



## Food for Thought

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

Paul E. Renaud<sup>1,2,\*†</sup>, Malin Daase<sup>3†</sup>, Neil S. Banas<sup>4†</sup>, Tove M. Gabrielsen<sup>2</sup>, Janne E. Søreide<sup>2</sup>, Øystein Varpe<sup>1,2</sup>, Finlo Cottier<sup>3,5</sup>, Stig Falk-Petersen<sup>1,3</sup>, Claudia Halsband<sup>1</sup>, Daniel Vogedes<sup>3</sup>, Kristin Heggland<sup>3</sup>, and Jørgen Berge<sup>2,3</sup>

<sup>1</sup>Akvaplan-niva. Fram Centre for Climate and the Environment, N-9296 Tromsø, Norway

<sup>2</sup>University Centre on Svalbard, PO Box 156, N-9171 Longyearbyen, Norway

<sup>3</sup>Faculty of Biosciences, Fisheries and Economics, University of Tromsø, N-9037 Tromsø, Norway

<sup>4</sup>Department of Mathematics and Statistics, University of Strathclyde, 26 Richmond Street, Glasgow G1 1XQ, UK

<sup>5</sup>Scottish Association for Marine Sciences, Scottish Marine Institute, Oban, Argyll PA37 1QA, Scotland, UK

\*Corresponding author: e-mail: [pr@akvaplan.niva.no](mailto:pr@akvaplan.niva.no).

†These three authors contributed equally to the article.

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

**Keywords:** Arctic ecosystem, *Calanus*, life-history modelling, secondary production

## Introduction

Large-scale re-organization of Arctic marine communities and significant functional changes in the ecosystem are expected as a result of accelerated climatic warming and sea-ice withdrawal

(Wassmann *et al.*, 2011; Sunday *et al.*, 2012; Fossheim *et al.*, 2015; Kortsch *et al.*, 2015). Empirical studies have already detected some structural and functional changes (Wassmann *et al.*, 2011; Wiedmann *et al.*, 2014; Fossheim *et al.*, 2015), but predicting

specific compositional changes and the ecosystem consequences of such changes is challenging. These consequences are not just of academic interest as seasonal migrations of tens of millions of seabirds, valuable commercial fisheries (Atlantic cod, Pacific pollock), and recovery of large baleen whales (blue, fin, bowhead, humpback) all depend on the temporally and spatially concentrated productivity of the Arctic and its marginal seas. A key link between primary producers and commercial stocks are large copepods of the genus *Calanus*, which usually dominate zooplankton biomass in temperate and polar seas. *Calanus* spp. can be thought of as part of the “wasp waist” in the food web (a concept usually applied to forage fish; Hunt and McKinnell, 2006), in the sense that they sit at a trophic nexus at which the organism- and population-level biology of just a few species has ecosystem-level consequences.

Large-scale biogeochemical models have predicted widespread changes in response to Arctic warming and sea-ice loss, particularly at and near the base of the food web. Such changes include a longer season of pelagic primary productivity, a moderate increase in total primary production (Slagstad et al., 2011, 2015), an increase in Atlantic zooplankton species (*Calanus finmarchicus*) and strong reduction in Arctic zooplankton (*Calanus glacialis*) in the Barents Sea, and spreading of *C. glacialis* along the Eurasian shelves (Slagstad et al., 2011; Feng et al., 2016). *C. finmarchicus* has expanded northward in the western Atlantic over the last 30 years (Chust et al., 2014), and is increasing in abundance at the expense of *C. glacialis* in the Barents Sea (Dalpadado et al., 2012). The fate of the third *Calanus* species in the region, *C. hyperboreus*, has so far not been considered (Slagstad et al., 2015; Feng et al., 2016, 2018). Although *C. hyperboreus* occurs on the shelf, it is primarily an oceanic species (Conover, 1988; Hirche, 1991; Kosobokova and Hirche, 2009) with markedly different life-history strategies, grows considerably larger than *C. glacialis* and *C. finmarchicus* (Falk-Petersen et al., 2009), and, therefore, is likely subject to different environmental forcing than the smaller, short-lived *Calanus* species.

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

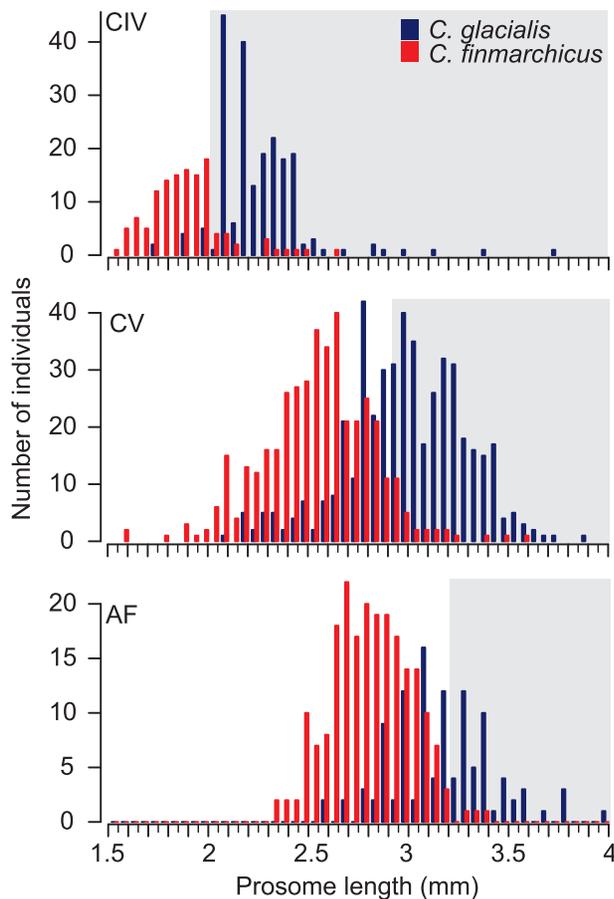
It can be misleading, however, to treat species as fixed types, with no plasticity or variation, in investigations of how ecosystems are likely to respond to unprecedented conditions. In fact, this kind of fixed-species approach can prevent important questions from being asked in the first place. It is increasingly clear that *C. glacialis* and *C. finmarchicus* have diverse and plastic

strategies for reproduction, foraging, and dormancy that are in part responses to environmental variation (Falk-Petersen et al., 2009; Daase et al., 2013; Melle et al., 2014). In addition, morphology-based identification of these two species has been shown to be unreliable in some areas (Lindeque et al., 2006; Gabrielsen et al., 2012; Choquet et al., 2018), and reports of hybridization between the two species (Parent et al., 2012) complicate the picture further still. In this study, we use a combination of molecular tools for species identification and a recent, well-validated life-history model (Banas et al., 2016a) to show that a trait-based, as opposed to species-based, approach allows us to formulate and test hypotheses that cut across the organismal, population, and community scales. We find that intra- and inter-specific variation in key organismal traits (body size, lipid content) may be more congruent across species than thought, allowing a huge conceptual simplification. The model, by placing individual life-history and population dynamics in a common mathematical frame, lets us scale up to the expected trade-off between these organismal traits and population productivity. In this framework, we can begin to reason systematically about whether the sum of these changes is a net gain or loss for particular classes of predator.

## A unified view of body size and energy content

To evaluate overlap in size between *C. finmarchicus* and *C. glacialis*, and whether lipid content is species or size dependent, we sampled *Calanus* in three fjords in Svalbard (78–81°N, 10–24°E, including Arctic and Atlantic hydrographic domains) using a Hydrobios Multi Plankton Sampler or a WP2 net (mesh size 200  $\mu\text{m}$ , mouth opening 0.25  $\text{m}^2$ ). Samples were taken between mid-September and early October in 2012 (Billefjorden 180–0 m, Rijpfjorden 265–0 m) and 2014 (Kongsfjorden 320–0 m, Rijpfjorden 265–0 m). This is the start of the overwintering period of *Calanus* spp. when lipid content is commonly at its highest, thus the variability in lipid content and size reflects natural variability in the population, but not seasonal variability. We measured the prosome length of >1500 individual copepods (copepodite IV and V, and adult females) and each specimen was preserved in absolute ethanol and identified to species using molecular techniques as described in Gabrielsen et al. (2012). Prior to being preserved,  $\sim 650$  individual copepods (copepodite stages IV, V, and VI) were photographed while still alive using a Leica MZ 95 stereomicroscope with a Motec camera. The pictures were used to measure prosome length, prosome area and area of the lipid sac. Total lipid content was calculated based on lipid sac area following Vogedes et al. (2010). To compare the lipid-size relationship in the *C. finmarchicus* and *C. glacialis* complex with that of the third *Calanus* congener in the study area, *C. hyperboreus*, we included measurements of prosome length and lipid sac area of 430 *C. hyperboreus* (CIII–CV and adult females) from Svalbard waters sampled between August and October (2010, 2012, 2014, max. sampled depth 2000 m). *C. hyperboreus* were not genetically identified as they are substantially larger than the other two *Calanus* species and can be distinguished morphologically by a spine at the last thoracic segment, which is present from stage CIV.

We found considerable overlap in prosome length of *C. glacialis* and *C. finmarchicus* identified to species using molecular tools (Figure 1), indicating that size-based classification is inaccurate for the larger developmental stages included in this study (copepodite IV, V, and females) (Figure 1). The relationship between



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

size and lipid content was statistically indistinguishable for the two species (Table 1; Figure 2). The relationship for copepodite stages CIII and CIV of *C. hyperboreus*, a range of body sizes that better matches *C. finmarchicus* and *C. glacialis* CIII–AF (Table 1, Figure 2), was also indistinguishable from that of the two smaller species. The relationship for all size classes of *C. hyperboreus* (Figure 2) displayed a significantly lower exponent coefficient ( $a$  in the equation in Table 1). This difference, however, appears to be an effect of scale—the range of body size considered in relation to intraspecific variability in lipid content—rather than a true species difference. Our results, therefore, suggest that there is little inherent, species-specific difference in lipid-storage capacity between the Arctic *C. glacialis* and the boreal *C. finmarchicus* (Figure 1), or indeed the younger stages of *C. hyperboreus*. The amount of lipid that can be stored, therefore, is dependent largely on body size (and developmental stage as it relates to size). This is in contrast to previous studies that have reported or assumed a higher species-specific lipid content in Arctic *C. glacialis* compared with *C. finmarchicus* (Falk-Petersen *et al.*, 2009; Scott *et al.*, 2000). This misconception has probably been caused by a general underrepresentation of *C. glacialis* in the community based on morphological identification (Choquet *et al.*, 2018).

**Table 1.** Results of exponential fits to total individual lipid content LC (in mg) as a function of prosome length PL (in mm), across *Calanus* spp. and life stages (see Figure 2). Each fit is specified by an exponent  $a$  and log coefficient  $b$  such that  $LC = e^b PL^a$ .

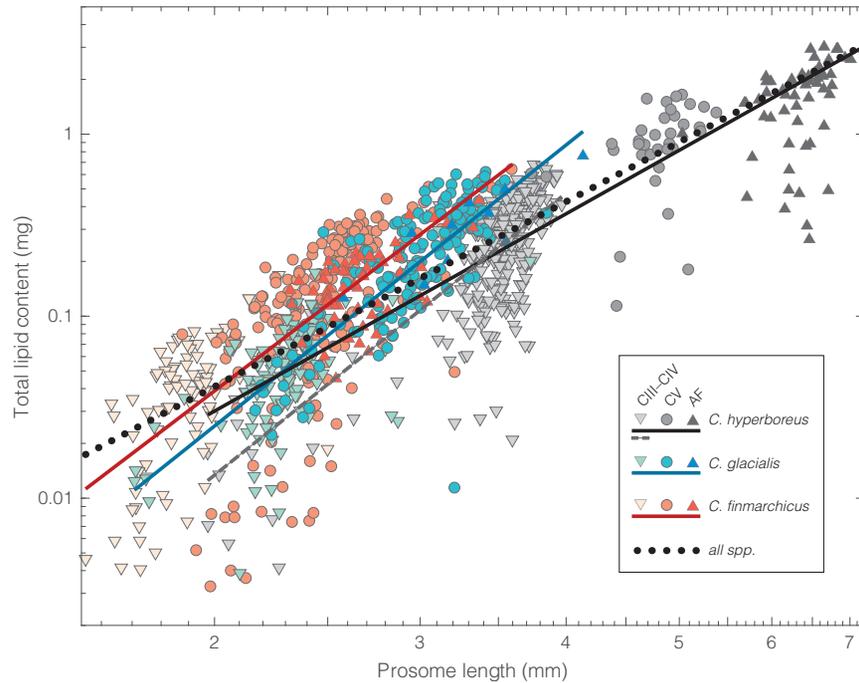
Species, stage	Exponent <sup>a</sup>	Log coefficient <sup>b</sup>
<i>C. finmarchicus</i> , CIII–AF	$4.9 \pm 0.5$	$-6.6 \pm 1.5$
<i>C. glacialis</i> , CIII–AF	$5.1 \pm 0.3$	$-7.2 \pm 1.0$
<i>C. hyperboreus</i> , CIII–CIV	$5.1 \pm 0.2$	$-7.9 \pm 1.1$
<i>C. hyperboreus</i> , CIII–AF	$3.6 \pm 0.2$	$-6.0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

Confidence limits at the 95% level are also given, and non-overlapping confidence intervals are considered statistically significant. All data are from live animals collected August to October. Outliers with LC < 0.002 mg have been omitted ( $n = 18$ , <2% of samples).

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

### Scaling up from individual traits to population productivity

As shown by the review of growth and development studies by Banas and Campbell (2016), body size in copepods can be thought of as a direct consequence of the combination of individual development time and the mean rate of energy gain during that time, i.e. life-history strategy and foraging strategy. In highly seasonal environments, these strategies are strongly constrained



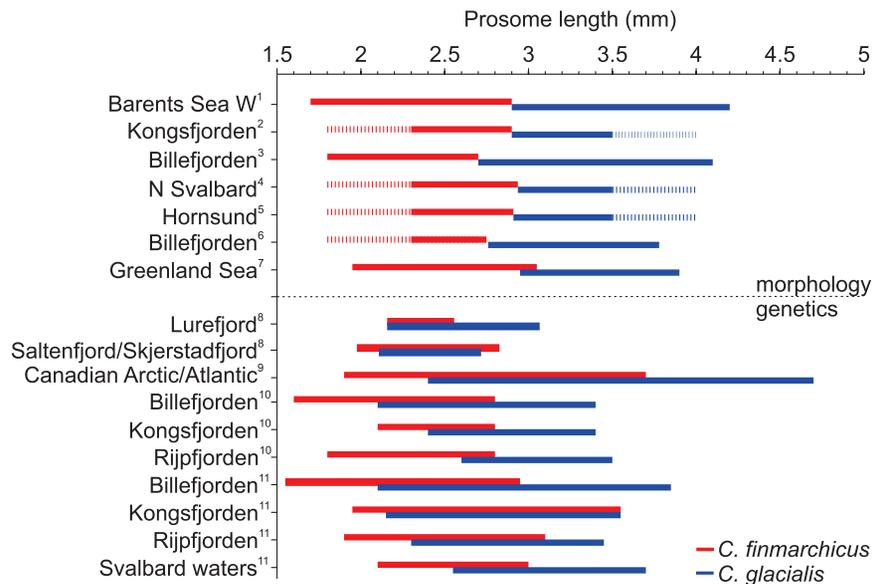
**Figure 2.** Total lipid content in relation to prosome length across *Calanus* species and stages. Five regression lines match the exponential fits and 95% CIs given in Table 1. Non-overlapping confidence intervals indicate statistically significant differences. *C. finmarchicus* CIII-AF (red;  $n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

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

The copepod life-history model Coltrane (Copepod Life-history Traits and Adaptation to New Environments) version 1.0 is described in detail by Banas *et al.* (2016a). Matlab source code is available at <http://github.com/neilbanas/coltrane>. Coltrane is an individual-based model that represents the time-evolution of one cohort of a clonal population, all bearing the same traits and spawned on the same date, with four state variables: relative developmental stage  $D$  (0 at spawning, 1 at adulthood), survivorship  $n$  (the fraction of initially spawned individuals that remain after some amount of cumulative predation mortality); structural biomass per individual  $S$ , and individual reserve or storage-lipid biomass  $R$  (Figure 4a). Families of cases of the cohort model are then combined to produce population- and community-level results, as shown in schematic form in (Banas *et al.*, 2016a) for a complete model description. A population in Coltrane (Figure 4b) is considered to have identical traits, and to have a

seasonal pattern of spawning dates that maximizes fitness (lifetime egg production per initial egg) while also solving internal life-history mismatch (Varpe *et al.*, 2007). Mathematically, this optimization involves running the cohort model (Figure 4a) for a complete spectrum of spawning dates and also a spectrum of imposed delays between maturation and the start of spawning (Figure 4b; Banas *et al.* 2016a). A community—or rather a meta-community, an estimate of “all possible ways to be a copepod” in a given environment—is generated in the present version of the model by varying a single life-history trait, the prey-saturated development rate  $u_0$ . This rate was varied from 0.005 to 0.01  $d^{-1}$ , corresponding to a total egg-to-adult development time of 100–200 d at 0°C under prey-saturated conditions (Banas and Campbell, 2016).

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



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

(survivorship) term over time to produce total energetic yield to predators

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

and the lipid fraction of that yield

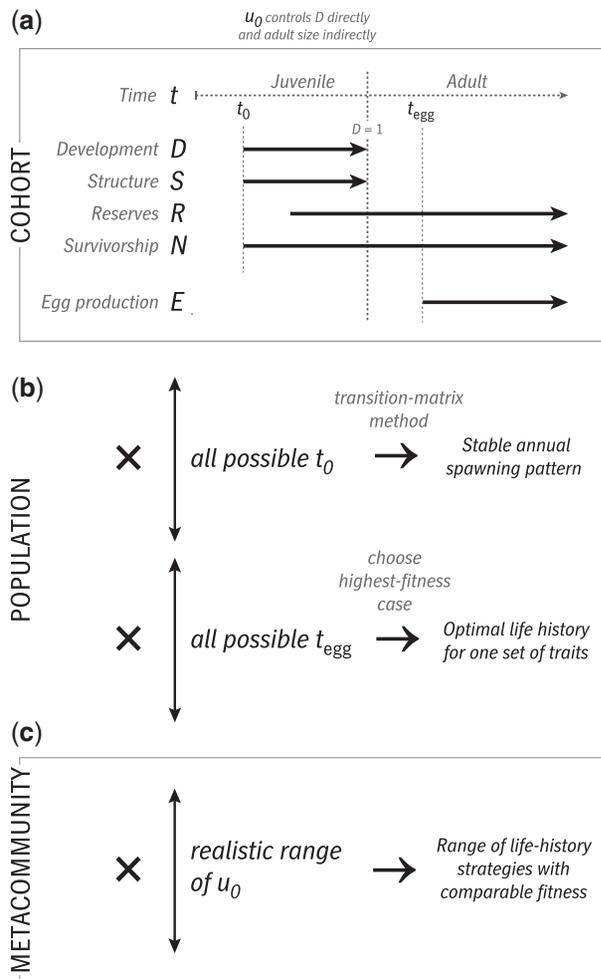
$$Y^{-1} \int mRN dt.$$

In this study, the model was run for a pair of idealized scenarios, which differed only in the duration of prey availability, in order to evaluate the common assumption that a longer ice-free period of spring-autumn pelagic phytoplankton production will lead to shrinking individual sizes and potential species shifts, and how such a shift toward smaller, faster-reproducing individuals would affect total secondary production by *Calanus*. The first of the two scenarios assumes phytoplankton prey occur in a Gaussian seasonal window equivalent to 3.5 months of saturating prey per year, as opposed to a window equivalent to 4.5 months in the second scenario (Figure 5a). These can be taken as idealisations of present-day and reduced-ice conditions in a West Svalbard fjord or a similar Arctic environment (mathematically, these cases correspond to the “global” experiment of Banas *et al.* (2016a) with  $\partial t' = 40, 50$  days). In reality, the length of the productive season need not correlate closely with the overall amount of food, or its nutritional quality, or its timing relative to the annual light cycle: all details that deserve consideration in a more complex, spatially resolved model study. Seasonal cycles were assumed to repeat exactly, such that the model results here describe optimal strategies in two contrasting but stable environments. For simplicity, both surface and deep temperature were held

constant at 0°C in both scenarios, although Banas *et al.* (2016a) explored the effect of temperature variation in relation to prey variation in the same model. Specific mortality  $m$  is assumed to follow the same allometry as specific ingestion (Banas *et al.*, 2016a): this simplifying assumption has a theoretical and coarse empirical basis (Hirst and Kiørboe, 2002), but may well be inappropriate in a high-latitude context where gradients in light availability and thus visual predation may be particularly strong (Varpe *et al.*, 2015).

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

Thus, the assumptions and review of laboratory data behind Coltrane (Banas and Campbell, 2016; Banas *et al.*, 2016a) support the idea that whether by plasticity, hybridization, evolution, or competitive replacement—the model is agnostic regarding the mechanism—we might indeed expect a shift in the changing Atlantic Arctic in which mid-sized, long-generation length



**Figure 4.** Schematic of the Coltrane copepod life-history model. (a) The time-evolution of one cohort of individuals, with identical traits and spawned on the same date  $t_0$ , are tracked by state variables representing development, structural and reserve biomass, and survivorship. Egg production by this cohort is calculated from these state variables, as a function of an additional strategy decision  $t_{egg}$ , which allows a delay between maturation and the start of spawning. (b) An annual routine representing a population is generated from the cohort solutions by varying  $t_0$  and  $t_{egg}$  systematically and identifying the seasonal pattern of spawning dates and the value of  $t_{egg}$  that maximize fitness while also solving internal life-history mismatch. (c) A metacommunity is generated by varying the relative-development-rate parameter  $u_0$ , which controls development time directly and adult size indirectly, as previously shown for a metastudy of laboratory experiments (Banas and Campbell, 2016). See Banas et al. (2016a) for a full description of the model.

*Calanus* are replaced by smaller, shorter-generation length organisms. Replacing a 2-year reproductive cycle with a one-year cycle increases survivorship and turnover, such that this shift is accompanied by more than a two-fold increase in lifetime egg production per adult (Figure 5e). More surprising, it is also accompanied by a more than twofold increase in specific energetic yield to predators (Figure 5f). The fraction of the yield to predators that consists of storage lipid decreases from  $\sim 30$  to  $\sim 20\%$  (Figure 5g; note that the lipid fraction of yield, summed across all

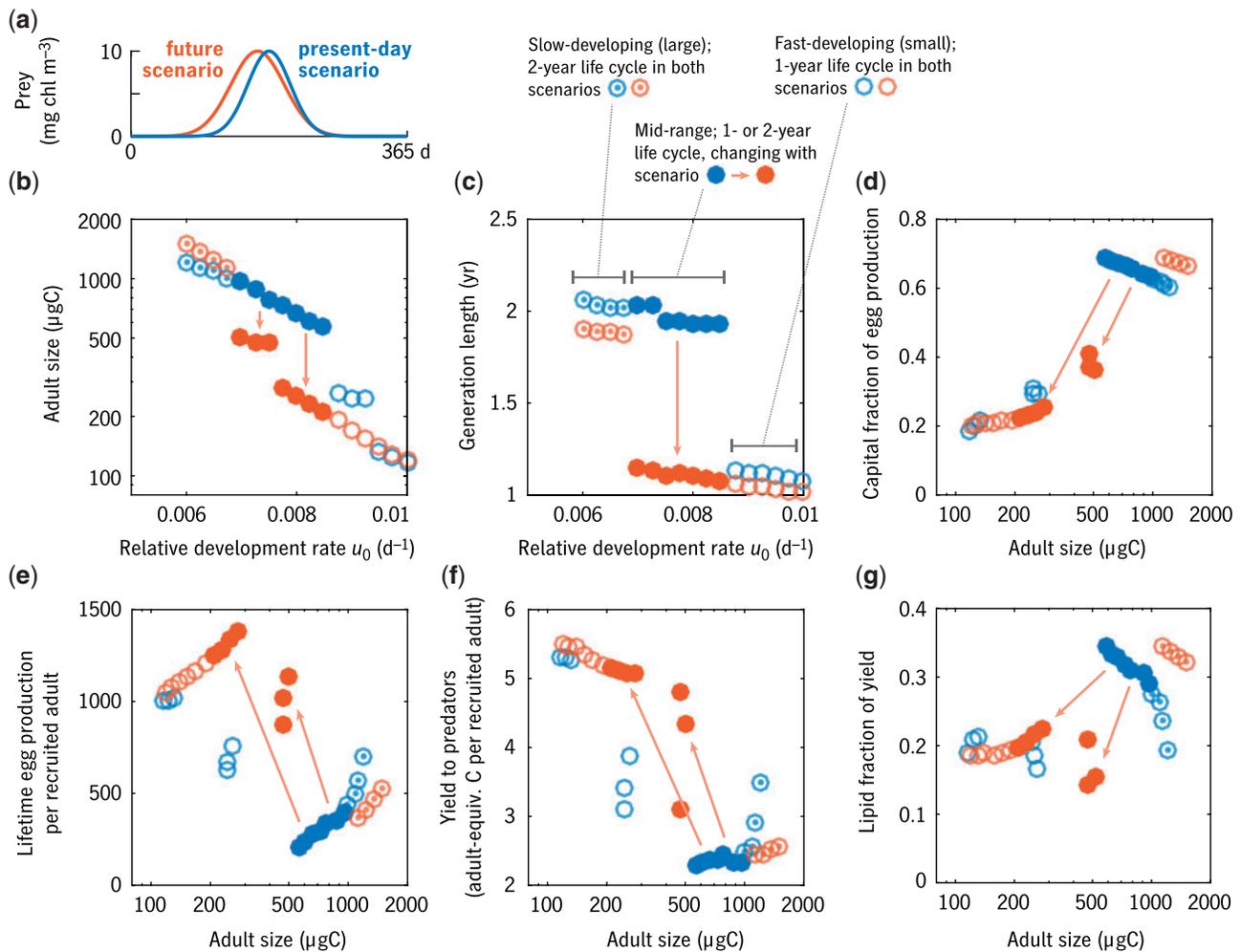
life stages, is not directly comparable to measurements of the lipid content of late stage individuals). However, the increase in total energetic yield outweighs the decrease in lipid fraction, so that the total yield of lipid to predators (per initial copepod egg) actually increases slightly in the longer-productive-season scenario.

Translating these trait-based results into species-specific predictions is ambiguous, particularly given the idealized nature of the model experiment. Body size depends on growth and development rates via a high exponent, such that 10% uncertainty in each of those rates translates into fourfold uncertainty in adult size (Banas and Campbell, 2016). Accordingly, body-size/generation-length combinations are likely to be skewed relative to the real *Calanus* populations (a more realistic application would address this through systematic parameter tuning). One could interpret the mid-sized cases that change generation length between scenarios as larger *C. glacialis* analogues, shifting toward a *C. finmarchicus*-like life-history under a longer productive season, or else as small *C. hyperboreus* analogues, replaced by *C. glacialis* and *C. finmarchicus* in a more boreal environment. Predicting these specific futures is a complex oceanographic and spatial-ecology problem, well beyond an idealized model (or for that matter any first-principles biological argument). It is likely that currently observed shifts in size distributions are consequences of internal population-level plasticity, and it is not clear whether any required genetic shifts (as climatic shifts surpass the range of phenotypic flexibility) could occur fast enough to reach these modelled optima. What we can conclude from this model experiment is that ecological shifts along the body size–lipid content curve in high-latitude *Calanus* (Figure 2) are likely to be accompanied by shifts in generation time and population turnover rate that have strong, compensating effects on energy transfer to predators.

### Ecosystem consequences

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

Parallel model experiments varying mean water temperature (Banas et al., 2016a) suggest that, at the community level, the direct effects of near-surface warming on *Calanus* trait patterns are similar to the effects of lengthening of the productive season, although at the population level, thermal thresholds (Alcaraz et al., 2014) may be limiting. This is another factor that complicates the translation of model results into species terms. Warming of deeper water, or loss of early spring ice-associated blooms, may drive some *Calanus* populations past thresholds of overwintering survival. This appears to be the case for the southeastern Bering Sea in warm, low-ice years (Hunt et al., 2011; Stabeno et al., 2012; Eisner et al., 2014), as the measured summer abundance of

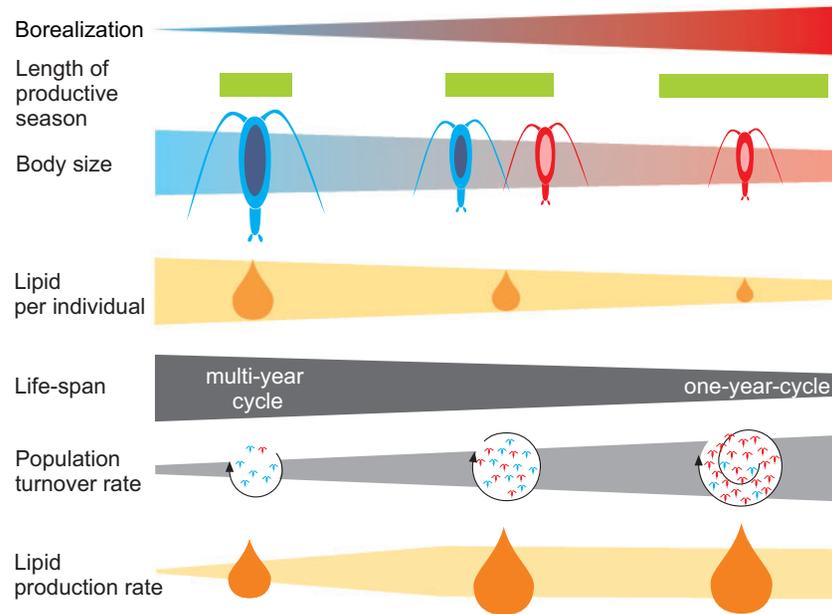


**Figure 5.** Results of the life-history model across the *Calanus* size spectrum, under a pair of idealized Arctic scenarios, which differ only in the duration of the availability of (a) phytoplankton prey. In all panels, blue symbols represent the shorter-duration, present-day scenario, and red symbols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

*C. glacialis/marshallae* crashes in temperature and ice conditions similar to those projected to be the new normal by the 2040s (Banas *et al.*, 2016b). Indeed, the same model that predicts the positive effects of extended pelagic productivity in this study (Figure 4) finds *Calanus* to be non-viable in the southeastern Bering Sea without an extended period of sea ice and ice algae (Banas *et al.*, 2016a).

Increasing air and sea temperatures and significant reductions in sea ice have already been observed in the Arctic (Stroeve *et al.*, 2014), and may impact food supply, growth rates, and relative distributions of *Calanus* spp. Furthermore, sea-ice loss changes the light regime of the water column, potentially altering seasonal

and/or size-specific predation pressure on zooplankton in a future Arctic Ocean (Varpe *et al.*, 2015). In addition, advection of heat, food, and species from boreal areas northward substantially alters plankton community structure in some regions (Orlova *et al.*, 2015). Any reconsideration of the paradigm of species replacement and its effect on ecosystem function, therefore, must consider the spatial variability in the drivers of change. Likewise, all the environmental drivers discussed here vary over a range of timescales as well, from interannual variability to true multidecadal trends. On very long timescales, it can be a powerful simplification to elide the differences among disparate mechanisms of adaptation—individual plasticity, competitive exclusion,



**Figure 6.** Conceptual understanding of the effects of borealization of the Arctic on length of productive season, body size, individual lipid content, life span and population turn over of Arctic (blue) and boreal (red) *Calanus* populations, and on total population lipid production. Where seasonal ice cover and low temperature prevail (central Arctic Ocean, towards the left of the continuum), large, lipid-rich and long-lived species may prevail, but population turn-over rates and total lipid production remain low. A high degree of borealization (right side) characterized by increased water temperatures, loss of sea ice and prolonged productive season, short life cycles, and high population turn over may lead to high population lipid production despite a shift towards smaller individual size and lipid content.

hybridization, range shifts and species replacement, true natural selection—as a trait-based approach allows one to do. However, these mechanisms have their own intrinsic timescales, and understanding shorter-term change in *Calanus* may require that we distinguish between mechanisms more precisely and apply trait- and optimality-based methods more selectively.

Our findings suggest that borealization of marginal seas in the European Arctic may not be detrimental in terms of either carbon- and lipid-based food-web contributions from *Calanus*, regardless of whether warming results in a species shift to *C. finmarchicus*, or in smaller sizes of *C. glacialis* (Figure 5). Record high stocks of age 3+ Atlantic cod in the Barents Sea in recent years suggest that there is no shortage of food, despite more than a decade of warming, a weakening in trophic links with their traditional prey (capelin) (Johannesen *et al.*, 2015), and a dominance of *C. finmarchicus* in many areas. A size shift in the zooplankton prey field may, however, impact predators that actively select larger individuals, regardless of the sensory mechanisms involved in the search process (Martens *et al.*, 2015). There are, however, only two explicit examples of this phenomenon from Arctic systems, and the results of one (Dalpadado *et al.*, 2000) could be explained by other mechanisms leading to apparent selection. The little auk (*Alle alle*) searches visually for its prey and actively selects larger individuals (Karnovsky *et al.*, 2003; Kwasniewski *et al.*, 2012; Vogedes *et al.*, 2014), and this predator may be negatively affected by shifts to a system with smaller prey (Kidawa *et al.*, 2015). One recent study, however, suggests that chick growth and adult body-condition may not decline when they fed on small zooplankton instead of larger congeners (Amélineau *et al.*, 2016).

Although we only consider bottom-up effects in this study, predation pressure may also be important in driving *Calanus*

life-history traits (Kaartvedt, 2000; Varpe *et al.*, 2007; Berge *et al.*, 2012). A continued northwards expansion of boreal fish, as well as increases in whale populations, may also select for Arctic *Calanus* species with shorter life-spans and smaller body sizes (Berge *et al.*, 2012), thus eliciting similar effects as shown in our models incorporating ocean warming and lengthening of the productive season. The effects of increased predation on zooplankton production and population size, however, are less clear.

### Conclusion and recommendations

Since climate change affects ecosystems both directly and indirectly, many unknowns could significantly affect the generality of our findings. Warmer temperatures, reduced ice cover, and the spread of boreal species are already affecting timing, quantity, and composition of phytoplankton production. Here we have focussed on a likely species shift within the *Calanus* species complex. Interactions of new taxa with both resident and other new species are difficult to predict (Williams and Jackson, 2007), and not incorporated into our conceptual model. A replacement of *Calanus* spp. with even smaller copepod species (i.e. *Pseudocalanus* spp., *Oithona similis*) having different nutritional values and life-history traits may prove to be much more detrimental in terms of available carbon and lipid for predators and food web structure (Coyle *et al.*, 2011) (Figure 6).

Our dataset is geographically and seasonally limited, and a large-scale survey of species and size specific lipid content would be necessary to assess the robustness of our regional observations. The use of a trait-based rather than a species-based approach to assess ecosystem changes may be particularly useful where species identification is challenging, which has become increasingly evident for *Calanus* (Choquet *et al.*, 2018). Our results clearly

demonstrate, however, that the basis for previous concerns regarding species replacement within the *Calanus* complex may be unfounded, or at least not universal, and that food subsidies from *Calanus* may continue to support many top predators in the European Arctic.

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