

Calanus copepods at the Arctic gateways

Modelling life history and energetics along
long-distance inflow corridors

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neilbanas.com/projects/coltrane



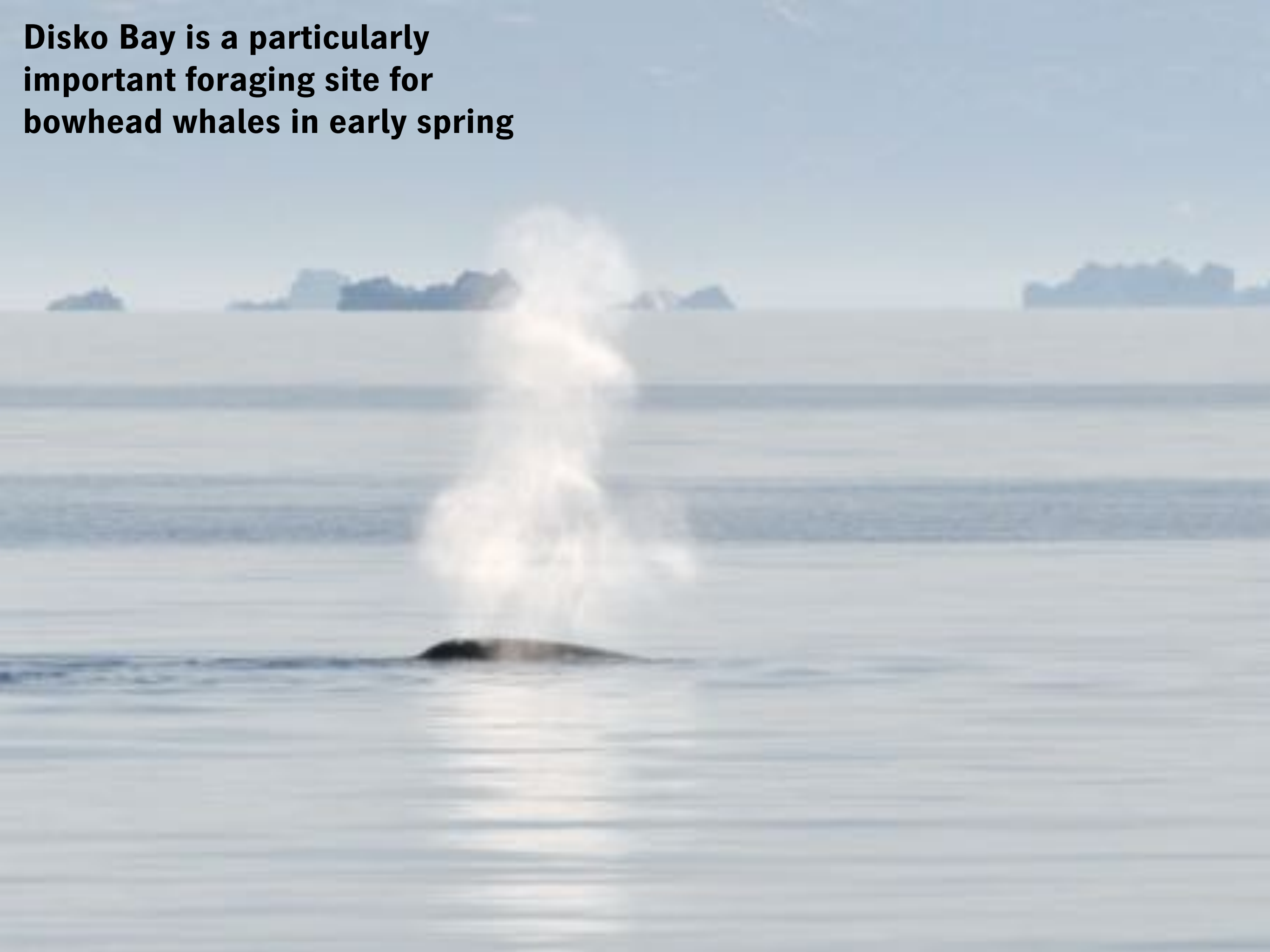
**Changing
Arctic
Ocean**



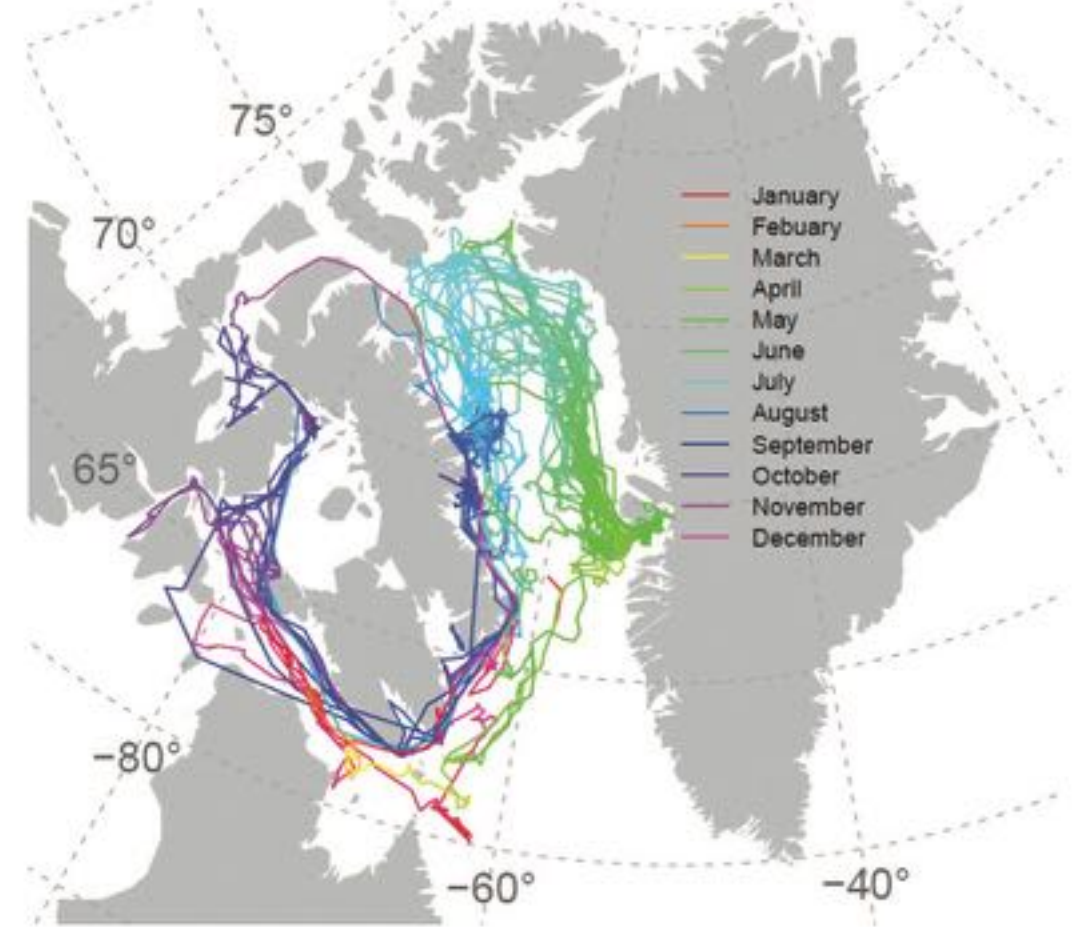
Natural
Environment
Research Council

Bowhead whales and copepods in Disko Bay

Disko Bay is a particularly important foraging site for bowhead whales in early spring

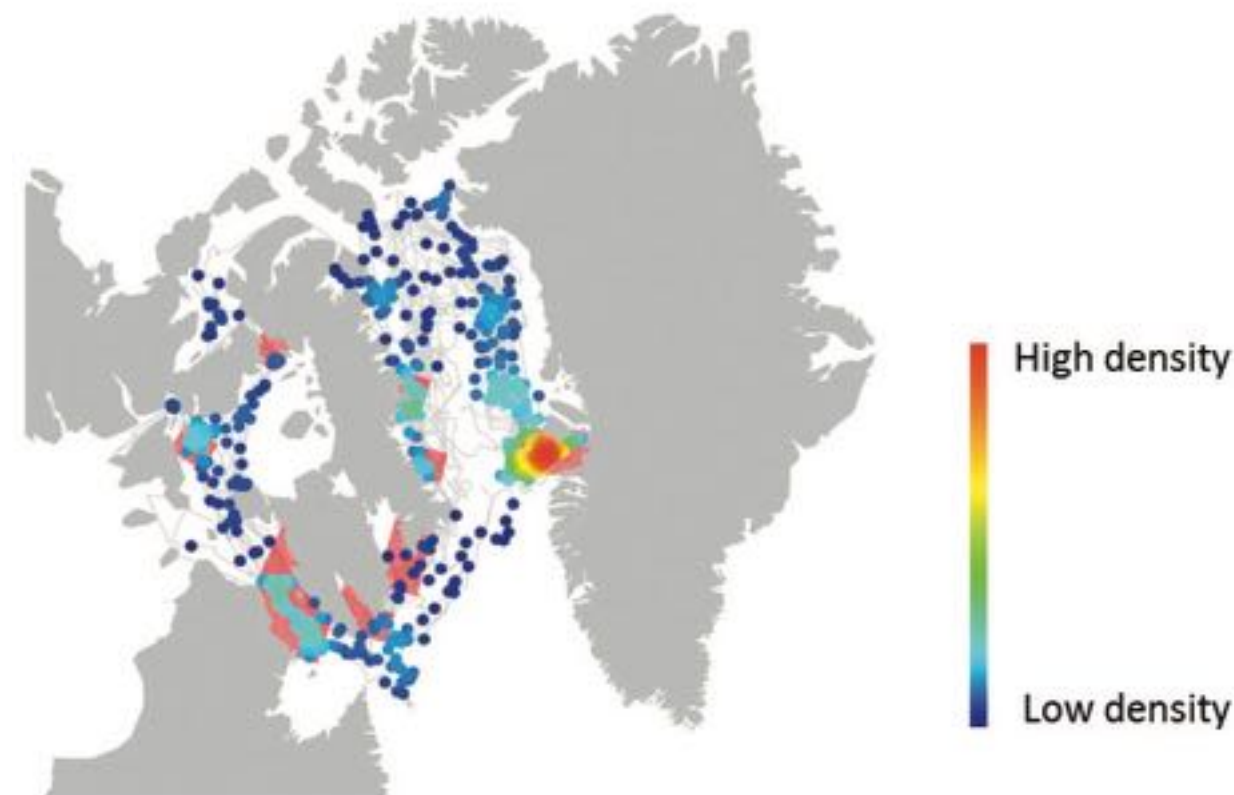


Disko Bay is a particularly important foraging site for bowhead whales in early spring



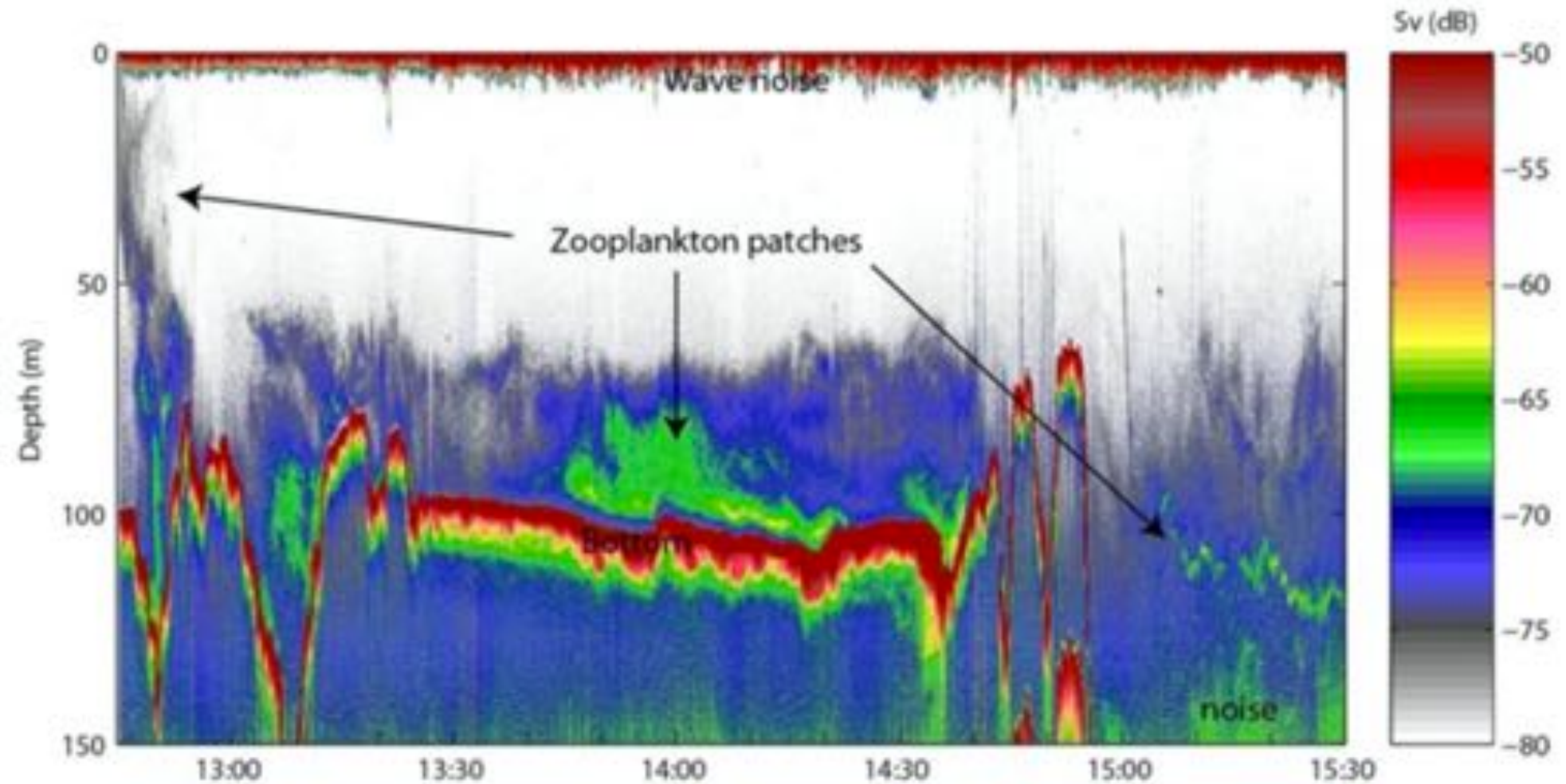
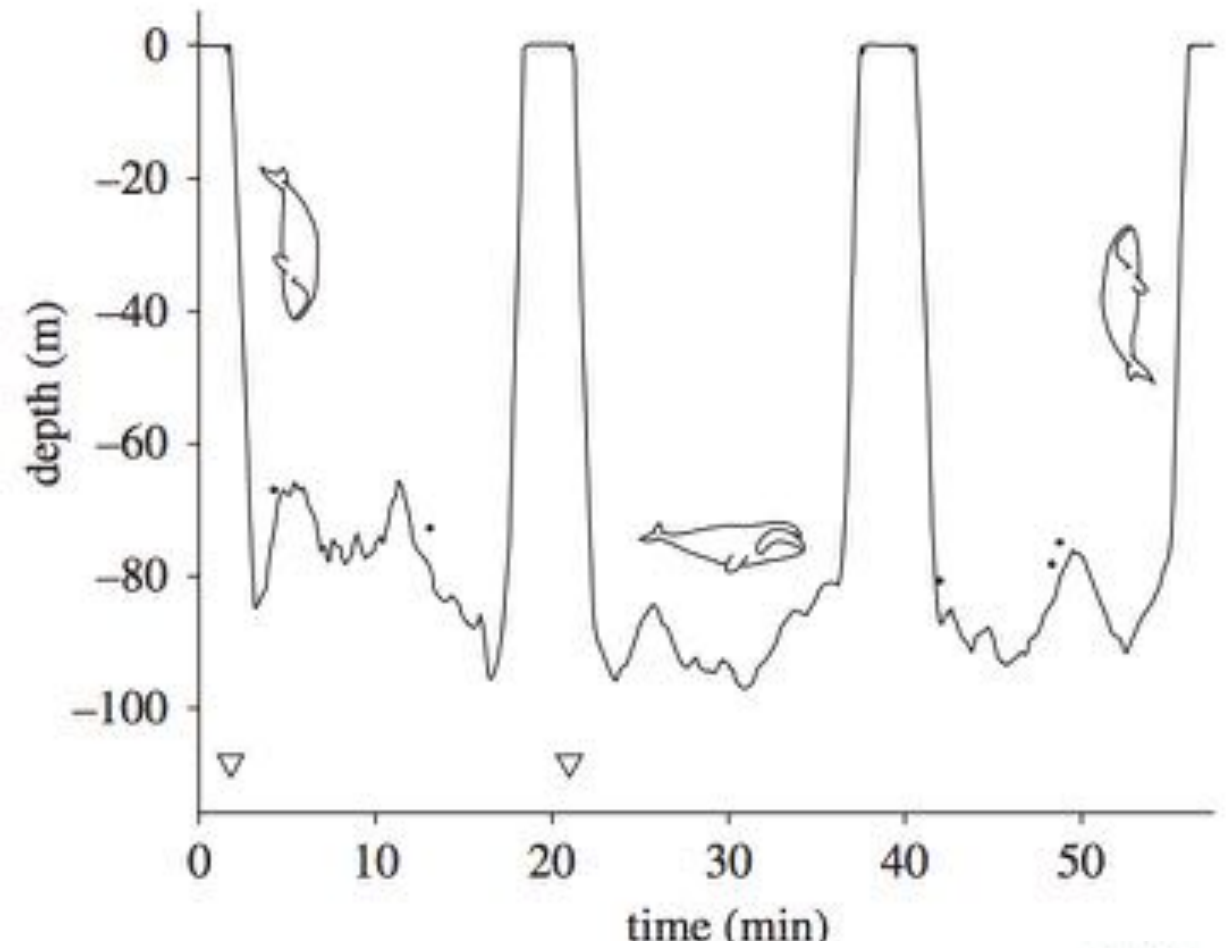
tagging study: Nielsen et al., *Arctic*, 2015

Dives per hour < 3

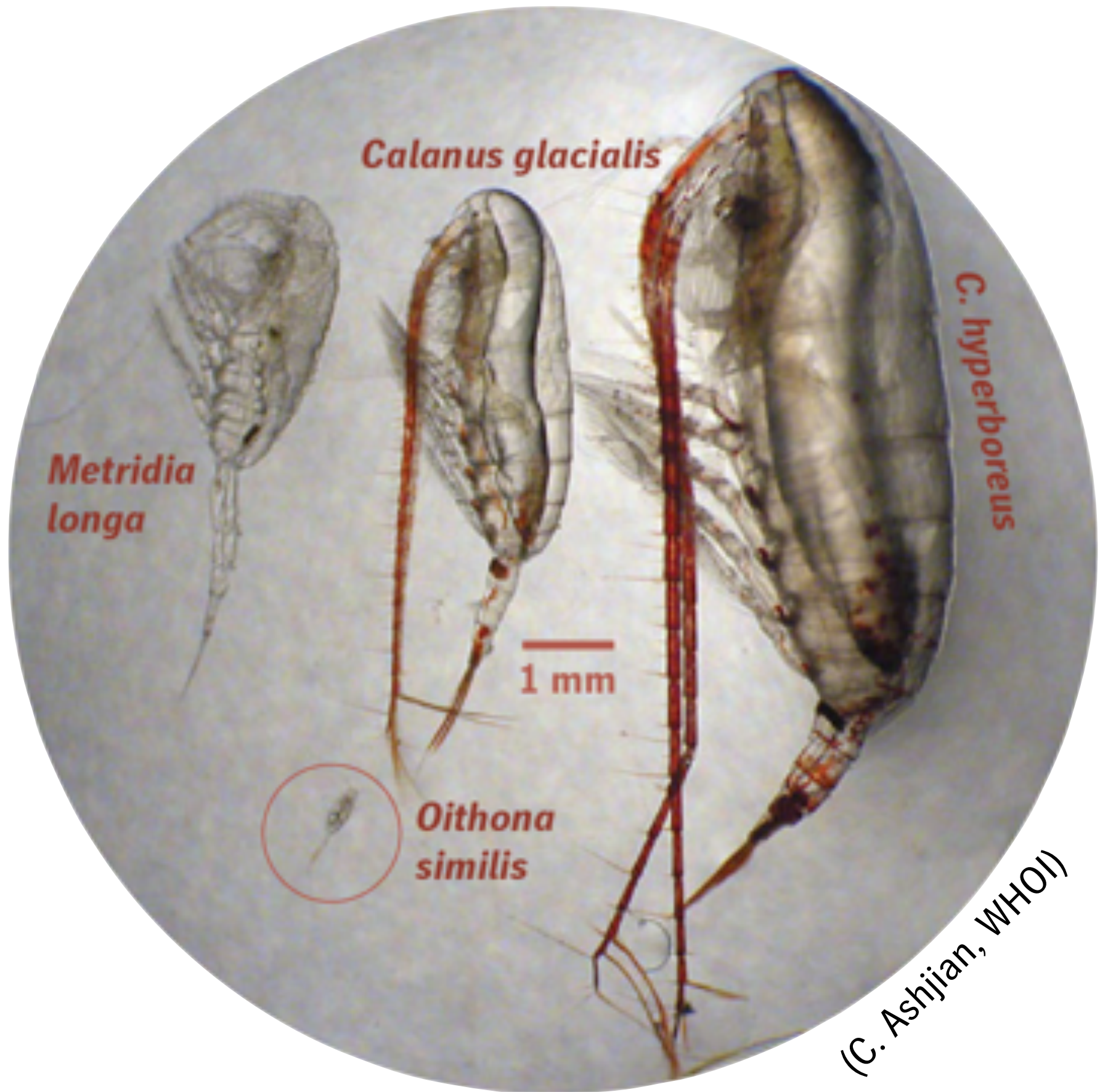


The whales feed directly on overwintering copepods

Simon et al.,
Proc. R. Soc. B, 2009



Heide-Jørgensen et al.,
Animal Telemetry, 2013



*Metridia
longa*

Calanus glacialis

1 mm

*Oithona
similis*

C. hyperboreus

(C. Ashjian, WHOI)

Behavioural observations, copepod abundance data, and bioenergetic considerations are consistent if **bowhead whales consume 26–75% of the copepod standing stock annually.**

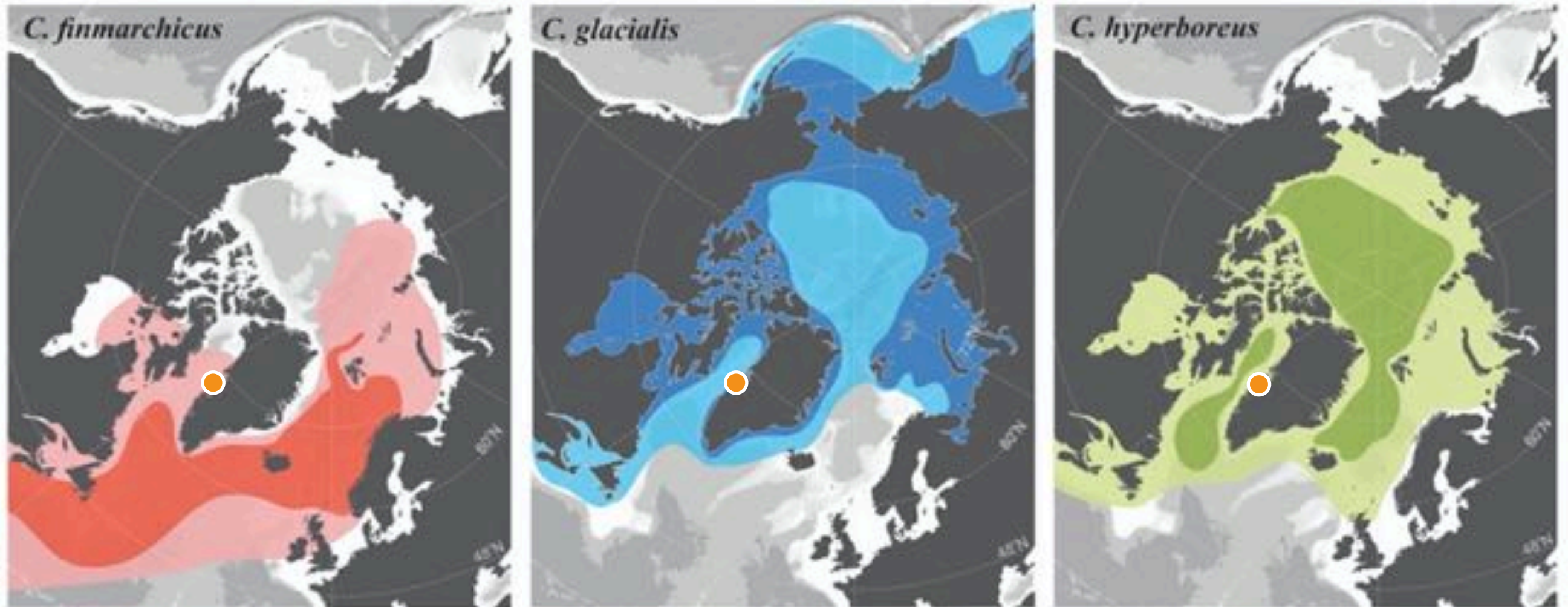


Table 1. Quantities used in estimation of bowhead whale foraging on copepods. Uncertainty is reported either as \pm standard deviation or as (5th, 95th percentiles).

Symbol	Definition	Units	Value	Uncertainty	Source
<i>Habitat parameters</i>					
A_{disko}	Bay area	km^2	6000		
h_{cop}	Thickness of deep copepod layer	m	5	(2, 18)	Heide-Jorgensen et al. 2013, Fig. 6
B_{cop}	Area-specific copepod biomass	gC m^{-2}	3.6	(0.14, 11)	
<i>Foraging parameters</i>					
N_{pop}	Number of whales in entire pop.		1500	(830, 2250)	Rekdal et al. (2015)
N_{graz}	Number foraging at one time		740	(360, 1460)	Rekdal et al. (2015)
a_{mouth}	Mouth area	m^2	4		Werth (2004)
u_{swim}	Swimming speed	m s^{-1}	0.7	± 0.1	Simon et al. (2009)
Δt_{graz}	Duration of foraging period	d	120	± 15	
f_{graz}	Fraction of day actively foraging		0.3	± 0.1	
<i>Bioenergetic parameters</i>					
E_{whale}	Indiv. metabolic requirement	kcal d^{-1}	1.1×10^6		Laidre et al. (2007), assuming 80% adult female + 10% adult male + 10% juveniles
e_{cop}	Energy density of copepods	kcal gC^{-1}	16		Karnovsky et al. (2003), assuming $0.4 \text{ gC (g dry wt)}^{-1}$

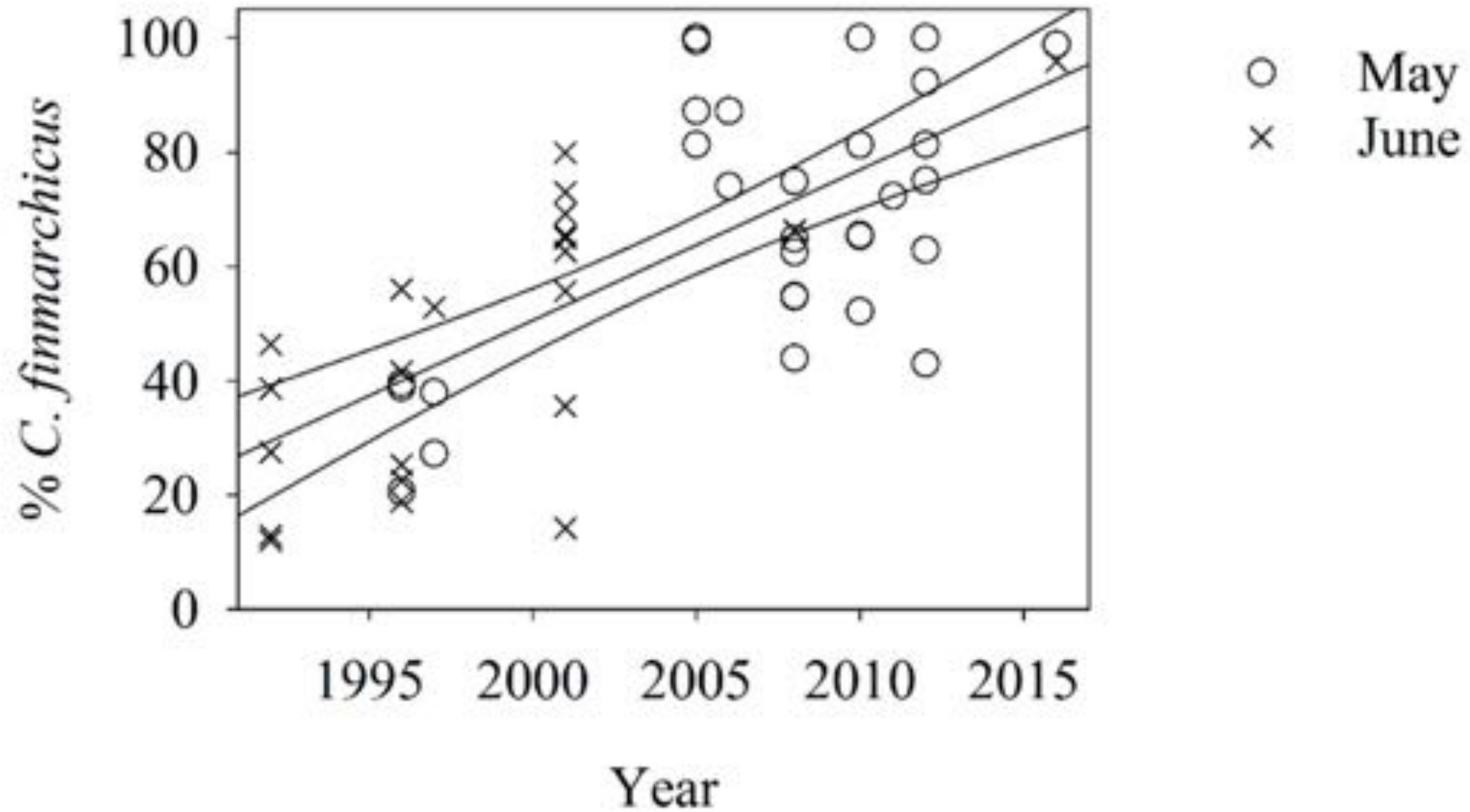
(Banas, Møller, Laidre, Simon, Ellingsen, Nielsen, in prep.)

Three *Calanus* spp. coexist in Disko Bay



(Choquet et al. 2017)

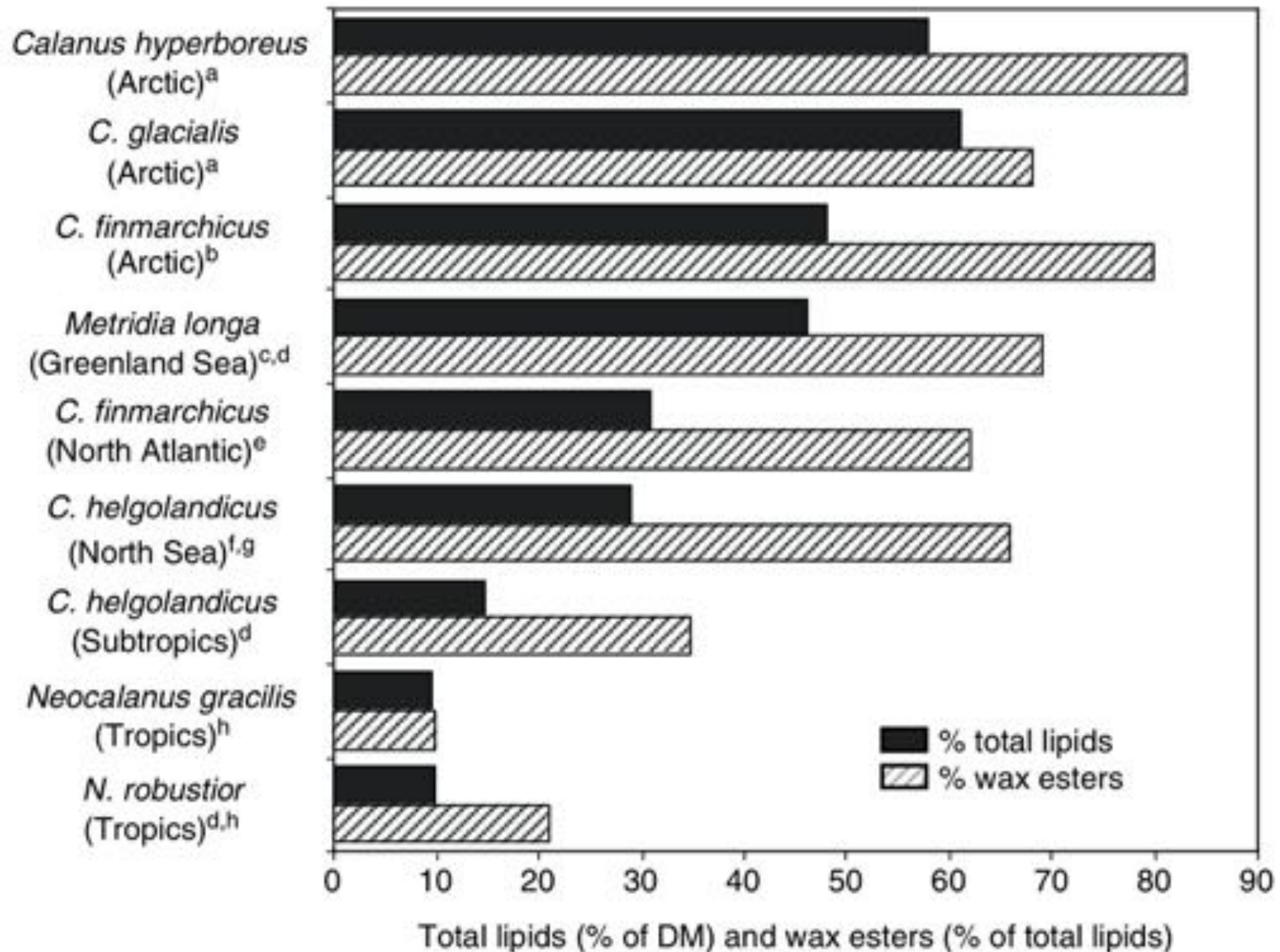
... but the proportions are shifting:
Atlantification / Borealisation



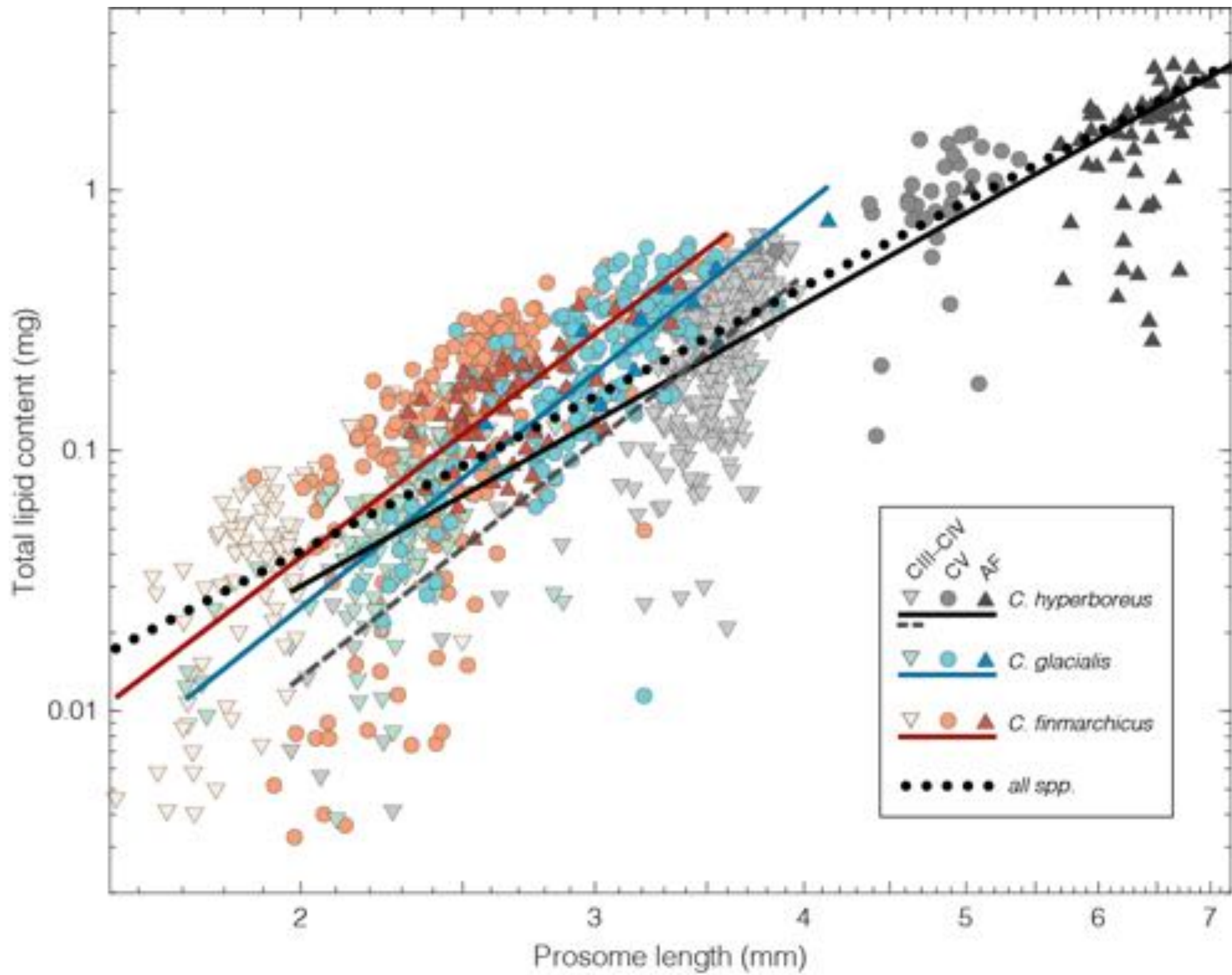
(Møller and Nielsen 2019)

Generalising

In general, lower-latitude copepods have lower lipid content (and therefore lower value as prey) than their high-latitude cousins



(Kattner and Hagen, 2002)



(Renaud et al., *ICES J Mar Sci*, 2018)

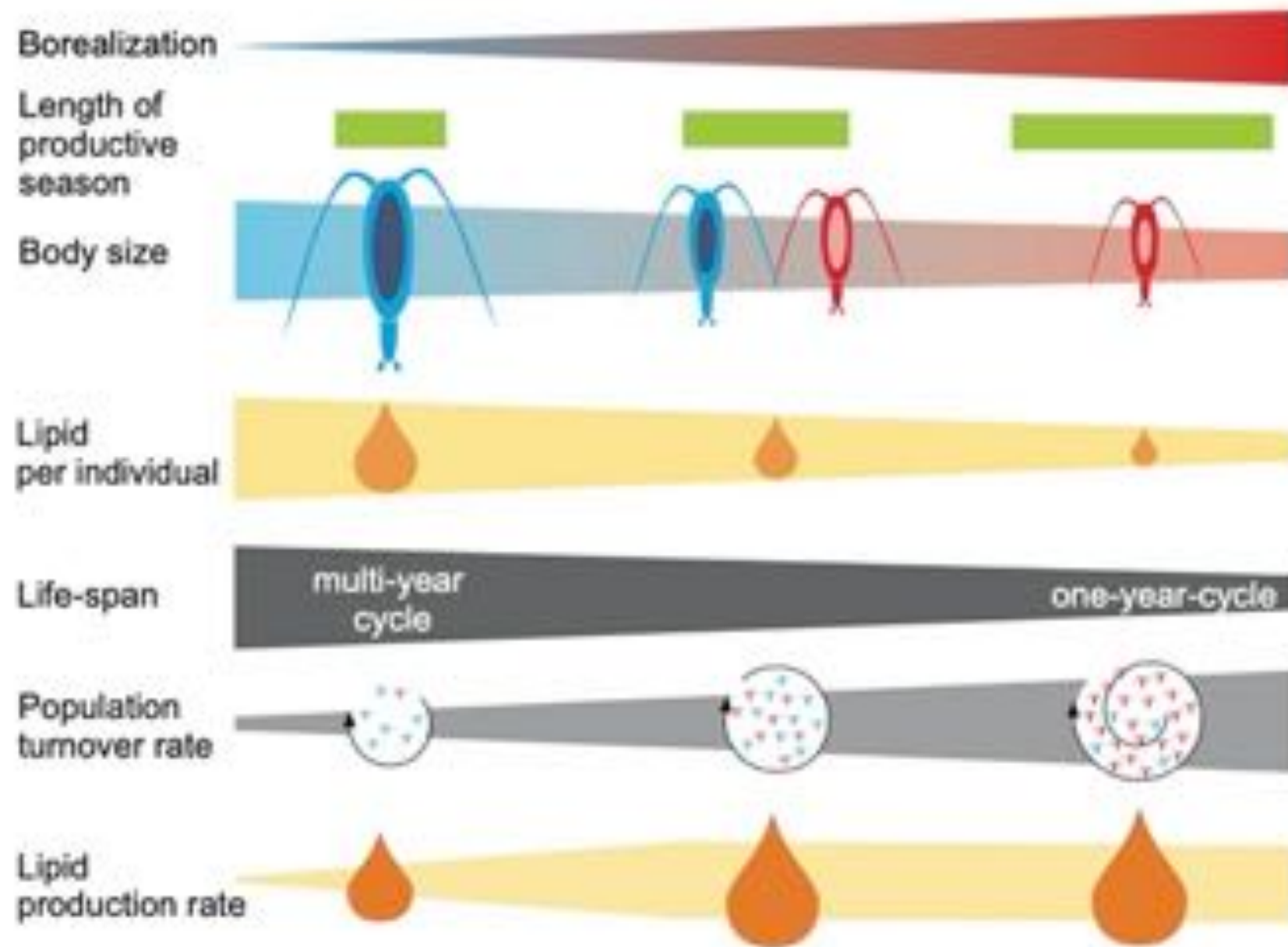


Figure 6. Conceptual understanding of the effects of borealization of the Arctic on length of productive season, body size, individual lipid content, life span and population turn over of Arctic (blue) and boreal (red) *Calanus* populations, and on total population lipid production. Where seasonal ice 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.

(Renaud et al., *ICES J Mar Sci*, 2018)

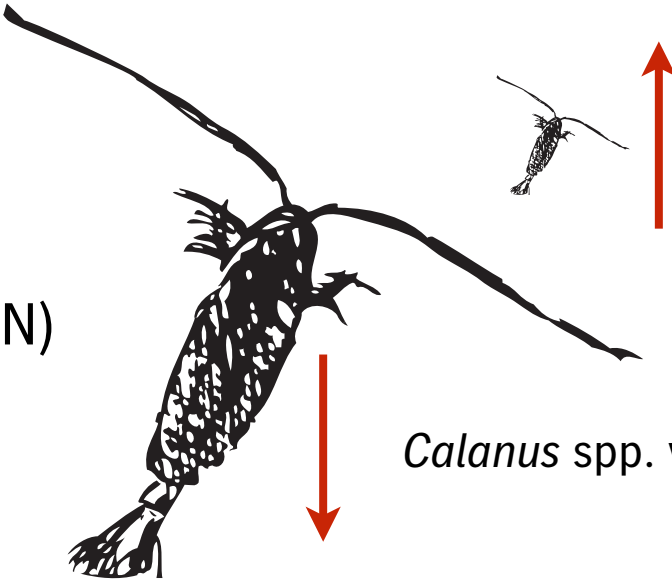
Region-specific shifts in zooplankton community composition

Bering Sea (60°N)

warm years;

US Pacific Northwest (45°N)

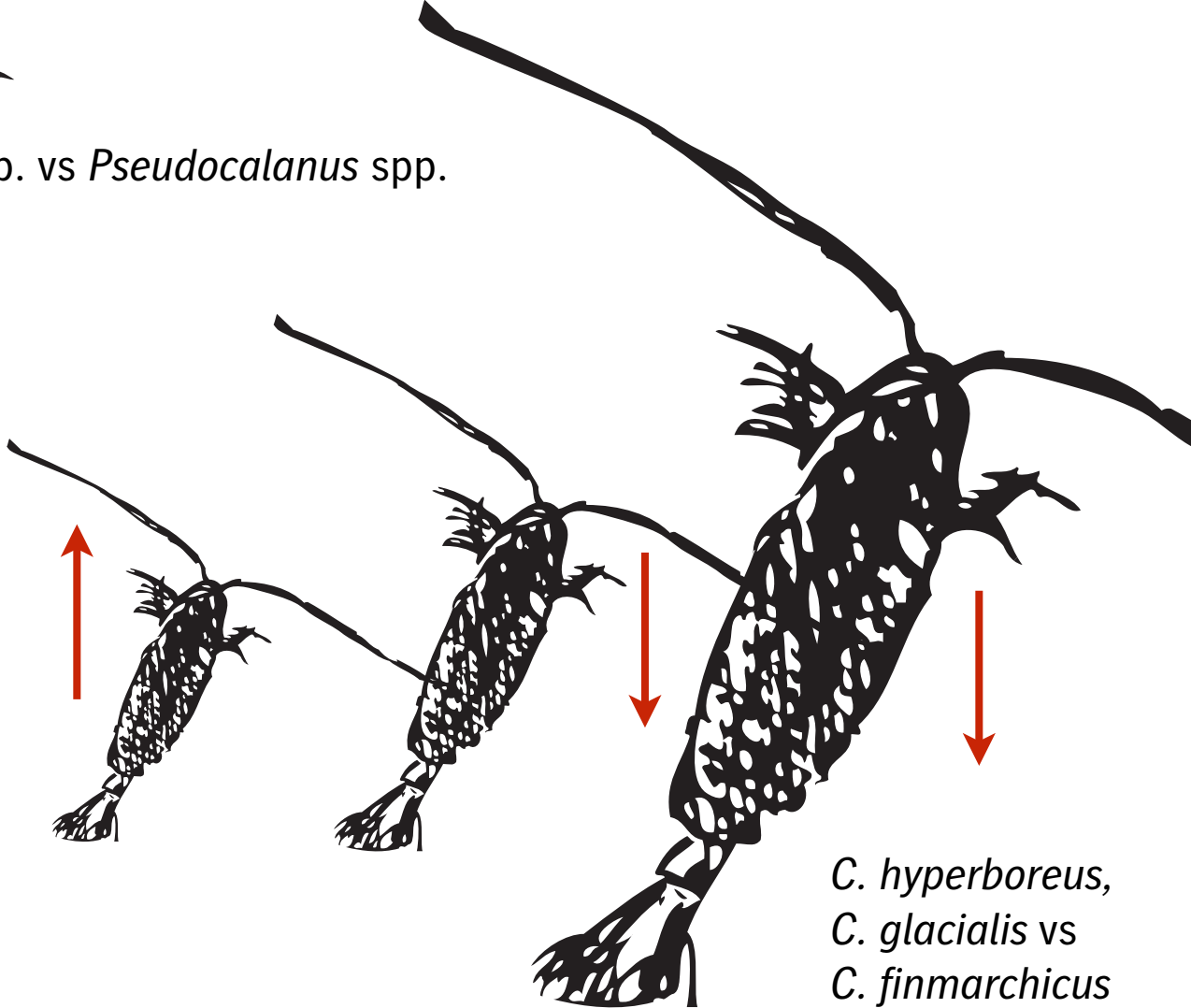
warm decades



Calanus spp. vs *Pseudocalanus* spp.

Disko Bay, West Greenland

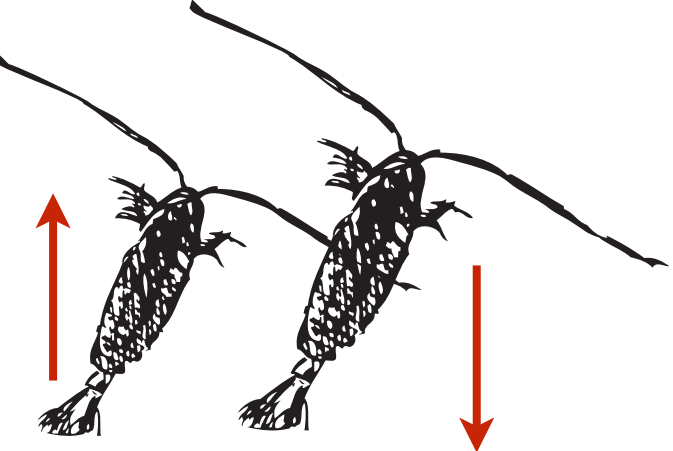
Atlantification, 2000s–



C. hyperboreus,
C. glacialis vs
C. finmarchicus

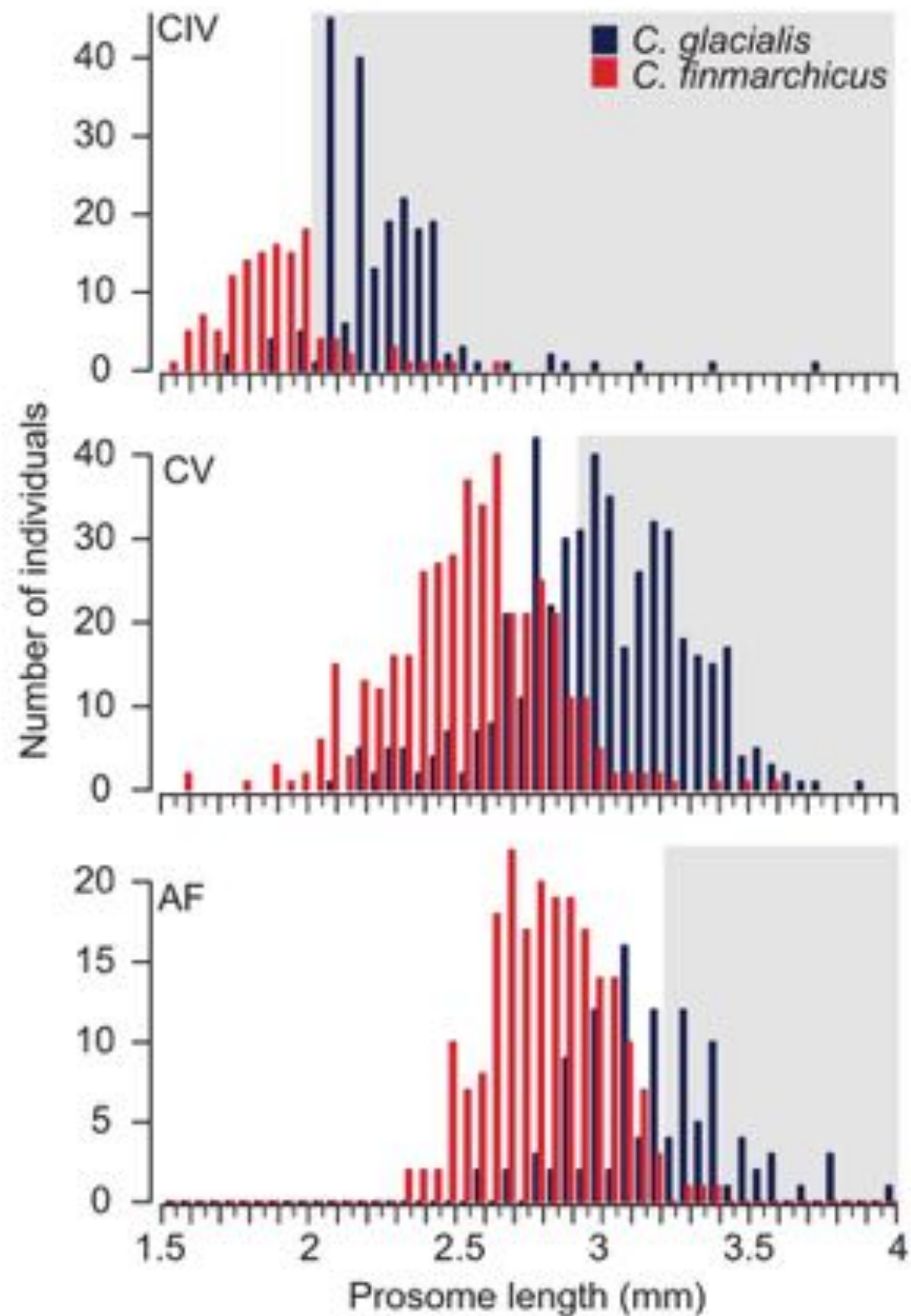
North Sea

warming trend, 1960s–

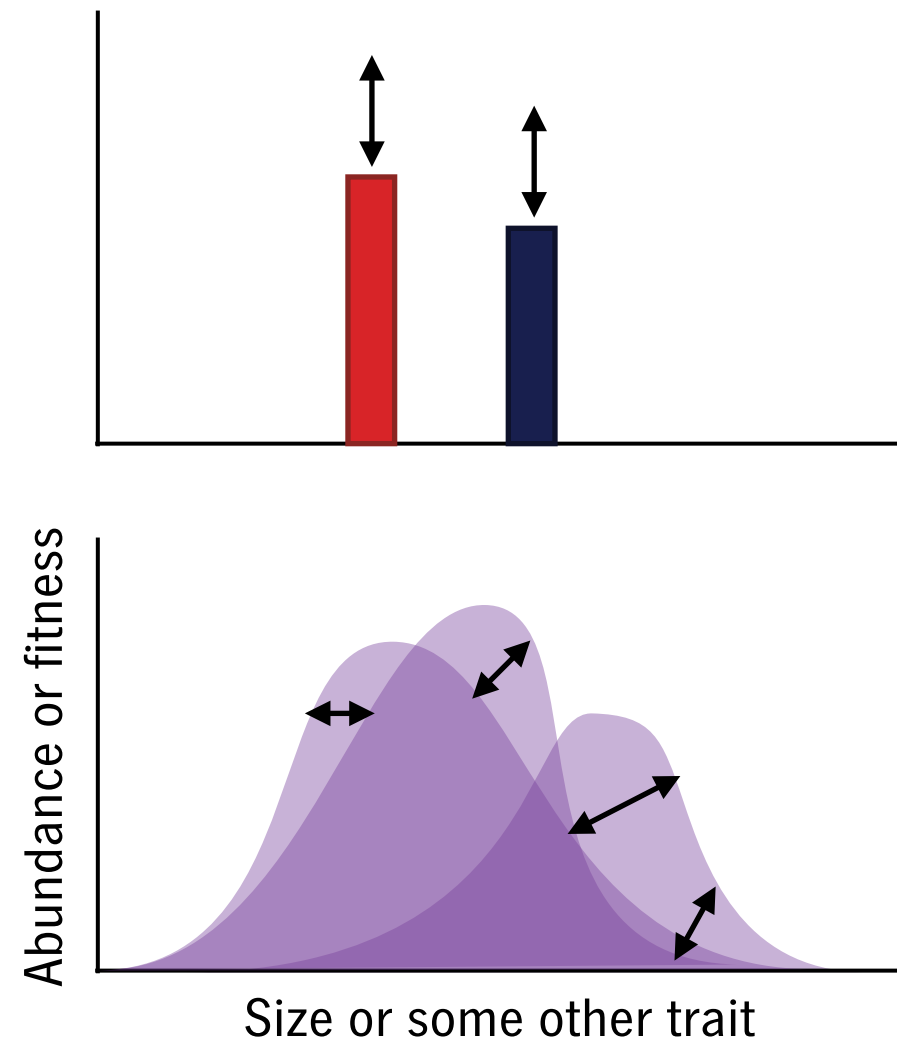


C. finmarchicus vs *C. helgolandicus*

Impacts on pollock, salmon, cod, forage fish, seabirds, whales...



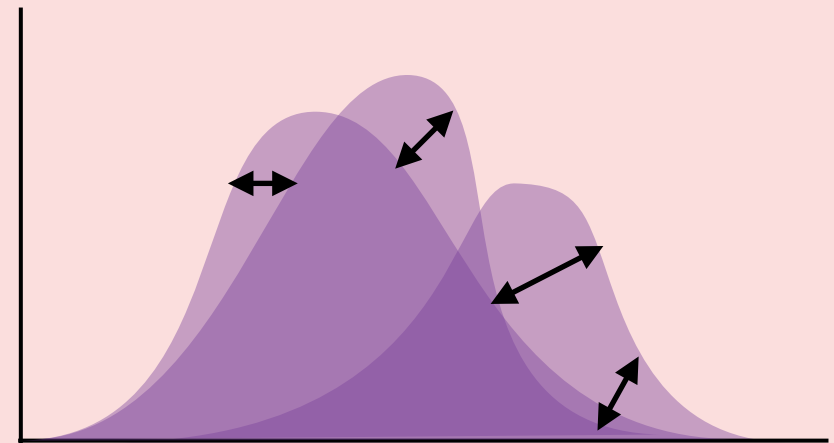
Should we model diverse, plastic reality as competing, distinct species or a continuous distribution of traits?



(Renaud et al. 2018)

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).

A trait-based model



Past approaches

Optimal annual routines

(Varpe et al. 2007, 2009; Houston & McNamara 1999, Clark & Mangel 2000)

focus on reserves
and timing

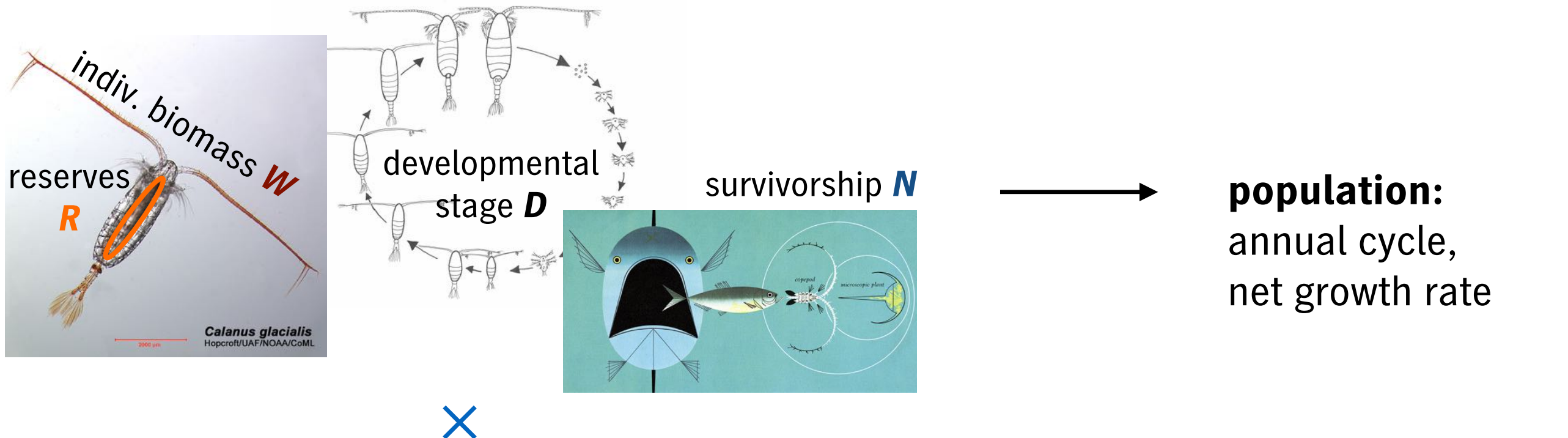
Emergent copepod communities

(Record et al. 2013)

trait-based
metacommunity

Coltrane (Copepod life-history traits and adaptation to novel environments)

(Banas et al. *Front. Mar. Res.*, 2016)

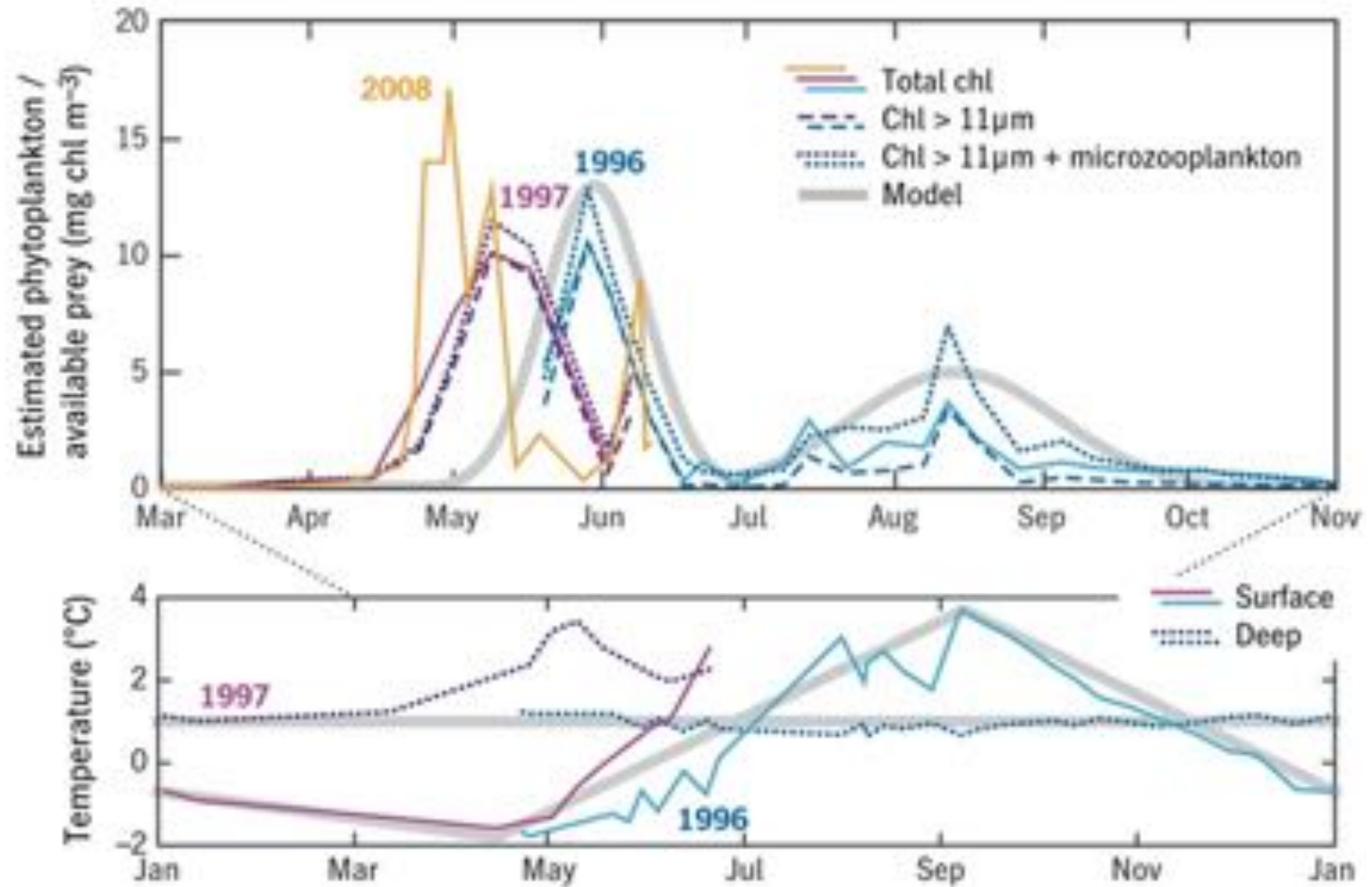


population:
annual cycle,
net growth rate

small number of variable traits

community
associated with a
given environment

An environment is defined by time series of **surface and deep temperature** and **prey availability**...



... and in future work, a relative measure of **predation risk**, defined in terms of **light**.

Steps (Coltrane 2.0)

Thresholds

For every combination of four **timing strategy** parameters, ←

spawn date × diapause entry
× diapause exit
× start of egg production

- Calculate **development** sequence.
(An environment in Coltrane is 3 time series:
Prey, surface temperature, deep temperature)



LEVEL 1

Diapause-capable
by winter

(cf. models of Arctic range
limits by Ji et al. 2011,
Feng et al. 2016, 2017)

Steps

For every combination of four **timing strategy** parameters, ←

spawn date × diapause entry
× diapause exit
× start of egg production

- Calculate **development** sequence.

- Calculate **net energy gain** (ingestion minus metabolism), **body size**, and **egg production**.



LEVEL 1

Diapause-capable by winter



LEVEL 2

Reach adulthood without starving

cf. other DEB models

Steps

For every combination of four **timing strategy** parameters, ←

spawn date × diapause entry
× diapause exit
× start of egg production

- Calculate **development** sequence.
- Calculate **net energy gain** (ingestion minus metabolism), **body size**, and **egg production**.
- Integrate predation mortality to produce a timeseries of **survivorship**, and calculate **fitness** (lifetime eggs egg⁻¹).

Thresholds



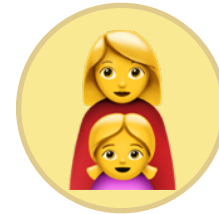
LEVEL 1

Diapause-capable by winter



LEVEL 2

Reach adulthood without starving



LEVEL 3

Reproduce at replacement rate

Steps

For every combination of four **timing strategy** parameters, ←

spawn date × diapause entry
× diapause exit
× start of egg production

- Calculate **development** sequence.
- Calculate **net energy gain** (ingestion minus metabolism), **body size**, and **egg production**.
- Integrate predation mortality to produce a timeseries of **survivorship**, and calculate **fitness** (lifetime eggs egg⁻¹).

Repeat fitness calculation across 2+ generations, to resolve **internal life history mismatch**.

(Varpe et al. 2007)

Thresholds



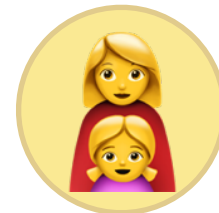
LEVEL 1

Diapause-capable by winter



LEVEL 2

Reach adulthood without starving



LEVEL 3

Reproduce at replacement rate

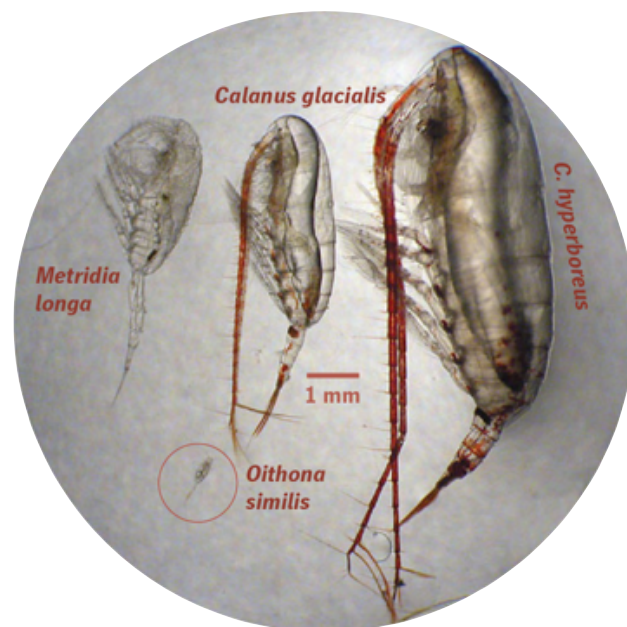


LEVEL 4

Replacement rate across 2 generations

= a long-term-viable **population**

It turns out that **two strategy traits** predict adult size in copepods across three orders of magnitude (*Oithona*–*Neocalanus* spp).



Traits controlling body size in copepods: separating general constraints from species-specific strategies

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²Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02881, USA

ABSTRACT: A new synthesis of laboratory measurements of food-saturated development and growth across diverse copepod taxa was conducted in a theoretical framework that distinguishes general allometric constraints on copepod physiology from contingent strategies that correlate with size for other reasons. After temperature correction, the allometry of growth rate is inconsistent between the ontogeny of *Calanus* spp., where it follows the classic -0.3 power-law scaling, and a broader spectrum of adult size W , (0.3 to $2000 \mu\text{g C}$, *Oithona* spp. to *Neocalanus* spp.), across which the classic scaling appears to represent only an upper limit. Over the full size spectrum, after temperature correction, a growth rate g , relative to the -0.3 power law correlates with adult size better than does relative (temperature-corrected) development rate u ; in contrast, at a finer scale of diversity (among *Calanus* spp., or among large ($>50 \mu\text{g C}$) calanoids in general), u is the better correlate with adult size and the effect of g , is insignificant. Across all these scales, the ratio of relative growth and development rates g/u , is a better predictor of adult size than g , or u , alone, consistent with a simple model of individual growth.

KEY WORDS: Copepods · Body size · Development rate · Growth rate · Zooplankton · Trait-based Diversity

INTRODUCTION

Body size is often cited as a 'master trait' controlling or serving as a proxy for many aspects of functional diversity in phytoplankton, zooplankton, and other guilds (Litchman & Klausmeier 2008, Klerboe & Hirst 2014). Allometric explanations have a long pedigree in biology (Bergmann 1847, Kleiber 1932, Brooks & Dodson 1965, Silvert & Platt 1978), and the past decade has seen a flourishing of size-based theory-building and data meta-analysis in plankton biology (Baird & Suthers 2007, Saiz & Calbet 2007, Banas 2011, Edwards et al. 2012, Ward et al. 2012, Wirtz 2012, Record et al. 2013, Andersen et al. 2015). Marine pelagic copepods have been the focus of much of this work, not only because of their abundance and trophic importance in the world ocean but also because their definite number of molts and

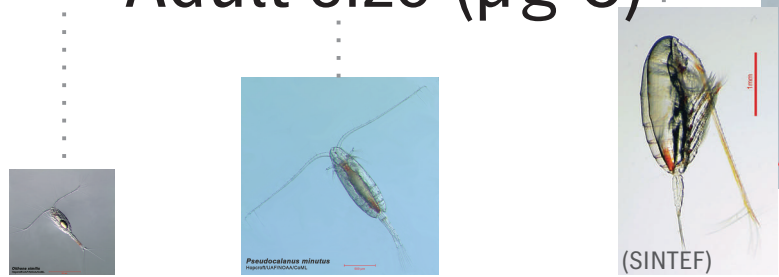
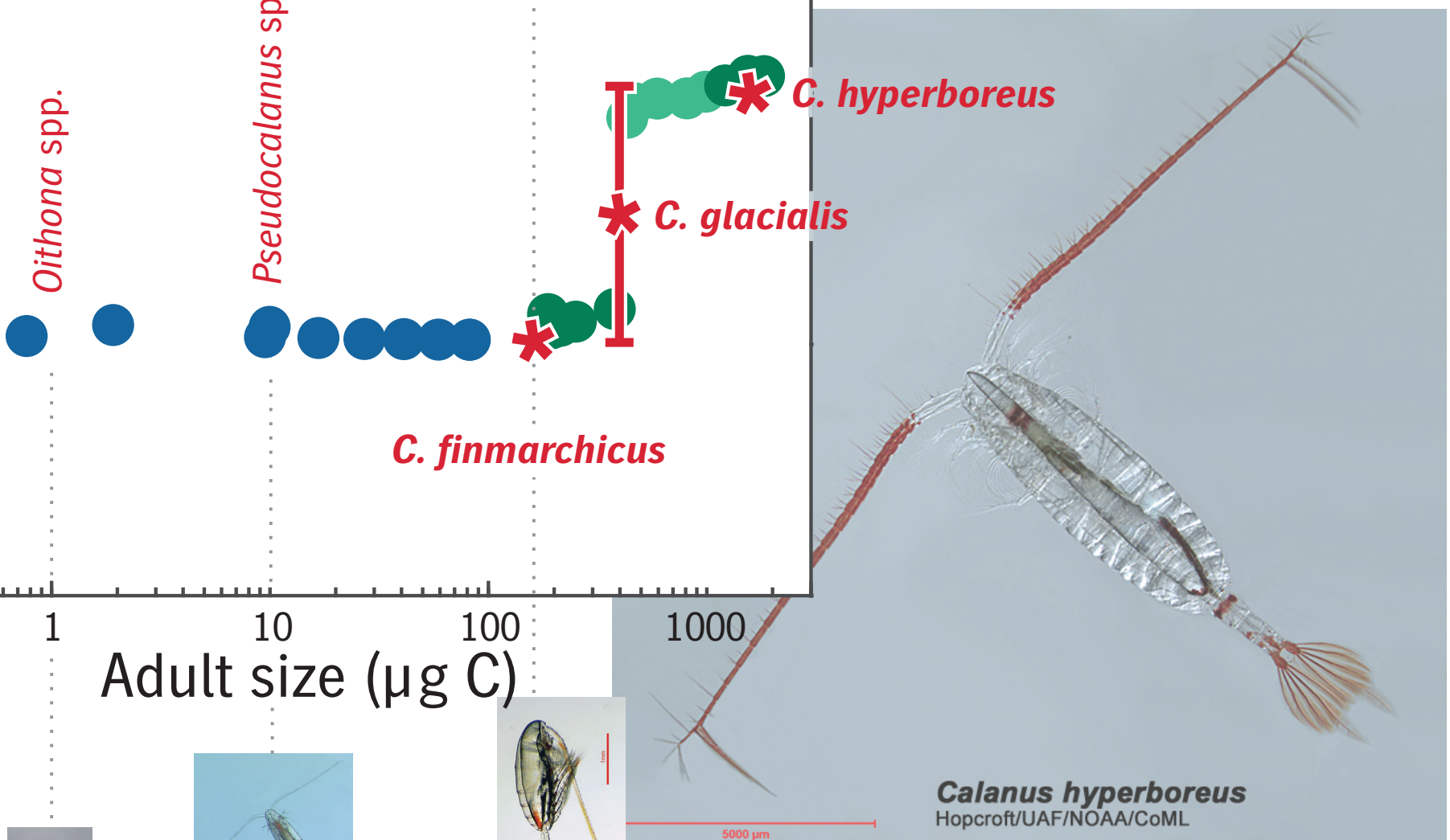
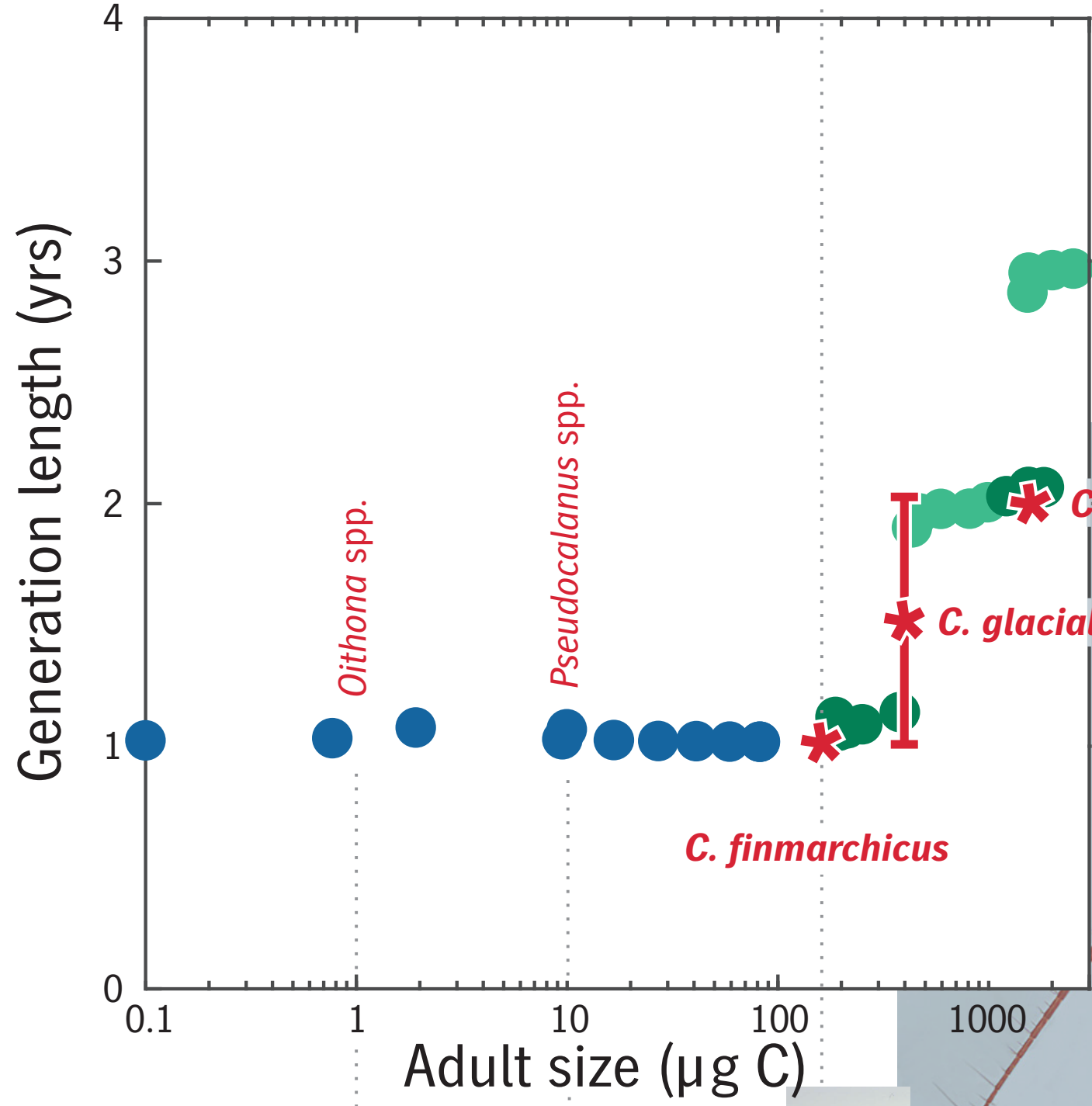
determinate growth make them good subjects for quantification of ontogenetic patterns in the lab (Foster et al. 2011). Numerous studies exist linking copepod vital rates (development, growth, ingestion, fecal pellet production, egg production) to size as well as temperature and prey (Klerboe & Sabatini 1995, Hansen et al. 1994, Hirst & Klerboe 2002, Bunker & Hirst 2004, Saiz & Calbet 2007, Klerboe & Hirst 2014).

Still, basic ambiguities remain in how growth rate, development rate, and adult body size are linked across copepod taxa. One can imagine an animal becoming a large adult either by growing quickly or maturing slowly; which of these ontogenetic models is more appropriate? Is it fair to think of growth rate as controlling adult size in this ontogenetic sense, or should we rather think of growth (or metabolic processes in general) as being controlled by body

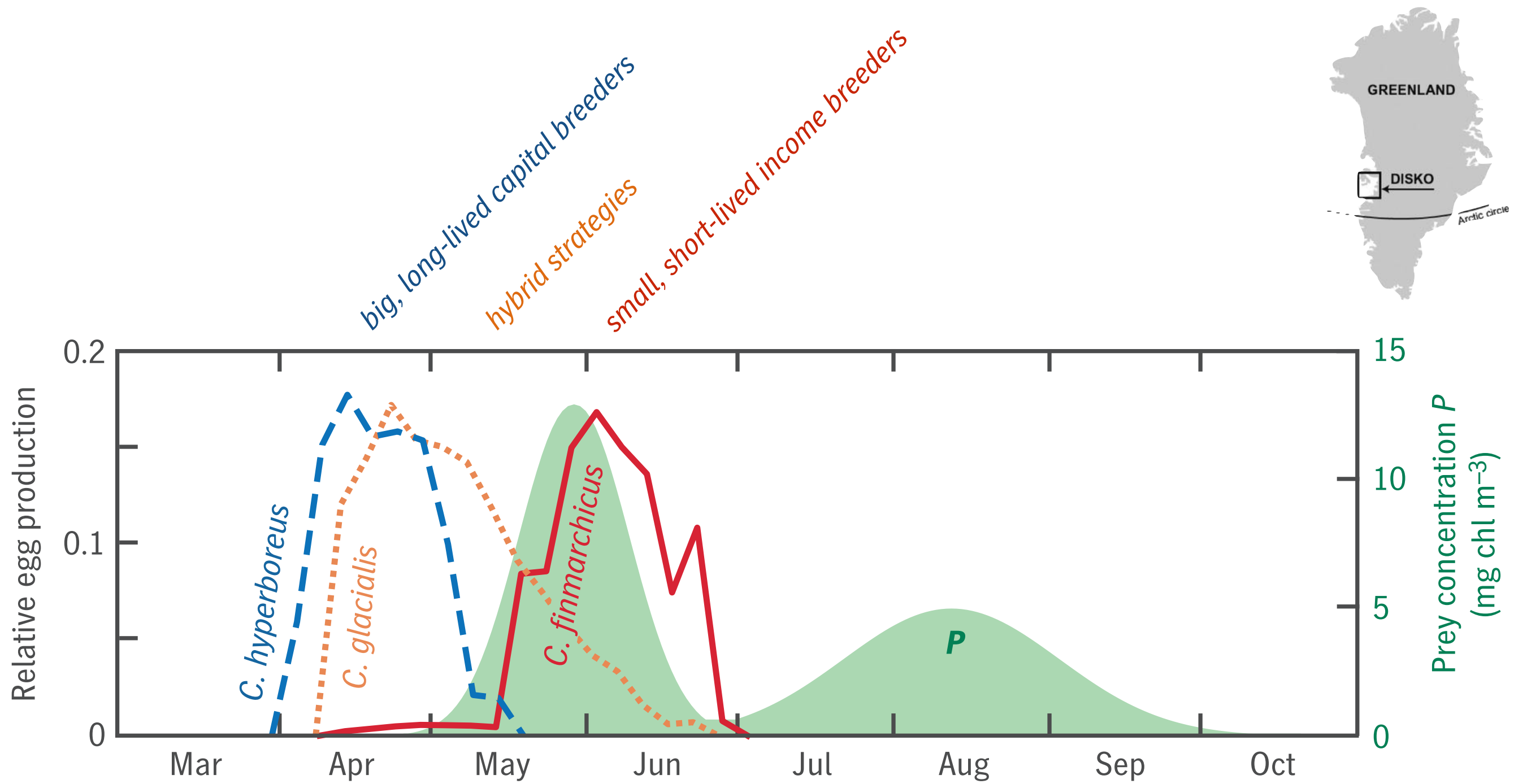
*Corresponding author: neil.banas@strath.ac.uk

varying relative *ingestion* rate
varying relative *development* rate

low-risk, low-reward ambush feeding
high-risk, high-reward active feeding
high-turnover income breeding
low-turnover capital breeding



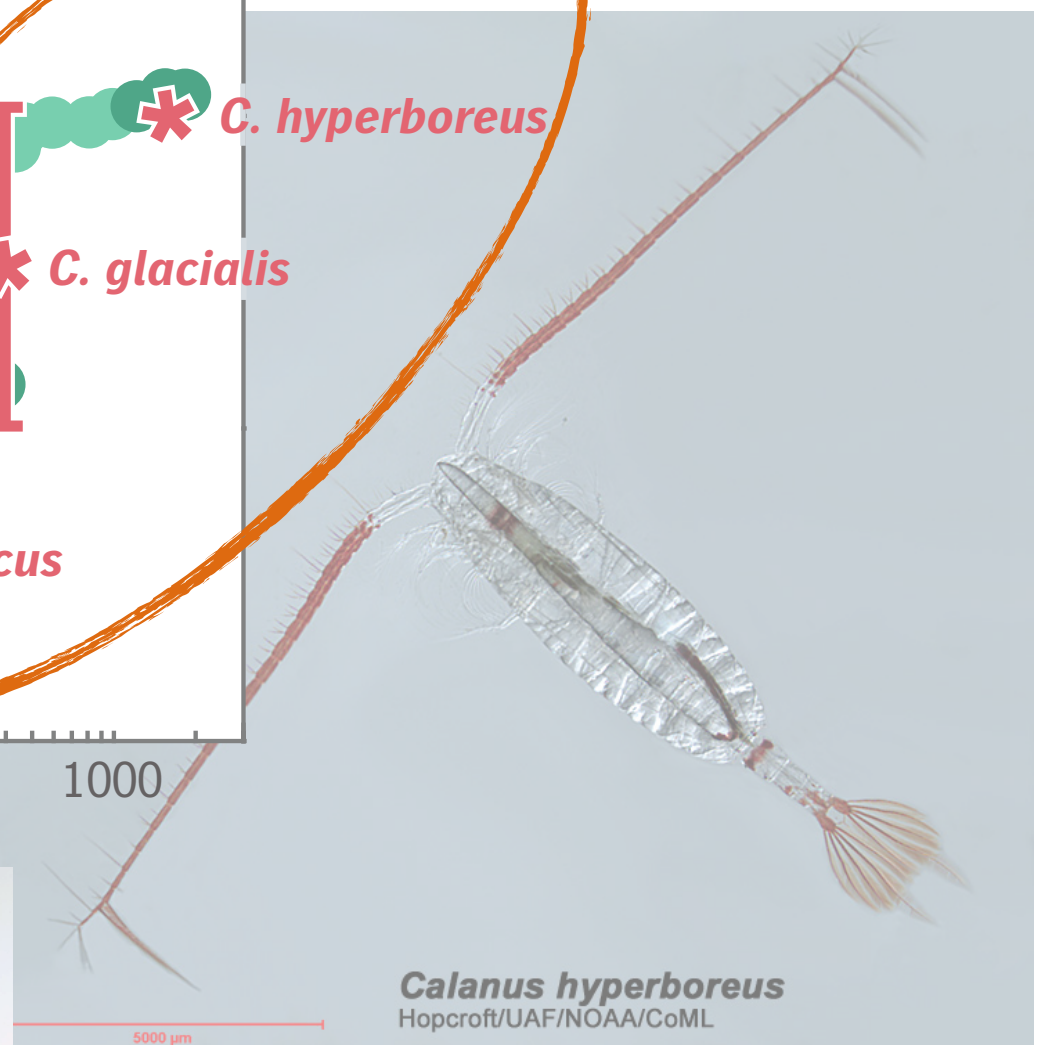
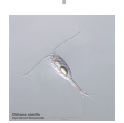
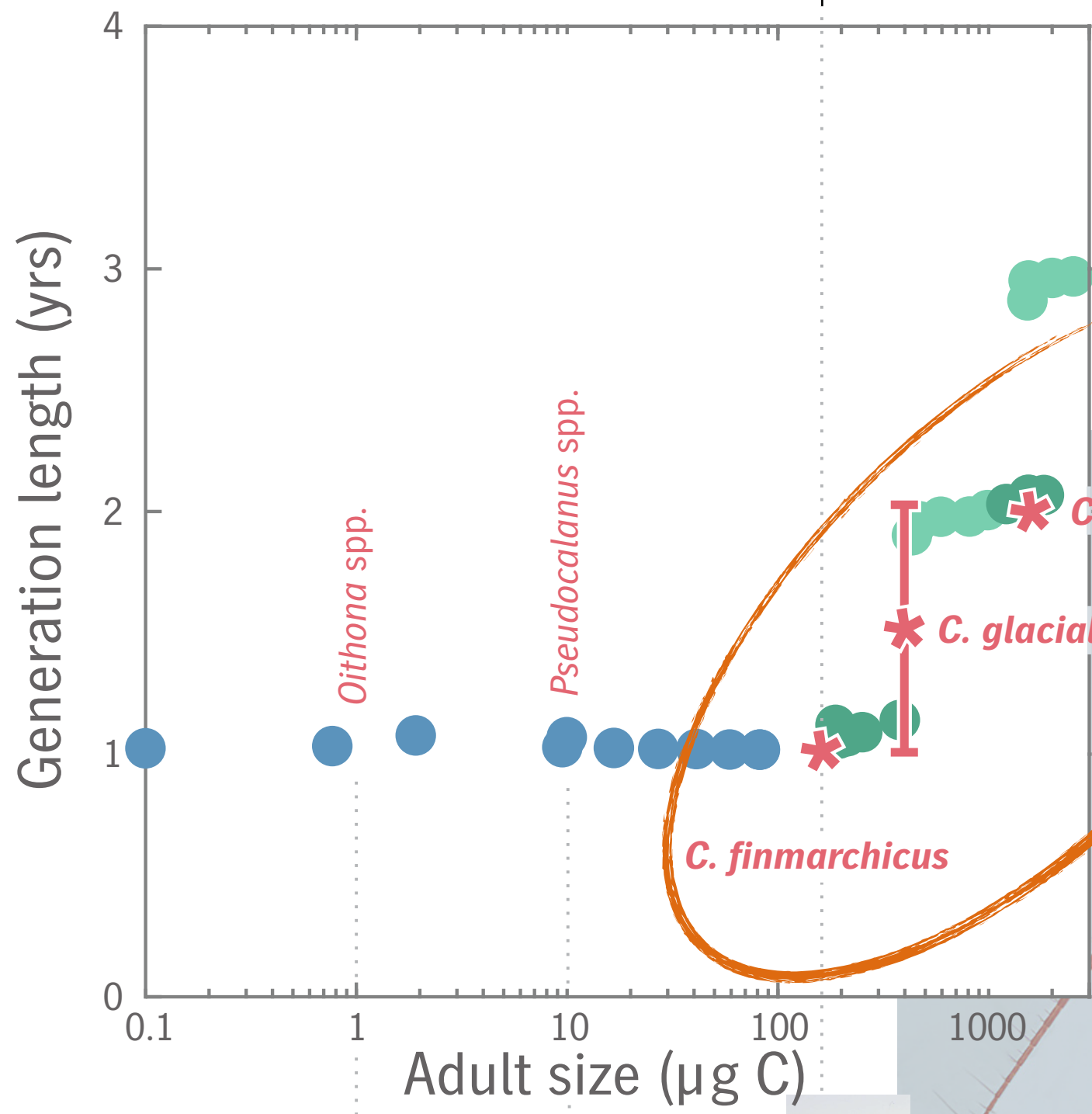
(Banas et al., *Front. Mar. Res.*, 2016)



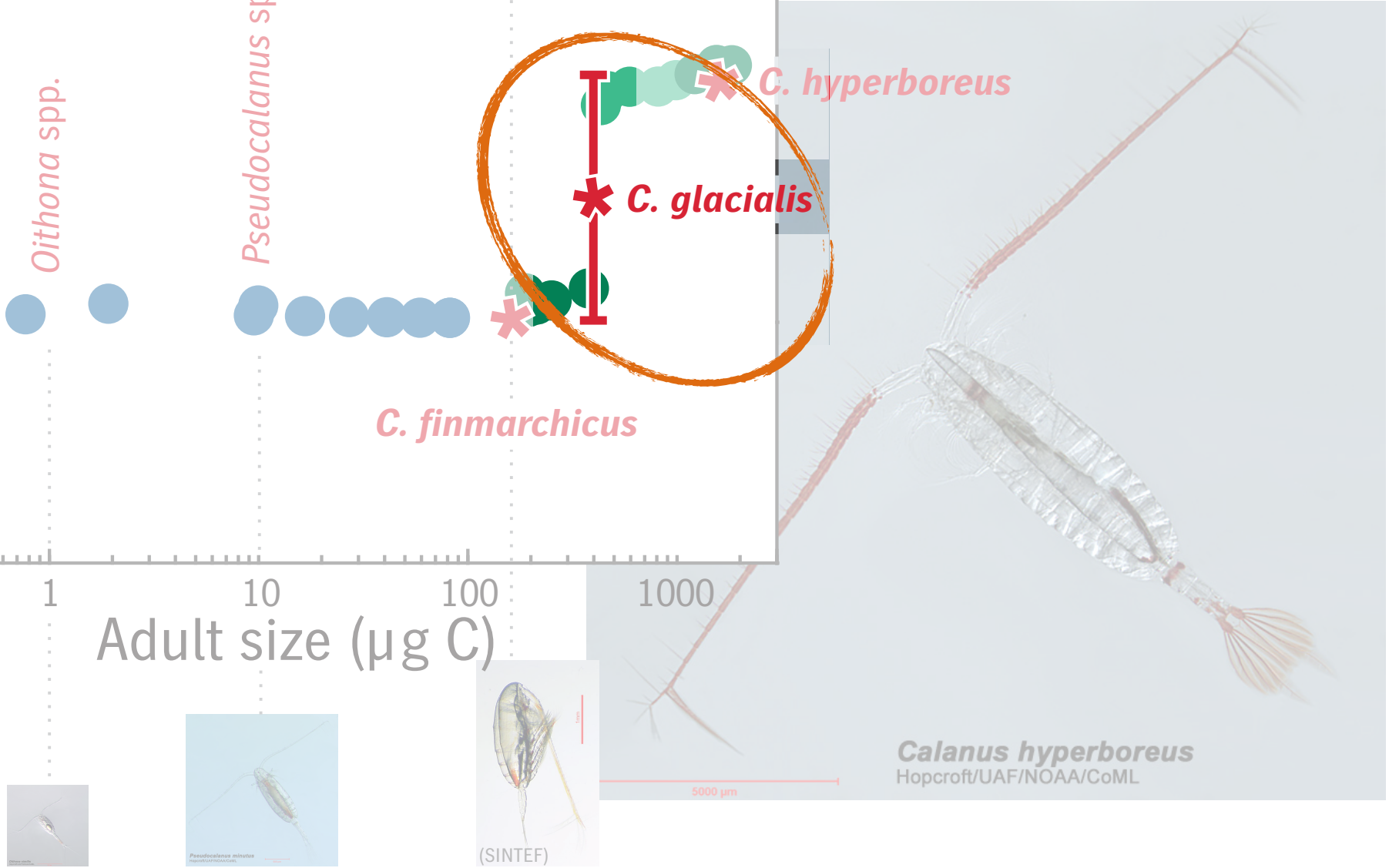
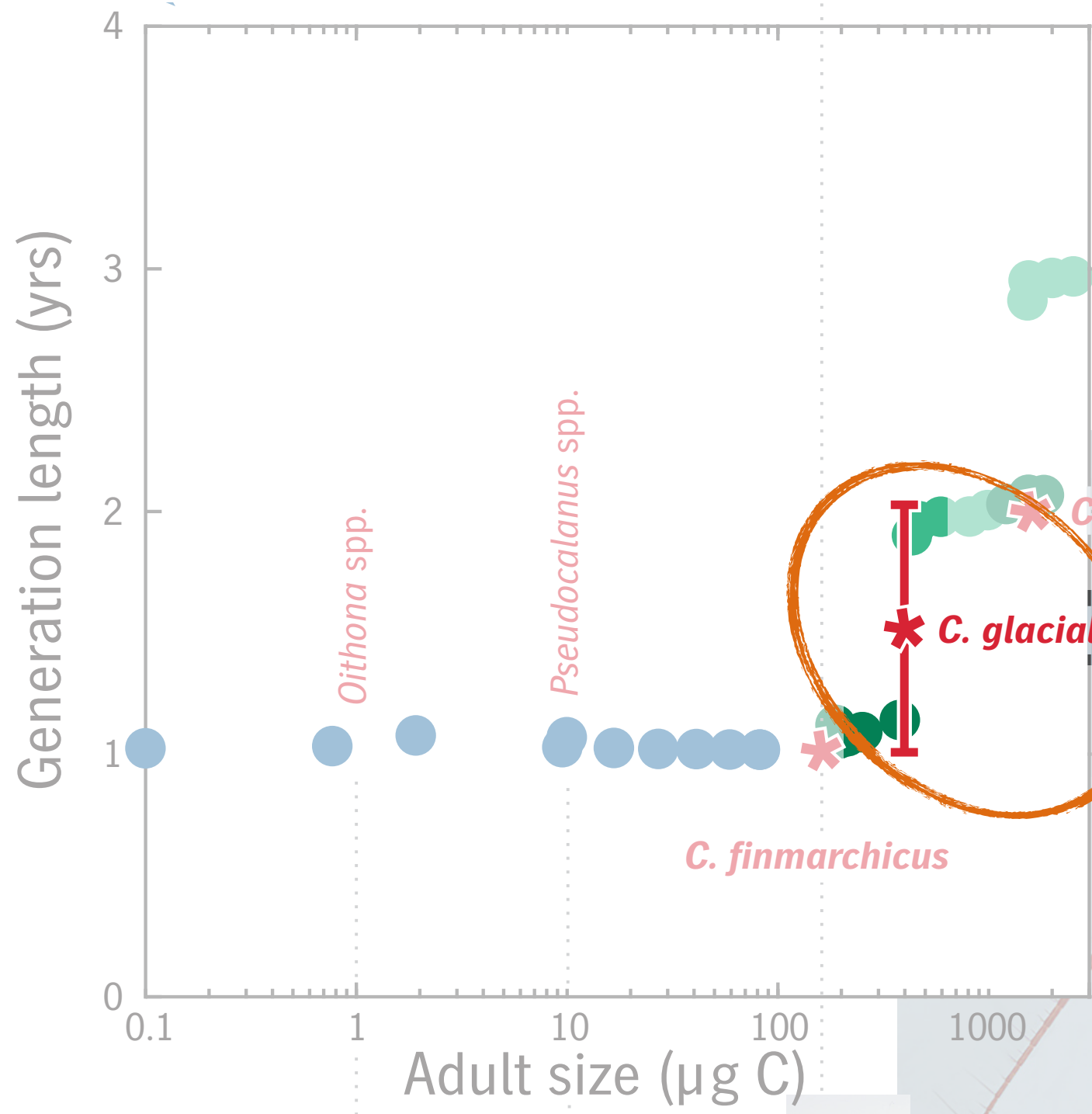
One recipe, many outcomes

This Disko Bay proof-of-concept is about viability of multiple *Calanus* recipes in one environment

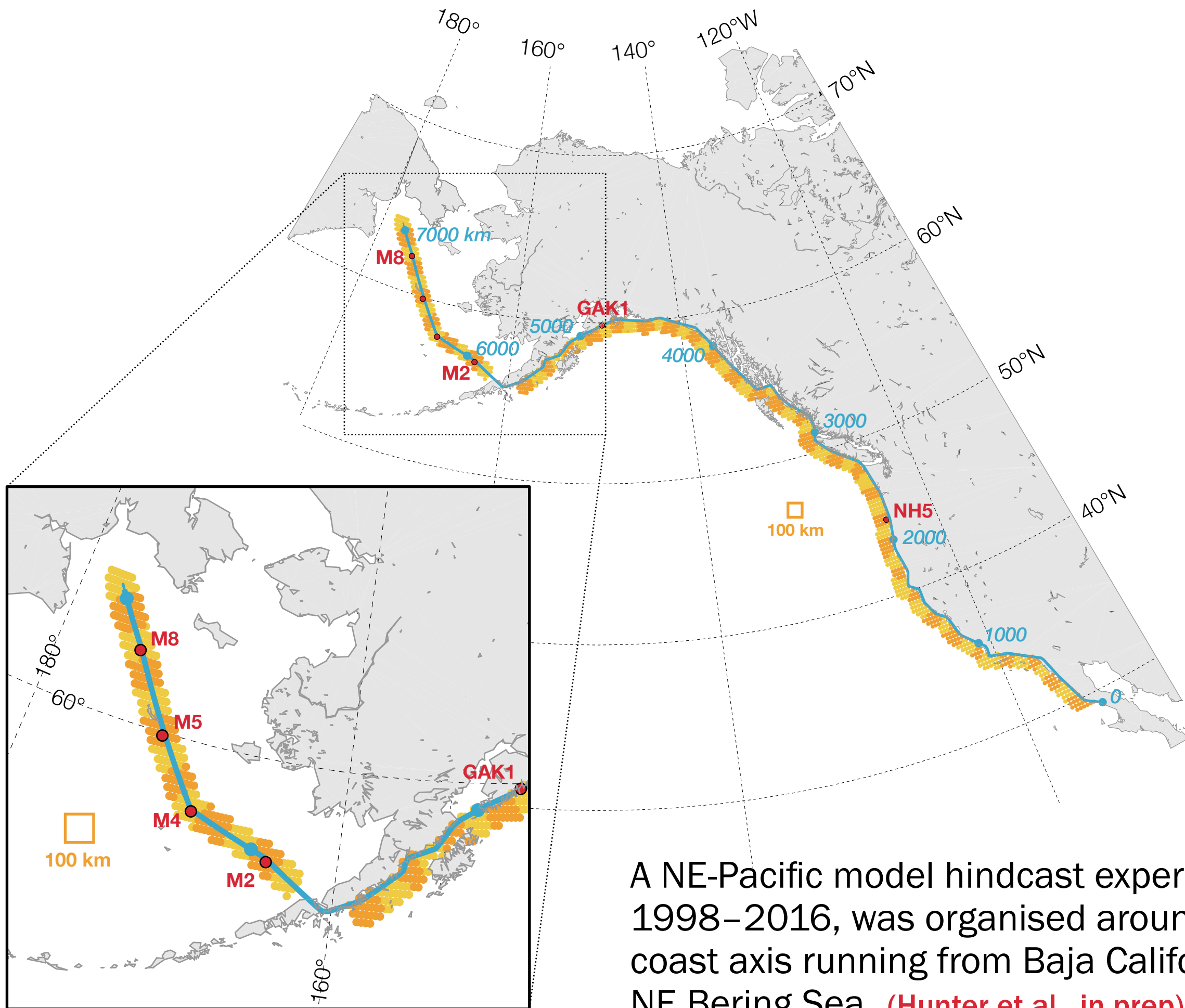
varying relative **development** rate



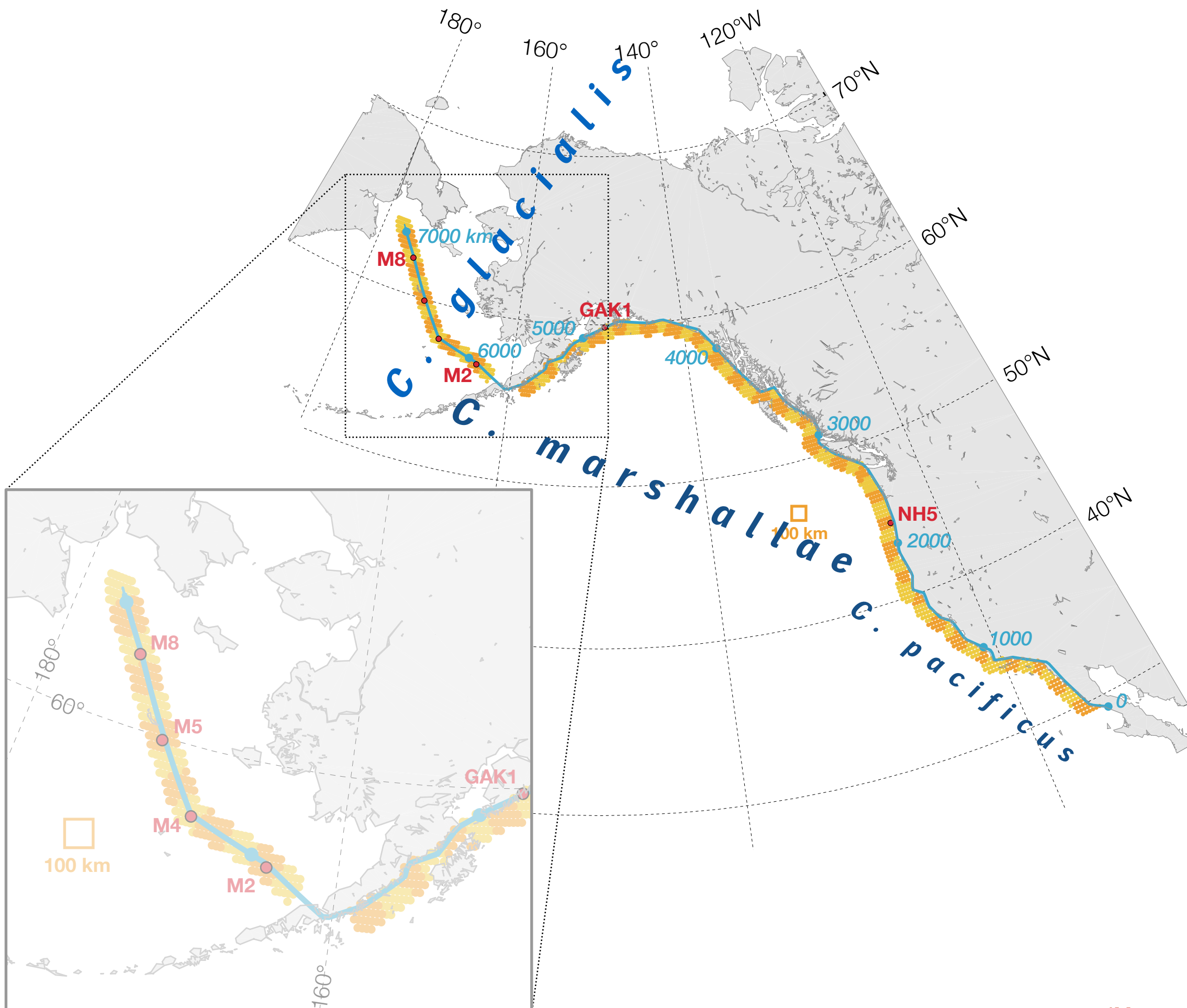
Next: how does a single *Calanus* recipe play out across multiple environments?



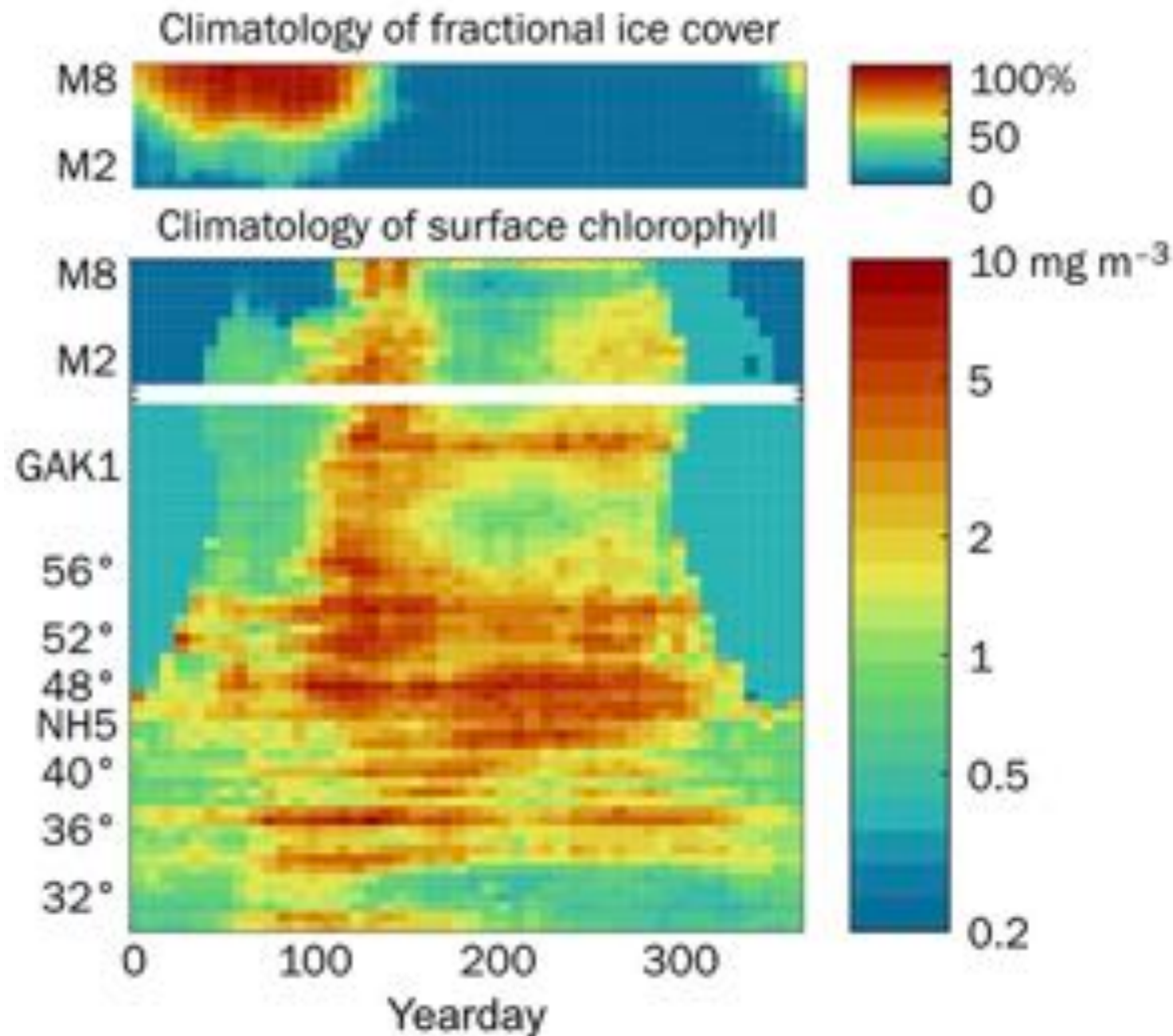
Calanus hyperboreus
Hopcroft/UAF/NOAA/CoML



A NE-Pacific model hindcast experiment, 1998–2016, was organised around an along-coast axis running from Baja California to the NE Bering Sea. (Hunter et al., in prep)

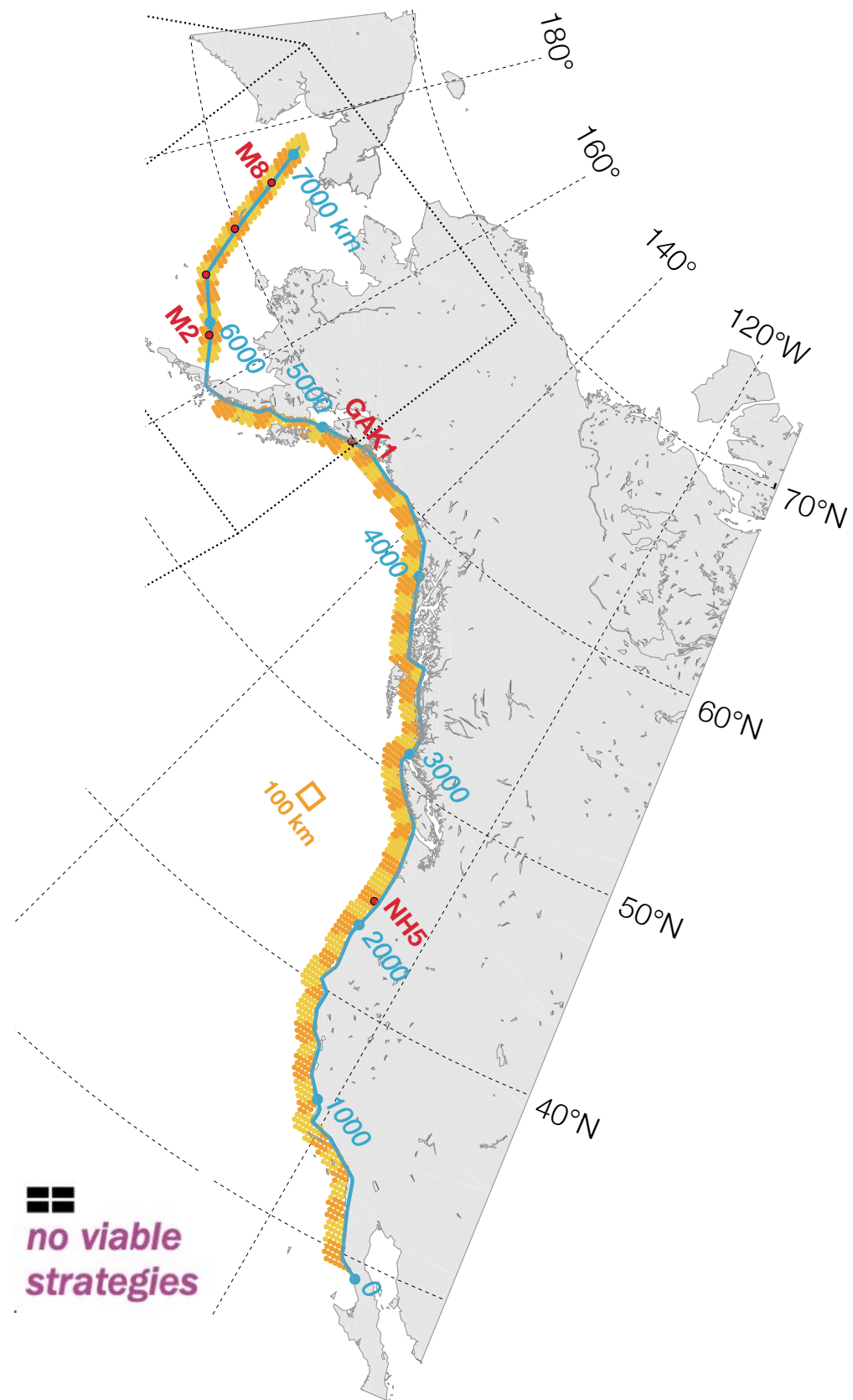
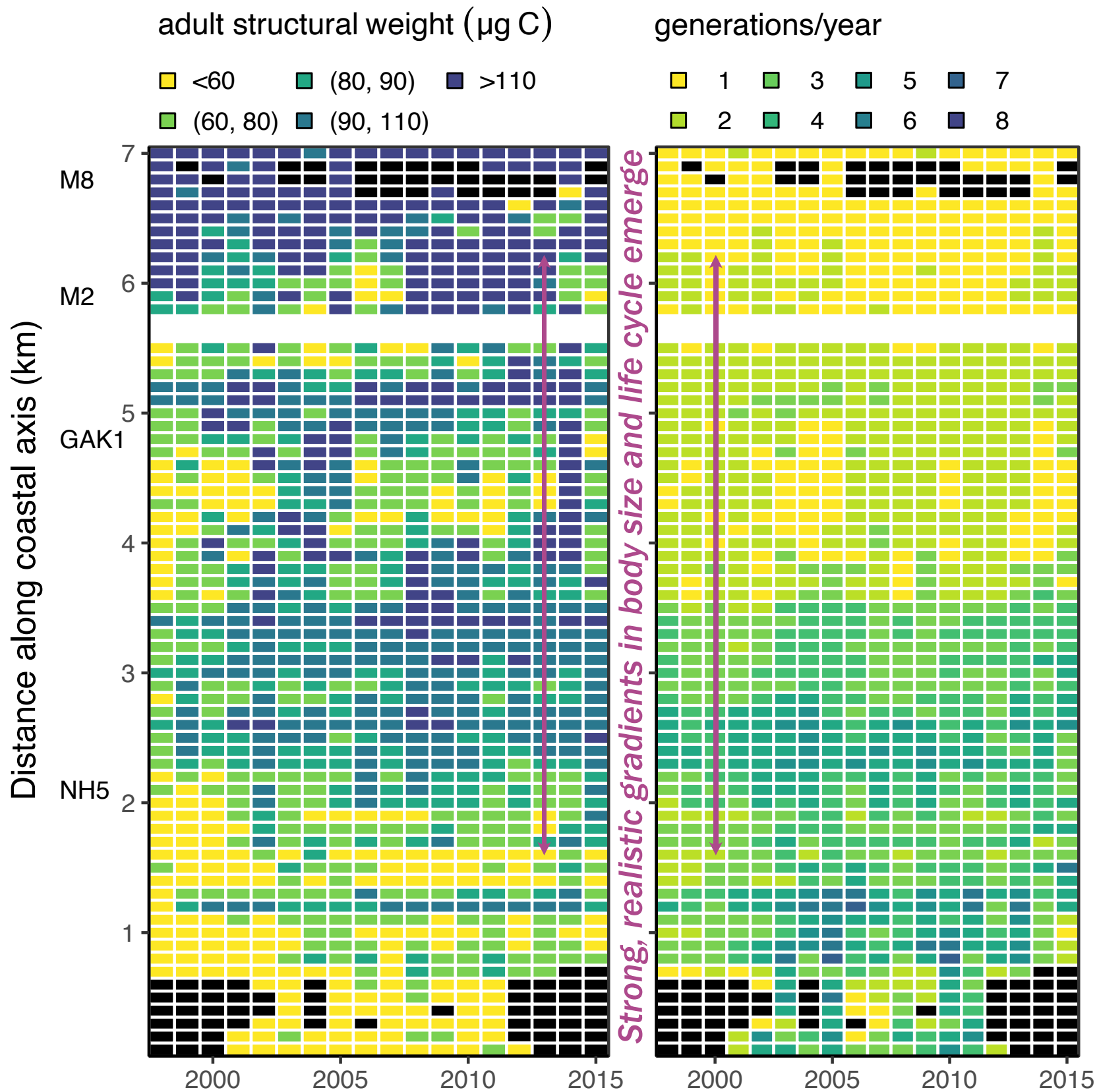


(Hunter et al. in prep)

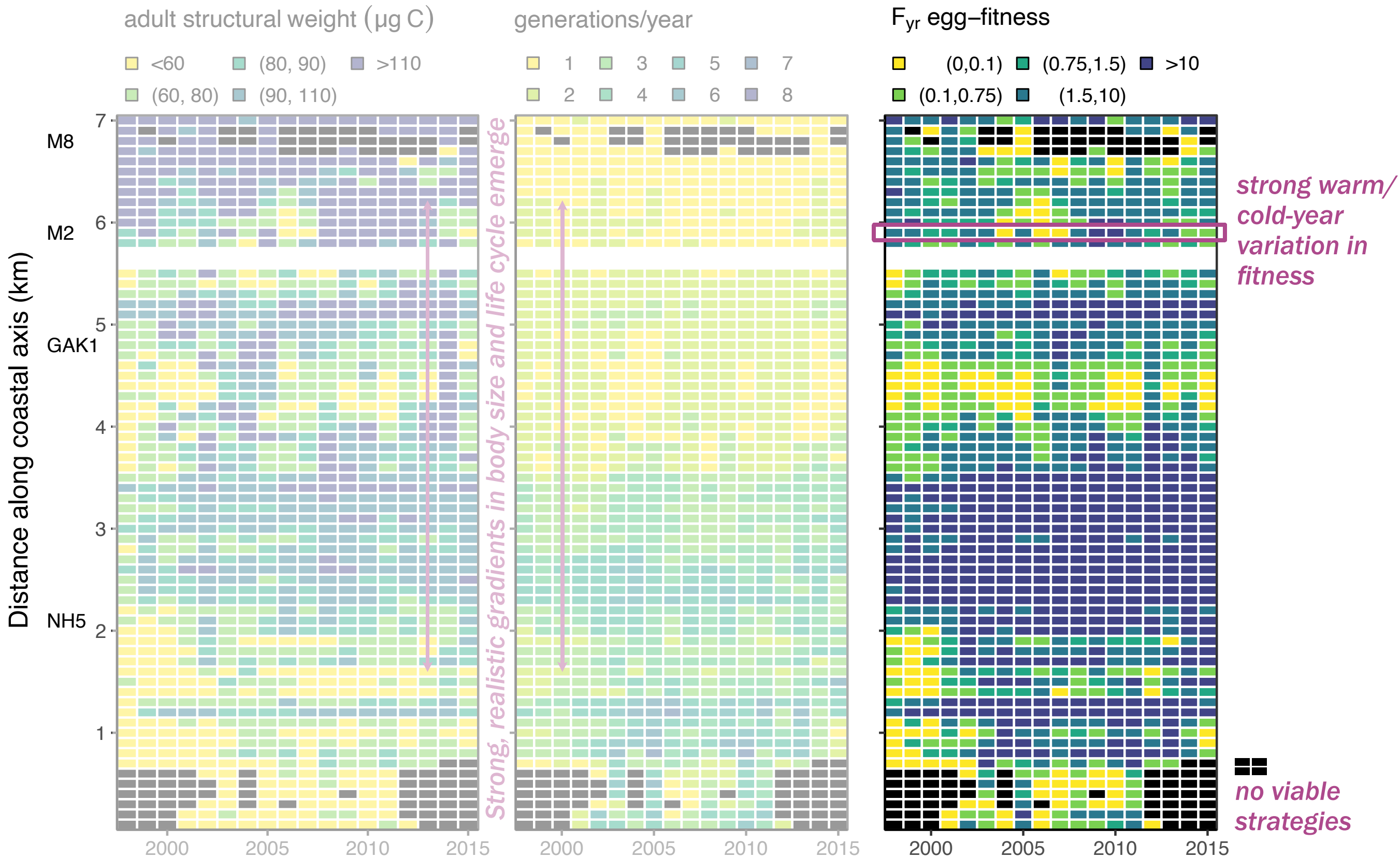


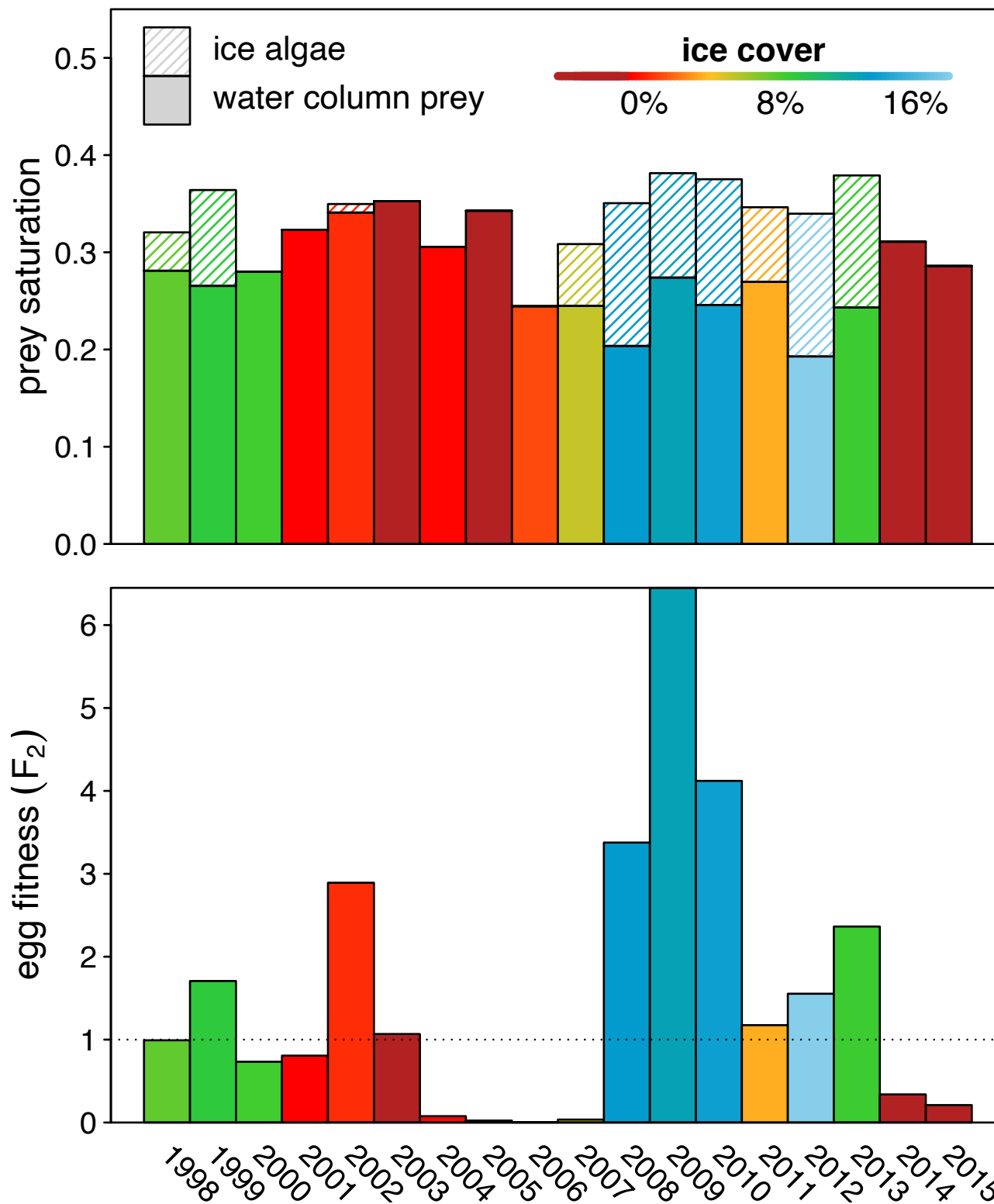
Model forcing was constructed from GlobColour merged-sensor chlorophyll, 1998–2016 (8 d, 25 km retrievals composited into 100×100 km averages), along with NOAA Optimal Interpolation SST, NSIDC ice cover, and WOA13 temperature at 500 m.

This experiment ignores advection.



(Hunter et al. in prep)



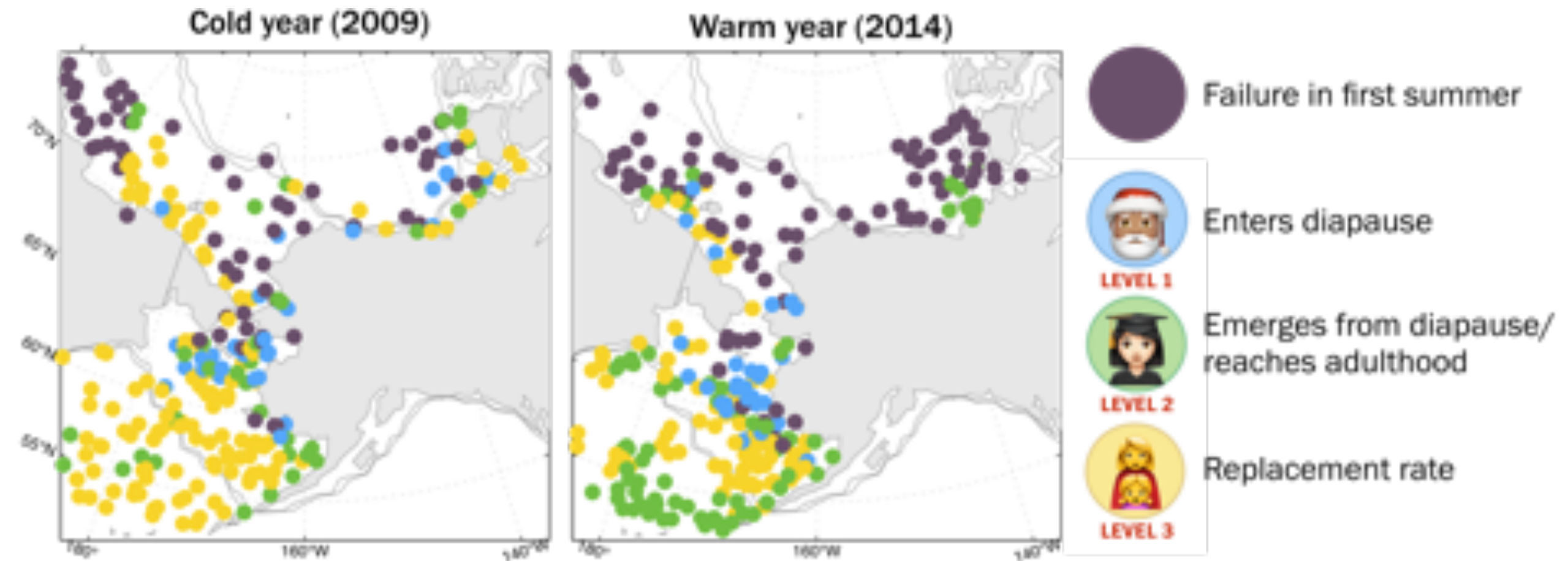


***cf. 1000-fold variation
in mean abundance
(Eisner et al. 2014,
Kimmel et al. 2017)***

Variations in available food (top; rescaled in terms of its effect on copepod development and growth rates) and the population response (bottom), at M2 in the SE Bering Sea

(Hunter et al. in prep)

Adding advection back in...



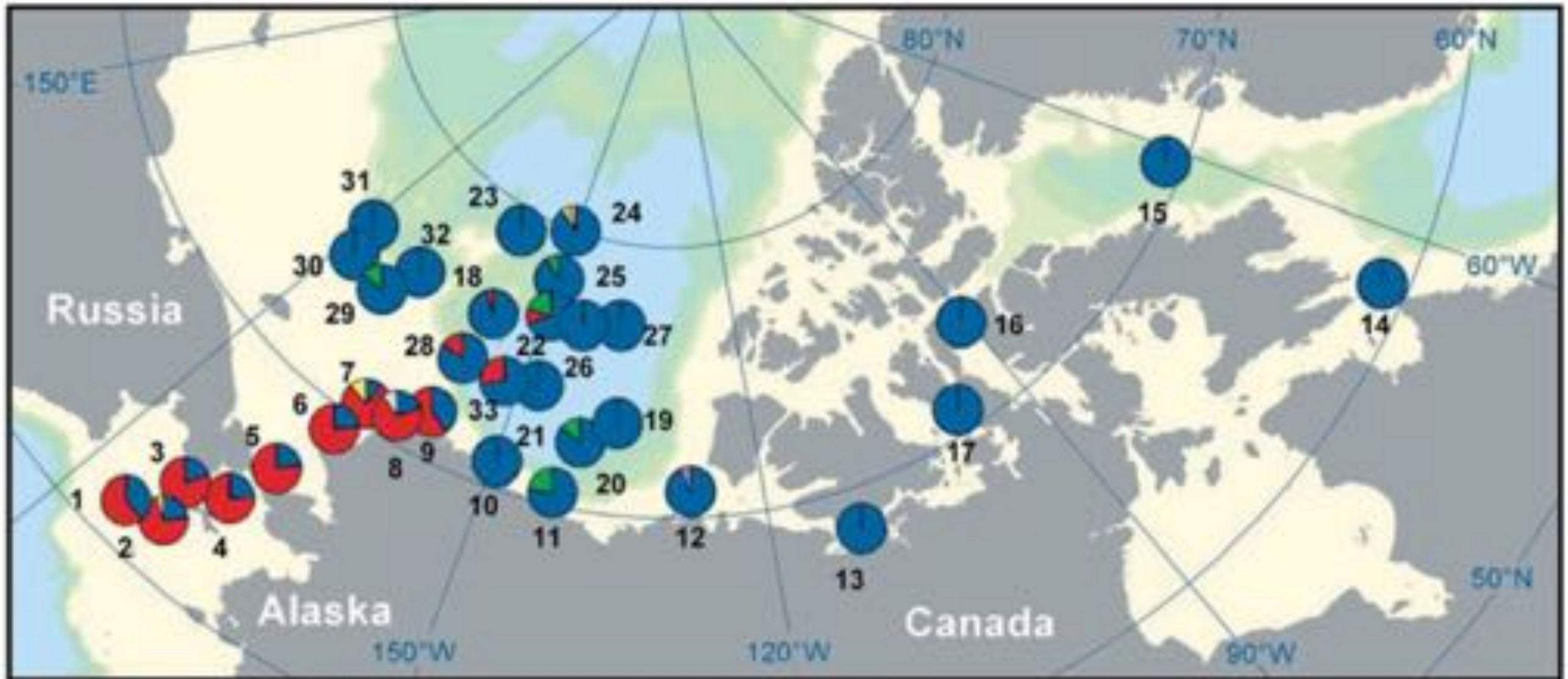
Each point represents the best outcome possible along a two-year flow trajectory (plotted at second summer).

The model also suggests a **strong but incomplete population bottleneck** that restricts the flux of successful individuals from the Bering Sea onto the Chukchi shelf and beyond, and keeps the reproductive capacity of the individuals that do pass through below replacement rate. This bottleneck appears to be stronger in warmer, lower-ice conditions.

Penetration of Pacific zooplankton into the western Arctic Ocean tracked with molecular population genetics

R. J. Nelson^{1,2,*}, E. C. Carmack¹, F. A. McLaughlin¹, G. A. Cooper²

(2009)



We construct pan-Arctic hindcasts and projections in Coltrane by running it along particle tracks in the 3D biophysical models **BIOMAS** (Pacific) and **SINMOD** (Atlantic).

M2 (Bering Sea)

NH5 (Newport)



Allowing $\pm 20\%$ variation in **development rate**

(along with flexibility in life-history/
diapause timing as before)

Longitude along Atlantic inflow

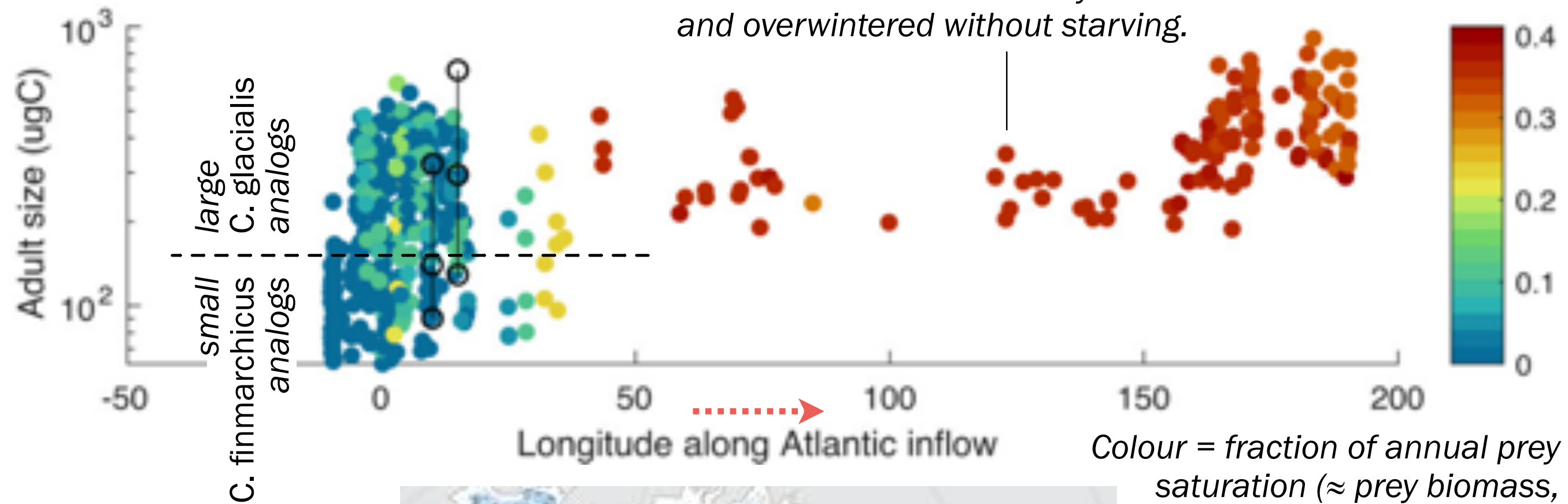


Allowing $\pm 20\%$ variation in development rate

development rate

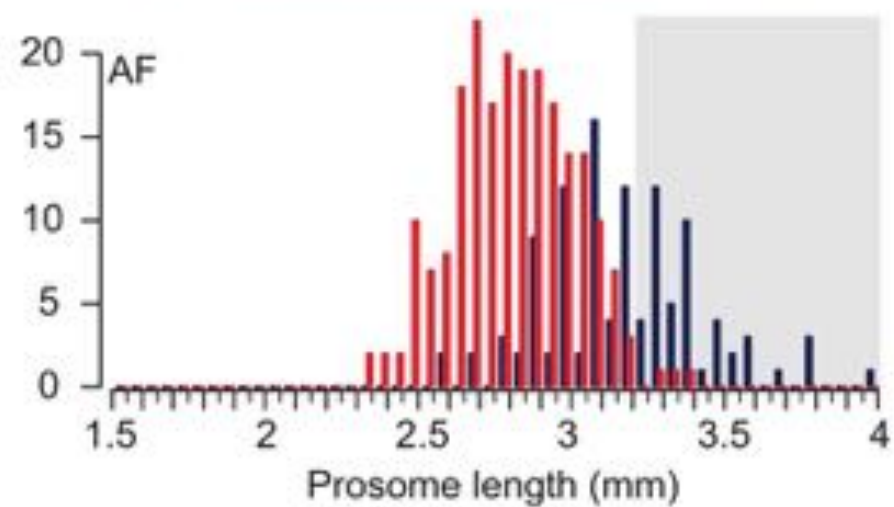
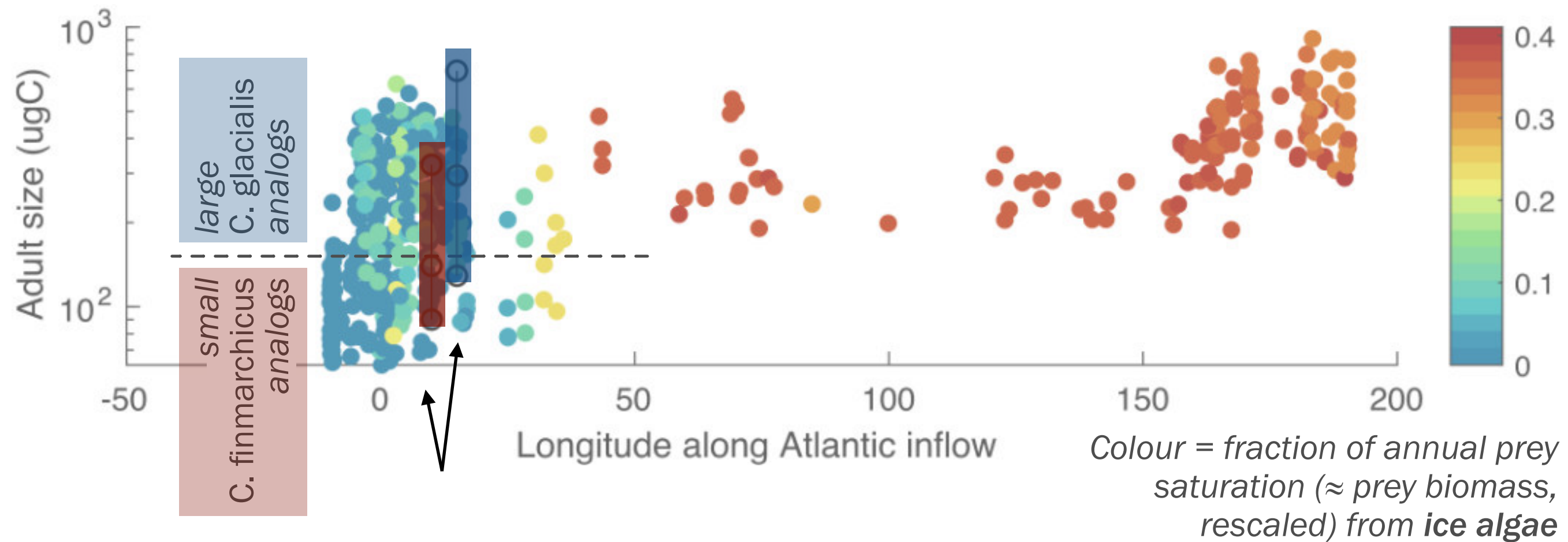
(along with flexibility in life-history/
diapause timing as before)

Each point represents the centre of mass of egg production by a Calanus cohort that has successfully matured and overwintered without starving.



*Colour = fraction of annual prey saturation (\approx prey biomass, rescaled) from **ice algae***

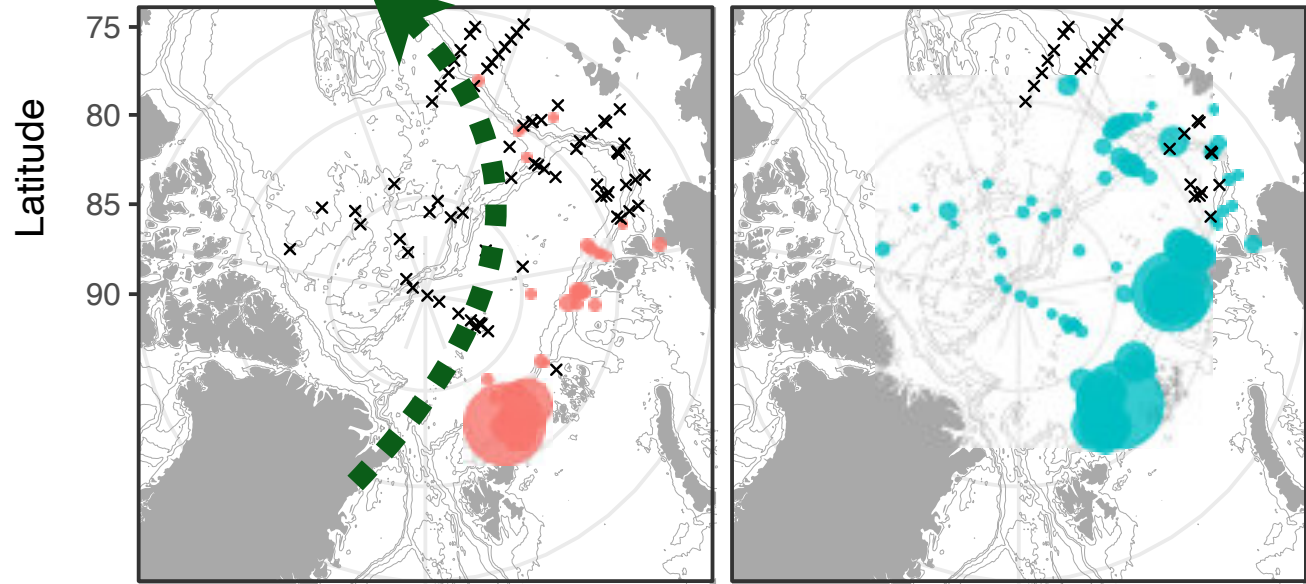




(Renaud et al. 2018)



C. finmarchicus



Life stage

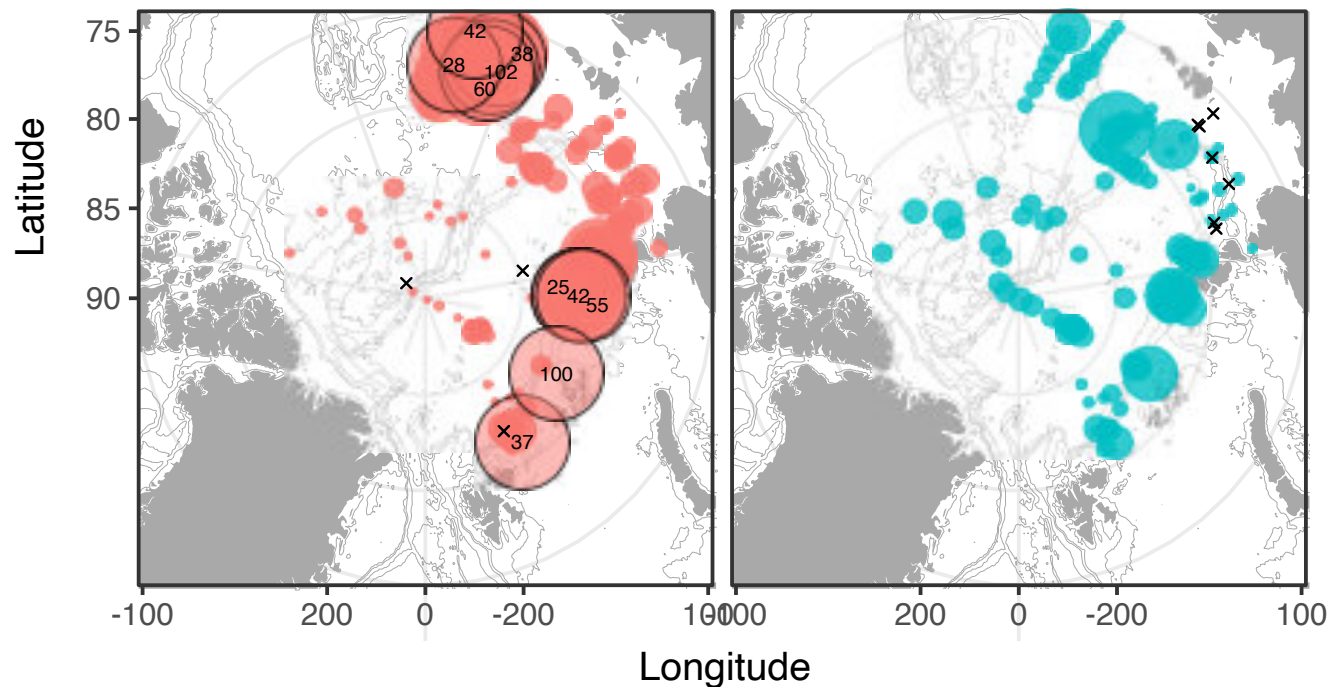
- C1-C4
- C5-AF/AM

**Abundance
(1000 ind m⁻²)**

- 5
- 10
- 15
- 20
- >25



C. glacialis

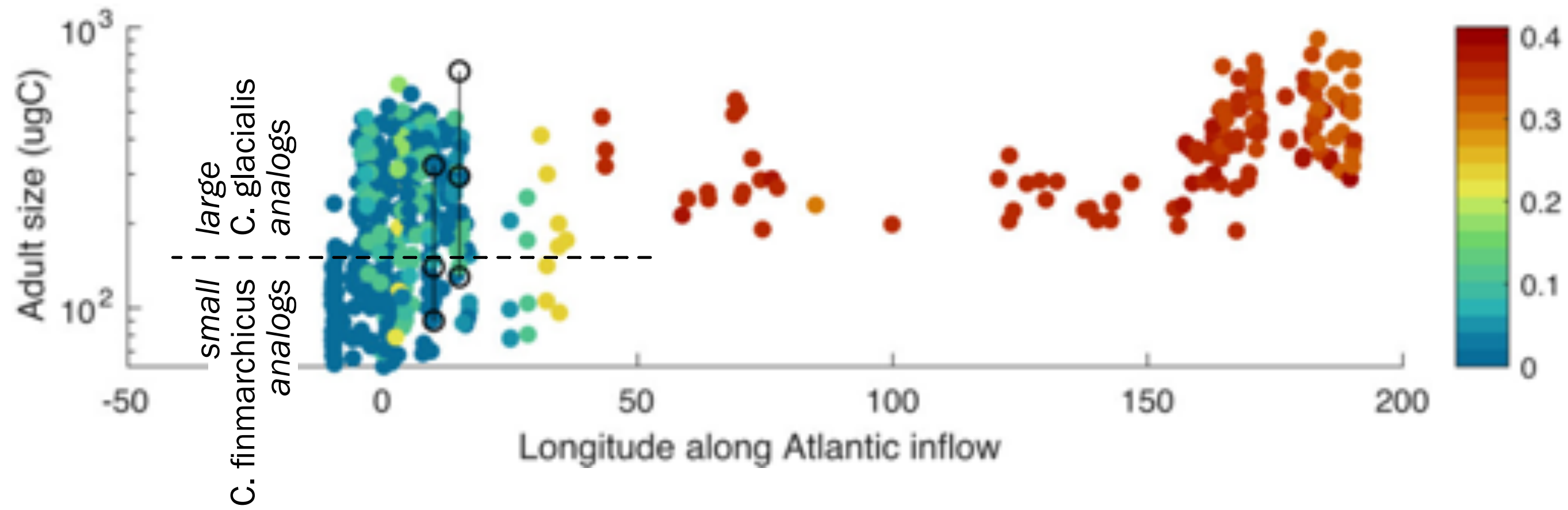


Abundance of *C. finmarchicus* (top) and *C. glacialis* (bottom) in summer surveys, 1993–2016.

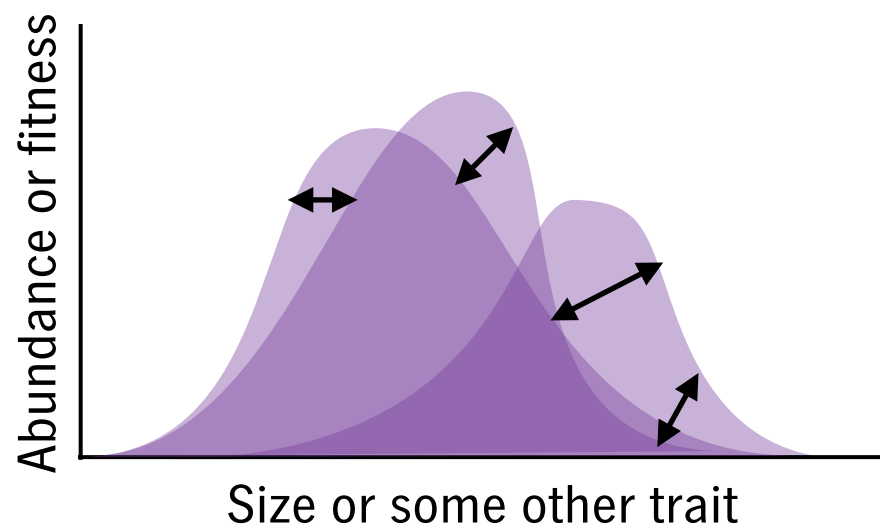
C. finmarchicus are found as far into the Eurasian Arctic as 90°E—but without the early life stages that indicate continuing reproduction. In contrast, early stages of *C. glacialis* are found into the E Siberian Sea and beyond.

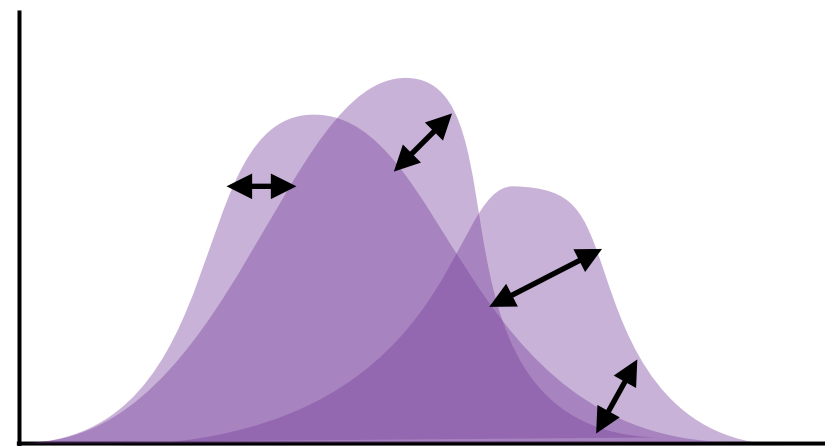
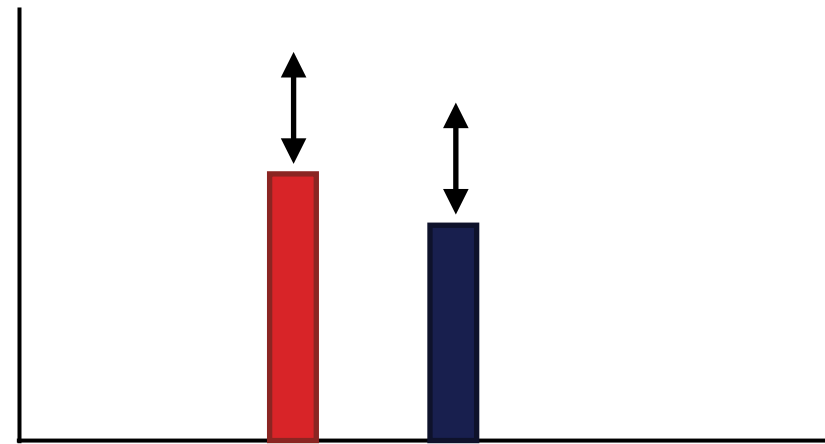
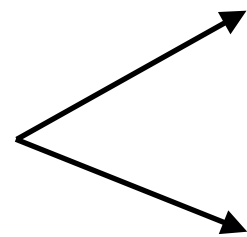
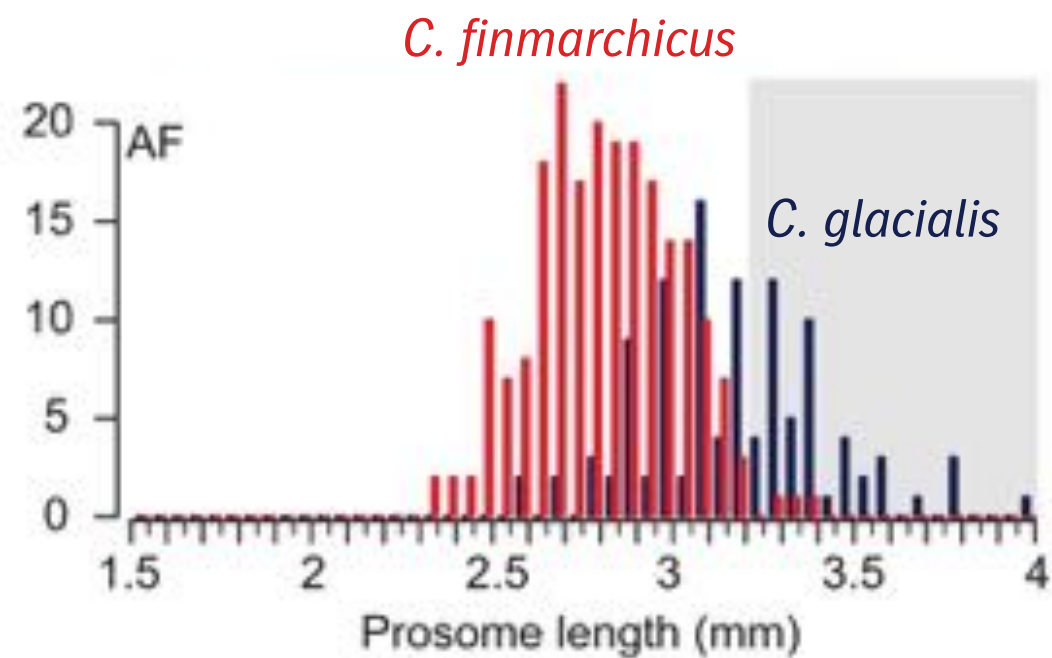
(E Ershova and K Kosobokova)

But where have the species gone?
(And does it matter?)



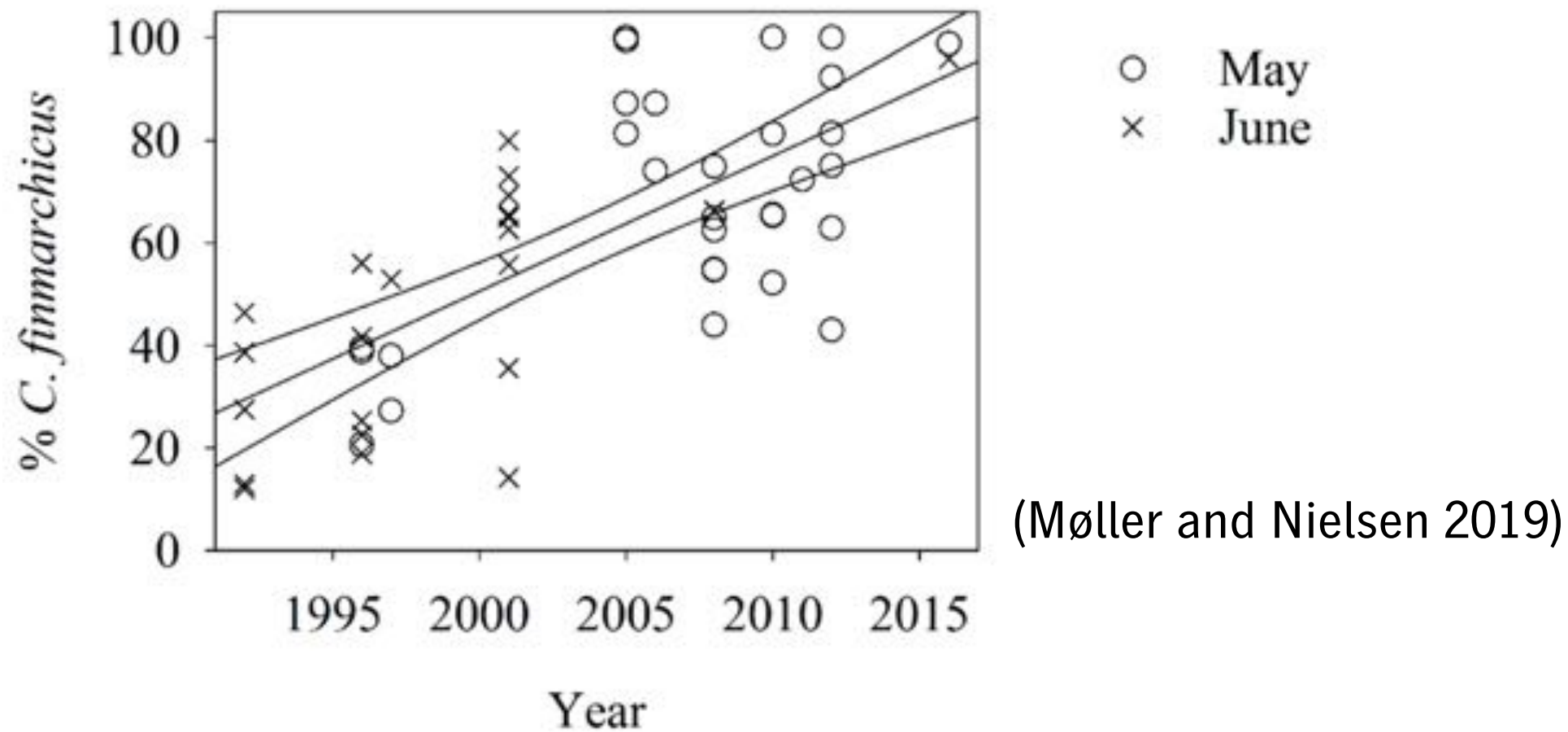
≈





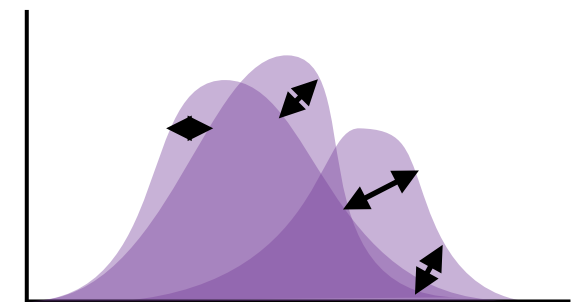
Whether to model diverse, plastic communities as competing, fixed-trait **species/populations** or continuous, fully plastic **trait distributions** isn't just a matter of preference or philosophy.

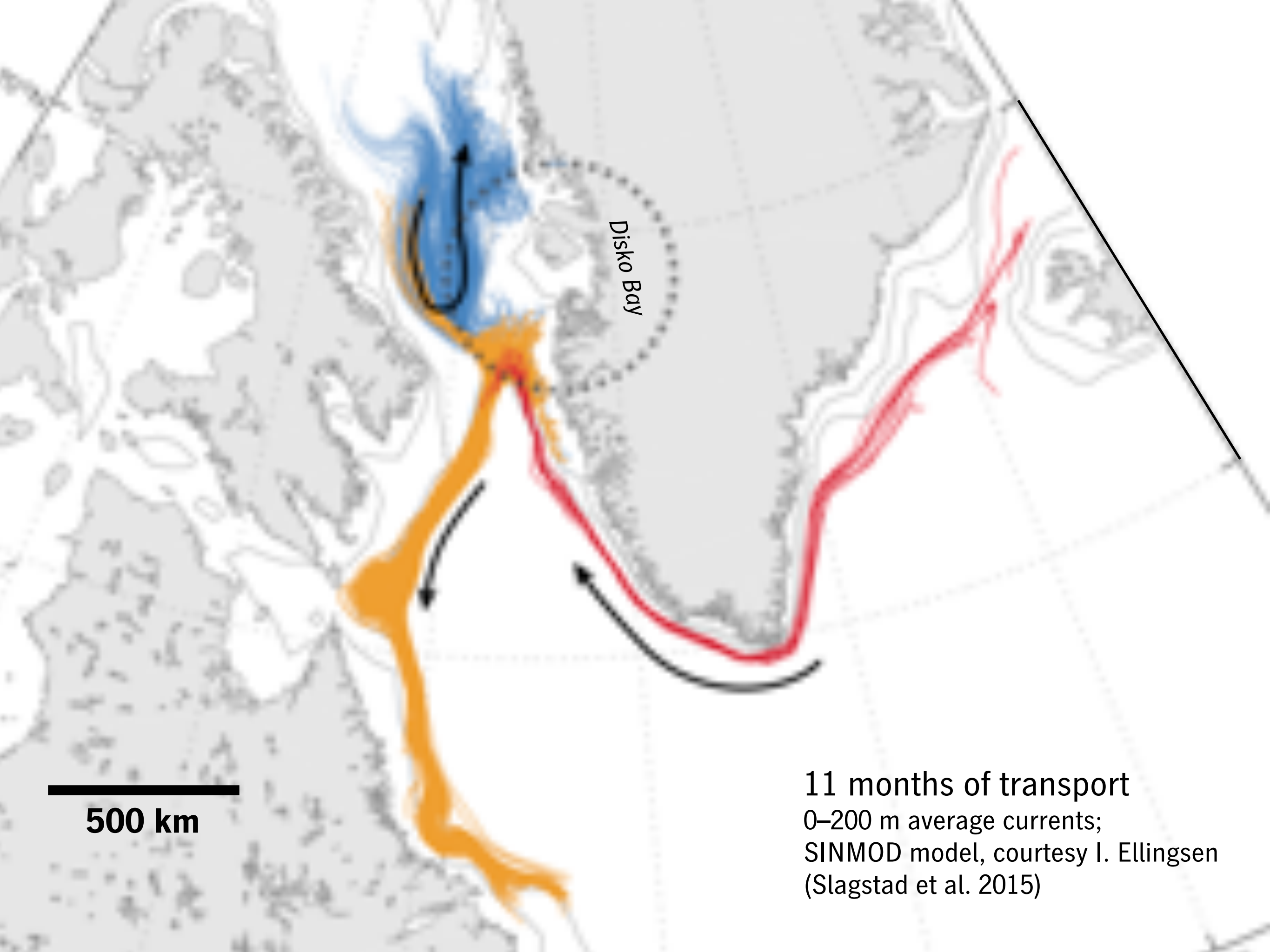
We don't know which of these better highlights the actual drivers of long-term change.



Does the Atlantification of Disko Bay zooplankton depict a shift in the fitness landscape driven by local environmental cycles?

Or is it really about oceanography and ecology upstream, on a large scale?





Disko Bay



500 km

11 months of transport
0–200 m average currents;
SINMOD model, courtesy I. Ellingsen
(Slagstad et al. 2015)



We're going to hypothesize recipes for *Calanus* species, not just individuals, e.g.

“Eurasian *C. finmarchicus* and *C. glacialis* are genetically distinct

H) because body size can only vary so much within one breeding population.”

H) because *C. glacialis* is uniquely adapted to eating ice algae.”

H) because they have unique overwintering strategies.”

H) for no functional reason at all; it's just about advection and connectivity.”

⋮

(The goal is to **reject** as many of these as possible.)

Conclusions

The Coltrane model implements the **hypothesis** (rooted in a lab meta-analysis) that trait differences across northern *Calanus* populations are the result of a **single, shared recipe for growth and development playing out across varying prey and temperature cycles.**

Banas and Campbell,
MEPS, 2016

Banas et al., *Front Mar Sci*, 2016

This hypothesis has proved surprisingly difficult to reject! Both the high adaptive capacity, and limits on adaptive capacity, of this way of being a copepod, arise in our simulations from this **general arithmetic** of development rate, growth rate, and days of net energy gain per year.

Hunter et al. in prep
McRae et al, in prep

This is a powerful result for large-scale modelling of future climate-change impacts. However, it means that identifying the role of **species-level adaptations and constraints** in shaping that future will require different kinds of evidence.

Renaud et al. *ICES JMS*, 2018

Hobbs et al., *Front Mar Sci*, submitted

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neilbanas.com/projects/coltrane