



CAN TEMPERATURE-DEPENDENT GROWTH BE USED TO MEASURE SECONDARY PRODUCTION OF COPEPODS IN COASTAL UPWELLING SYSTEMS?

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PICES, Hiroshima 2012



Copepods as secondary producers

- They dominate virtually all marine systems
- They contribute significantly to zooplankton biomass (usually >60%)
- In the food web they capture and transfer C very fast (short life cycles)
- They are main prey of fish and other predators
- Many species.....many ecological capacities---
-many chances to occupy all kind of habitats


Copepods in upwelling systems: Humboldt Current as an example

- Low diversity high abundance and biomass
- Large sized copepods present, but usually medium size and even small copepods dominate (number and biomass)
- Large-sized herbivores are not the main pathway of C, but omnivore small-sized copepods seem the major channel for C in the food web
- They usually reproduce year round (continuous production)
- In the spring they feed on diatoms and in the winter the swicht to an heterotrophic diet.



If food is sufficient to sustain continuous growth, then we ask:

Can temperature control the dynamics of copepods in upwelling systems?

- Copepods are ectotherms
 - Development rate is temperature dependent
 - They show exponential growth, then g depends on DR, which is T° dependent
 - $DW/DT = W_0 \text{Exp}(g t)$
- 

TEMPERATURE IS A KEY FACTOR FOR COPEPOD ECOLOGY

Temperature and development

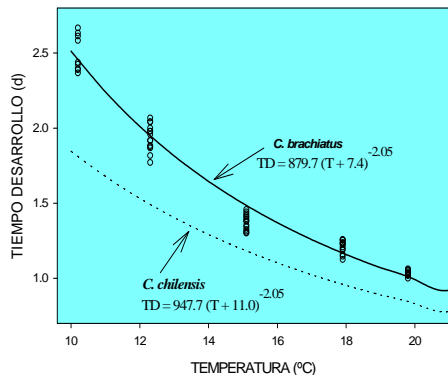
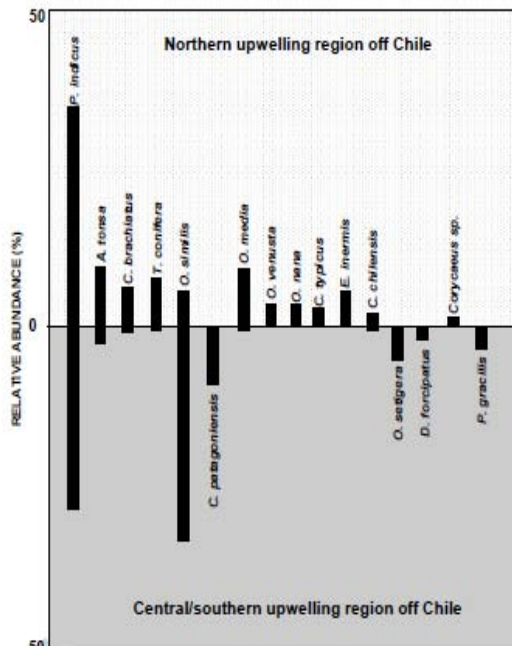


Table 1. Observed copepod species grouped by water-type affiliation.

Assemblage	Taxa	
Cold neritic	<i>Acartia hudsonica</i>	
	<i>Acartia longirostris</i>	
	<i>Calanus marshallae</i>	
	<i>Centropages abdominalis</i>	
	<i>Epithalpus amphioxys</i>	
	<i>Paracalanus crassus</i>	
	<i>Totanus albobrunneus</i>	
	<i>Mesocyclops pacificus</i>	
	<i>Mesocyclops pusillus</i>	
	<i>Mesocyclops plumbeus</i>	
Subarctic	<i>Scutellinella minor</i>	
	<i>Acartia tonsa</i>	
	<i>Coronula angulata</i>	
	<i>Caeculanus varius</i>	
	<i>Paracalanus parvus</i>	
	Warm neritic	<i>Acartia danae</i>
		<i>Calanus pacificus</i>
		<i>Calocalanus pavo</i>
		<i>Calocalanus tenuis</i>
		<i>Canthata bipinnata</i>
<i>Cliscolocanus arcuicornis</i>		
<i>C. furcatus</i>		
<i>C. tridax</i>		
<i>C. marginatus</i>		
<i>C. parvipes</i>		
Warm oceanic	<i>C. pusillus</i>	
	<i>C. perezii</i>	
	<i>Fucalcanus hutchinsoni</i>	
	<i>Fuchirella contracta</i>	
	<i>Mesocyclops lewinsonis</i>	
	<i>Platysolenites abdominalis</i>	
	<i>Rhinocalanus muelleri</i>	
	<i>Sapphirina</i> sp.	
	<i>Aetideus pacificus</i>	
	<i>Centropages brevis</i>	
Other	<i>Ch. somersi contracta</i>	
	<i>Fucalcanus</i> spp.	
	<i>Fuchirella</i> spp.	
	<i>Lacinia flavicornis</i>	
	<i>Mesocyclops</i> spp.	
	<i>Mesocyclops</i> spp.	
	<i>Oithona similis</i>	
	<i>Oithona speciosa</i>	
	<i>Oncocys</i> spp.	
	<i>Paracalanus</i> sp.	
<i>Racovitzia antarctica</i>		

WARM OR COLD ADAPTED COPEPODS SPECIES ARE EVERYWHERE

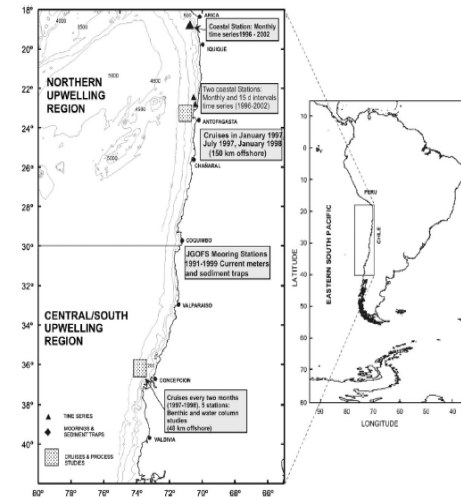
Norht Pacific (Hoofs & Peterson, 2006)



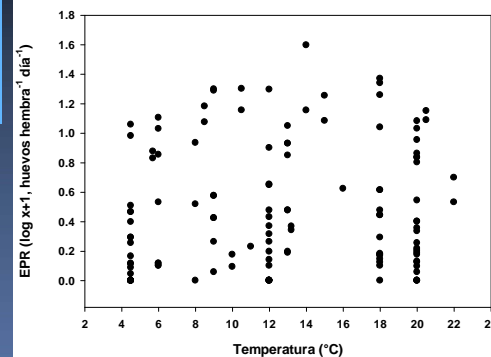
Rapid adjustment to highly variable temperature in upwelling systems

EPR vs Temperature (*C. patagoniensis*, *P. indicus*, *A. tonsa*)

WARM OR COLD ADAPTED SPECIES

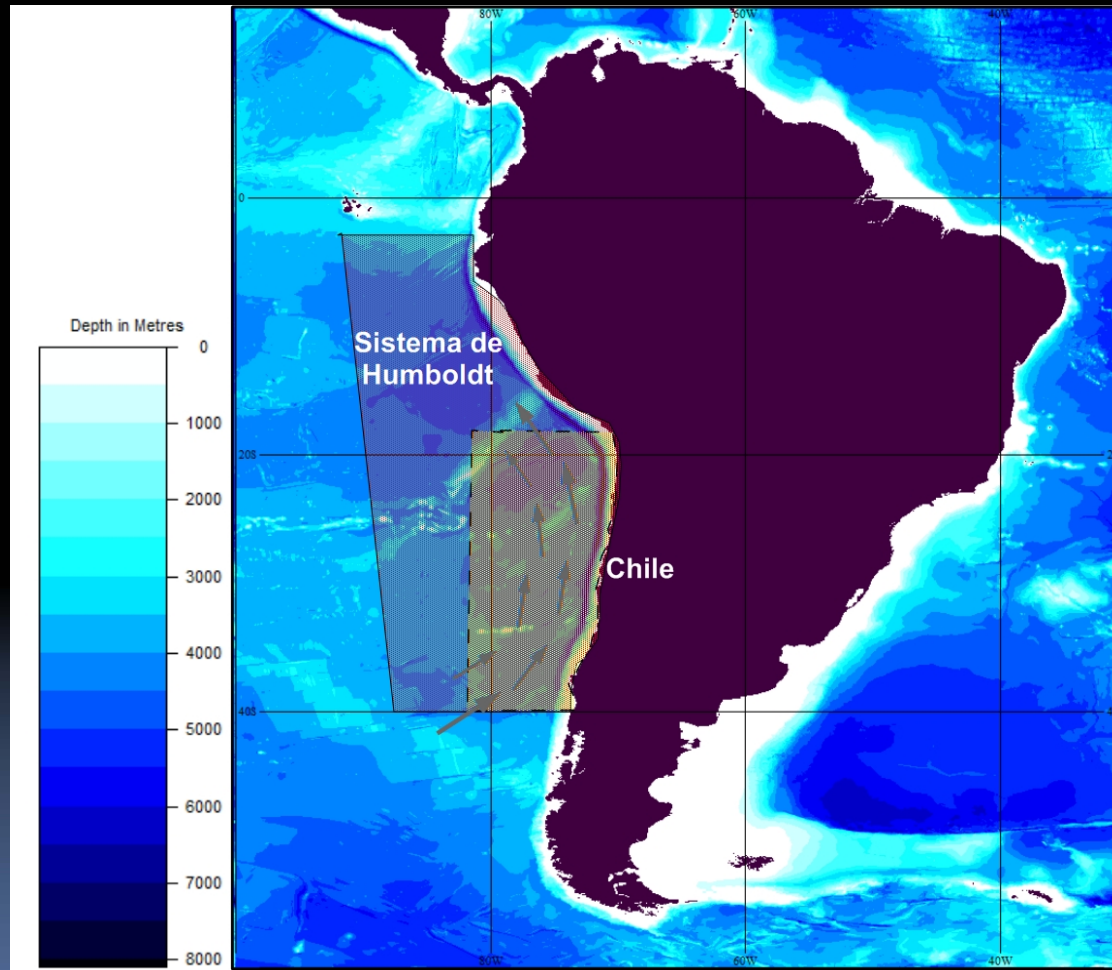


Hidalgo et al. (2010 DSR-II)



Fredericks & Escrivano, in prep.

COPEPODS IN THE HUMBOLDT CURRENT

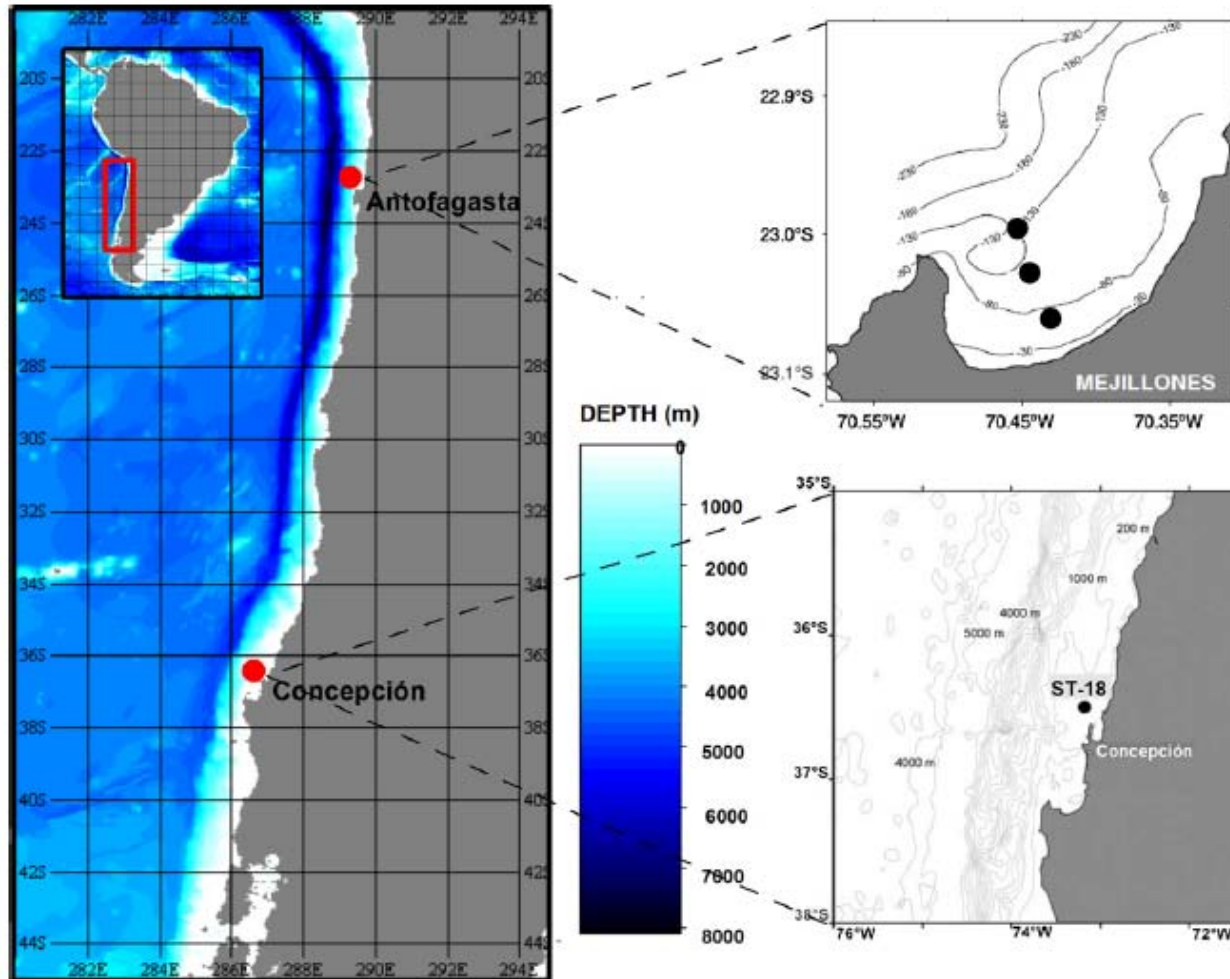


Paracalanus indicus
Calanus chilensis
Centropages brachiatus
Acartia tonsa
Calanoides patagoniensis
Eucalanus inermis
Rhincalanus nasutus

Most species distribute along a latitudinal gradient of ca 4500 km
This is a temperature range of about 8 to 25 °C in the upper 50 m

Therefore, the HCS is a natural experiment to test T° effects on copepods dynamics

Study Area for experimental work



20 and 10 years of study on copepod dynamics

Data on oceanographic variability (time series studies)

Copepod biomass, abundance and diversity

**In 2002-2003 and 2011
Live samples for experiments on development rate and temperature, using egg development approach**

Egg development experiments (No food effect)

- Estimating species clutch size, hatching success and the embryonic development time at controlled temperatures..T° range in the upper 50 m layer
- Fitting an equation to egg development rate as a function of T°
- $DR = a (T + \alpha)^c$ (Belerhàdek equation)
- $DR = a (\exp^{bT})$ (Exponential model)
- Using DR as a proxy to estimate species generation time (GT)
- Finally, estimating the potential number of generations a year (NGY)

RESULTS FOR THREE DOMINANT SPECIES

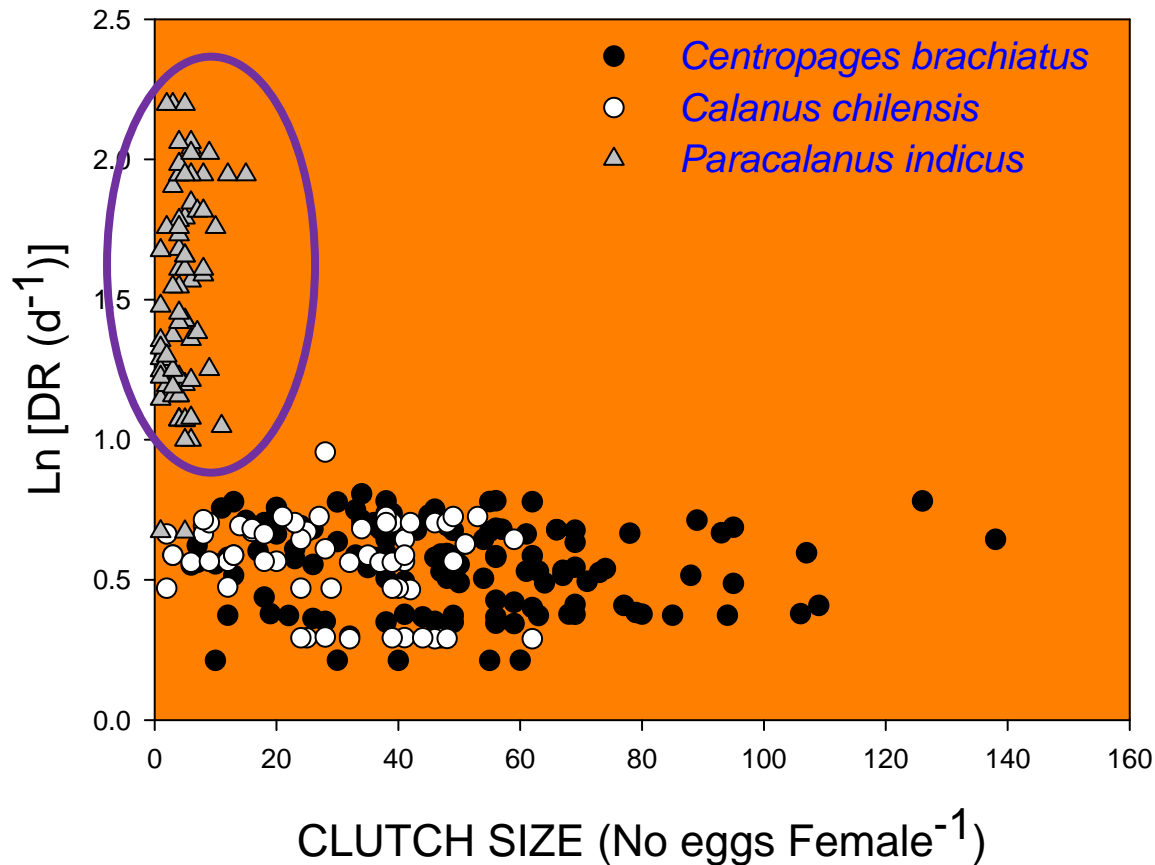
CLUTCH SIZE AND DEVELOPMENT RATE

CLUTCH SIZE= No. of eggs spawned at once per female (within 2 h)

Species	Clutch size (eggs female ⁻¹)	Hatching success (%)		DT (d)	
	Mean ±SE	Mean ±SE	n1	Mean ±SD	n2
<i>C. chilensis</i>	29.3 ± 1.97	32.0 ± 3.93	63	1.42 ± 0.074	79
<i>C. brachiatus</i>	43.3 ± 2.43	58.5 ± 4.93	141	1.60 ± 0.058	173
<i>P. indicus</i>	4.7 ± 0.31	51.9 ± 2.99	75	0.38 ± 0.019	100

THE RELATIONSHIP BETWEEN CLUTCH SIZE AND DR

CLUTCH SIZE VS DEVELOPMENT RATE



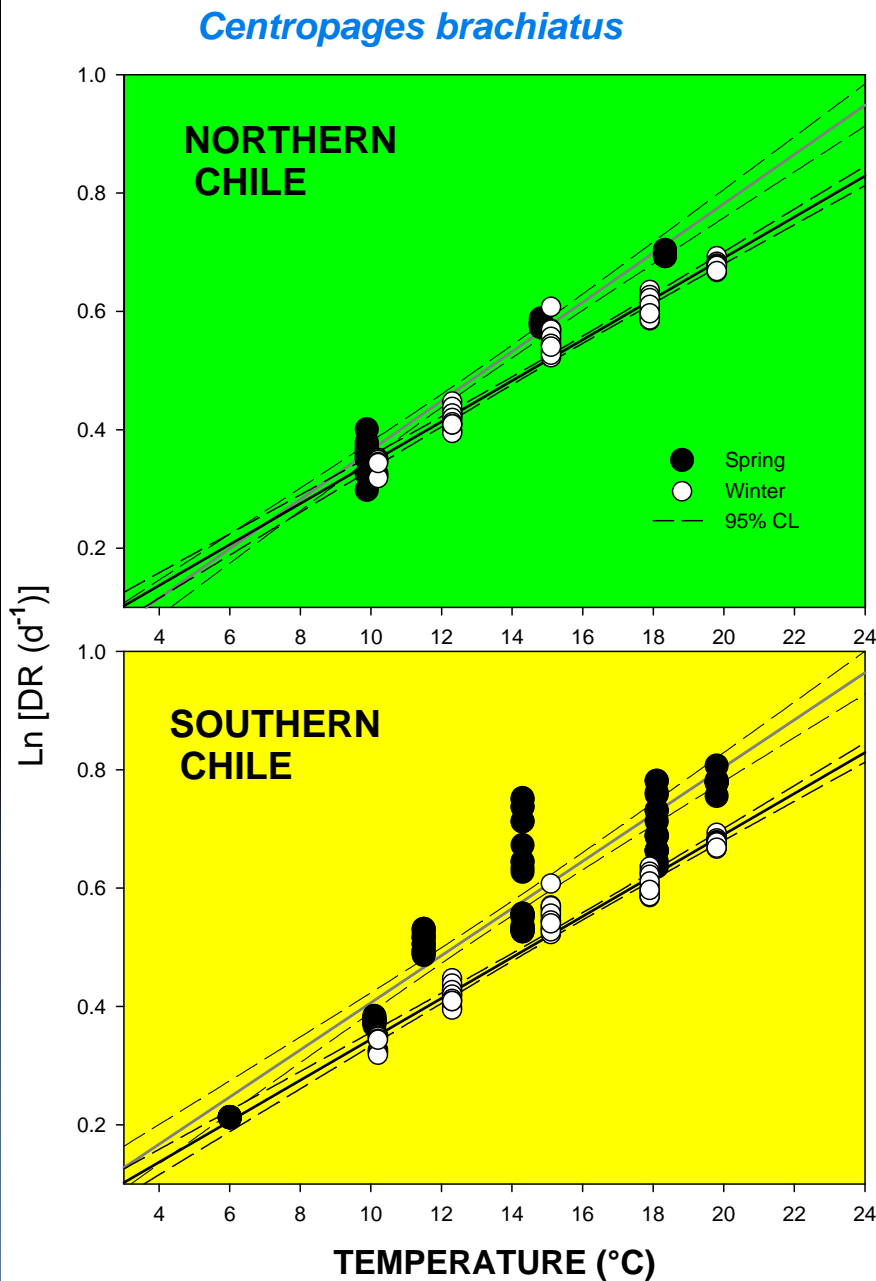
C. brachiatus and *C. chilensis* similar DR, but larger CS in the former

P. indicus extremely low CS, but very high DR

No seasonal effects on CS

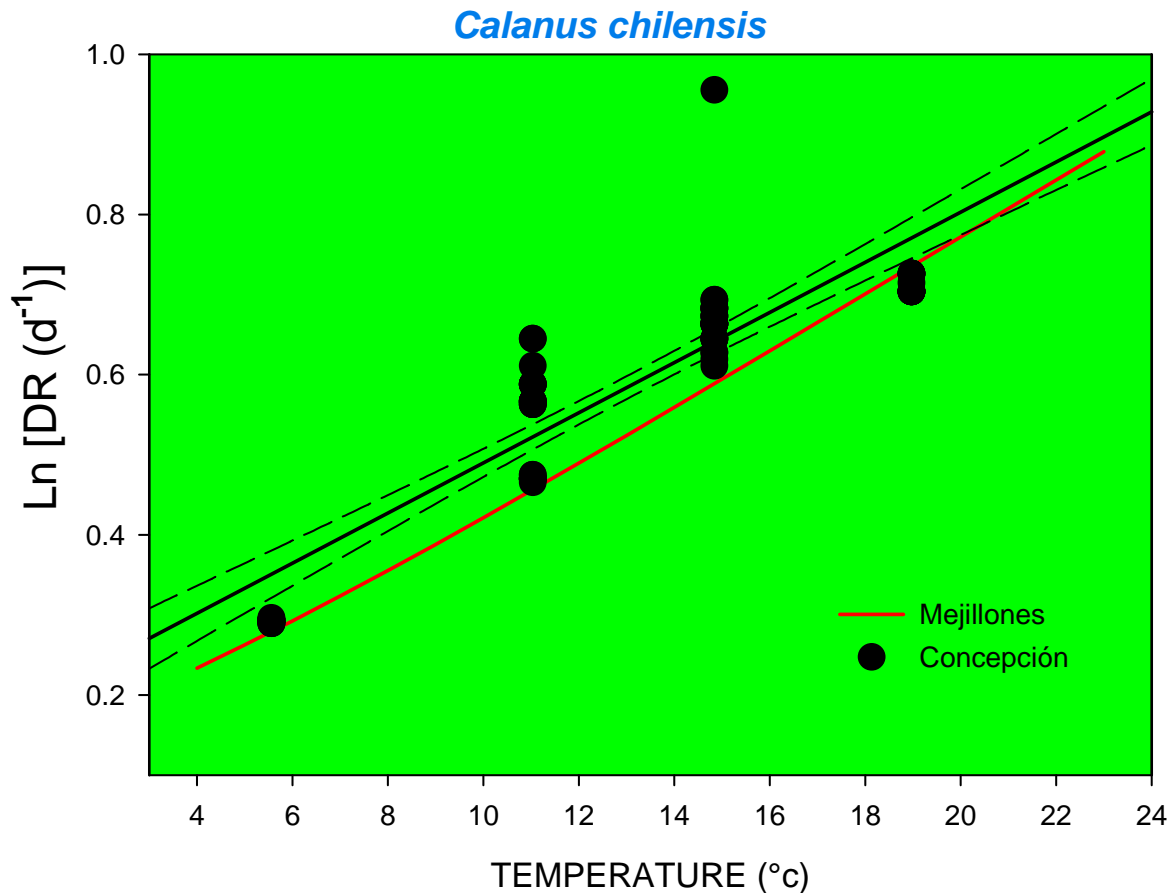
No regional effects on CS

SEASONAL AND REGIONAL EFFECTS ON DR OF EGGS



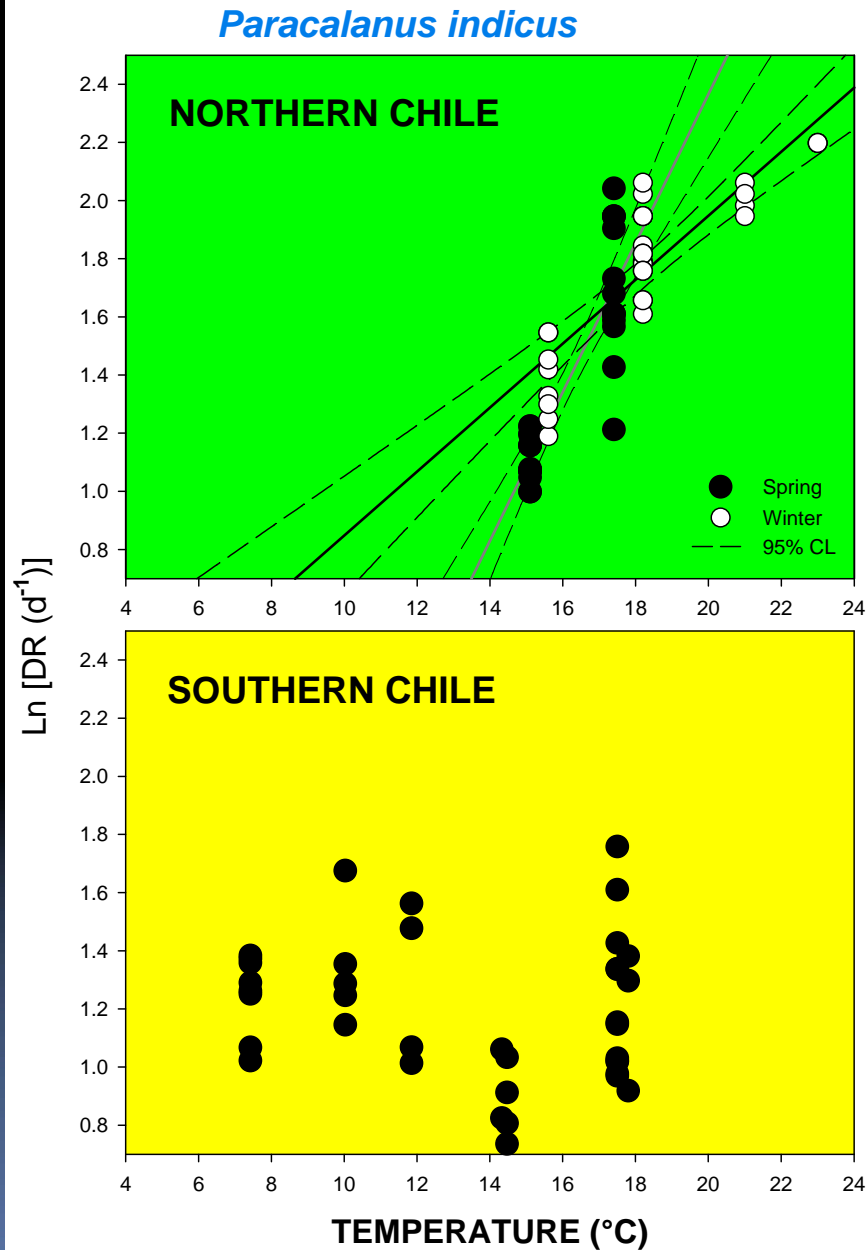
- 1) DR is higher in the spring
- 2) DR is higher in northern Chile
- 3) warm adapted species

SEASONAL AND REGIONAL EFFECTS ON DR OF EGGS



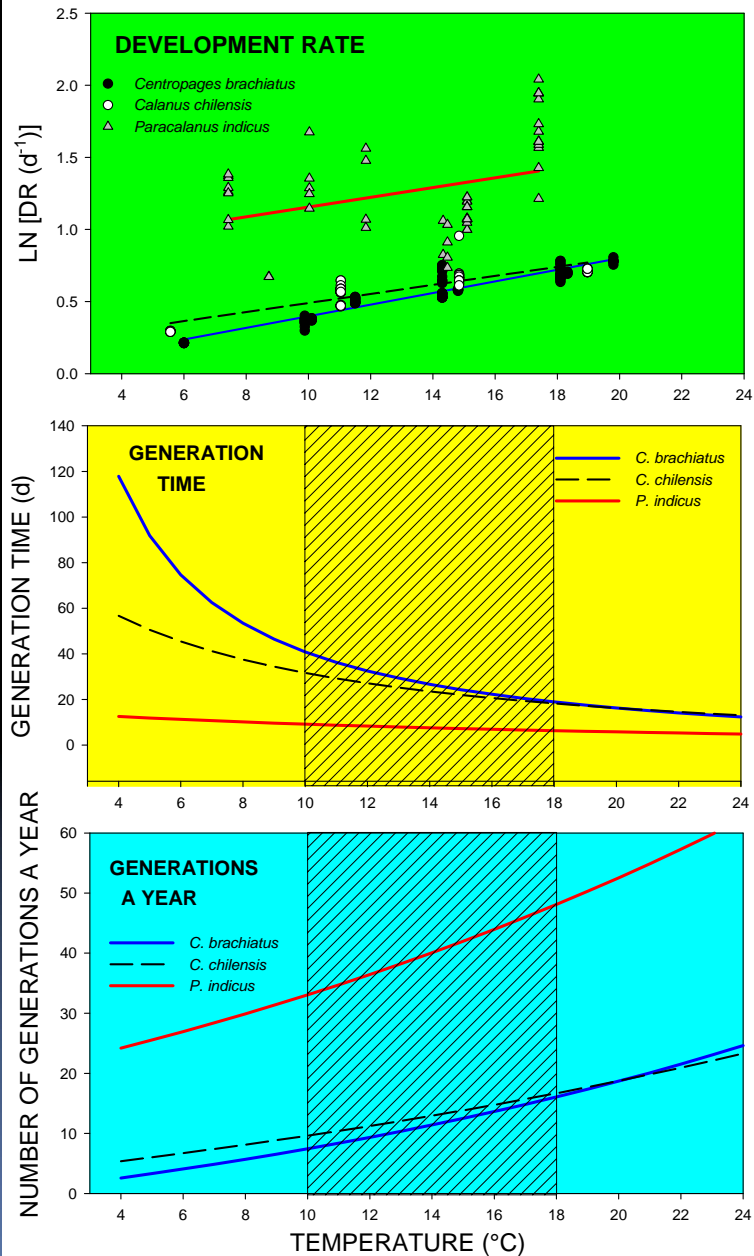
- 1) Only spring condition, hardly present in winter in southern Chile
- 2) Fitted line for Mejillones is from Escribano et al. (1998)
- 3) DR is not different between northern and southern Chile
- 3) warm adapted species (Escribano et al. 1998)

SEASONAL AND REGIONAL EFFECTS ON DR OF EGGS



- 1) The response to T° depended on the temperature range
- 2) At low T° (<15 °C) eggs develop faster than expected (compensation?)
- 3) DR is not different between northern and southern Chile
- 3) Cold adapted species. It shows similar DR's at cold and warm conditions

COMBINED DATA OF THE THREE SPECIES



1. The Small *P. indicus* is a ver fast developing species
2. *C. brachiatus* and *C. chilensis* are very similar
3. GT estimated assuming that egg development is 5% of GT (Escribano et al. 1998, also equiproportional rule from Corkett et al. 1986)
4. Potential NGY estimated assuming continuous reproduction and 10% of GT as a tiem lag to initiate spawning
5. Shaded area in the current observed range of T° in the upper 50 m
6. At any T° the small *P. indicus* will produce more generations a year
7. Low temperature clearly favours the small *P. indicus*

IMPLICATIONS

PREDICTIONS FROM THE TEMPERATURE RESPONSE

Species	Location	Mean T°	Estimated GT	Potential NGY
<i>C. brachiatus</i>	Northern	15°C	24.3	12.5
<i>C. chilensis</i>	Northern	15°C	22.0	13.8
<i>P. indicus</i>	Northern	15°C	7.2	41.9

Species	Location	Mean T°	Estimated GT	Potential NGY
<i>C. brachiatus</i>	Southern	12°C	32.5	9.3
<i>C. chilensis</i>	Southern	12°C	27.1	11.2
<i>P. indicus</i>	Southern	12°C	8.3	36.4

FIELD OBSERVATIONS

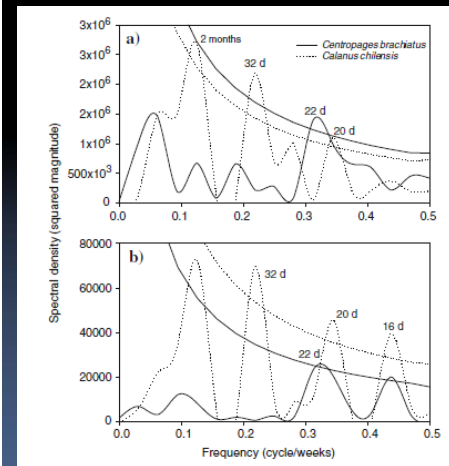
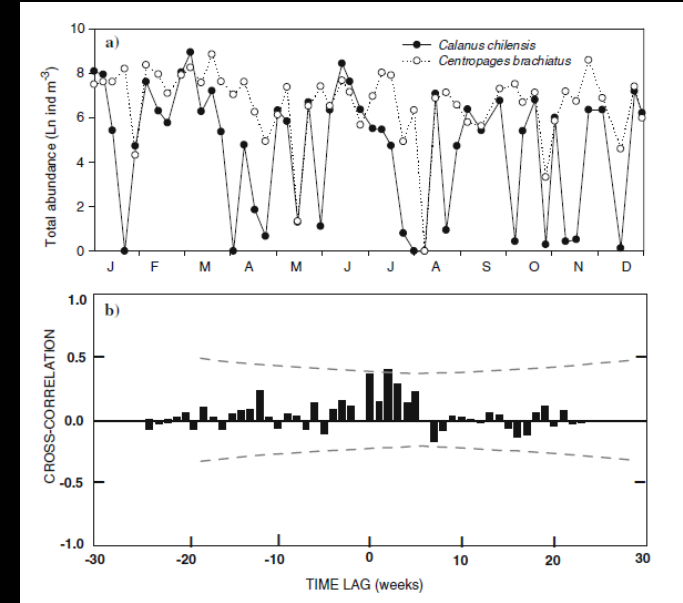
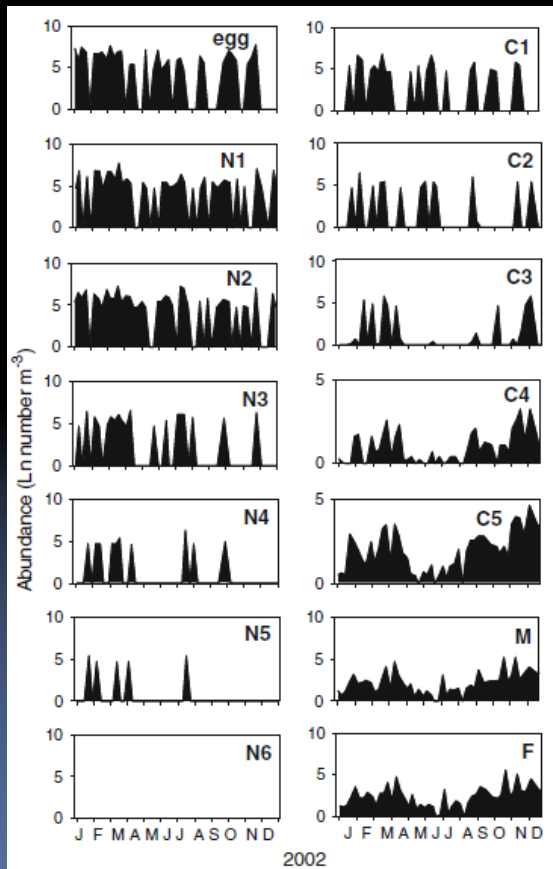
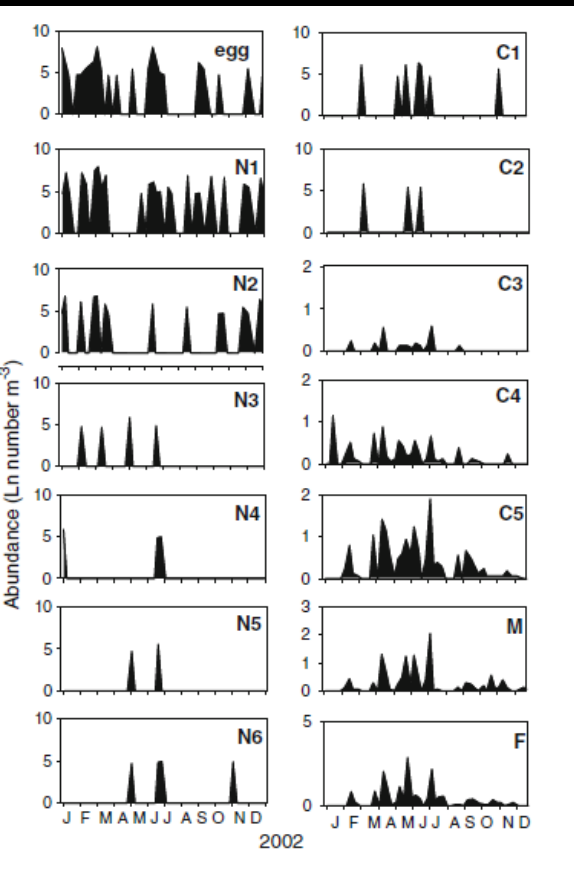
C. brachiatus and *C. chilensis* at northern Chile

2 years time series (15 d sampling interval)

Both spp strongly associated with continuous reproduction and cohort development

C. brachiatus

C. chilensis

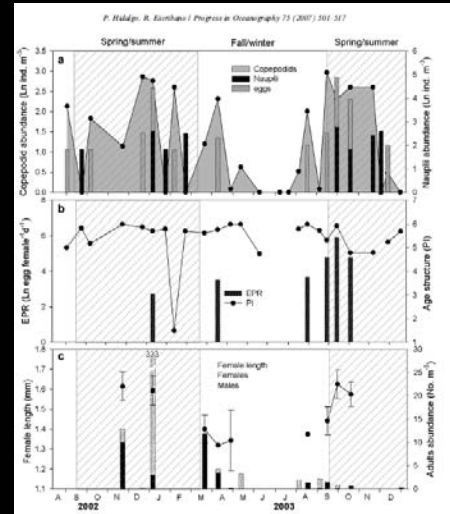


GT=22 d for *C. brachiatus* and 20 d for *C. chilensis*

About 16 generations a year for both spp

FIELD OBSERVATIONS

C. brachiatus

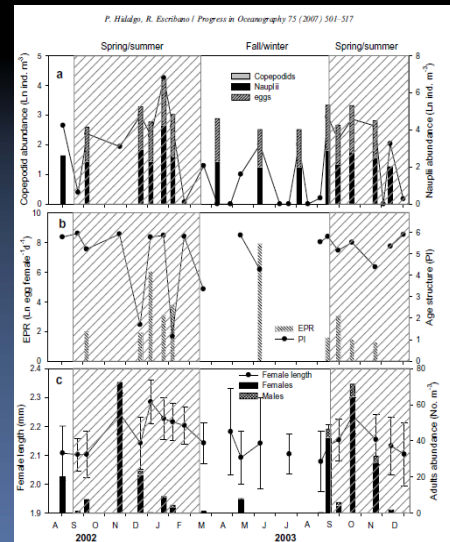


C. brachiatus and *C. chilensis* at southern Chile

2 years time series (15-30 d sampling interval)

Both spp also associated with continuous reproduction and cohort development

C. chilensis



No time series analysis

Tracking cohorts suggested:

GT= 30-35 d *C. brachiatus*

GT= 25-30 d *C. chilensis*

NGY = 10 *C. brachiatus*

12 *C. chilensis*

PREDICTIONS VS OBSERVATIONS

NORTHERN CHILE

Species	T°	GT predicted	GT observed	NGY predicted	NGY Observed
<i>C. brachiatus</i>	15-16°C	22-24 d	22 d	13 – 14	Ca. 16
<i>C. chilensis</i>	15-16°C	20-22 d	20 d	14- 15	Ca. 16
<i>P. indicus</i>	15-16°C	7	NA	42-44	NA

SOUTHERN CHILE

Species	T°	GT predicted	GT observed	NGY predicted	NGY Observed
<i>C. brachiatus</i>	12-13°C	29- 33 d	30-35 d	10	10
<i>C. chilensis</i>	12-13°C	25-27 d	25 . 30 d	11- 12	12
<i>P. indicus</i>	12-13°C	8	NA	36-38	NA

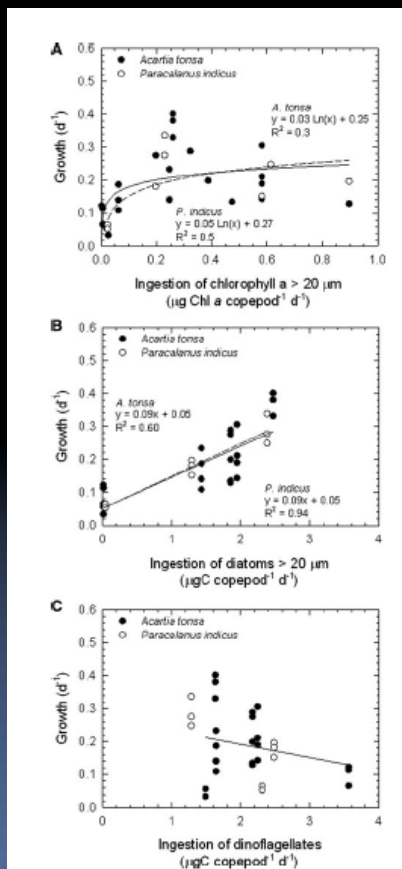
PREDICTIONS FROM AN TEMPERATURE_DEPENDENT ESTIMATE OF THE NGY ARE SURPRINSINGLY CONSISTENT WITH INDEPENTD FIELD DATA
 NO FIELD DATA AVAILABLE FOR *P. indicus*, but this is numerically dominant and persistent year-round at both places (Escribano et al. 2007)

Are the populations controlled by temperature?

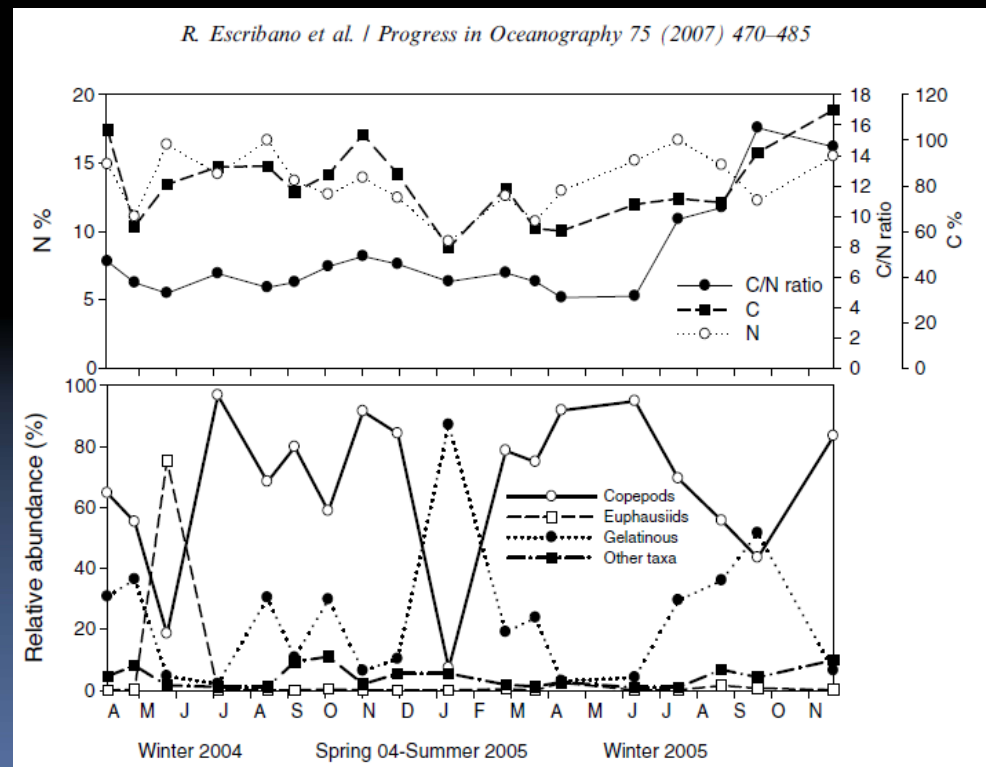
Is therefore growth temperature-dependent?

Food influences seasonal growth

However, greater growth in the spring implies more C from diatoms.. Copepods are overweighed. The C/N ratio increases in the spring (>C) while in winter is about 7

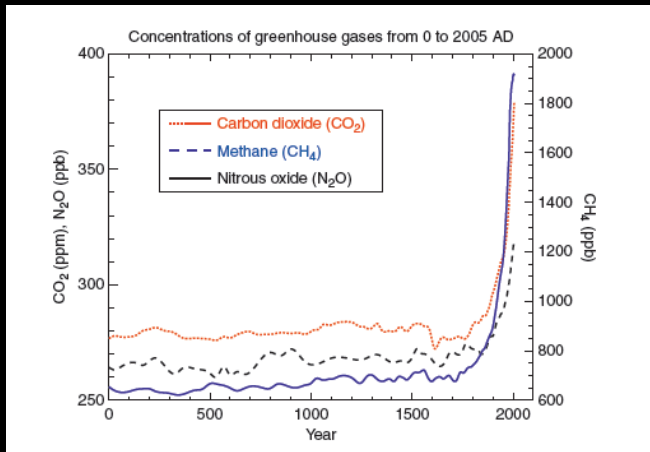


Vargas et al. 2010

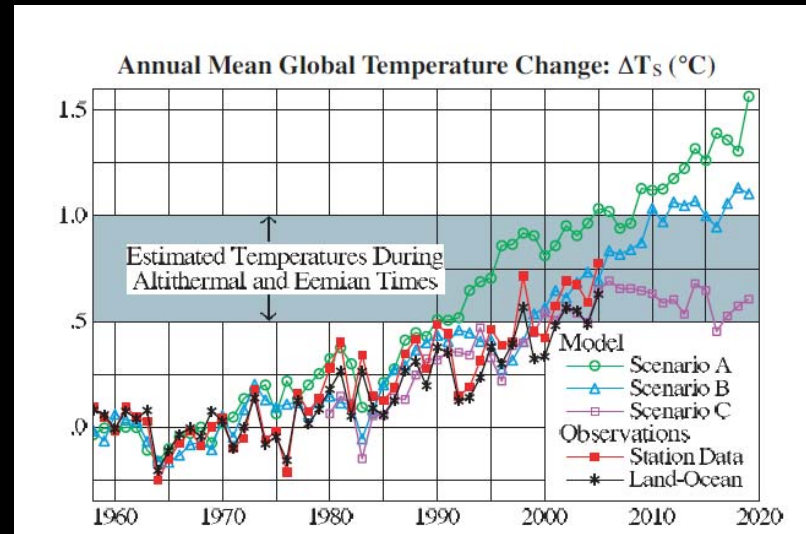


Escibano et al. 2007

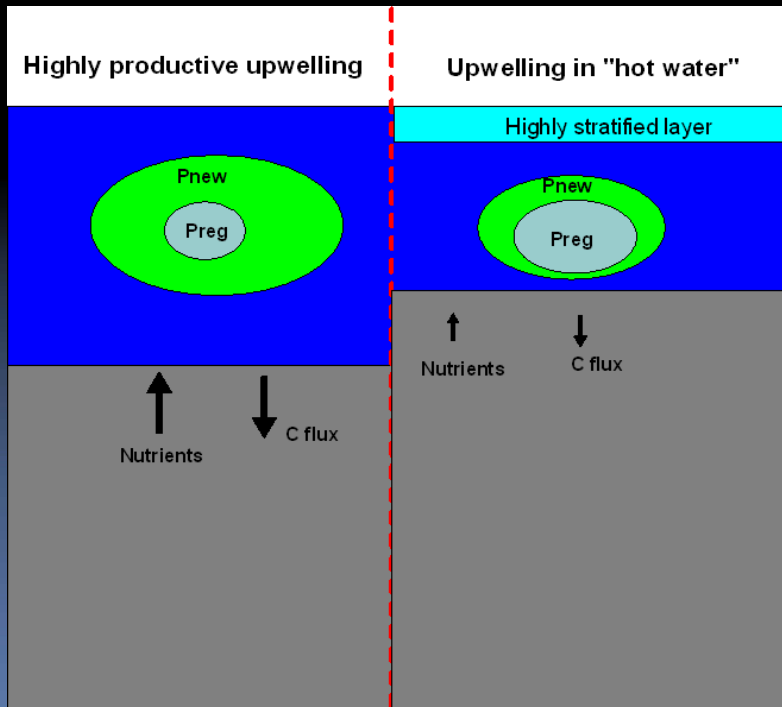
TEMPERATURE CONTROL OF COPEPOD DYNAMICS UPON GLOBAL WARMING



Reid et al. 2009 Adv. Mar. Ecol.



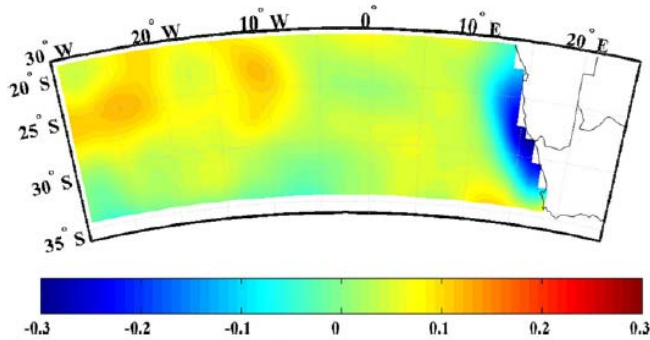
Hansen et al 2006 PNAS



Should we expect more copepods upon warmer conditions?

Ulloa et al. (2001) described an increase of *C. chilensis* population during the 1997-98 El Niño because of higher temperature

BUT, GLOBAL WARMING IS COOLING DOWN THE UPWELLING SYSTEMS

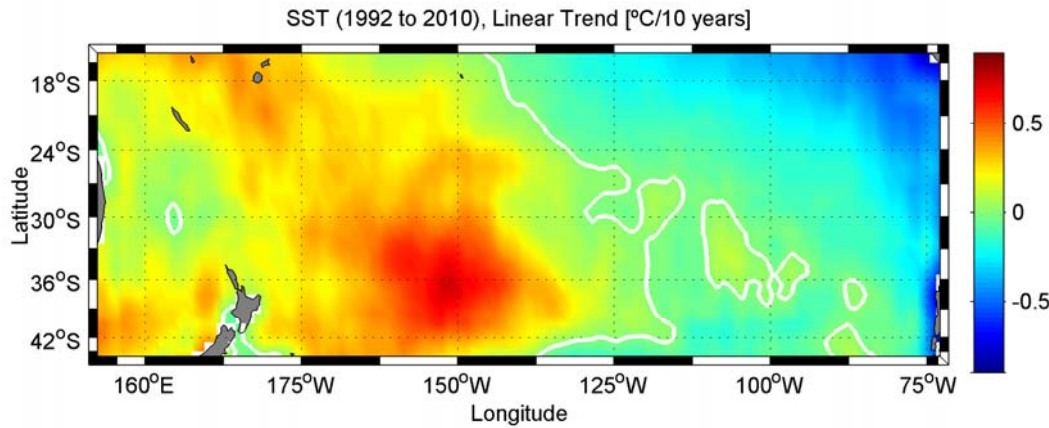


Benguela current

Fig. 3. Annual SST trend ($^{\circ}\text{C dec}^{-1}$) for the area under study from 1970 to 2009.

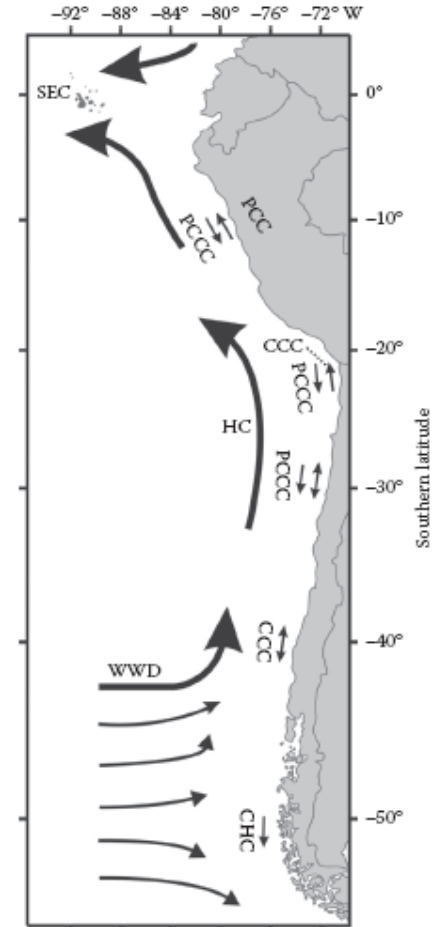
Santos et al. 2012 CSR

Humboldt current



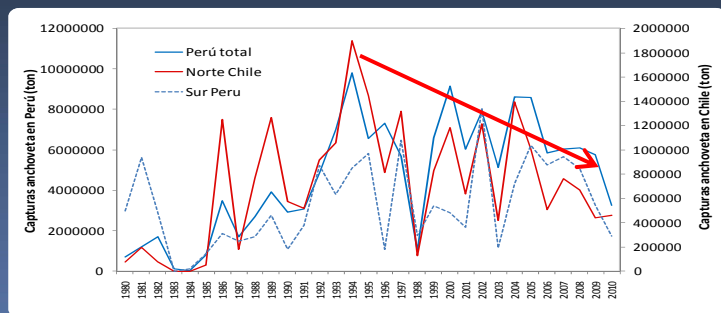
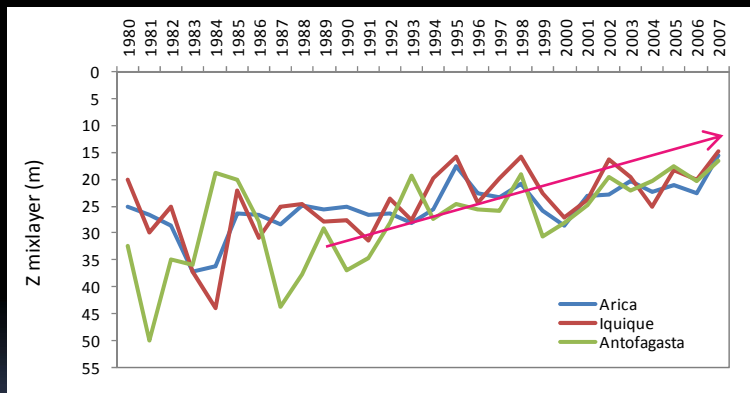
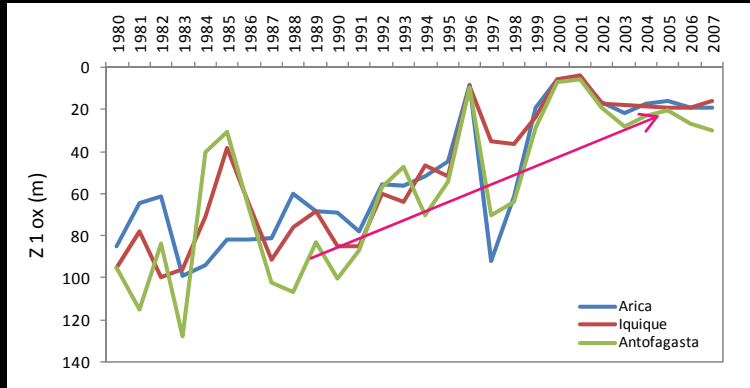
NEGATIVE TREND IN TEMPERATURE

THEN COLDER AND FRESHER IN THE LAST 20 YEARS



IN SITU DATA CLEARLY SHOW INCREASING UPWELLING

NORTHERN CHILE LAST 30 YEARS

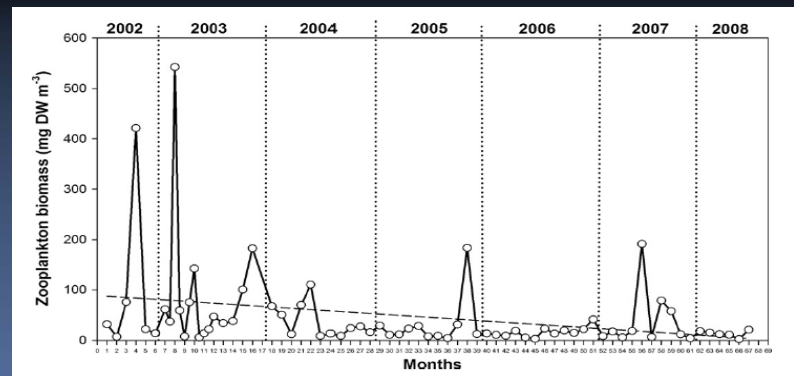
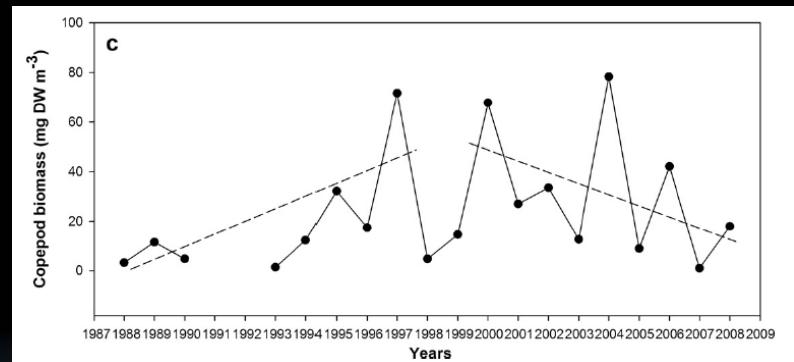


Escribano et al (unpublished)

INCREASED UPWELLING MEANS A NARROW MIXING LAYER AND SHALLOWER OZM

CONSEQUENCES ARE UNCERTAIN

MORE UPWELLING MAY NOT BE AS GOOD



Escribano et al (2012)

SOME REMARKS

THE HUMBOLDT CURRENT IS JUST AN EXAMPLE ON HOW TEMPERATURE CAN CONTROL COPEPOD DYNAMICS. FINDINGS MAY APPLY TO SIMILAR UPWELLING SYSTEMS

HIGH-LATITUDE COPEPODS MAY NOT RESPOND TO TEMPERATURE SIMILARLY, BECAUSE OF FOOD LIMITATION, PRESENCE OF DIAPAUSE, ALSO BECAUSE T° REGIME IS MORE ESTABLE

TEMPERATURE-DEPENDENCE CANNOT BE SEEN OVER SHOR-TERM VARIABILITY (INTRASEASONAL, SEASONAL, LOCAL)

PRODUCTION DURING A YEAR CYCLE DEPEND ON HOW MANY GENERATIONS THE POPULATION CAN PRODUCE. THIS DEPEND ON THE GENERATION TIME, WHICH IS TEMPERATURE-DEPENDENT

HOPING THESE FINDINGS CAN HELP DEVELOP AN EMPIRICAL MODEL TO ESTIMATE COPEPOD PRODUCTION IN MARINE ECOSYSTEMS

Acknowledgements

CONICYT of Chile
COPAS Center
GLOBEC Program
Many students



THANK YOU!