energy transfer to predators.

## 277 **Ecosystem consequences**

278 As long as there are still large *C. glacialis* and small *C. finmarchicus* found in the same region, energy  
279 transfer from the mesozooplankton to predators can still be species dependent as well as size  
280 dependent, with *C. hyperboreus* functioning as an especially lipid-rich treat. For many predators,  
281 however, total nutrition available from the mesozooplankton community may be more dependent on  
282 secondary production at the population level, than on mean individual lipid content. Crucially, results  
283 of the life-history model suggest that changes in population-level energy content accompanying a shift  
284 to smaller body size outweigh the effects of a body-size reduction on individual lipid content (Figure  
285 4, 5). Predators that target individual copepods and predators that feed on copepods *en masse* may  
286 thus experience opposite trends in their prey.

287 Parallel model experiments varying mean water temperature (Banas *et al.*, 2016a) suggest that, at the  
288 community level, the direct effects of near-surface warming on *Calanus* trait patterns are similar to  
289 the effects of lengthening of the productive season, although at the population level, thermal  
290 thresholds (Alcaraz *et al.*, 2014) may be limiting. This is another factor that complicates the translation  
291 of model results into species terms. Warming of deeper water, or loss of early-spring ice-associated  
292 blooms, may drive some *Calanus* populations past thresholds of overwintering survival. This appears  
293 to be the case for the southeastern Bering Sea in warm, low-ice years (Hunt *et al.*, 2011; Stabeno *et*  
294 *al.*, 2012; Eisner *et al.*, 2014), as the measured summer abundance of *C. glacialis/marshallae* crashes  
295 in temperature and ice conditions similar to those projected to be the new normal by the 2040s (Banas  
296 *et al.*, 2016b). Indeed, the same model that predicts the positive effects of extended pelagic

297 productivity in this study (Figure 4) finds *Calanus* to be non-viable in the southeastern Bering Sea  
298 without an extended period of sea ice and ice algae (Banas *et al.*, 2016a).

299 Increasing air and sea temperatures and significant reductions in sea ice have already been observed  
300 in the Arctic (Stroeve *et al.*, 2014), and may impact food supply, growth rates, and relative distributions  
301 of *Calanus* spp. Furthermore, sea-ice loss changes the light regime of the water column, potentially  
302 altering seasonal and/or size-specific predation pressure on zooplankton in a future Arctic Ocean  
303 (Varpe *et al.*, 2015). In addition, advection of heat, food, and species from boreal areas northward  
304 substantially alters plankton community structure in some regions (Orlova *et al.*, 2015). Any  
305 reconsideration of the paradigm of species replacement and its effect on ecosystem function,  
306 therefore, must consider the spatial variability in the drivers of change. Likewise, all the environmental  
307 drivers discussed here vary over a range of timescales as well, from interannual variability to true  
308 multidecadal trends. On very long timescales, it can be a powerful simplification to elide the  
309 differences among disparate mechanisms of adaptation—individual plasticity, competitive exclusion,  
310 hybridisation, range shifts and species replacement, true natural selection—as a trait-based approach  
311 allows one to do. However, these mechanisms have their own intrinsic timescales, and understanding  
312 shorter-term change in *Calanus* may require that we distinguish between mechanisms more precisely  
313 and apply trait- and optimality-based methods more selectively.

314 Our findings suggest that borealisation of marginal seas in the European Arctic may not be detrimental  
315 in terms of either carbon- and lipid-based food-web contributions from *Calanus*, regardless of whether  
316 warming results in a species shift to *C. finmarchicus*, or in smaller sizes of *C. glacialis* (Figure 5). Record  
317 high stocks of age 3+ Atlantic cod in the Barents Sea in recent years suggest that there is no shortage  
318 of food, despite more than a decade of warming, a weakening in trophic links with their traditional  
319 prey (capelin) (Johannesen *et al.*, 2015), and a dominance of *C. finmarchicus* in many areas. A size shift  
320 in the zooplankton prey field may, however, impact predators that actively select larger individuals,  
321 regardless of the sensory mechanisms involved in the search process (Martens *et al.*, 2015). There are,

322 however, only two explicit examples of this phenomenon from Arctic systems, and the results of one  
323 (Dalpadado *et al.*, 2000) could be explained by other mechanisms leading to apparent selection. The  
324 little auk (*Alle alle*) searches visually for its prey and actively selects larger individuals (Karnovsky *et*  
325 *al.*, 2003; Kwasniewski *et al.*, 2012; Vogedes *et al.*, 2014), and this predator may be negatively affected  
326 by shifts to a system with smaller prey (Kidawa *et al.*, 2015). One recent study, however, suggests that  
327 chick growth and adult body-condition may not decline when they fed on small zooplankton instead  
328 of larger congeners (Amélineau *et al.*, 2016).

329 While we only consider bottom-up effects in this study, predation pressure may also be important in  
330 driving *Calanus* life-history traits (Kaartvedt, 2000; Varpe *et al.*, 2007; Berge *et al.*, 2012). A continued  
331 northwards expansion of boreal fish, as well as increases in whale populations, may also select for  
332 Arctic *Calanus* species with shorter life-spans and smaller body sizes (Berge *et al.*, 2012), thus eliciting  
333 similar effects as shown in our models incorporating ocean warming and lengthening of the productive  
334 season. The effects of increased predation on zooplankton production and population size, however,  
335 are less clear.

### 336 **Conclusion and recommendations**

337 Since climate change affects ecosystems both directly and indirectly, many unknowns could  
338 significantly affect the generality of our findings. Warmer temperatures, reduced ice cover, and the  
339 spread of boreal species are already affecting timing, quantity, and composition of phytoplankton  
340 production. Here we have focused on a likely species shift within the *Calanus* species complex.  
341 Interactions of new taxa with both resident and other new species are difficult to predict (Williams  
342 and Jackson, 2007), and not incorporated into our conceptual model. A replacement of *Calanus* spp.  
343 with even smaller copepod species (i.e. *Pseudocalanus* spp., *Oithona similis*) having different  
344 nutritional values and life history traits may prove to be much more detrimental in terms of available  
345 carbon and lipid for predators and food web structure (Coyle *et al.*, 2011).

346 Our dataset is geographically and seasonally limited, and a large-scale survey of species and size  
347 specific lipid content would be necessary to assess the robustness of our regional observations. The  
348 use of a trait-based rather than a species based approach to assess ecosystem changes may be  
349 particularly useful where species identification is challenging, which has become increasingly evident  
350 for *Calanus* (Choquet *et al.*, 2018). Our results clearly demonstrate, however, that the basis for  
351 previous concerns regarding species replacement within the *Calanus* complex may be unfounded, or  
352 at least not universal, and that food subsidies from *Calanus* may continue to support many top  
353 predators in the European Arctic.

354

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365

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547 **Table 1:** Results of exponential fits to total individual lipid content LC (in mg) as a function of  
 548 prosome length PL (in mm), across *Calanus* spp. and life stages (see Figure 2). Each fit is specified by  
 549 an exponent  $a$  and log coefficient  $b$  such that  $LC = e^b PL^a$ . Confidence limits at the 95% level are also  
 550 given, and non-overlapping confidence intervals are considered statistically significant. All data are  
 551 from live animals collected Aug–Oct. Outliers with  $LC < 0.002$  mg have been omitted ( $n=18$ ,  $< 2\%$  of  
 552 samples).

553

Species, stage	Exponent $a$	Log coefficient $b$
<i>C. finmarchicus</i> , CIII–AF	$4.9 \pm 0.5$	$-6.6 \pm 1.5$
<i>C. glacialis</i> , CIII–AF	$5.1 \pm 0.3$	$-7.2 \pm 1.0$
<i>C. hyperboreus</i> , CIII–CIV	$5.1 \pm 0.2$	$-7.9 \pm 1.1$
<i>C. hyperboreus</i> , CIII–AF	$3.6 \pm 0.2$	$-6.0 \pm 1.2$
all species, CIII–AF	$3.4 \pm 0.1$	$-5.5 \pm 1.3$

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556

557 **Figure legends**

558 **Figure 1:** Prosome length frequency distribution of copepodite stages CIV (N=341) and CV (N=886) and  
559 adult females (AF, N=329) of *C. glacialis* (blue) and *C. finmarchicus* (red). Species determined based  
560 on genetics. Grey shaded area indicates size classes classified as *C. glacialis* (Daase and Eiane, 2007)  
561 (see also Figure 3).

562 **Figure 2:** Total lipid content in relation to prosome length across *Calanus* species and stages. Five  
563 regression lines match the exponential fits and 95% confidence intervals given in Table 1. Non-  
564 overlapping confidence intervals indicate statistically significant differences. *C. finmarchicus* CIII–AF  
565 (red; n=373), *C. glacialis* CIII–AF (blue; n=290), *C. hyperboreus* CIII–AF (black, solid; n=430) and CIII–  
566 CIV only (gray, dashed; N=337), and all species (dotted).

567 **Figure 3:** Length range of prosome length of copepodite stage CV of *Calanus finmarchicus* (red) and *C.*  
568 *glacialis* (blue) based on size-frequency analysis (morphology) and genetic analysis (genetics). Broken  
569 lines: no minimum/maximum size defined. References: 1. Tande *et al.* (1985); 2. Kwasniewski *et al.*  
570 (2003); 3. Arnkværn (2005); 4. Daase and Eiane (2007); 5. Weydmann and Kwasniewski (2008); 6.  
571 Breur (2003); 7. Hirche *et al.* (1994); 8. Choquet *et al.* (2018) 9. Parent *et al.* (2011); 10. Gabrielsen *et*  
572 *al.* (2012); 11. This study (includes data from Gabrielsen *et al.* (2012)). Svalbard waters: Stations in  
573 open water, outside fjords.

574 **Figure 4:** Schematic of the Coltrane copepod life-history model. (a) The time-evolution of one cohort  
575 of individuals, with identical traits and spawned on the same date  $t_0$ , are tracked by state variables  
576 representing development, structural and reserve biomass, and survivorship. Egg production by this  
577 cohort is calculated from these state variables, as a function of an additional strategy decision  $t_{\text{egg}}$ ,  
578 which allows a delay between maturation and the start of spawning. (b) An annual routine  
579 representing a population is generated from the cohort solutions by varying  $t_0$  and  $t_{\text{egg}}$  systematically  
580 and identifying the seasonal pattern of spawning dates and the value of  $t_{\text{egg}}$  that maximise fitness while  
581 also solving internal life-history mismatch. (c) A metacommunity is generated by varying the relative-



582 development-rate parameter  $u_0$ , which controls development time directly and adult size indirectly,  
583 as previously shown for a metastudy of laboratory experiments (Banas and Campbell 2016). See Banas  
584 et al. (2016a) for a full description of the model.

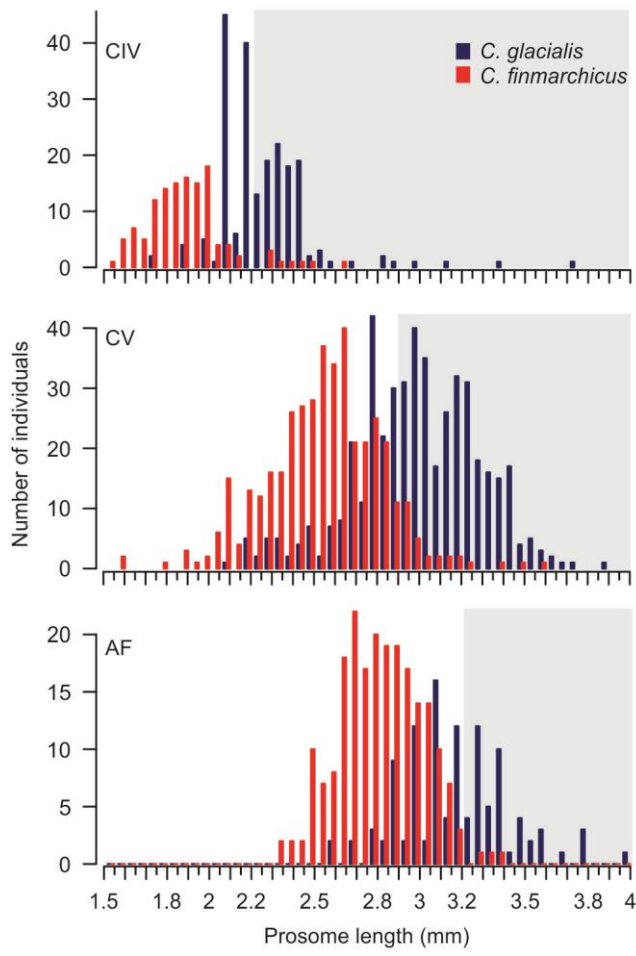
585 **Figure 5:** Results of the life-history model across the *Calanus* size spectrum, under a pair of idealized  
586 Arctic scenarios, which differ only in the duration of the availability of (a) phytoplankton prey. In all  
587 panels, blue symbols represent the shorter-duration, present-day scenario, and red symbols the  
588 longer-season, future scenario. (b) A size spectrum from *C. finmarchicus* analogs at the small end to *C.*  
589 *hyperboreus* analogs at the large end is generated by varying the food-saturated development rate  $u_0$ .  
590 A single red or blue symbol represents a model population (Fig. 4b) and the set of blue symbols or red  
591 symbols represents a model metacommunity (Fig. 4c). (c) At the small, fast-developing (*C.*  
592 *finmarchicus*-like) end of the spectrum, the model predicts that a 1-year life cycle is optimal in both  
593 environmental scenarios (open circles). At the large, slow-developing (*C. hyperboreus*-like) end, 2  
594 years is optimal in both (dotted circles). Over a middle range, the optimal strategy changes from a 2-  
595 year cycle in the shorter productive season to 1 year in the longer case (solid circles). Note that these  
596 three cases, which are distinguished by symbol type in all panels, are not imposed but rather a  
597 classification of the emergent results in (c). (d) The middle-range cases that change generation length  
598 (solid symbols) also switch from a hybrid income/capital breeding strategy to an almost pure income-  
599 breeding strategy. These changes are accompanied by (e) more than doubling of lifetime egg  
600 production per successful adult and (f) more than doubling of the specific energetic yield to predators.  
601 (g) The fraction of the yield to predators that consists of storage lipid decreases, from ~30% to ~20%.

602 **Figure 6:** Conceptual understanding of the effects of borealization of the Arctic on length of productive  
603 season, body size, individual lipid content, life span and population turn over of Arctic (blue) and boreal  
604 (red) *Calanus* populations, and on total population lipid production. Where seasonal ice cover and low  
605 temperature prevail (central Arctic Ocean, towards the left of the continuum), large, lipid-rich and  
606 long-lived species may prevail, but population turn-over rates and total lipid production remain low.

607 A high degree of borealisation (right side) characterized by increased water temperatures, loss of sea  
608 ice and prolonged productive season, short life cycles and high population turn over may lead to high  
609 population lipid production despite a shift towards smaller individual size and lipid content.

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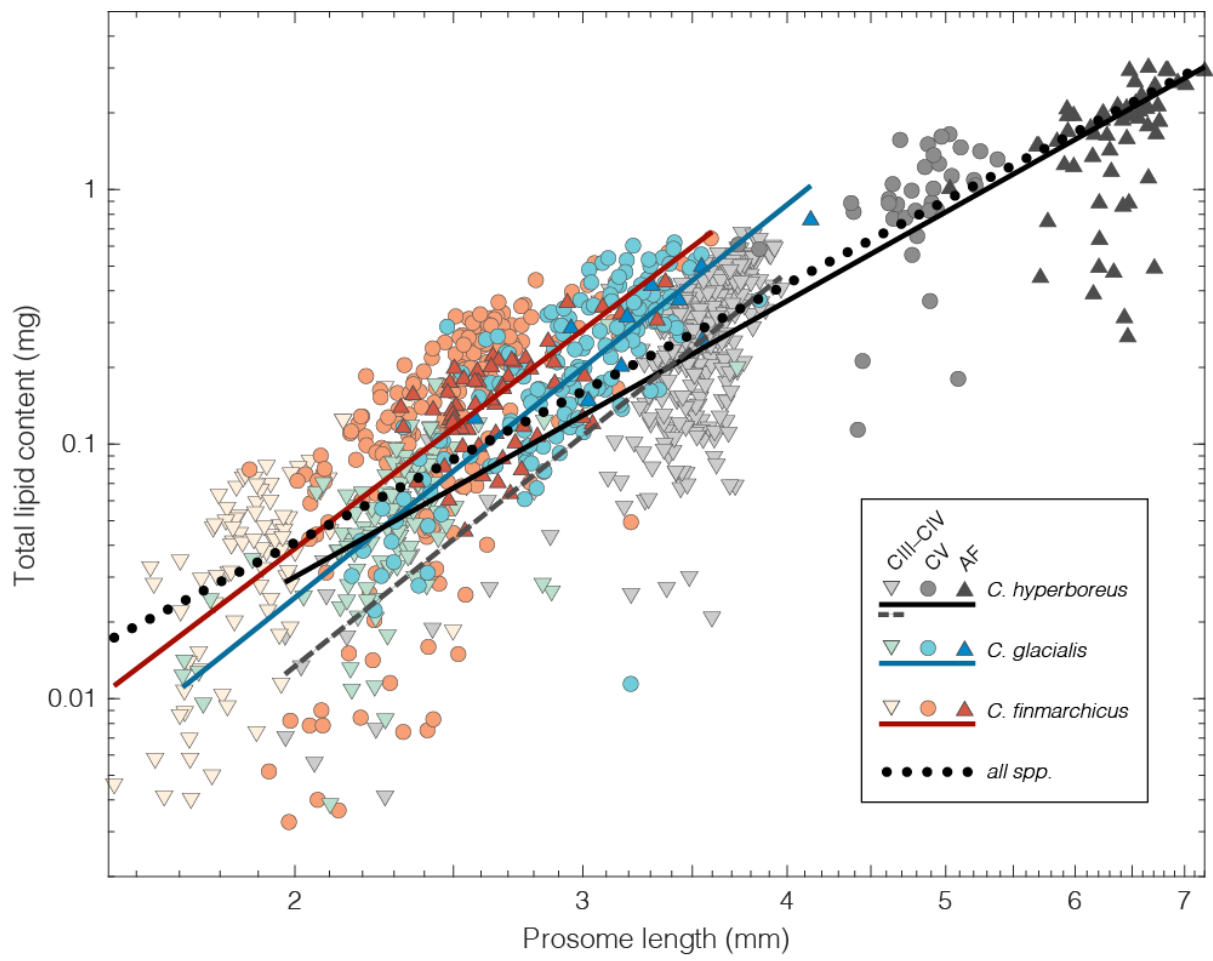


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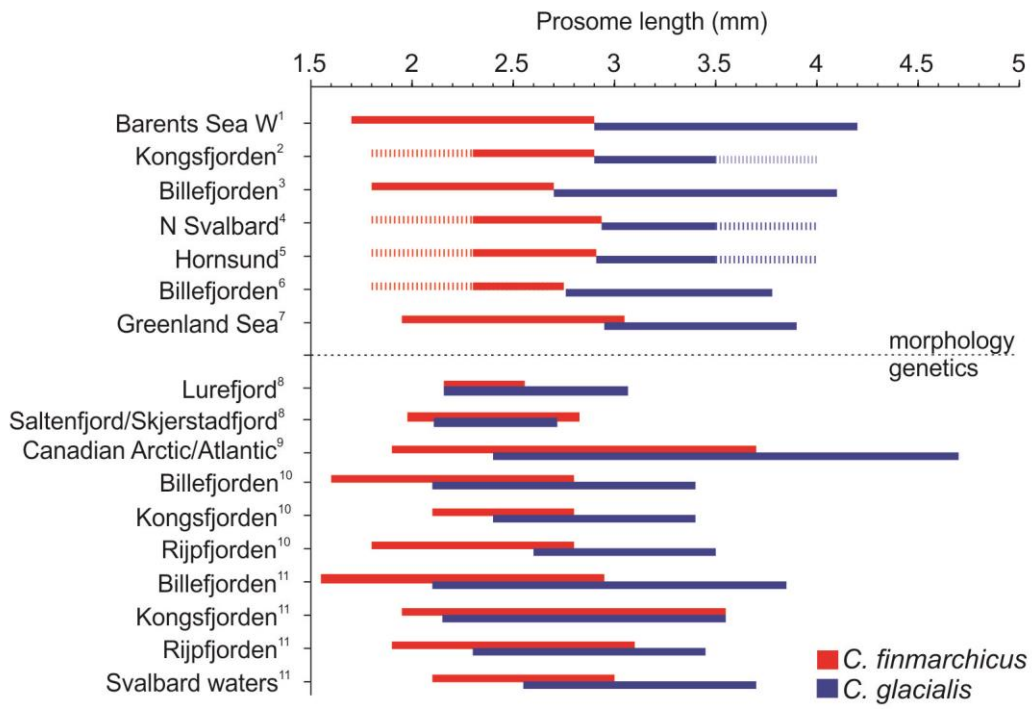
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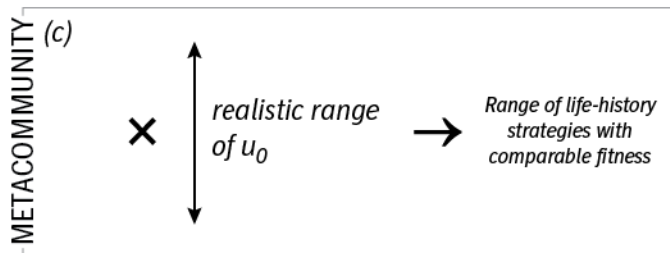
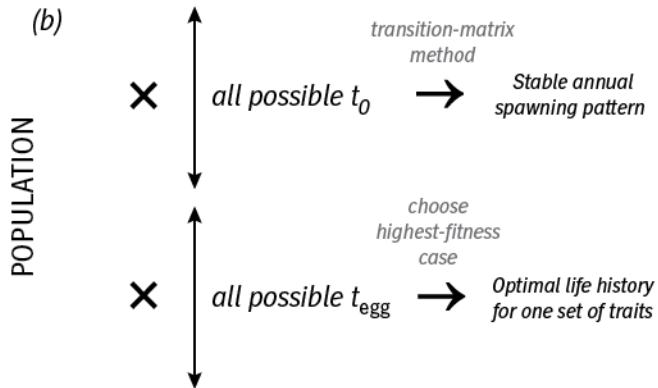
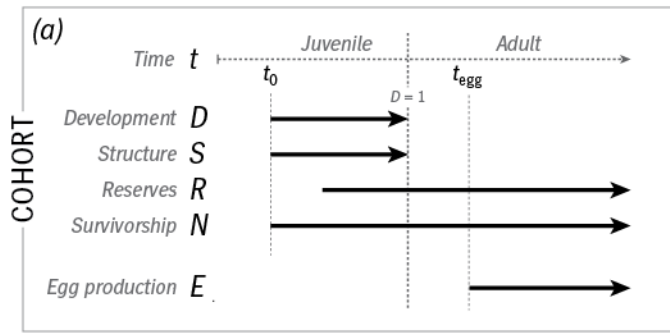


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620

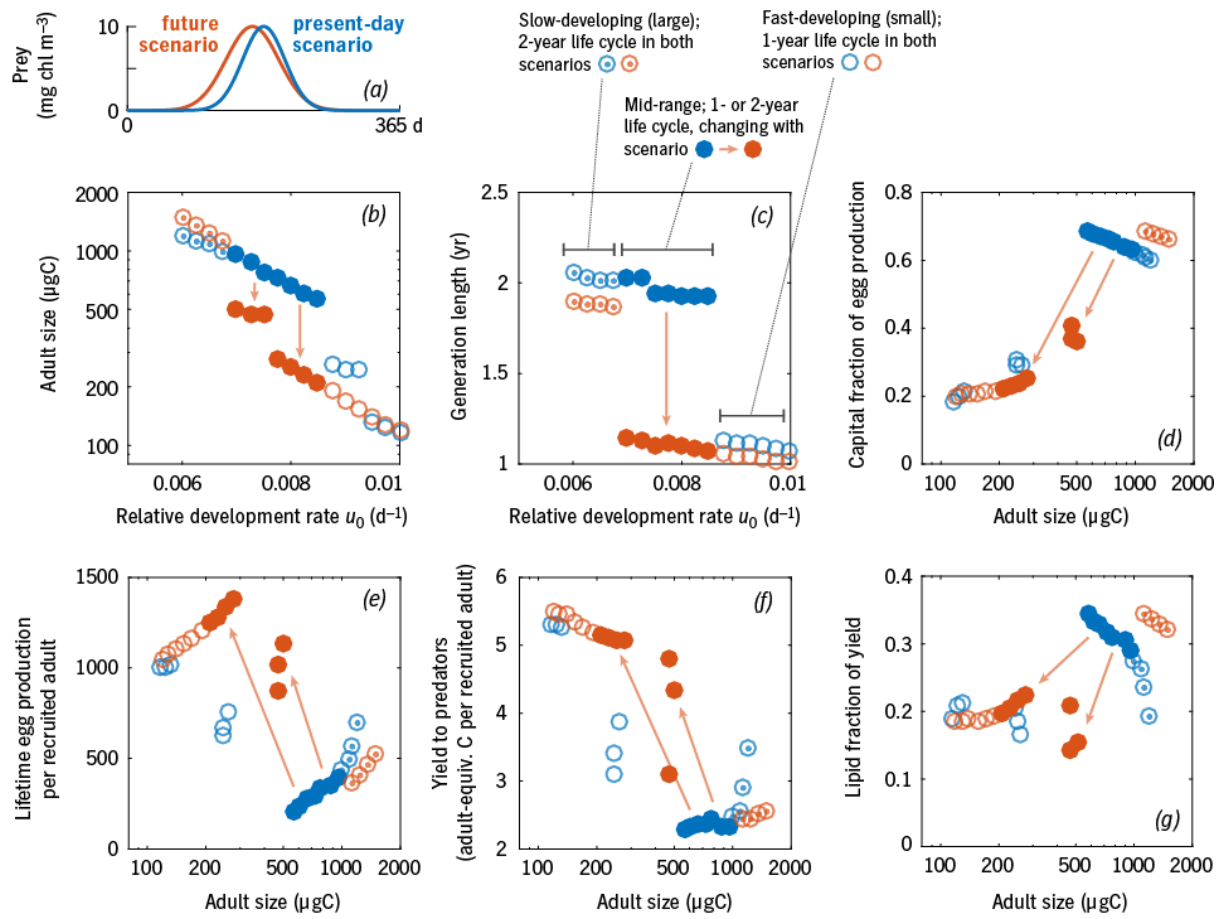
621

$u_0$  controls  $D$  directly  
and adult size Indirectly



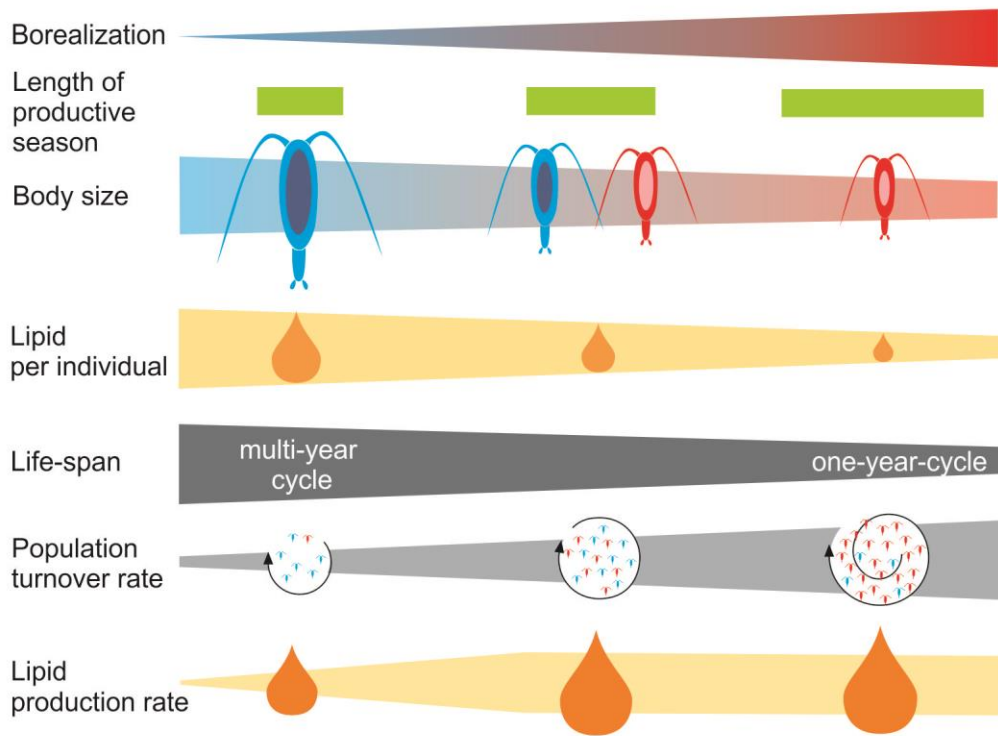
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