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Clocks & Rhythms in Polar Pelagic Organisms

Krill population cycles

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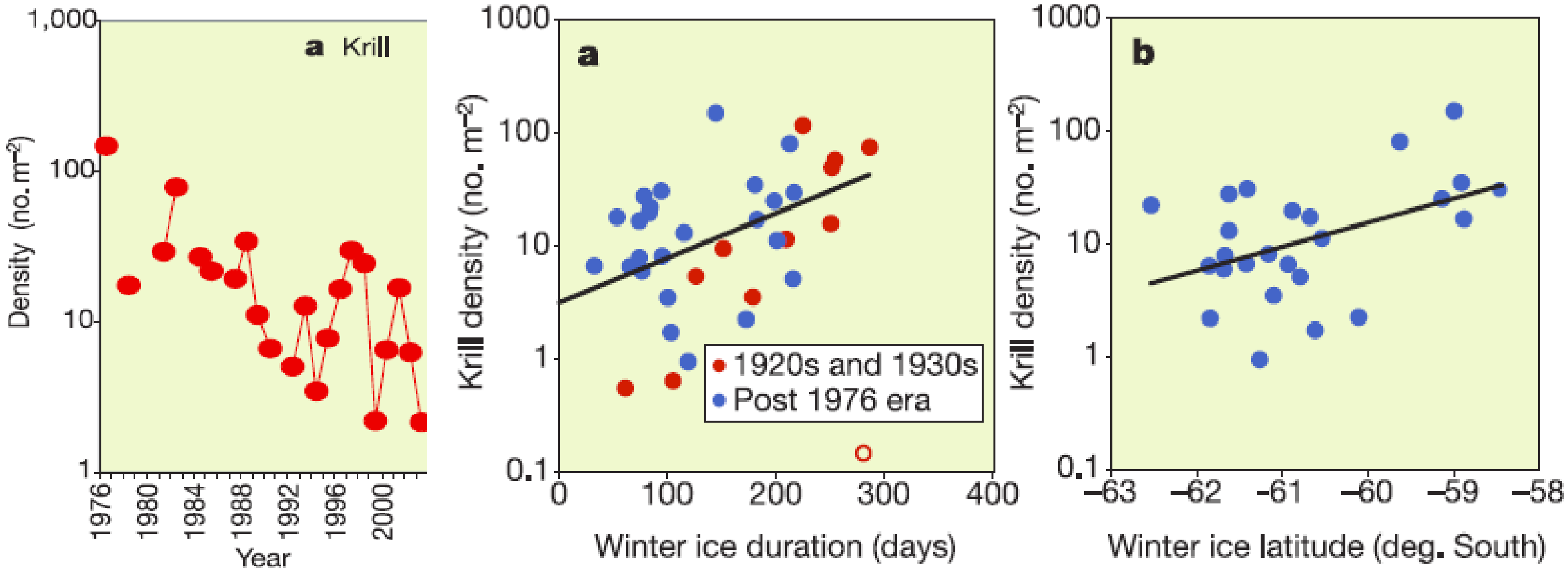
Australian Antarctic Division

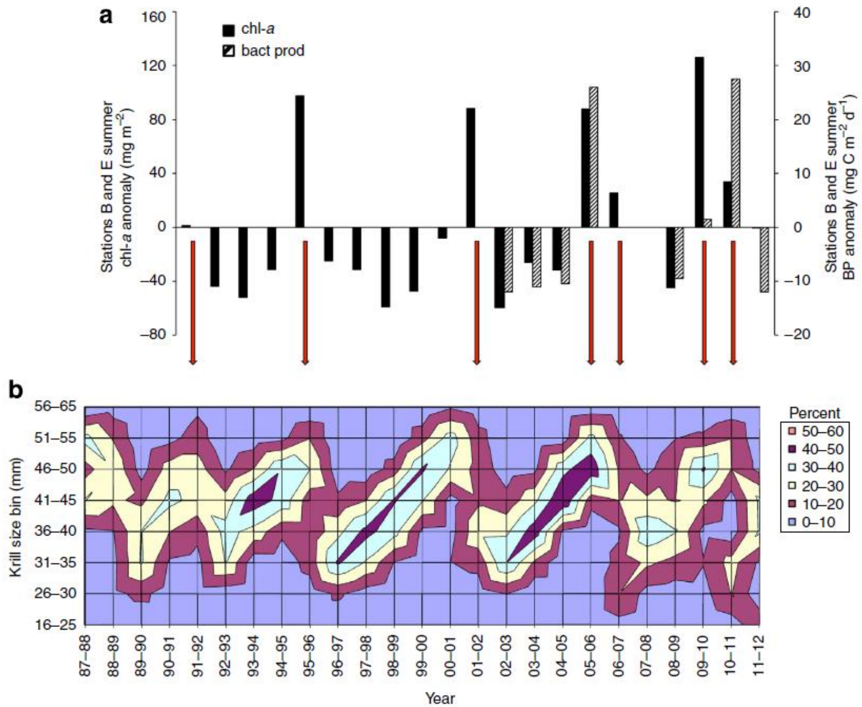
Why does krill abundance oscillate?

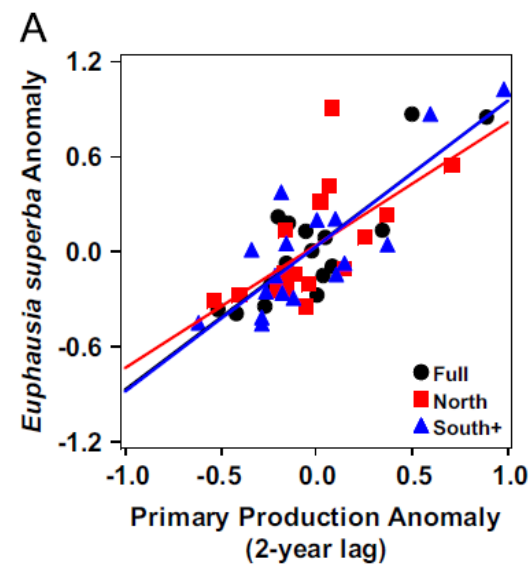


Atkinson et al. 2004

Sea ice and summer conditions are the main drivers of krill abundance

Effects of summer chlorophyll



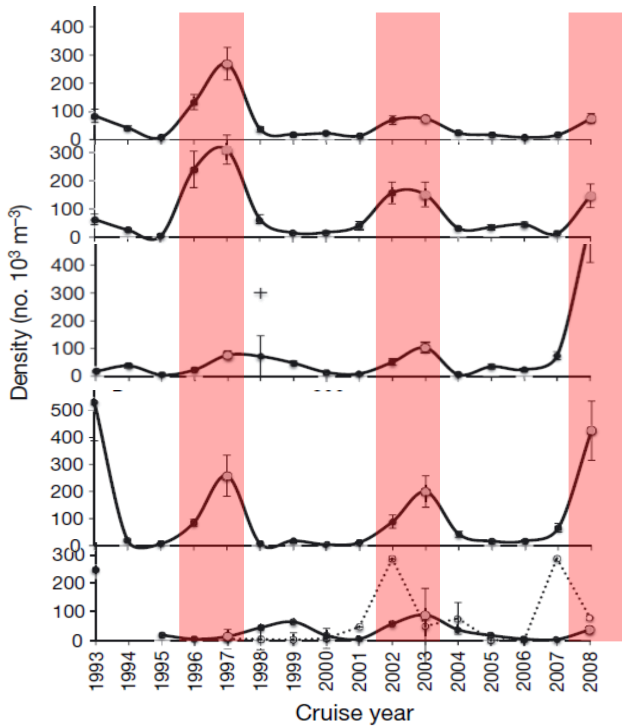


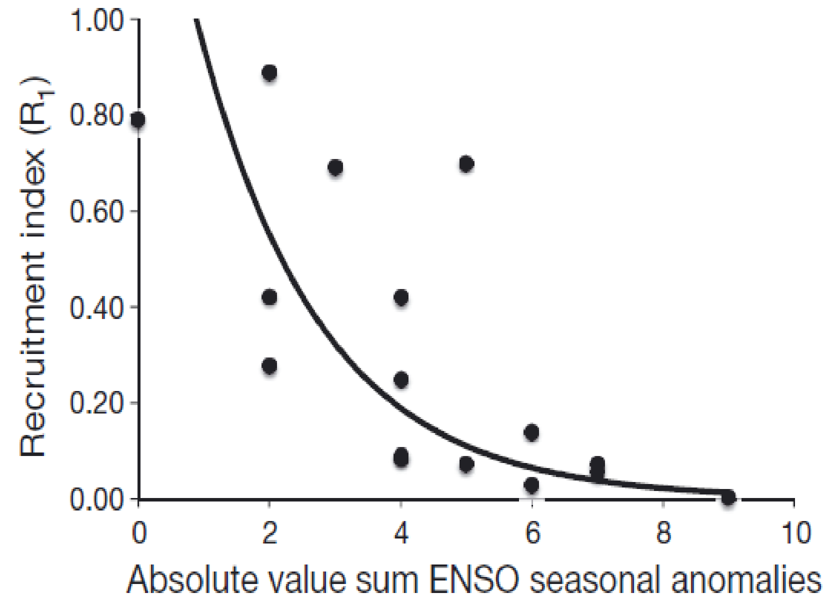
Survival of new cohorts was associated with anomalies in summer chlorophyll level or in primary production

Sabe et al. 2014, Nat Commun

Steinberg et al. 2015, Deep Sea Res

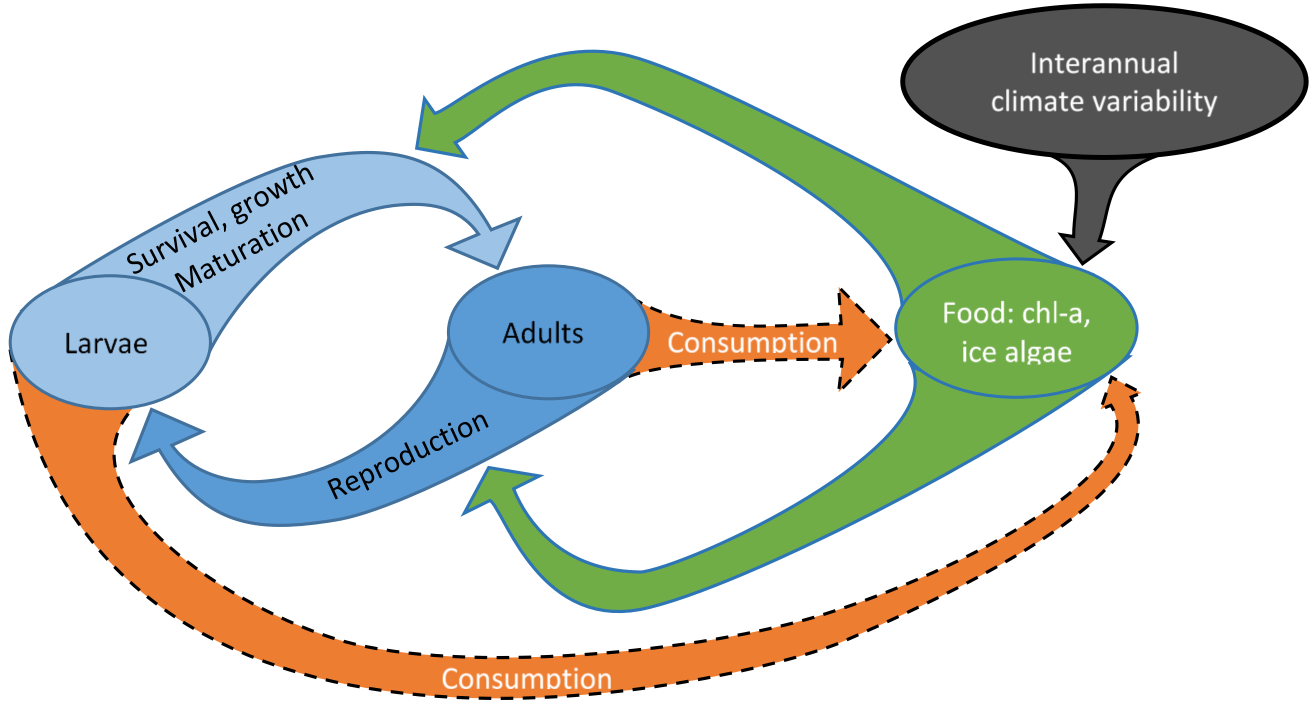
Sea ice duration, ENSO index





Ross et al. 2014, MEPS

Recruitment success has been linked to the El Niño-Southern Oscillation (ENSO) cycle



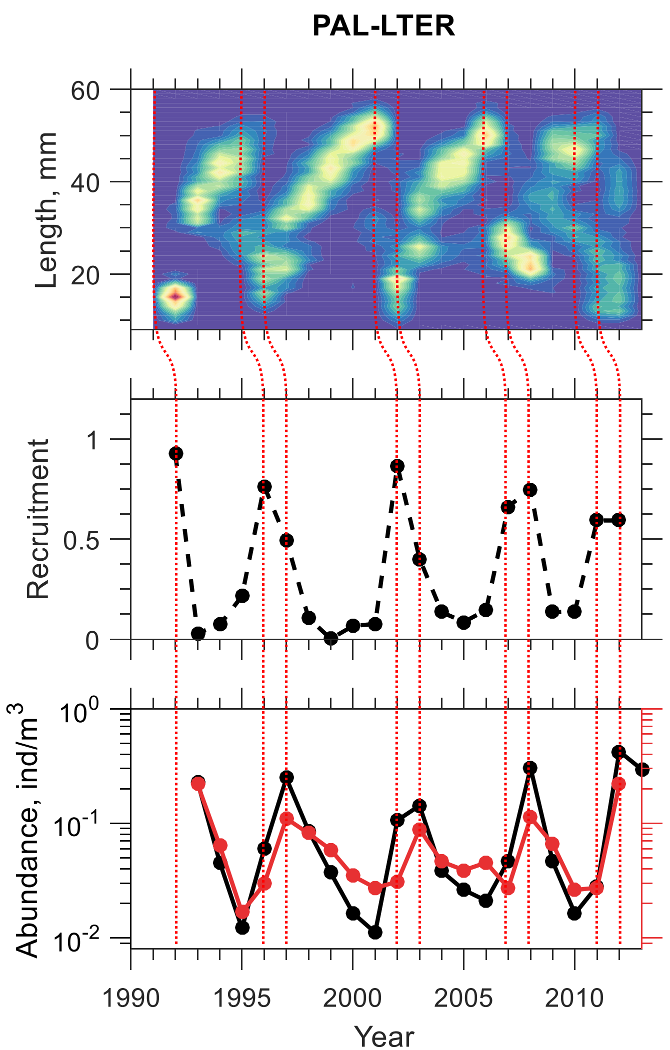
The krill population dynamics is driven by food availability

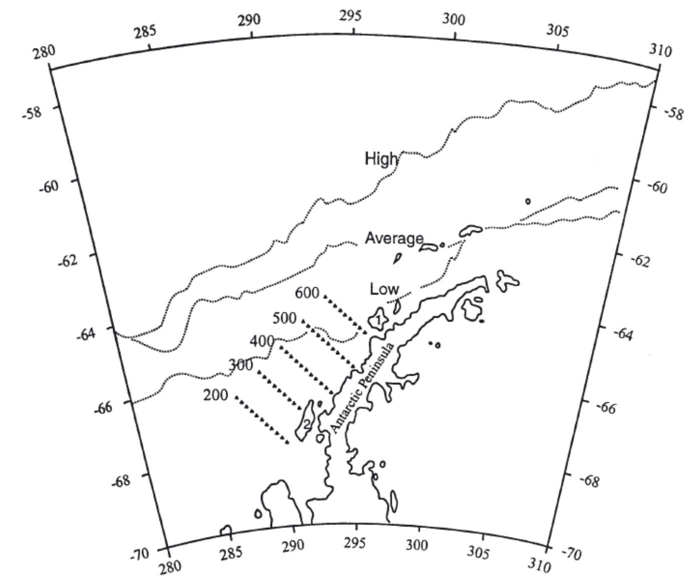
But the food availability can be affected either by external factors (climate variability) or by grazing (if the population is resource limited)

Too strong consumption can reduce reproduction or maturation

An ontogenetic asymmetry (e.g., a difference in weight specific food assimilation between larvae and adults) can lead to oscillations in abundance in a stage-structured population

Persson & de Roos, *Ecology* **94**

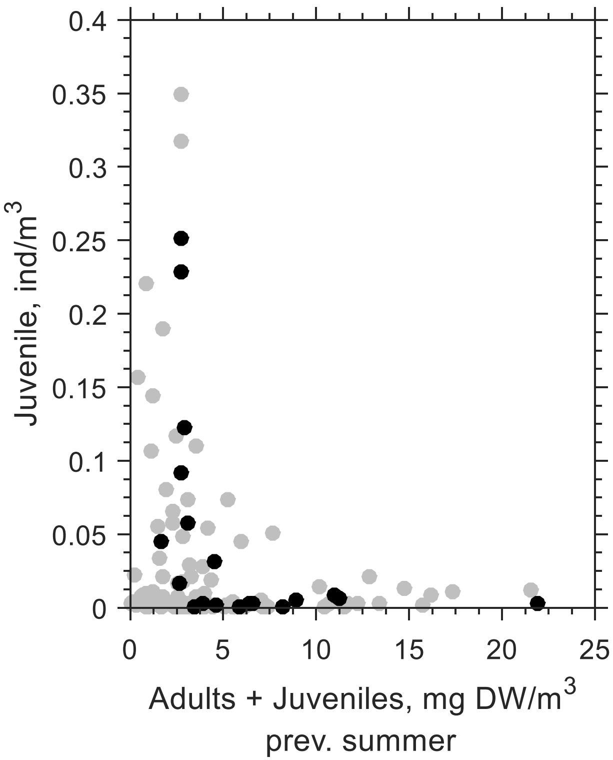


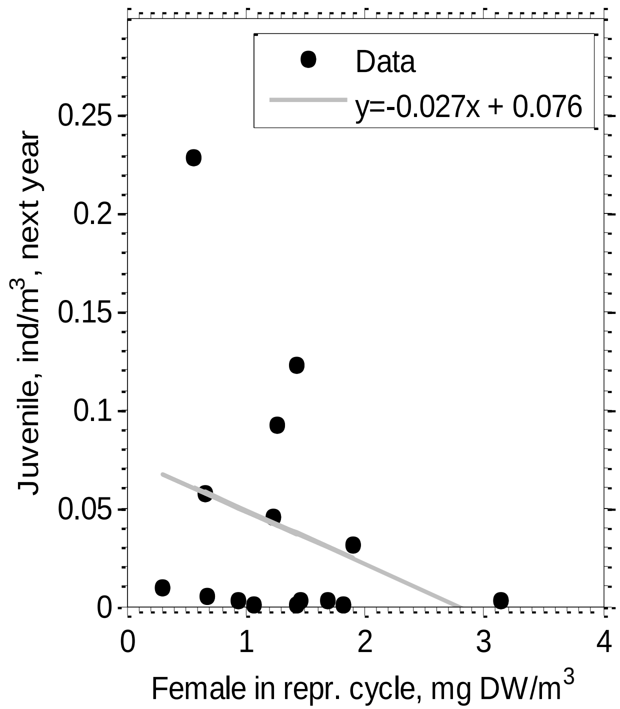


Quetin & Ross 2003, 2014

The cycle period is around 5-6 years with 2 successive years of good recruitment and 3-4 years without recruitment

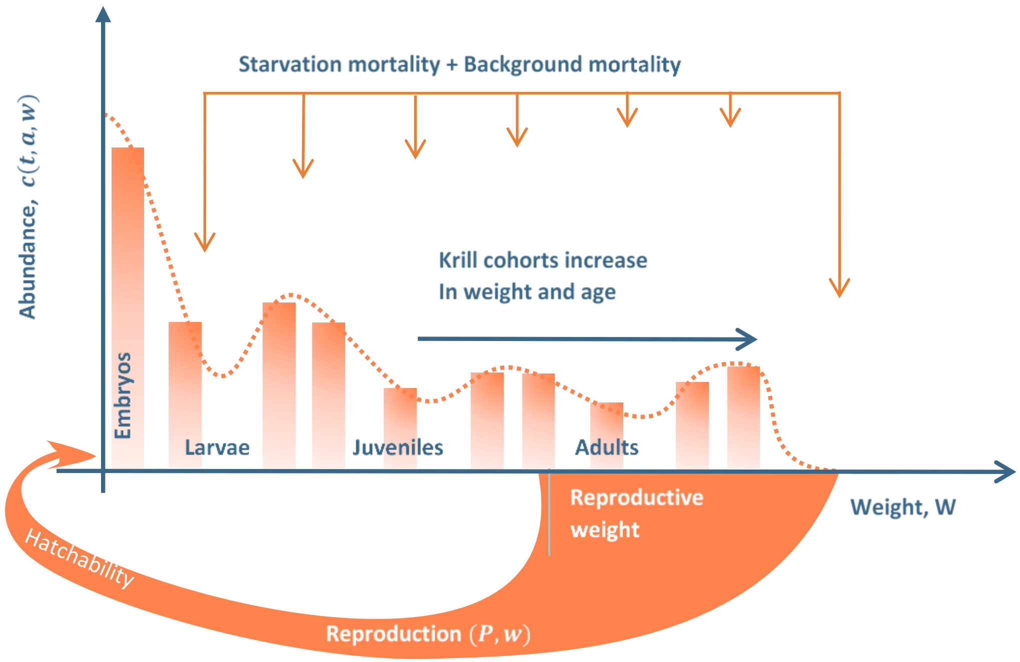
The appearance of a new strong cohort is synchronized with extinction of an old strong cohort



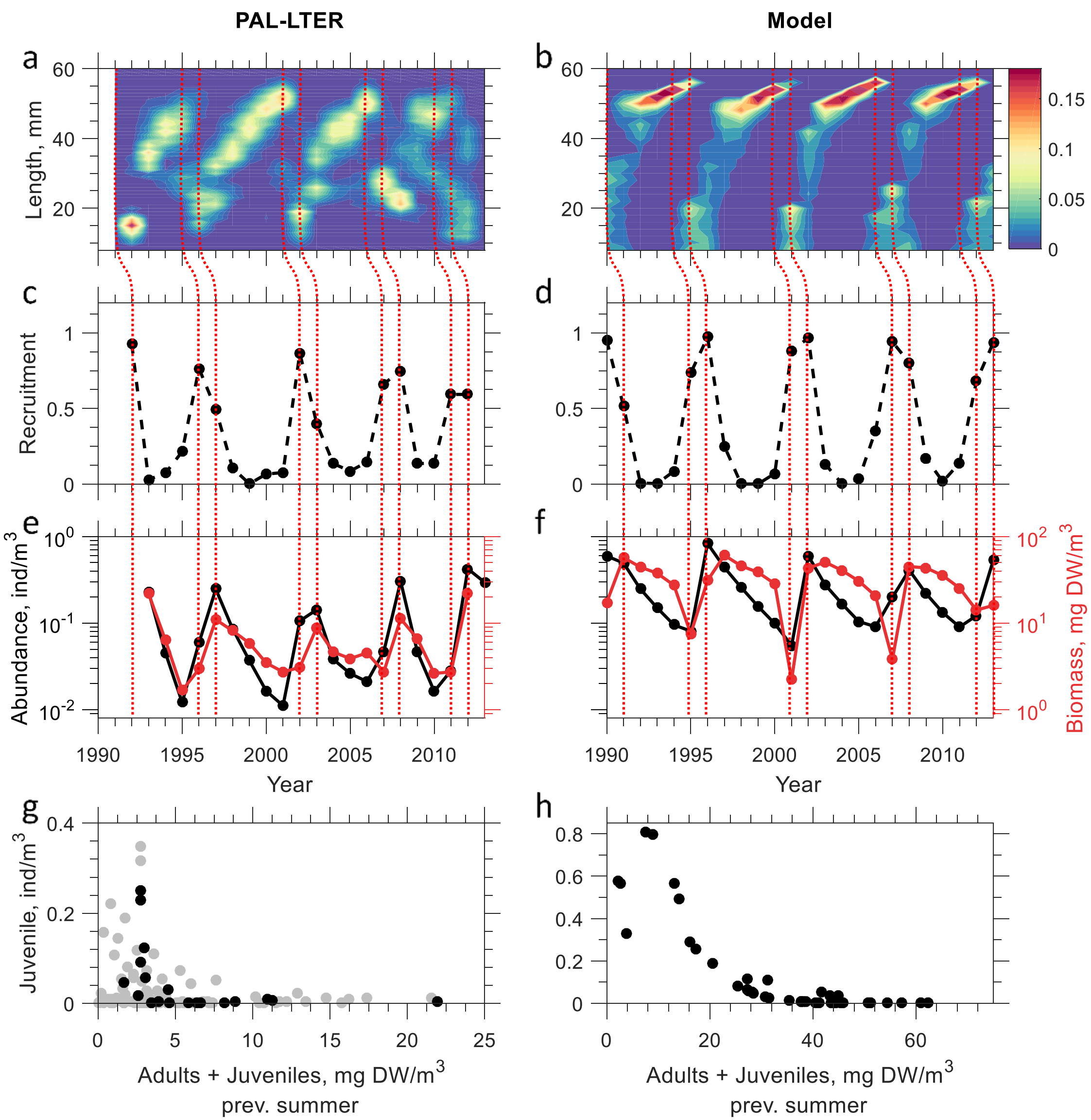


There is a negative effect of krill biomass and on krill recruitment, which implies resource limitation of the whole population

Model

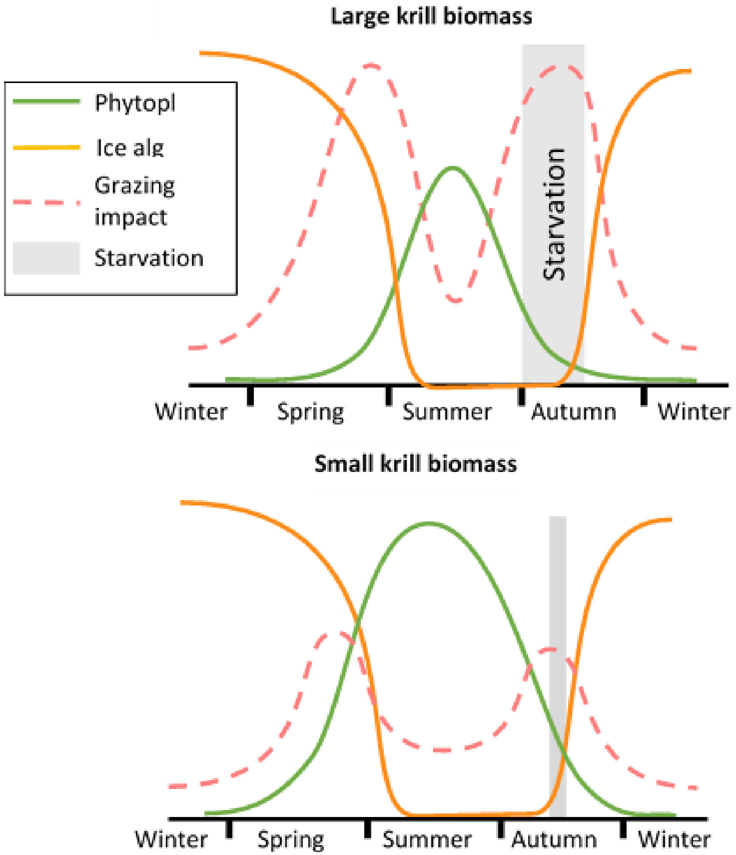


- The model captures the effects of seasonality on reproduction and ontogenetic development of krill.
- Growth and fertility are proportional to a difference between ingestion and maintenance rates
- In summer: all feeding stages compete for phytoplankton
- In winter: Adults can starve, larvae need to feed on ice algae, because larvae have a significant starvation mortality



- In the model, population cycles can occur even in the absence of interannual variability in phytoplankton production
- two successive years of successful recruitment followed by 3-4 years of unsuccessful recruitment
- a new cohort appears when an old strong cohort dies
- the negative effect of krill biomass on the juvenile abundance one year later

The mechanism of the cycles

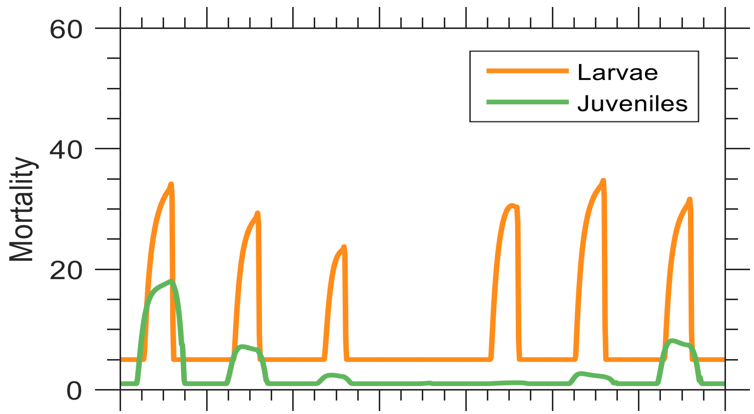


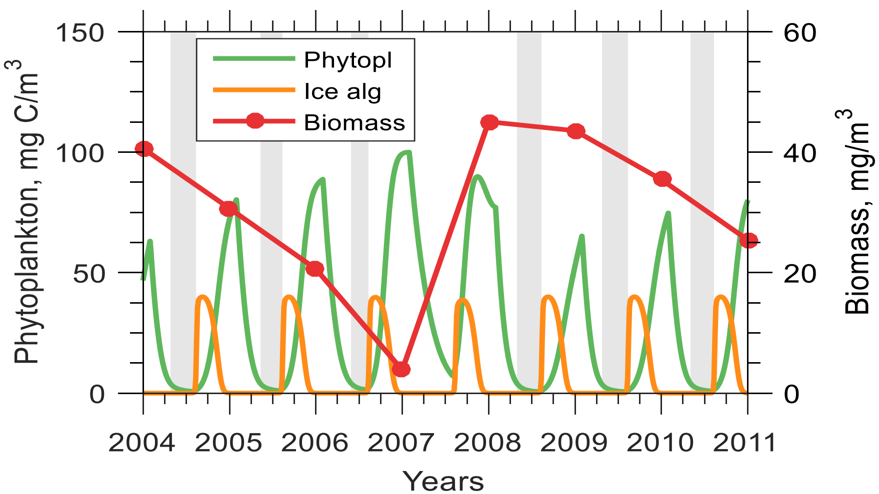
During autumn the phytoplankton concentrations and duration of the starvation periods are strongly sensitive to krill biomass density.

An abundant krill population (adults and/or larvae) depletes phytoplankton and leads to a long starvation period of larvae during autumn.

A small population has a smaller impact on phytoplankton, and phytoplankton concentrations are sufficient for larvae to survive.

The mechanism of the cycles



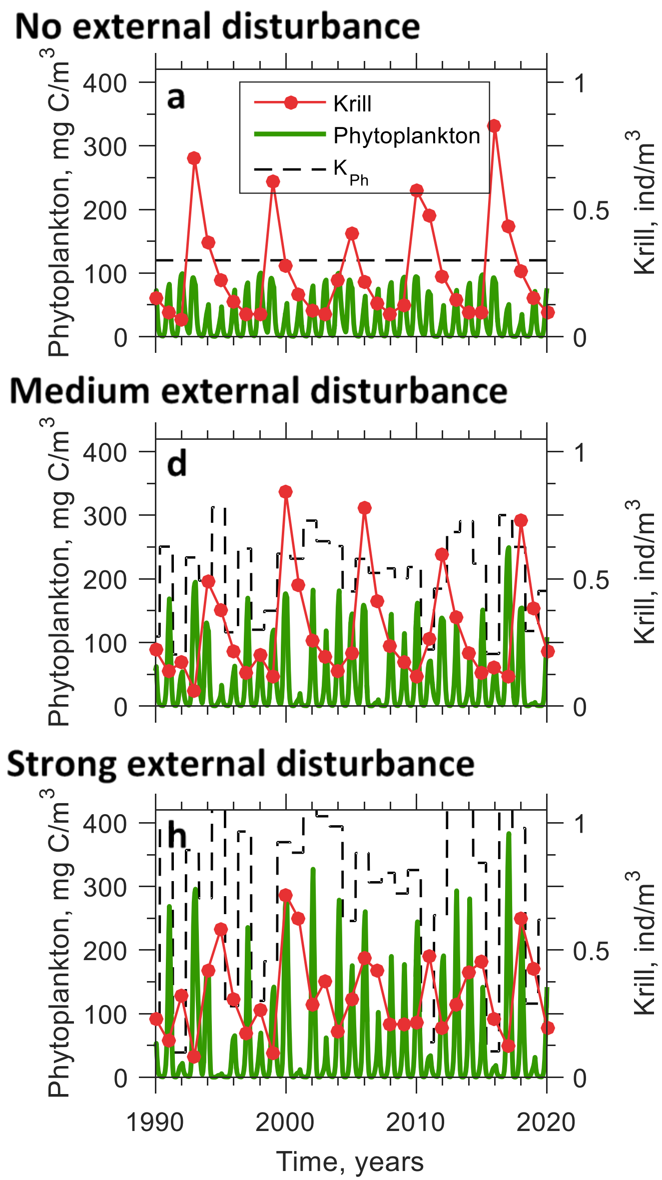


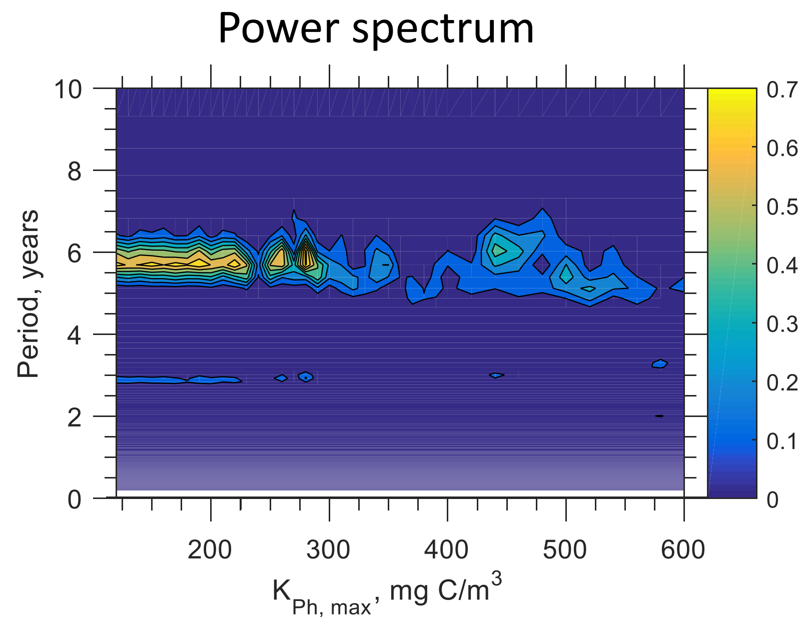
The cyclic changes in the biomass lead to cyclic changes in mortality.

Large biomass -> large starvation mortality -> small absolute recruitment -> a decrease on total biomass.

Small biomass -> small starvation mortality -> over reproduction-> Large biomass -> ….

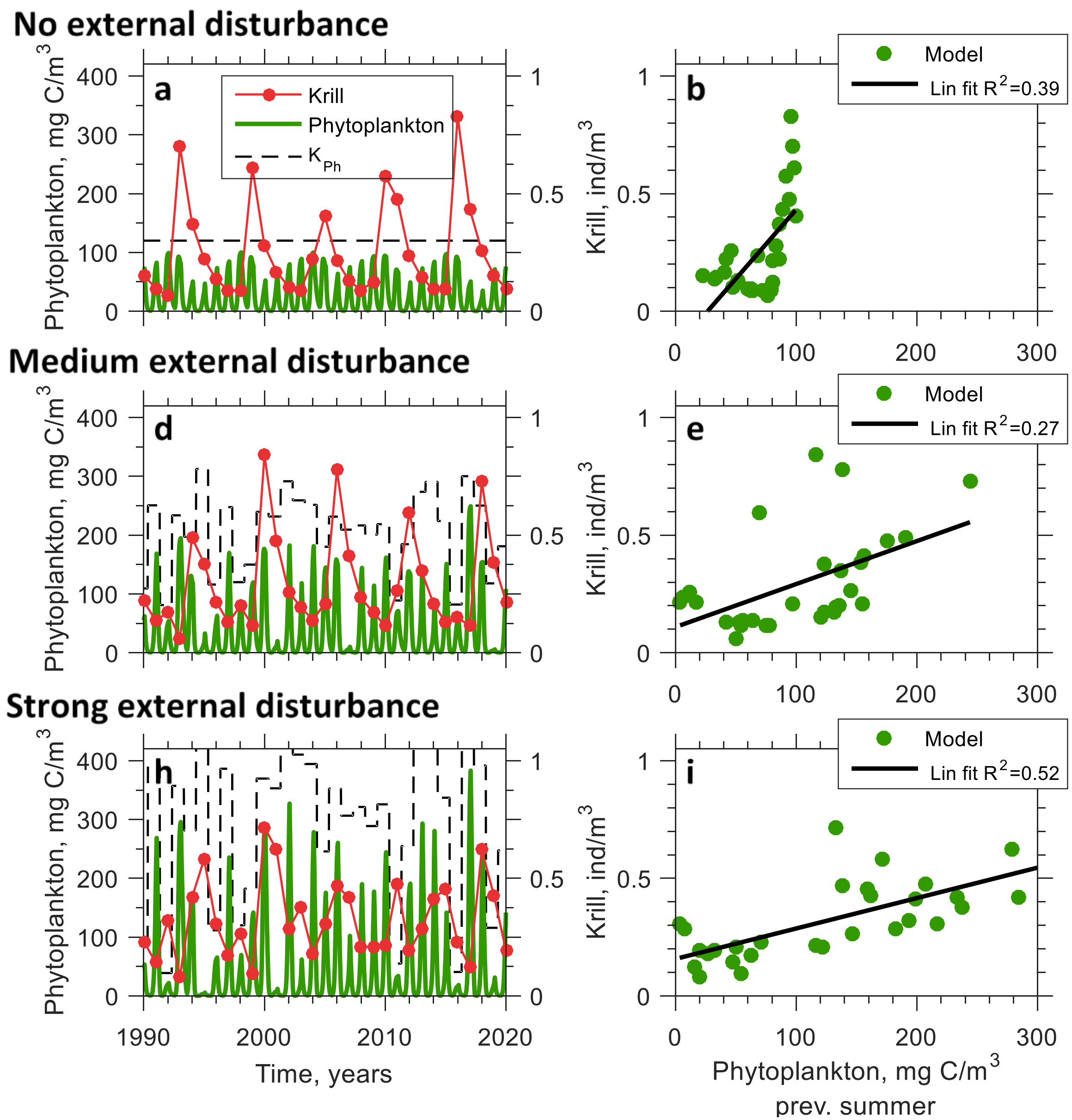
Effects of climate variability





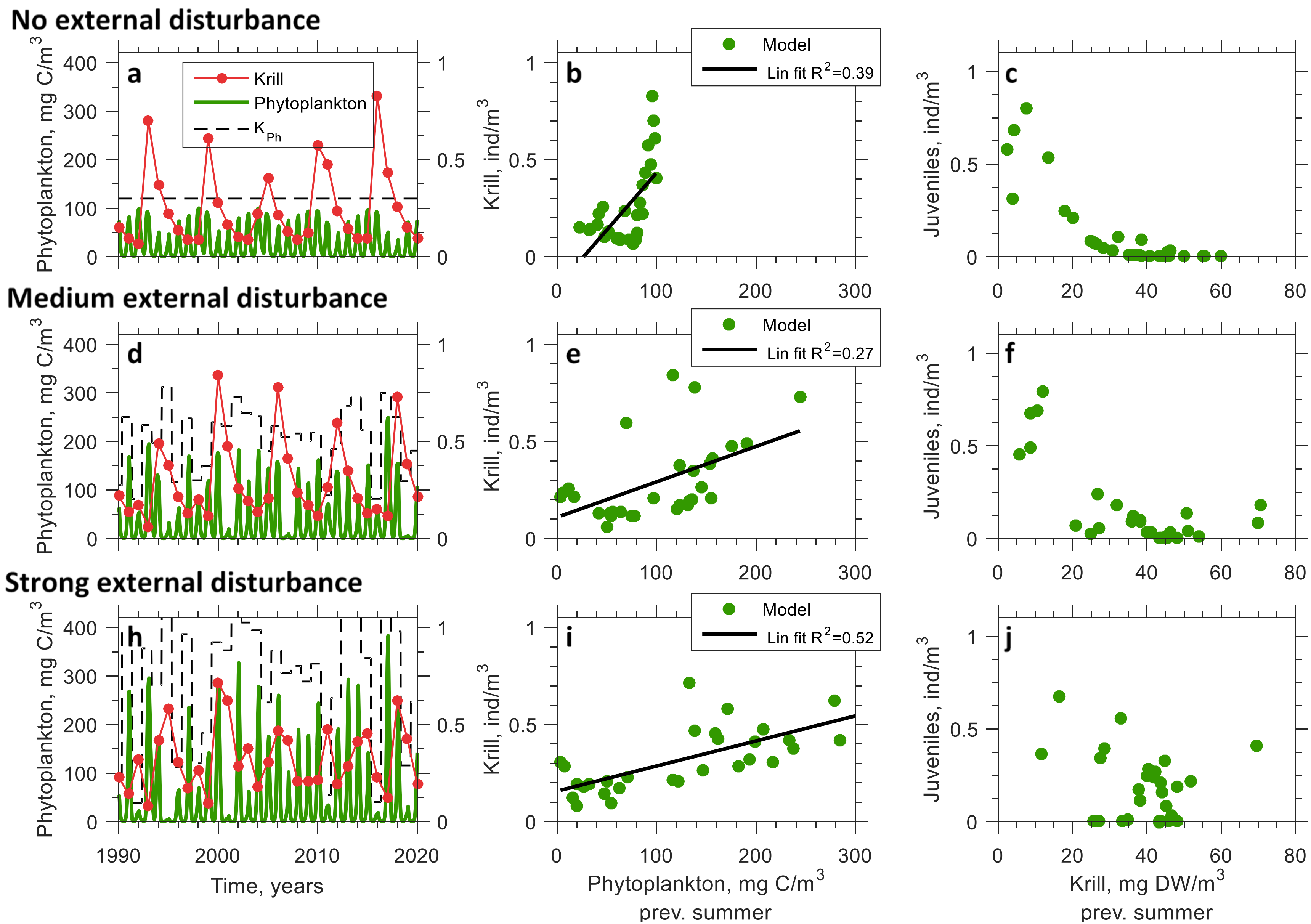
The six year oscillation cycle is retained in the model with among-year random variations in algal productivity

Effects of climate variability

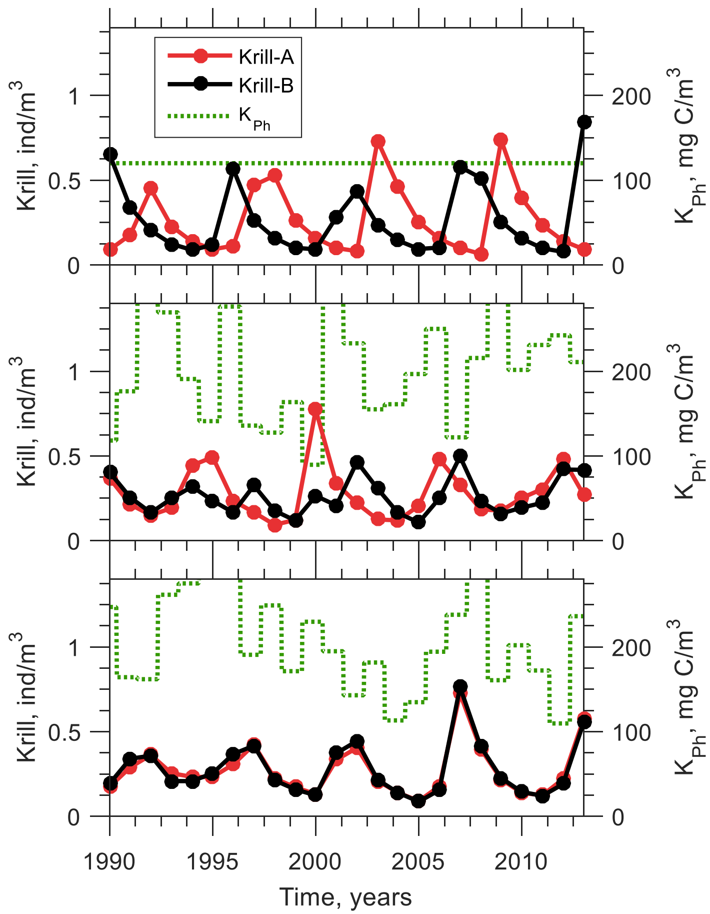


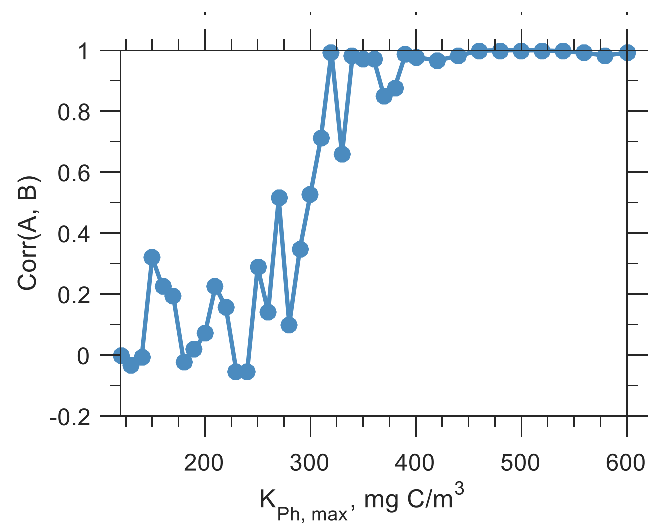
The correlation between summer chlorophyll level and krill abundance next summer increases with increasing perturbation level.

Effects of climate variability



Synchronization of two uncoupled population by climate (Moran effect)



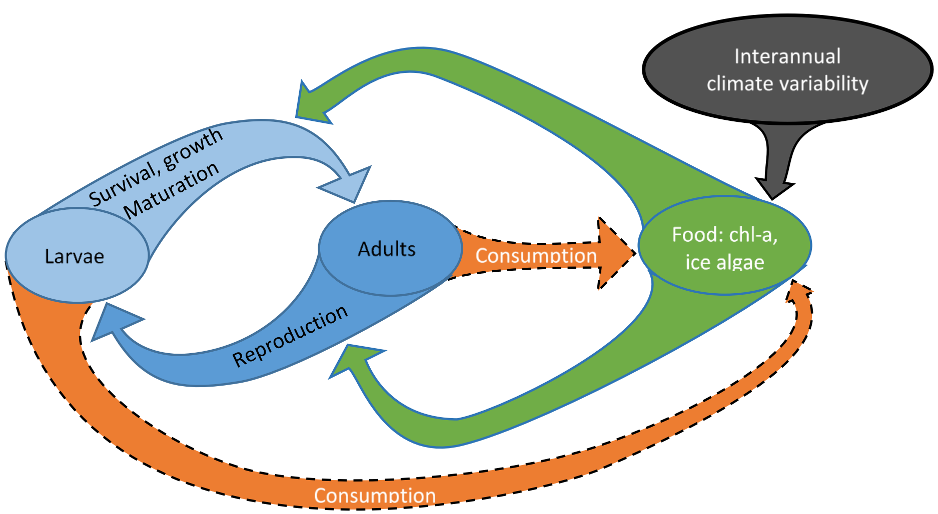


The correlation between two separate populations increases with the level of environmental disturbances, leading ultimately to a complete synchronization of two uncoupled populations

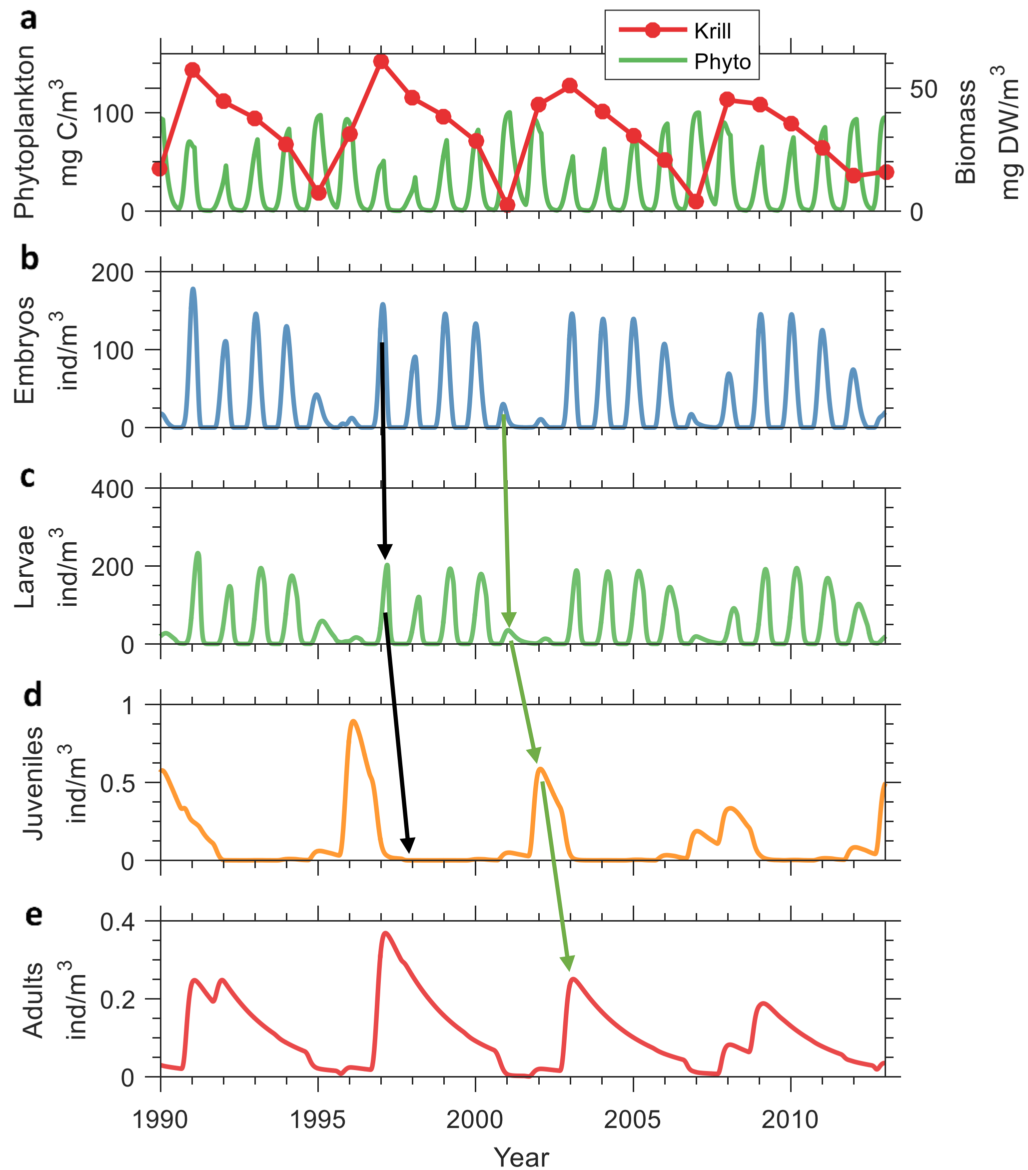
- Krill population cycles can be induced by competition between different cohorts for food

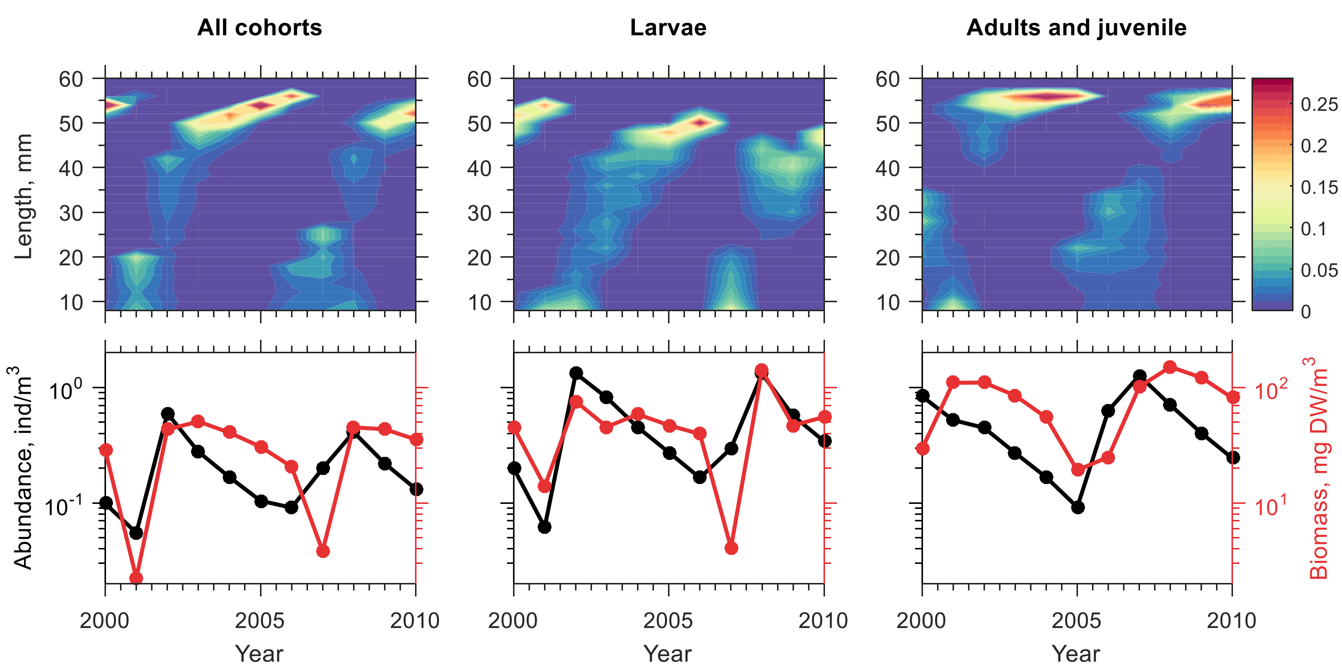
- The model can naturally explain the presence of
  - two successive years of successful recruitment followed by 3-4 years of unsuccessful recruitment
  - a new strong cohort appears when an old strong cohort becomes extinct
  - total krill biomass has a negative effect on the juvenile abundance one year later

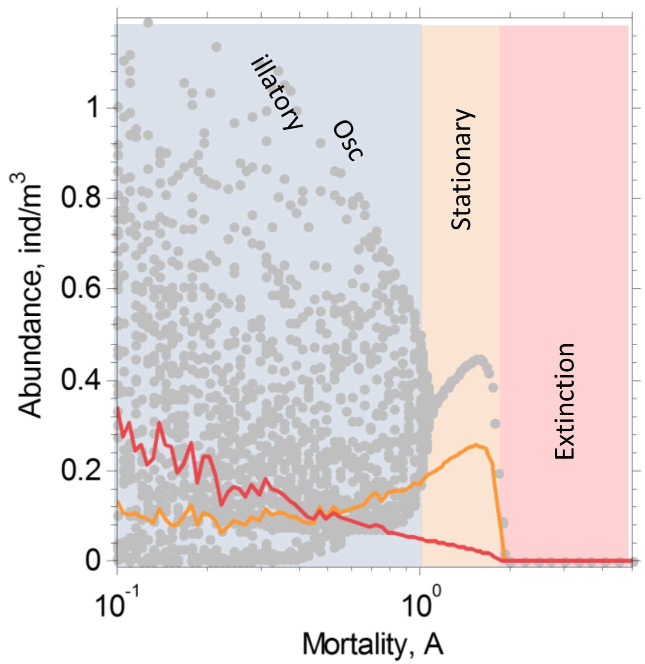
- External climatological factors can modulate the cycle phase and duration and also can synchronize the cycles over large scales



It is important to take into account the effect of consumers on food availability, especially for the periods when the food is depleted


a
Krill
Phyto
Phytoplankton mg C/m3
Biomass mg DW/m3
100
0
50
0
b
Embryos ind/m3
200
100
0
c
Larvae ind/m3
400
200
0
d
Juveniles ind/m3
1
0.5
0
e
Adults ind/m3
0.4
0.2
0
1990
1995
2000
2005
2010
Year

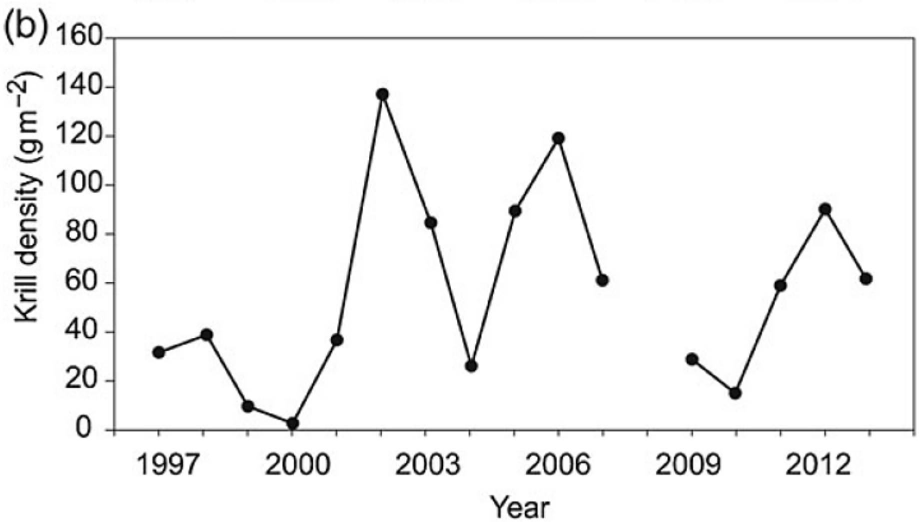

All cohorts
Larvae
Adults and juvenile
Length, mm
60
50
40
30
20
10
0.25
0.2
0.15
0.1
0.05
0
Abundance, ind/m^3
10^0
10^{-1}
Biomass, mg DW/m^3
10^2
10^1
2000
2005
2010
Year

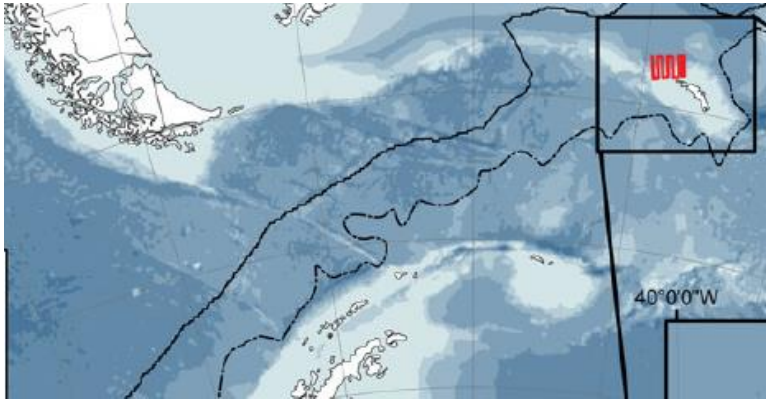


Osc
illatory
Stationary
Extinction
Abundance, ind/m3
1
0.8
0.6
0.4
0.2
0
10-1
100
Mortality, A

Why does krill abundance oscillate?

Fielding et al. 2014



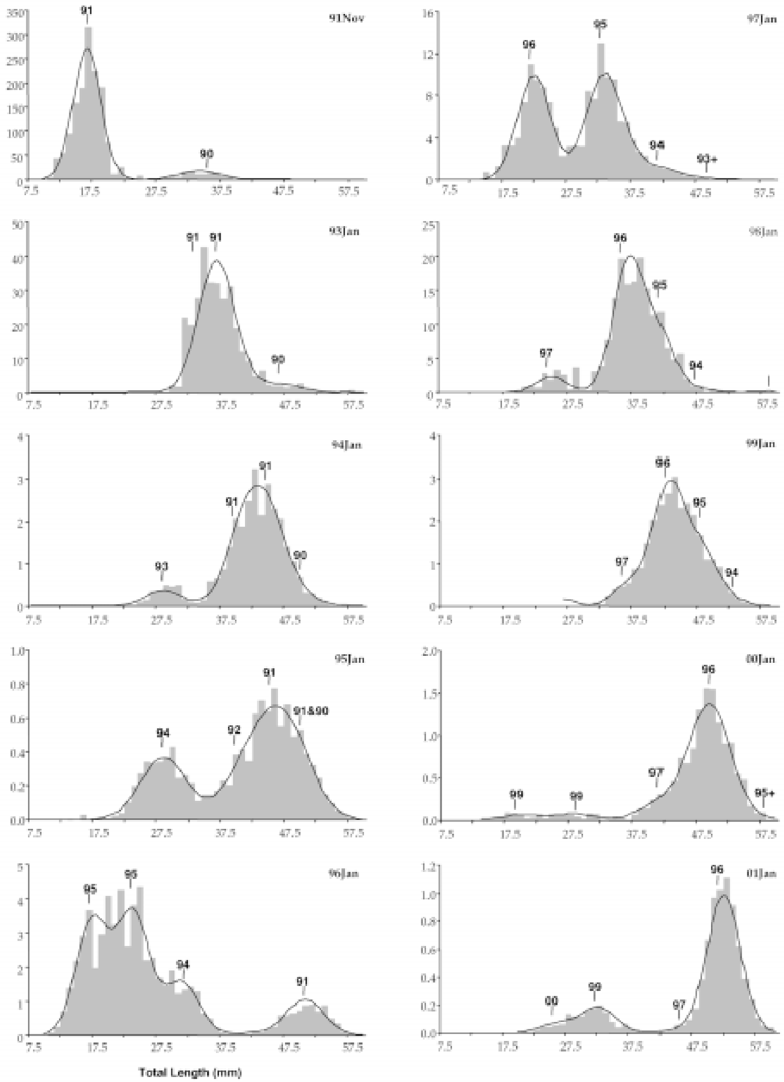


Only surface temperature with 5 month lag was significantly correlated with krill density. The effect of **SAM and ENSO was not significant**

Table 3. Summary of Pearson's correlation probability (p) and factor (f) of SDWBA krill density and indices of SAM, ENSO, and SST for 0 – 12 month lagged data.

Lag (month)	0	1	2	3	4	5	6	7	8	9	10	11	12
SAM (p)	0.35	0.39	0.74	0.27	0.38	0.74	0.42	0.68	0.02	0.12	0.38	0.39	0.52
SAM (f)	−0.25	−0.23	0.09	−0.29	0.24	−0.09	−0.22	0.11	−0.58	0.41	−0.24	−0.23	−0.18
ENSO (p)	0.71	0.79	0.74	0.64	0.65	0.42	0.37	0.14	0.45	0.58	0.93	0.94	0.99
ENSO (f)	0.10	0.07	0.09	0.13	0.12	0.22	0.24	0.39	0.20	0.15	0.03	0.02	0.00
SST (p)	−0.68	0.88	0.36	0.03	0.02	**0.01**	0.57	0.48	0.22	0.24	0.40	0.66	0.37
SST (f)	0.11	−0.04	−0.25	−0.54	−0.57	**−0.64**	−0.16	−0.16	−0.33	−0.31	−0.23	−0.12	0.24

Factors significantly correlated with SDWBA krill density (at a level of $p < 0.1$, which is adjusted to $p < 0.0083$ using the sequential Bonferroni correction; Holm, 1979) are in bold.



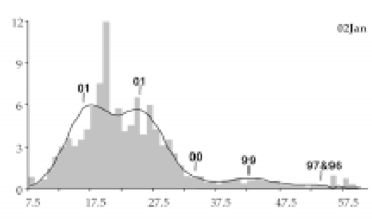
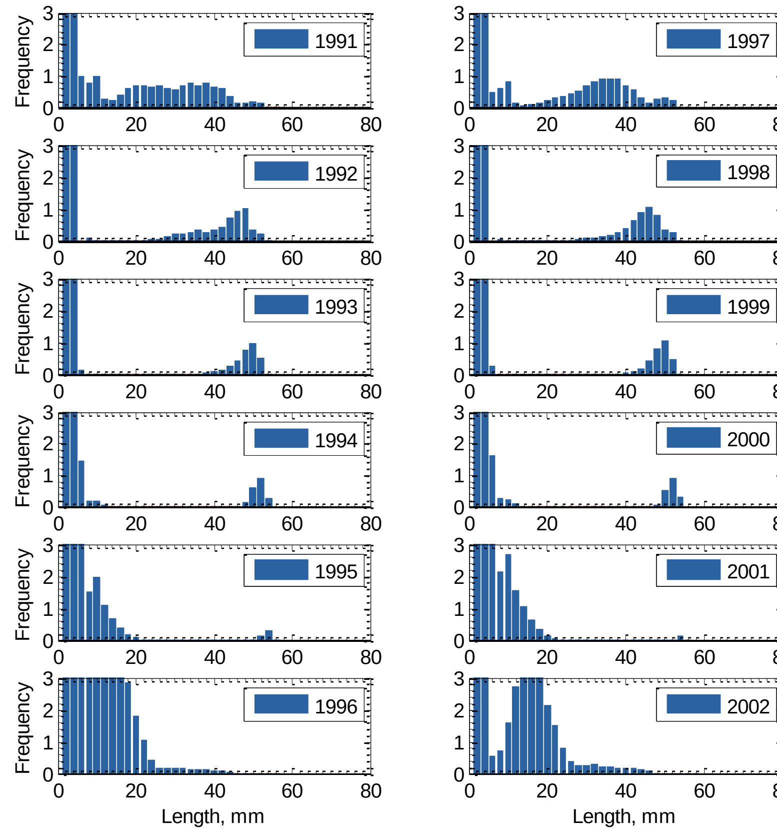
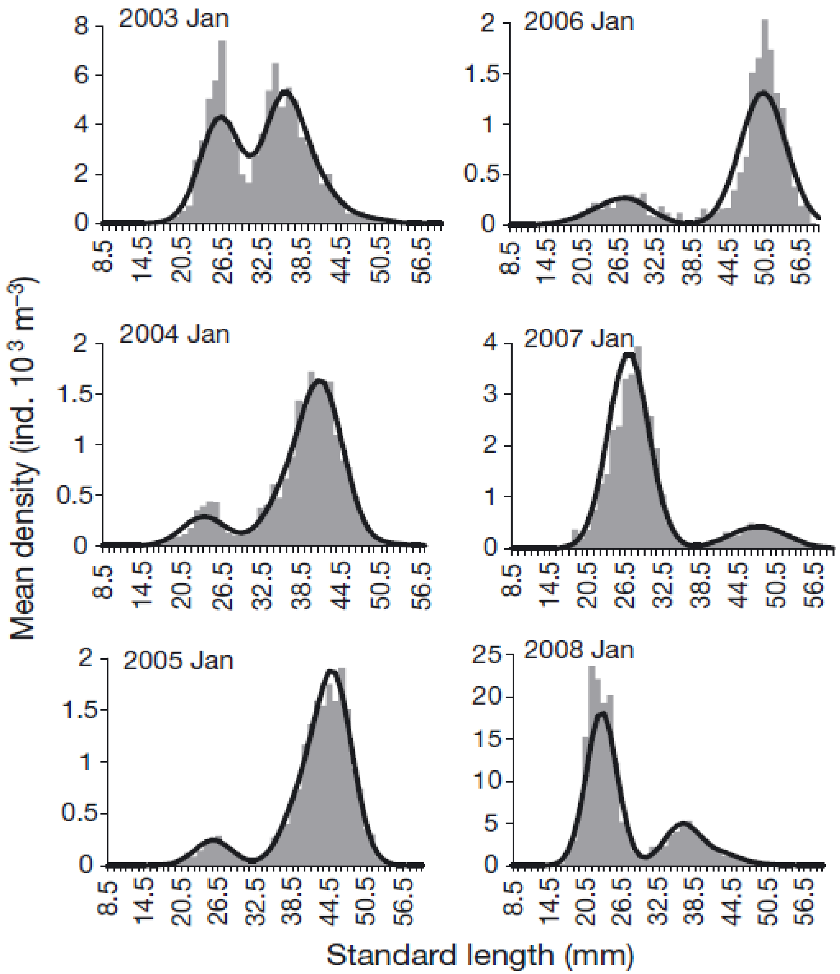


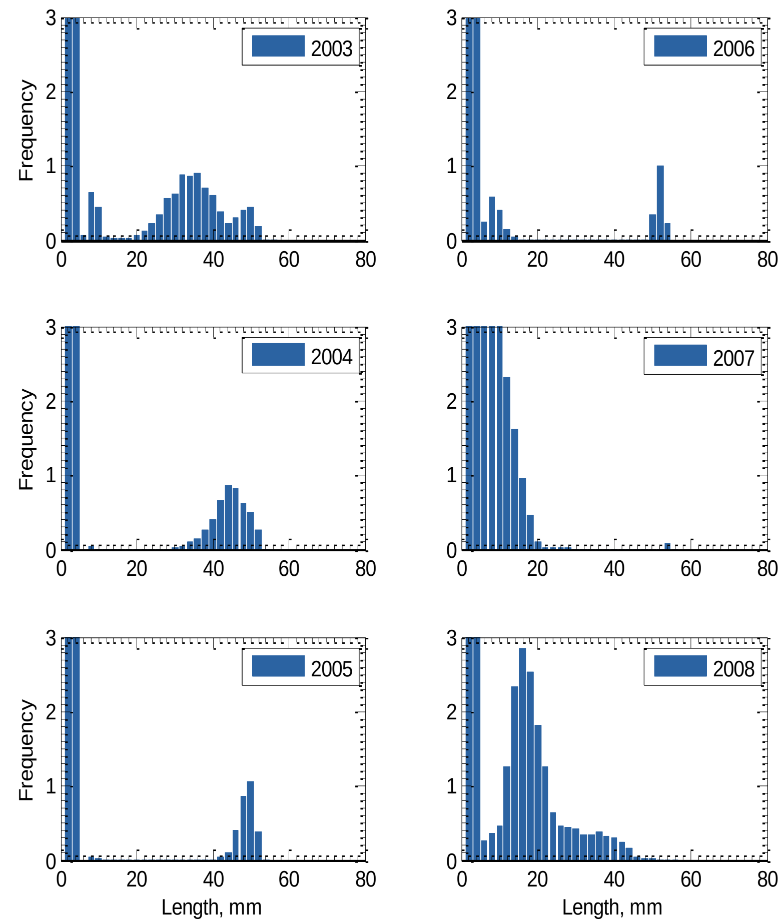
Fig. 2. *Euphausia superba*. Length–density distributions for the 11 cruises with observed densities in each length bin as solid columns and expected densities from the mixture solution derived with CMIX as the line. The vertical line and number indicate the mean total length of krill in a mode and the year class (YC) of that mode respectively. Two modes are shown for Age Class 1 for YC1995, YC1999 and YC2001



Quetin et al 2003

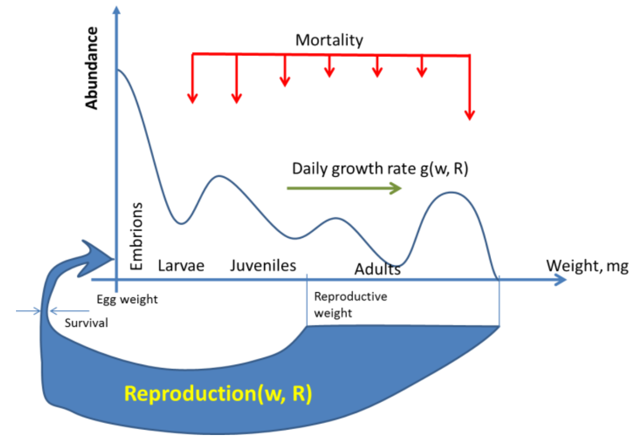
Length distributions





Quetin et al 2014

Modeling equations



Change = Growth − Mortality

$$\frac{\partial c(t,w)}{\partial t} = -\frac{\partial g(R,w)c(t,w)}{\partial w} - d(R,w)c(t,w)$$

w dry weight, t time

$c(t,w)$ density of the cohort (individuals/(m^3 mg))

$g(R,w)$ is daily growth rate (mg/day)

$d(R,w)$ mortality ($year^{-1}$).

Reproduction

$$g(R,w_{egg})c(t,w_{egg}) = S\int_{w_{repr}}^{w_{max}} \mu(R,w)c(t,w)dw$$

Resource dynamics

$$\frac{dR}{dt} = D(G(t) - R) - \int_{w_{Larv}}^{w_{max}} I(R,w)c(t,w)dw\,;$$