

Copepod life strategy and population viability in response to prey timing and temperature: Testing a new model across latitude, time, and the size spectrum

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2 ABSTRACT

3 A new model ("Coltrane": Copepod Life-history Traits and Adaptation to Novel Environments)
4 describes environmental controls on copepod populations via 1) phenology and life history and
5 2) temperature and energy budgets in a unified framework. A set of complementary model
6 experiments are used to determine what patterns in copepod community composition and
7 productivity can be predicted from only a few key constraints on the individual energy budget: the
8 total energy available in a given environment per year; the energy and time required to build an
9 adult body; the metabolic and predation penalties for taking too long to reproduce; and the size
10 and temperature dependence of the vital rates involved. In an idealized global-scale testbed, the
11 model correctly predicts life strategies in large *Calanus* spp. ranging from multiple generations
12 per year to multiple years per generation. In a Bering Sea testbed, the model replicates the
13 dramatic variability in the abundance of *C. glacialis/marshallae* observed between warm and
14 cold years of the 2000s, and indicates that prey phenology linked to sea ice is a more important
15 driver than temperature per se. In a Disko Bay, West Greenland testbed, the model predicts the
16 viability of a spectrum of large-copepod strategies from income breeders with a adult size ~ 100
17 μgC reproducing once per year through capital breeders with an adult size $> 1000 \mu\text{gC}$ with
18 a multiple-year life cycle. This spectrum corresponds closely to the observed life histories and
19 physiology of local populations of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*.

20 **Keywords:** Zooplankton, copepod, life history, annual routine, diversity, biogeography, modelling, community ecology, Arctic

1 INTRODUCTION

21 Calanoid copepods occupy a crucial position in marine food chains, the dominant mesozooplankton in
22 many temperate and polar systems, important to packaging of microbial production in a form accessible
23 to higher predators. They also represent the point at which biogeochemical processes, and numerical
24 approaches like NPZ (nutrient–phytoplankton–zooplankton) models, start to be significantly modulated by
25 life-history and behavioural constraints. The population- and community-level response of copepods to
26 environmental change (temperature, prey availability, seasonality) thus forms a crucial filter lying between
27 the biogeochemical impacts of climate change on primary production patterns and the food-web impacts
28 that follow.

29 Across many scales in many systems, the response of fish, seabirds, and marine mammals to climate
30 change has been observed, or hypothesized, to follow copepod community composition more closely than
31 it follows total copepod or total zooplankton production. Examples include interannual variation in pollock
32 recruitment in the Eastern Bering Sea (Coyle et al., 2011; Eisner et al., 2014), interdecadal fluctuations in
33 salmon marine survival across the Northeast Pacific (Mantua et al., 1997; Hooff and Peterson, 2006; Burke
34 et al., 2013), and long-term trends in forage fish and seabird abundance in the North Sea (Beaugrand and
35 Kirby, 2010; MacDonald et al., 2015). These cases can be all be schematized as following the “junk food”
36 hypothesis (Österblom et al., 2008) in which the crucial axis of variation is not between high and low total
37 prey productivity, but rather between high and low relative abundance of large, lipid-rich prey taxa.

38 Calanoid copepods range in adult body size by more than two orders of magnitude, from <10 to $>1000 \mu\text{g}$
39 C. Lipid storage is likewise quite variable among species, and linked to both overwintering and reproductive
40 strategy (Kattner and Hagen, 2009; Falk-Petersen et al., 2009). Many but not all species enter a seasonal
41 period of diapause in deep water, in which they do not feed and basal metabolism is reduced to $\sim 1/4$ of
42 what it is during active periods (Maps et al., 2014). Reproductive strategies include both income breeding
43 (egg production fueled by ingestion of fresh prey during phytoplankton blooms) and capital breeding (egg
44 production fueled by stored lipids in winter), as well as hybrids between the two strategies (Hirche and
45 Kattner, 1993; Daase et al., 2013). Generation lengths vary from several weeks to several years.

46 This paper describes a numerical approach, appropriate for both regional and global scales, that predicts
47 many of these traits—adult size, average lipid/energy content, life cycle, and seasonal timing—from first
48 principles based on interactions among growth, development, reproduction, and survivorship. Our approach
49 draws on two currents in recent modelling work. First, it builds on the *optimal annual routine* approach
50 (McNamara and Houston, 2008) previously applied to copepods by Varpe et al. (2007, 2009) and others.
51 We borrow from this tradition the hypothesis, or instinct, that timing is everything in seasonal environments,
52 as well as the technical strategy of separately tracking structural and reserve energy stores, with the latter
53 variable forming a link between copepod survival strategy and the value of the copepods as prey. Second,
54 we embed this optimal-annual-routine logic in a *trait-based metacommunity* (Follows et al., 2007; Record
55 et al., 2013), in which a small number of traits is used to parsimoniously represent the possibility space of
56 “all ways there are to be a copepod.”

57 The model experiments below pose the question: How many of the high-level associations among copepod
58 body size, body composition, generation length, reproductive strategy, and annual routine, at global or
59 regional scales, can be explained by a small handful of traits and tradeoffs that regulate how individual
60 animals best allocate energy over time? We will show that the scheme introduced here reproduces patterns
61 in space (large-scale trait biogeography), time (variability of one *Calanus* sp. in the Bering Sea), and along

62 the size spectrum (differences among three coexisting *Calanus* spp. in Disko Bay, West Greenland), in
63 response to annual cycles of temperature and prey availability.

2 MODEL DESCRIPTION

64 2.1 General approach

65 The model introduced here is “Coltrane” (Copepod Life-history Traits and Adaptation to New
66 Environments) version 1.0. Like many individual-based models Fiksen and Carlotti (1998), Coltrane
67 represents the time-evolution of one cohort of a clonal population, all bearing the same traits and spawned
68 on the same date t_0 , with a set of ODEs. The state variables describing a cohort are relative developmental
69 stage D , where $D = 0$ represents a newly spawned egg and $D = 1$ an adult; survivorship N , the fraction
70 of initially spawned individuals that remain after some amount of cumulative predation mortality; activity
71 level a , 1 for normal activity and 0 for diapause; structural biomass per individual S , and “potential”
72 or “free scope” φ , which represents all net energy gain not committed to structure, i.e. a combination
73 of internal energy reserves and eggs already produced. Combining reserves and eggs into one pool in
74 this way lets us cleanly separate results that depend only on the fundamental energy budget (gain from
75 ingestion, loss to metabolism, and energy required to build somatic structure) from results that depend on
76 particular assumptions about egg production (costs, cues, and strategies). An alternate form of the model
77 explicitly divides φ into internal reserves R and income and capital egg production rates E_{inc} and E_{cap} :
78 the simpler model without this distinction will be called the “potential” or φ model and the fuller version
79 the “egg/reserve” or ER model.

80 Because our goal is to describe a broad landscape of potentially coexisting strategies rather than a single,
81 optimal strategy, the model is written as a family of parallel, forward-in-time integrations with traits varying
82 among cases, rather than using the backwards-in-time solving method of the classic optimal annual routine
83 approach (Houston et al., 1993; Varpe et al., 2007). The model uses a family of cases varying spawning
84 date t_0 over the year to produce population-level results, and families of cases varying one or more traits to
85 produce community-level results.

86 In contrast to Record et al. (2013), we do not include interactions between competing species or explicitly
87 resolve coexistence and its limits, keeping our representation of predation mortality simple and linear to
88 make this possible. The purpose of this simplification (beyond a huge increase in computational efficiency)
89 is to separate bottom-up from top-down mechanisms as fully as possible, for the sake of interpretability.
90 Record et al. (2013) show that the choice of mortality closure has a huge effect on predictions of community
91 structure and diversity, and this dependence can easily obscure one’s understanding of how temperature
92 and prey cycles affect community characteristics by themselves.

93 Because we are willfully ignoring competition and coupling through predation, we will evaluate model
94 results in terms of the *landscape of viable strategies in a given environment*, rather than treating the results
95 as detailed predictions of relative abundance. A particular environment is defined by annual cycles of three
96 variables, total concentration of phytoplankton/microzooplankton prey P , surface temperature T_0 , and deep
97 temperature T_d . At present, these annual cycles are assumed to be perfectly repeatable, so that a “viable”
98 strategy can be defined as a set of traits that lead to annual egg production above the replacement rate,
99 given P , T_0 , and T_d as functions of yearday t . The effect of interannual variability on strategy is left for
100 future work.

101 **2.2 Time evolution of one cohort**

102 **2.2.1 Ontogenetic development**

103 Calanoid copepods have a determinate developmental sequence, comprising the embryonic period, six
 104 naupliar stages (N1–6), five copepodid stages (C1–5) and adulthood (C6). Similar to Maps et al. (2012),
 105 conversions between relative developmental stage D and the actual 13-stage sequence have been done using
 106 relative stage durations for *C. finmarchicus* from (Campbell et al., 2001), which appear to be appropriate
 107 for other *Calanus* spp. with the proviso that C5 duration is particularly variable and strategy-dependent.
 108 Development in the model follows

$$\frac{dD}{dt} = u, \quad D \leq 1 \quad (1)$$

109 where developmental rate u is

$$u = a q_d \sigma u_0 \quad (2)$$

110 and

$$q_d \equiv Q_d^{T/10^\circ\text{C}} \quad (3)$$

$$T = a T_0 + (1 - a) T_d \quad (4)$$

$$\sigma \equiv \frac{P}{K_s + P} \quad (5)$$

111 All variables and parameters are defined in Table 1. The temperature-dependent factor q_d describes a
 112 power-law response with a Q_{10} of Q_d , where temperature is assumed to be T_0 during active feeding
 113 ($a = 1$) and T_d during diapause ($a = 0$). Prey saturation σ is a simple Michaelis-Menten function with
 114 half-saturation K_s . The parameter u_0 , the development rate corrected to 0°C , was found by Banas and
 115 Campbell (2016) to be the primary trait responsible for differences in adult body size among *Calanus* spp.
 116 and other calanoids $>50 \mu\text{g C}$ adult size, although not at a broader scale of diversity.

117 **2.2.2 Energy gain and loss**

118 Energy gain from ingestion is given by

$$I = a r_a \sigma q_g I_0 S^{\theta-1} \quad (6)$$

119 Ingestion is assumed to follow a Kleiber's Law-like size dependence, with $\theta = 0.7$ (Kleiber, 1932; Saiz and
 120 Calbet, 2007). I_0 is specific ingestion rate at saturating prey concentration, $T=0^\circ\text{C}$, and $S=1 \mu\text{g C}$.

121 The factor $q_g \equiv Q_g^{T/10^\circ\text{C}}$ is a power-law temperature response for growth parallel to that for development
 122 but with a different Q_{10} . Q_{10} values have been found to vary among copepod species but Banas and
 123 Campbell (2016) argue that common values derived from a fit across community-level data are more
 124 appropriate for comparing species near their thermal optima. Based on Forster et al. (2011), we use $Q_g =$
 125 2.5 and $Q_d = 3.0$.

126 Energy loss to metabolism is given by

$$M = a^* r_m q_g I_0 S^{\theta-1} \quad (7)$$

127 where r_m is the ratio of metabolism to ingestion when prey is saturating. Unlike dD/dt and I , which are 0
 128 during diapause ($a = 0$: see below) because of the factor a in (2) and (6), M during diapause is nonzero,

129 although reduced by a factor r_b :

$$a^* = r_b + (1 - r_b)a \quad (8)$$

130 In this formalism, gross growth efficiency ϵ can be written

$$\epsilon = \frac{I - M}{r_a^{-1} I} = \sigma r_a - r_m \quad (9)$$

131 We have set $r_m = 0.14$ such that $\epsilon \approx 0.3$ when $P \approx 2K_s$ and $\epsilon = 0$ when $P = 1/4 K_s$.

132 2.2.3 Allocation of net gain

133 Net mass-specific energy gain G is simply $I - M$. The two energy stores S and φ follow

$$\frac{dS}{dt} = f_s GS \quad (10)$$

134

$$\frac{d\varphi}{dt} = (1 - f_s)GS \quad (11)$$

135 in the case where $G \geq 0$ and development is past the first feeding stage, $D \geq D_f$. For $D < D_f$, we assume
136 $G = 0$ for simplicity. Positive gain is allocated between structure and potential according to the factor f_s ,
137 which commits net gain entirely to structure before a developmental point D_s , entirely to potential during
138 adulthood, and to a combination of them in between:

$$f_s = \begin{cases} 1, & D < D_s \\ \frac{1-D}{1-D_s}, & D_s \leq D \leq 1 \\ 0, & D = 1 \end{cases} \quad (12)$$

139 When $G \leq 0$, the deficit is taken entirely from reserves (eq. (11) with $f_s=0$).

140 Potential φ is allowed to run modestly negative, to represent consumption of body structure during
141 starvation conditions. A cohort is terminated by starvation if

$$\varphi < -r_{starv} S \quad (13)$$

142 where in this study $r_{starv} = 0.1$. A convenient numerical implementation of this scheme is to integrate S
143 implicitly so that it is guaranteed > 0 , and to integrate φ explicitly so that it is allowed to change sign, with
144 no change of dynamics at $\varphi = 0$.

145 2.2.4 Reserves vs. potential reserves

146 If the φ model just described is elaborated with an explicit scheme for calculating total egg production
147 over time $E(t)$, then it is possible to define $R(t)$, individual storage/reserve biomass, and interpret R as a
148 state variable and φ as a derived quantity. The relationship between the two is

$$\frac{dR}{dt} = (1 - f_s)GS - E \quad (14)$$

$$\varphi(t) = R(t) + \int_{t_0}^t E(t') dt' \quad (15)$$

149 Thus φ tracks the reserves that an animal would have remaining if it had not previously started egg
 150 production. This is a useful metric for optimising reproductive timing, as we will show (Section 2.3).

151 2.2.5 Predation mortality

152 Predation mortality is assumed to have the same dependence on temperature and body size as ingestion,
 153 metabolism, and net gain (Hirst and Kiørboe, 2002). Survivorship N is set to 1 initially and decreases
 154 according to

$$\frac{d(\ln N)}{dt} = -m \quad (16)$$

155 where

$$m = a q_g S^{\theta-1} m_0 \quad (17)$$

156 so that predation pressure relative to energy gain is encapsulated in a single parameter m_0 . In practice m_0
 157 is a tuning parameter but we can solve for the value that would lead to an approximate equilibrium between
 158 growth and mortality. Solving for

$$\frac{1}{NS} \frac{d(NS)}{dt} = 0 \quad (18)$$

159 after some algebra yields $m = f_s G$, and with $a = 1$ this becomes

$$\frac{m_0}{I_0} = \epsilon f_s \quad (19)$$

160 Averaging f_s over the maturation period $0 \leq D \leq 1$ with $D_s = 0.35$ and assuming $\epsilon \approx 0.3$ gives
 161 $m_0/I_0 = 0.2$. This is the default level of predation in the model except where otherwise specified.

162 2.2.6 Activity level and diapause

163 Modulation of activity level a has been treated as simply as possible, using a “myopic” criterion that
 164 considers only the instantaneous energy budget, rather than an optimisation over the annual routine
 165 or lifetime (Sainmont et al., 2015). Furthermore, we treat a as a binary switch—diapause or full
 166 foraging activity—although intermediate overwintering states have been sometimes observed, e.g., *C.
 167 glacialis/marshallae* on the Eastern Bering Sea shelf in November (R. G. Campbell, pers. comm.), and
 168 a continuously varying a could be used to represent modulations in diel vertical migration or foraging
 169 strategy more generally. In the present model, we set $a = 0$ if $D > D_{dia}$ (the stage at which diapause first
 170 becomes possible) and prey saturation σ is below a threshold σ_{crit} , and set $a = 1$ otherwise. The prey
 171 saturation threshold is determined by maximising the rate of total population energy gain as a function of
 172 a . When d/d_a of this quantity is positive, active foraging $a = 1$ is the optimal instantaneous strategy and
 173 when it is negative, $a = 0$ is optimal. I.e., the threshold

$$\frac{d}{da} \frac{d}{dt} (\varphi + S) N = 0 \quad (20)$$

174 can be rearranged to give

$$\sigma_{crit} = \frac{r_m(1 - r_b)}{r_a} + \frac{C_{dia}}{r_a} \frac{m_0}{I_0} \quad (21)$$

175 where $C_{dia} = 1 + \varphi/S$. The first term in (21) can be derived more simply by setting $dG/da = 0$, a criterion
 176 based on ingestion and metabolism alone. The second term adjusts this criterion by discouraging foraging
 177 at marginal prey concentrations when predation is high. This second term, however, tends to produce

178 unrealistic, rapid oscillations in which the copepods briefly “top up” on prey and then hide in a brief
 179 “diapause” to burn them: this is the limitation of a myopic criterion in which diapause is not explicitly
 180 required to be seasonal, and of combining actual lipid reserves and potential egg production into a single
 181 state variable. Pragmatically, the issue can be eliminated by replacing C_{dia} with $1 + R/S$; or, to preserve
 182 the self-sufficiency of the φ model, by approximating C_{dia} as

$$C_{dia} = \max \left[0, 1 + \min \left(r_{\varphi}^{max}, \frac{\varphi}{S} \right) \right] \quad (22)$$

183 where $r_{\varphi}^{max} = 1.5$.

184 2.3 Population-level response

185 The viability of a trait combination in a given environment can be expressed in terms of the egg fitness F ,
 186 future egg production per egg (Varpe et al., 2007). F depends on spawning timing t_0 , which we assume
 187 a copepod population is completely free to optimise: we do not impose any constraints representing
 188 environmental cues or additional physiological requirements. The approach to optimising t_0 and solving
 189 for F differs between the φ and ER versions of the model, which we will discuss separately. However, both
 190 methods require an estimate of individual egg biomass W_e in order to convert $\varphi(t)$ or $E(t)$ from carbon
 191 units into a number of eggs, and so a digression on the determination of W_e is required.

192 2.3.1 Egg and adult size

193 The problem of estimating W_e can be replaced by the problem of estimating adult size W_a using the
 194 empirical relationship for broadcast spawners determined by Kiørboe and Sabatini (1995):

$$\ln W_e \approx \ln r_{ea} + \theta_{ea} \ln W_a \quad (23)$$

195 where $r_{ea} = 0.013$, $\theta_{ea} = 0.62$. (In the ER model, $W_a \equiv S + R$ at $D = 1$, but in the φ model we
 196 approximate it as S alone for simplicity.) Adult size itself is an important trait for the model to predict, but
 197 the controls on it are rather buried in the model formulation above. Banas and Campbell (2016) describe a
 198 theory relating body size to the ratio of development rate to growth rate based on a review of laboratory
 199 data for copepods with adult body sizes 0.3–2000 μgC . In our notation, their model can be derived as
 200 follows: if we approximate (10), (11) in terms of a single biomass variable as

$$\frac{dW}{dt} = \epsilon' q_g I_0 W^{\theta}, \quad D \geq D_f \quad (24)$$

201 then integrating from spawning to maturation gives

$$\frac{1}{1-\theta} W^{1-\theta} \Big|_{D=0}^{D=1} = (1 - D_f) \epsilon' q_g I_0 \frac{1}{u} \quad (25)$$

202 since u is the reciprocal of the total development time. Growth rate has been written in terms of I_0 and an
 203 effective growth efficiency over the development period ϵ' . If we assume that egg biomass $W_e = W|_{D=0}$ is
 204 much smaller than $W_a = W|_{D=1}$, then combining (25) with (2) gives

$$W_a \approx \left[(1 - \theta) (1 - D_f) \epsilon' \left(\frac{Q_g}{Q_d} \right)^{T/10^\circ\text{C}} \frac{I_0}{u_0} \right]^{\frac{1}{1-\theta}} \quad (26)$$

Table 1. Parameter values and other symbols used in the manuscript.

Symbol	Definition	Value	Units	Source
a	Activity level			
a^*	Variation of metabolism with a			
C_{dia}	Coefficient arising in the diapause criterion			
D	Relative developmental stage			
D_{dia}	Stage at which diapause becomes possible	0.49		stage C3
D_f	Stage of first feeding	0.1		stage N3; Campbell et al. (2001)
D_s	Stage at which lipid storage begins	0.35		stage C1
E	Total egg production		$\mu\text{gC d}^{-1}$	
E_{cap}	Capital egg production		$\mu\text{gC d}^{-1}$	
E_{inc}	Income egg production		$\mu\text{gC d}^{-1}$	
E_{max}	Maximum egg production rate		$\mu\text{gC d}^{-1}$	
F	Egg fitness			
$F_{1/2}, F_1, F_2$	Maximum egg fitness at 1/2, 1, 2 generations per year			
f_s	Fraction of G allocated to S			
G	Net gain (ingestion minus metabolism)		d^{-1}	
I	Specific ingestion		d^{-1}	
I_0	Specific ingestion at $\sigma = 1, T = 0^\circ\text{C}, S = 1 \mu\text{gC}$	0.4	d^{-1}	Banas and Campbell (2016)
K_s	Half-saturation for ingestion	See Table 2	mg chl m^{-3}	Møller et al. (????), Campbell et al. (2016)
M	Specific metabolism		d^{-1}	
m	Specific predation mortality		d^{-1}	
m_0	Specific predation mortality at $T = 0^\circ\text{C}, S = 1 \mu\text{gC}$	See Table 2	d^{-1}	
N	Survivorship			
P	Prey concentration		mg chl m^{-3}	
Q_d	Q_{10} for development	3.0		Forster et al. (2011)
Q_g	Q_{10} for growth	2.5		Forster et al. (2011)
q_d	Temperature dependence of development			
q_g	Temperature dependence of growth			
R	Individual reserve biomass		μgC	
r_a	Fraction of ingestion assimilated	0.67		
r_b	Diapause metabolism relative to active metabolism	0.25		Maps et al. (2014)
r_{ea}	Scaling constant for egg:adult size ratio	0.013		Kiørboe and Sabatini (1995)
r_m	Metabolism relative to prey-saturated ingestion	0.14		
r_{starv}	Fraction of S consumable under starvation conditions			
r_φ^{max}	Upper limit on φ/S used in diapause criterion	1.5		<i>C. hyperboreus</i> lipid fraction: Swalethorpe et al. (2011)
S	Individual structural biomass		μgC	
T	Temperature experienced by the organism		$^\circ\text{C}$	
T_0	Surface temperature		$^\circ\text{C}$	
T_d	Deep temperature		$^\circ\text{C}$	
t	Simulation time		d	
t_{egg}	Earliest possible date of egg production	See Table 2	d	
t_0	Yearday of spawning		d	
u	Ontogenetic development rate		d^{-1}	
u_0	Development rate corrected to 0°C	See Table 2	d^{-1}	
W_a	Adult body size		μgC	
W_e	Egg biomass		μgC	
δt	Effective duration of prey availability (global testbed)			
$\delta t'$	Width of P window (global testbed)			
ϵ	Gross growth efficiency			
ϵ'	Effective ϵ over the development period			
θ	Allometric exponent for vital rates	0.7		Saiz and Calbet (2007)
θ_{ea}	Allometric exponent for egg:adult size ratio	0.62		Kiørboe and Sabatini (1995)
λ	Population growth rate		yr^{-1}	
σ	Prey saturation			
σ_{crit}	Critical prey saturation for diapause criterion			
φ	Potential reserves and egg production		μgC	

205 Properly speaking, both ϵ' and T in (26) are functions of t_0 since they depend on the alignment of the
 206 development period with the annual cycle. Since we are trying to use (23) and (26) to optimise t_0 , we
 207 have a circular problem. Record et al. (2013) derive an expression similar to (26) and apply it iteratively
 208 because of this circularity. Some applications of Coltrane might require the same level of accuracy, but in
 209 the present study we take the expedient approach of simply assuming that T is the annual mean of T_0 and
 210 that $\epsilon' \approx 1/3$: i.e., that after t_0 is optimised, some diapause/spawning strategy will emerge that aligns the
 211 maturation period moderately well with a period of high prey availability. This assumption eliminates the
 212 need to run the model before estimating W_e via (23) and (26).

213 2.3.2 Optimal timing in the φ model

214 With a method for approximating W_e in hand, we can define egg fitness F as a function of φ . If a cohort
 215 spawned on t_0 were to convert all of its accumulated free scope φ —all net energy gain beyond that required
 216 to build an adult body structure—into eggs on a single day t_1 , the eggs produced per starting egg would be

$$F(t_0 \rightarrow t_1) = \frac{\varphi(t_1)}{W_e} N(t_1) \quad (27)$$

217 This expression condenses one copepod generation into a *mapping* F similar to the “circle map” of Gurney
 218 et al. (1992). Once the ODE model has been run for a family of t_0 cases, this mapping can be used to
 219 quickly identify optimal life cycles of any length. The optimal one-generation-per-year strategy is the t_0
 220 that maximizes $F_1 = F(t_0 \rightarrow t_0 + 365)$. The optimal one-generation-per-two-years strategy has t_0 that
 221 maximizes $F_{1/2} = F(t_0 \rightarrow t_0 + 2 \cdot 365)$. The optimal two-generation-per-year strategy has spawning dates
 222 t_0, t_1 that maximize the product $F_2 = F(t_0 \rightarrow t_1) \cdot F(t_1 \rightarrow t_0 + 365)$; and so on. A viable strategy is a
 223 combination of spawning dates and model parameters that give $F \geq 1$.

224 2.3.3 Optimal timing in the ER model

225 In reality, of course, copepods are not free to physically store indefinite amounts of reserves within
 226 their bodies and then instantaneously convert them into eggs when the timing is optimal. If a scheme for
 227 calculating egg production over time $E(t)$ is added to the model (and note that this scheme has not yet
 228 been specified in our discussion), then the per-generation mapping represented by F takes a different form.
 229 First, we use the assumption that the environmental annual cycle repeats indefinitely to convert the time
 230 series of EN —egg production discounted by survivorship—from a function of days since spawning to a
 231 function of yearday. By combining time series of EN/W_e from a family of cases varying t_0 , we construct
 232 a *transition matrix* V that gives eggs spawned on each yearday in generation $k + 1$, given eggs per yearday
 233 in generation k :

$$n_{k+1} = V \cdot n_k \quad (28)$$

234 where n is a discrete time series spanning one year (in practice we discretize the year into 5 d segments
 235 rather than yeardays per se). The first eigenvector of V then gives a seasonal pattern of egg production
 236 that is stable in shape, with the corresponding eigenvalue λ giving one plus the population growth rate per
 237 generation: $n_{k+1}(t) = V \cdot n_k(t) = \lambda \cdot n_k(t)$. A strict criterion for strategy viability would then be $\lambda \geq 1$,
 238 although this criterion is unhelpfully sensitive to predation mortality. A more robust criterion (which we
 239 use in Section 3.4 below) is to consider a strategy viable if it yields lifetime egg production above the
 240 replacement rate: if $E(t_0; t)$ and $N(t_0; t)$ are the time series of egg production and survivorship for a cohort

241 spawned on t_0 , and $n(t_0)$ is a normalized annual cycle of egg production,

$$\int_0^{365} \int_0^{\infty} n(t_0) \frac{E(t_0; t) N(t_0; t)}{W_e} dt dt_0 \geq 1 \quad (29)$$

242 Thus in the ER version of the model, as in the φ version, we have an efficient method that describes the
 243 long-term viability of a trait combination under a stable annual cycle, along with the optimal spawning
 244 timing associated with those traits in that environment; and these methods only require us to explicitly
 245 simulate one generation.

246 2.4 Assembling communities

247 Community-level predictions in Coltrane take the form of bounds on combinations of traits that lead to
 248 viable populations in a given environment. There are many copepod traits represented in the model that one
 249 might consider to be axes of diversity or degrees of freedom in life strategy: u_0 , I_0 , θ , D_s , K_s , W_e/W_a ,
 250 and even m_0 to the extent that predation pressure is a function of behaviour (Visser et al., 2008). Record
 251 et al. (2013) allowed five traits to vary among competitors in their copepod community model. We have
 252 taken a minimalist approach, where in the φ model we allow only one degree of freedom: variation in u_0
 253 from 0.005–0.01 d⁻¹. Banas and Campbell (2016) showed from a review of lab studies that u_0 variations
 254 appear to be the primary mode of variation in adult size among large calanoids ($W_a > 50 \mu\text{gC}$) including
 255 *Calanus* and *Neocalanus* spp., with slower development leading to larger adult sizes. That study also
 256 suggests that variation in I_0 is responsible for copepod size diversity on a broader size or taxonomic scale
 257 (e.g. between *Calanus* and small cyclopoids like *Oithona*). However, variation in I_0 (energy gain from
 258 foraging) probably only makes sense as part of a tradeoff with predation risk or egg survivorship (Kiørboe
 259 and Sabatini, 1995) and we have left the formulation of that tradeoff for future work. We therefore expect
 260 Coltrane 1.0 to generate analogs for large and small *Calanus* spp. ($\sim 100\text{--}1000 \mu\text{gC}$ adult size) but not
 261 analogs for *Oithona* spp. or even small calanoids like *Pseudocalanus* or *Acartia*.

262 Choices regarding reproductive strategy require another degree of freedom. In the φ model, this does
 263 not require additional parameters, because the difference between, e.g., capital spawning in winter and
 264 income spawning in spring is simply a matter of the time t at which F is evaluated in postprocessing: each
 265 model run effectively includes all timing possibilities (eq. (27)). In the ER model, however, diversity in
 266 reproductive timing must be made explicit. In the one experiment below that uses the ER model (Section
 267 3.4), we use the following scheme for egg production. $E(t)$ is the sum of income egg production E_{inc}
 268 and capital egg production E_{cap} , which are 0 until maturity is reached ($D = 1$) and an additional timing
 269 threshold has been passed ($t > t_{egg}$). Past those thresholds, they are calculated as $E_{inc} = G$ if $G > 0$
 270 and $E_{cap} = E_{max} - E_{inc}$ if $R > 0$, where E_{max} is a maximum egg production rate which we assume
 271 to be equal to the food-saturated ingestion rate $r_a q_g I_0 S^\theta$. Thus the trait t_{egg} determines whether egg
 272 production begins immediately upon maturation or after some additional delay. Instead of t_{egg} , expressed
 273 in terms of calendar day, one could introduce the same timing freedom through a trait linked to light, an
 274 ontogenetic clock that continues past $D = 1$, or a more subtle physiological scheme. However, since we
 275 run a complete spectrum of trait values in each environmental case, it is not important to the results how the
 276 delay is formulated, provided we only compare model output, rather than actual trait values, across cases.

277 2.5 Model experiments

278 This study comprises three complementary experiments (Table 2). The first of these is an idealized
 279 global testbed which addresses broad *biogeographic* patterns. The second is a testbed representing the

Table 2. Setup of model experiments. All other parameters are as in Table 1.

Experiment	Environmental forcing	Variable traits	K_s	m_0	Model
Global	Surface, deep temperatures constant; Gaussian window of prey availability	$u_0 = 0.005 - 0.01 \text{ d}^{-1}$	1 mg chl m^{-3}	0.08 d^{-1}	φ
Bering	Family of seasonal cycles on the middle shelf: see Appendix	$u_0 = 0.007 \text{ d}^{-1}$	3	0.08	φ
Disko	One seasonal cycle (1996–97): see Appendix	$u_0 = 0.005 - 0.01 \text{ d}^{-1}$, $t_{egg} = 0 - 1095$	1	0.06	ER

280 Eastern Bering Sea shelf, which addresses *time-variability* in one population in one environment. The last
 281 is a testbed representing Disko Bay, West Greenland, which addresses *trait relationships along the size*
 282 *spectrum* in detail. The first two are evaluated entirely in terms of the φ model, while in the Disko Bay
 283 case we use the ER model to allow more specific comparisons with observations.

284 The global testbed consists of a family of idealized environments in which surface temperature T_0 is held
 285 constant, and prey availability is a Gaussian window of width $\delta t'$ centered on yearday 365/2:

$$P(t) = (10 \text{ mg chl m}^{-3}) \exp \left[- \left(\frac{t - \frac{365}{2}}{\delta t'} \right)^2 \right] \quad (30)$$

286 We assume that deep, overwintering temperature $T_d = 0.4 T_0$. The ratio 0.4 matches results of a regression
 287 between mean temperature at 0 and 1000 m in the Atlantic between 20–90°N, or 0 and 500 m in the Pacific
 288 over the same latitudes (World Ocean Atlas 2013: <http://www.nodc.noaa.gov/OC5/woa13/>). We compare
 289 environmental cases in terms of T_0 and an effective season length $\delta t = \int \sigma dt$, which rescales the $\delta t'$ cases
 290 in terms of the equivalent number of days of saturating prey per year.

291 The Bering Sea testbed considers interannual variation in temperature, ice cover, and the effect of ice
 292 cover on in-ice and pelagic phytoplankton production (Stabeno et al., 2012b; Sigler et al., 2014; Banas
 293 et al., 2016). Variation between warm, low-ice years and cold, high-ice years has previously been linked to
 294 the relative abundance of large zooplankton including *Calanus glacialis/marshallae* (Eisner et al., 2014),
 295 and we test Coltrane predictions against 8 years of *C. glacialis/marshallae* observations from the BASIS
 296 program. Seasonal cycles of T_0 , T_d , and P are parameterized using empirical relationships between ice
 297 and phytoplankton from Sigler et al. (2014) and a 42-year physical hindcast using BESTMAS (Bering
 298 Ecosystem Study Ice-ocean Modeling and Assimilation System: Zhang et al. (2010); Banas et al. (2016)).
 299 Details are given in the Appendix.

300 The Disko Bay testbed represents one seasonal cycle of temperature and phytoplankton and
 301 microzooplankton prey, based on the 1996–97 time series described by Madsen et al. (2001). We use
 302 this particular dataset not primarily as a guide to the current or future state of Disko Bay but rather as a
 303 specific circumstance in which the life-history patterns of three coexisting *Calanus* spp. (*C. finmarchicus*,
 304 *C. glacialis*, *C. hyperboreus*) were documented (Madsen et al., 2001). Details are given in Section 3.4 and
 305 the Appendix.

3 RESULTS

306 3.1 An example population

307 One case from the global experiment with $u_0 = 0.007 \text{ d}^{-1}$, $T_0 = 1^\circ\text{C}$, and $\delta t = 135$ is shown in detail in
308 Fig. 2 to illustrate the analysis method described in Section 2.3.2. In this case, out of cohorts spawned over
309 the full first year, only those spawned in spring reached adulthood without starving (Fig. 2b, blue-green
310 lines; non-viable cohorts not shown). The fitness function F (eq. 27) declines during winter diapause and
311 rises during the following summer when prey are available. There is no equivalent peak during the third
312 summer, indicating that by this time cumulative predation mortality is so high that there is no net advantage
313 to continuing to forage before spawning.

314 The maximum value of F for most cohorts (\star , Fig 2c) comes at ~ 1.5 yr into the simulation, at the peak
315 in prey availability following maturation. This point in the annual cycle, however, does not fall within the
316 window of spawning dates at which maturation is possible (compare year 2 in Fig. 2c with year 1 in Fig.
317 2b), and thus is an example of “internal life history mismatch” (Varpe et al., 2007), the common situation
318 in which the spawning timing that maximizes egg production by the parent is not optimal for the offspring.
319 The long-term egg fitness corresponding to stable 1-year and 2-year cycles is marked for each cohort (Fig.
320 2c, red, orange circles). Some but not all of the cohorts that reach maturity are able to achieve $F > 1$,
321 egg production above the replacement rate, in these cyclical solutions (solid circles). The best one-year
322 and two-year strategies achieve similar maximum fitness values (red vs. orange solid dots), although they
323 require slightly different seasonal timing.

324 3.2 Global behaviour

325 In the global experiment, populations like that shown in Fig. 2 were run for a spectrum of u_0 values,
326 across combinations of T_0 and δt from $-2\text{--}16^\circ\text{C}$ and $0\text{--}310$ d (the latter corresponding to $\delta t'$ from $0\text{--}150$
327 d). Across these cases, at a given u_0 , the model predicts a log-linear relationship between adult size and
328 temperature, which is not much perturbed by variation in prey availability (Fig. 3). The slope of this
329 relationship is equivalent to a Q_{10} of 1.8–2.0, significantly steeper than the size dependence explicitly
330 imposed by the growth/development parameterization ($Q_d/Q_g = 1.2$; eq. 26). This suggests that not only
331 physiological mechanisms (Forster and Hirst, 2012) but additional, emergent, ecological mechanisms are
332 contributing. Provocatively, a similar contrast exists between laboratory measurements of temperature
333 dependence in *C. finmarchicus* ($Q_d/Q_g = 1.3$, Campbell et al. (2001)) and field observations of size in
334 relation to temperature in *C. finmarchicus* and *C. helgolandicus* across the North Atlantic ($Q_{10} = 1.65$,
335 Wilson et al. (2015), with prosome length converted to carbon weight based on Runge et al. (2006)).

336 The intercept of the size-temperature relationship depends on u_0 (Fig. 3), with $u_0 = 0.005\text{--}0.01 \text{ d}^{-1}$
337 corresponding to the range of adult size from *C. finmarchicus* to *C. hyperboreus* at the cold end of the
338 temperature spectrum (Disko Bay, $\sim 0^\circ\text{C}$: Swalethorp et al. (2011)). It is not always fair, however, to
339 associate a particular u_0 value with a particular species over the full range of temperatures included. As
340 Banas and Campbell (2016) discuss further, the temperature response of an individual species is often
341 dome-shaped, a window of habitat tolerance (Møller et al., 2012; Alcaraz et al., 2014), whereas Coltrane
342 1.0 uses the monotonic, power-law response observable at the community level (Forster et al., 2011)). *C.*
343 *finmarchicus*, for example, is fit well by $u_0 = 0.007 \text{ d}^{-1}$ at higher temperatures ($4\text{--}12^\circ\text{C}$), whereas near
344 0°C in Disko Bay, it has been observed to be considerably smaller than extrapolation along the $u_0 = 0.007$
345 d^{-1} power law would predict. Past studies have also found *C. finmarchicus* growth and ingestion to be

346 suppressed at low temperatures, i.e., to show a very high Q_{10} compared with the community-level value
 347 (Campbell et al., 2001; Møller et al., 2012).

348 With this caveat on the interpretation of u_0 , we can observe a sensible gradation in life strategy along the
 349 u_0 axis (Fig. 4). From $u_0 = 0.01 \text{ d}^{-1}$ (*C. finmarchicus*-like at 0°C) to $u_0 = 0.005 \text{ d}^{-1}$ (*C. hyperboreus*-like),
 350 the environmental window in which multi-year life cycles are viable ($F_{1/2} \geq 1$) expands dramatically.
 351 This window overlaps significantly with the window of viability for one-year life cycles ($F_1 \geq 1$; Fig. 4,
 352 black vs. gray contours). In all u_0 cases, there is a non-monotonic pattern in maximum fitness as a function
 353 of either temperature or prey (Fig. 4, color contours), as environments align and misalign with integer
 354 numbers of generations per year or years per generation.

355 The number of generations per year in the timing strategy that optimizes F for each $(T_0, \delta t)$ habitat
 356 combination is shown in Fig. 5 for $u_0 = 0.007 \text{ d}^{-1}$. This u_0 value corresponds in adult size to Arctic *C.*
 357 *glacialis* and temperate *C. marshallae* populations in the Pacific (Fig. 3), species which coexist and are
 358 nearly indistinguishable in the Bering Sea. In the lowest-prey conditions, no timing strategy is found to
 359 be viable. As prey and temperature increase, the model predicts bands proceeding monotonically from
 360 multiple years per generation to multiple generations per year. Validating these model predictions requires
 361 parameterizing places (in terms of T_0 and δt) in addition to parameterizing their inhabitants, and thus the
 362 meaning of either success or failure is ambiguous. Still, we can observe the following. Ice Station Sheba in
 363 the high Pacific Arctic (Fig. 1) falls in the non-viable regime (Fig. 5), consistent with the conclusion of
 364 Ashjian et al. (2003) that *Calanus* spp. are unable to complete their life cycle there. Disko Bay falls on
 365 the boundary of one- and two-year generation lengths, consistent with observations of *C. glacialis* there
 366 (Madsen et al., 2001). At Newport, Oregon, near the southern end of the range of *C. marshallae*, the model
 367 predicts multiple generations per year, consistent with observations by Peterson (1979).

368 3.3 A high-latitude habitat limit in detail: The Eastern Bering Sea

369 These idealized experiments (Figs. 4,5) suggest that very short productive seasons place a hard limit
 370 on the viability of *Calanus* spp., regardless of size, temperature, generation length, or match/mismatch
 371 considerations (although these factors affect where exactly the limit falls). A decade of observations in the
 372 Eastern Bering Sea provide a unique opportunity to resolve this viability limit with greater precision. This
 373 analysis takes advantage of the natural variability on the Southeastern Bering Sea shelf described by the
 374 “oscillating control hypothesis” of Hunt et al. (2002, 2011): in warm, low-ice years, the spring bloom in
 375 this region is late (\sim yearday 150: Sigler et al. (2014)) and the abundance of large crustacean zooplankton
 376 including *C. glacialis/marshallae* is very low, while in colder years with greater ice cover, the pelagic
 377 spring bloom is earlier, ice algae are present in late winter, and large crustacean zooplankton are much
 378 more abundant. The task of replicating these observations serves to test the Coltrane parameterization, and
 379 situating them within a complete spectrum of temperature/ice cover cases also allows the model to provide
 380 some insight into mechanisms.

381 Mean surface temperature \bar{T}_0 was used to index annual cycles of surface and bottom temperature on the
 382 Eastern Bering Sea middle shelf (Appendix; insets in Fig. 6). Date of ice retreat t_{ice} was likewise used
 383 to index phytoplankton availability over each calendar year (Appendix; insets in Fig. 6). Coltrane was
 384 run for each (\bar{T}_0, t_{ice}) combination with $u_0 = 0.007 \text{ d}^{-1}$, thus consistent with Fig. 5 except for the more
 385 refined treatment of environmental forcing, and an adjustment to K_s to match results of Bering Sea feeding
 386 experiments (Campbell et al., 2016)). The maximum egg fitness F for a one-generation-per-year strategy is
 387 shown as a function of \bar{T}_0 and t_{ice} in the main panel of Fig. 6. Coltrane predicts that one generation per
 388 year is the optimal life cycle length everywhere in this parameter space except for the cold/ice-free and

389 warm/high-ice-cover extremes (white contours), combinations which do not occur anywhere in a hindcast
390 of middle-shelf conditions back to 1971 (Fig. 6, red and blue dots).

391 Late summer measurements of *C. glacialis/marshallae* abundance (individuals m⁻²), averaged over the
392 middle/outer shelf south of 60°N, are shown in Fig. 6 for 2003–2010 ($n=364$ over the 8 years; Eisner
393 et al. (2014)). Both these observations and the predicted maximum F from Coltrane show a dramatic
394 contrast between the warm years of 2003–05 ($t_{ice} = 0$) and the cold years of 2007–10 ($t_{ice}=100–130$),
395 with the transitional year 2006 harder to interpret. Eisner et al. (2014) found that there was less contrast
396 between cold year/warm year abundance patterns on the northern middle/outer shelf, consistent with the
397 model prediction that all hindcast years on the northern shelf fall within the “viable” habitat range for *C.*
398 *glacialis/marshallae* (Fig. 6, blue dots).

399 The viability threshold that the Southeastern Bering Sea appears to straddle is qualitatively similar
400 to that in the more idealized global experiment (Figs. 5,4), primarily aligned with the phenological
401 index (horizontal axis) rather than the temperature index (vertical axis). The threshold in the Bering
402 Sea experiment falls somewhat beyond the dividing line imposed in the experiment setup between early,
403 ice-retreat-associated blooms and late, open-water blooms ($t_{ice} = 75$: see Appendix, Sigler et al. (2014)).
404 This gap (whose width depends on the mortality level m_0 : not shown) indicates that some period of ice
405 algae availability is required by *C. glacialis/marshallae* in this system, in addition to a favorable pelagic
406 bloom timing.

407 3.4 Coexisting life strategies in detail: Disko Bay

408 The experiments above test the ability of Coltrane 1.0 to reproduce first-order patterns in latitude and time
409 but do not provide sensitive tests of the model biology. A model case study in Disko Bay, where populations
410 of three *Calanus* spp. coexist and have been described in detail (Madsen et al., 2001; Swalethorp et al.,
411 2011), allows a closer examination of the relationships among traits within the family of viable life
412 strategies predicted by Coltrane.

413 The model forcing (Fig. 7 describes a single annual cycle, starting with the 1996 spring bloom. This
414 represents a cold, high-ice state of the system, compared with more recent years in which the spring bloom
415 is earlier (e.g. 2008, Fig. 7, Swalethorp et al. (2011)) and the deep layer is warmed by Atlantic water
416 intrusions (Hansen et al., 2012). This particular year was chosen because measurements of prey availability
417 and *Calanus* response by Madsen et al. (2001) were particularly complete and coordinated. A simple
418 attempt to correct the prey field for quality and *Calanus* preference was made by keeping only the >11 µm
419 size fraction of phytoplankton and adding total microzooplankton, in µg C. The measured phytoplankton
420 C:chl ratio was used to convert the sum to an equivalent chlorophyll concentration, and this time series was
421 then slightly idealized for clarity (Fig. 7, Appendix).

422 Sensible results were only possible after tuning the predation mortality scale coefficient m_0 . It is likely
423 that our simple mortality scheme introduces some form of bias, compared with the reality in this system of
424 predation by successive waves of visual and non-visual predators, which will be considered in a separate
425 study. Still, a sensitivity experiment using the φ model shows that varying m_0 has, as intended, a simple,
426 uniform effect on fitness/population growth (Fig. 8) that leaves other trait relationships along the size
427 spectrum unaffected. The φ model predicts that copepods similar to *C. finmarchicus* in size have much
428 greater fitness at a generation length of one year than at two years or more; that *C. hyperboreus* would be
429 unable to complete its life cycle in one year, but is well-suited to a two-year cycle; and that *C. glacialis*
430 falls in the size range where one- and two-year life cycles have comparable fitness value. These results are

431 consistent with observations (Madsen et al., 2001) and more general surveys of life strategies in the three
432 species (Falk-Petersen et al., 2009; Daase et al., 2013).

433 For greater specificity, we switched from the φ to the ER model version, running a spectrum of t_{egg} cases
434 (see section 2.4) along with a spectrum of u_0 cases. The ER model imposes additional constraints on the
435 model organisms—e.g., they are no longer allowed an infinite egg production rate—and to compensate we
436 reduced m_0 from 0.08 d^{-1} to 0.06 d^{-1} . The relationship between generation length and adult size across all
437 (u_0 , t_{egg}) combinations is shown in Fig. 9. Results are consistent with the φ model (Fig. 8): only a one-year
438 life cycle is viable for *C. finmarchicus* in this environment, only a two-year or longer cycle is viable for *C.*
439 *hyperboreus*, and *C. glacialis* again lies near the boundary where the two strategies are comparable.

440 The ER model predicts a time series of egg production associated with each trait combination, not just
441 an optimal date (Section 2.3.3), and compositing these over all viable cases within 30% of the average
442 measured adult size for each species allows us to compare modelled egg production patterns directly with
443 observations. The model predicts that *C. finmarchicus* analogs spawn in close association with the spring
444 bloom, that *C. hyperboreus* spawns well before the spring bloom, and that *C. glacialis* is intermediate
445 (Fig. 10, Fig. 11a). These patterns are all in accordance with Disko Bay observations (Madsen et al., 2001;
446 Swalethorp et al., 2011), although the absolute range is muted: Madsen et al. (2001) report *C. hyperboreus*
447 spawning as early as February. As one would expect from these timing patterns, the model predicts a
448 significant trend between size and the capital fraction of total egg production $E_{cap}/(E_{inc} + E_{cap})$ (Fig. 11c).
449 Again, the pattern is qualitatively correct but muted: Coltrane predicts 80% income breeding at the size of
450 *C. finmarchicus* (a pure income breeder in reality) and 80% capital breeding at the size of *C. hyperboreus* (a
451 pure capital breeder in reality). More notable than the error is how much of the income/capital spectrum can
452 apparently be reproduced as a consequence of optimal timing alone, without imposing the physiological
453 difference between the two strategies as an independent trait (Ejmond et al., 2015).

454 The model predicts (Fig. 11b) that the largest model organisms, with the longest generation lengths, enter
455 their first diapause near the boundary between copepodite stages C4 and C5 ($D \approx 0.75$), whereas smaller
456 organisms enter first diapause well into stage C5. Madsen et al. (2001) found that both *C. glacialis* and
457 *C. hyperboreus* diapause as C4, C5, and adults in Disko Bay, suggesting that the model is biased toward
458 fast maturation. The discrepancy could also be related to intraspecific variation in the real populations
459 or non-equiproportional development in the late stages, i.e., a variable conversion scale between actual
460 developmental stage and D .

461 Finally, the ER version of Coltrane allows an estimate of the fraction of individual carbon in the form of
462 storage lipids $R/(R + S)$ (Fig. 11d). Averaging each model population from $D = D_{dia}$ through adulthood,
463 weighted by survivorship N , yields an overall range that compares well with the species-mean wax ester
464 fractions measured by Swalethorp et al. (2011): $\sim 30\%$ for *C. finmarchicus* to $\sim 60\%$ for *C. hyperboreus*.
465 In the middle of the size spectrum, reserve fraction is highly variable across viable two-year strategies, a
466 warning that the success of this final model prediction may be partly fortuitous. Still, taken as a whole,
467 this experiment has yielded a striking result: that a small set of energetic and timing contraints is able to
468 correctly predict, a priori, that Disko Bay should be able to support a spectrum of calanoid copepods from
469 income breeders with an adult size $\sim 100 \mu\text{g C}$, a one-year life cycle, and a wax ester fraction $\sim 30\%$ to
470 capital breeders with an adult size $\sim 1000 \mu\text{g C}$, a two-or-more-year life cycle, and a wax ester fraction
471 $\sim 60\%$.

4 DISCUSSION

472 4.1 Uncertainties

473 The biology in Coltrane could be refined in many ways, but two issues stand out as being both
474 mechanistically uncertain and sensitive controls on model behaviour. These correspond to the two
475 parameters that it was necessary to tune among model experiments (Table 2): the obstacles to formulation
476 of a single, fully portable scheme.

477 The first of these is the perennial problem of the mortality closure. We modelled predation mortality as
478 size-dependent according to the same power law used for ingestion and metabolism, a choice which is
479 mathematically convenient and makes the effect of top-down controls, if not minor, then at least simple
480 and easy to detect (Fig. 8). This size scaling is consistent with the review by Hirst and Kiørboe (2002) but
481 that study also shows that the variation in copepod mortality not explained by allometry spans orders of
482 magnitude (cf. Ohman et al. (2004)). Indeed, in some cases one might posit exactly the opposite pattern, in
483 which mortality due to visual predators like larval fish increases with prey body size (Fiksen et al., 1998;
484 Varpe et al., 2015). This latter pattern is one hypothesis for why in reality *C. hyperboreus* is confined to
485 high latitudes, whereas the model predicts no southern (warm, high-prey) habitat limit to *C. hyperboreus*
486 analogs based on bottom-up considerations (Fig. 4). Merging Coltrane 1.0 with a light- and size-based
487 predation scheme similar to Varpe et al. (2015) or Ohman and Romagnan (2015) would allow one to better
488 test the balance of bottom-up and top-down controls on calanoid biogeography.

489 Second, our experience constructing the Bering Sea and Disko Bay cases suggests that the greatest
490 uncertainty in the model bioenergetics is actually not the physiology itself—empirical reviews like Saiz
491 and Calbet (2007), Maps et al. (2014), Kiørboe and Hirst (2014), and Banas and Campbell (2016) have
492 constrained the key rates moderately well—but rather the problem of translating a prey field into a rate
493 of ingestion. Within each of our model testbeds, the prey time series P remains subject to uncertainty in
494 relative grazing rates on ice algae, large and small pelagic phytoplankton, and microzooplankton, despite a
495 wealth of local observations and a history of work on this problem in *Calanus* specifically (Olson et al.,
496 2006; Campbell et al., 2016). The precision of each testbed, and even moreso the ambition of generalizing
497 across them, is also limited by uncertainty in the half-saturation coefficient, which does not appear to be
498 consistent across site-specific studies (Campbell et al., 2016; Møller et al., ?????) or well-constrained by
499 general reviews (Hansen et al., 1997), and more generally by uncertainty in the functional form (Gentleman
500 et al., 2003). This ambiguity is perhaps not surprising when one considers that ingestion as a function of
501 chlorophyll or prey carbon is not a simple biomechanical property, but in fact a plastic behavioural choice.
502 Accordingly, it might well be responsive not only to mean or maximum prey concentration but also to
503 the prey distribution over the water column, the tradeoff between energy gain and predation risk (Visser
504 and Fiksen, 2013), prey composition and nutritional value, and the context of the annual routine. These
505 issues are fundamental to concretely modelling the effect of microplankton dynamics on mesozooplankton
506 grazers. Addressing them systematically in models will require novel integration between what could be
507 called oceanographic and marine-biological perspectives on large zooplankton.

508 4.2 Temperature and timing

509 Despite these uncertainties, one pattern in the copepod response to environment appears to hold in
510 Coltrane whether prey availability is treated simply (Fig. 5,4) or with site-specific detail (Fig. 6). Namely,
511 the viability of the calanoid community, at least near its high-latitude limit, is more sensitive to prey
512 abundance and phenology than to temperature. Alcaraz et al. (2014) suggested based on lab experiments

513 that *C. glacialis* reaches an bioenergetic limit near 6°C, and Holding et al. (2013) and others have
514 hypothesized that thermal limits will produce ecosystem-level tipping points in the warming Arctic. Our
515 results, in contrast, suggest that thermal tipping points, even if present at the population level, do not
516 generalize to the community level in copepods. Rather, the model predicts complete continuity between the
517 life strategy of Arctic *C. glacialis* and temperate congeners like *C. marshallae* (Fig. 5). It also suggests that
518 even on the population level in the Bering Sea, warm/cold-year variation in prey availability is a sufficient
519 explanation of variability in the abundance of *C. glacialis/marshallae* (Fig. 6), without the invocation of a
520 thermal threshhold.

521 Both the global and Bering experiments suggest, furthermore, that increasing water temperature per
522 se is not necessarily a stressor on copepod communities, even high-latitude communities. In both cases,
523 the low-prey viability threshhold actually relaxes (i.e. is tilted toward lower prey values) as temperature
524 increases, indicating that in these testbeds, the positive effect of temperature on growth and maturation
525 rate actually outweighs the effect of temperature on metabolic losses and overwinter survival. In cases
526 where deep, overwintering temperatures increase faster than surface temperatures (Hansen et al., 2012) this
527 balance may not hold, and in the real ocean changes in temperature are highly confounded with changes
528 in phytoplankton production and phenology. Still, it is notable that the model predicts that warming
529 temperatures will have a non-monotonic effect on copepod populations ($\partial F/\partial T_0 \geq 0$, Figs. 5,4) even
530 when metabolic thermal threshholds *sensu* Alcaraz et al. (2014) and changes in prey availability are
531 not considered. These results are a caution against overly simple climate-impacts projections based on
532 temperature alone.

5 CONCLUSION

533 Coltrane 1.0, introduced here, is a minimalist model of copepod life history and population dynamics,
534 a metacommunity-level framework on which additional species- or population-level constraints can
535 be layered. Many present and future patterns in large copepods might well prove to be sensitive to
536 species-specific constraints that Coltrane 1.0 does not resolve, such as thermal adaptation, physiological
537 requirements for egg production, or cues for diapause entry and exit. Nevertheless, the model experiments
538 above demonstrate that many patterns in latitude, time, and trait space can be replicated numerically even
539 when we only consider a few key constraints on the individual energy budget: the total energy available
540 in a given environment per year; the energy and time required to build an adult body; the metabolic and
541 predation penalties for taking too long to reproduce; and the size and temperature dependence of the vital
542 rates involved.

543 Results of the global and Bering experiments (Figs. 5,4,6) suggest that timing and seasonality are
544 crucial to large copepods, but not because of match/mismatch (Edwards and Richardson, 2004): the model
545 organisms are free to resolve timing mismatches with complete plasticity. Rather, these results highlight
546 the role of seasonality in the sense of total energy available for growth and development per year, or the
547 number of weeks per year of net energy gain relative to the number of weeks of net deficit. The simplicity
548 of this view means that the model scheme and results may generalize far beyond copepods with only minor
549 modification.

550 The exercise of parameterizing the Bering Sea and Disko Bay cases, and of attempting to map real
551 environments onto an idealized parameter space in the global experiment (Fig. 5), highlighted that the
552 real limit on our ability to predict the fate of copepods in changing oceans may not be our incomplete
553 knowledge of their biology, but rather our incomplete knowledge of how their environments appear from

their point of view. How do standard oceanographic measures of chlorophyll and particulate chemistry relate to prey quality, and how much risk a copepod should take on in order to forage in the euphotic zone? How do bathymetry, the light field, and other metrics relate to the predator regime? Further experiments in a simple, fast, mechanistically transparent model like Coltrane may suggest new priorities for field observations, in addition to new approaches to regional and global modelling.

APPENDIX: REGIONAL TESTBED FORMULATIONS

559 Eastern Bering Sea

560 This Appendix specifies the formulation of the Bering Sea and Disko Bay testbeds in detail.

561 Interannual variation in the Bering Sea was parameterized for a swath of the middle shelf bounded by two
 562 long-term mooring sites on the 70 m isobath: M2 (57°N), representing the southern shelf where seasonal
 563 ice cover is highly variable and some winters are ice-free, and M8 (62°N), representing the northern shelf
 564 where seasonal ice cover is more consistent (Stabeno et al., 2012a). An annual cycle at one station is
 565 parameterized in terms of the annual mean surface temperature $\overline{T_0}$ and yearday of spring/summer ice retreat
 566 t_{ice} .

567 Annual cycles of surface and bottom temperature $T_0(t)$, $T_d(t)$ were associated with $\overline{T_0}$ using results from
 568 a 1971–2012 three-dimensional, assimilative hindcast using the BESTMAS model (Zhang et al., 2010;
 569 Banas et al., 2016). This hindcast compares well with observations of ice area and thickness, in both the
 570 mean seasonal cycle and interannual anomalies (Zhang et al., 2010). It also shows excellent agreement
 571 with the areal mean and standard deviation of surface and bottom temperatures on the shelf (Zhang et al.,
 572 2012). Fitting idealized curves to daily BESTMAS output at M2, M8, and the intermediate mooring sites
 573 M4, M5 lets us concisely represent $T_0(t)$ in terms of $\overline{T_0}$ as two half-sinusoids:

$$T_0(t) = \max(-1.8^{\circ}\text{C}, -3.1^{\circ}\text{C} + 1.5 \overline{T_0} + \Delta T \cdot \cos\left(\frac{2\pi}{365}(t - t_{max})\right))$$

$$\Delta T = \begin{cases} -0.62 \overline{T_0} + 9.6^{\circ}\text{C} & , |t - t_{max}| < 365/4 \\ 0.76 \overline{T_0} + 0.2^{\circ}\text{C} & , |t - t_{max}| \geq 365/4 \end{cases}$$

where t_{max} = yearday 245. A parallel polynomial expression for $T_d(t)$ is

$$T_d(t) = \max[-1.8^{\circ}\text{C}, 1.75^{\circ}\text{C} \cdot (\hat{t} - \hat{t}^5)]$$

574 where $\hat{t} = 2t/365 - 1$.

575 Banas et al. (2016) present a plankton model run with forcing from the same BESTMAS hindcast at the
 576 same stations, but that model covers the spring bloom period only, and so we have not used it here. Instead,
 577 we define a semi-idealized cycle of phytoplankton production based on observed patterns in spring and fall
 578 bloom timing and magnitude from moored chlorophyll sensors (Sigler et al., 2014). $P(t)$ is assembled as
 579 the day-by-day maximum of a Gaussian spring bloom P_{spr} ; Gaussian autumn bloom P_{aut} ; constant, low
 580 summer value in between the two P_{sum} ; constant, even lower winter value P_{win} ; and period of ice-algal

581 availability in late winter/early spring P_{IA} . These are given by

$$\begin{aligned} P_{win} &= 0.1, & t_{aut} < t < t_{spr} \\ P_{IA} &= \hat{P}_{IA}, & t \geq 45 \text{ and } t < t_{ice} + 10 \\ P_{spr} &= \hat{P}_{spr} \exp\left(-[(t - t_{spr})/15]^2\right) \\ P_{sum} &= \frac{1}{10} \hat{P}_{spr}, & t_{spr} < t < t_{aut} \\ P_{aut} &= \left(\frac{1}{2} \hat{P}_{spr}\right) \exp\left(-[(t - t_{aut})/15]^2\right) \end{aligned}$$

582 $\hat{P}_{spr} = 16 \text{ mg chl m}^{-3}$ (Sigler et al., 2014). Prey saturation during the ice algal production period (mid
 583 February until ice retreat: R. Gradinger, pers. comm.) has been assumed to be very high, comparable to
 584 the peak of the spring bloom: $\hat{P}_{IA} = \hat{P}_{spr}$. This is a gloss over a number of competing considerations. In
 585 reality, in the Eastern Bering Sea, ice algae comprise a much smaller integrated standing stock than the
 586 pelagic bloom (Cooper et al., 2013) and they are likely available to *Calanus* only intermittently in time.
 587 However, they are extraordinarily concentrated when they are present; they dominate the gut contents of
 588 *Calanus* during late winter (Durbin and Casas, 2014); and feeding experiments (Campbell et al., 2016)
 589 show that *Calanus* ingest them at a rate that far exceeds the functional response to pelagic phytoplankton
 590 we have otherwise assumed.

The date of the autumn bloom maximum t_{aut} , which Sigler et al. (2014) show to be relatively invariant, is 265. The date of the spring bloom maximum t_{spr} has the nonlinear relationship with ice-retreat date t_{ice} described by the “oscillating control hypothesis” (Hunt et al., 2002):

$$t_{spr} = \begin{cases} 150 & , t_{ice} < 75 \\ t_{ice} + 10 & , t_{ice} \geq 75 \end{cases}$$

591 Ice-free years are represented by $t_{ice} = 0$.

592 Disko Bay

593 The Disko Bay testbed was constructed using observations of temperature, phytoplankton, and
 594 microzooplankton from 1996–97 as shown in Fig. 7 (Madsen et al., 2001). For ease of interpretation, we
 595 slightly idealized the forcing time series (instead of interpolating between raw observations) as follows.

596 Surface temperature is a piecewise linear function between -0.7°C on yearday 1, a late-winter minimum
 597 of -1.8°C on yearday 105, and a summer maximum of 3.7°C on yearday 250. Deep temperature is set to
 598 1°C year-round, which matches 1996 observations but omits the arrival of warmer Atlantic deep water in
 599 spring 1997 (Hansen et al., 2012).

600 Prey P is assumed to consist of large phytoplankton and microzooplankton. These were summed in
 601 carbon units and then converted to an equivalent chlorophyll concentration using the observed mean
 602 phytoplankton C:chl ratio. Similar to the Bering Sea testbed, it is assembled from the day-by-day maximum

603 of a Gaussian spring bloom, Gaussian autumn bloom, and constant summer and winter minima:

$$\begin{aligned} P_{win} &= 0.1, & t_{aut} < t < t_{spr} \\ P_{spr} &= \hat{P}_{spr} \exp\left(-[(t - t_{spr})/15]^2\right) \\ P_{sum} &= \frac{1}{20} \hat{P}_{spr}, & t_{spr} < t < t_{aut} \\ P_{aut} &= \left(\frac{1}{2} \hat{P}_{spr}\right) \exp\left(-[(t - t_{aut})/30]^2\right) \end{aligned}$$

604 $\hat{P}_{spr} = 13 \text{ mg chl m}^{-3}$, $\hat{P}_{spr} = 5 \text{ mg chl m}^{-3}$, $t_{spr} = \text{yearday } 150$, and $t_{aut} = \text{yearday } 225$. These timing
 605 parameters are not appropriate for more recent years with less ice cover (e.g., 2008, Fig. 7) but evaluating
 606 the effect of interannual variation on model copepods in Disko Bay, parallel to the Bering Sea experiment
 607 above, is left for future work.

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

608 The authors declare that the research was conducted in the absence of any commercial or financial
 609 relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

610 NSB designed the model, performed the analysis, and led the writing of the manuscript. EFM and TGN
 611 helped formulate and interpret the Disko Bay case study, and LBE the Bering Sea case study. All authors
 612 contributed to revision of the manuscript.

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FIGURES

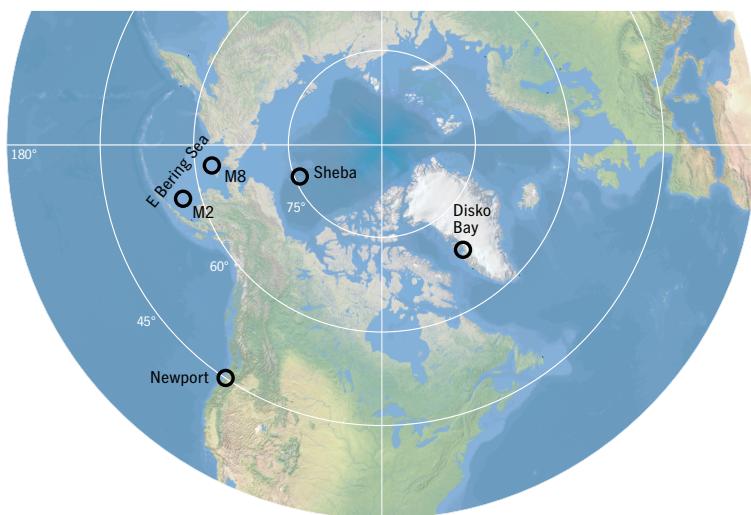


Figure 1. Locations of model testbeds. The “global” model experiment spans a gradient from approximately Ice Station Sheba to Newport, Oregon and beyond.

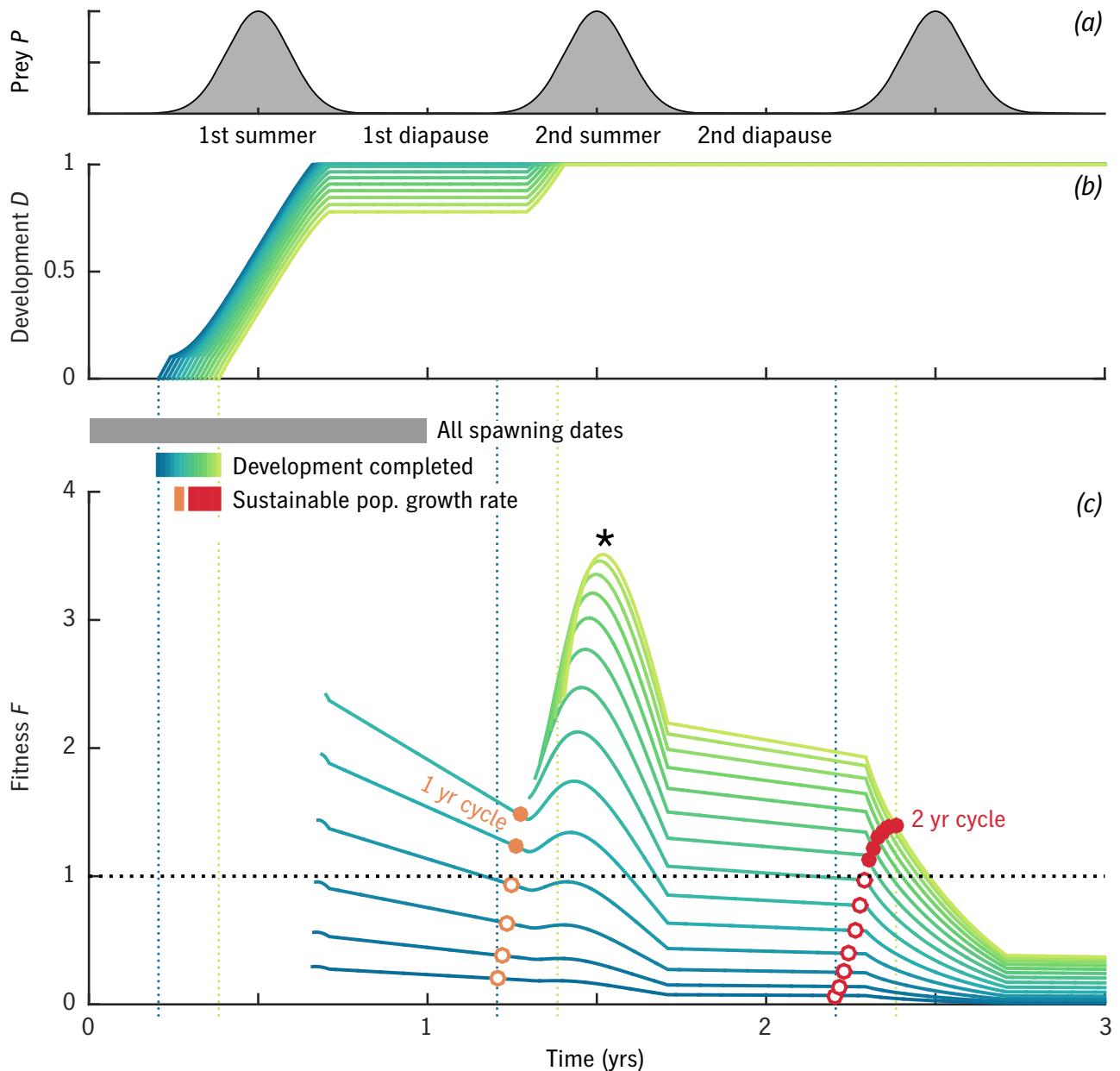


Figure 2. Results of an example model case with $u_0 = 0.007 \text{ d}^{-1}$, $T_0 = 1^\circ\text{C}$, and $\delta t = 135$.

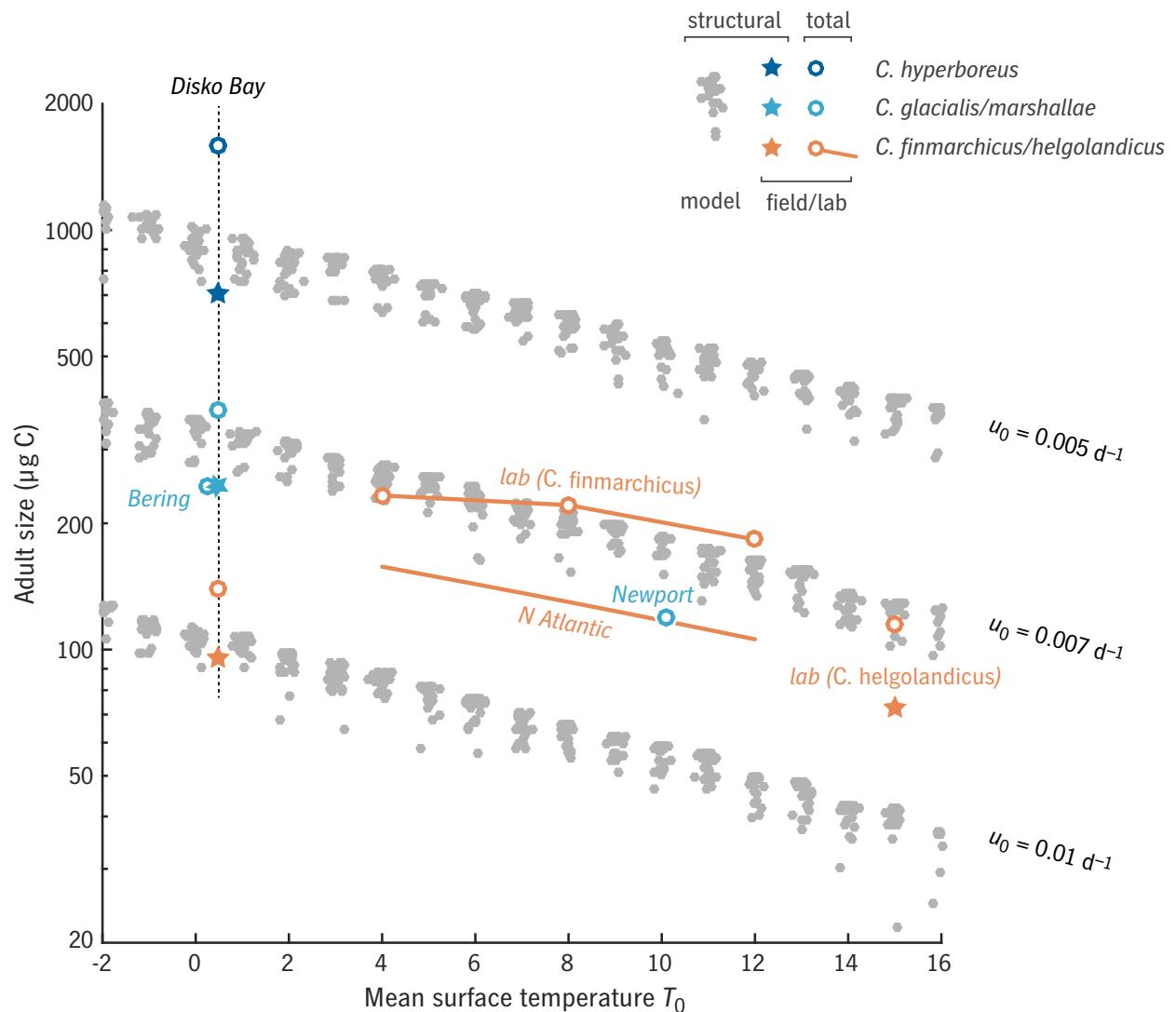


Figure 3. Relationship between adult size W_a and mean temperature T_0 in the “global” model experiment, for three values of u_0 , in comparison with observations and laboratory results. Model results (gray dots) represent structural biomass S , as do observations marked with a $*$; observations marked with a \circ represent total biomass $R + S$.

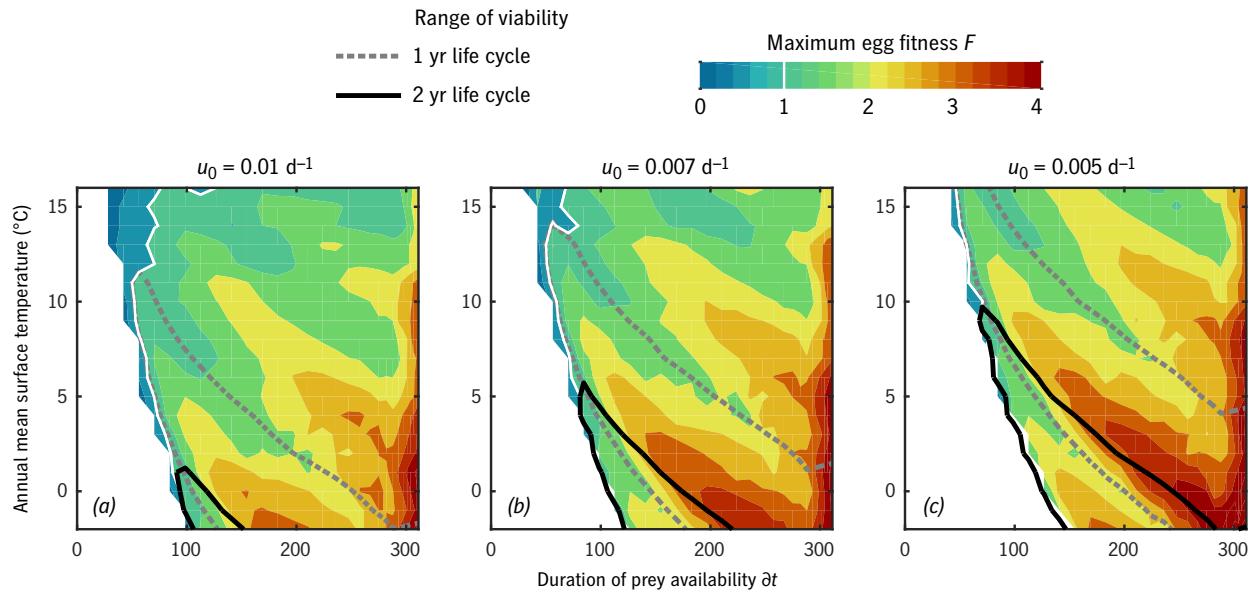


Figure 4. Maximum egg fitness (eggs per starting egg per generation) across all combinations of temperature and duration of prey availability in the “global” experiment. Unfilled contour lines give the environmental range over which one-year (gray, dotted) and two-year (black, solid) life cycles are viable. The white regions at low prey availability indicate environments in which no timing strategy exists that allows successful maturation.

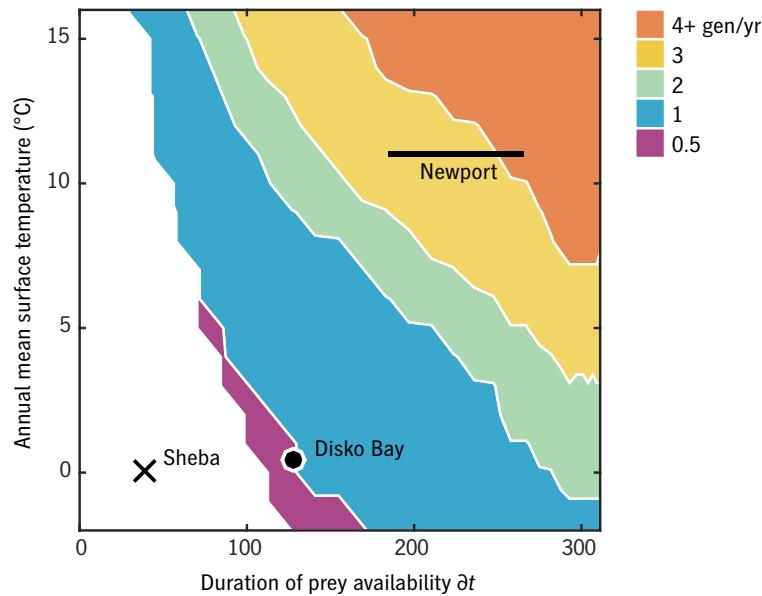


Figure 5. Generations per year of the optimal strategy in each environmental combination for $u_0 = 0.007 \text{ d}^{-1}$. Ice Station Sheba, Disko Bay, and Newport (Fig. 1) have been placed approximately for comparison.

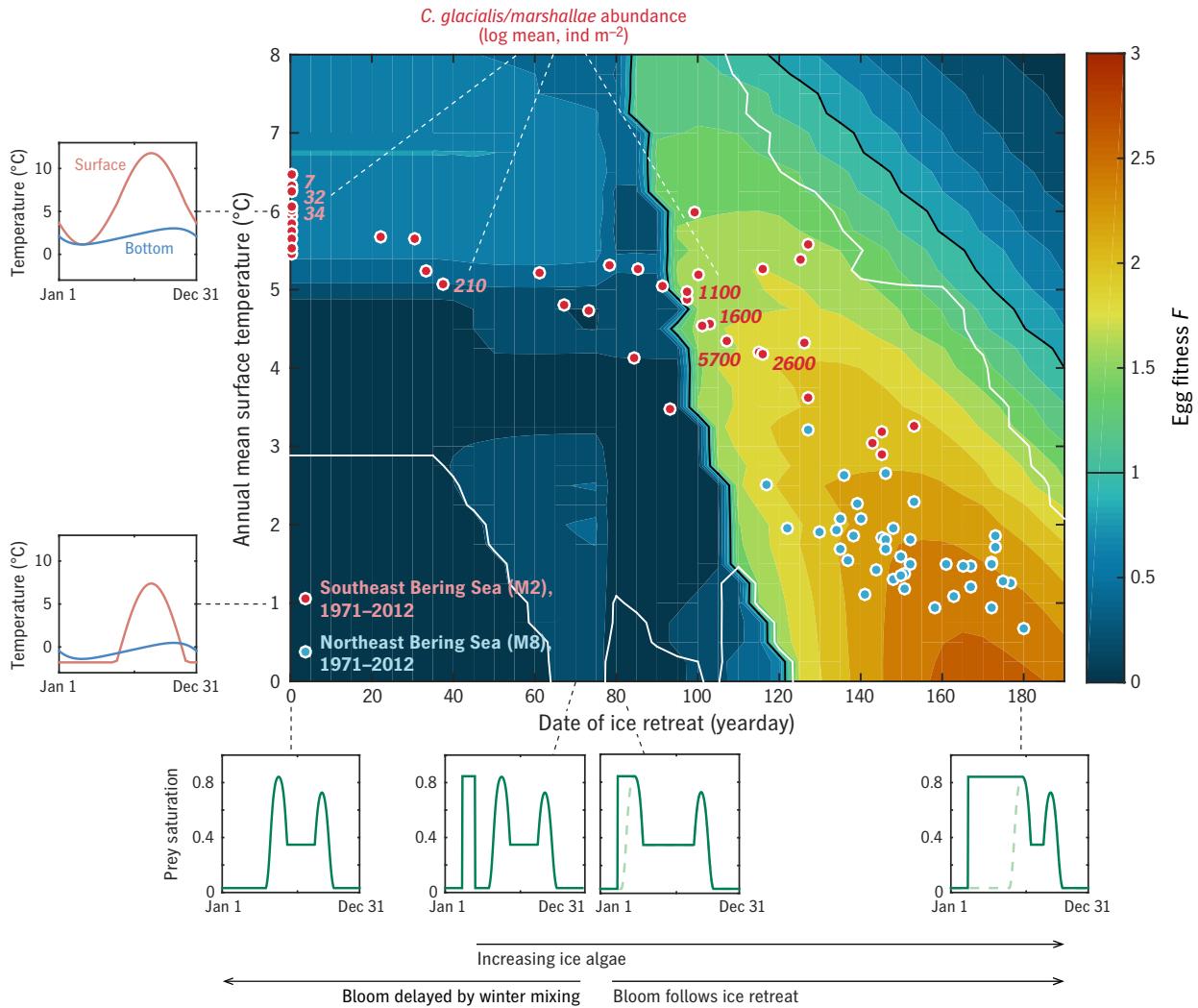


Figure 6. Results of the “Bering” experiment. Color contours give the predicted egg fitness of a *C. glacialis/marshallae* analog under combinations of ice retreat timing (assumed to control spring bloom timing: Appendix) and temperature. Examples of the annual cycles of prey availability \bar{P} and surface and bottom temperature T_0, T_d are given at left and bottom. Dots locate years 1971–2012 in this timing/temperature parameter space, for the northern (blue) and southern (red) middle shelf. Numbers give the measured abundance of *C. glacialis/marshallae* in summer.

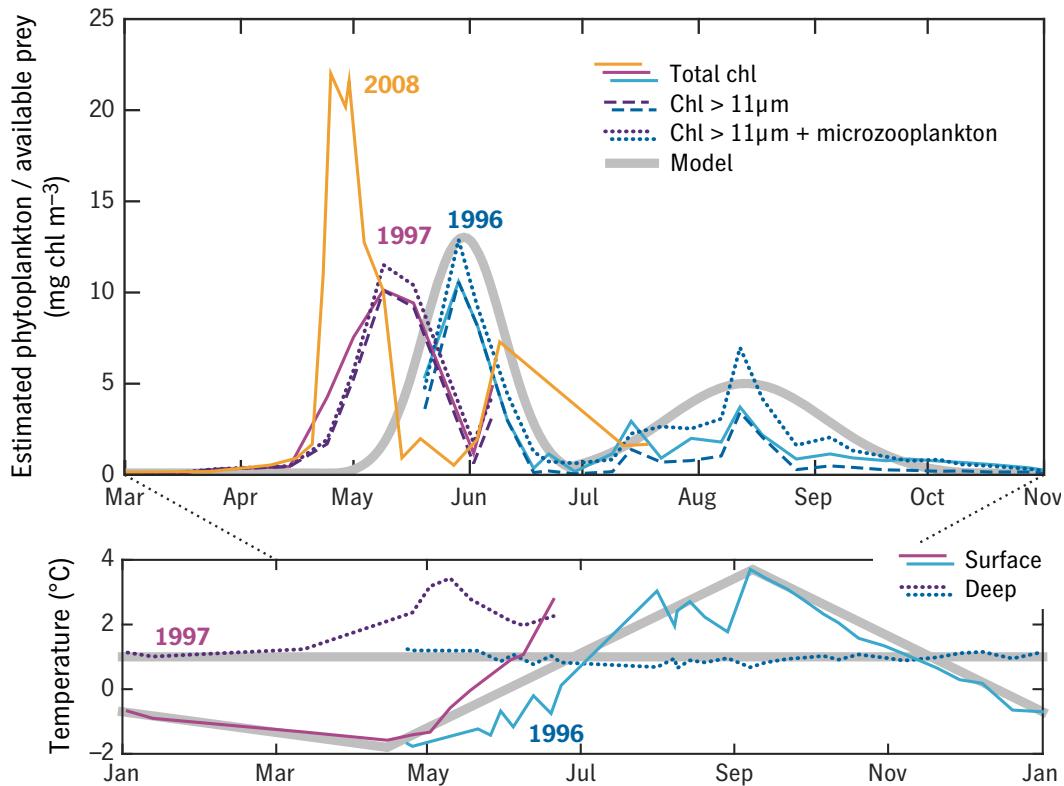


Figure 7. Observations of temperature and prey in Disko Bay 1996–97 from Madsen et al. (2001) (blue and purple thin lines) used to construct semi-idealized forcing time series for the model (thick grey lines). Three estimates of the prey field are shown, in each case averaged between the surface and subsurface fluorescence maximum: total chlorophyll (solid), chlorophyll in the $>11\text{ }\mu\text{m}$ size fraction (dashed), and $>11\text{ }\mu\text{m}$ chlorophyll plus a correction for microzooplankton (dotted). A 2008 phytoplankton time series is shown for comparison (orange), based on integrated phytoplankton carbon scaled to matched the spring maximum in chlorophyll units. Temperature in the upper 50 m (“surface”) and water-column minimum temperature (“deep”) are also shown.

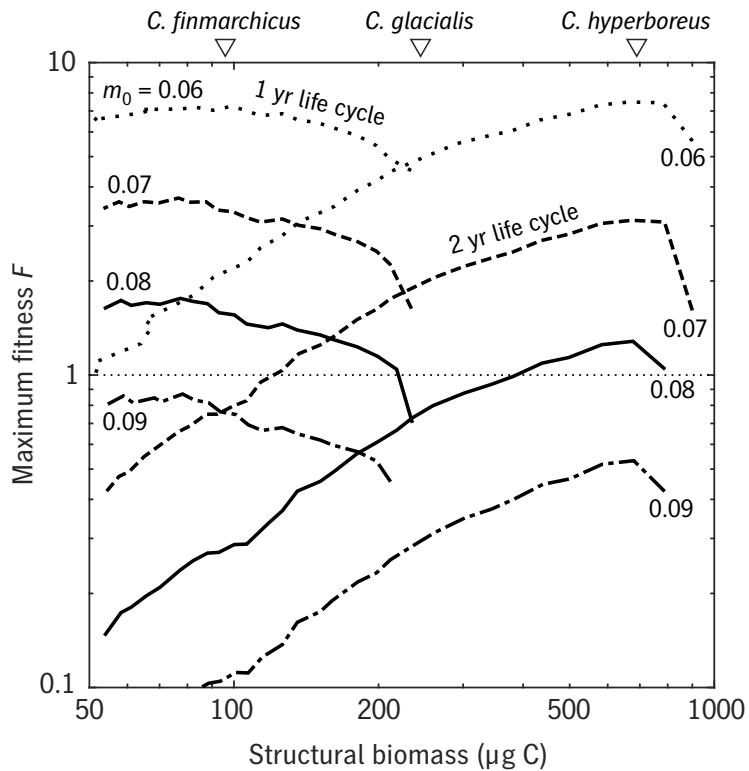


Figure 8. Results of the φ model for a range of u_0 values in the Disko Bay testbed (Fig. 7). Maximum egg fitness F is plotted for one-year and two-year strategies, for each of four values of the mortality scaling parameter m_0 ($0.06–0.09 \text{ d}^{-1}$), as a function of adult size S . The mean structural weights of the three *Calanus* spp. that coexist in Disko Bay are also shown (white triangles, top). Curves of F are shown over ranges where survival to adulthood without starvation is possible.

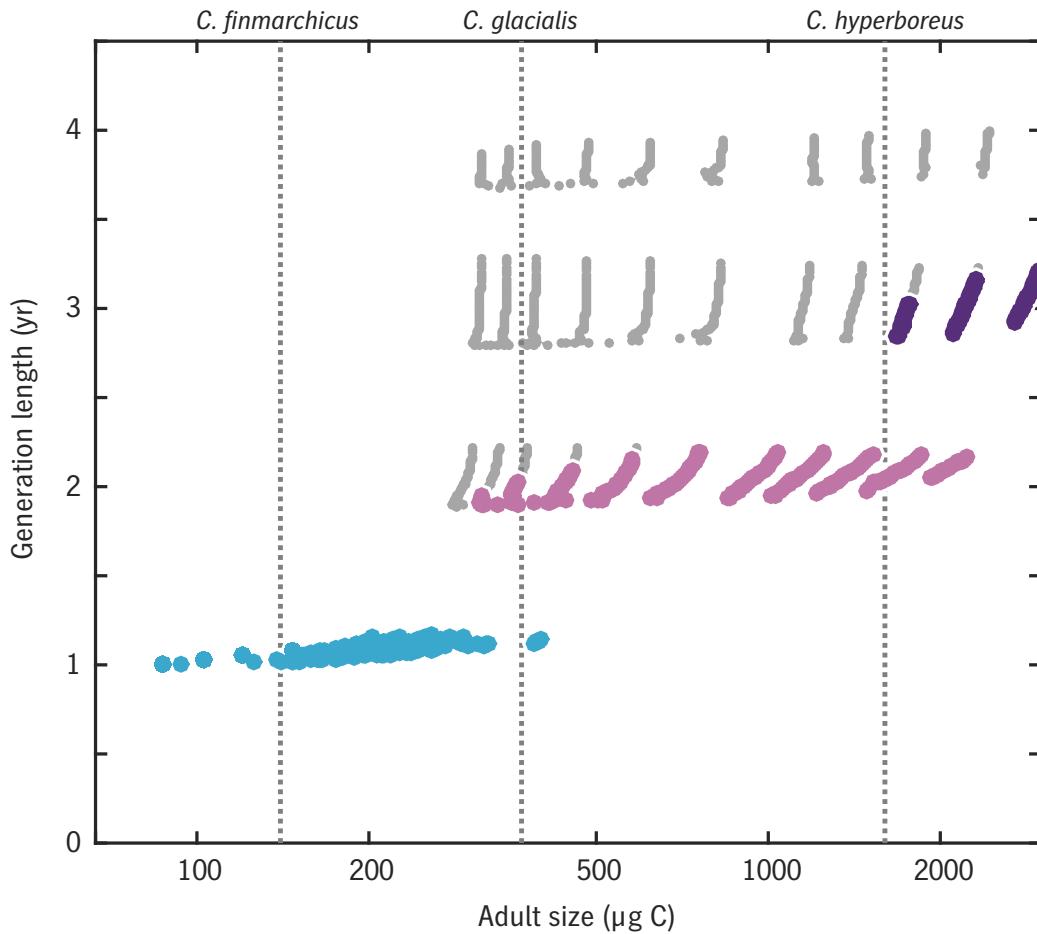


Figure 9. Emergent relationship between generation length and adult size in the Disko Bay model experiment. Large colored dots indicate results for trait combinations that achieve a viable rate of egg production per generation (color coding matches that in Fig. 11) while small gray dots indicate trait combinations that reach maturity without starvation but have egg production rates below replacement level.

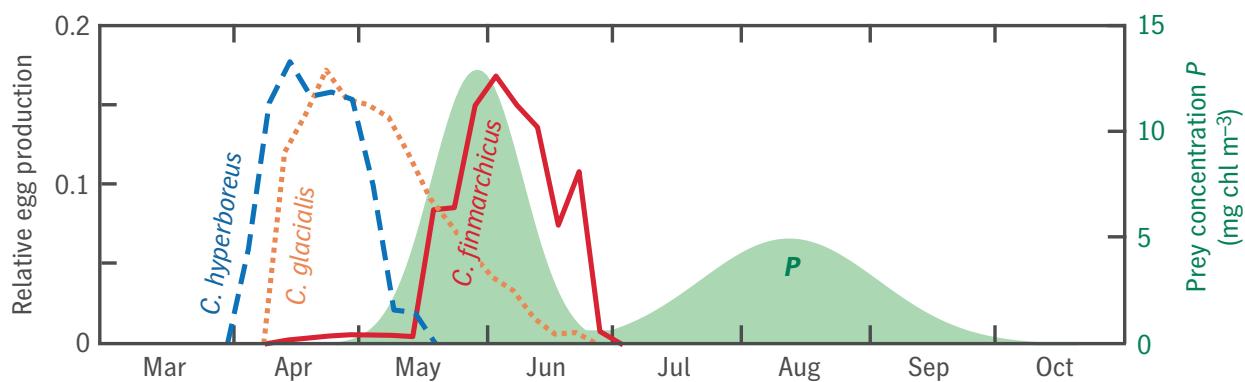


Figure 10. Seasonal progression of egg production in model analogs for three *Calanus* spp. in Disko Bay (lines), in relation to prey concentration P (shaded). Egg production time series consist of $n(t_0)$, the first eigenvector of the transition matrix V discussed in Sec. 2.3.3, normalized to integrate to 1.

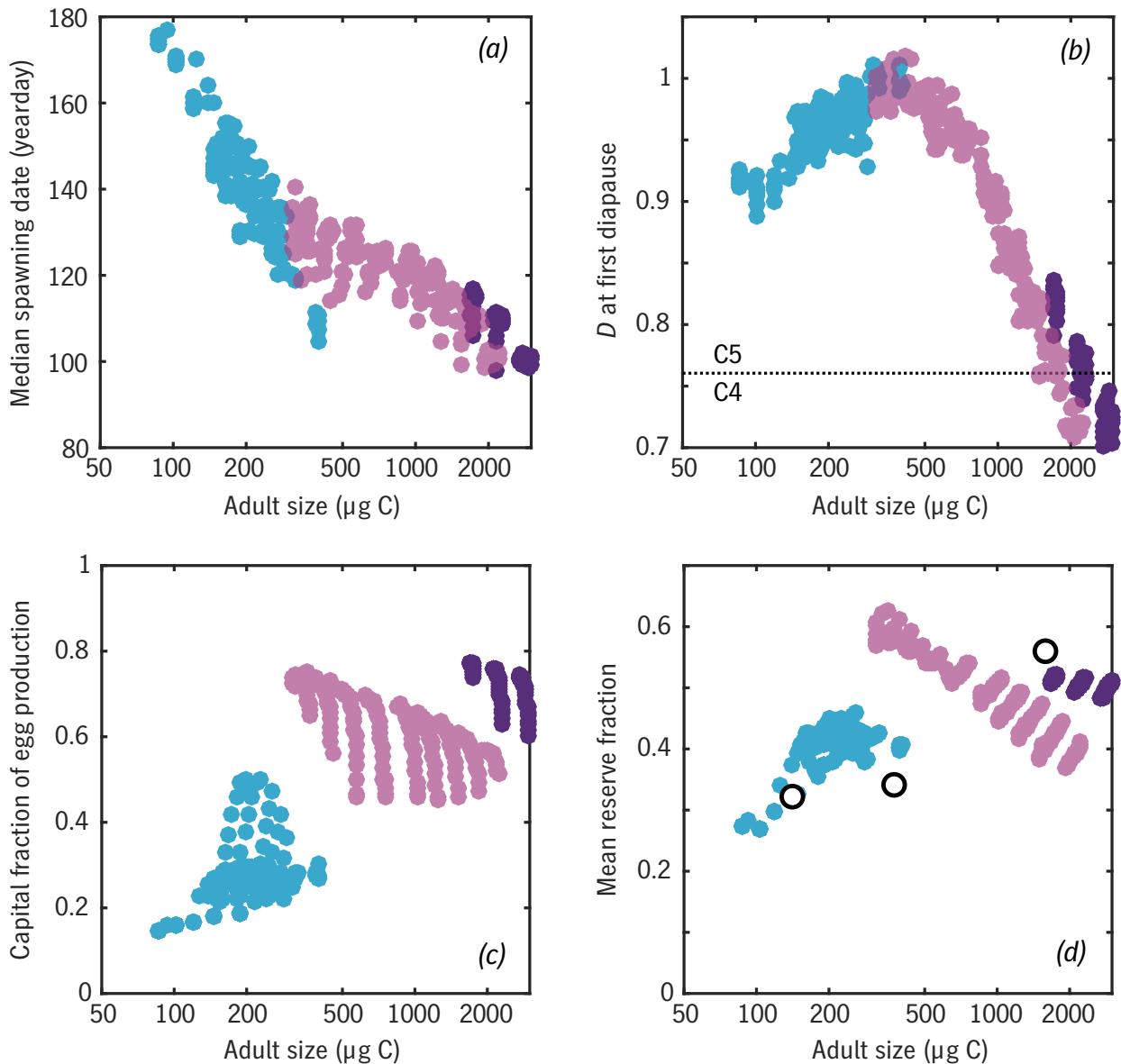


Figure 11. Relationships between a number of emergent traits with adult body size in the Disko Bay experiment. Color coding matches Fig. 9, distinguishing one-year (blue), two-year (light purple) and three-year (dark purple) life cycles. (a) Median spawning date: compare peaks of egg production curves in Fig. 10. (b) Earliest developmental stage D at which diapause ($a = 0$) occurs: values have been jittered slightly in the vertical for clarity. (c) Capital fraction of egg production $E_{cap}/(E_{inc} + E_{cap})$. (d) Mean reserve fraction of individual biomass $R/(R + S)$, compared with wax esters as a fraction of total body carbon for three *Calanus* spp. from Swalethorpe et al. (2011) (open circles).