What Determines the Distributions of *Calanus* Endemic and Expatriate Species in the Arctic Ocean?

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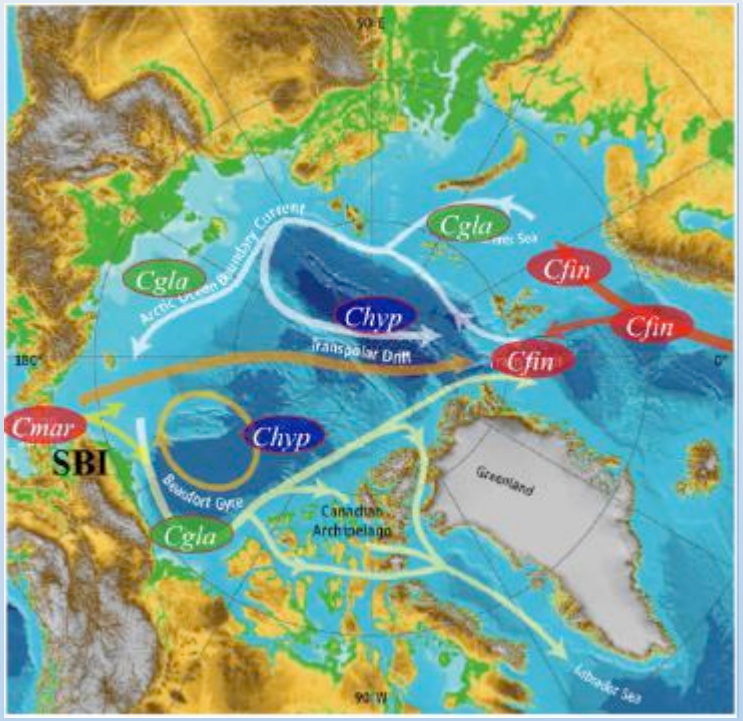
Shelf Basins Interactions Program, Phase III

Four species of the copepod genus *Calanus* are found in the Arctic and/or adjacent seas

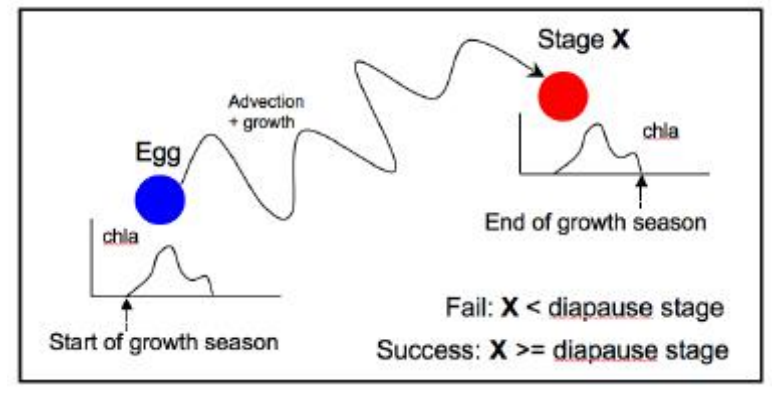


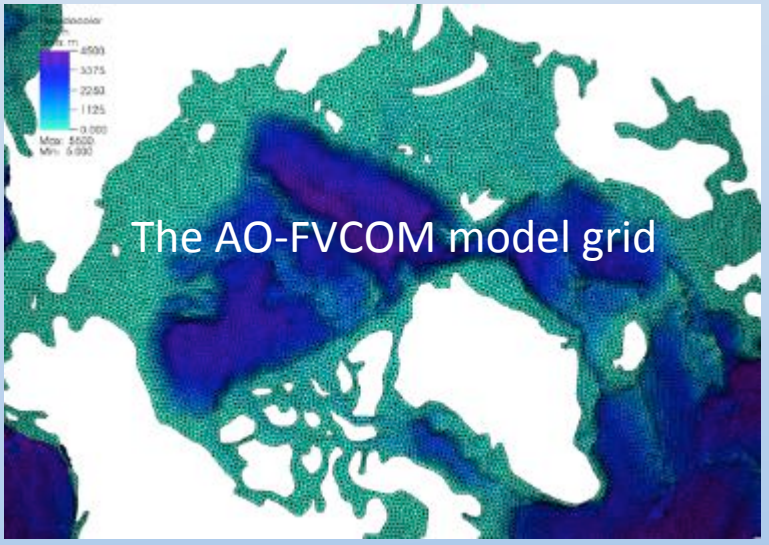
- *Calanus* spp. are key components of arctic and subarctic food webs
- Two in the northern Atlantic (*C. finmarchicus*) or northern Pacific (*C. marshallae*), expatriate in the Arctic
- Two endemic to the Arctic (*C. glacialis, C. hyperboreus*)
- All four follow a life history that includes overwintering in diapause at a less than adult life stage

Questions

- What maintains the persistent biogeographical patterns of distribution?
- Can species that are transported into the Arctic persist (reproduce successfully) and become endemic?
- Will climate change modify these patterns?

Modeling *Calanus* spp.





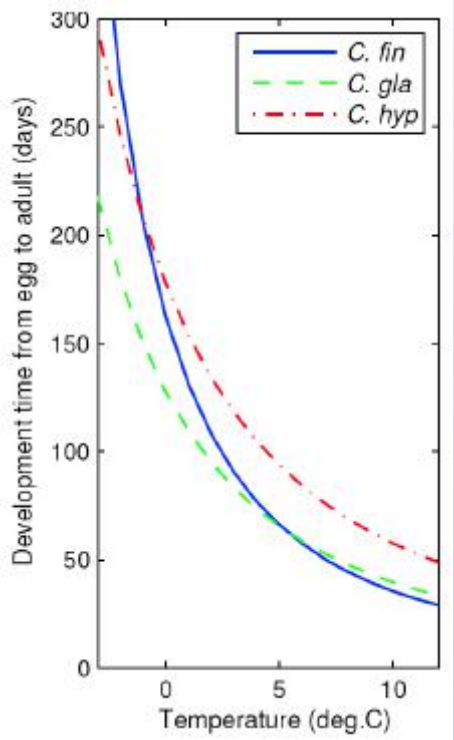
GOALS: Identify locations to which animals could be transported and successfully achieve the diapause stage and thus persist under present and potential future conditions

- Individual based modeling study – IBM model coupled to AO-FVCOM physical model
- Temperature and food dependent development rates
- Modeled circulation and water temperature
- Growth season length for each node from satellite ocean color or from snow melt, radiation levels for end
- Each "copepod" starts when food is required (N3 for *C. hyperboreus*, egg for other 3 species)
- Advect and develop copepod through growth season and see where and at what stage (diapause or not) they end up

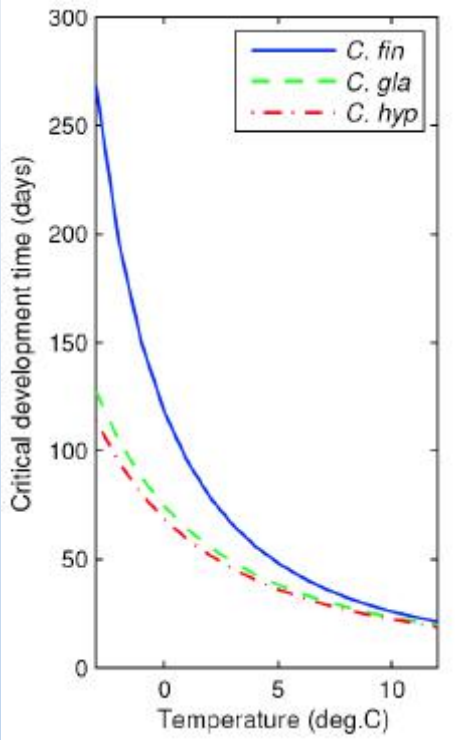
Ji, Ashjian, Campbell, et al. 2012. Progress in Oceanography 96: 40-56.

Temperature Dependent Development Times

All Stages



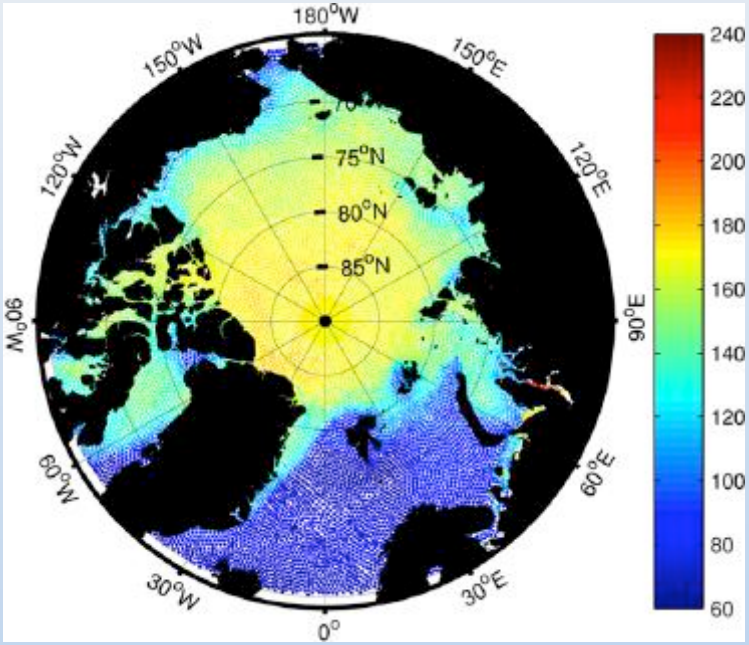
Critical (egg/first feeding to diapause)



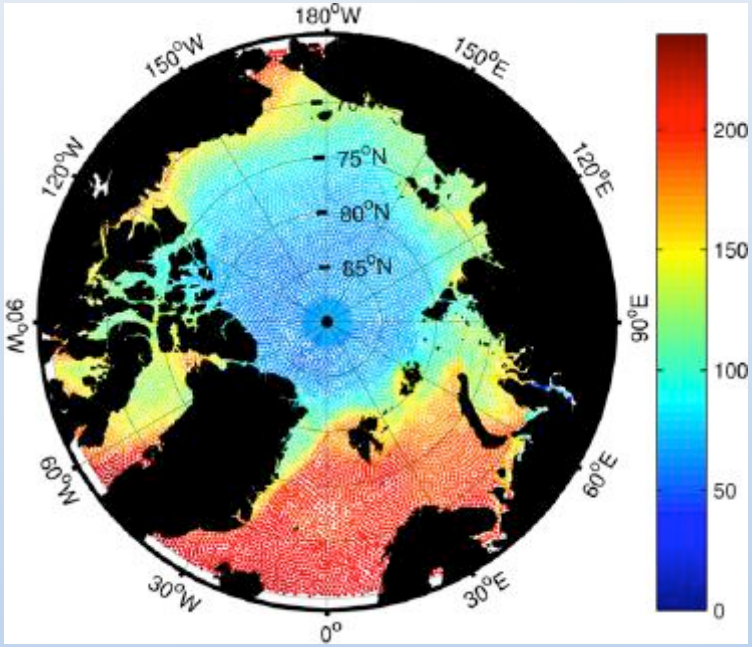
- At cold temperatures, the two Arctic species develop more quickly than the subarctic/temperate species. This is particularly acute for the development to the diapause stage.
- We could not derive development times for *C. marshallae*, the Pacific sub-arctic species (not enough observational data).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

Growth Season

Growth Season Start (Day)



Duration of Growth Season



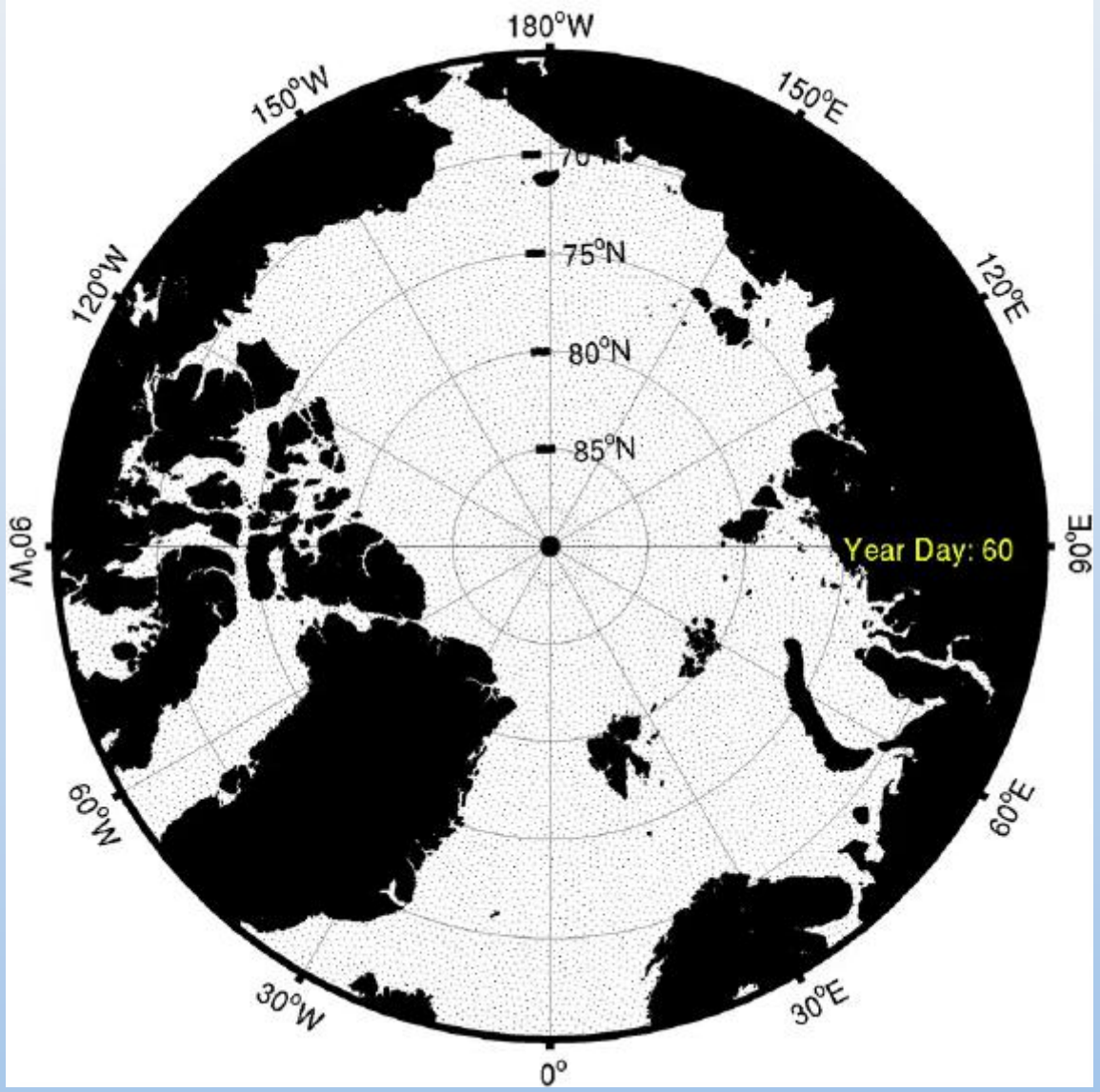
(Snow Melt Climatology from Drobot and Anderson, 2001, updated 2009; Satellite chlorophyll from SeaWifs climatology)

- Predictably, growth season starts earliest in subarctic/marginal seas and ends latest there
- This determination of growth season length may not consider all types of available food so the actual growth season may be longer
- We were able to use temperature and food dependent development rates for the expatriate species for some simulations using the chlorophyll from the SeaWifs climatology

The Simulations

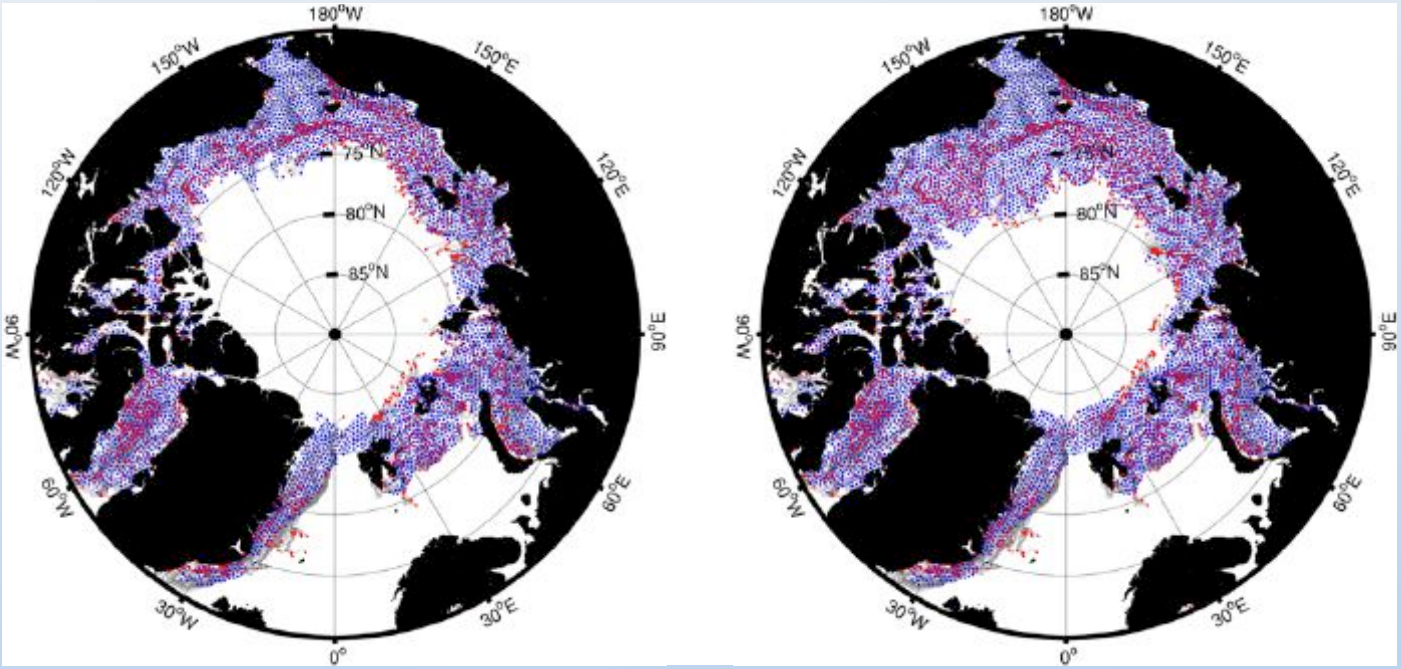
Species	Development		Diapause	A) 2 Week Earlier Growth Season Start	B) 2° C Warming	Both A) and B)	Start Stage	Diapause Stage
	Temperature -Dependent	Temperature- and Food- Dependent						
C. finmarchicus	0 m 50 m	0 m 50 m	200 m	0 m	0 m	0 m	Egg	C5
C. marshallae	0 m 50 m	0 m 50 m	200 m	0 m	0 m	0 m	Egg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

C. glacialis - Arctic endemic (T Dependent, @ Surface)



The Arctic Species (T Dependent, @ Surface)

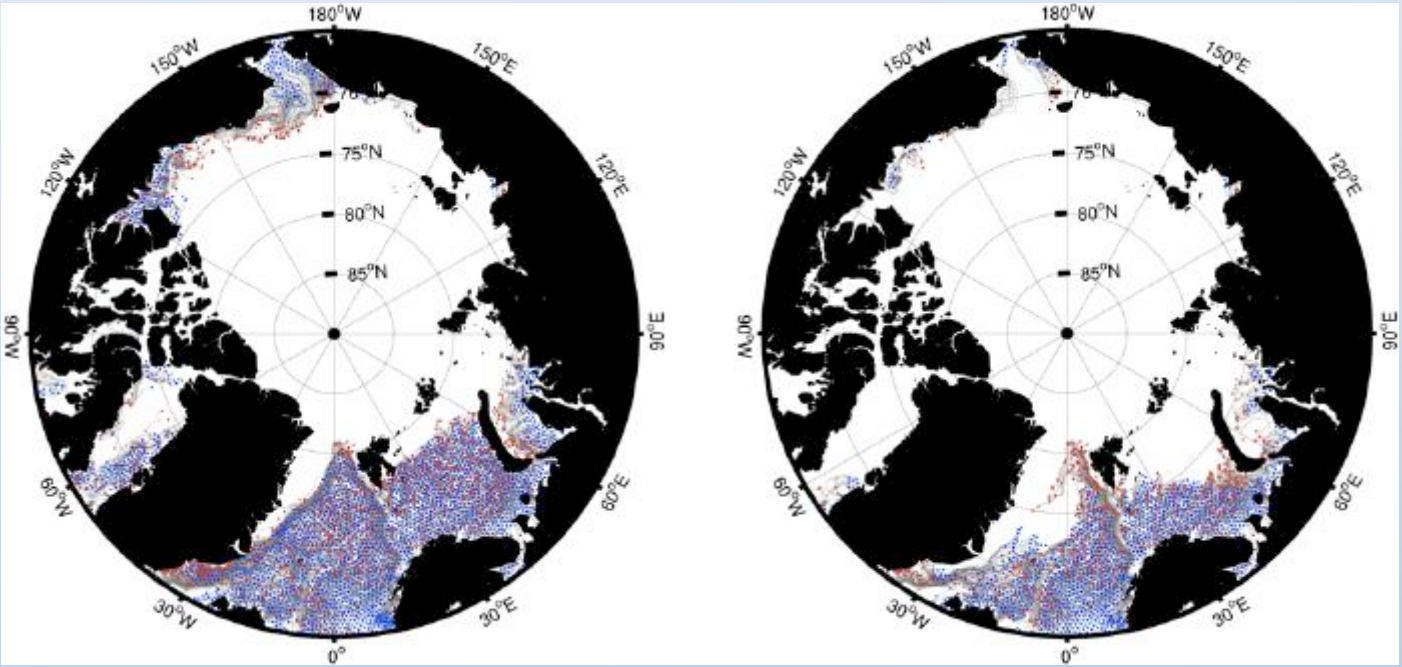
C. glacialis *C. hyperboreus*



- Neither could reach diapause in the Central Arctic; *C. hyperboreus* was successful slightly further to the N than was *C. glacialis* which is restricted to the shelves and slopes
- The inability of *C. hyperboreus* to reach diapause in the Central Arctic was curious, since this species is found there
- It has been suggested that *C. hyperboreus* is expatriate in the Central Arctic (Olli et al., 2007)

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

Temperature Dependent @ Surface Temperature and Food Dependent @ Surface



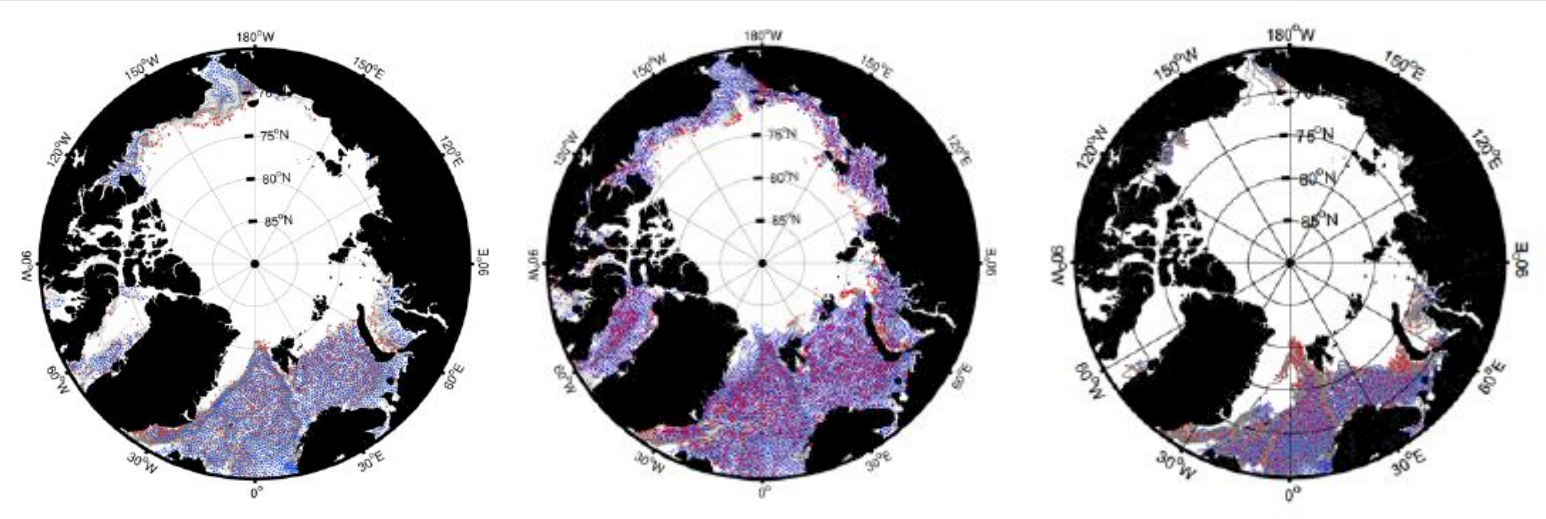
- Neither species can "make it" (achieve the diapause stage) in the Central Arctic
- The situation is worse with food dependent development rate; food must be limiting
- Although these species may be transported into the Central Arctic, they develop too slowly at the ambient temperatures to reach diapause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

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

Present Temperature and Growth Season Length

Temperature Increased 2°C

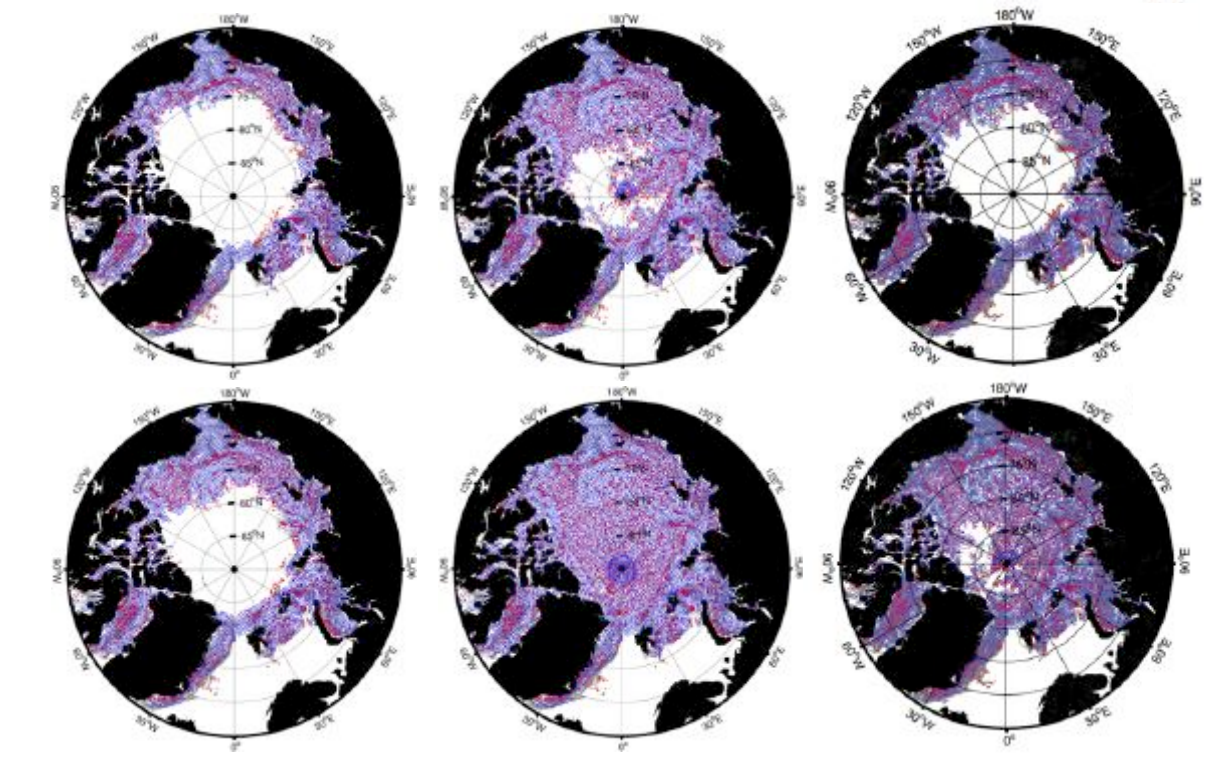
Growth Season Lengthened 2 Weeks



- Even when temperature is increased by 2°C (and thus development rates are increased) and/or the growth season is lengthened by two weeks, these species still cannot persist in the Central Arctic

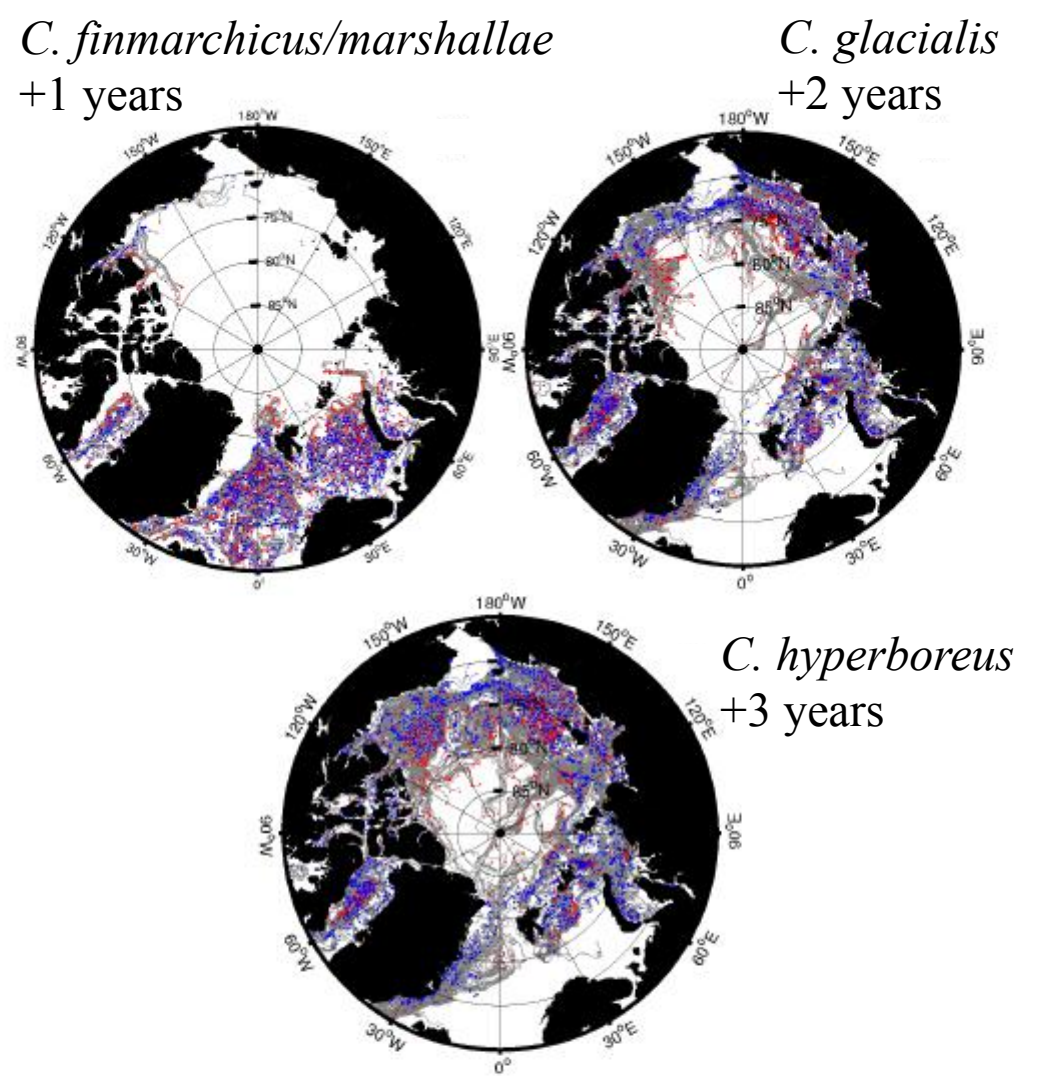
Arctic Species

	Present Temperature and Growth Season Length	Temperature Increased 2°C	Growth Season Lengthened 2 Weeks
C. glacialis			
C. hyperboreus			



- Under present temperature and growth season length, distribution is restricted to shelves and slopes, consistent with observations
- A 2°C temperature increase greatly expands the potential range over which these species can persist. Lengthening of the growth season has a somewhat lesser effect for *C. glacialis* but is still very helpful to *C. hyperboreus*

Add Advection during Diapause



- Continued advection and development including diapause at 200 m for 1-3 additional years
- Range is extended into the Central Arctic for the Arctic endemics but not for the two expatriates for which there is little range expansion
- Many of the locations reached in the Central Arctic are those where previous simulations showed the animals could not achieve diapause

Conclusions

- 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 Arctic
- 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 Central Arctic
- Simulations with the animals at different depths did not change these results

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 – need more observational data
- 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

Development Equations

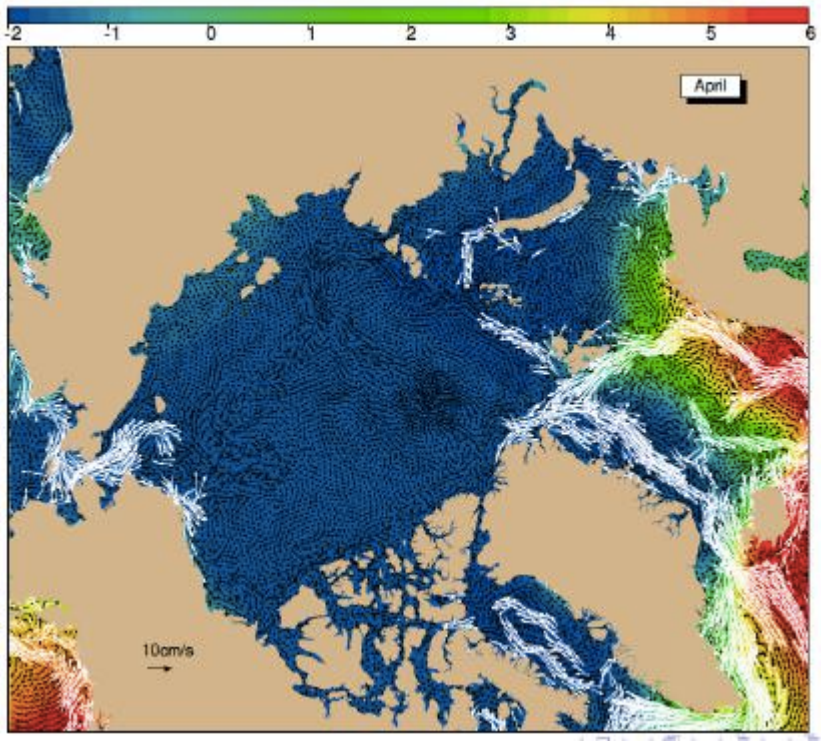
Temperature Dependent $D = a\,(T+\alpha)^{\beta}$

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

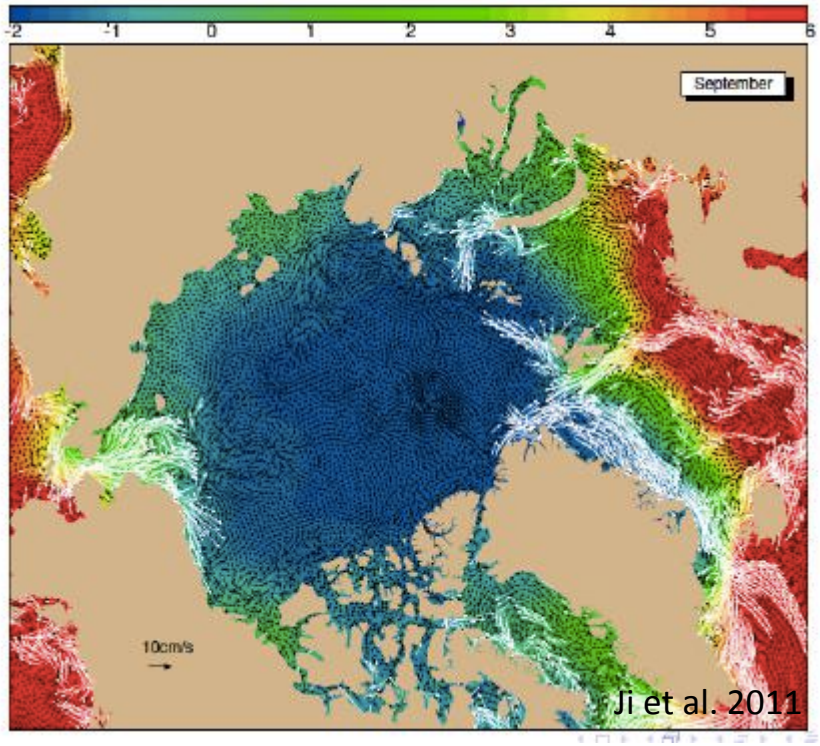
- Can only simulate the food dependent cases for the sub-arctic species where SeaWIFS climatology is available to supply food levels
  - Here satellite-derived chlorophyll is used as a proxy for food availability; likely there is more food because the copepods also eat microzooplankton

Modeled Circulation and Water Temperature from AO-FVCOM

April



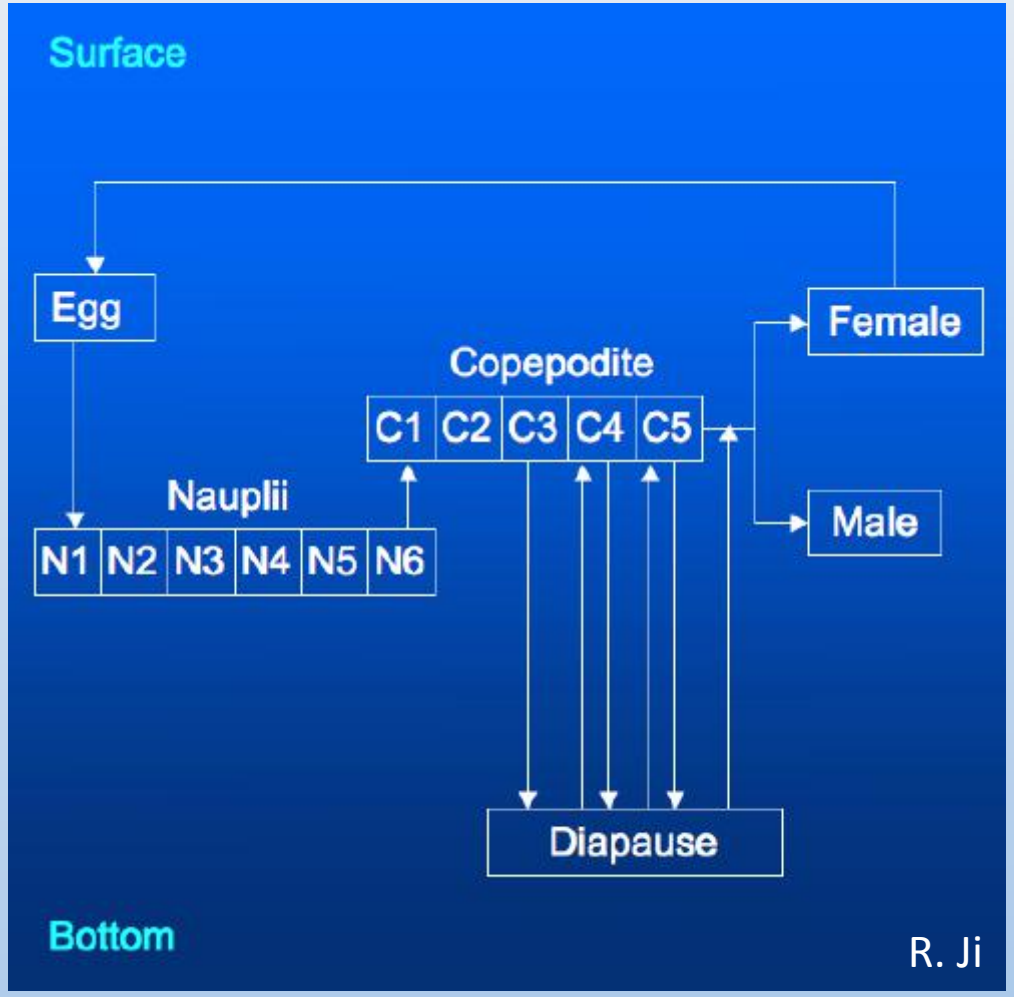
September



Ji et al. 2011

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

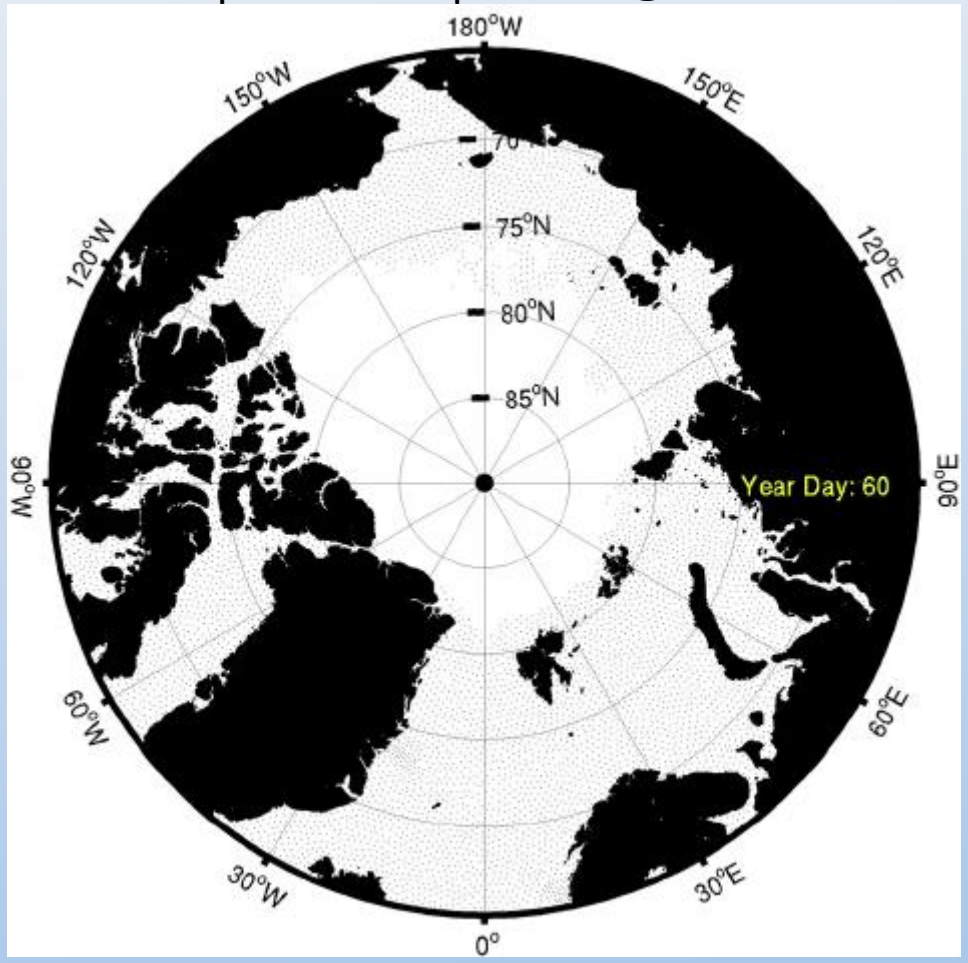
Calanus spp. Life Cycle



- 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*

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

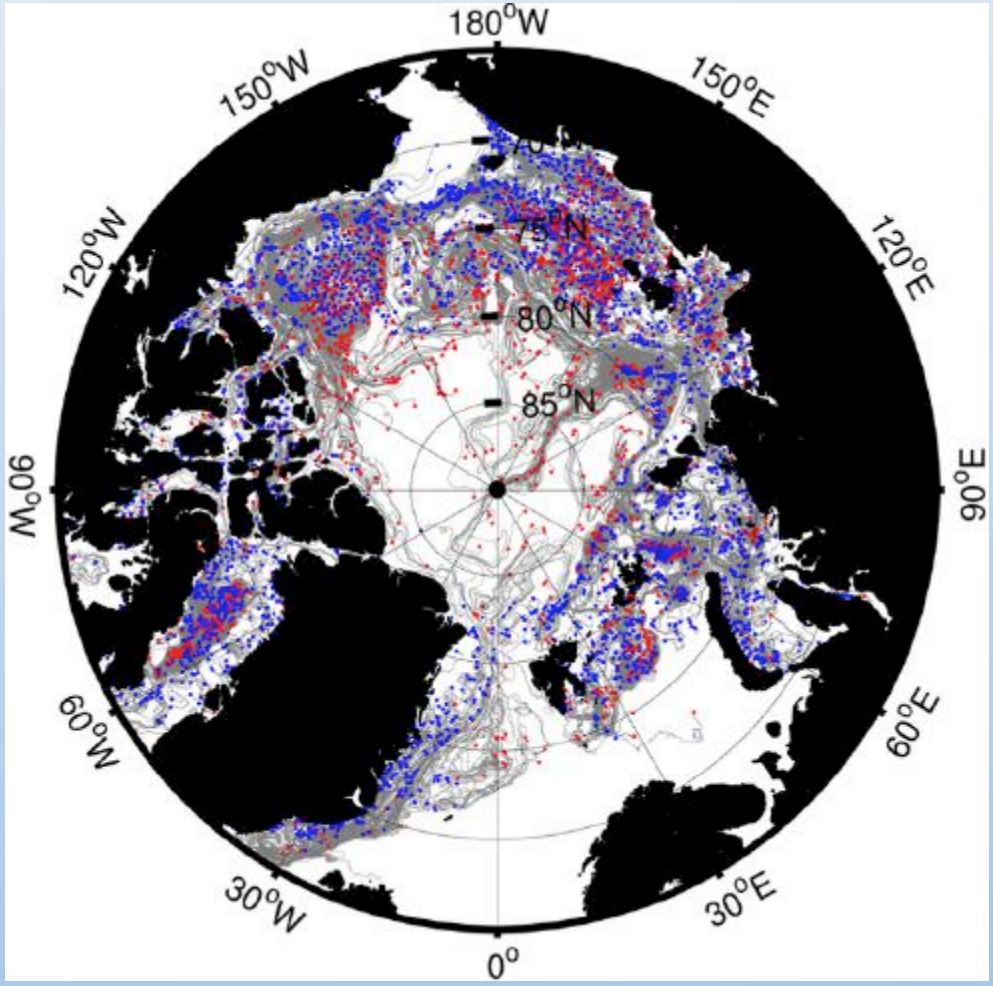
Temperature Dependent @ Surface



- Neither species can "make it" (achieve the diapause stage) in the Central Arctic

Add Advection during Diapause

C. hyperboreus



- For this species, continued advection and development including diapause at 200 m for two additional years
- 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