The Future of Arctic Marine Ecosystems

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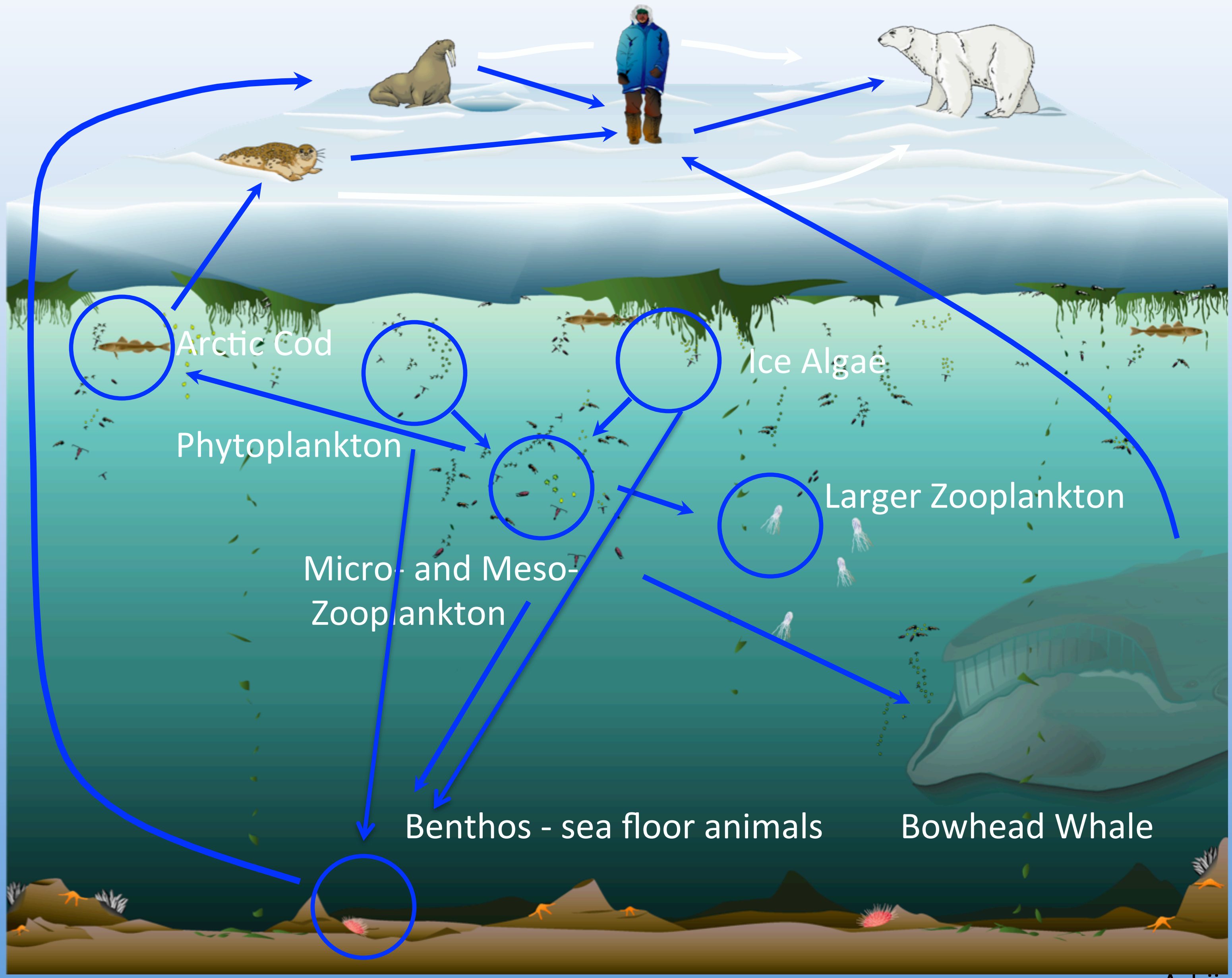
Arctic Marine Food Web



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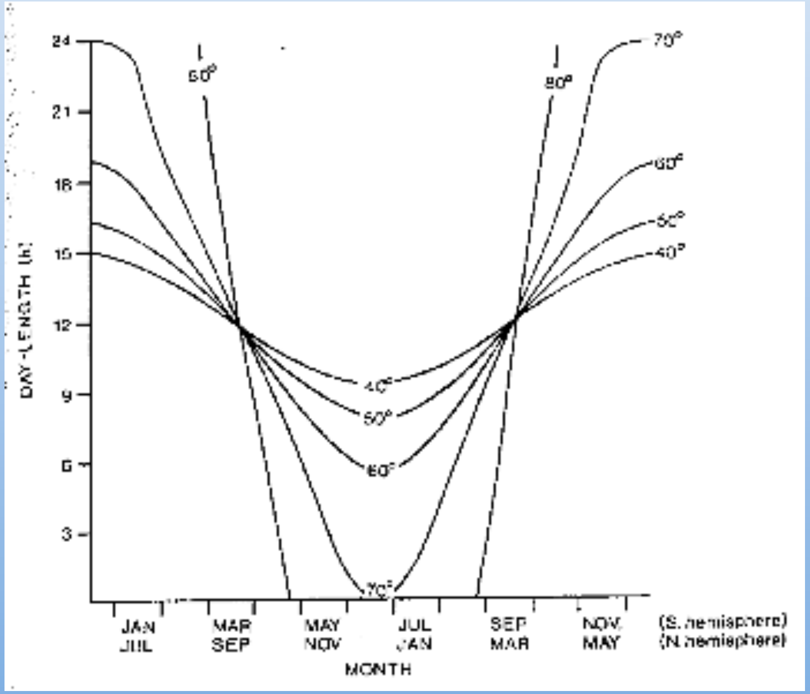
What Controls Marine Ecosystems in the Arctic?

- Arctic marine ecology is profoundly impacted by the seasonal variations in temperature, light, and ice cover
- Life histories of organisms are timed to the seasonal cycles

  - Light - drives photosynthesis, absent during winter
  - Temperature- water temperature (min. -1.8°C); many lower trophic level organisms are poikilothermic so their metabolism (growth) is slow
  - Nutrients-required by phytoplankton and algae for photosynthesis
  - Sea Ice-barrier to light and heat; critical substrate for organisms ranging from phytoplankton to mammals
  - Hydrographic Structure-vertical structure of water column defines plankton distributions
  - Advection- source of organisms, nutrients, redistributes plankton
  - Seasonally varying food supply



Smith and Sakshaug 1990

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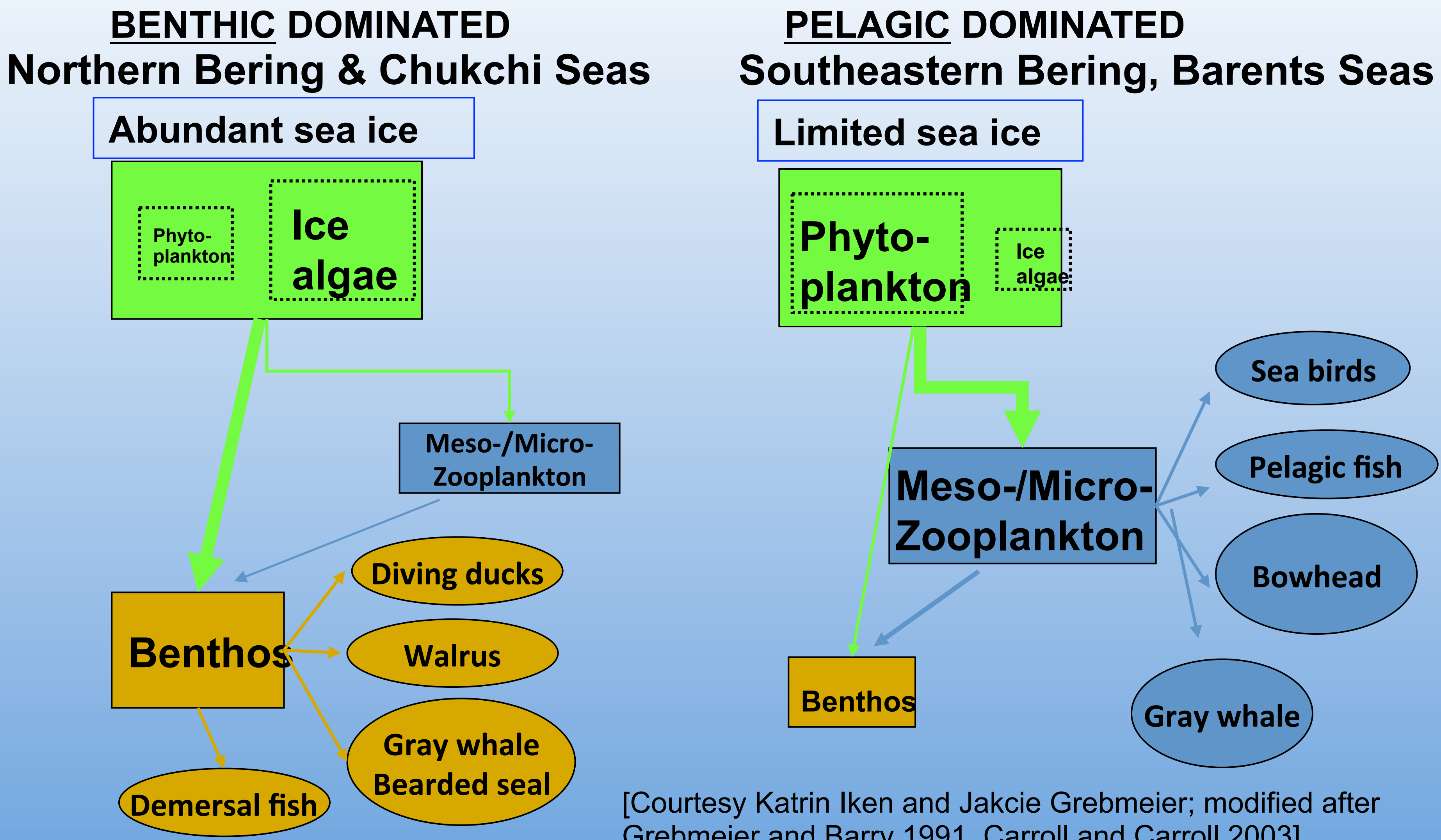
Benthic vs. Pelagic Dominated Ecosystems



[Courtesy Katrin Iken and Jakcie Grebmeier; modified after Grebmeier and Barry 1991, Carroll and Carroll 2003]

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How might climate change impact this ecosystem?

- Change in circulation, input of nutrients and heat (water temperature), and biota
- Reduction of ice that can have serious consequences for ice obligate animals that live in/on the ice as well as changing the ice and light environment
- Changes in the ranges of organisms
- Changes in the marine food web
  - Changes in dominant organisms
  - Changes in food web linkages (e.g., more/less predation)
  - Changes in allocation of carbon between different components of the food web
  - Change from benthically dominated to pelagically dominated and vice-versa
- Changes in environmental seasonality

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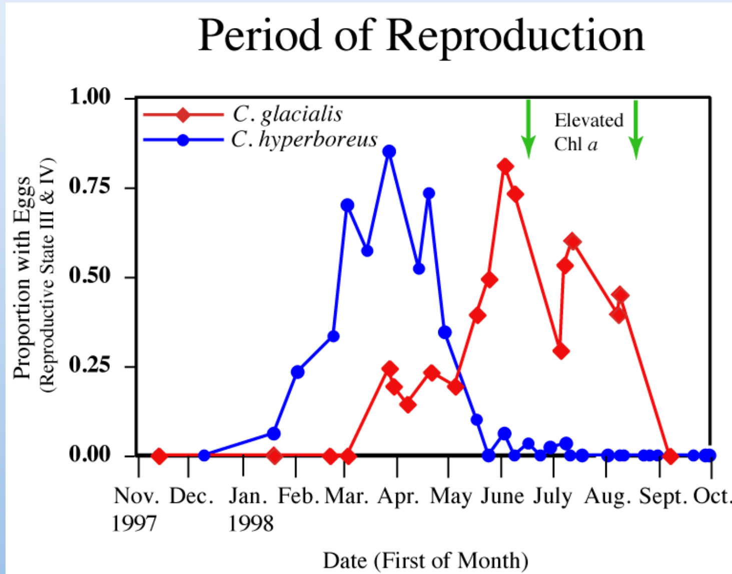
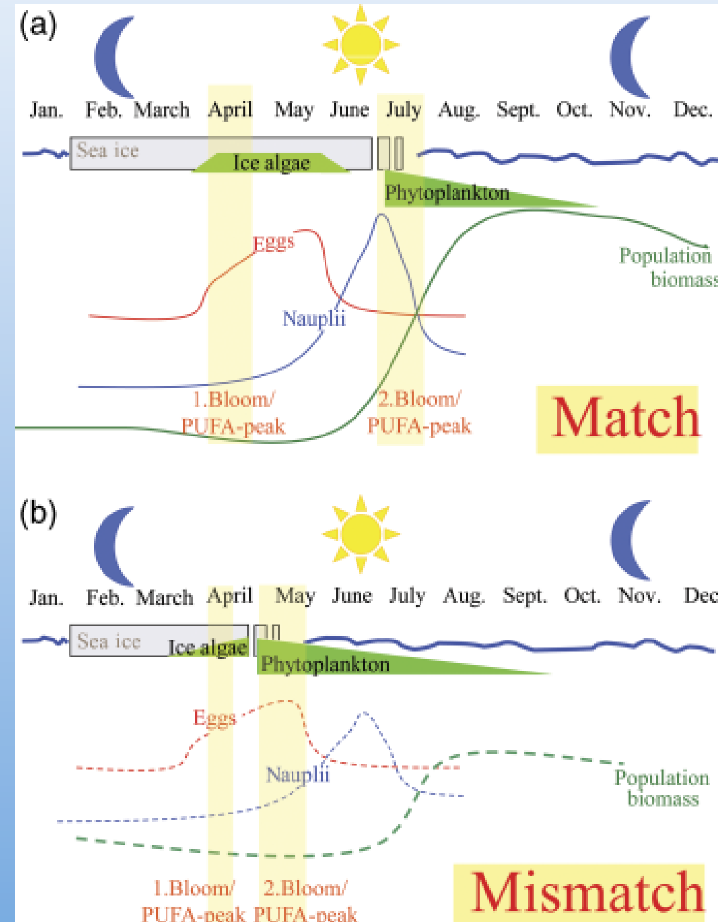
Changes in Seasonality are Hypothesized to Impact the Marine Ecosystem- Match/Mismatch



Campbell and Ashjian



Søreide et al. 2010

- Reproduction in Arctic species is timed to coincide with the availability of food (phytoplankton or ice algae) or so that their young start to feed coincident with the availability of food.
- The idea that earlier ice melt will result in mismatch between these events is being explored in modeling, but field observations are needed

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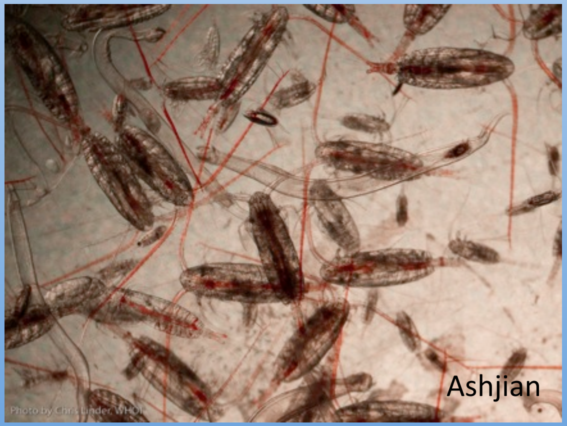
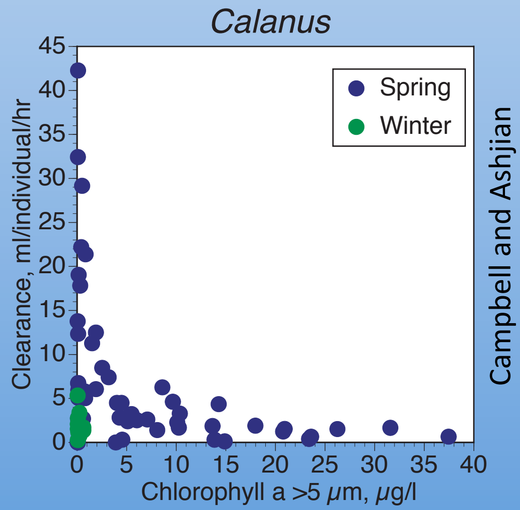
How do we study the Arctic marine ecosystem?

- Sampling – Collection of organisms (determination of species, abundances, biomass), observations of upper trophic level organisms, sensors on ships, moorings, ice-tethered profilers
  - Difficulty in access means that sampling is limited and most has been done during spring/summer/fall, little work in winter
- Experimentation – Determination of vital rates (grazing, egg production, growth, development, primary production, respiration)
- Modeling





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Why model the ecosystem?

- Predict future conditions
  - Informed management decisions (short-term predictions)
  - Understand the impact of environmental/climate change (production changes, range shifts of organisms, changing seasonality)
- Understand how the ecosystem works and why we see the patterns that we do
  - How do extrinsic factors (environmental characteristics (T, S, nutrients, ice/snow cover, light, circulation) impact distributions, production cycles, carbon cycling?
  - How do interactions within the ecosystem impact function?

Approaches to Modeling

- Individual based modeling
  - Focuses on a single species or organism, models their life history relative to environmental conditions
- NPZ or ecosystem type modeling
  - Focuses on ecosystem compartments (e.g., large zooplankton) and the fluxes between compartments
- Both can be coupled to physical models that model circulation, temperature, salinity, ice cover, light, etc.

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Some Considerations in Modeling

- Environmental characteristics are very important to biology:
  - Temperature governs rate processes
    - Growth (put on weight), development (advance through life stages), primary production, respiration…
  - Light in the Arctic is particularly important in governing biological activity because of its impact on primary production
    - Light impacted by ice cover, snow cover on ice, annual cycle
  - Food/nutrient QUANTITY, TYPE, and TIMING is critical to production
- Interactions between ecosystem compartments
  - Grazing, predation
- In order to model the ecosystem, need data from observations (e.g., biomass) and from experiments (rates)
- Can sometimes use empirical relationships (e.g., modeling respiration based on biomass and Q_{10})
- NPZ type models usually are validated through comparison with observations

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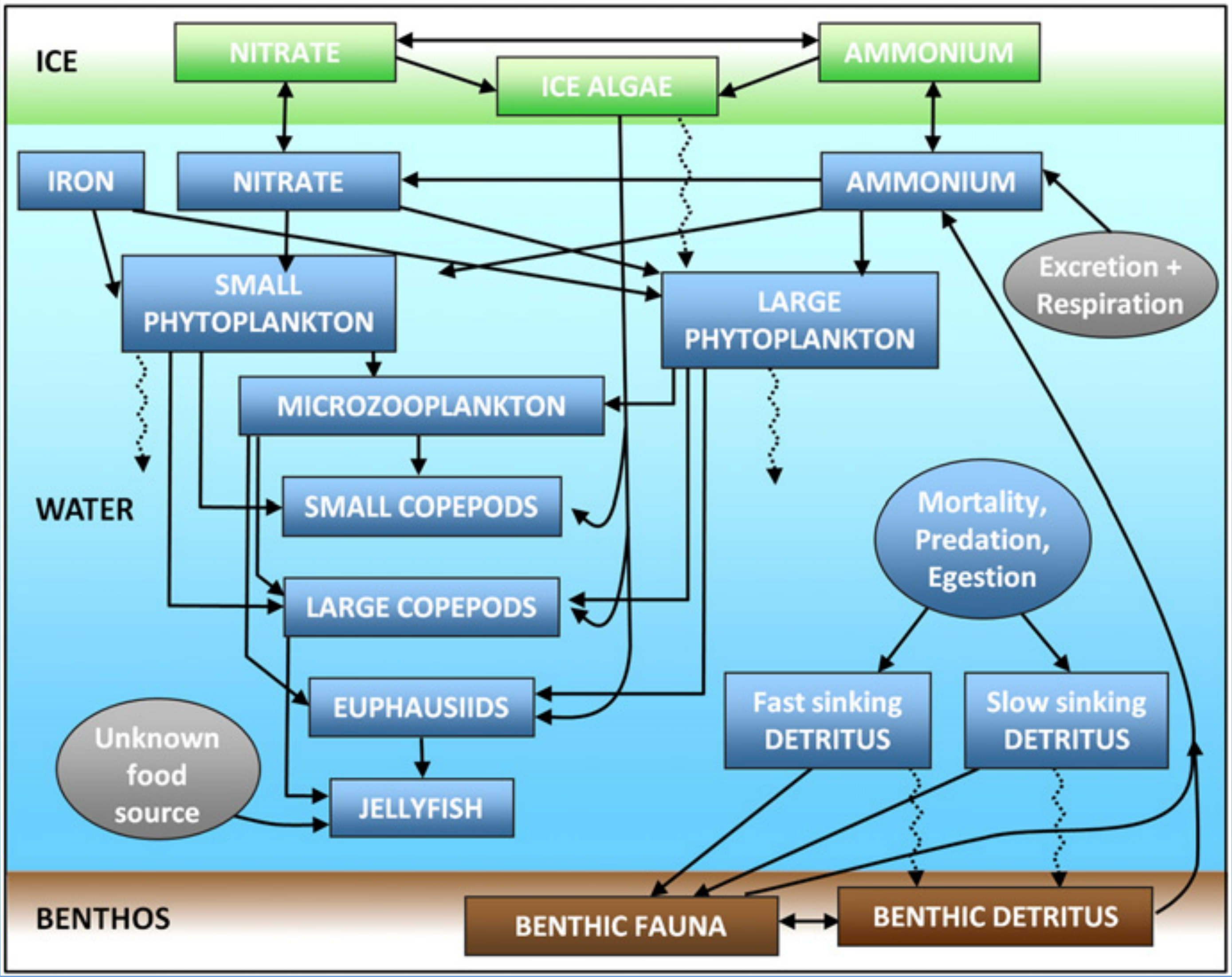
An Example of a NPZ Model –Bering Sea



Gibson and Spitz 2011

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Equations from the Gibson and Spitz (2011) paper for the NPZ Model

Table 1
Model equations for the *BEST–NPZD* model. For clarity advection and diffusion terms have been omitted. Sub equations are presented in Table 2.

State variable	Equation
Nitrate (NO_3)	$\frac{\partial NO_3}{\partial t} = -\xi\left(PS\cdot Pmax_{PS}\cdot \min\left(Lim_{LightPS}, Lim_{\mathrm{NO_3}PS}, Lim_{FePS} + PL\cdot Pmax_{PL}\cdot \min\left(Lim_{LightPL}, Lim_{\mathrm{NO_3}PL}, Lim_{FePL}\right)\right) + Nitrif$
Ammonium (NH_4)	$\frac{\partial NH_4}{\partial t} = -\xi\begin{pmatrix} PS\cdot Pmax_{PS}\cdot \min\left(Lim_{LightPS}, Lim_{\mathrm{NH_4}PS}\right) \\ + PL\cdot Pmax_{PL}\cdot \min\left(Lim_{LightPL}, Lim_{\mathrm{NH_4}PL}\right) \\ + Resp_{PS} + Resp_{PL} + Resp_{ZM} + Resp_{ZS} \\ + Resp_{ZL} + Resp_{E} + Resp_{J} + Resp_{B} \end{pmatrix} - Nitrif$

Grazing on Small Phyto

Grazing on Large Phyto

Grazing on Microzoo

$$\frac{\partial ZL}{\partial t} = \gamma_{ZL}\cdot\left(Graz_{ZLPS} + Graz_{ZLPL} + Graz_{ZLZM}\right) - Graz_{ZLJ} - Resp_{ZL} - Pred_{ZL}$$

Assimilation Efficiency

Predation by Jellyfish

Respiration

Other Predation/Mortality

State variable	Equation
Benthic detritus (BD)	$\frac{\partial BD}{\partial t} = Defec_{B} + Mort_{BD} + Pred_{BD} + \left(Sink_{PS}(z=h) + Sink_{PL}(z=h) + Sink_{D}(z=h) + Sink_{DF}(z=h)\right)\cdot Hz - Graz_{BBD} - Remin_{BD}$
Slow sinking detritus (D)	$\frac{\partial D}{\partial t} = (1-\gamma_{ZM})\cdot\left(Graz_{ZMPS} + Graz_{ZMPL}\right) + Mort_{PS} + Mort_{PL} + Pred_{ZM} - Graz_{DB}\cdot H_{Z=1}^{-1} - Remin_{D} - Sink_{D}$
Fast sinking detritus (DF)	$\frac{\partial DF}{\partial t} = (1-\gamma_{ZS})\cdot\left(Graz_{ZSPS} + Graz_{ZSPL} + Graz_{ZSZM}\right) + (1-\gamma_{ZL})\cdot\left(Graz_{ZLPS} + Graz_{ZLPL} + Graz_{ZLZM}\right) + (1-\gamma_{E})\cdot\left(Graz_{EPS} + Graz_{EPL} + Graz_{EZM} + Graz_{EZS}\right) + \min(0, 1-\gamma_{J})\cdot\left(Graz_{JZS} + Graz_{JZL} + Graz_{JE}\right) + Pred_{ZS} + Pred_{ZL} + Pred_{E} + Pred_{J} - Graz_{DFB}\cdot H_{Z=1}^{-1} - Remin_{DF} - Sink_{DF}$

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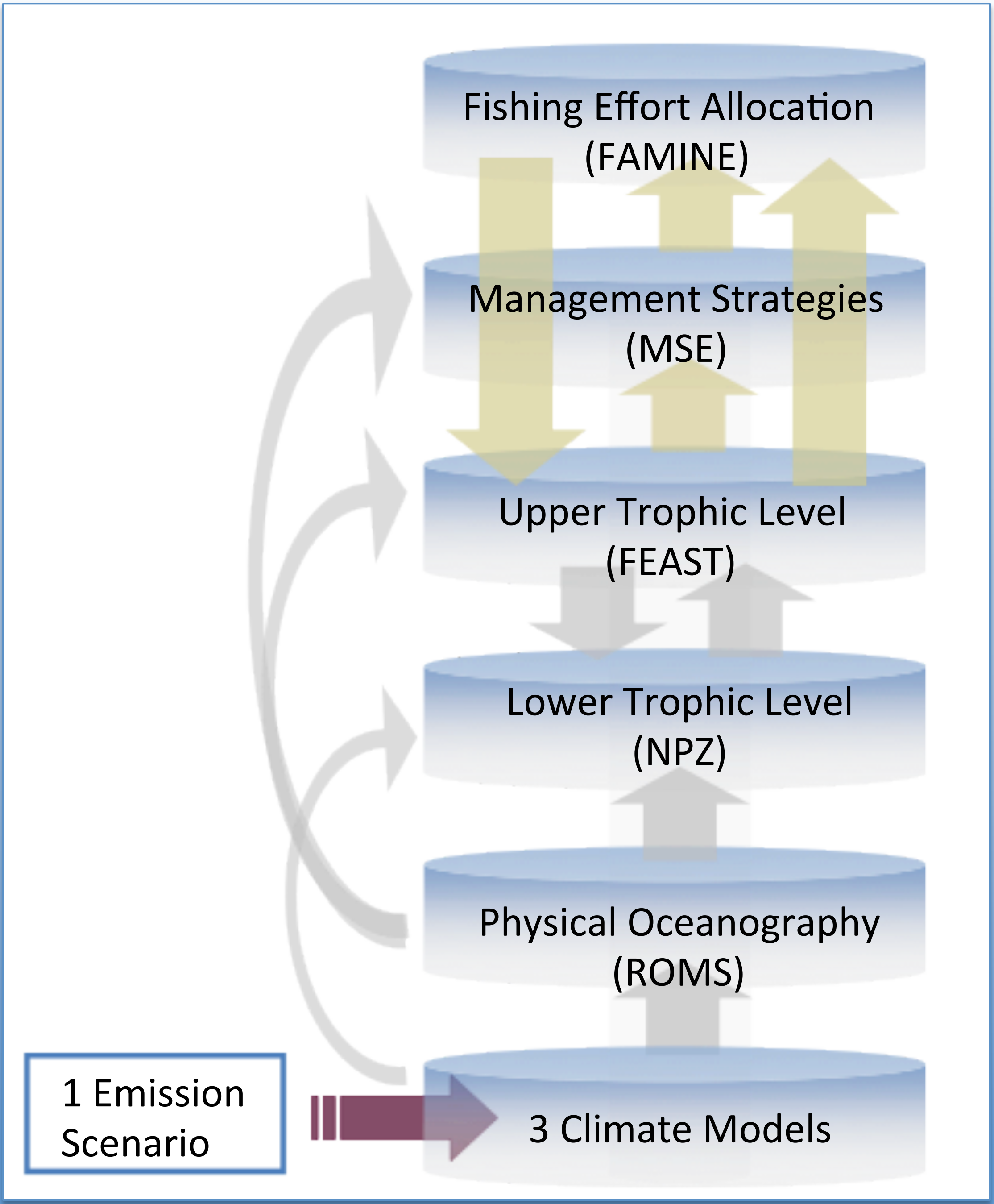

Bering Sea Vertically Integrated and Coupled Ecosystem Modeling

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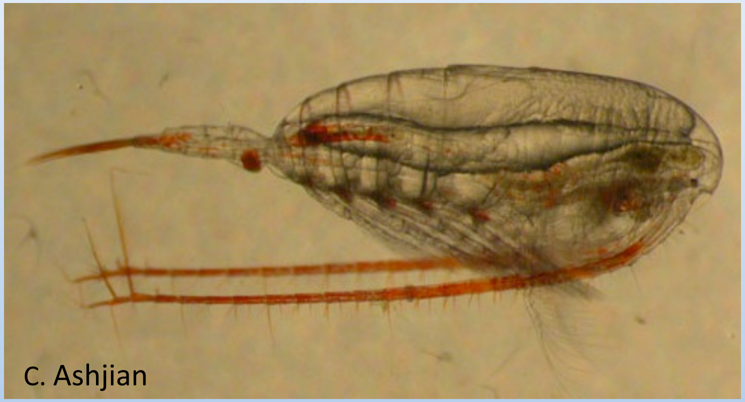
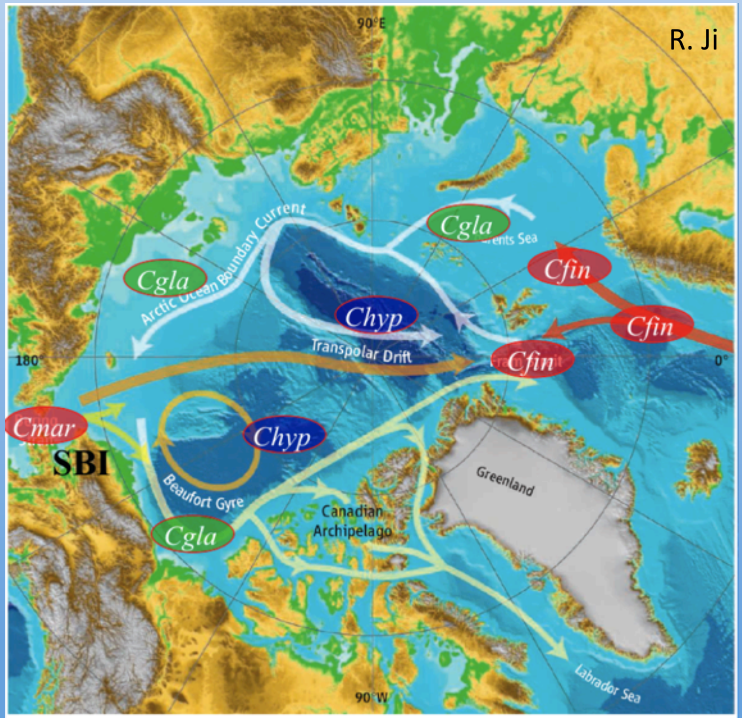
Biogeography of *Calanus* spp., a key ecosystem component





- Four species of the copepod genus *Calanus* are found in the Arctic and/or adjacent seas
  - *C. finmarchicus* is in the temperature and subarctic Atlantic Ocean and enters Arctic
  - *C. marshallae* is in the Gulf of Alaska and Bering Sea
  - *C. glacialis* is most abundant on shelf/slope regions in the Arctic as well as in the Bering Sea and Sub-Arctic Atlantic
  - *C. hyperboreus* is truly "Arctic" and is found on the shelf/slopes and basin
- Advection transports the species between regions yet they have persistent, biogeographical patterns of distribution

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An Example using IBM linked to circulation model output

- What determines the distribution/biogeography of *Calanus* spp. in the Arctic and adjacent seas?
  - How do their life histories and temperature/food specific development rates, coupled to advection, determine where the species persist and where they are only expatriates?
- How might this change under ongoing climate and environmental change?
  - Will environmental change result in range expansion or contraction and changing biogeography of the different species?

Ji, R., Ashjian, C.J., Campbell, R.G., Chen, C., Gao, G., Davis, C.S., Cowles, G.W., Beardsley, R.C. 2011. Life history and biogeography of *Calanus* copepods in the Arctic Ocean: An individual-based modeling study. Progress in Oceanography, 96: 40-56.

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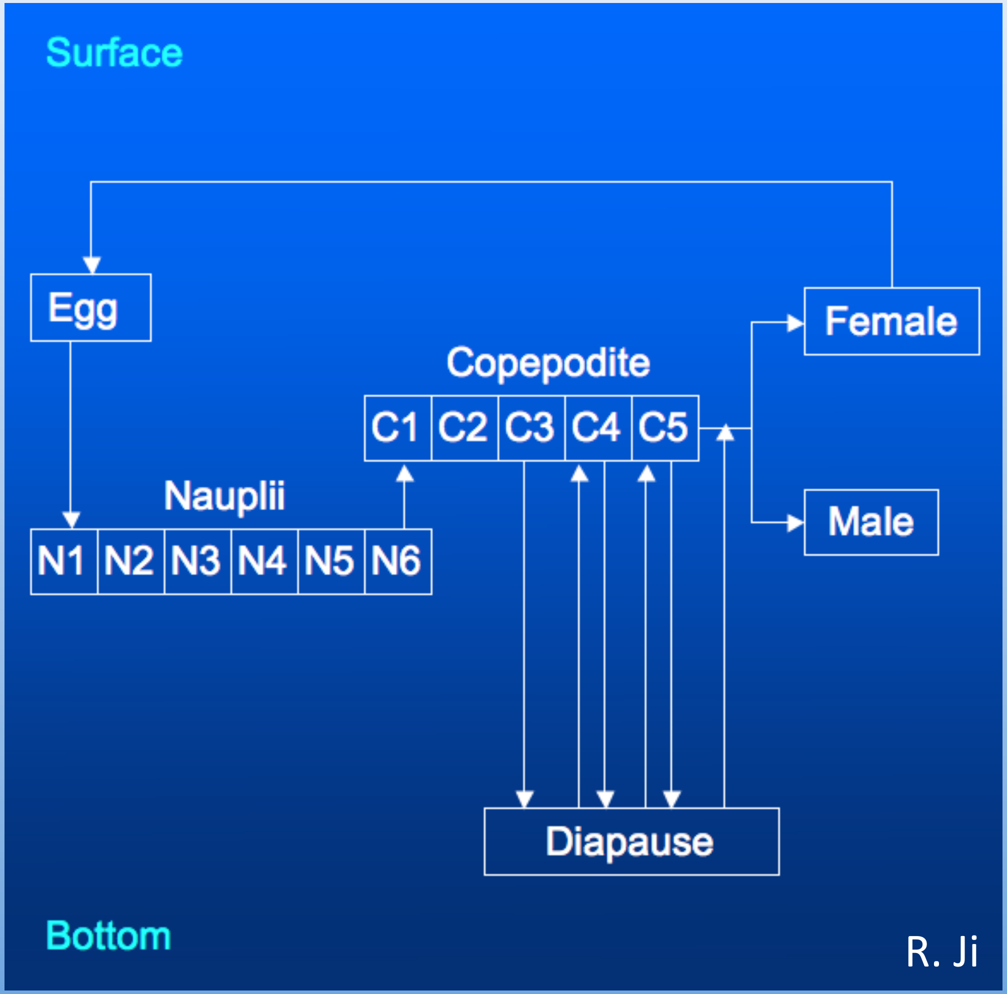
Calanus spp. Life Cycle



- Six naupliar and five copepodid stages before the adult stage is reached
- Multiyear in the Arctic because of cold temperatures
- Egg production is food-dependent and occurs near the surface except for *C. hyperboreus* (Arctic species) that reproduces based on stored lipid at depth
- Feeding and lipid storage (and thus growth and development) occurs during the productive season
- Diapause occurs during winter; the animals migrate to depth (200 m), reduce metabolic activity, do not develop further, and do not feed
- Diapause at C4, C5 for *glacialis*, C5 for *finmarchicus, marshallae*; C3, C4 for *hyperboreus*

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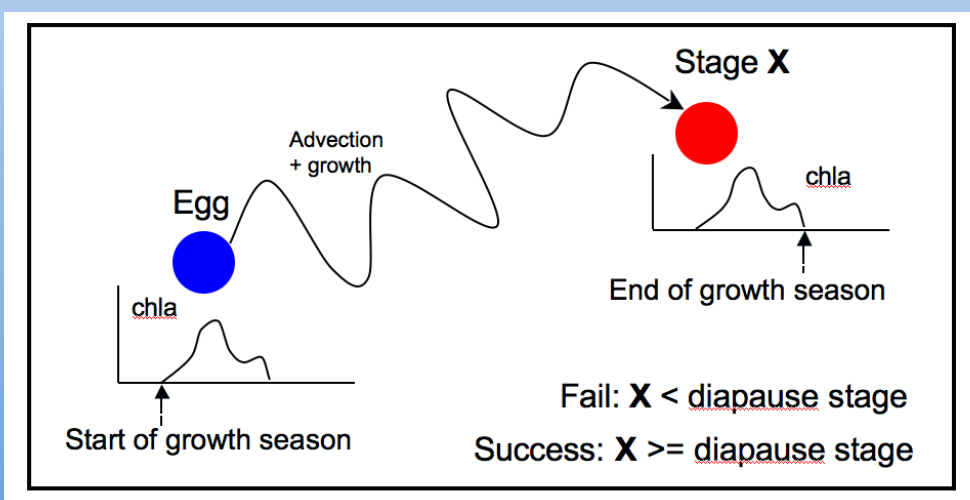
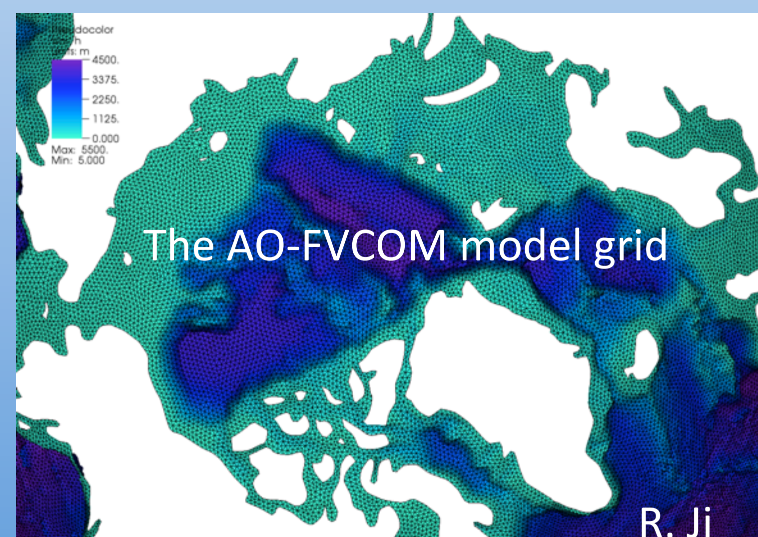
Approach: Use physical model (AO-FVCOM; Chen et al. 2009; Ji et al. 2011) with an IBM

- Advect the “copepods” using the model circulation
- Temperature comes from the modeled temperature at each grid point
- In the IBM, allow the copepods to develop from egg or first feeding stage to critical life stage during the growth season and see where they end up
- Start=first date of growth season; End=end of growth season
- Critical life stage is the first diapausing life stage for each species (different for the different species)
- Animals that reach the diapausing stage SUCCEED; those that do not FAIL and cannot persist at that location (they will not overwinter successfully)





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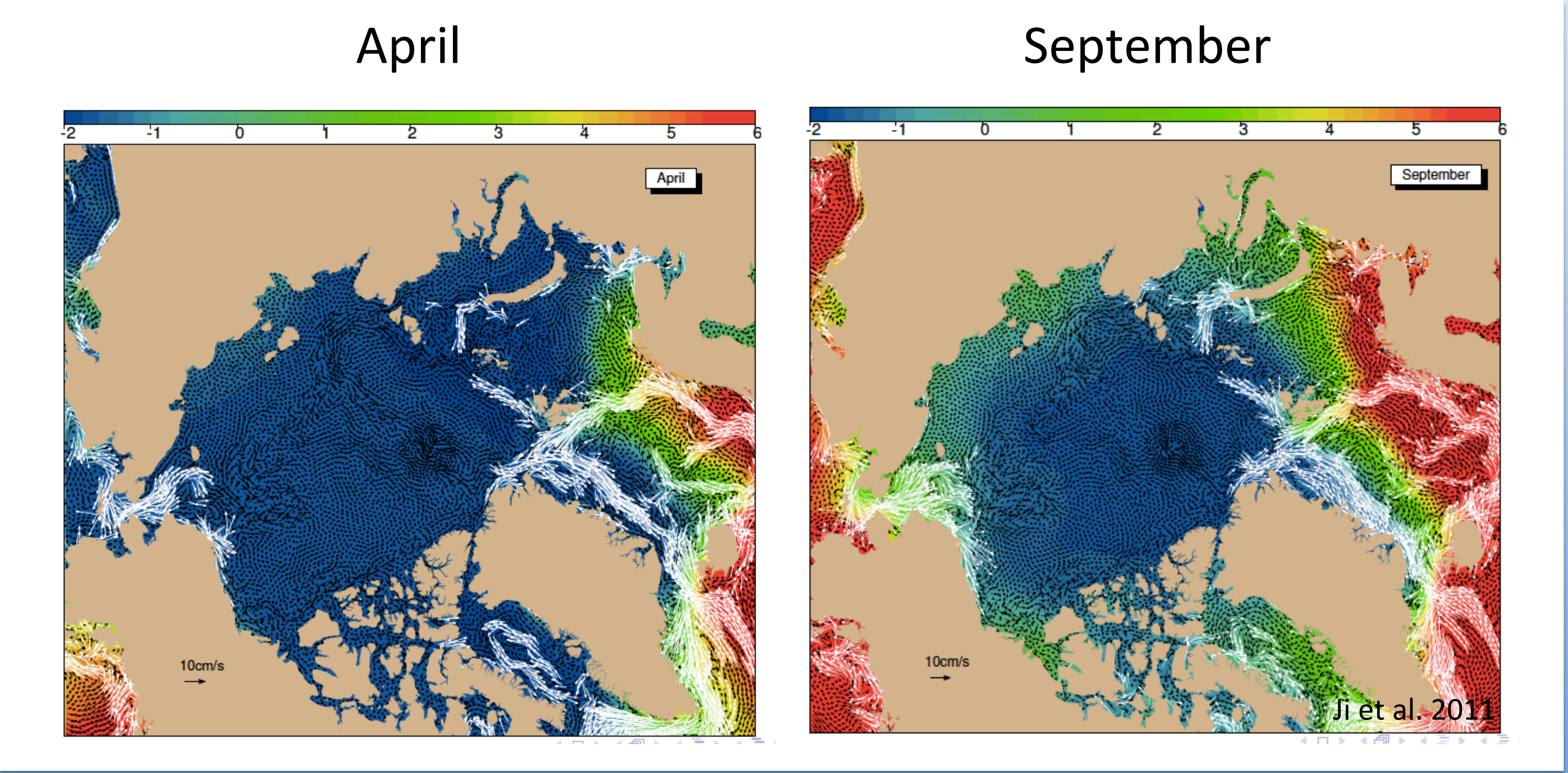
Modeled Circulation and Water Temperature from AO-FVCOM



- Model does a good job of simulating the dominant circulation and temperature

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Needs:

- The length of the growth season for each location
  - This is loosely defined as the period in which food is available to fuel development. Food=both phytoplankton and microzooplankton
- Temperature and food-dependent development rates for each copepod species

How to determine the length of the growth season?

- Use satellite measured chlorophyll (SeaWifs climatology) for seasonally ice-covered regions.
  - No satellite data from under sea ice so this is useful only in the seasonally ice-covered marginal seas and sub-arctic regions (Northern Atlantic, Bering, Southern Chukchi
  - Does not show ice algal production
  - Will also yield a chlorophyll concentration that can be used to supply food
  - Start/end of season would be defined by critical level of chlorophyll
- Use satellite-derived onset of snow melt for permanently ice-covered areas (Basin) for start and solar radiation for end.
  - We know that primary production under sea ice starts when snow melts because enough light can get through
  - Use solar radiation level (daily mean short wave radiation) for end of season (critical level <20 W/m^2)
  - Snow melt climatology from Drobot and Anderson, 2001, updated 2009

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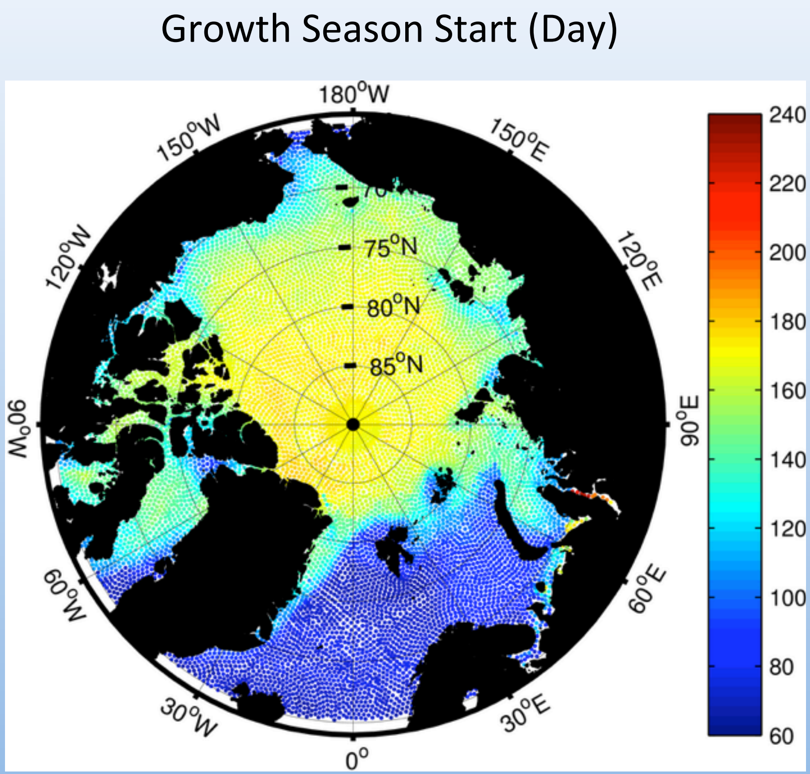
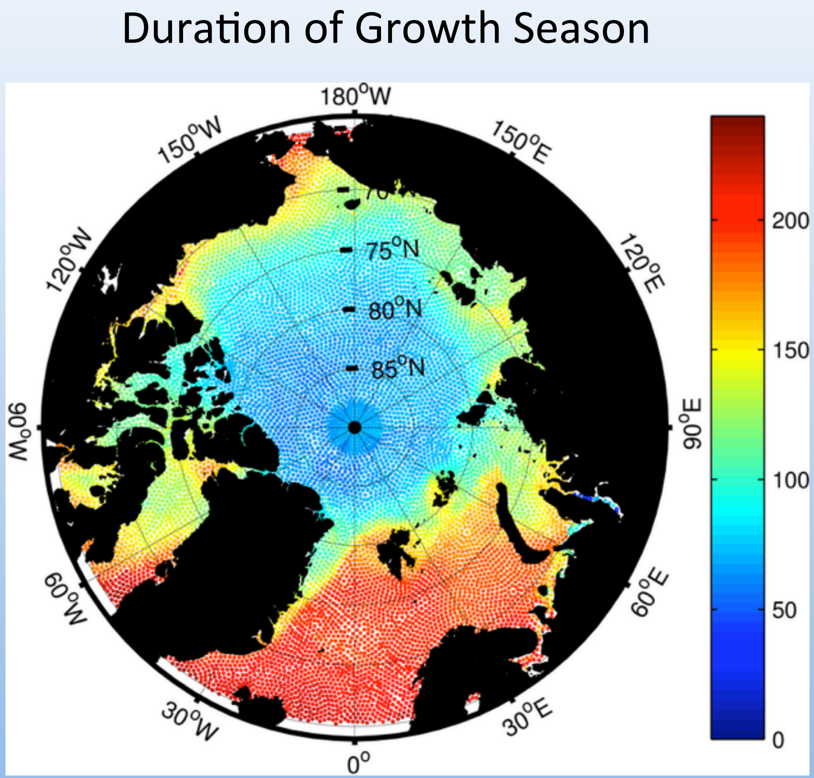
Growth Season





(Snow Melt Climatology from Drobot and Anderson, 2001, updated 2009; Satellite chlorophyll from SeaWifs climatology)

- Predictably, growth season starts earliest in subarctic/marginal seas and ends latest there
- Sub-Arctic copepods (*C. finmarchicus/marshallae*) starting locations were where SeaWifs chlorophyll was available
- Arctic copepods (*C. glacialis and C. hyperboreus*) starting locations were where winter sea ice was present

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Development Equations

Temperature Dependent $D = a\,(T+\alpha)^{\beta}$

Temperature and Food Dependent $D = a\,(T+\alpha)^{\beta}[1-\exp(-F/K)]$

- Can only simulate the food dependent cases for the sub-arctic species where SeaWIFS climatology is available to supply food levels
  - Here satellite-derived chlorophyll is used as a proxy for food availability; likely there is more food because the copepods also eat microzooplankton

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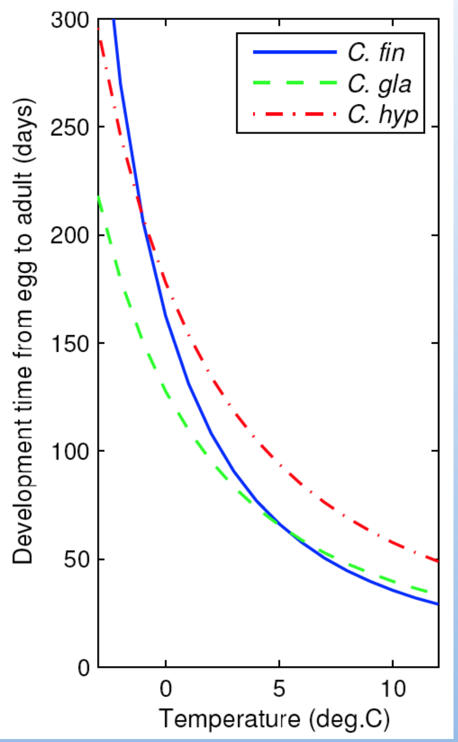
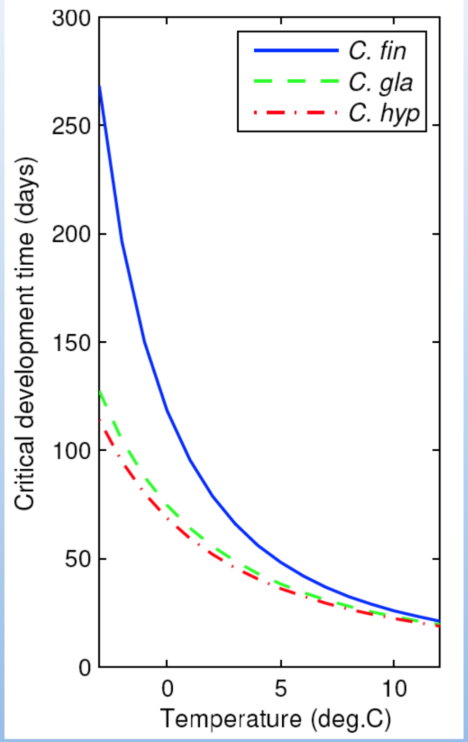
Development Times

All Stages



Critical (egg/first feeding to diapause)



Ji et al. 2011

- At cold temperatures, the two Arctic species develop more quickly than the subarctic/temperate species. This is particularly acute for the development to the diapause stage
- We could not derive development times for *C. marshallae*, the Pacific sub-arctic species (not enough observational data). We used the times for *C. finmarchicus* in our simulations

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The Simulations

Species	Development		Diapause	A) 2 Week Earlier Growth Season Start	B) 2° C Warming	Both A) and B)	Start Stage	Diapause Stage
	Temperature -Dependent	Temperature- and Food-Dependent						
C. finmarchicus	0 m 50 m	0 m 50 m	200 m	0 m	0 m	0 m	Egg	C5
C. marshallae	0 m 50 m	0 m 50 m	200 m	0 m	0 m	0 m	Egg	C5
C. glacialis	0 m 50 m	- -	200 m	0 m	0 m	-	Egg	C4, C5
C. hyperboreus	0 m 50 m	- -	200 m	0 m	0 m	-	N3	C3, C4

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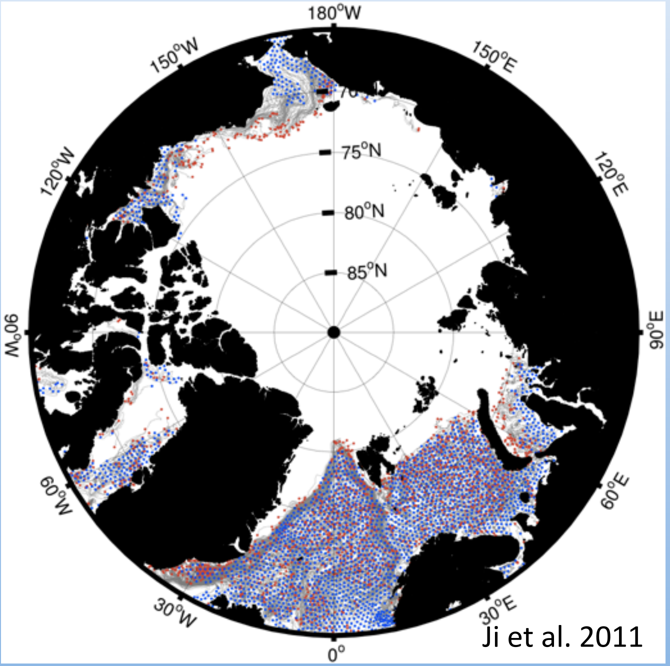
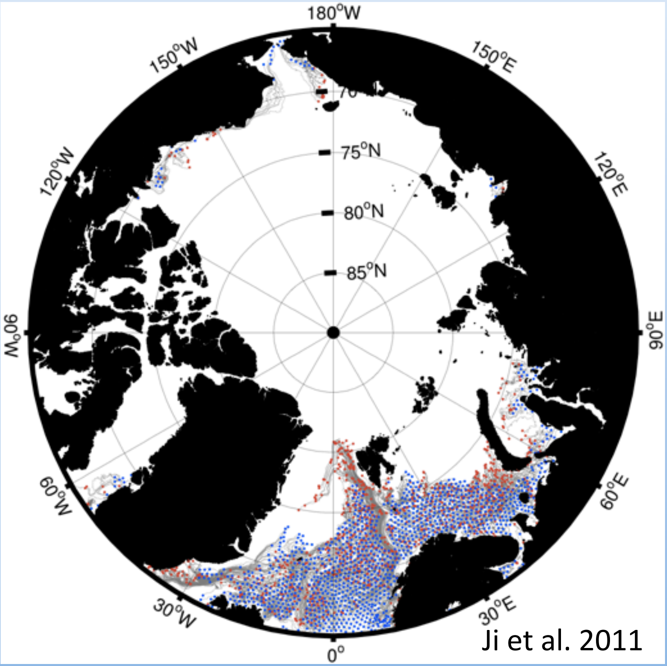
The Sub-Arctic Species (*C. finmarchicus* (Atlantic side) and *C. marshallae* (Pacific side)

Temperature Dependent @ Surface



Temperature and Food Dependent @ Surface



- Neither species can "make it" (achieve the diapause stage) in the Central Arctic
- The situation is worse with food dependent development rate; food must be limiting
- Although these species may be transported into the Central Arctic, they develop too slowly at the ambient temperatures to reach diapause during the growth season

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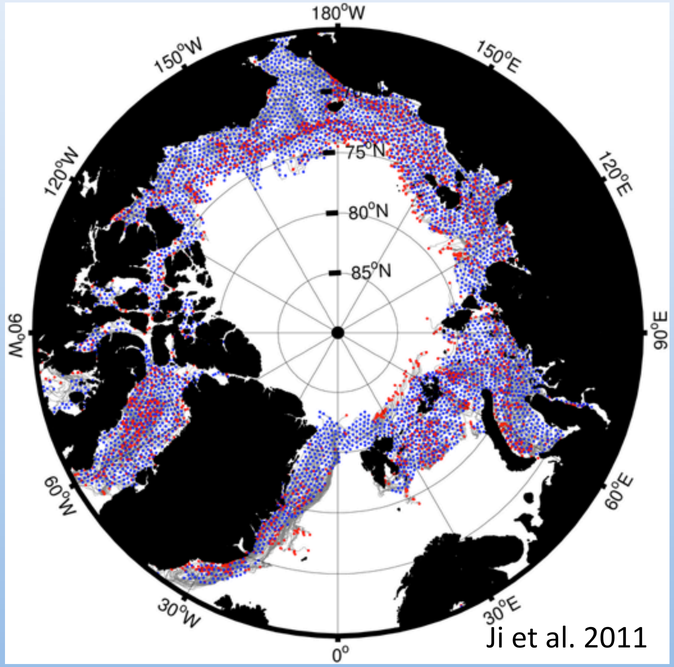
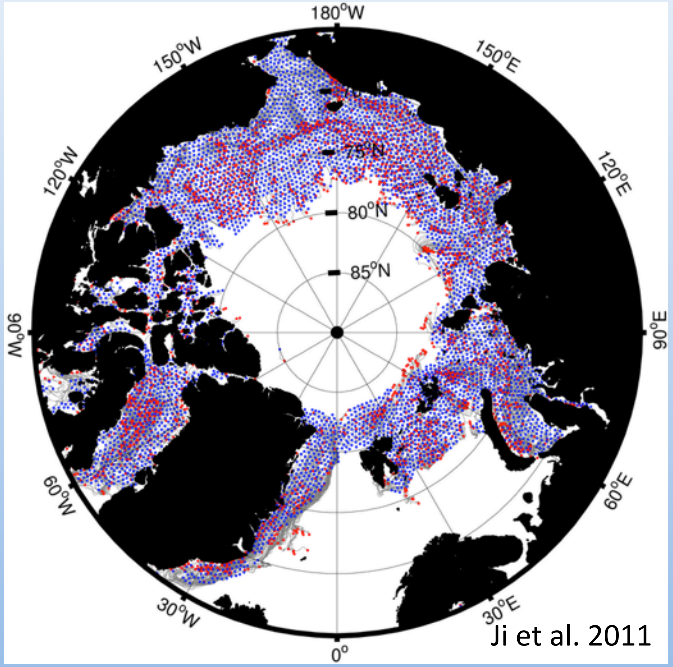
The Arctic Species (T Dependent, @ Surface)

C. glacialis



C. hyperboreus



- Neither could reach diapause in the Central Arctic; *C. hyperboreus* was successful slightly further to the N than was *C. glacialis*
- This was counter to what we know of the distribution of *C. hyperboreus* which is found in the Central Arctic
- There are a number of reasons why this could be, including several having to do with our assumptions and methodology

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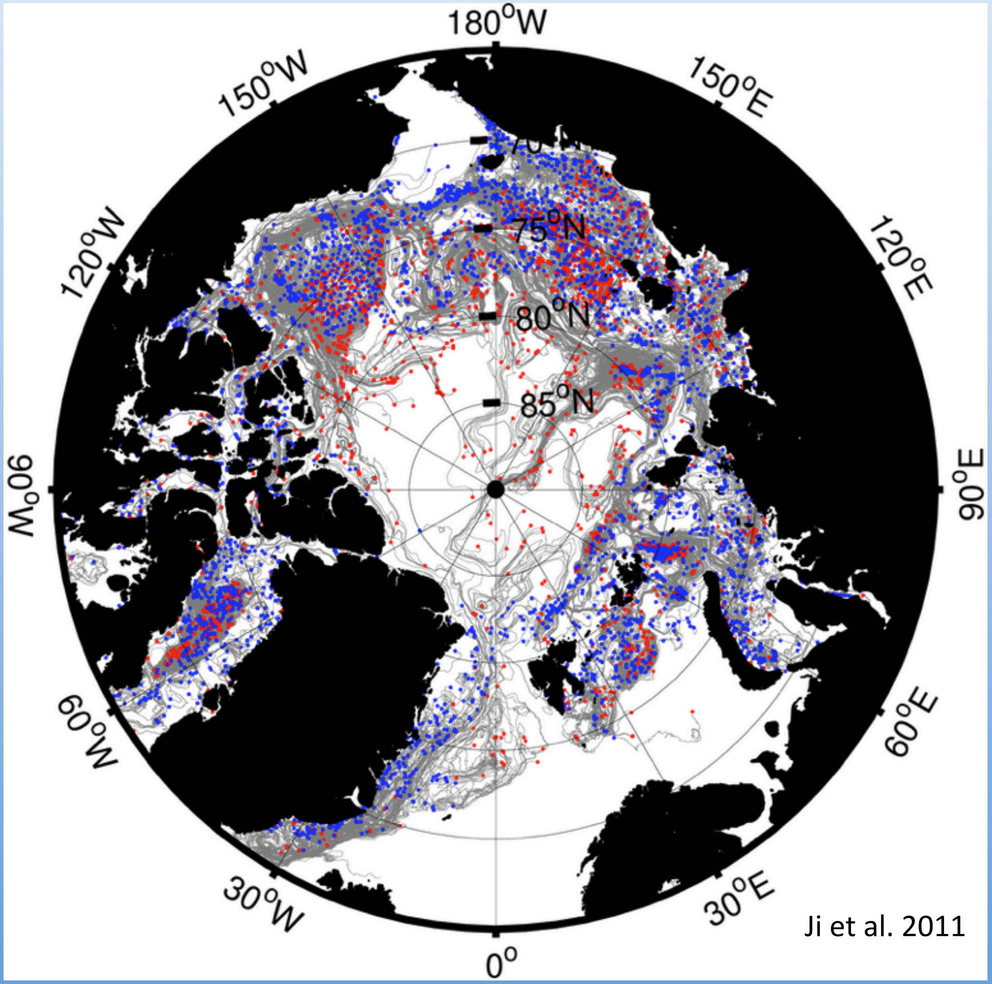
Add Advection during Diapause For Two Additional Years

C. hyperboreus



Ji et al. 2011

- Range is extended into the Central Arctic if the animals that reach diapause in the first year are advected and continue to develop (and diapause) for an additional two years

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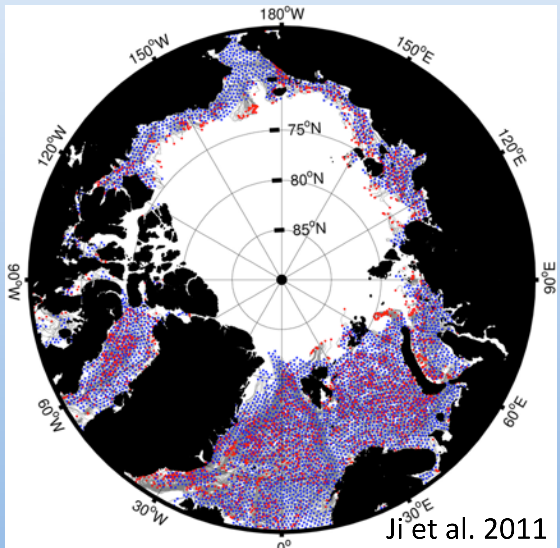
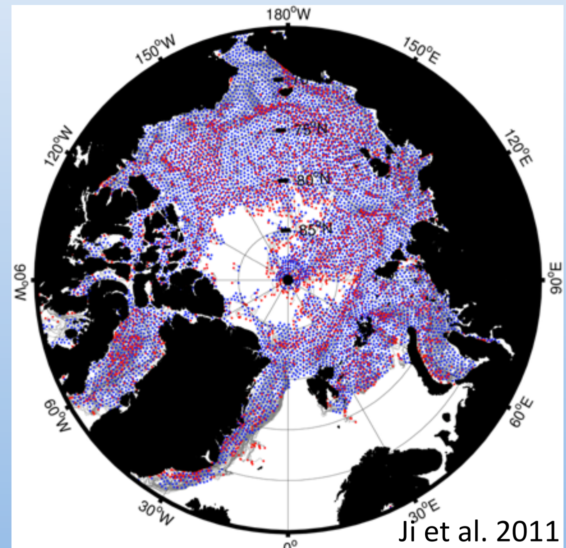
Effect of 2 °C Warming (Increased Development Rates)

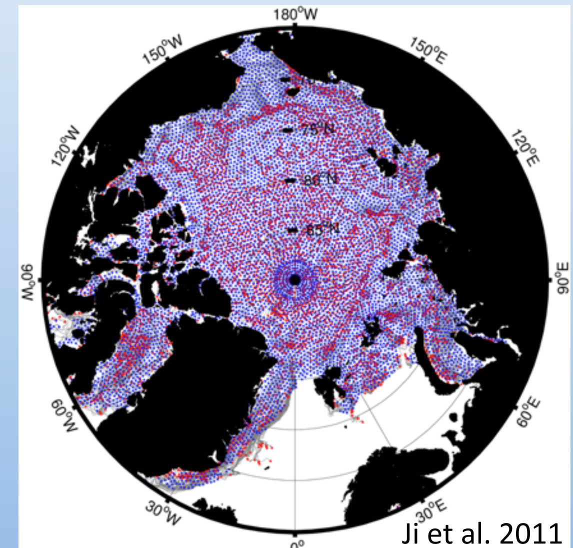
C. finmarchicus/marshallae



C. glacialis



C. hyperboreus



- All four species expand their range.
  - The Atlantic/Pacific species only expand slightly
  - *C. glacialis* expands into the Central Arctic
  - *C. hyperboreus* covers the entire Central Arctic
- Note that the length of the growing season remains the same as in the previous simulations

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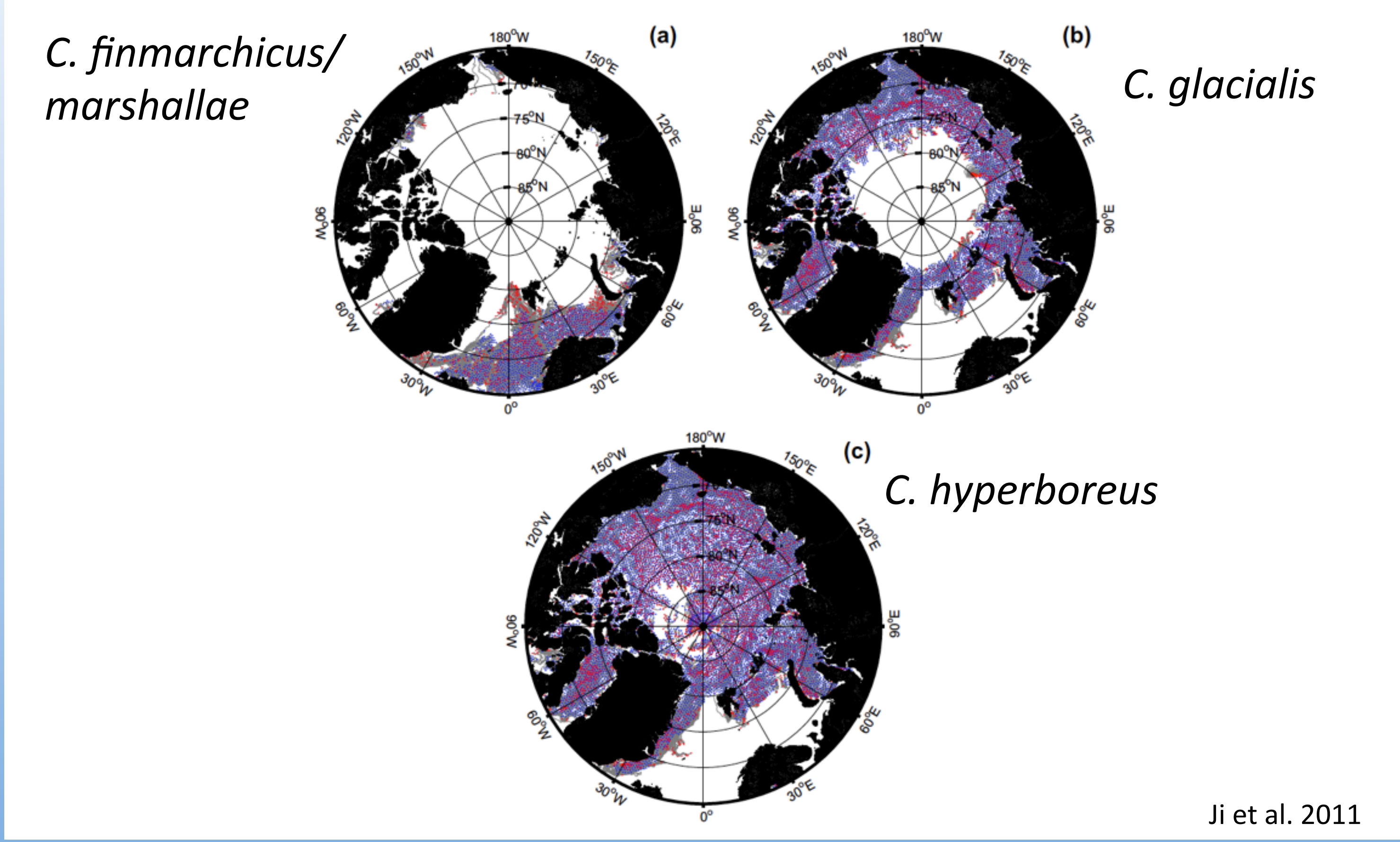
Effect of Lengthening the Growing Season by 2 Weeks



- Little/no expansion in range for the Sub-Arctic Species (*C. fin/C. marsh*)
- Some expansion in range for *C. glacialis*
- *C. hyperboreus* can persist in most of the Central Arctic

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Conclusions from Modeling

- The observed biogeographic distributions of the species could be explained by life history characteristics and development rates coupled to water temperature, length of the growth season, and advection
- Both expatriate *Calanus* species cannot under present conditions colonize the Central Arctic because the growth season is too short to permit development to the diapausing stage
- Both endemic *Calanus* species can maintain viable populations in the Arctic marginal seas and Central Basin
- Only the Arctic endemics responded to increased temperature and the longer growing season, by increasing the range of where they could reach diapause, suggesting that even with moderate warming and changes in seasonality, the expatriate species will not be able to expand their range and colonize the Arctic

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Some Limitations to the Modeling

- Food-dependent development rates could not be used for the Arctic species because we have no information on food concentrations under the sea ice
  - Perhaps link this effort to an NPZ model that predicts food concentration?
  - These simulations are "best case" scenarios
- The development rate coefficients were dependent on extrapolations from limited experimental data
- The start date of the growth season in both ice-free and ice-covered regions is not well constrained
- We assumed that the predominant first stage of diapause was the critical stage; if younger stages can overwinter, then the critical development time would be reduced
- The warming scenario did not include changes in ice coverage and food availability that might result from warming

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Overall

- The use of the IBM coupled to the circulation was an effective way to:
  - Explain and understand the observed distributions of these four congeneric species
  - Identify how climate change might, or might not, impact their biogeography
  - Identify shortfalls in our knowledge and understanding that can guide future field and modeling research
- Ecosystem models can offer similar insights
- Successful marine ecosystem modeling depends on good physical and sea ice modeling
- We need more observations both to understand the system and also to provide better inputs to the modeling efforts (e.g., Central Arctic chlorophyll, *C. marshallae* development rates)

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